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THE FEEDING MECHANISM AND PHYSIOLOGY OF DIGESTION IN SABELLA PAVONINA.

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INTRODUCTION.

Recent work has directed much attention to the subject of feeding mechanisms and digestive enzymes in the Invertebrates.

The groups worked on previously have been chiefly the Mollusca and Crustacea, and it was felt that a study of the Polychaetes in this connection would be of considerable interest in itself as well as for comparative purposes. An examination of the literature showed that the amount of detailed work on Polychaetes from the physiological point of view was extremely small, and, in the case of the digestive processes, out of date. I have therefore begun a study of the feeding mechanisms and physiology of digestion in the Polychaetes, choosing a filter-feeding form as a starting point, so that a direct comparison can be made with such Molluscs as Mya arenaria and Ostrea edulis which feed on similar material.

Sabella pavonina has been chosen chiefly because of the ease with which it can be kept in the laboratory and also on account of its large size and relative abundance.

Previous Work.

The Sabellidae have attracted the attention of naturalists

since the earliest times. Most of the work has however been done at foreign Marine Stations where Spirographis spallanzani is the commonest form, and the majority of papers refer to it instead of to Sabella pavonina. Fauvel in the volume on Sedentary Polychaetes in the Faune de France has the following note.

> "Les deux genres ne se distinguent que par leur panache branchial et peut-être par leur tube un peu different."

The internal anatomy of Spirographis is also similar, so that it is necessary to consider the literature on that form as carefully as that on Sabella.

Although the anatomy of various members of the group has been described at considerable length, in no case has the feeding mechanism been worked out in detail and with the exception of two papers, only scattered references to cilia and their direction of beat occur along with general anatomical details.

The first to investigate the internal anatomy of a Sabellid was GRUBE(1838). He describes the general structure of the gill region, the collar folds and ventral gland shields of Spirographis spallanzani under the name of Sabella unispira. He mentions the palps but not the lips or ventral sacs; and although he was aware of the presence of cilia on the gills he does not describe their distribution or function. He divides the gut into two regions; an anterior region, distinguished by its greater width and thicker walls, and a posterior, slightly convoluted, part. The gut is fastened in position by muscular

septa which contract to widen the lumen. The vascular system consists of two zig-zagging lateral vessels giving off alternating vessels to the dorsal and ventral body-wall. These longitudinal vessels run into the gill region where they join, after giving off a large vessel to the gills on each side, to form a median dorsal vessel which runs in a posterior direction above the gut for some distance before communicating again with the lateral vessels by a mass of anastomosing capillaries. The vessel running to each gill fan breaks up into single strands for each filament, which give off single lateral capillaries to the pinnules. He also refers to a longitudinal vessel below the gut with lateral, loop-like branches but does not give any of its connections. He considers that the blood passes along the lateral vessels into the gills, thence to the dorsal vessel and back to the laterals by the cross capillaries. He also refers to the action of the muscles of the branchial region in rolling up the gills before retraction into the tube.

MILNE-EDWARDS(1838) gives a description of the circulatory system of a Sabellid from dissection. He mentions a very fine vessel on the dorsal surface of the gut which receives at each septum a pair of lateral vessels, and also a median ventral vessel with looped lateral branches. No mention is made of the intestinal sinus or of the vessels of the branchial region, but blind vesicles are described as projecting into the body cavity at every segment.

LEYDIG(1851) describes a skeletogenous structure in the branchial region of Amphicora.

DALYELL(1853) figures and describes the external features of Sabella pavonina under the name of Amphitrite ventilabrum. He is the first to make observations on the currents of the branchial region. He describes the collecting of fine mud for the process of tube building. Although he uses the word "cilium", he applies it to the pinnules themselves and suggests the presence of smaller lateral projections without actually seeing them. He also describes the streams of mucus from the tips of the palps.

DE QUATREFAGES(1865) gives a general description of the anatomy of Sabellids and Serpulids as an introduction to his systematic account of these groups. It is often difficult to ascertain to which subdivision he is referring; indeed some doubt must have existed in his own mind about their differentiation, since he ascribes an internal supporting structure similar to that found in the Sabellids to the Serpulids as well. It is described as a very delicate cartilage surrounded by a much stronger perichondrium which gives the gills their characteristic shape. The whole structure serves only for the support of the real respiratory parts of the gills.

> "Ces parties sont les barbules placés sur les côtes des dernières branches de l'appareil et dans ces barbules on voit reparaître toute la structure caractéristique et la mollesse des organes

branchiaux ordinaires."

He is the first to suggest that the gills unfold entirely by the elasticity of the cartilage. He also describes the vascular system of the branchial region as consisting of a double system of vessels and states that it is possible to observe the blood coursing through them. He also describes the gut, dividing it into several regions; the mouth leading into the proboscis and followed by a stomach and a straight intestine. The proboscis is divisible into two regions, a muscular portion and a wide, sac-like portion occupying one segment only. The intestine is wide anteriorly and narrows as the posterior end is approached. It is covered on the exterior by a layer of velvety texture representing the liver, thickest in front and often absent behind. The gut is lined by a mucosa covered with short cilia.

CLAPARÈDE(1873) was the first to study the anatomy of the Sabellids by means of sections and consequently his is the first detailed account of the internal anatomy and histology of the group. He describes in Spirographis the internal supporting axis of the gills as consisting of a central portion of large, vacuolated cells surrounded by a sheath of hyaline material containing numerous groups of cells. The whole forms a horse-shoe-shaped basal supporting lamella and not a complete ring as described by GRUBE. The musculature of the branchial region is described in detail. The fibrils folding the pinnules together and the oblique muscle concerned with the rolling and drawing together of the branchial crown are mentioned, as is also a

muscle running from side to side below the transverse bar of the supporting axis, which causes the branchial funnel to be opened widely. He describes two pairs of tentacles, a dorsal, elongated pair, and a short ventral pair. These are convex to the outside and the inner surface is ciliated. They are in reality the ventral sacs, whose nature and function CLAPARÈDE entirely failed to understand. He gives a detailed description of the circulatory system. The ventral vessel gives off lateral vessels which enter the gut sinus which is separated from the gut epithelium by a thin layer of muscles and peritoneum. The lateral vessels mentioned by GRUBE are also linked up to the lateral branches of the ventral vessel in each segment. At the anterior end the ventral vessel divides into two, the oesophageal connectives, which together with the gut sinus break up and form the peri-oesophageal plexus which occupies the first body segment and gives off a dorsal vessel which goes to the connective tissue of the brain. In the same region occur vessels running to the collar folds(to which,since they are ciliated, he attributes a secondary respiratory function), and two large vessels to the gills. He states that the blood passes forwards in the sinus into the plexus and from there into the anterior vessels which have highly muscular, and in consequence, contractile walls.

"Les mouvements de systole sont dus à une couche externe de larges fibres musculaires. Quant à la diastole elle paraît due à la simple élasticité des parois, du moins

n'ai-je pu découvrir aucune fibre longitudinale dans le paroi du vaisseau."

The blood is then forced back into the plexus and out of it into the ventral vessel.

The walls of the gut are described as consisting of columnar ciliated cells with the nucleus at the middle of the height of the cell. The height of the cells varies considerably, but the nuclei always retain this relation. Unicellular glands occur in certain regions, and in Branchiomma curious rosette-like compound glands are to be found in the oesophagus. He describes a subepithelial tissue occurring principally in the oesophageal region, lying under the muscle layer and consisting of nerves, blood vessels and connective tissue. The alimentary canal is always separated from the body cavity by the peritoneum. The muscle coat consists of an outer layer of circular fibres and an inner incomplete layer of longitudinal fibres immediately below the epithelium.

MACÉ(1882) mentions the collecting of mud on the gills of Sabella in connection with tube building.

ÖRLEY(1884) gives a short description of the gill filaments of Sabellids. He describes the horseshoe-shaped basal support of cartilage strongly resembling that of the radula of Molluscs. The skeleton has two backwardly projecting processes joined by a transverse muscle which he regards as belonging to the oblique muscle system and which draws the two parts of the gill crown together. He gives a figure also of inter-filamentar transverse

transverse muscles which pull the filaments together for closing.

VIALLANES(1885) gives a detailed description of the skeletal supporting structure of the branchial region of Sabella. He describes the histology of the central cells and also of the surrounding sheath, two very different tissues having no relation ship beyond that of position. The central cells are thick-walled and contain a transparent fluid; there is very little protoplasm. The perichondrium or sheathing material is non-cellular and consists of a hyaline, homogeneous "substance fondamental". It is interspersed with anastomosing connective tissue cells in varying numbers. This sheath on the outside of the central axis is in direct contact with the cells of the epidermis; on the inside it serves for the attachment of the muscles. The gills are spread by the elasticity of the cartilage alone.

PRUVOT(1885) gives a brief account of the external features of Sabella. He describes the terminal mouth surrounded by the gill crown whose base is formed by the union of the longitudinal muscles of the body. He describes the nervous system in some detail. The brain is composed of four parts; two small internal ganglia fused in the middle line which give off a small nerve to a pair of very short conical appendages hidden beneath the swollen base of the gills; and two large lateral ganglia, which are united by the internal ganglia and give off, a) a nerve to the muscles of the gills, b) a branchial nerve dividing up and sending one branch to each filament, c) a nerve to the blood plexus. This last nerve breaks up into many branches, a few of

which run to the buccal epithelium. It is the remains of the stomato-gastric system and therefore the lateral ganglia are in reality the suboesophageal ganglia drawn forward. Consequently the branchial crown and so-called antennae are not antennae or tentacles but much divided palps, and the small conical appendages are the true antennae.

JAQUET(1886) in a paper on the vascular system of Annelids describes the condition found in Spirographis. There is only one well developed vessel, the ventral, which runs in the mesentery below the gut and breaks up into a plexus in the thoracic region In each segment the vessel gives off two sinuous lateral vessels which run to the parapodia. The gut is surrounded by a sinus. On the lateral body-walls two other vessels occur which give off two branches in each segment, one running to the dorsal surface, the other to the parapodia. He also describes the structure of the gill filaments, their cartilaginous axis and the single blood vessel running up each. He mentions two rows of cilia on the pinnules, one of close, short cilia, the other of thick cilia eight to ten times the length of the first row and in fixed material folded across the middle of their length.

MEYER(1887,1888) in his first paper is concerned with a study of the thoracic excretory organs of various Polychaetes. He describes the thoracic organs of Spirographis in detail and states that they are excretory in function and play no part in the formation of the tube. He notes strings of mucus passing off from the tips of the palps. In the same paper he gives a

figure of the vascular system of the anterior end of the body in Spirographis, which does not differ materially from those of previous workers. In the second paper he considers the group and its relations phylogenetically, comparing the structure of the Sabellids and Serpulids with that of the Hermellids and Spionids. He describes the external features of the gill crown in detail and states that there are two pairs of antennae, a long, pointed pair on the dorsal lip, and a second, greatly reduced pair similar to those described by PRUVOT in Sabella. He describes the ventral gland shields and the epidermis of the body-wall in detail and discusses the homologies of the gill-supports and collar folds.

BRUNOTTE(1888) working on Branchiomma, differs from some of CLAPARÈDE'S views. He describes the gut as a straight tube swollen into oval chambers between the septa, the epithelium being composed of ciliated cells, with no differentiated gland cells. He reinvestigated the compound glands described by CLAPARÈDE in the oesophageal region, and showed them to be pits formed by the folding of the epithelium, the so-called duct being the narrow side branch of the lumen of the oesophagus cut transversely. He finds no trace of a subepithelial layer, and states that the fibres of ~~the fibres~~ of the muscular coat are not differentiated into two layers but are intermixed. He confirms CLAPARÈDE'S observations on the position of the gut sinus lying between the peritoneum and the muscle fibres.

SOULIER(1891) was the first to describe the ciliary currents

on the gills of Serpulids and Sabellids in any detail. From the second group he examined Spirographis, Sabella, Branchiomma and and Myxicola. His results are mainly concerned with the rejection tracts since his experimental methods were crude. He transfixed the worm with a needle to prevent retraction into the tube, or narcotised it with dilute alcohol to prevent movement. In either case the branchial region was irritated, and large quantities of mucus were secreted, almost completely masking the collecting tracts. He does describe the passage of fine particles down the axes of the filaments and along the basal groove of the lips to the mouth, but completely disregards the sorting mechanism on the basal folds. He gives an account of the entangling of foreign matter in a thin sheet of mucus and its removal from the tube by the combined action of the cilia of the ventral groove, the dorsal lip and the palps; also of the currents on the lateral lips and the formation of mucus strings, containing particles, on the "bourrelets branchiaux" or basal folds. He considers that the function of these organs is to form foreign particles into strings with mucus in preparation for their removal by the cilia of the palps. He fails entirely to discover the function of the ventral sacs; he shows that they contain particles collected from the filaments and considers them to be storage organs for reserve food material. He gives an accurate and detailed account of the anatomy of the branchial region. An account of the anatomy ~~of the anatomy~~ and histology of the alimentary canal is also given. The gut is a straight tube

constricted by each septum but not divisible into regions except for the oesophagus which occupies the first segment and projects slightly into the first sac of the intestine. The epithelium of the gut is composed of ciliated cells. Mucous glands only occur in the oesophagus and again at the extreme posterior end of the intestine. The nuclei of the epithelial cells occur in a band in the centre of the cells. Other nuclei belonging to replacement cells from the connective tissue occur at the base of the epithelium. Yellowish granules occurring most frequently in the posterior region are described as absorbed food, since they are less frequent in starving animals. The gut is surrounded by a blood sinus which lies between the longitudinal and the circular muscles, and the whole is covered by a complete layer of peritoneum.

DE ST. JOSEPH(1894) gives a general account of the internal and external anatomy of Sabella.

ORTON(1912) in a paper on the ciliation of the gills of Molluscs, Brachiopods and cryptocephalous Polychaetes states that the ciliation on the gills of these worms is identical with that of Molluscs. He gives however neither description nor figures in support of this statament.

M'INTOSH(1916,1923) describes the external characters of Sabella and states that" the inrush of water along the inner surface of the branchial fan would thus be swept towards the mouth, the tentacles and their webs probably aiding in this function and keeping the stream in each fan to its own side, as

it rushes down the groove by the outer border of the smaller anterior web into the mouth". (1916) In the British Marine Annelids (1922) he gives an account of the internal and external anatomy of Sabella without however adding anything to the accounts of previous writers.

ROMIEU(1923) describes the "éléocytes" of the body cavity of Sabella. These are of two kinds; one colourless and crowded with large spherules of fat as well as with smaller droplets; the other a modification of the first, coloured brick-red with excretory products.

JOHANSON(1927) describes the feeding mechanism in various Sabellids and Serpulids. The food is carried in suspension in a current entering between the filaments of the branchial crown. The current is produced by the lateral cilia of the pinnules, and particles are embedded in mucus and passed to the short cilia between the others. They are then carried in a mucus string down the filament to a groove along the base of each half of the gill crown to the mouth. The palps, renamed the "Mund anhänge", in Sabella are well developed because of the weakness of the current between the gills, and serve to throw out waste material. The central dorsal portion of the palp is ciliated but the current is weak, while that on the edge is strong. On the inner face the cilia beat weakly towards the mouth.

BIONOMICS.

Sabella pavonina is to be found in suitable localities all round the coast of Britain, either singly or in considerable numbers and can be collected in many places at low spring tides. In the Salcombe estuary in South Devon where most of the material for this paper was obtained, it occurs in very large numbers. With a suitable tide the tubes can be seen projecting from the mud in thousands (Plate I, fig.1); at low water mark in clumps of twenty or more of all sizes covered with algae, tunicates and the tubes of young Sabella; (Plate I, fig.2); and higher up , singly along with Branchiomma and Myxicola , two other sedentary Polychaetes with somewhat similar methods of feeding. It also occurs as a deep-water form and is often dredged from the Cellaria beds off Plymouth. At Millport and other places on the west coast of Scotland it can be collected singly at extremely low tides from the zostera beds.

A small percentage of the worms from the Salcombe estuary when taken, show regenerating anterior ends. Whether the loss of the branchial crown is a periodic autotomy due to a need to renew the food collecting mechanism or is caused by the attacks of natural enemies is not known. Sabella heads are reported as occurring in the stomachs of various fishes. They form part of the food of the Pleuronectidae (TODD 1903) and of the cod(M'INTOSH 1875) and BLEGVAD (1914) reports that Sabellids are eaten by Pleuronectes limanda and also by Aphrodite aculeata.

GENERAL ANATOMY.

Methods.

Considerable difficulty was experienced in obtaining suitably fixed material. For the general internal anatomy Zenker's fluid, formol-bichromate, acetic sublimate, and sublimate formol gave bad results. Bouin's fixative gave unsatisfactory fixation of the cilia of the branchial region; the posterior region of the gut was fairly well fixed but the anterior region, even when previously removed from the body was useless, the cells being disintegrated and the nuclei distorted. This effect was not due to autolysis of the gut wall previous to killing as worms fixed five minutes after being collected were equally unsatisfactory; nor was it due to overhardening in the course of embedding as material cleared in oil of wintergreen from 90% alcohol and embedded in wax of 40°C. melting point was very little better. The alcoholic mixture of Duboscq and Brasil was however found to give very good results. The cilia of the branchial region showed basal granules and intracellular fibrils. When the worm was fixed whole, lateral incisions being made to allow of penetration, the general fixation was satisfactory as shown by the absence of shrinkage in the giant fibres of the nervous system; the epithelium of the fore-gut however was still unsatisfactory. Removal of the gut from the body and fixing of por-

tions of not more than half a centimetre in length gave good results. Various other fixatives were tried on isolated portions of the gut. Fleming's fluid with and without acetic gave unsatisfactory results also Champy's and Allen's fluids. Hermann's fixative however gave results very similar to those obtained by Dubosc's and Brasil's method, fixing in addition granules of a fatty nature . Sections were cut by the paraffin method usually 6u in thickness and stained in Heidenhain's haematoxylin. Mucus was shown by staining with Mayer's mucicarmine. An attempt was made to differentiate the secreting cells of the gut epithelium and a large number of stains were tried. Mann's methyl blue-eosin Bensley's gentian violet, Auerbach's methyl green - acid fuchsin, methyl green - pyronin, Jarotsky's nigrosin following after haematoxylin, acid fuchsin and light green all gave uniform staining of the cells of the gut, whether ciliated or secreting. For the study of the reserve food supplies material was fixed in Carnoy's fluid for glycogen reserve and in Hermann's fixative and in 5% formalin for fat reserve and sections cut by the freezing method. To show the distribution of glycogen in the body material was stained by Langerhan's iodine method and with Best's carmine after Delafield's haematoxylin. The distribution of fat was shown by staining with sudan III and scharlach R. An examination was also made of the contents of the body cavity from fresh material staining in sudan III and nile blue sulphate.

External features.

The length of the worm is very variable and depends largely on age and to a lesser degree on regeneration. The average length of an adult worm containing well developed ova is from 15 to 20 cm.. The body is narrow, about 0.5 cm. across and of uniform width, except at the posterior end where it tapers to a blunt point. The number of segments is variable, usually 200 to 250; of these the first eight form the so-called thoracic region, but this is subject to considerable variation. The first segment bears, besides the branchial crown, four muscular and glandular flaps, the collar folds. The dorsal pair are small and do not meet in the middle line, but the ventral pair are large , their under sides being covered by extensions of the first ventral gland-shield, and slightly overlap each other in the middle line. The ventral shields are a series of glandular cushions on the ventral surface of every segment of the body which secrete the mucus lining the tube. Those of the thoracic region are uninterrupted in the middle line, but in the rest of the body the right and left halves of each shield are divided by the mid ventral ciliated groove. This groove runs from the anus forward to segment nine where it passes round to the right between the gland-shields of the eighth and ninth segments and runs obliquely to the base of the palps as a shallow, slightly pigmented depression It conveys the faeces from the posterior end to be discharged from the tips of the palps.

The Parapodia.

A pair of parapodia is present on every segment of the body. They are of two kinds: those of the thoracic region consist of a dorsal bristle bundle and a ventral row of uncini, while in the rest of the body the bristle bundles are ventral and the uncini which are dorsal, are situated on a small, muscular lobe projecting from the posterior margin of the segment.

The Branchial Crown.

The branchial crown is composed of two lateral lobes which are joined at the base on the dorsal side only. They curve round on either side of the mouth and are greatly prolonged ventrally. Each bears numerous filaments, usually about thirty on each side; but the number may be considerably more and is by no means constant for different worms or for the two sides of the same branchial crown. The three most ventral filaments on either side become progressively shorter and the most dorsal one is often darkly pigmented. Each filament when fully developed is about 4 cm. in length and bears a double row of alternating pinnules. At the base these give place to a pair of parallel ridges, the gill-folds, which run along the filaments for the first 4-5 mm.

The filaments form a wide funnel in the centre of which is the mouth. On the dorsal side of this arise two long tapering structures, the palps.* They are joined to each other and to the

* Considerable confusion exists with regard to the nomen-

first dorsal gill-filament on each side by a fold of epithelium which forms the dorsal lip of the mouth. This lip arises as a continuation of the outer basal fold of the most dorsal gill-filament. The two lateral lips bordering the sides of the triangular mouth arise in a similar manner from the ventral gill-filaments. These lips run all along the bases of the branchial folds

clature of the anterior end of the Sabelliformia.

DE QUATREFAGES(1865) called all outgrowths from the anterior end which were innervated from the cerebral ganglia, antennae.

PRUVOT(1885) investigated the problem further and divided the brain of Polychaetes into three parts, a stomato-gastric region innervating the palps, an anterior antennal region innervating a pair of anterior antennae, and a posterior antennal region innervating a pair of posterior antennae and when present a median antenna. In Sabella he found that the whole of the appendages of the head were innervated from the first of these regions and were in consequence palps. Reduced antennae were found by PRUVOT on the dorsal part of the gill complex.

MEYER(1888) discards the term "palp" and called the outgrowths of the dorsal lip the "neural head tentacles", and the reduced antennae the "haemal head tentacles".

JOHANSON(1927) has examined again the innervation of the head appendages of various Polychaetes and finds that the whole of the gill complex of the Sabelliformia is developed from in front of the prototroch in the larva, and in the adult is innervated from the anterior median ganglion except for a small branch which leaves the stomato-gastric ganglion and joins the main nerve as soon as it leaves the brain." Ferner meine ich das die Palpen bei den Hermelliformia mit dem Siebapparate bei den Sabelliformia identisch sind und ich bezeichne diese zwei stark verzweigten Hälften desselben ebenfalls als Palpen."

In this paper, while recognising that upon the evidence advanced by JOHANSON and previous writers all parts of the gill complex of Sabella are part of the same structure and can be homologised with the palps of other Polychaetes, it has been thought best to retain the nomenclature which is used by FAUVEL in the Faune de France, Polychètes Sédentaires, and call the filtering part of the palp the branchial crown, while the name palp is retained for the specialised portion of the dorsal lip which is concerned with the rejection of waste material

until they reach the level of the palps, where they turn towards each other and finally pass ventrally on either side of the mouth meeting again below it in the middle line. At this point the bases fuse to form the ventral wall of the oesophagus, but the free edges are folded and hollowed to form a pair of structures, the ventral sacs, lying one on either side of the midventral line The posterior edges are then continued back for a short distance as a pair of thick, parallel folds which end abruptly between the ventral collar folds.

Between the dorsal lip and the dorsal body wall is a deep pit formed by an inpushing of the surface epithelium. The shape of the pit in transverse section is roughly triangular, the base lying along the dorsal body wall and the apex filling the angular fold in the dorsal lip. The epithelium lining the pit is similar to that of the dorsal body wall. The cells are columnar with the nuclei in the centre of the cell. Mucous glands are numerous as well as ciliated cells. There is a thick cuticle through which the cilia project in tufts. The pit runs back until it reaches the anterior margin of the cerebral ganglia. Immediately in front of this point on the dorsal wall of the pit are two small projecting ridges; here the epithelial cells are higher and narrower with very long cilia and their bases are associated with ganglion cells which appear to be in direct communication with the cerebral ganglia. From their structure these appear to be some sort of sensory organ. They may possibly be the reduced antennae described by PRUVOT. JOHANSSON does not

mention them nor was he able to find the antennal structures of PRUVOT.

On a level with the anterior margin of the cerebral ganglia the pit divides into three finger-like processes lying in the same plane but of unequal lengths. The central one runs back for a short distance and ends in the groove between the cerebral ganglia in a mass of mucous cells. Some of the cells have sunk below the level of the rest of the epithelium, and the whole mass is surrounded by a few muscle fibres. The lateral processes pass backwards in the angle between the cerebral ganglia and the lateral connectives and end on a level with the most posterior portion of the internal supporting skeleton. Their structure is peculiar At the same level as the end of the central process the lumen of the lateral processes becomes very narrow and the lining cuticle fuses together to form a central, hyaline rod; pigment appears in the cells towards the middle line and ganglion cells become associated with the epithelium on that side also. The general structure is similar to that of many Invertebrate eyes and similar structures have been described by HESSE(1898) in Branchiomma and Spirographis as eyes. It is difficult however to see what possible visual function they can exercise in the position in which they occur.

The Anatomy and Histology of the Branchial Region.

The Branchial Skeleton.

The branchial crown of Sabella contains an internal support

ing tissue of large, vacuolated cells usually described as cartilage, but which bears no resemblance to vertebrate cartilage either histologically or chemically.

The following description of the skeleton agrees closely with that of VIALLANES(1885). It has however been augmented at several points.

It was found that a more successful method of preparing the branchial skeleton than that of VIALLANES (who macerated the anterior end of the worm for several days in 30% alcohol) was to soak the branchial region for 24 hours in isotonic magnesium chloride when with the help of needles and a brush the whole of the epidermis and underlying muscles could easily be removed. The central so-called cartilaginous cells can then be stained with methylene blue and the whole skeleton examined under the binocular microscope.

The supporting structure consists of two triangular lamellae greatly prolonged into ventral horns which fit into the long, curved projections of the lower lip. The lamellae are concave towards the middle line and the ventral projections are somewhat twisted so that the face that is towards the centre in the dorsal region, in the ventral, is turned forwards. The dorsal margins of the triangles are joined by a narrow transverse bar, so that the skeleton appears in transverse section in this region, as a horseshoe-shaped band. The anterior margins bear the supporting axes of the filaments. Owing to the twisting forwards of the lamellae, in serial sections through this region the supports of

the filaments arise earlier on the ventral part than on the dorsal. Each gives off two rows of slender axes which support the pinnules. The palps also have a skeletal axis which arises from the inner face of the basal lamellae near the dorsal margin. The posterior dorsal angles of the basal lamellae project backwards in the neck region and serve as attachments for the longitudinal muscle bundles of the body.

The skeletogenous tissue is composed of two separate parts, a central axis of large thick-walled cells and a surrounding sheath of varying thickness. (Plate II, fig. 1.) The central, thick-walled cells contain a nucleus supported by a few strands of protoplasm, and are filled with a clear fluid. In the basal lamellae these cells show no definite arrangement or number but those in the filaments occur in successive layers of four cells, the pair facing the centre of the branchial funnel being the larger. The cells in the living state are turgid and by this means retain the rigidity of the branchial crown. A single column of cells enters the palp as well as the pinnules. In the pinnule the first cell of the column is elongated in an antero-posterior direction and is attached to four or five cells of the axis of the filament. The subsequent cells decrease in width until the ninth which is approximately cuboidal. (Plate II, fig. 2) The more distal cells increase greatly in length and very slightly in breadth until the relative proportion of length to breadth is as two to one. The ninth cell forms a universal bending joint about

which the muscles of the base of the pinnule work.

The sheath surrounding this axis is composed of a clear, hyaline substance having the same staining properties as the basement membrane, interspersed with a varying number of anastomosing cells. It has been fully described by VIALLANES. On the two sides of the basal lamella it varies in character. On the outside it is homogeneous and contains very few cells, but on the inside, i. e. towards the middle line, cells occur in large numbers, often in groups, while the hyaline material occurs in strands between them. (Plate II, fig. 1). CLAPARÈDE describes in Spirographis in certain regions of this sheath, and particularily where the longitudinal body muscles are attached, three distinct layers, a) a thin layer of normal connective tissue, to which the longitudinal muscles are attached; b) a layer formed by groups of nuclei embedded in connective tissue; and c) a layer of connective tissue with the usual small groups of nuclei, much thicker than the other two, traversed by numerous fine striations These he describes as:

" des faisceaux de striés ou de fibres tres-fines partant des grappes de nucleus de la couche précédente et perforant le tissu connectif, perpendiculairement à la surface du cartilage. Ces striés, qu'elles sont ou non l'expression de véritables fibres, paraissent émaner de l'interieur des grappes de nucleus, mais vu leur finesse, il n'est guère possible de determiner s'il y en a une ou plusieurs aboutissant à chaque nucleus.....La direction de ces derniers, reste toujours exactement perpendiculaire à la

surface du cartilage."

He describes a similar arrangement of layers on the outside of the sheath.

In Sabella the arrangement of parts is not nearly so clearly defined, CLAPARÈDE'S region of groups of nuclei being replaced by connective tissue in which run short bundles of fibres and relatively few nuclei. The striations however are very clearly marked at the posterior end but are absent on the outside where the epidermis abuts directly on the sheath with no intermediate tissue of any kind (Plate II, fig. 1). The insertion of the muscles of the branchial region on the sheath cause it to break up into a loose network . On the filaments it is thickest on the outside and the anastomosing cells do not penetrate the hyaline material but occur here and there pressed between the base of the epidermis and the outside layer of the sheath (Plate II, fig. 1). In the pinnule the sheath is absent.

There is no evidence in favour of the view that this tissue is cartilage. VIALLANES has shown that the sheath contains cells and cannot therefore be regarded as the matrix secreted by the central axis with which it is connected merely by virtue of position, the two being readily separable. KRUKENBERG(1880) compares the chemical composition with that of vertebrate cartilage and finds no resemblance. The names cartilage and perichondrium employed by VIALLANES and all previous workers are therefore not applicable; those of supporting axis and sheath are much more applicable.

The Musculature of the Branchial Region.

The muscular system of Sabella consists entirely of plain muscle.

In the pinnules longitudinal muscles only are present. The muscle fibrils are extremely fine and are not easily identified in transverse sections. Certain flattened nuclei which are occasionally evident in the sections may belong to these fibrils or to the membrane lining the cavity of the pinnule. (Plate III. fig. 3) In longitudinal sections the muscle fibrils can be seen to lie closely pressed against the base of the epidermis and appear as a thin, darkly staining, wavy line(PlateIII, fig. 4). That this is not a case of precipitation of the stain on the basal membrane of the epidermal cells is shown by the fact that in some preparations the fibrils can be seen, at the proximal end of the pinnule, to leave their position at the base of the epidermis and become inserted on the sheath of the central skeletal support of the filament. In addition to these fibrils, which are concerned with the movements of the pinnules during the collection of food, there is a second group, which also helps with the general movements, but is very particularly concerned with the closing of the branchial fans before retraction into the tube. These are the muscle fibres mentioned in connection with the universal bending joint of the pinnules. They are inserted on the sheath of the pinnule for a few cells distal to the ninth and their origin is on the sheath of the skeleton of the filament (Plate III

Fig. 4

Plate II
figs. 2 and 3). In transverse sections they appear as a lining to the cavity of the pinnule on the sides and front but not on the back* where the epidermis and the skeletal sheath are in close contact(Text-fig. 1).

The palps have longitudinal muscles only. These lie along the sheath of the central axis on the lateral and ventral sides. In transverse section the muscle fibres appear as parallel bands with the nuclei attached to the edge which projects into the coelomic space (Text-fig. 3).

In the filaments again only longitudinal muscles are present they occur in the cavity surrounding the branchial blood vessel, but on the lateral portions only. In transverse section they project from the walls of the cavity and show large oval nuclei at their free ends (Plate III, fig. 4). In longitudinal section they appear as bands of muscle with scattered nuclei, running from end to end of the filament, the individual fibres arising at intervals from the skeletal sheath. At the base of the filaments near the lower limits of the branchial folds these bundles increase greatly in size and come to lie on either side of a central projection of the skeletal sheath, from which many of the fibres arise. A little lower down on a level with the extreme base of the filament a large mass of muscle is present, lying

* In considering the orientation of the filaments and pinnules the surface towards the centre of the branchial funnel is considered to be the frontal face, that towards the outside of the funnel the abfrontal face, and those to the sides the lateral faces. This nomenclature will be used throughout the paper.

between the blood vessel and the supporting sheath(Text-fig. 4a). In longitudinal sections cut parallel to the dorsal surface of the worm, these bundles can be seen to be inserted on the skeletal sheath of the branchial crown below the level of the ventral lip and on a level with the main blood-vessel supplying the vessels of the filaments (Text-fig. 2).

On a level with the bases of the muscles described above a band of oblique muscles arises (Text-fig.4b). This runs from the ventral corner of the branchial crown parallel with the lower lip, gathering up fibres as it progresses, and is partly inserted on the transverse skeletal bar and partly forms a band of transverse muscles immediately above it(Text-fig. 2). On a level with the transverse bar the more ventral portions of the oblique muscles have disappeared, and a stout muscle bundle stretches across the angle of the lamella, from the lateral portion to the transverse bar on either side of the middle line, passing internally to the branchial blood-vessel(Text-fig.4c). Another band of muscles also runs across from side to side immediately below the skeletal bar in the neck region(Text-figs. 2 and 4d). The longitudinal body muscles are also attached to the backwardly directed processes of the branchial crown in this region, the ventral bundles being inserted in a more anterior position on the inside of the posterior processes of the internal supporting structure than the dorsal ones, which are attached to the outside.

The movements of the branchial region can be divided into three main groups according as they are concerned with a) the spreading of the branchial crown, b) the closing of the branchial crown, and c) movements of the whole branchial region.

a) VIALLANES states in his paper on the skeleton of Sabella that the spreading of the branchial crown is entirely due to the elasticity of the "cartilage". This does not appear to be the case. It is true that the pinnules and filaments appear to spread by elasticity alone but it is more probable that the transverse muscle band joining the posterior skeletal projections in the first body segment has for its function the spreading of the branchial crown to its fullest extent, by pulling their bases together posterior to the transverse bar. A similar function has been ascribed to a band of muscles occurring in the same position by CLAPARÈDE. ÖRLEY on the other hand describes the muscle band as belonging to the system of muscles which close the branchial crown.

b) The withdrawal of the worm into its tube follows after a complicated series of movements involving all the remaining muscles of the branchial region. The pinnules are drawn together in the middle line and also laid along the length of the filaments with their tips pointing forwards; this is due to the contraction of the frontal and antero-lateral portions of the basal muscles of the pinnules. The filaments are brought together by the agency of their longitudinal muscles, which, by their contraction, raise the filaments on the branchial crown, so bringing them to lie

side by side and serving in place of the interfilamentar muscles described by ORLEY in Branchiomma. The gill complex is rolled round on itself from the ventral corner by means of the oblique muscles and pulled together by the transverse muscle anterior to the skeletal bar, which acts in direct antagonism to the muscle bundle directly below it. The rapidity with which all the muscles act is so great that it is impossible to follow the sequence of events with any degree of certainty.

c) The angle of spread of the branchial crown depends on contraction of the longitudinal muscles of the body. The gill crown is usually held in a position at right angles to the axis of the body, but may occasionally be inclined towards the ventral surface or to the side. The first position appears to be brought about by the localised contraction of the anterior end of the ventral longitudinal muscles, the second by the contraction of the dorsal and ventral body muscles of one side or the other. During the process of tube building the anterior end of the worm is rotated and may sometimes describe as much as two and a half turns. The posterior part of the worm does not take part in the movement but remains fixed relative to the tube by the parapodia. The parapodia of the thoracic region are responsible for the rotation; alternate parapodia on each side are retracted, rotated sideways, protruded and the bristles inserted into the mucus lining of the tube. The muscles infront of the parapodia then contract and the body is pulled round a short distance and held in position while the rest of the parapodia

are swung forward into place and the cycle of movements is repeated. Usually not more than a complete turn is performed before the movement is reversed, but should it continue further the body of the worm is spirally twisted inside the tube. If retraction should now occur then the branchial crown revolves rapidly as it disappears from sight. Retraction within the tube is brought about by a sudden contraction of the longitudinal muscles of the body. The parapodia of a region near the posterior end remain fixed to the walls of the tube while the anterior and the extreme posterior parts of the body suddenly contract up to it. The rapid contraction of the whole body is due to the action of the giant cells and their fibres which run from end to end of the ventral nerve chord.

The Histology of the Branchial Epithelium.

The cells forming the epithelium of the pinnules are of three kinds, a) cells bearing cilia, b) cells without cilia, and c) cells secreting mucus. The ciliated cells occur on the frontal and abfrontal faces of the pinnules. In transverse section those on the abfrontal face are usually two or three in number and contain large, oval nuclei with scattered, darkly staining chromatin and a small nucleolus. Their free ends are covered with cilia which pass through the thin cuticle and are attached to a well marked basal plate which does not however show individual basal granules(Plate III, fig. 2). The cells on the frontal face are

divisible into two series. A longitudinal row of large cells occupies the corners of the base of the somewhat triangular filament. In section the rows appear as a pair of large oval cells. Between these latero-frontal cells are three or four columnar cells forming the second series. The latero-frontal cells contain very large oval nuclei with scattered, lightly staining, reticular chromatin and a large nucleolus situated rather to one side. To the free ends of the cells are attached what are apparently a group of long fine cilia. In the living animal this is in reality a single stout cilium which when at rest presents a peculiar appearance. Each cilium is folded across the middle and is slightly swollen at the bend so that the effect of a row of pins is produced. A similar arrangement is described for Spirographis by JAQUET. The cilia are attached to a small basal plate situated immediately below the thin cuticle;from it a group of fine fibrils runs into the cell, terminating on the median side of the nucleus in a fine rootlet(Plate III, fig. 2). The frontal cells are usually three in number. These are not arranged in definite ranks but interlock considerably so that, although three nuclei are usually present, the cilia appear to be arranged in a greater number of groups. The size and shape of the nuclei varies considerably, depending on the degree of crowding, but they are similar to those found on the abfrontal face. The cilia towards the outside are longer than those towards the centre, and the basal granules are in many cases distinct, with clearly marked fibrils running to the nucleus. Those in the centre are shorter

and more numerous, are situated on a basal plate and are connected with the central and usually largest nucleus by less clearly defined fibrils (Plate II, fig. 5). The non-ciliated cells are smaller and situated on the sides of the pinnules. Their nuclei are smaller and rounder, the chromatin stains more darkly and is aggregated into larger particles and the nucleolus is not distinguishable. In certain regions of the gill filaments the non-ciliated cells are crowded with brown pigment granules which are most numerous towards the periphery of the cell. In such regions the pigment is also found in the ciliated cells of the abfrontal face. The mucus cells occur sparingly on the sides of the pinnule. The secretion greatly distends the cells and pushes the nuclei to the circumference. The nuclei stain very darkly and are much distorted (Plate II, fig. 5).

The epithelium of the branchial filaments is composed of the same types of cell as that of the pinnules. The outer epithelium of the filament is formed almost entirely of columnar non-ciliated cells whose bases abut directly on the sheathing material of the skeleton and end in fine processes penetrating its surface. Occasionally a mucus cell is present. On the sides of the filaments the epithelium is lower and the nuclei rounder. It passes gradually into that found on the sides of the pinnules. The epithelium of the inner face of the filaments is elevated into a series of parallel folds. These are in reality the posteriorly prolonged bases of the pinnules (Text-fig. 1). They are formed by a double layer of epithelium separated by a well developed

basement membrane. On the outside of these folds the mucus cells increase greatly in number and in some places four or five may be contiguous. The cells are spherical, distended with secretion and the nuclei are greatly compressed, often forming a lens-shaped cap at the side or end of the cell and staining a uniform black. The inner face of the filamentar folds is covered with epithelium of much greater depth, with very few mucous cells The nuclei are round or oval With darkly staining nucleoli and chromatin; occasionally one can be seen in mitotic division. All the cells bear cilia but no definite intracellular apparatus could be demonstrated. The cuticle is absent from the inside of the groove (Plate III, fig. 4).

The basal folds are composed of two layers of epithelium separated by a basement membrane. The inner face is formed of ciliated columnar epithelium of varying height. It reaches a maximum at the free edge and in the centre of the fold where it increases suddenly so that a ridge is formed on either side almost cutting off the lower part of the groove. The height then decreases regularly until the floor of the groove is reached where it increases again slightly. All the cells are covered with a dense brush of long cilia; basal granules and fibrils are not distinguishable and mucous cells are absent except for an occasional one on the floor of the groove (Text-fig. 4). The epithelium of the outer faces of the folds is formed of low cubical cells. The nuclei are round and the free edges of the cells are covered by a very thin cuticle. Cilia occur in tufts on isolated

cells and are inserted on very small basal plates. Mucous cells are abundant, especially towards the tips of the folds. The epithelium in the pockets at the extreme base of the folds, formed by their fusing together in pairs, is composed almost entirely of mucous cells (Text-fig. 4).

The basal membrane which unites the bases of the filaments is also composed of two layers of epithelium separated by a basement membrane. The outer cell layer is continuous with that of the outside of the filaments and the inner with that of the outer wall of the basal folds. Cilia are absent.

Each palp consists of a solid central core upon which are set two narrow ridges in such a way that the surface of the support is divided into a short and a long arc. The long arc is on the dorsal surface, the short arc on the ventral. The core consists of a single pillar of supporting cells surrounded by a large mass of sheath material, a number of muscle fibres and a blood vessel. Sometimes more than one vessel is present but this may be considered as an abnormal condition. The whole is surrounded by an epithelium of tall columnar cells which is pulled out into the lateral ridges; these are formed from two layers of epithelium separated by a basement membrane. The epithelium on the inner face of the palp differs from that on the outer, although both layers are formed of ciliated and mucus cells. On the outer surface the ciliated cells each bear a tuft of long stout cilia which arise from basal granules and show faint intracellular fibrils running towards the nucleus. The nuclei are ellip-

tical, lightly staining and contain a dark nucleolus. In certain areas of the epithelium the distal ends of the cells are packed with brown pigment granules. The mucus cells are evenly distributed and numerous; in some worms they may be so developed that a few sink into the subepithelial connective tissue as they do in the ventral gland shields. The whole epithelium is covered by a delicate cuticle (Text-fig. 3 and Plate III, fig. 1). The epithelium of the inner face is similar to the epithelium of the buccal cavity and differs from that on the outside of the palp in several points. The cuticle is absent, pigment granules are never present and the cilia, instead of being grouped in tufts are shorter and form a continucus covering. These differences are of considerable interest when considered in connection with JOHANSSON'S work on the innervation of the branchial crown. The epithelium on the outer face resembles that of the dorsal body wall while that of the inner face is indistinguishable from that of the buccal cavity and oesophagus. JOHANSSON finds a mixed nerve supply to the branchial crown ,part of which is derived from the stomato-gastric system which innervates the buccal epithelium, the oesophagus and the anterior end at least of the stomach. It appears then as if there was an evagination of endoderm at the anterior end similar to that found at the anus. A study of the larval developement is required to confirm this suggestion.

The epithelium of the buccal funnel is a continuation of that of the inner face of the palps and does not in any way differ from it. Mucus cells are very numerous and their basal

nuclei are conspicuous. SOULIER states that the nuclei at the base of the epithelium are those of the "cellules de remplacement" which are derived from the subepithelial connective tissue A careful examination has led to the conclusion that this is not correct. Dividing nuclei are frequent and occur always immediately below the free edge of the cell. The resulting nuclei are smaller than those of the ciliated cells but it is reasonable to supposetthat they are ultimately converted into them. The nuclei occurring at the base of the epithelium do not then belong to replacing cells but are the nuclei of the mucus cells and can be seen lying at the side of such cells distorted and flattened by the secretion. SOULIER'S suggestion that cells migrate from the connective tissue is unlikely for he does not mention that he ever saw cells in the act of passing through the basement membrane, nor does the present work reveal any such. The changes during secretion of the mucus-secreting cells are difficult to follow. The secretion at first appears to be slightly granular and stains diffusely with iron haematoxylin, while later it has an alveolar appearance and stains with muci-carmine. As activity increases the nuclei become darker and smaller, are often unevenly shrunk and finally appear to break down completely. The dark globules which can be seen in parts of the epithelium may be the residue. Sections occasionally show extrusion of the bodies.

The ventral sacs are formed by the outer fold of the lateral lip which is pushed out and folded on either side so that a

pair of vesicles is formed with their openings facing each other in the middle line. The walls are thin and formed of two layers of epithelium separated by a layer of connective tissue. The outer epithelium is continuous with that of the lower lip. The cells are elongated and the nuclei oval. Mucus cells are rare. In many places the protoplasm contains round granules staining dark blue with iron haematoxylin. In certain regions also the outer epithelium may be crowded with brown pigment granules. In some worms the whole of the ventral sacs may be pigmented but in others the walls may be quite transparent. Ciliated cells are not common but are evenly distributed over the outer surface The inner epithelium is a continuation of that of the branchial funnel. In the region anterior to the point of fusion of the ventral wall of the oesophagus the characteristic height of the buccal epithelium is retained on the dorsal wall of the sacs, but after the fusion of the two lips only a small area in the mid-ventral line retains the high epithelium and plentiful mucus cells of the lateral lips. The lateral and ventral walls are lined by low epithelium bearing cilia and without a cuticle. Only a few scattered mucus cells are present except in certain parts. Along the free edges of the lower part of the sacs and in the mid-ventral line under the oesophagus mucus cells are developed to such an extent that they sink below the level of the epithelium and invade the subepithelial connective tissue layer. They are collected in groups in the spaces of the tissue and retain their connection with the exterior only by a narrow

neck which is invisible except when distended with secretion. The cells are swollen and the nuclei much distorted.

The parallel folds are formed of two layers of epithelium, similar to those of the ventral sacs, separated by a thick layer of subepithelial connective tissue whose interstices are filled with large mucous glands which discharge their contents between the folds. The inner epithelium is covered with a dense fringe of long cilia.

The Vascular System.

The vascular system of Sabella is well developed and although no specially contractile regions are present, the circulation, contrary to what is generally stated, is complete and efficient.

The blood contains chlorocruorin in solution which has been shown by MUNRO FOX(1923) to be capable of acting as a respiratory pigment, but no detailed study has yet been made of the respiration of the living animal. It is hoped to extend the outline account given here, both anatomically and physiologically.

The blood of Sabella is a clear liquid. ROMIEU(1923) states that cells are present. He does not find them in the gills but in the gut sinus, where they are recognisable by the deeply staining nucleus and small amount of lightly staining protoplasm. These cells have not been found with any degree of certainty; but the blood of the sinus contains numerous clear droplets, a

fact which may be connected with the observations of ROMIEU; no nuclei were however observed.

The blood is fluorescent, being green by transmitted, red by reflected light. The pH is about 6.8.

The vessels in which it is contained are thin walled and apparently without a muscular coat. FEDERIGHI(1928) describes the walls of the capillaries of Nereis virens as consisting of an endothelium only. In the larger vessels a cuticula is present and an outer incomplete layer of muscle cells. The muscle cells he demonstrates by means of vital staining with methylene blue. In Sabella the endothelium is a clear membrane with nuclei at frequent intervals. No cuticula has been seen in any vessel but staining with methylene blue shows a discontinuous layer of stellate cells over the outside of all the vessels of the body-cavity. Whether these are muscle cells as FEDERIGHI claims for Nereis virens, or are nerve cells associated with the vessels, has not yet been determined. The endothelium itself is contractile and upon its activity depends the whole circulation of the blood.

The Vessels of the Branchial Region.

The system of vessels in the branchial region is single, so that no continuous circulation of the blood is possible in this region. A large basal vessel runs from the most ventral point of the lateral lip round its base to the corner of the mouth. From this vessel are given off at intervals single vessels which

run on the inner side of the skeletal supports right to the very tip of each filament, sending a number of very short vessels to each basal fold and longer ones to each pinnule. The vessels for the group of filaments dorsal to the corner of the mouth are all given off close together. At the corner of the mouth the main branchial vessel bends sharply at right angles and runs in a posterior direction, between the skeletal sheath and the oblique muscle bundle, to the dorsal side of the brain, giving off on the way a single vessel on either side which runs to the palp. The branchial vessel lies free in an outgrowth of the body cavity which invades the branchial crown. This cavity, at least in the region surrounding the main branchial blood vessel, is lined by peritoneum. Certain nuclei in the cavity of the pinnule probably also belong to the peritoneum but might be those of the longitudinal muscle fibrils (Plate III, fig. 2).

When the blood vessel reaches the dorsal side of the brain it runs obliquely backwards between the anterior ganglion and the lateral commissure, where it joins a transverse vessel lying between the anterior cerebral ganglia and the oesophagus. This transverse vessel receives the branchial vessels at its ends. From the ends are also given off posteriorly two vessels which run obliquely backwards and towards the ventral surface where they fuse to form the ventral vessel at the septum between segments two and three. Lateral branches of these oesophageal connectives appear to run into and fuse with the vessels of the plexus surrounding the oesophagus, but whether this is actually

the case

is still doubtful. The capillaries may merely carry oxygenated blood to the muscle fibrils and tissues of the plexus.

A third vessel is given off from the transverse vessel in the mid-dorsal line, which runs backwards for a short distance, divides into two and runs into the oesophageal plexus where its identity is completely lost. The oesophageal plexus consists of a network of capillaries which surrounds the oesophagus in the first segment, is prolonged in an anterior direction below the cerebral ganglia and invades the tissue spaces of the lower lip where perhaps it reaches its greatest developement.

The Vessels of the Body.

The vascular system of the body consists mainly of longitudinal vessels but these are joined together in every segment by transverse connections.

The principal vessel is the ventral which is formed by the fusion of the oesophageal connectives and runs in the ventral mesentery for the whole length of the body. It is somewhat constricted by the septa so that when blood is passing along it, it takes the form of a number of swellings. In each segment it, is surrounded by chloragogen cells of a blackish brown colour which outline it sharply. In young Sabellas less than an inch in length the chloragogen cells have not yet acquired this characteristic colour and the ventral vessel when empty of blood is not

visible through the ventral body-wall.

On each side on the lateral body-wall is a vessel which runs in the body-cavity closely adpressed to the dorsal longitudinal muscle bundle. These vessels are not straight but describe a double curve in each segment, running first to the ventral and then towards the dorsal body-wall. From the crest of the first curve a vessel is given off to the parapodium, and from the second a vessel which runs upwards and forwards towards the mid-dorsal line where it ends. There are no longitudinal dorsal vessels as described by MILNE-EDWARDS. Both these vessels give off very numerous blind sacs which project far into the coelome and are unsupported by any mesentery. These sacs, although they are without muscle fibrils in their walls are strongly contractile, and empty and fill at each pulsation of the lateral vessels.

In addition to these vessels there is a large blood sinus surrounding the gut. It runs from one end of the body to the other and lies between the basement membrane of the gut epithelium and the muscular coat. In the thorax, where it reaches its greatest developement, it runs forward to the junction of the oesophagus with the stomach and breaks up there to form the oesophageal plexus.

A series of transverse vessels in each segment joins up the various longitudinal vessels. From the ventral vessel in the anterior part of each segment, is given off a pair of large transverse vessels which describe a double curve before they run to the lateral body-wall. The walls of the curved portion are thick

ly covered with chloragogen cells. The vessels run immediately behind the septum to the lateral body wall, then round the curve of the body and across the septum to the gut sinus which they enter in the mid-lateral line. At the point at which they touch the lateral body-wall they give off a vessel which joins the lateral longitudinal vessel close to the septum.

A second transverse vessel runs across the floor of the coelome in each segment just anterior to the septum. This vessel is very fine and passes ventrally and diagonally towards the middle line, through the ventral longitudinal muscle bundle to the ventral gland shield, where it breaks up into very numerous capillaries. The other end of this vessel is connected with the vessels of the parapodia and through them with the lateral vessels.

The collar folds and ventral gland shields of the first segment receive a very rich blood supply from the oesophageal plexus

The Direction of Flow of the Blood.

The circulation of the blood in Sabella is much more thorough than is generally supposed.

The blood passes along the vessels at a definite rate and in a definite direction. Only on one occasion was a reversal of flow observed in a lateral vessel, but other disturbances of the circulation showed that this was abnormal.

The blood passes in a posterior direction along the ventral vessel and in an anterior direction along the lateral vessels

and the gut sinus in a series of pulsations, the vessels being alternately empty and full in different parts of their length. In the branchial crown where the vessels are single all the vessels of one side are full at the same time, the most dorsal filaments filling first and emptying last while the more ventral ones fill and then empty in succession. As soon as all the vessels are full to the tip a wave of contraction passes towards the base pushing all the blood infront of it and emptying the vessel completely. The rate of emptying and filling is carefully timed in the various filaments so that as each vessel becomes empty the contraction in the main branchial vessel, which begins at the ventral end and passes dorsally, reaches the base of that filament. As soon as the gill crown is empty it fills again. It appears that while filling of the branchial crown on one side is taking place from the transverse vessel behind the brain, the oesophageal vessel on that side is constricted and when emptying, that part is open while the corresponding part of the transverse vessel is closed, although conclusive observations have not yet been made. Indeed no other mechanism would serve, since the two sides of the branchial crowns are filled alternately from the same transverse vessel and the ventral vessel is filled twice as often as each half of the branchial crown.

The function of the oesophageal and lateral lip plexuses have not yet been worked out. They do not appear to act as a "heart" as might be supposed from their position.

The circulation in the lateral vessels can also be watched.

Here again the two sides of the worm are not synchronised, the wave of contraction occurring later on one side than the other. A wave of contraction passes up the lateral vessel forcing the blood before it. At the posterior end the number of segments whose vessels are filled with blood at each contraction is small, but as the wave of contraction passes forwards the blood already in the lateral vessel and derived from the transverse vessels is gathered up, until at the anterior end as many as ten or twelve segments may be filled at the same time. As the blood passes along the lateral vessel it is forced into all the branches and the blind sacs given off from them. As soon as these are full they contract and force the blood back into the lateral vessels just as the wave of contraction passes the base of the lateral branches. a certain amount of blood appears to enter the transverse vessels also, but this is forced back again by the next contraction of the lateral vessel.

The number of contractions in the various vessels is not constant for worms of a similar size, as can be seen from the accompanying table giving the measurements and rates of circulation of eight worms of different sizes. There is no more than an indication of an increased rate of circulation in the smaller worms.

No. of beats per. min. in:	Worms I.	II.	III.	IV.	V.	VI.	VII.	VIII.
1/2 gill crown.	5	9	5	6.5	7	6	6	6.5
Whole gill crown.	10	19	10	12	14	12	13	13
Ventral vessel.	-	20	-	20	13	11	-	13
Lateral vessel.	4	11	6	5	6	7	5	5
Gut sinus.	23	34	20	20	28	20	12	23
Length of body. in cm.	7.5	1.1	6.5	1.0	2.7	1.1	0.7	7.0
Length of gills in cm.	3.2	0.7	2.8	0.9	1.5	0.9	0.5	3.0

Although earlier workers such as GRUBE(1838), MILNE-EDWARDS (1838) and CLAPARÈDE(1873) describe the circulation of the blood in various vessels of Spirographis no complete account has been given. MUNRO FOX(1924) gives an account of the contractions in some of the vessels of Sabellids, but states that no circulation in the true sense could take place, since the blood only oscillated back and forwards in a short region of the vessel. There is no doubt however that there is normally an efficient circulation of the blood in Sabella and that the gill crowns, though primarily modified for the capture of food must play an important part also in respiratory exchange.

The observations of BOUNHIOL(1902) upon the respiration of Spirographis with and without the gill crown show that the gills are only responsible for one quarter of the total respiration.

Their considerable area, thin walls, blood supply and continually changing water stream would point to a greater significance than this. Although there is a constant slow current of water through the tube, the only parts of the body which have a good peripheral blood supply are the parapodia and the ventral gland shields, and in both cases it seems more likely that the blood is supplying oxygen to the tissues rather than absorbing it from the surrounding water.

The Anatomy and Histology of the Alimentary Canal.

When the body cavity of Sabella is opened the alimentary canal can be seen as a simple tube without diverticula or convolutions of any kind. Although histologically several regions can be distinguished, they are variable in their limits and by no means clearly defined, and the same applies to their anatomical differentiation. The anterior portion of the gut is greatly constricted by the septa and swells out between them into a series of almost spherical chambers.

Towards the posterior end, which is often distended with faeces, the portion of gut in each segment is longer than the distance between the septa and bends now to one side, now to the other.

The intermediate portion is straight and only slightly constricted. If however it is much distended with food it may take

on the appearance of the anterior part but to a lesser degree.

The walls of the gut typically consist of four layers; a) An outer peritoneal layer, the lining of the body cavity, b) A muscular coat of circular and longitudinal fibres which do not occur in two definite coats as in the earthworm, but are intermingled, the longitudinal fibres, fewer in number running in the interstices of the circular. c) A vascular sinus surrounding the gut on all sides. This sinus commences behind the septum between segments two and three and extends to the posterior end of the body, where however it becomes so thin as almost to disappear. d) A ciliated and glandular epithelium resting on a well developed basement membrane.

Histologically the alimentary tract can be divided into four regions.

a). The oesophagus.
b). The stomach.
c). The intestine.
d). The rectum.

The oesophagus.

The exact point at which the buccal funnel ends and the oesophagus begins is marked neither anatomically nor histologically. For the sake of convenience the oesophagus may be taken as the region between the point of fusion of the lateral lips in the mid ventral line and the posterior end of segment two. At the anterior end the lumen is triradiate in section (Text-fig.4b). This configuration continues backwards for some distance until on a

level with the posterior edge of the transverse bar of the skeleton the oesophagus finally becomes narrow and slit-like (Text-fig.6). The whole of the oesophagus is surrounded by blood plexuses, first those of the lateral lips, then by their posteriorly directed continuation in the first two body segments. The muscle coat lies immediately below the plexus. It consists almost entirely of circular fibres. At the anterior end of the oesophagus a few fibrils are developed but these seem to be related rather to the blood plexus than to the oesophageal wall, although the two are touching. Just posterior to this however on a level with the posterior projections of the branchial skeleton, the circular muscle coat reaches a greater degree of development than in any other part of the alimentary tract. In transverse section longitudinal fibrils cannot be distinguished but in longitudinal section a few are visible running among the circular fibres.

The blood sinus which in other parts of the gut lies immediately below the muscle layer is not yet present.

The epithelium rests upon a well developed basement membrane It is similar to that of the buccal funnel but is more developed and thrown into numerous ridges. The mucus cells are more frequent in the ventral part of the epithelium, while in the dorsal part they may be entirely absent. Many dividing nuclei may be seen at the periphery of the epithelium. This appears to be a characteristic of the secretory epithelia of Sabella as it occurs frequently in the branchial funnel, the oesophagus, the stomach

and the rectum, but not in the intestine which does not contain any secretory cells.

The stomach.

The oesophagus opens into the stomach behind the second septum. The walls are formed by the four typical tissue layers. The peritoneum covers the muscular layer which consists of mixed longitudinal and circular fibres. Immediately below the muscular layer is the gut sinus which is particularly well developed in the anterior region (Text-fig. 7).

The epithelium itself varies greatly in height in different parts depending partly on the degree of distension of the gut with food.

The cells of the epithelium appear to exist in two physiological states, which are sharply defined, the majority of cells in a region being either secreting or ciliated.

The ciliated cells have oval nuclei with a dense chromatin network and a small nucleolus. The cytoplasm is pale and granular. The cilia are long and delicate and show neither basal granules nor intracellular fibrils. In the ciliated phase of the epithelium dividing nuclei are very plentiful and always occur immediately below the free edge of the cells(Plate III, fig.3). Evidence of degeneration of nuclei is also present. Spherules which stain uniformly with iron haematoxylin occur at all levels in the epithelium. They occur singly or two or three at a time inside a clear

vacuole and when towards the base of the epithelium may be associated with a lens-shaped nucleus(Plate III, fig3). These agree closely with the description given by BRASIL (1904) of degenerating nuclei in various Polychaetes.

In other regions of the gut a very different appearance is found. The cells have lost their cilia, are not actively dividing and show considerable changes in the nuclei. The cells are club-shaped with the rounded ends projecting into the lumen. The nuclei are oval and show a large nucleolus and a fine network of chromatin. In many cells between the nucleus and the free end large clear vacuoles of secretion fill up the cell. The lumen of the gut is filled with a granular coagulum which is formed by the coalescence of the round globules, each surrounded by a denser membrane, which can be seen towards the periphery. These globules can be seen issuing from the club-shaped ends of the cells(Plate III, fig. 4). When secretion is commencing the globules are pushed out between the cilia which appear to be thrown off and not retracted (Plate IV, fig. 3).

Although in Polychaetes the appearance of droplets of secretion being liberated from the free ends of the cells has often been described it has frequently been attributed to bad fixation. In Sabella however, in fresh preparations the gut is full of greenish brown droplets and if the epithelium is examined in sea water these can be seen protruding from the cells and are finally liberated from their ends.

The Intestine.

The exact point at which the stomach passes into the intestine is indefinite, the characteristic ventral folds of the intestine appearing before the secretory epithelium of the stomach gives place to the intestinal epithelium, so that an intermediate region of varying length results.

The intestine is of a more uniform diameter than the stomach and does not expand between the septa to the same extent. As in the other regions of the gut the outermost layer of the wall is formed by the peritoneum. Immediately below this lies the circular muscle coat which is fairly well developed. Longitudinal muscles occur in bundles lying between the circular fibrils and the blood sinus. The number of bundles is not fixed, nor do they occur in any definite position although a median dorsal and a median ventral bundle are usually present. The muscle bands can be seen in the fresh gut as light coloured stripes running in a longitudinal direction. The blood sinus lies below the muscular layer. In sections it is usually most obvious on the ventral side of the gut, where it forms two large spaces below the ventral folds. There is a well marked basement membrane on which the epithelium rests.(Text-fig. 8)

The epithelium is very unequal in height and is thrown up into two very large ventral folds characteristic of this region (Text-fig. 8). These folds vary somewhat in general form but are always present, sometimes as angular, sometimes as flat-topped projections. This region of the gut is slightly sinuous when fixed, as the

posterior end of the body is greatly extensible, and consequently transverse sections often show the epithelium cut at various angles In a completely transverse section the ventral folds stand out clearly and are sometimes flanked by lower folds of a similar nature. The cells of which they are composed vary greatly in height, those towards the centre of the fold being longer than the peripheral ones. Their free ends are covered with long cilia. The nuclei are elongated and rodlike and form a zone one-third of the height of the cell from the free edge; they frequently show two nucleoli. In addition to this band of nuclei numerous others are scattered in the basal portion of the epithelium, many of them darkly staining (Plate IV, fig. 6). These do not belong to mucous cells as staining with mucicarmine shows that none are present. The cytoplasm of the cells is finely granular and shows no vacuoles or inclusions. No trace of the yellow granules described by SOULIER have been found. The epithelium of the rest of the wall is low and is composed of almost cubical cells; they are ciliated and their nuclei are round and large containing a large nucleolus and very little chromatin (Plate IV, fig. 7). No dividing nuclei can be seen in any part of the intestinal epithelium.

The Rectum.

The rectum is separated from the intestine by an intermediate zone where the epithelium gradually increases in height on the dorsal and ventral walls and a few mucous glands appear. The circular muscle coat of the rectum lies immediately below the peri-

toneum and is greatly reduced. The longitudinal muscle fibres are absent. The blood sinus is still present but is also greatly reduced. The epithelium is enormously developed and thrown up into four large folds which almost obliterate the lumen of the gut when empty (Text-fig. 9).

The mucus glands of the epithelium are so greatly developed that the ciliated cells among them can only be recognised from their nuclei and the slightly expanded distal ends bearing cilia. In section across the length of the cells the ciliated cells appear as a fine network with greatly distended mucous cells filling up the meshes (Plate IV, fig. 8). The nuclei of the ciliated cells appear as faint grey rods in the distal part of the epithelium, while the nuclei of the mucus cells stain very darkly and are scattered through the basal portion of the epithelium forming in particular a zone at the base. Dividing nuclei are to be seen at the periphery (Plate IV, fig. 8). The more closely is the anus approached the more ~~closely~~ greatly are the mucous glands developed.

At the anus itself there is no ectodermal invagination. The anus is terminal, and on either side is a cushion-like outgrowth of rectal epithelium (Text-fig. 10). Mucous glands are greatly developed and serve to lubricate the faeces up to the moment when they enter the ventral groove (Text-fig. 11). These projections also serve to close the anus and can be brought together in the middle line for that purpose.

THE CILIARY FEEDING MECHANISM.

Methods.

It is possible to keep most of the Sabellids which are found in Britain, in good condition for several weeks at least in wide mouthed dishes without either a water circulation or air supply, and for longer periods embedded in clean sand, as in their natural habitat, with a few inches of water over them. Food is supplied from diatom cultures.

During the study of the ciliary currents of the branchial region of Sabella the worm was kept as far as possible under natural conditions. A suitable specimen with stiff gill filaments and as little pigment as possible about the lips and branchiae was chosen and placed, still in its own tube, inside a glass tube of slightly greater diameter. This was placed in a tall jar filled with sea water, and could be fixed in any position required by means of thin wire loops. The observations were made with a binocular dissecting microscope, usually using a magnification of 20 diameters. The worm was illumined from below by a strong light which was first passed through an alum bath to cut off the heat rays.

Upon first using an animal for observation difficulty was often experienced owing to extraneous vibrations and movements, but after a time this sensitivity was found to pass off.

The finer details of the ciliary tracts were ascertained by

examining excised portions of the branchiae in sea water under a higher power, but where ever possible these observations were confirmed on the complete animal. The substances used for demonstrating the currents were carmine powder, starch stained with iodine, various grades of carborundum, fine plankton and mud. It was in all cases found necessary to use only very small quantities of suspended material, otherwise the normal functioning of the various parts of the gills was not obtained.

The Collecting Currents.

When the anterior part of the worm is protruded so that the basal portion of the branchial region is free from the tube and the gill-crown is fully expanded, feeding commences. The maximum degree of expansion varies with the individual; in some the two halves of the branchial crown are drawn apart until an almost flat plate is formed, in others a wide and shallow funnel surrounds the mouth. The filaments forming the branchial crown stand out stiffly at regular intervals and are kept in position by the membranous web at their base. The pinnules on each filament are arranged in two rows which make an angle with each other rather greater than 90°. Towards the base of the filament they interlock; but gradually come to lie tip to tip, and finally towards the distal end they are wide apart. By this means a very effective filtering area is formed which acts as a food trap.

Water is drawn into this filtering funnel from the outside by

the cilia on the back of the pinnules, along whose length, from the base to the tip, they beat very strongly and continuously. These cilia are the abfrontals (Text-fig.12). The entering current deflected between the pinnules by the latero-frontal cilia (Text-fig.12), beating in a direction at right angles to the abfrontals, passes through the network of pinnules into the branchial funnel (Text-fig.13). Along with this stream enter small particles in suspension in the water. The particles are thrown by the latero-frontal cilia onto the shallow groove running along the inner face of each pinnule, and are carried to the base by the activity of the frontal cilia (Text-fig.12). The collecting of particles is partly brought about by the eddy formed in front of the pinnule by the water flowing past the sides. A region of reduced pressure is thus formed causing, along with the current produced by the latero-frontals, an inflow of water from the sides bearing the suspended particles.

The various rows of cilia show different reactions towards adverse conditions. Shock for example, affects the frontals and abfrontals to a very much less degree than the latero-frontal cilia The removal of a filament from the branchial crown will stop the movement of most of the latero-frontals on it, leaving only an isolated cilium beating here and there, while the activity of the other rows continues unabated. In this connection it is interesting to note that YONGE (1923) makes the following observations on Mya.

" Moreover in many cases, when examining animals that had been kept in the laboratory for some time, it was found

that the gills were black in parts. This was due to the presence of mud in the inter-lamellar cavities owing to the atrophy of the latero-frontal cilia, which apparently are much more easily affected by adverse conditions than the lateral cilia."

Specimens of Sabella are fairly frquently collected without, or with regenerating branchial crowns. In many cases no doubt, the loss of the branchiae is due to the voracity of passing fish, but it may also be the normal reaction to the wearing out of, or damage to, the all important latero-frontal cilia. Under Aquarium conditions it is often found that worms throw off the entire branchial crown and retire into their tubes to reappear again ten days or a fortnight later with small but perfect gill fans which rapidly reach their full size.

The rate of passage of water through the filtering funnel is slightly affected by a current, probably respiratory, which enters and leaves the mouth of the tube. While feeding is going on the body of the worm is in a constant state of movement, waves of contraction passing along it in succession, so that a stream of water enters the tube slowly and is more rapidly expelled. This pumping action of the body alters the speed of the current passing between the gills, increasing it on the downward, decreasing it on the upward stream. The means by which this current is brought about can be observed in two ways. In certain old and thick-walled tubes it is possible to scrape off the outer layer on one side. The removal of the muddy covering leaves exposed a thin, relatively

transparent membrane through which the greater part of the length of the worm can be seen. It is also possible to transfer a worm from its own to a tightly fitting glass tube which has been coated internally with a thick solution of gelatine to provide a grip for the parapodia. Observations on the manner of forming the current agree which ever method is used. The thoracic parapodia are protruded and anchor the anterior end of the worm in the tube. Immediately behind this region a swelling is formed by a shortening and thickening of the body for about half an inch, so that, with retracted parapodia it entirely fills the tube. This contracted piston-like portion then passes slowly backwards, segments drawing up to its advancing margin and relaxing behind until the posterior end is reached. The contracted area, dying away behind, begins to reform in front while the body returns to its normal length. The passing backwards of the piston causes water to be drawn in in front in the mid-ventral line and on the dorsal surface, points where the tube is not entirely blocked by the collar folds. The less strong upward current of shorter duration is formed by the returning of the worm to its normal length and the re-forming of the piston in front.

Timing the waves of contraction at 13°C. gave the following results. The time was taken from the commencement of the backward movement of the piston to the moment when it ceased to progress at the posterior end. The time of formation of the piston is not included but took about three seconds. An average of 23.87 seconds for the duration of the backward passage of the piston was obtained

from fifteen observations. At this point tube building movements commenced and the anterior twelve segments which were previouly protruding from the tube were drawn in and the piston formed further forward. An average of 25.5 seconds was then obtained. Later the temperature rose to 15°C. when further readings were taken giving an average of 21.5 seconds. At this more rapid rate, observations were made of the number of waves of contraction in five minutes. This gave an average of 17, showing that a slight overlap occurred, so that a second piston is formed and begins to pass backwards before the first has entirely died away.

When the particles collected by the latero-frontal cilia reach the frontal groove they are transported by the cilia on it to the base where they pass between the basal expansions of one pinnule and the next and enter the longitudinal groove of the gill axis down which they are driven as far as the gill folds by the cilia which line it. Heavy particles such as coarse sand grains falling from above are prevented from entering this groove by the basal expansions of the pinnules which over arch it.

The Sorting Mechanism.

The gill folds are arranged in pairs with their inner faces almost touching and are ciliated on both sides. The cilia on the outside all beat towards the free edge, but on the inner face, although the majority beat in the same direction, there are three parallel horizontal tracts on which the cilia beat towards the base of the filament (Text-fig. 14). One tract passes along the edge

of each fold, one along the middle situated on a fold of epithelium and one along the extreme base. The beating of the cilia on the outside causes a vortex to be formed and particles can be seen rushing down between the folds and rising up the sides in such a way that the inner surface of the basal supportng web appears to be ciliated; but this is not the case. By the interaction of the various currents on the inner surfaces of the gill-folds collected material is sorted into three grades. Large particles cannot enter between the gill-folds which are kept firmly pressed together; they are forced upwards by the cilia of their ends and carried along the edges to the dorsal or ventral lip. Medium sized particles pass between the folds on a level with the longitudinal ridges and are carried along these and discharged at their lower ends. Very fine particles pass straight down between the folds in the basal grooves (Text-fig. 14).

If the gill crown is irritated by too great a concentration of suspended matter , a copious secretion from the mucous glands of the filaments results and bulky strings of mucus with the particles embedded in them areproduced. These strings cannot enter the basal grooves, and are carried along the middle groove, or if they are still larger, along the tract on the edges of the fold. In this connection the distribution of mucous cells on the folds is noteworthy. They occur only on the outside and on the free edges, as bulky, well compacted strings are necessary for the proper functioning of the rejection tracts, while only the finest loose particles can be taken by the collecting tracts (Text-fig. 5).

The lower ends of the folds abut on the lateral or dorsal lips according to their position in the branchial crown, along which three corresponding tracts are developed; one along the free edge (Text-fig. 16), one along the middle and one along the free edge (Text-fig. 15). Waste material is carried to the palps. Medium sized particles from the dorsal group of filaments pass along a ridge on the dorsal lip as far as the palp. At this point the dorsal and lateral lips are in contact and the material crosses over to the groove on the lateral lip (Text-fig. 15). Rejected material on the dorsal lip passes along the free edge which is directly continued as the lateral wing of the palp (Text-fig. 16).

The Rejecting Mechanisms.

So far the rejection tracts have only been referred to in connection with the general processes of food collecting and sorting. In addition various ciliated regions are concerned with the removal of waste material settling upon the upper part of the body and the bases of the gills. Faeces , sand grains, caste off setae and any foreign particles from the inside of the tube pass up the ventral groove, round onto the dorsal surface of the thorax and are dragged forwards in a thin film of mucus by the action of the cilia on the neck and palps. This film passes between the two most dorsal gill filaments and is deflected into two divergent streams by the activity of the cilia on the palps. Material carried straight forward across the opening of the dorsal pit onto the dorsal surface of the lip is

driven sideways onto the palp where it joins the main streams. The cilia on both sides of the palp beat towards the tip, so that particles are carried away from the mouth along all parts of it (Text-fig. 16). In one specimen there appeared to be a feeble current on the ventral face of the palp carrying particles downwards, but in no other example was this found.

Foreign material accumulating on the unciliated ventral surface collar folds and bases of the gills is entangled in a thin sheet of mucus which is dragged forwards by the activity of the cilia on the lateral lips. Particles falling on the ventral sacs are caught by the scarce cilia of the posterior part and passed to the lateral lips.

The cilia of the outside of the lateral lip beat exceedingly actively and cause a current over its surface from behind forwards towards the free edge and slightly towards the ventral corner (Text-fig. 16). The direction of beat of the cilia on the free edge varies with the part of the lip. The currents on the central part, bordering the mouth, passes from below upwards towards the palps, while that on the part bordering the gills is in the contrary direction (Text-fig. 16). The two meet at a point directly opposite the palp where the mucus strings unite and are dragged off by the cilia of the palp.

The force of the current on the lateral lips is often so great that particles which are being carried towards it along the edges of the branchial folds are rolled back upon themselves and become entangled in mucus from the lower lip and formed into transverse

strings at the base of the pinnules. These are either dragged off by the palps or ejected from the branchial funnel by the animal retracting rapidly into the tube.

In a certain number of worms another rejection tract can be seen. This is situated at the sides of each filament. Particles are carried by it from the basal regions of the filaments to the tips. In no case have the cilia been seen in sections, but in certain worms a flickering can be seen over the surface of the filament while particles move rapidly and steadily upwards. In other specimens no trace of this current can be found.

The relative parts played by ciliary and muscular activity in the above processes can be clearly demonstrated by narcotising a Sabella in a mixture of three quarters by volume of isotonic magnesium chloride and one quarter of calcium chloride at pH 8, when the whole branchial region becomes limp. The cilia however continue beating. The proper functioning of the filtering apparatus clearly depends on the muscular tonus of the filaments and pinnules, but the cilia continue to collect particles whenever possible, passing them down the gill-axis to the branchial folds. These instead of standing up stiffly with parallel walls are quite flaccid, so that particles of any size passing along the gill-axis can push them apart and pass straight down to the base. Similarily the lateral and dorsal lips are without stiffness and none of the sorting mechanisms works although the cilia continue to beat, and even the largest particles pass to the oesophagus. In this case again the proper functioning depends on muscular tonus and on the maintenance of a

correct relationship between the lower lip and the base of the branchial folds.

Discussion.

ORTON (1914) in a paper on ciliary mechanisms states that:

"The cephalic gills of cryptocephalous Polychaetes have current-producing lateral cilia and frontal food collecting cilia essentially similar to those of Brachiopods, Lamellibranchs and other groups mentioned above."

The other groups are Tunicates, Protochordates and certain Gastropods such as Crepidula which have become almost entirely sedentary. In all these forms with the exception of some of the Lamellibranchs there are four rows of cilia on the meshes of the filtering apparatus, one abfrontal, one frontal and two lateral. In all cases the beat of the lateral cilia is from the frontal to the abfrontal face of the filament, and the current of water impinges first on the frontal cilia and then passes between the filaments.

In certain Lamellibranchs such as Ostrea and Mytilus two extra rows of cilia are developed, the latero-frontals. These are very stout compound cilia which are set in a single row as combs in the path of the current passing between the filaments; they beat in the oposite direction to the laterals and filter particles from the water jerking them forwards again into the frontal groove whence the cilia carry them away. ORTON groups the cryptocephalus Polychaetes with the main body of forms; but this does not seem to be justifiable,

for the arrangement is more like that in the aberrant Ostrea group. It does not seem possible to compare the current-producing cilia of Sabella with the laterals of other groups from which they differ in four important points.

1.) They are arranged as a single row.
2.) They are compound in structure.
3.) They beat in the opposite direction.
4.) They are much more sensitive to adverse conditions.

These characters however point to a definite similarity to the latero-frontals of the aberrant Lamellibranchs. (Text-fig. 17).

If it were possible to shave off the lateral cilia from the gill of Mytilus one would find that the latero-frontals would take on the function of current producers, the water would pass between the filaments from behind, and fine particles would be carried to the frontal cilia, partly by eddy currents, partly by means of the latero-frontal cilia; and a feeding mechanism almost identical with that of Sabella would result.

In the tube-living Polychaetes the absence of lateral cilia may be connected with the instability of the gill-complex: rapid and frequent retraction into the tube necessitating a lateral folding of the pinnules. ~~(Text-fig. 20)~~.

Considerable stress has been laid by various authors on the part played by mucus in the collecting of particles by ciliary activity.

ORTON (1913) makes the following observations.

"In all these gills there can be no doubt that mucus formation plays a very important part in the process of food collecting..... ..... In Lamellibranchs and Crepidula it has been suggested that

the corresponding mucus formation (to that of the endostyle in Amphioxus and Ascidians) takes place in the frontal epithelium of the gill filaments, and indeed swollen cells which are almost certainly mucus cells, have already been figured in the epithelium of the filaments of Mytilus . Similar globules occur also in the filaments of Glycimeris, Crania, Terebratula and Rhynchonella."

An examination of the literature shows that mucus cells are figured in various Lamellibranchs such as Ostrea (YONGE 1927) but RIDEWOOD (1903) makes no reference to them in his extensive paper on the gills of Lamellibranchs.

One difficulty lies in the way of accepting the importance of the part played by mucus in ciliary collecting mechanisms. It is this: the formation of strings of mucus in which all particles, regardles of size, are embedded seems incompatible with a subsequent sorting mechanism such as occurs on the palps of Lamellibranchs, depending on the size or weight of the particles.

The force of this argument is not weakened by the case of Amphioxus and the Tunicates, for there what sorting does occur is performed by the buccal tentacles in Amphioxus (ORTON 1913) and by the peribranchial processes in Tunicates (ORTON 1913) forming a sieve which strains off the larger particles before they reach the collecting pharyngeal region. In Brachiopods and Gastropods such as Crepidula the only sorting which occurs is due to the sudden expansion of the passage for the entering water inside the mantle cavity which allows heavy particles to fall onto the mantle surface

and be ejected by the ciliary tracts of the mantle. In Sabella it has been shown that mucus cells are chiefly associated with the rejection areas such as the free edges of the branchial folds, the outside of the lateral and dorsal lips and both faces of the palps. Mucus-secreting cells are present on the collecting tracts but in no great numbers and appear usually to serve the purpose of lubrication. It is interesting to note in this connection that mucus cells first appear on the collecting tracts in the filamentar grooves where lubrication of the cilia is more necessary owing to the constricted space in which they work. On the frontal grooves of the pinnules where contact is not so intimate mucus does not appear.

When, however, too numerous or too large particles falling from above instead of being drawn through from below, irritate the walls of the axial grooves of the filaments, then it seems that the cells are stimulated to empty all their contents and cause bulky strings of mucus to be formed which are seized by the rejection tracts. How far this idea of the function of the mucus cells on ciliary tracts collecting food particles can be applied to the case of Molluscs can only be determined by further experiment, but work done by GRAHAM on the feeding mechanism of Ensis siliqua confirms its applicability there also; any particles which become embedded in mucus strings are rejected regardless of size.

Although the collecting mechanism is so similar to that of Molluscs, the sorting mechanism differs fundamentally. In describing the sorting process in Mya arenaria (YONGE 1923) says:

"All heavy particles which make their way onto the palp face will naturally tend to settle down, and, if they are not more than a certain weight, they will, inspite of the proximal currents, come to rest in the grooves formed between the upper distal slope of the one fold and the summit of the preceding one..... On the other hand, the lighter particles, such as carmine grains, will be, as it were, thrown over these grooves from upper distal slope to upper distal slope until they reach the oral groove..... The whole palp mechanism tends to separate small from large particles, the criterion of size being weight."

In Sabella the sorting is reversed. The small, light particles travel along the base of the folds in the grooves, while the large, heavy ones are carried up the ends and along the free margins, the criterion of suitability being very emphatically size and not weight

The method of formation of the current inside the tube is also of interest when compared with that of the closely related Serpulids where a dorsal membrane is developed in the thorax. Miss FAULKNER (1928) describes in Filograna the course taken by particles of carmine inside the tube. Water enters posteriorly and passes forwards over the abdomen both dorsally and ventrally. When the posterior margin of the thoracic membrane is reached by the current on the ventral face the water stream is directed dorsally on both sides and joins the dorsal abdominal current on the dorsal surface of the thoracic membrane. The suction of this dorsal current causes water to be drawn in at the mouth of the tube on the

ventral surface, which passes round the posterior margin of the thoracic membrane and out on the dorsal surface. The whole current is produced by ciliary activity, no part being played by muscular contraction.

In Sabella on the other hand , although the faeces are carried forwards by the activity of the cilia of the ventral groove and the dorsal surface of the thorax, the water current inside the tube enters entirely by the anterior end and is produced solely by muscular contractions of the whole body.

THE PROCESS OF TUBE BUILDING.

Previous Work.

Although the tube which Sabella inhabits is so conspicuous and plays such an important part in the life of the animal, few authors have considered its formation in any detail.

Apart from brief notes on its dimensions and consistancy, the first to describe its formation was DALYELL (1853). He uses the name Amphitrite ventilabrum, but from his description and plate there can be no doubt that the species under consideration is Sabella pavonina. After describing the expansion of a worm in a jar of fresh sea-water he writes of the process of tube formation.

> "But if a drop of liquid mud fall amid the element from above disturbing its purity, then while the plume unfolds to its utmost capacity does the animal begin a slow revolution, the body also passing around within the tube. Now are all the thousands of cilia (pinnules) fringing the ribs of the branchiae discovered to be in vigourous activity and their office to be wondrous. A loose muddy mass is soon afterwards visibly accumulating in the bottom of the funnel; meantime the neck or first segment of the body, rising unusually high above the orifice of the tube exhibits two trowels beating down the thin

edge as they fold and clasp over the margin, like our fingers pressing a flattened cake against the palm of the hand. During these operations the muddy collections are seen descending between the roots of the fans towards the trowels, while another organ, perhaps the mouth, is also occupied, it may be, in compounding the preparation with adhesive matter. Still does the partial or complete revolution of the plumes above, and of the body within the tube, continue; the bulk of the muddy mass diminishes, activity abates; it is succeeded by repose, when the tube is found to have received evident prolongation."

CLAPARÈDE (1873) considers that in the Sabellidae the mucus from which the tube is formed is secreted by the "tubiparous glands" which are now known to be the thoracic excretory organs. After a detailed study of the ventral gland shields he first upholds their glandular nature and then decides that, since they occur most frequently in the thoracic region, they are to be regarded as protective cushions preventing injury by the edge of the tube.

MACÉ (1882) studied in detail the structure of the tube of Sabella. He describes two layers over and above the coating of mud, the outer layer being secreted by the skin, the inner by the"tubiparous glands". He recognises the importance of the gills in the process of tube building, stating that the absence of muddy coating in certain cases was due to the excessive size and unsuitability of the particles collected by the gills.

"C'est que l'animal pendant la formation de ces tubes ou partis de ces tubes, n'a trouve à la porté de ces cirrhes branchials

préhensiles que des materiaux trop grossiers pour être employés à la construction de son habitat."

BRUNOTTE (1888) in Branchiomma considers that the mucus forming the tube is secreted by the epidermis in general and the ventral gland shields in particular.

MEYER (1888) describes the ventral collar folds as secretory and as tools used in forming the tube.

SOULIER (1898) working on Sabella confirms the observations of BRUNOTTE and MEYER with regard to the secretion of mucus for the tube. He also records the formation of a transparent zone on the anterior end of the tubes of Sabella as occurring in captivity. The normal outer coating of mud he attributes to particles carried against the tube by the water currents, and adhering to the freshly secreted mucus.

The Tube.

Sabellas can be obtained from two localities, from the intertidal zone where they occur embedded in mud, and from deep water where they are not buried in the substratum but are dredged entire from the Cellaria beds.

The tubes from the two localities differ slightly. Those from the mud are composed of two portions, a tough leathery part some but not all of which projects above the mud, and a posterior part which is semi-transparent, thin and collapsible. The tube is extremely long, often as much as two feet in length, and cannot be obtained complete, but even so there is a distinct reduction in diameter of

the tube towards the posterior end. In very small worms the tube tapers to a point but the extreme end is ragged and does not end in a smooth pore as in Branchiomma.

In worms from the Cellaria the tube, although not so large is about eight inches long and one quarter of an inch in diameter. Throughout the greater part of its length it is of uniform leathery consistency and of uniform diameter. At the posterior end there is about half an inch of thin membranous tube which is attached to the Cellaria and tapers to a point. The extreme tip is again ragged.

The limited extent to which the tubes protrude from the estuarine mud, their relatively constant diameter and the fact that even young worms when removed from their tubes cannot burrow into the mud and build again, points to a distinct problem concerned with the relation of growth to tube diameter. Only a study of the whole life-history of the worm can show by what method the tube is adapted to the increasing diameter of the body.

Addition to the Anterior End.

The ventral sacs are filled from the longitudinal groove of the lower lip as has been described in the section on the collecting currents. Since the ventral sacs themselves are formed from a folding of the outer wall of the groove, it opens towards the base of th sac posterior to the upper ends of the parallel folds. Material passing down the groove is carried down to its base, round the bend in its outer wall and forced between it and the ventral wall of the

oesophagus to the base of the sac. It is there coated with mucus. If it is present in small amount it is carried up to the central region of the sac where it meets the currents descending from the upper part (Text-fig.18). If present in large amount it is pushed up by fresh material coming up from below, until the sac is completely full. If more material is still brought down and tube-building is delayed, the surplus material overflows and is caught by the rejection currents of the lower lips.

The process of tube building is not continuous but depends on a good supply of mud in suspension. Nevertheless a low edging of transparent mucus may be laid down in the course of time in order to smooth the edge of the tube if mud is not forthcoming.

When tube-building is about to commence the anterior end of the worm is pushed out of the tube until the ventral collar folds lie over the edge. The worm then begins to rotate , while the collar folds commence a complex series of movements. The rotation is brought about by the levering action of the thoracic parapodia, as has already been described (page 31). At the same time the ventral collar folds begin their movements. Working together these undergo a rhythmic contraction which begins at the fixed base and spreads towards the free tips. At the same time they move towards and away from the body, smoothing the tube up towards its edge. The commencement of each cycle of movements causes the ventral folds to be drawn slightly apart so that the cilia have free play. At the same time the ventral parallel folds secrete mucus so that a continuous string is formed, in which are embedded particles of mud from the ventral

sacs. More mucus is added as this passes between the collar folds from the very plentiful glands on either side. As soon as the string is long enough it is attached to the edge of the tube by the mucous secretion and the tooling action of the collar folds (Text-fig. 19 20). It is then pulled out by the rotating action of the worm and laid like a rope along the edge of the tube, being cemented into position by the mucus of the collar folds. Most of the cilia of the parallel folds are functionless at this time, but those of the upper end of the groove retain their work of feeding particles to the upper end of the groove where they are added to the mucus string. The ventral collar folds press the new material together between their tips and the body wall, or may be used to smooth the inner wall by pressing upwards and outwards with the tips inserted into the mouth of the tube. This mode of construction gives rise to numerous transverse striations which were mentioned by MACÉ as corresponding to the segmentation of the body. The inner smooth lining of the tube, so obvious in sections is without doubt laid down by the activity of the ventral gland shields throughout the life of the animal, since it is much thinner in the anterior and more recent part of the tube.

Discussion.

From this description it can be seen how much more closely the observations of DALYELL approached the truth than those of later writers. His outline of the process is correct and although

he failed to understand the storing function of the ventral sacs, which he mistook for " a tongue or scoop", he recognised them as playing some part in the process of tube building. That the thoracic excretory organs do not function in the formation of the tube, as CLAPARÈDE thought, is perfectly clear, as their contents can be seen to be liberated from the renal papillae as a stream of liquid containing greenish granules which are caught in the dorsal rejection tracts and carried to the tips of the palps. SOULIER was especially interested in the formation of the tube, but entirely failed to understand the process. Although he described the occurrence of particles in the ventral sacs and between the ventral folds and showed experimentally that they are derived from the collecting and not from the rejecting tracts, he considered them to be most likely a reserve food supply.

An examination of other members of the Sabellidae shows that ventral sacs and collar folds, the two most essential parts of the building apparatus are not universally present. In Eispira and Potamilla both collar folds and ventral sacs are well developed and the consistency of the tube is the same as that of Sabella; the method of formation is also the same. In Myxicola the ventral sacs and the collar folds are absent, the tube being formed entirely of mucus secreted by the whole body-wall, the gland shields occurring dorsally as well as ventrally. In Branchiomma the method of formation of the tube is very different. The basal folds on which sorting of food material occurs in Sabella are almost absent and the structures named the ventral sacs by SOULIER, who believed them

to be identical with those of Sabella, are in reality very different The narrow diameter of the branchial funnel and the absence of ventral prolongations of the gill crowns cause the lateral lips to bend round sharply on themselves as they leave the gill filaments to border the mouth. Their edge is greatly curved outwards away from the filaments and it is the cavity surrounded by each lip and overarched by the recurved edge that SOULIER names the " ampoule ventrale ", a very different thing from the ventral sac of Sabella.

The tube of Branchiomma, of a very different consistency, is made from individual sand grains in place of mud. In aquaria where the water is still, disturbed only by the food-collecting currents of the worms themselves, additions are made to the tube of moderately large sand grains . The surface of the sand, discoloured by a dark brown growth of diatoms, shows no sign of disturbance such as might be caused by the worm bending from the tube and collecting particles from the surface with the gills; the particles used are light in colour and can only be derived from the layers below the surface. It seems likely that they are collected by the posterior end of the worm and passed up the ciliated groove to the anterior end. The method by which this is brought about, and the treatment of the sand grains before they are attached to the edge of the tube has not yet been worked out, but should prove of great interest.

The method of formation of the tube in other Polychaetes has been to a certain extent described by WATSON but in no case has a similar process to that of Sabella been found, individual sand grains laid on separately being used in all cases examined.

THE PHYSIOLOGY OF DIGESTION.

Previous Work.

The processes of digestion and the hydrogen ion concentration of the gut of Polychaetes are practically unknown, only a few isolated observations on the action of gut extracts on the principal classes of food-stuffs having been made under unknown conditions.

The earliest record is that of FREDERICQ (1878) who found that an extract of the whole body of Nereis pelagica contained a very st strong proteolytic enzyme capable of digesting in two hours, in alkaline medium, a weight of fibrin equivalent to the weight of worm used in making the extract. The resulting solution gave a positive reaction to tests for peptone.

WIREN (1887) found that the contents of the intestinal caeca of Arenicola, and also the intestine gave an acid reaction to litmus

KRUKENBERG (1881) found a proteolytic enzyme acting in alkaline medium in the gut of Hermione, Aphrodite, Arenicola and Spirographis

DARBOUX (1899) described an enzyme from the intestinal caeca of Aphrodite acting on fibrin.

BRASIL (1903 and1904) examined the effect of an alcoholic extract of the intestinal caeca of Arenicola on starch and fibrin in various media. Fibrin only was digested. In the presence of dilute acid no digestion took place, only a slight amount in neutral solution and the maximum amount in alkaline solution. The reaction of the caecal contents was neutral, while that of the gut was

alkaline. He also (1904) made observations on the digestive enzymes of Lagis korenii. A starch digesting enzyme was found in the descending arm of the intestinal loop and also minute traces of a lipase. A proteolytic enzyme acting in alkaline medium was obtained from the ascending arm of the intestine.

The Food of Sabella.

From the nature of the food collecting mechanism it is clear that Sabella feeds exclusively on very finely divided matter in suspension in the water. While studying the food of various bottom living forms HUNT (1925) examined the gut contents of Sabella and describes the food as finely sorted plankton and detritus. The chief constituents were bottom-living diatoms, although when present typical planktonic forms made up the bulk of the food. Peridinians, Silicoflagellates, Foraminifera and Tintinnids also occurred.

An examination of the gut contents both in April and September confirmed HUNT'S observations. A large part of the ingested material consists of finely divided detritus and very small grains of sand, but at both seasons diatoms occur in large numbers. The commonest are the bottom-living naviculoid forms, but planktonic diatoms Rhizosolenia are also present. In some worms large numbers of diatoms may be found, while in others collected on the same ground at the same time there may be relatively few diatoms but enormous numbers of planktonic dinoflagellates. In all are found, in addition to sand grains, numerous annelid and crustacean bristles

small portions of copepods, pieces of red and green algae, encysted flagellates, very numerous coccolithophores and an occasional Tintinopsis . Since an examination of the gut contents could not be made for six to eighteen hours after the worms were collected, all protozoa, eggs and larvae ingested were rendered unidentifiable by the action of the enzymes, although they were undoubtedly present originally in large numbers. Measurements of material found in the gut show that only very fine particles are taken in. The following are typical measurements for the largest particles found.

Substance.	Dimensions.
Sand grains.	114u x 86u. 100u x 86u. 240u x 240u. 170u x 140u.
Navicula.	160u x 17u.
Acnanthe.	160u x 81u.
Paralia chains.	280u x 170. 240u x 20u. 100u x 35u.

In annelid and crustacean bristles the length may be considerably greater but the breadth is such that falling into the grooves lengthwise they would pass the sorting mechanisms on the gill folds and enter the gut.

A certain amount of individual variation occurs in the size of the particles. In almost all cases where unusually large sand grains in the gut were found, the worms had been for some time

under laboratory conditions and were probably suffering from lack of muscular tonus.

Transport of Food Along the Gut.

When the gut is opened it is found to be filled in the anterior region with a dark brown liquid, the digestive juice.

In the centre of the gut is a string of mucus in which are embedded the particles of food. The mucus may be continuous through many segments and stained by the digestive juice which diffuses all through it. The mucus is partly derived from the branchial funnel but mostly from the bases of the lips and the oesophagus.

At the posterior end the gut contents appear as a compact mass of fine sand, detritus and diatom cases. The mucus in which the particles were embedded is no longer evident and the faeces readily break up. When however they are expelled they do not show the same tendency to disintegrate owing to the quantity of mucus secreted by the extreme posterior end of the gut which forms an outer binding coat.

The gut is uniformly ciliated throughout, but how far muscular activity is responsible for the passage of food along the gut is not clear. Judging by the poorness of the muscular coat and its position outside the sinus it is more likely to be concerned with the circulation of blood than with the transport of food along the gut.

The Rate of Passage of Food along the Gut.

The rate of passage of food along the gut was measured at 16°C. A carmine suspension was fed to a number of worms and the time taken until red faeces were expelled, was noted. The number of segments in each worm were counted and the average time required for the passage of food through the gut obtained. Individual worms when tested several times in succession showed considerable consistency. At 16°C. the average time taken was 22.8 hours for an average length of 234.7 segments.

No. of Worm.	No. of hours.	No. of segments.	Average rate in segs. per hr.
1.	21	265	12.6
2.	24	210	9.0
	24	210	9.0
3.	7.75 *	250	33.6
	8.0	250	31.0
4.	24	210	8.8
	17	210	12.3
	25	210	8.4
5.	26.5	255	9.6
	22	255	11.6
6.	22.5	230	10.2
	26	230	8.1
7.	18	210	11.7
8.	23.5	240	10.1
9.	25.5	255	10.0
10.	21	250	11.9
	21.5	250	11.8

* No explanation of this result could be found.

The Hydrogen Ion Concentration of the Gut.

No observations have been made at all on the pH of the gut of Polychaetes.

In the Sabellidae the determination of the hydrogen ion concentration with accuracy is difficult owing to the ease with which contamination with blood from the sinus or with coelomic fluid occurs; both of these fluids appear to be more strongly buffered than the gut contents and tend to give samples from the gut a pH value of 6.8.

Estimations of the pH of the gut of a large number of worms were made by the following method. The worms were opened along their whole length and the coelome on each side of the gut broken into, the septa being cut through. The body cavity was washed out with distilled water and dried with clean filter paper. Samples of the gut contents were then taken with a fine, blunt ended pipette at every tenth segment. The pH was measured either by the spot method of CLARKE and LUBS or by comparison with colour standards in small test tubes of 1 cc. capacity. Owing to the dark brown colour of the gut contents it was found that the second method gave the better results, as it was then possible to dilute the sample considerably with distilled water. At the posterior end, however, where the faeces are solid it is necessary to use the spot method, after mixing the faeces with a little distilled water on a white plate. Although the results are by no means constant when compared segment for segment, the general pictures obtained

are very similar. The results of a number of estimations are given in Table I.

The pH of the first ten to thirty segments is low, about pH 6.8, but rises steadily to pH 8 or even as high as pH 8.4 about the hundredth segment. Posterior to this it drops suddenly to pH 7, then falls more slowly to pH 6.

The enzymes of the gut begin to be secreted at the extreme anterior end of the gut, and are still active at the extreme posterior end; in consequence, the pH range through which they must act is pH 6 to pH 8.4.

The Enzymes of the Gut.

Methods.

In all experiments a crude water extract of the walls and contents of the gut was used as a source of enzyme, as it was found to be quite impossible to collect sufficient enzyme from the contents of the narrow lumen. For each experiment theguts of a number of worms were removed, weighed and ground up in a mortar with sand and a few drops of toluol. They were then extracted on ice for an hour, filtered and diluted ~~to~~ with distilled water to the strength required.

Considerable difficulty was experienced in controlling the pH of the experiments, since in the case of protein and more especially fat digestion the end products are acids which quickly

lower the pH when the mixture is unbuffered. At first no suitable buffer covering the long pH range could be found, and the citric acid-sodium phosphate mixtures of MacIlvaine (CLARK 1927) giving a pH range from 2.2 to 8 were used, followed by the boric acid-sodium carbonate buffers of ATKINS and PANTIN (1926) giving a range from pH 7.6 to 11. These were found to give very unsatisfactory results, as the salts of which they are composed affect the rate of digestion, the amount digested at pH 8, for example, with the same enzyme extract and concentration of substrate, being very much greater with one buffer than the other. In the digestion of glycogen and starch more digestion takes place with the buffer covering the high pH range than with that covering the lower. With the digestion of methyl acetate the oposite result is obtained. The results of two typical experiments showing this effect are given in Table II. The buffer mixture given by NORTHROP (1919) was then tried after substituting sodium acetate for the sodium citrate given in his formula. This was found to give good results with protein digestion, only a slight change in pH occurring after a period of twelve hours.

It was found however that owing to the liberation of fatty acids no amount of buffer would cause the pH in fat digestion experiments to remain constant. But by reducing the quantities of enzyme and substrate used to one tenth the volume of buffer, and estimating the fatty acids formed at the end of two or three hours, it was possible to reduce the change in hydrogen ion concen-

tration to about pH 1, the pH of the experiment being taken as the average pH, as a rough ~~estimation~~ approximation.

When first determining the optimum hydrogen ion concentration of carbohydrate digestion the pH was adjusted by the addition of dilute acid and alkali and was found to remain constant. When, however in September 1929 the experiments were repeated, it was found that a higher optimum was obtained. It was then found that the pH had changed greatly in the course of the experiment, and that when the average pH. instead of the initial pH. was taken as the pH of the experiment the same optimum was obtained. As this change did not occur before, it is possibly due to the autolysis of fat stored in the walls of the gut after a period of exceptionally warm weather. An experiment was therefore set up to investigate the extent of the autolytic processes. The details of the experiment are given in Table III. The results show that the alteration in pH during autolysis is considerable and indicates that as the optimum pH for autolysis is about pH 7.6 while that for the digestion of fat is about pH 7.4 , the abnormal alteration in pH during the digestion of carbohydrates is due to the presence of large quantities of fat in the cells of the gut. Owing to lack of material from April 1928 it is impossible to confirm this by direct fat analysis.

The method employed to estimate the products of digestion of carbohydrates is the modification of the blood-sugar technique of HAGEDORN and JENSEN (1922) used by BOYLAND (1928) to estimate the carbohydrates in muscle. This was found to give reliable and con-

stant results.

The products of digestion of proteins were estimated by the formol titration method of SÖRENSEN using a mixture of phenolphthalein and methylene blue as indicator. This was found to give better results than phenolphthalein alone, especially by artificial light. The method employed by DERNBY (quoted by BODANSKY and ROSE 1922) proved unsatisfactory, as the activity of the enzyme even when greatly diluted was so great as to cause all the tubes round the optimum to liquify apparently simultaneously.

The products of digestion of fat were estimated by direct titration of the fatty acids with sodium hydroxide using the same indicator as was used in the estimation of amino acids.

The Localisation of the Enzymes.

Since there is a distinct histological difference in the walls of the anterior and posterior portions of the gut, a series of experiments was set up to determine whether the enzymes were secreted by the anterior portion alone, as is indicated by the cellular structure, or by every region of the gut.

Since the enzymes are still active at the extreme posterior end of the gut it was necessary to remove every trace of the gut contents from the lumen of the hind gut. A second difficulty was that of separating the anterior from the posterior part of the gut owing to the absence of anatomical differentiation. It is probably due to this source of error rather than to the other that a certain amount of enzyme appears to be present in the walls of the hind

gut.

The method which gave the best results was to open the worm along its whole length, cut through the septa, slit up the gut from end to end and wash out the contents with distilled water. Portions of the two regions were then removed, ground up with sand , and the activity of the extract upon starch and gelatine determined. The results of the experiments are summarised in Table IV.

Although the result are not conclusive the great discrepancy in the amounts digested in the two regions of the gut shows that the apparent presence of enzymes in the wall of the hind gut is probably due to one of the sources of error mentioned above.

The Digestion of Carbohydrates.

Specificity.

A series of experiments was set up to determine the range of activity of the carbohydrate digesting enzymes of the gut. Table V gives the results of a typical set of experiments.

It was found that both starch and glycogen were readily digested by an extract of the gut wall. The glucoside salicin was also digested but not cane sugar, lactose or maltose.

In view of the statement made by BOYSEN JENSEN (1914) that large quantities of cellulose and pentosans are present in the detritus of the sea-bottom and are most likely utilised by animals as a source of food, experiments were performed to show whether enzymes capable of digesting these substances were present in the

gut of Sabella. The results of the experiment are given in Table VI. No trace of enzymes acting on these substances were found even after seven days' incubation at 30°C.

Activity at Posterior End of Gut.

An experiment was performed to determine whether the carbohydrate digesting enzymes are still active at the posterior end of the gut. Freshly formed faeces were used as a source of enzyme which was extracted in the usual way. The result of the experiment, which was confirmed by others, is given in Table VII.

The enzymes were found to be still active in the faeces, so that the digestion of carbohydrates can occur, under suitable conditions, in all regions of the gut.

A detailed study of the properties of the amylase was made.

The Influence of the Hydrogen Ion Concentration on the Digestion of Starch.

i. The determination of the pH optimum.

A number of experiments were performed to determine the optimum pH of starch digestion. The results obtained were very uniform, in all cases the optimum falling between pH 6.5 and 6.85 with an average of pH 6.8. Very little digestion takes place below pH 5 or above pH 9. Table VIII gives the results of an experiment of eight hours' duration at a temperature of 31°C. The activity of the enzyme falling off very rapidly on either side of the optimum, gives 50% digestion between pH 5.5 and 7.5.

ii. The influence of time upon the optimum pH.

Experiments were performed to determine whether the duration of the experiment had any effect on the optimum hydrogen ion concentration . Three experiments were set up as described for the optimum pH, using the same enzyme extract and concentration of substrate, and incubated for eight, sixteen and twenty four hours at 31°C. Table IX gives the results of the experiments. No change in the optimum pH occurred throughout the experiment.

iii. The influence of temperature on the pH optimum.

Table X gives the results of an experiment performed to investigate the influence of the temperature of incubation on the optimum pH. Three experiments were set up as described already and incubated for eight hours at 39°C., 31°C. and 18°C. A change of 0.15 pH resulted but the variation is too small to be of any significance under the conditions of the experiment.

The Influence of Temperature on the Digestion of Starch.

i. The determination of the temperature optimum.

BLACKMAN (1902) has shown that the optimum temperature at which an enzyme acts does not depend on any property of the enzyme, but is merely the temperature at which the acceleration due to the increase of temperature and the destruction due to the same cause exactly balance each other, and is directly dependent upon the duration of the experiment. In consequence the determination of the temperature optimum has very little significance, but has been determined for Sabella because of its possible relation to other factors.

For a digestive period of ten hours it was found to lie at about 30°C. Details of the experiment are given in Table XI.

ii. The temperature of destruction.

The temperature of destruction of the enzyme was determined by heating the enzyme to various temperatures for fifteen minutes and subsequently incubating with starch solution at 30°C. for seven hours. Details of the experiment are given in Table XII. It was found that the temperature of total destruction of the enzyme after fifteen minutes heating was at or a little below 65°C. at pH 6.4.

iii. Digestion at 0°C.

From experiments on the temperature optima it was found that the enzyme was almost inactive at 0°C. and prolonged experiments showed a small but definite increase in the amount of reducing sugar present. The enzyme then is not destroyed by a low temperature.

iv. The influence of pH on the temperature optimum.

An experiment was set up to test the possible effect of the hydrogen ion concentration on the temperature optimum. A series of experiments were set up at three different pHs and incubated at various temperatures for nine hours. Table XIII shows the results. Although a slight change was found in the temperature optimum comparable to that found by COMPTON (1915) for the enzymes of yeast yet the change is so small that no reliance can be placed on the result until it is repeated with a more delicately regulated and graded thermostat.

v. The effect of time on the temperature optimum.

When determining the optimum temperature for the digestion of starch the results obtained seemed to indicate that an increased incubation period for the experiment caused a fall in the optimum temperature, and it was thought that a clue had been obtained to the explanation of the very high temperature optima of the enzymes of many marine animals. A number of experiments were performed to investigate this point further. Indications were obtained that for the time taken by the food to pass through the gut, about 22 hours at 16°C., the optimum fell below 20°C., but beyond this no conclusive results were arrived at. Table XIV gives details of an experiment which showed a very definite lowering of the optimum temperature upto eighteen hours incubation; subsequently the optimum remained at the lower temperature or even rose slightly until thirty-six hours, when the experiment was stopped. The enzyme remained active until the end. No explanation can yet be given of this result which occurred several times.

The Optimum Hydrogen Ion Concentration for Glycogen Digestion.

The optimum pH was determined for the digestion of glycogen. Table XV gives the results of an experiment which was incubated for ten hours at 32°C. The greatest amount of digestion was found to occur at pH 6.8.

The Digestion of Proteins.

The only observation on the protease of a Sabellid is that of KRUKENBERG who found an enzyme acting on protein in alkaline medium in the gut of Spirographis. A similar enzyme has been found in Sabella.

Specificity.

A series of experiments was set up to determine the range of activity of the protease present in extracts of the gut-wall. Table XVI gives the results of one of these experiments. It was found that casein, fibrin, peptone and gelatine were all digested; free amino- acids were formed in each case, as shown by a rose coloration with bromine water. Coagulated egg albumin was not digested A more detailed study of the digestion of gelatine was then made.

The Influence of the Hydrogen Ion Concentration on Gelatine Digestion.

A preliminary investigation on the digestion of gelatine over a pH range of 2.2 to 11 showed that only one optimum was present about pH 7.8 & no digestion occurred below pH 4. The pH optimum was then determined with greater accuracy and was found to lie at pH 8. 50% activity occurred between pH 7.5 and 9.2 . Table XVII gives the details of this experiment.

The Influence of Temperature on Gelatine Digestion.

i. Temperature of destruction of Protease.

A number of experiments were performed to determine the temperature of destruction of the enzyme. The extract was heated to various temperatures for fifteen minutes and subsequently incubated with gelatine solution for 12 hours at 32°C. Table XVIII gives details of an experiment which was confirmed by others. The temperature of destruction of protease lies about 70°C. for fifteen minutes heating at pH 6.4.

The Digestion of Fat.

Determination of the Presence of a Lipase.

A preliminary experiment was performed with phenol-red milk to test for the presence of lipase in the gut extract of Sabella. 10 cc. milk were boiled and rendered alkaline with phenol-red. The milk was divided into two portions; to one was added 5 cc. of 2% gut extract and to the other the same amount after boiling. Both were incubated at 30°C.. The colour in the experimental tube changed from red to yellow in 2 hours while the control remained red up till 18 hours.

A lipase was therefore present in the gut of Sabella.

Specificity.

An experiment was set up to determine the range of digestion of the lipase. The details of the experiment are given in TableXIX.

Olive oil, lecithin and methyl acetate were all digested.

The Influence of Hydrogen Ion Concentration on Fat Digestion.

i. The optimum pH.

A number of experiments were performed to find the optimum pH of the lipase. Table XX gives the results of a typical experiment. Very little digestion takes place below pH 6 or above pH 8. The optimum for the digestion of methyl acetate lies at pH 7.4 after 2 hours incubation at 30°C.

The Influence of Temperature on Fat Digestion.

i. The Temperature of Destruction.

Experiments were set up to find the temperature of destruction of the lipase. The enzyme extract was heated to various temperatures for fifteen minutes and then incubated with ethyl butyrate for ten hours at 30°C. Table XXI gives the details of the experiment. The lipase is completely destroyed by heating for fifteen minutes at a temperature of 60°C. at pH 6.4.

Absorption of the Products of Digestion.

Since the gut of Sabella is narrow and the walls extremely delicate it was found to be impossible to study the permeability of the gut wall by direct experimental methods. An attempt was made, therefore , to define the absorptive region by the iron saccharate method used by JORDAN (1904) for Aphrodite . While specially

useful in cases where phagocytosis or intracellular digestion occurs. The method has also been successfully used for Ciona (YONGE 1925), where absorption of dissolved food substances takes place. In Sabella absolutely negative results were obtained. Although the iron in the lumen of the gut stained clearly no trace of it could be found in the cells of the gut wall at any period from two hours up to four days. Although the method was of use for Aphrodite it does not appear to be of universal application to the Polychaetes, as Miss FAULKNER (1929) also obtained negative results for Filograna.

SCULIER (1898) describes the presence of yellowish food granules in the gut epithelium especially towards the posterior end. No trace of these was found; but in the region of the stomach, in cells which though not actually secreting, occurred between others which were pouring enzymes into the lumen, numerous small black granules were to be seen in material fixed in Hermann's fluid, (Plate IV, fig. 2). These were not found in non-osmicated material, which suggests that they were of a fatty nature. If these are droplets of absorbed fat then fat-absorbing cells occur between the secreting cells of the stomach and in no other region. The great difficulty of obtaining well fixed material has prevented a further study of absorption by histochemical methods.

Discussion.

The enzymes of the gut of Sabella are unusually well adapted to work in the medium in which they are found. In all cases

the optimum pH of the enzyme falls well inside the limits of pH of the gut. The 50% activity range of the various enzymes is given below.

Amylase	pH 6 - 7.5.	Protease	pH 7.5 - 9.
Glycogenase	pH 6 - 7.5.	Lipase	pH 6.5 - 8.

Except for part of the range of the protease all of these fall inside the average pH values for the gut of pH 6 - 8.4.

The relative strengths of the enzymes are also well adapted to the nature of the food. BRANDT (1900) gives the following values for the composition of diatoms and peridinians which form a considerable proportion of the food of Sabella.

	Diatoms,	Peridinians.
Protein	28.7%	13.7%
Fat	8.0%	1.37%
Carbohydrate	63.0%	84.9%

In Sabella the best developed enzyme is the amylase, followed by the protease and then the lipase.

BERRILL (1929) shows the extreme importance of the time factor in the digestion of carbohydrates and proteins in Tunicates. An attempt to show the same effect in Sabella has failed. In it, the amylase at any rate, appears to be relatively stable, the temperature optimum only falling slightly with experiments of long duration.

COMPTON (1915) gives the following summary of the factors which are to influence the temperature optima and pH optima of enzyme action in certain cases.

Optimum Temperature.

i. Independent of the concentration of the enzyme.

ii. Independent of the concentration of the substrate.

iii. Dependent on the pH of the medium.

iv. Dependent on the duration of the experiment.

Optimum Hydrogen Ion Concentration.

i. Independent of the concentration of the enzyme.

ii. Dependent on the concentration of the substrate.

iii. Dependent on the temperature of the experiment.

iv. Dependent on the duration of the experiment.

In Sabella an attempt was made to show the influence of some of these factors on the digestion of starch by the enzymes of the gut. Since only a crude water extract of the gut wall was used as a source of enzyme and the concentration necessarily varied with every fresh sample the influence of the concentration of the enzyme and substrate was not investigated. The other four factors were however investigated and in no case was definite positive evidence obtained of their influence on the process of digestion.

RESERVE FOOD MATERIAL.

A detailed study of the reserve food material of Sabella has not yet been made.

A preliminary investigation shows that both glycogen and fat are present.

Large quantities of glycogen occur in the eggs in droplets but

has not yet been identified in other tissues.

Fat occurs in droplets in the cells at the base of the parapod ia and in the body cavity in enormous quantities. The eggs are full of large droplets as well as many smaller ones. When the contents of the body cavity are treated with Sudan III. all the droplets in the eggs stain very deeply except a few which are probably vacuoles containing the glycogen masses.

The wandering cells are also full of small droplets and occur in large clusters round the eggs. When stained with Nile blue sulphate these droplets stain every colour from blue to red, showing that fat in all stages of elaboration is present.

Up to the present only female worms have been examined, but it is intended to complete these observations and extend them to males and young worms killed at various times of the year.

GENERAL DISCUSSION.

An examination of the gill crowns of other tube-living Polychaetes of the groups Sabellidae and Serpulidae shows that the actual collecting mechanism, in the British members at any rate, is very similar to that of Sabella. In Bispira, Branchiomma, Dasychone, Myxicola and Potamilla the same four rows of cilia are present and function in exactly the same way as in Sabella. In the Serpulids Filograna, Hydroides, Pomatoceros, Protula, Serpula and Spirorbis only three of these rows are present. The abfrontal cilia are not developed and the whole of the current which enters the branchial funnel is produced by the latero-frontals. The smaller number of filaments and the wider spread of the pinnules probably make this arrangement possible in the Serpulids, the water entering the branchial funnel at right angles instead of at a very small angle as in the Sabellids (Text-fig. 2D).

The complex sorting mechanisms of Sabella occur also in Bispira and Potamilla. In the other forms referred to above a brief examination has shown that in each the branchial folds are greatly reduced or absent. In Sabella the sorting of food is entirely carried out on these organs, so that if rigorous sorting does occur in these other forms it must be by some entirely different method.

Very little is known about the methods of food collecting in other groups of Polychaetes.

A ciliary mechanism is known to occur in the Spionidae, Terebellidae, Ampharetidae, Hermellidae, Chlorhaemidae and Chaetopteridae .

In the Spionidae the long palps which project from the tube bear a ciliated groove. They twist actively in all directions and particles with which they come in contact are passed to the mouth partly by ciliary activity, partly by shortening of the palps.

In the Terebellidae and Ampharetidae (HESSLE 1924) the method of food collecting is similar. In neither group is the sorting mechanism known.

In the Hermellidae the method of collecting the food appears to be very similar to that found in Sabellids. According to JOHANSSON (1927) the palps are the organs modified for the collecting of food in this group also. They take the form of parallel rows of processes on either side of the mouth and a brief examination of the living animal shows that particles in suspension pass between the processes and are caught and carried by ciliary activity down a groove to the base of each process and thence to the mouth. The sorting mechanism is not known.

In the Chlorhaemidae the feeding mechanism varies in the different groups, but in Flabelligera a ciliary mechanism is developed. Both the tentacles above the mouth and the palp-like organs which project in front of it are ciliated. The current produced by the tentacles is probably purely respiratory but the palps have ciliated grooves on their under surface and as the animal moves about they are pushed along the surface of the ground and all small particles are carried along the grooves to the mouth.

In Chaetopterus (JOYEUX-LAFFUIE 1890) the respiratory current which passes through the tube brings particles in suspension to the

mouth of the tube. These particles are collected in two different regions by ciliary tracts although no filtering mechanism is developed. The water entering the mouth of the tube comes in contact with the ciliated lips of the buccal funnel and particles in suspension are carried direct to the mouth. The water then passes along the dorsal surface and comes in contact with the respiratory-current-producing fans of segment twelve. Each has a ciliated groove on its edge down which particles pass to a median dorsal groove which runs forward to the buccal funnel.

In other groups besides the Polychaetes it might be supposed that sedentary forms with ciliated crowns at the anterior end would show a similar mechanism. No very satisfactory account exists of the ciliary currents in Polyzoa, Phoronis or Cephalodiscus. An examination of a living Phoronis shows that the cilia of the tentacles are differentiated into three rows as in Serpulids, two latero-frontal in position and one frontal row. The current of water, however , enters between the whorls of tentacles and is drawn in both directions between the tentacles by the activity of the paired rows of cilia. The water impinges first on the frontal cilia, then passes through between the tentacles, an arrangement similar to that found in many Molluscs and Brachiopods as well as in Tunicates and in Amphioxus.

The direction of flow of the water current is the same in the Ectoproct Polyzoa where the water passes down the centre of the funnel and out between the tentacles.

In the Endoproct Polyzoa on the other hand, the condition is different. The arrangement of cilia is the same as in Serpulids.

Very strongly beating latero-frontal cilia draw a current of water through the filaments and throw particles onto the cilia of the frontal face which carry them to the basal groove. This passes round the base of the tentacles to the mouth. The arrangement is very similar to that found in Polychaetes.

A detailed comparison has already been made with the collecting mechanisms of Lamellibranchs, sedentary Gastropods, Brachiopods, Tunicates and Amphioxus (pages 67 to 70), but the developement of a similar mode of feeding in such widely different groups as Molluscs, Brachiopods, Protochordates, Polyzoa and Polychaetes involving such widely fifferent organs as pharynx, tentacles and body-wall can only be regarded as another interesting example of convergence correlated with a similar mode of life.

A comparison can not yet be made between the digestive processes in Sabella and those in other Polychaetes, but it is possible to compare them with those of Molluscs and Tunicates. Mya arenaria(YONGE 1923) and Ostrea edulis (YONGE 1926) both occur along with Sabella in the estuarine mud and take into their alimentary canals similar food material.

In the Lamellibranchs the digestive tract is specialised for intracellular digestion; digestion of all particles except those of a carbohydrate nature occurs in the phagocytic cells of the digestive diverticula or in the phagocytes themselves. The digestion of carbohydrates is emphasised in every direction and the only enzyme which is found free in the gut is the very strong amylase of the crystalline style.

In Tunicates, which also occur attached to stones and weed in a similar habitat, the processes of digestion are somewhat different. In Ciona (YONGE 1925) which does not appear to be typical of the group, although digestion is extracellular the carbohydrate-digesting enzyme again is the only one present in any quantity, while the protease and lipase are very weak. In the Pyurid ascidians (BERRILL 1929) where there is a well defined secretory liver, a strong amylase and a moderately strong protease and lipase are all poured into the lumen of the gut and the process of digestion appears to be similar to that of Sabella.

Since BOYSEN JENSEN (1914) published his account of the available food supply of the sea-bottom and showed that a considerable amount of carbohydrate was present in the detritus as cellulose and pentosans, various workers have attempted to find an enzyme acting on these substances in the gut of of detritus feeders. Since in no typical member of any of the four principal groups of detritus feeders, Echinoderms, Lamellibranchs, Tunicates and Polychaetes has an enzyme acting on either cellulose or pentosans been found, it can be said that plant detritus is not a widespread source of nourishment for the bottom fauna and is probably not utilised at all, passing through the alimentary canal unchanged.

The only groups of marine Invertebrates in which the digestion of these substances is known to occur are the specialised wood-boring Teredinidae and one Tectibranch, Aplysia; the one digesting wood, the other the cell walls of living plants.

SUMMARY.

Sabella pavonina is a tube-living Polychaete occurring in estuarine mud in great numbers in certain localities.

The branchial crown, which projects from the anterior end of the body, is a specialised ciliary filtering organ which collects small particles in suspension from the water. The branchial crown is formed by two symmetrical portions each composed of a basal lamella bearing numerous filaments which in turn bear a pair of basal folds and two rows of short pinnules. The basal lamella and the axis of each filament and pinnule contain a specialised supporting structure of large vacuolated cells surrounded by a connective tissue sheath on which are inserted muscles for opening and closing the branchial crown. The mouth is terminal and is enclosed between two lateral and a dorsal lip which bears two elongated structures, the palps. The lateral lips fuse to form the floor of the oesophagus and their free edges are continued as a pair of ventral sacs which lie just anterior to the collar folds of the first body segment

The vascular system is well developed and the blood circulates rapidly in all parts of the body.

The pinnules are ciliated and cause a current of water to flow between the filaments into the branchial funnel; particles in suspension are caught by the cilia and carried to a groove on each filament, down which they pass to the basal folds. On these they are sorted into three grades, the criterion being size, not weight. The largest sized particles are carried to the palps and rejected;

the medium sized are carried to the ventral sacs and stored there; the finest are conveyed to the mouth.

The ventral ciliated groove and the palps are concerned with the rejection of waste material from the anus, the inside of the tube and the branchial funnel. Mucus glands are almost exclusively associated with the rejection tracts and play very little part in the collecting of food.

A constant current of water is kept up inside the tube by muscular contractions of the body of the worm.

Additions are made to the anterior end of the tube with the material stored in the ventral sacs. The particles are mixed with mucus and, by the rotation of the anterior end of the worm and the tooling action of the collar folds, are laid like a rope along the edge of the tube and cemented into place by the mucous secretion of the first body segment.

The alimentary canal is straight and without diverticula. It can be divided into four regions upon histological grounds only. The second portion is the secretory region.

The gut contents consist of fine sand, detritus, peridinians, flagellates, algal spores and diatoms. The food takes an average of twenty-two and a half hours to pass through the gut at 16°C.. The enzymes present are an amylase acting on starch, glycogen and glucosides; a protease acing on fibrin, casein, peptone and gelatine and a lipase acting on olive oil, lecithin and esters. The optimum pHs at which these enzymes act are 6.8, 8.0 and 7.4 respectively, all of which fall within the limits of the range of hydrogen ion

concentration of the gut, pH 6 to 8.4.

The reserve materials stored in the body are fat and glycogen.

DESCRIPTION OF PLATES.

List of Abbreviations used.

ab. c.	absorbing cell.
ab. f. c.	abfrontal cilia.
ax. sh.	sheath of internal supporting axis.
ax. sh. fil.	axis sheath of filament.
b. m.	basement membrane.
b. m. pin.	basal muscles of pinnule.
bend. jt.	bending joint of pinnule.
bl. v. fil.	blood vessel of filament.
bl. v. pin.	blood vessel of pinnule.
cil.	cilia.
cil. c.	ciliated cell.
cil. r.	ciliary rootlet.
circ. m. g.	circular muscles of gut.
con. t. c.	connective tissue cell.
cut.	cuticle.
d. n.	dividing nuclei.
deg. n.	degenerating nuclei.
dr. sec.	droplets of secretion.
ep.	epidermis.
fr. cil.	frontal cilia.
g. s.	gut sinus.
l. n.	lens shaped nucleus of degenerating cell.
lat. b. m. f.	lateral basal muscle fibres.
l. fr. cil.	latero-frontal cilia.
long. bod. m.	longitudinal muscles of body.
long. gr. fil.	longitudinal groove of filament.
long. m. f.	longitudinal muscle fibres.
long. m. pin.	longitudinal muscles of pinnules.
m. gl.	mucous gland-cell.
m. sec.	mucous secretion.
n.	nucleus.
ner.	nerve.
n. cil. c.	nucleus of ciliated cell.
n. l. m. f.	nucleus of longitudinal muscle fibre.
n. m. gl.	nucleus of mucus gland-cell.
n. per.	nucleus of peritoneum.
p. c.	pericardial cell.
sec.	secretion.
sh. bn. f.	short bundles of fibres.
st.	striations.
sup. ax. fil.	supporting axis of filament.
sup. ax. pin.	supporting axis of pinnule.
sup. ax. p. p.	supporting axis of posterior projection.

Plate I.

Fig. 1. The Salcombe collecting ground at low tide. The tubes of Sabella pavonina project from the mud in large numbers.

Fig. 2. A clump of tubes projecting from the water.

Plate II.

Fig. I. Longitudinal section through part of the branchial region, showing the posterior projection of the skeletal supporting structure and the muscles attached to it. x 146.

Fig. 2. Longitudinal section through the base of a pinnule to show the bending joint and the basal muscles. x 292.

Fig. 3. Longitudinal section through the base of the same pinnule to show the insertion of one of the basal muscles on the supporting axis of the pinnule. x 292.

Fig. 4. Transverse section through a gill filament which has passed longitudinally through a pinnule, to show the musculature, blood supply and histology of both. x 292.

Fig. 5. Transverse section through the outer epithelium of the palp to show the ciliation, and histology. x 730.

Plate III.

Fig. 1. Transverse section through the outer epithelium of the palp to show the ciliation and histology. x 538.

Fig. 2. Transverse section through the epithelium of the buccal funnel, to show the ciliation and histology. x 538.

Fig. 3. Transverse section through the epithelium of the stomach in the ciliated phase , to show the histology. x 538.

Fig. 4. Transverse section through the epithelium of the stomach in the secreting phase, to show the secreting and absorbing cells. x 538.

Fig. 5. Transverse section through the epithelium of the stomach at the commencement of secretion to show the fate of the cilia. x 233.

Fig. 6. Transverse section through onr of the ventral folds of the epithelium of the intestine, to show the histology. x 538.

Fig. 7. Transverse section through the epithelium of the intestine on the dorsal side to show the histology. x 538.

Fig. 8. Transverse section through the epithelium of the rectum, to show the histology. x 525.

Fig. 9. Transverse section across the epithelial cells of the rectum, showing the great developement of mucous cells and the obliteration of the ciliated cells. x 525.

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APPENDIX.

TABLE I.

The Hydrogen Ion Concentration of the Gut.

No. of seg.	Worm I.	Worm II.	Worm III.	Worm IV.
10	6.8	7.2	7.0	6.6
20	-	-	7.2	7.2
30	7.2	-	-	-
40	7.4	7.4	-	-
50	7.7	7.6	7.7	7.7
60	7.8	8.2	7.9	7.9
70	7.9	-	8.2	8.2
80	7.9	8.0	8.2	8.2
90	7.9	8.0	-	7.0
100	-	7.5	7.4	-
110	8.0	-	-	-
120	-	-	-	6.7
130	7.2	-	-	-
140	-	7.0	-	-
150	-	-	7.0	-
160	6.8	6.6	-	-
-	-	-	-	-
-	-	-	-	-
-	-	-	-	-
200	6.4	6.4	6.6	6.0
-	-		-	
-	-		-	
-	-		-	
250	6.0		6.0	

TABLE II.

The Effect of McIlvaine's & Atkins & Pantin's Buffers.

I. On the Digestion of Glycogen.

2 ccs. 1% Glycogen + 5ccs. Buffer + 2 ccs. Enzyme.
2 ccs. 1% Glycogen + 5ccs. Buffer + 2ccs. Enzyme(boiled).

McIlvaine = pH 5.4 - 7.0
Atkins & Pantin = 7.6 - 9.0.

Duration of Experiment = 10 hours.
Temperature of Experiment = 32°C.

pH.	Experiment ccs. N/100 Thio.	Control. ccs. N/100 Thio.	Difference.	Mgms. Sugar 2ccs	10ccs.
9.0	6.3	9.0	2.7	0.8	0.4
8.0	4.6	8.8	4.4	1.3	6.5
7.6	3.6	9.0	5.4	1.65	8.25
7.0	6.65	9.0	2.35	0.7	3.5
6.8	5.9	9.0	3.1	0.95	4.75
6.4	6.45	9.0	2.55	0.8	4.0
6.0	7.4	9.0	1.6	0.5	2.5
5.4	8.6	9.0	0.4	0.15	0.75

The pH remained constant throughout the experiment.

II. On the Digestion of Methyl Acetate.

2 ccs. 2% Enzyme + 1/2 cc. Methyl acetate + 2½ ccs. H2O + 5cc Buffer.
2 ccs. 2% Enzyme(boiled) + 1/2 cc. Methyl acetate + 21/2 ccs. H2O + 5 ccs. Buffer.

Duration of Experiment= 22 hours.
Temperature of Experiment = 32°C.

pH.	Experiment. ccs. N/20 NaOH.	Control. ccs. N/20 NaOH.	Difference.
10.0	2.3	1.4	0.9
9.4	3.1	1.2	1.9
9.0	3.4	1.1	2.4
8.6	3.5	1.3	2.2
8.4	2.8	1.3	1.5
8.2	3.2	1.4	1.8
8.0	3.1	1.5	1.6
7.8	3.1	1.7	1.4
7.6	2.9	2.0	0.9
7.0	9.0	5.9	3.1
6.4	10.1	7.8	2.3
6.0	10.4	8.7	1.7
5.4	11.3	10.1	1.2
5.0	12.0	11.0	1.0

Owing to a mistake only the initial pH was recorded.

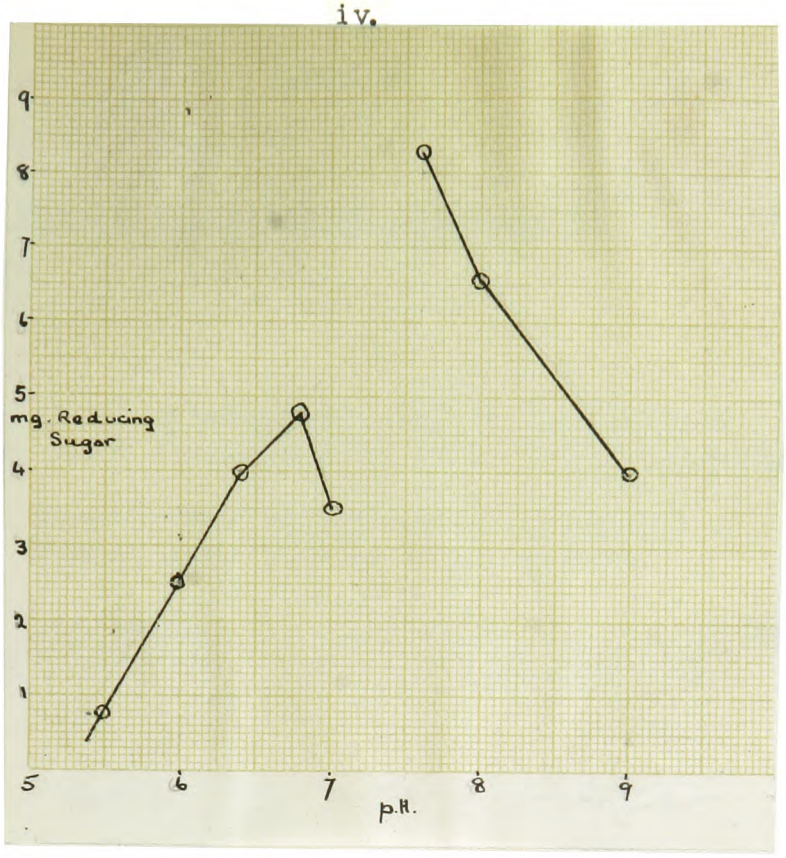
TABLE III.

Autolysis of the Gut.

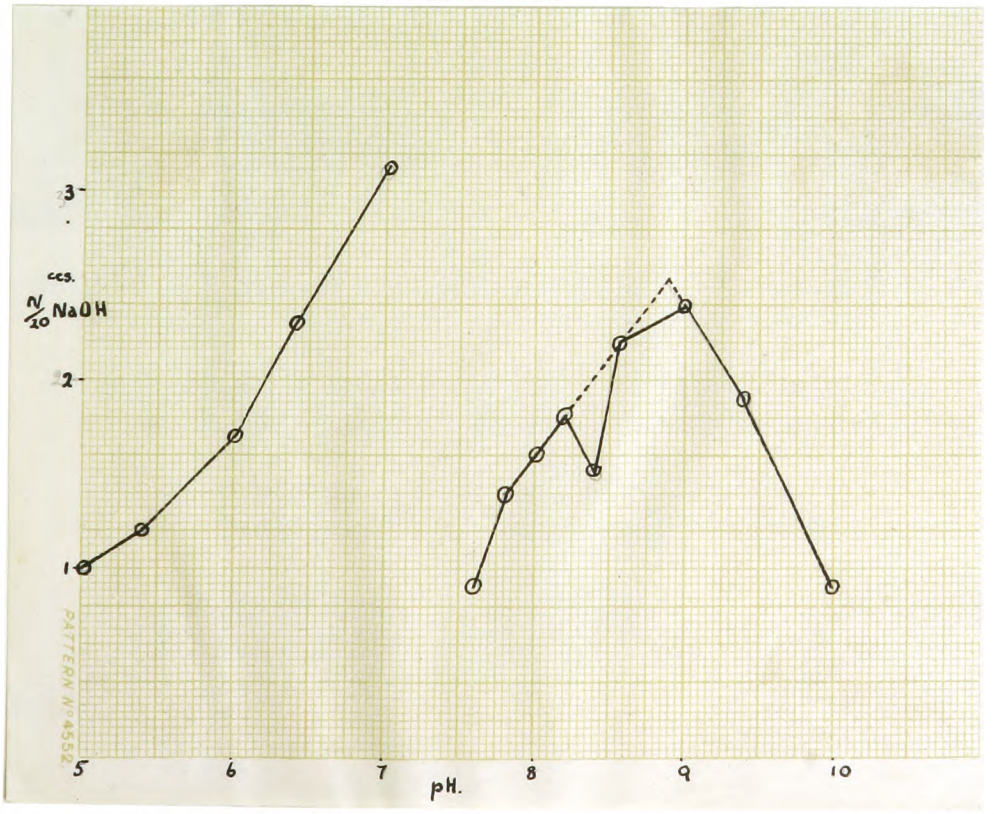
N/20 NaOH + Water + 5ccs. 2% Enzyme.
N/20 NaOH + Water + 5ccs. 2% Enzyme(boiled).

Duration of Experiment = 18 hours.
Temperature of Experiment = 29 C.

Initial pH.	Final pH.	Aver. pH.	ccs. NaOH for pH.	ccs. Water	Control. ccs. NaOH.	Experiment. ccs. NaOH.	Differ,
10.0	9.0	9.5	0.7	0.3	0.0	0.00	0.00
9.6	8.4	9.0	0.4	0.6	0.3	0.42	0.12
8.8	7.0	7.9	0.3	0.7	0.4	0.56	0.16
8.2	7.0	7.6	0.2	0.8	0.5	0.84	0.34
7.4	6.4	6.9	0.1	0.9	0.6	0.70	0.10
6.4	6.0	6.2	0.0	1.0	0.7	0.70	0.00



Effect of McIlvaine's and Atkins and Pantin's Buffers on Glycogen Digestion.



Effect of McIlvaine's and Atkins and Pantin's Buffers on Fat Digestion.

TABLE IV.

The localisation of the Enzymes.

Amylase.

3cc. 2.5% Starch + 5cc. 2% Enzyme extract.
3cc. 2.5% Starch + 5cc. 2% Enzyme extract(boiled).

Duration of Experiment = 12 hours.
Temperature of Experiment = 30°C.

	Experiment. cc. N/100Thio.	Control. cc. N/100Thio.	Difference. 1cc.	10cc.
Mid-gut.	2.0	6.1	4.1	41.0
Hind-gut.	4.6	5.7	0.9	9.0

5cc. 2.5% Starch + 2.5cc. 1% Enzyme extract.
5cc. 2.5% Starch + 2.5cc. 1% Enzyme extract(boiled).

Duration of Experiment = 8 hours.
Temperature of Experiment = 34°C.

	Experiment. cc. N/100Thio.	Control. cc. N/100Thio.	Difference. 1cc.	10cc.
Mid-gut.	0.5	8.4	7.9 7.9	79.0
Hind-gut.	8.2	8.4	0.2	2.0

5cc. 2.5% Starch + 2.5cc. 1% Enzyme extract.
5cc. 2.5% Starch + 2.5cc. 1% Enzyme extract(boiled).

Duration of Experiment = 10 hours.
Temperature of Experiment = 34°C.

	Experiment. cc. N/100Thio.	Control. cc. N/100Thio.	Difference. 1cc.	10cc.
Mid-gut.	2.7	8.4	5.5	55.0
Hind-gut.	7.7	8.4	0.7	7.0

TABLE IV (continued).

Protease.

3cc. 2.5% Gelatine + 5cc. 2.5% Enzyme extract.
3cc. 2.5% Gelatine + 5cc. 2.5% Enzyme extract(boiled).

Duration of Experiment = 12 hours.
Temperature of Experiment = 30°C.

	Experiment. cc. N/20NaOH.	Control. cc. N/20NaOH.	Difference. 5cc.	10cc.
Mid-gut.	6.2	1.8	4.4	8.8
Hind-gut.	1.3	1.4	0.1	0.2

5cc. 2.5% Gelatine + 2cc. 2.5% Enzyme extract.
5cc. 2.5% Gelatine + 2cc. 2.5% Enzyme extract(boiled).

Duration of Experiment = 12 hours.
Temperature of Experiment = 30°C.

	Experiment. cc. N/20NaOH.	Control. cc. N/20NaOH.	Difference. 5cc.	10cc.
Mid-gut.	4.7	1.7	3.0	6.0
Hind-gut.	1.0	1.0	0.0	0.0

TABLE V.

The Specificity of the Carbohydrate-digesting Enzyme.

5cc. Substrate + 5cc. 1% Enzyme extract.
5cc. Substrate + 5cc. 1% Enzyme extract(boiled).

Duration of Experiment = 8 hours.
Temperature of Experiment = 30°C.
pH of Experiment = 6.4.

Substrate.	Experiment. cc. N/100Thio.	Control. cc. N/100Thio.	Difference. 2cc.	10cc.
2% Salicin	7.0	11.0	4.0	20.0
2% Sucrose	6.2	6.2	0.0	0.0
1% Glycogen	8.8	11.0	2.2	11.0
5% Starch	8.2	10.9	2.7	13.5
2% Lactose	No reduction with Barfoed's reagent.			
2% Maltose	No reduction with Barfoed's reagent.			

TABLE VI.

The Digestion of Cellulose and Pentosans.

Cellulose.

E. 0.5 gm. Sawdust + 10cc. 2% Enzyme extract.
C.1. 0.5 gm. Sawdust + 10cc. 2% Enzyme extract (boiled).
C.2 0.5 gm. Sawdust + 10cc. Distilled water.
C.3 10cc. Enzyme extract alone.

Duration of Experiment = 7 days.
Temperature of Experiment = 28°C.

Experiment. cc. N/100Thio.	Control. cc. N/100Thio.		Difference for 2cc.
	C.1	5.4	
5.2	C.2	5.2	0.0
	C.3	5.85	

Pentosans.

E. 5cc. 5% Gum arabic + 5cc. 2% Enzyme extract.
C.1 5cc. 5% Gum arabic + 5cc. 2% Enzyme extract (boiled).
C.2 5cc. 5% Gum arabic + 5cc. Distilled water.
C.3 5cc. 2% Enzyme extract + 5cc. Distilled water.

Experiment. cc. N/100Thio.	Control. cc. N/100Thio.		Difference for 2cc.
	C.1	3.2	
2.6	C.2	2.6	0.0
	C.3	5.7	

TABLE VII.

Activity of the Amylase at the Posterior End.

5cc. 2.5% Starch + 2.5cc. 2% Enzyme extract.
5cc. 2.5% Starch + 2.5cc. 2% Enzyme extract(boiled).

Duration of Experiment = 7 hours.
Temperature of Experiment = 34°C.
pH of Experiment = 6.4.

Experiment. cc. N/100 Thio.	Control. cc. N/100 Thio.	Difference for 2cc.
3.7	7.4	3.7

TABLE VIII.

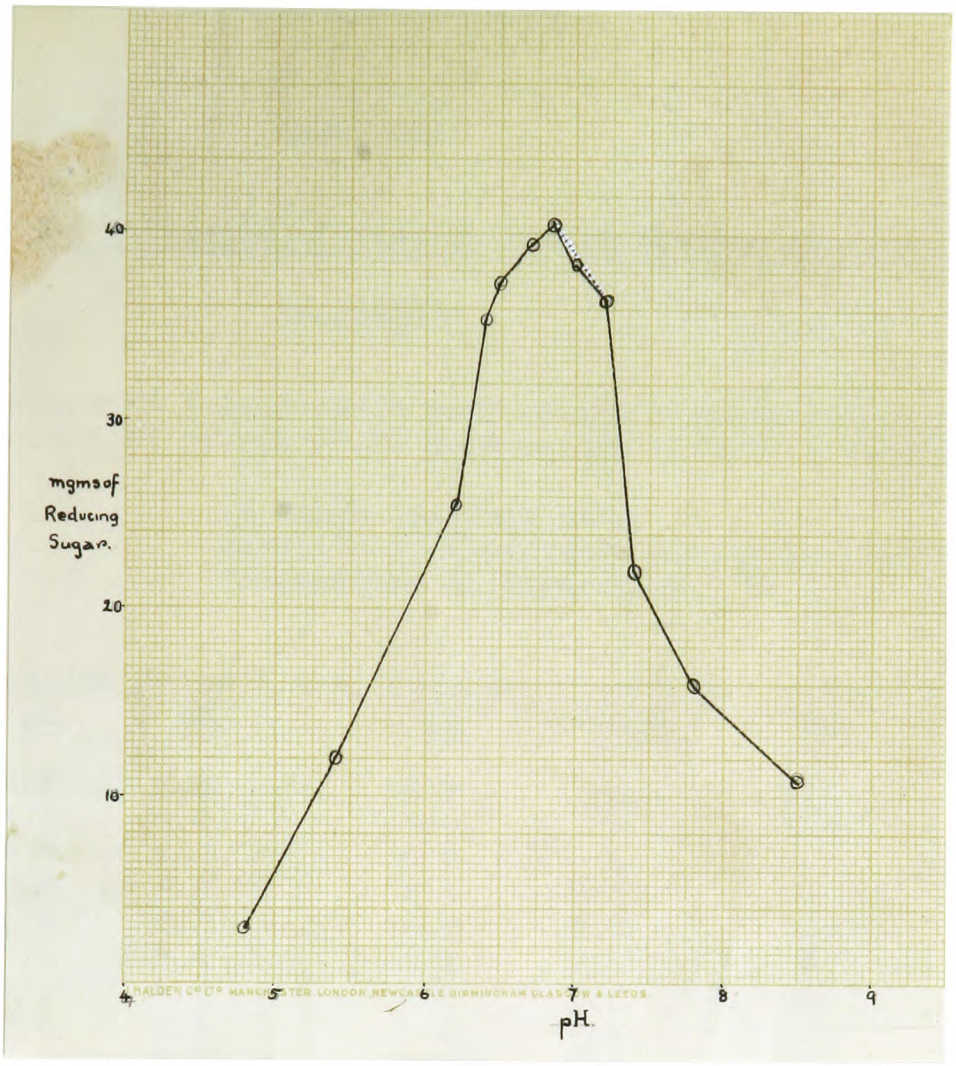
The Influence of the Hydrogen Ion Concentration on the Digestion of Starch.

5 ccs. 2.5% Starch + N/20 NaOH or HCl + water + 2ccs. Enzyme =8.2cc
5 ccs. 2.5% Starch + N/20 NaOH or HCl + water + 2ccs. Enzyme(boiled)

1% Enzyme extract used.
Duration of Experiment = 8 hours.
Temperature of Experiment = 31 C.

pH.	ccs. N/20 NaOH.	ccs. N/20 HCl.	ccs. Water.
4.8	-	0.5	0.7
5.4	-	0.25	0.95
6.2	-	-	1.2
6.6	0.1	-	1.1
6.8	0.2	-	1.0
7.0	0.25	-	0.95
7.2	0.3	-	0.9
7.4	0.4	-	0.8
7.6	0.5	-	0.7
7.8	0.7	-	0.5
8.2	1.0	-	0.2
9.0	1.2	-	0.0

Initial pH.	Final pH.	Average pH.	Control ccs. N/100 Thio.	Experiment ccs. N/100 Thio.	Differ.	Mgms Red. Sugar 1ccs.	10ccs.
4.8	4.8	4.8	14.7	13.7	1.0	0.3	3.0
5.4	5.4	5.4	14.7	10.9	3.8	1.2	12.0
6.2	6.2	6.2	14.8	6.5	8.2	2.55	25.5
6.6	6.2	6.4	14.7	3.1	11.6	3.55	35.5
6.8	6.2	6.5	14.7	2.7	12.0	3.75	37.5
7.0	6.4	6.7	14.6	1.9	12.8	3.95	39.5
7.2	6.4	6.8	14.7	1.5	13.2	4.05	40.5
7.4	6.6	7.0	14.7	2.5	12.2	3.8	38.0
7.6	6.8	7.2	14.8	2.9	11.8	3.65	36.5
7.8	7.0	7.4	14.7	7.7	7.0	2.2	22.0
8.2	7.0	7.6	14.6	9.4	5.3	1.65	16.5
9.0	8.0	8.5	14.7	12.1	2.6	0.8	8.0



The Influence of the Hydrogen Ion Concentration on the Digestion of Starch.

TABLE IX.

The Influence of Time on the pH Optimum for the Digestion of Starch.

5ccs. 2.5% Starch +N/20 NaOH or HCl + Water + 2ccs. Enzyme = 8.2ccs
5ccs. 2.5% Starch +N/20 NaOH or HCl + Water + 2ccs Enzyme(boiled).

1% Enzyme extract used.
Duration of Experiment = 8, 16, and 24 hours.
Temperature of Experiment = 31 C.

Initial pH.	After 8 hrs. pH.	Average pH.	ccs. N/20 NaOH.	ccs. N/20 HCl.	ccs. Water.
4.8	4.8	4.8	-	0.5	0.7
5.4	5.4	5.4	-	0.25	0.95
6.2	6.2	6.2	-	-	1.2
6.6	6.2	6.4	0.1	-	1.1
6.8	6.2	6.5	0.2	-	1.0
7.0	6.4	6.7	0.25	-	0.95
7.2	6.4	6.8	0.3	-	0.9
7.4	6.6	7.0	0.4	-	0.8
7.6	6.8	7.2	0.5	-	0.7
7.8	7.0	7.4	0.7	-	0.5
8.2	7.0	7.6	1.0	-	0.2
9.0	8.0	8.5	1.2	-	0.0

After 8 hours the pH remained constant.

Mgms. of Reducing Sugar produced after 8 hours.

pH.	Control. ccs. N/100 Thio.	Experiment. ccs. N/100 Thio.	Differ.	Mgms Red. Sugar 1cc.	10 ccs.
4.8	14.8	13.8	1.0	0.3	3.0
5.4	14.8	11.0	3.8	1.2	12.0
6.2	14.6	6.6	8.2	2.55	25.5
6.4	14.8	3.2	11.6	3.55	35.5
6.5	14.9	2.8	12.0	3.75	37.5
6.7	14.9	2.0	12.8	3.95	39.5
6.8	14.8	1.6	13.2	4.05	40.5
7.0	14.7	2.6	12.2	3.8	38.0
7.2	14.8	3.0	11.8	3.55	35.5
7.4	14.7	7.8	7.0	2.2	22.0
7.6	14.8	9.5	5.3	1.65	16.5
8.5	14.8	12.1	2.6	0.8	8.0

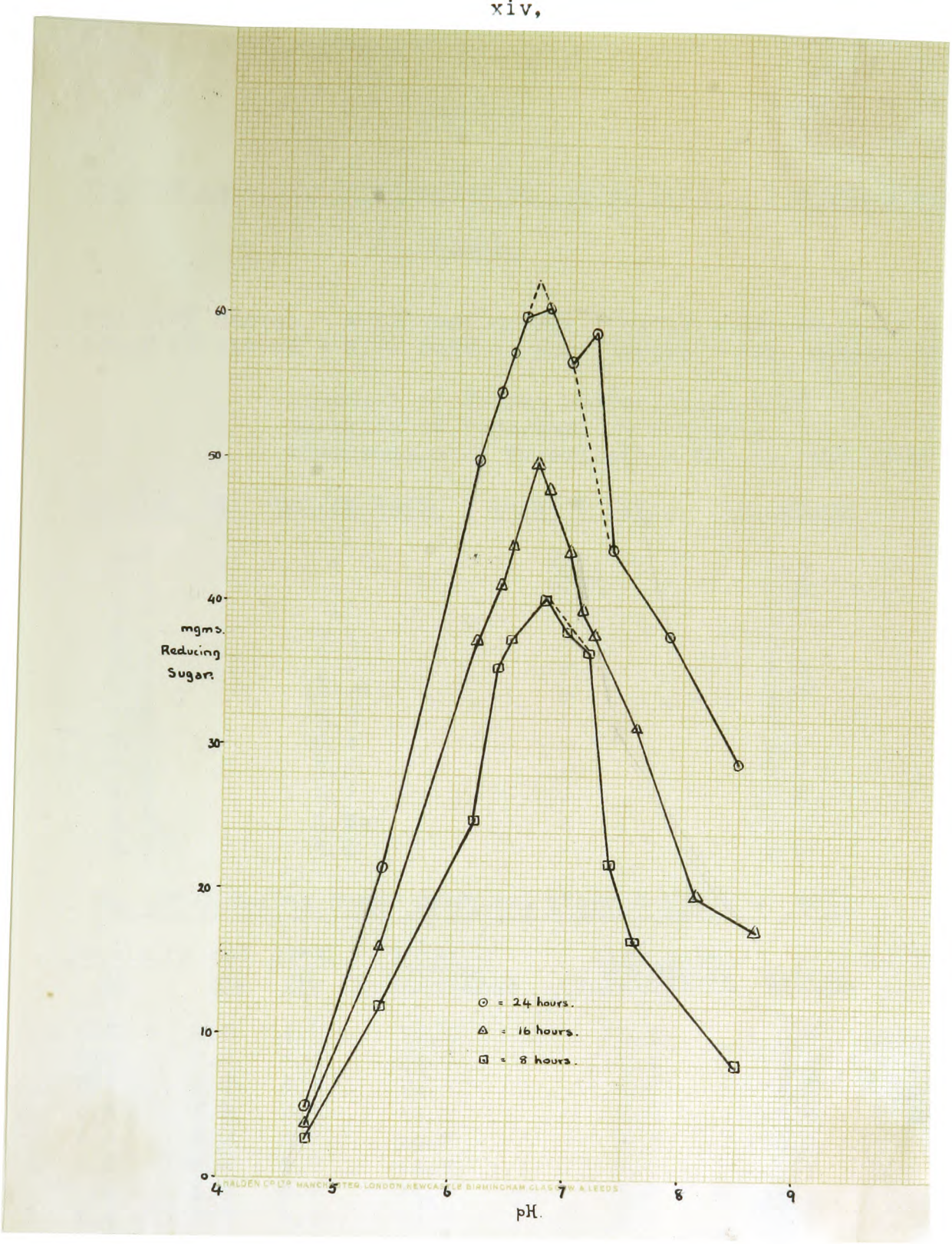
TABLE IX. (continued)

16 hours.

pH.	Control ccs. N/100 Thio.	Experiment. ccs. N/100 Thio.	Differ.	Mgms. Red. Sugar 1cc.	10ccs.
4.8	19.6	17.2	1.4	0.4	4.0
5.4	19.4	14.3	5.3	1.6	16.0
6.2	19.4	7.6	12.0	3.75	37.5
6.4	19.6	6.2	13.4	4.15	41.5
6.5	19.6	5.4	14.2	4.4	44.0
6.7	19.6	3.6	16.0	5.0	50.0
6.8	19.7	4.2	15.4	4.8	48.0
7.0	19.6	5.5	14.1	4.35	43.5
7.2	19.6	6.9	12.7	3.95	39.5
7.4	19.8	7.4	12.2	3.8	38.0
7.6	19.6	9.4	10.2	3.15	31.5
8.5	19.6	13.1	6.5	1.95	19.5
		13.9	5.7	1.75	17.5

24hours.

pH.	Control. ccs. N/100 Thio.	Experiment. ccs. N/100 Thio.	Differ.	Mgms. Red. Sugar 1cc.	10ccs.
4.8	24.6	22.9	1.6	0.5	5.0
5.4	24.6 24.5	17.6	6.9	2.15	21.5
6.2	24.5	8.5	16.0	5.0	50.0
6.4	24.5	6.9	17.6	5.5	55.0
6.5	24.4	6.1	18.4	5.75	57.5
6.7	24.5	5.3	19.2	6.0	60.0
6.8	24.5	5.1	19.4	6.05	60.5
7.0	24.6	6.3	18.2	5.7	57.0
7.2	24.5	5.5	19.0	5.9	59.0
7.4	24.5	10.2	14.3	4.4	44.0
7.6	24.4	12.2	12.3	3.8	38.0
8.5	24.5	15.1	9.4	2.9	29.0



The Influence of Time on the pH Optimum of the Digestion of Starch.

TABLE X.

The Influence of Temperature on the pH Optimum for the Digestion of Starch.

5cc. 2.5% Starch + N/20 NaOH or HCl + Water + 2cc. Enzyme = 8.2cc.
5cc. 2.5% Starch + N/20 NaOH or HCl + Water + 2cc. Enzyme(boiled).

Strength of Enzyme extract used = 1%.
Duration of Experiment = 8 hours.
Temperature of Experiment = 39, 31, and 18°C.

Initial pH.	ccN/20 NaOH.	cc. N/20 HCl.	cc. Water.
4.8	-	0.5	0.7
5.4	-	0.25	0.95
6.2	-	-	1.2
6.6	0.1	-	1.1
6.8	0.2	-	1.0
7.0	0.25	-	0.95
7.2	0.3	-	0.9
7.4	0.4	-	0.8
7.6	0.5	-	0.7
7.8	0.7	-	0.5
8.2	1.0	-	0.2
9.0	1.2	-	0.0

Mg. of Reducing Sugar produced after 8 hours at 39°C.

Initial pH.	Final pH.	Aver. pH.	Control. cc. N/100Thio.	Experiment. cc. N/100Thio.	Differ.	Mg. Red. Sugar 1cc.	Mg. Red. Sugar 10cc.
4.8	4.8	4.8	14.8	14.0	0.7	0.25	2.5
5.4	5.4	5.4	14.7	11.4	3.3	1.0	10.0
6.2	6.2	6.2	14.9	8.5	6.2	1.9	19.0
6.6	6.2	6.4	14.7	6.8	7.9	2.45	24.5
6.8	6.2	6.5	14.7	6.3	8.4	2.6	26.0
7.0	6.4	6.7	14.6	5.1	9.6	3.0	30.0
7.2	6.4	6.8	14.7	3.3	11.4	3.55	35.5
7.4	6.6	7.0	14.7	4.2	10.5	3.25	32.5
7.6	6.8	7.2	14.7	5.7	9.0	2.8	28.0
7.8	7.0	7.4	14.6	7.7	7.0	2.15	21.5
8.2	7.2	7.7	14.7	8.9	5.8	1.8	18.0
9.0	8.0	8.5	14.7	11.3	3.4	1.1	11.0

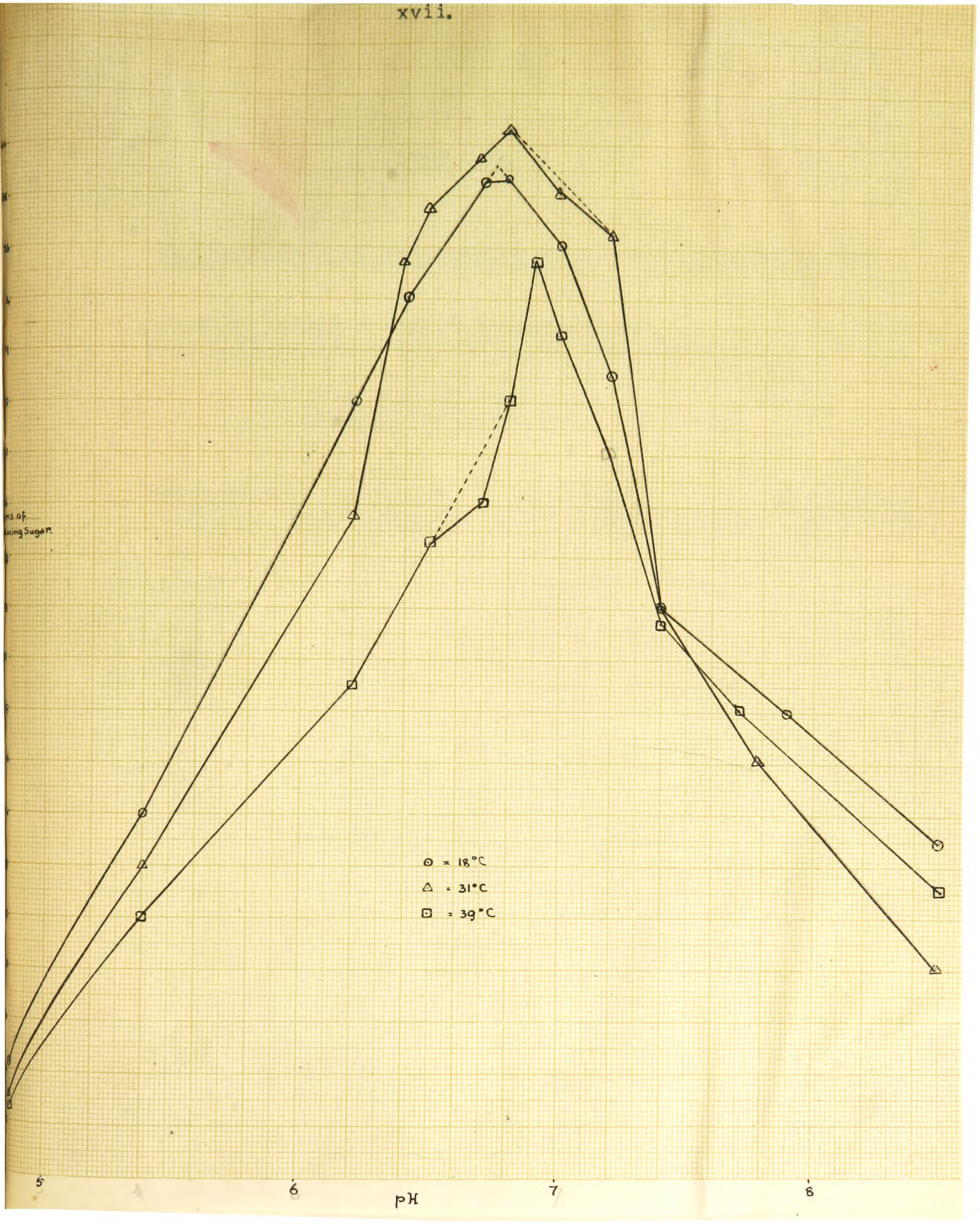
TABLE X. (continued)

8 hours at 31°C.

Initial pH.	Final pH.	Aver. pH.	Control. cc. N/100Thio.	Experiment. cc. N/100Thio.	Differ.	Mg. Red. Sugar. 1cc.	10cc.
4.8	4.8	4.8	14.6	13.7	1.0	0.3	3.0
5.4	5.4	5.4	14.6	10.9	3.8	1.2	12.0
6.2	6.2	6.2	14.7	6.5	8.2	2.55	25.5
6.6	6.2	6.4	14.7	3.1	11.6	3.55	35.5
6.8	6.2	6.5	14.7	2.7	12.0	3.75	37.5
7.0	6.4	6.7	14.8	1.9	12.8	3.95	39.5
7.2	6.4	6.8	14.8	1.5	13.2	4.05	40.5
7.4	6.6	7.0	14.7	2.5	12.2	3.8	38.0
7.6	6.8	7.2	14.7	2.9	11.8	3.65	36.5
7.8	7.0	7.4	14.7	7.7	7.0	2.2	22.0
8.2	7.4	7.8	14.8	9.4	5.3	1.65	16.5
9.0	8.0	8.5	14.7	12.1	2.6	0.8	8.0

8 hours at 18°C.

Initial pH.	Final pH.	Aver. pH.	Control. cc. N/100Thio.	Experiment. cc. N/100Thio.	Differ.	Mg. Red. Sugar. 1cc.	10cc.
4.8	4.8	4.8	14.8	12.4	1.3	0.4	4.0
5.4	5.4	5.4	14.7	10.2	4.5	1.4	14.0
6.2	6.2	6.2	14.8	4.9	9.8	3.0	30.0
6.6	6.2	6.4	14.6	3.7	11.0	3.4	34.0
6.8	6.6	6.7	14.6	2.3	12.4	3.85	38.5
7.0	6.6	6.8	14.7	2.3	12.4	3.85	38.5
7.2	6.8	7.0	14.7	3.0	11.7	3.6	36.0
7.4	7.0	7.2	14.7	4.7	10.0	3.1	31.0
7.6	7.2	7.4	14.6	7.7	7.0	2.2	22.0
7.8	7.4	7.6	14.7	-	-	-	-
8.2	7.6	7.9	14.7	8.9	5.8	1.8	18.0
9.0	8.0	8.5	14.7	10.7	4.2	1.3	13.0



The Influence of Temperature on the pH Optimum for the Digestion of Starch.

TABLE XI.

The Influence of Temperature on the Digestion of Starch.

5cc. 2.5% Starch + 2cc. 1% Enzyme extract.
5cc. 2.5% Starch + 2cc. 1% Enzyme extract(boiled).

pH of Experiment = 6.4.
Duration of Experiment = 10 hours.

Temperature °C.	Control. cc. N/100Thio.	Experiment. cc. N/100Thio.	Differ.	Mg. Reducing Sugar 1cc.	10cc.
3.0	19.7	17.4	2.4	0.7	7.0
9.0	19.2	15.6	4.2	1.3	13.0
13.0	19.7	13.4	6.4	1.95	19.5
19.0	19.9	11.0	8.8	2.7	27.0
24.0	19.8	8.6	11.2	3.4	34.0
26.0	19.8	8.2	11.6	3.6	36.0
32.0	19.8	8.0	11.8	3.65	36.5
38.0	19.8	9.6	10.2	3.15	31.5
50.0	19.9	11.6	8.2	2.55	25.5
70.0					9.0

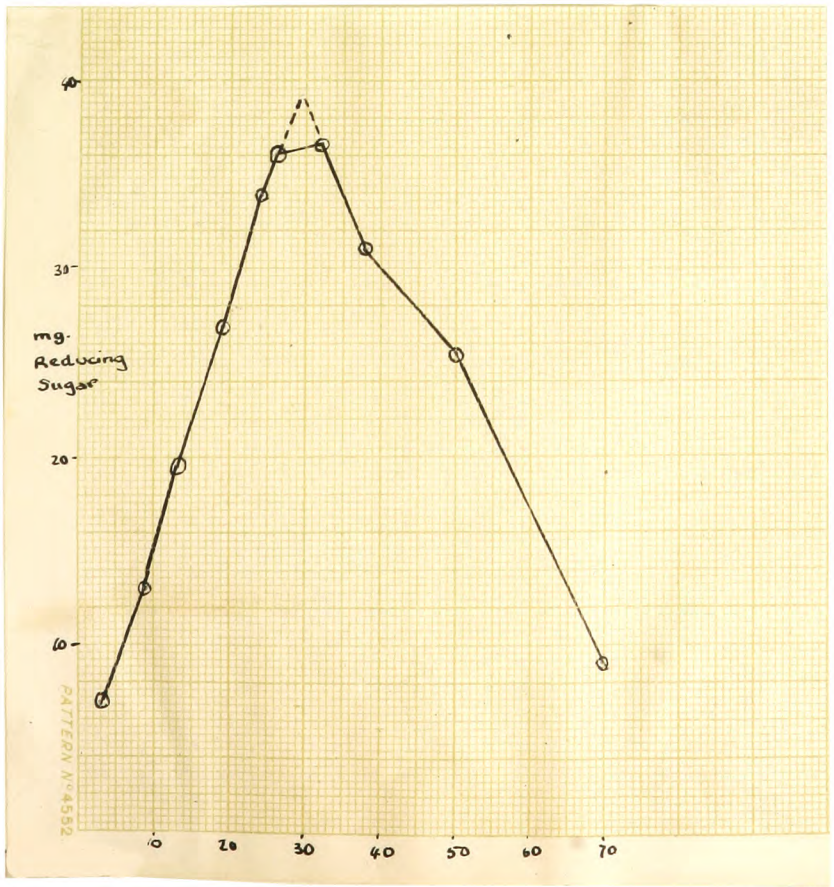


TABLE XII.

The Temperature of Destruction of Amylase.

2cc. 1% Enzyme + 5cc. 2.5% Starch.

The enzyme extract was heated for 15 minutes at various temperatures previous to setting up the experiment.

Duration of Experiment = 8 hours.
Temperature of Experiment = 30°C.
pH of Experiment = 6.4.

Temperature. °C.	Control. cc. N/100Thio.	Experiment. cc. N/100Thio.	Differ.	Mg. Reducing Sugar 1 cc.	10 cc.
100		5.1	0.4	0.12	1.2
90		5.1	0.4	0.12	1.2
85		5.1	0.4	0.12	1.2
80		5.1	0.4	0.12	1.2
75		5.1	0.4	0.12	1.2
70	5.5	5.1	0.4	0.12	1.2
65		5.1	0.4	0.12	1.2
60		4.5	1.0	0.31	3.1
55		3.8	1.7	0.53	5.3
50		3.2	2.3	0.7	7.0

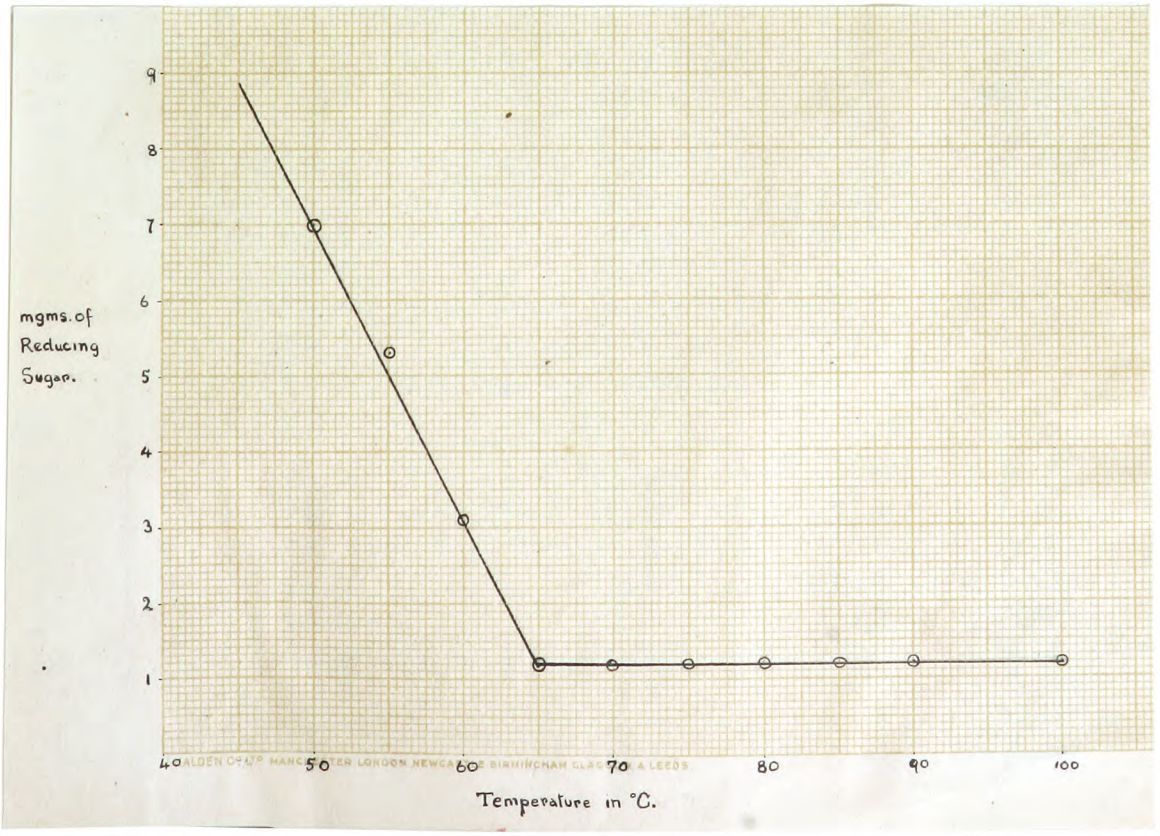


TABLE XIII.

The Influence of Hydrogen Ion Concentration on the Optimum Temperature for the Digestion of Starch.

3cc. 2.5% Starch + 2cc. 2% Enzyme + NaOH N/20.
3cc. 2.5% Starch + 2cc. 2% Enzyme (boiled) + N/20 NaOH.

Duration of Experiment = 8 hours.
Temperature of Experiment = 31°C.
pH of Experiment = 6, 7.2 and 8.2.

pH 6.

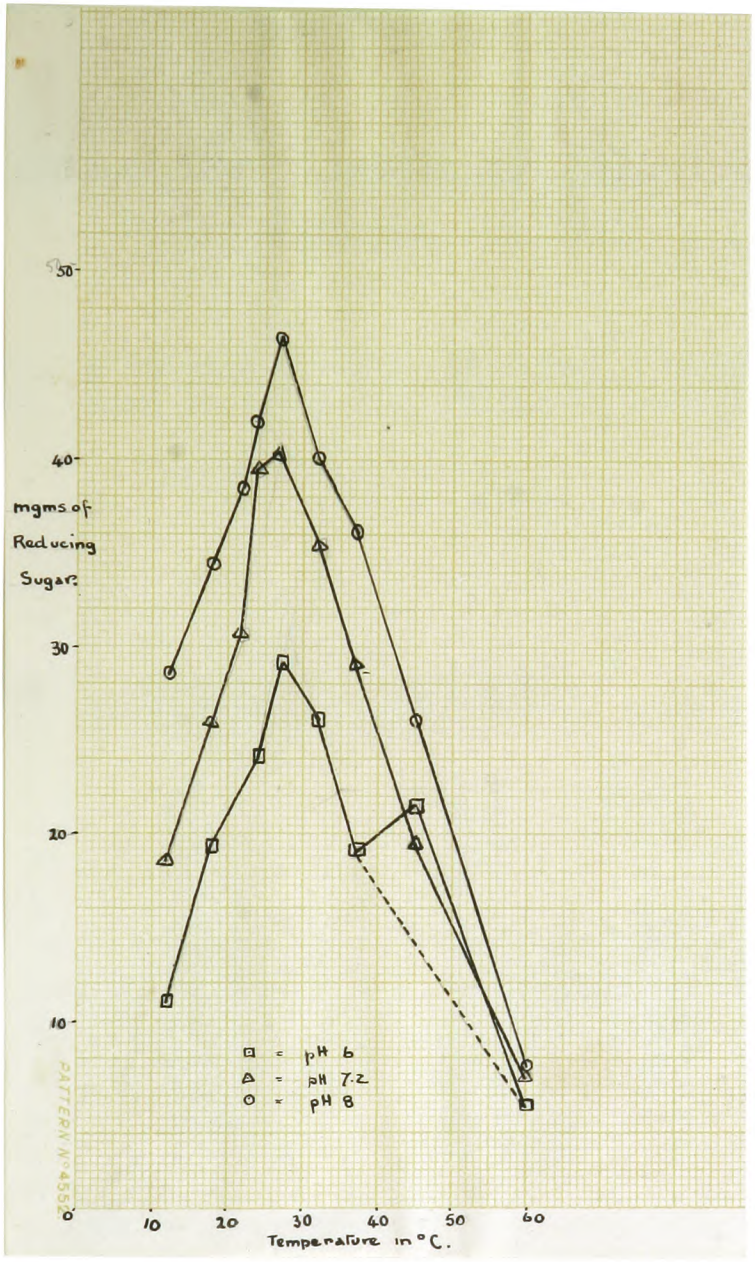
Temperature °C.	Control. cc.N/100 Thio.	Experiment. cc. N/100 Thio.	Differ.	Mg. Reducing Sugar 1cc.	10cc.
60	14.6	12.9	1.8	0.55	5.5
45	14.6	7?.8	6.9	2.15	21.5
37	14.7	8.6	6.1	1.9	19.0
32	14.8	6.4	8.3	2.6	26.0
27	14.7	5.3	9.4	2.9	29.0
24	14.7	6.9	7.8	2.4	24.0
22	14.7	-	-	-	--
18	14.8	8.4	6.3	1.95	19.5
12	14.8	11.2	3.5	1.1	11.0

pH 7.2.

60	14.7	12.4	2.3	0.7	7.0
45	14.7	8.4	16.3	11.95	19.5
37	14.8	5.4	9.3	2.9	29.0
32	14.8	3.3	11.4	3.55	35.5
27	14.7	1.7	13.0	4.05	40.5
24	14.7	2.0	12.7	3.95	39.5
22	14.6	4.8	9.9	3.05	30.5
18	14.6	6.3	8.4	2.6	26.0
12	14.7	8.7	6.0	1.85	18.5

pH 8.

60	14.6	12.2	2.5	0.75	7.5
45	14.6	6.3	8.4	2.6	26.0
37	14.7	3.0	11.7	3.6	36.0
32	14.7	1.8	12.9	4.0	40.0
27	14.7	0.1	14.6	4.65	46.5
24	14.8	1.2	13.5	4.2	42.0
22	14.7	2.4	12.3	3.85	38.5
18	14.7	3.6	11.1	3.45	34.5
12	14.8	5.5	9.2	2.85	28.5



The Influence of the Hydrogen Ion Concentration on the Optimum Temperature for the Digestion of Starch.

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TABLE XIV.

The Influence of Time on the Optimum Temperature of Starch Digestion.

5cc. 2.5% Starch + 2cc. 2% Enzyme extract.
3cc. 2.5% Starch + 2cc. 2% Enzyme extract (boiled).

pH of Experiment = 6.4.

10 hours.

Temperature °C.	Control. cc. N/100Thio.	Experiment. cc. N/100Thio.	Differ.	Mg. Reducing Sugar. 1cc.	10cc.
61	14.8	13.4	1.3	0.4	4.0
45	14.7	9.7	5.0	1.5	15.0
37	14.7	7.6	7.1	2.2	22.0
29	14.7	7.1	7.6	2.35	23.5
24	14.8	7.5	7.2	2.25	22.5
22	14.6	8.1	6.6	2.05	20.5
19	14.7	8.4	6.3	1.95	19.5
16	14.7	9.3	5.4	1.75	17.5
8	14.8	11.3	3.4	1.05	10.5
5	14.8	12.3	2.5	0.8	8.0
0	14.6	13.2	1.5	0.4	4.0

10 hours.

61.	14.6	13.2	1.5	0.45	4.5
45	14.7	8.7	6.0	1.85	18.5
37	14.6	6.6	8.1	2.5	25.0
29	14.8	4.9	9.8	3.05	30.5
24	14.7	5.2	9.5	2.95	29.5
22	14.7	6.1	8.6	2.65	26.5
19	14.7	7.1	7.6	2.35	23.5
16	14.7	7.0	6.8	2.1	21.0
8	14.6	10.1	4.6	1.4	14.0
5	14.7	11.1	3.6	1.1	11.0
0	14.8	12.0	2.7	0.8	8.0

TABLE XIV. (continued).

18 hours.

Temperature °C.	Control. cc. N/100 Thio.	Experiment. cc. N/100 Thio.	Differ.	Mg. Reducing Sug 1cc.	10cc.
61	14.6	13.2	1.5	0.45	4.5
45	14.7	7.9	6.8	2.1	21.0
37	14.7	5.1	9.6	3.0	30.0
29	14.7	3.9	10.8	3.35	35.5
24	14.6	4.0	10.7	3.3	33.0
22	14.8	5.1	9.6	2.95	29.5
19	14.8	-	-	-	-
16	14.7	6.7	8.0	2.50	25.0
8	14.7	9.5	5.2	1.65	16.5
5	14.7	10.3	4.4	1.35	13.5
0	14.7	11.4	3.3	1.0	10.0

22 hours.

61	14.8	13.2	1.5	0.45	4.5
45	14.8	7.5	7.2	2.25	22.5
37	14.6	4.5	10.2	3.15	31.5
29	14.7	2.9	11.8	3.65	36.5
24	14.7	3.0	11.7	3.6	36.0
22	14.7	4.7	10.0	3.1	31.0
19	14.6	6.1	8.6	2.7	27.0
16	14.5	6.1	8.6	2.7	27.0
8	14.7	8.9	5.8	1.8	18.0
5	14.7	9.7	5.0	1.55	15.5
0	14.9	9.9	4.8	1.45	14.5

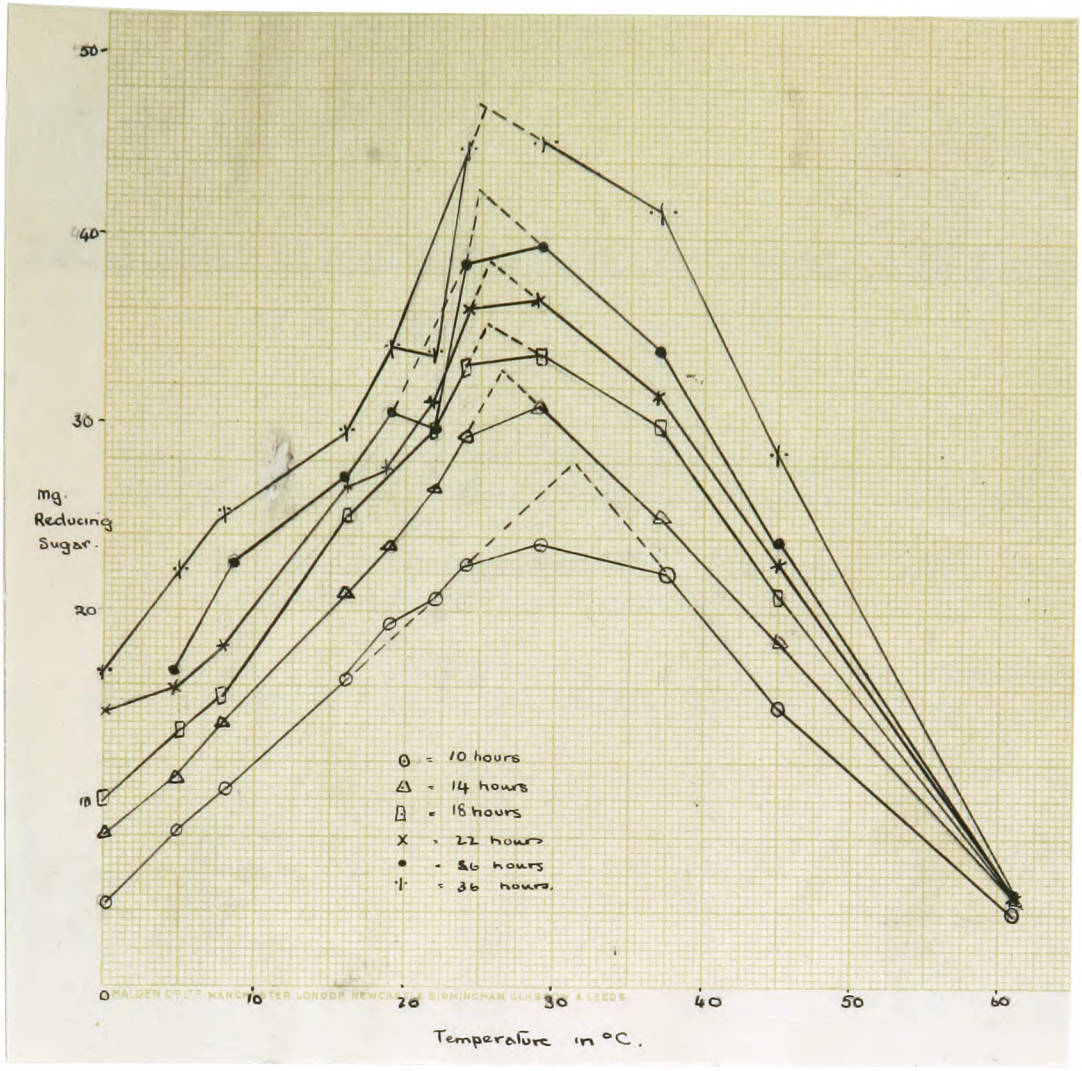
26 hours.

61	14.8	13.2	1.5	0.45	4.5
45	14.6	7.0	7.7	2.40	24.0
37	14.6	4.7	11.0	3.40	34.0
29	14.7	2.0	12.7	3.95	39.5
24	14.7	2.2	12.5	3.85	38.5
22	14.7	5.3	9.4	2.90	29.0
19	14.7	4.8	9.9	3.05	30.5
16	14.6	6.0	8.7	2.7	27.0
8	14.7	7.4	7.3	2.25	22.5
5	14.7	9.5	5.2	1.65	16.5
0	14.7	-	-	-	-

TABLE XIV (continued).

36 hours.

Temperature °C.	Control. cc. N/100 Thio.	Experiment. cc. N/100 Thio.	Differ.	Mg. Red. Sugar. 1cc.	10cc.
61	14.8	13.2	1.5	0.45	4.5
45	14.8	5.7	9.2	2.85	28.5
37	14.7	1.4	13.3	4.15	41.5
29	14.7	0.2	14.5	4.5	45.0
24	14.7	0.4	14.3	4.45	44.5
22	14.6	3.8	10.9	3.4	34.0
19	14.7	3.7	11.0	3.4	34.0
16	14.7	5.2	9.5	2.95	29.5
8	14.6	6.7	8.0	2.5	25.0
5	14.7	7.6	7.1	2.2	22.0
0	14.8	9.5	5.2	1.65	16.5



Influence of Time on the Temperature Optimum of Starch Digestion

TABLE XV.

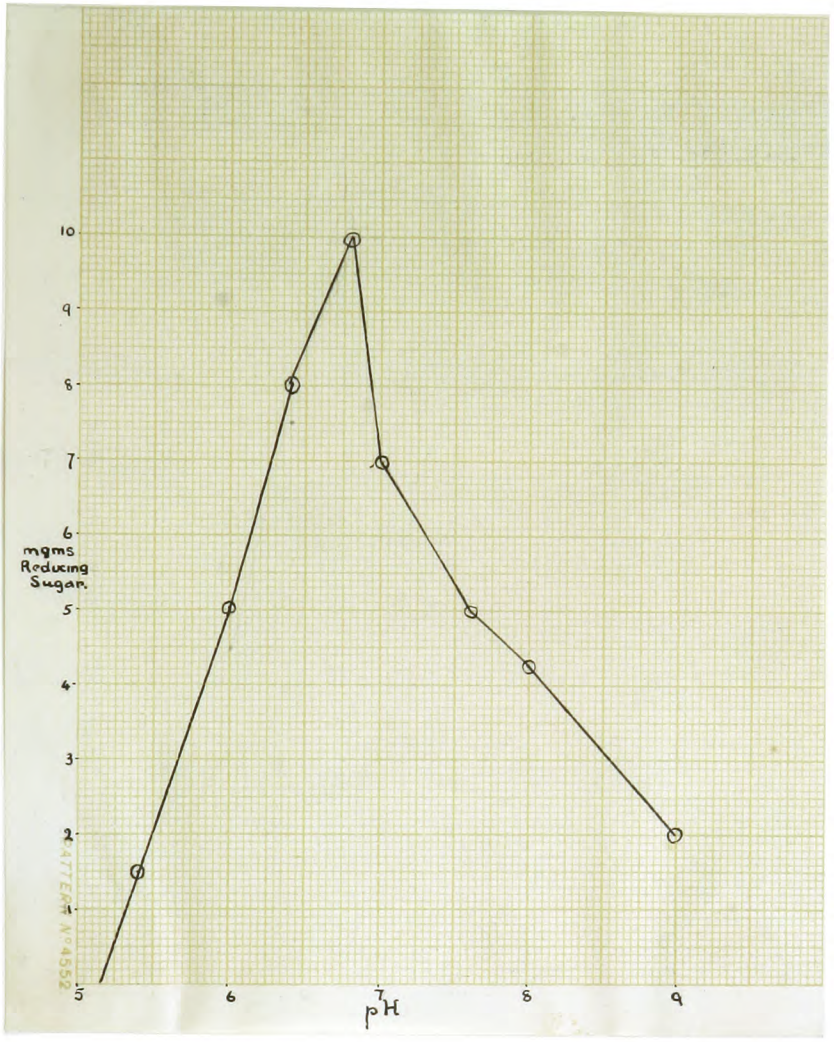
The Infuence of the Hydrogen Ion Concentration on the Digestion of Glycogen.

2cc. 1% Glycogen + 2cc. 2% Enzyme extract.
2cc. 1% Glycogen + 2cc. 2% Enzyme extract (boiled).

Duration of Experiment = 10 hours.
Temperature of Experiment = 32°C.

pH.	Control. cc. N/100 Thio.	Experiment. cc. N/100 Thio.	Differ.	Mg. Reducing Sugar. 1 cc.	10cc.
5.4	9.0	8.6	0.4	0.15	1.5
6.0	8.9	7.4	1.6	0.5	5.0
6.4	9.0	6.45	2.55	0.8	8.0
6.8	9.0	5.9	3.1	1.0	10.0
7.0	9.0	6.65	2.35	0.7	7.0
7.6	9.0	7.4	1.6	0.5	5.0
8.0	8.8	7.7	1.3	0.43	4.3
9.0	8.9	8.4	0.6	0.2	2.0

The pH was adjusted with N/20 NaOH and HCl.



The Influence of the Hydrogen Ion Concentration on the Digestion of Glycogen.

TABLE XVI.

The Specificity of the Protease.

5 cc. Substrate + 5 cc. 1% Enzyme extract.
5 cc. Substrate + 5 cc. 1% Enzyme extract (boiled).

Duration of Experiment = 22 hours.
Temperature of Experiment = 31°C.
Initial pH of Experiment = 8.4.

Substrate.	Control. cc. N/20NaOH.	Experiment. cc. N/20NaOH.	Differ.	Mg. Nitrogen.
2% egg albumen	1.75	1.85	0.1	0.07
2% casein	7.0	10.0	3.3	2.31
.5 gm. fibrin	2.7	6.7	4.0	2.8
1% gelatin	2.7	9.1	6.4	4.48
2% peptone	10.6	15.8	5.2	3.64

TABLE XVII.

The Influence of Hydrogen Ion Concentration on the Digestion of Gelatin.

5cc. 2.5% Gelatin + 5cc. Buffer + 2cc. 1% Enzyme extract.
5cc. 2.5% Gelatin + 5cc. Buffer + 2cc. 1% Enzyme extract(boiled).

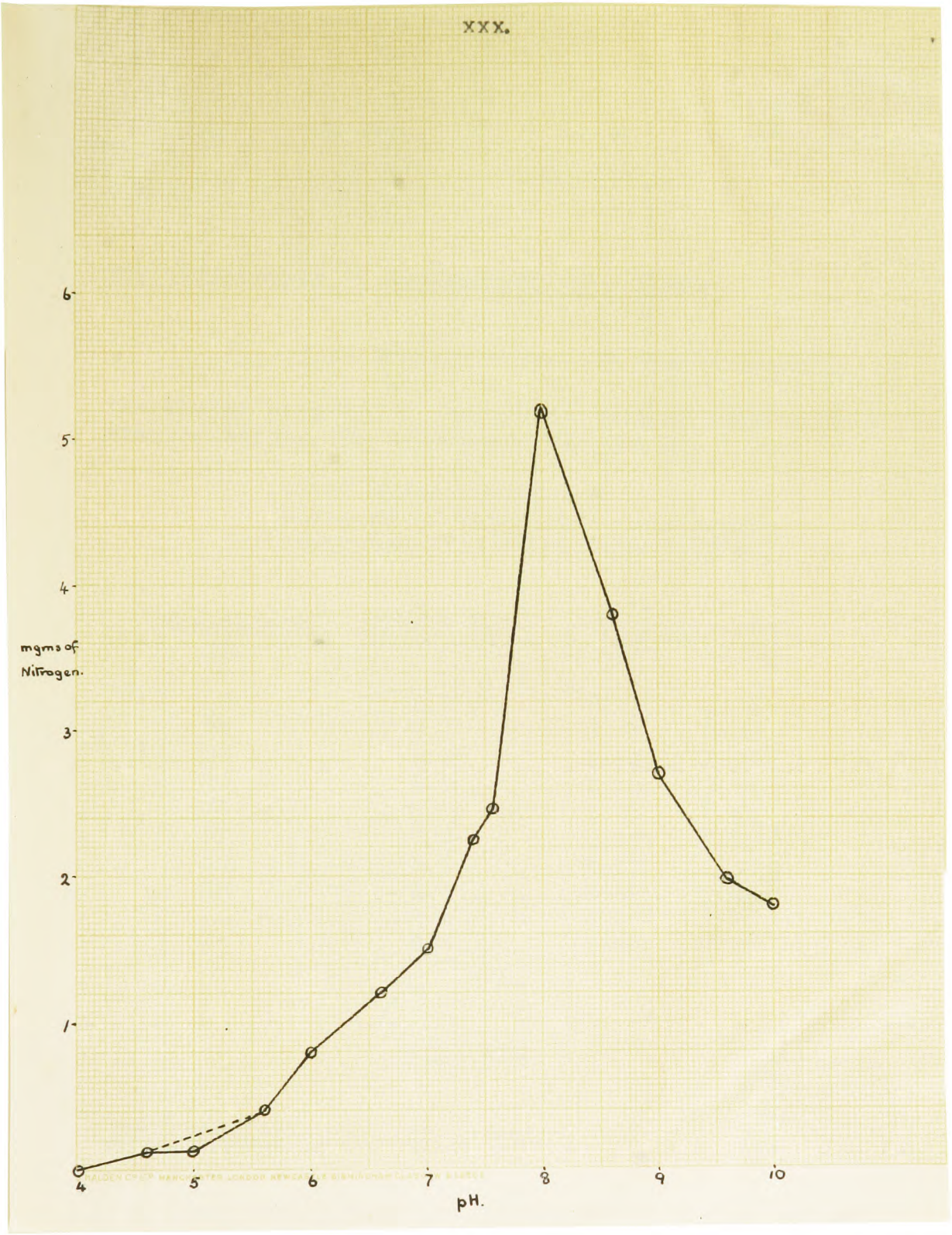
Buffer =McIlvaine pH 4 - 7.4.
Atkins and Pantin pH 7.6 - 10.

Strength of NaOH = N/20.
Strength of HCl = N/20.

Duration of Experiment = 12 hours.
Temperature of Experiment = 32°C.

	Control.		Experiment.			Mg. Nitrogen	
pH.	cc. NaOH.	cc. HCl.	cc. NaOH.	cc. HCl.	Differ.	5cc.	10cc.
4.0	4.3	-	4.3	-	0.0	0.0	0.0
4.6	3.9	-	4.0	-	0.1	0.075	0.15
5.0	3.5	-	3.6	-	0.1	0.075	0.15
5.6	3.1	-	3.4	-	0.3	0.22	0.42
6.0	2.7	-	3.25	-	0.55	0.4	0.8
6.6	2.2	-	3.05	-	0.85	0.6	1.2
7.0	1.65	-	2.7	-	1.05	0.75	1.5
7.4	0.8	-	2.4	-	1.6	1.13	2.26
7.6	4.35	-	6.1	-	1.75	1.25	2.5
8.0	3.6	-	7.3	-	3.7	2.6	5.2
8.6	1.9	-	4.6	-	2.7	1.9	3.8
9.0	0.6	-	2.5	-	1.9	1.35	2.7
9.6	-	1.0	0.4	-	1.4	0.975	1.95
10.0	-	2.7	-	1.4	1.3	0.9	1.8

The pH remained constant throughout the experiment.



The Influence of the Hydrogen Ion Concentration on the Digestion of Gelatine.

TABLE XVIII.

The Temperature of Destruction of Protease.

5cc. 2.5% Gelatin + 5cc. 2% Enzyme extract.

The enzyme extract was heated to various temperatures for 15 minutes before the experiment was set up.

pH of Experiment = 6.4.
Duration of Experiment = 12 hours.
Temperature of experiment = 34°C.

Temperature. °C.	cc. N/20 NaOH.	Mg. Nitrogen. 5 cc.	10 cc.
100	0.2	0.14	0.28
85	0.2	0.14	0.28
80	0.2	0.14	0.28
75	0.2	0.14	0.28
70	0.3	0.21	0.42
65	0.7	0.49	0.98
60	1.1	0.77	1.54
55	0.6	0.42	0.84
50	2.1	1.47	2.94
45	2.5	1.75	3.50

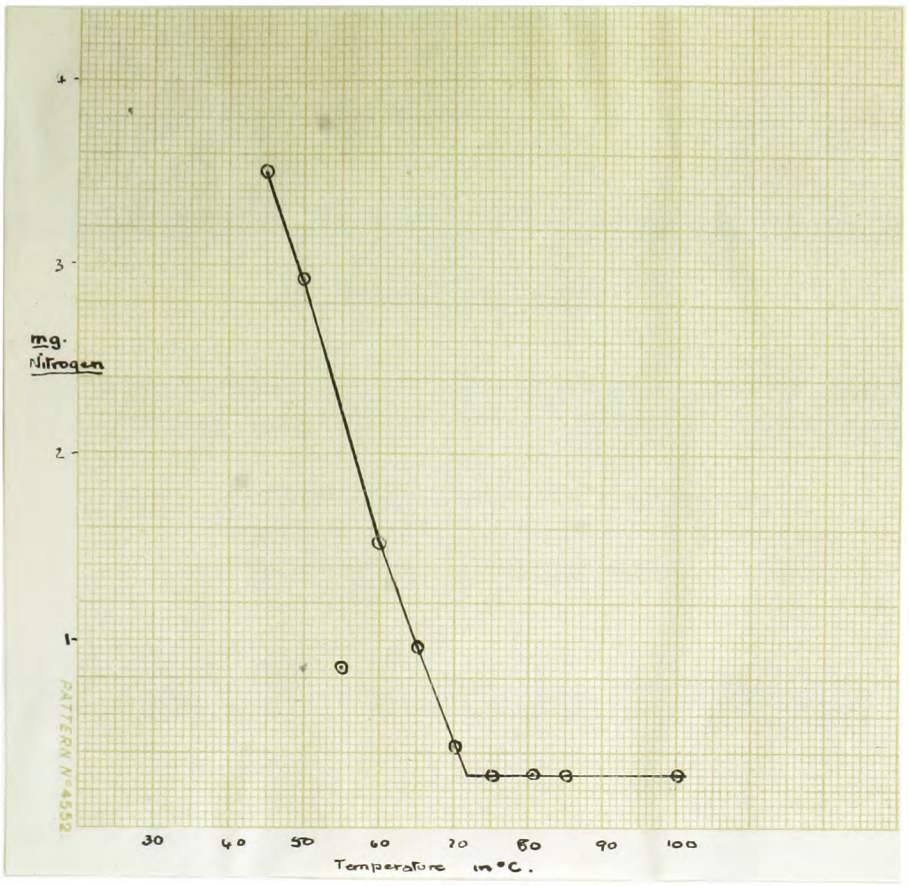
TABLE XIX.

The Specificity of the Lipase.

xcc. Substrate + 5cc. Buffer + 5cc. Enzyme extract.
xcc. Substrate + 5cc. Buffer + 5cc. Enzyme extract(boiled).

Buffer = Atkins and Pantin pH 8.2.
Duration of Experiment = 22 hours.
Temperature of Experiment = 30°C.

Substrate.	Control. cc. N/20 NaOH.	Experiment. cc. N/20 NaOH.	Difference.
5cc. lecithin sol.	2.8	3.5	0.7
1cc. methyl acetate	8.3	13.9	5.6
1cc. olive oil	6.0	7.3	11.3



Temperature of Destruction of Protease.

TABLE XX.

The Influence of Hydrogen Ion Concentration on the Digestion of Methyl Acetate.

0.5cc. Methyl acetate + 10cc. Buffer + 1cc. 1% Enzyme extract.
0.5cc. Methyl acetate + 10cc. Buffer + 1cc. 1% Enzyme extr. (boiled)

Buffer = Northrop's (modified).
Duration of Experiment = 2 hours.
Temperature of Experiment = 30°C.

Initial pH.	Final pH.	Aver. pH.	Control. cc. N/20 NaOH.	Experiment. cc. N/20 NaOH.	Difference. 5 cc.	Difference. 10 cc.
9.2	8.4	8.8	3.0	3.0	0.0	0.0
8.8	7.8	8.3	4.0	4.3	0.3	0.6
8.4	7.4	7.9	4.1	4.5	0.4	0.8
8.0	7.2	7.6	4.2	4.5	0.3	0.6
7.8	7.0	7.4	4.4	5.2	0.8	1.6
7.4	7.0	7.2	5.3	6.0	0.7	1.4
7.0	6.8	6.9	6.0	6.6	0.6	1.2
6.6	6.6	6.6	7.6	8.1	0.5	1.0
5.8	5.8	5.8	11.2	11.3	0.1	0.2
4.6	4.6	4.6	19.0	19.0	0.0	0.0

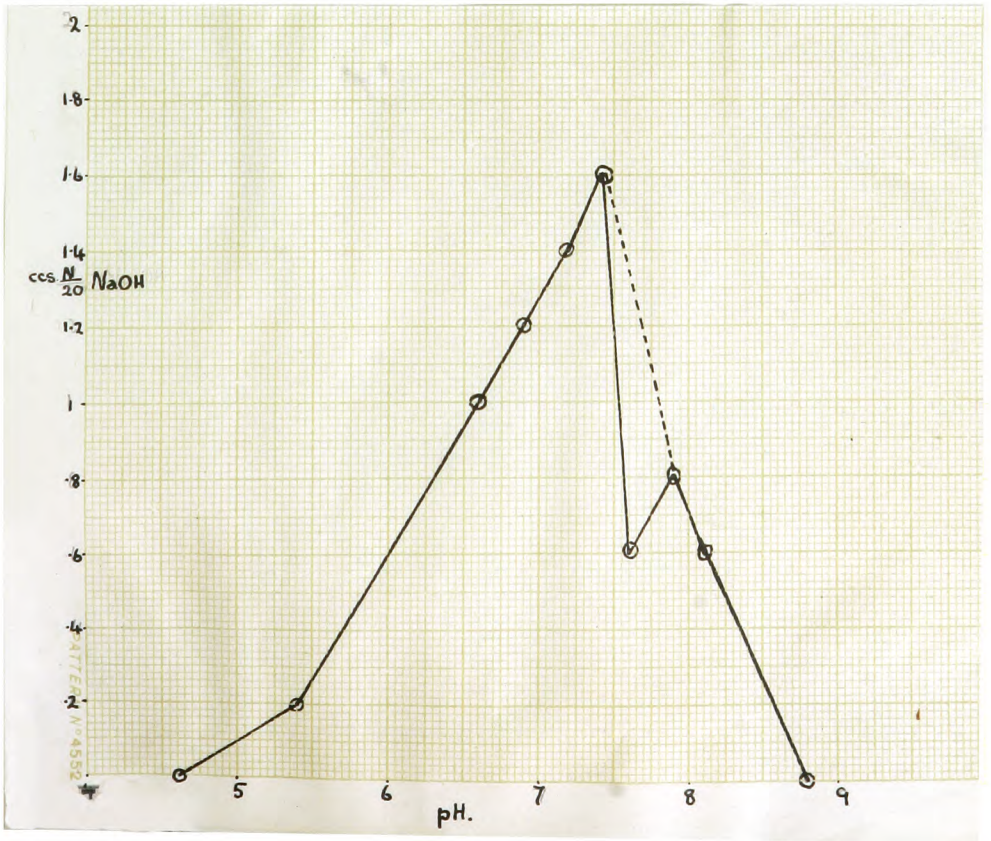


TABLE XXI

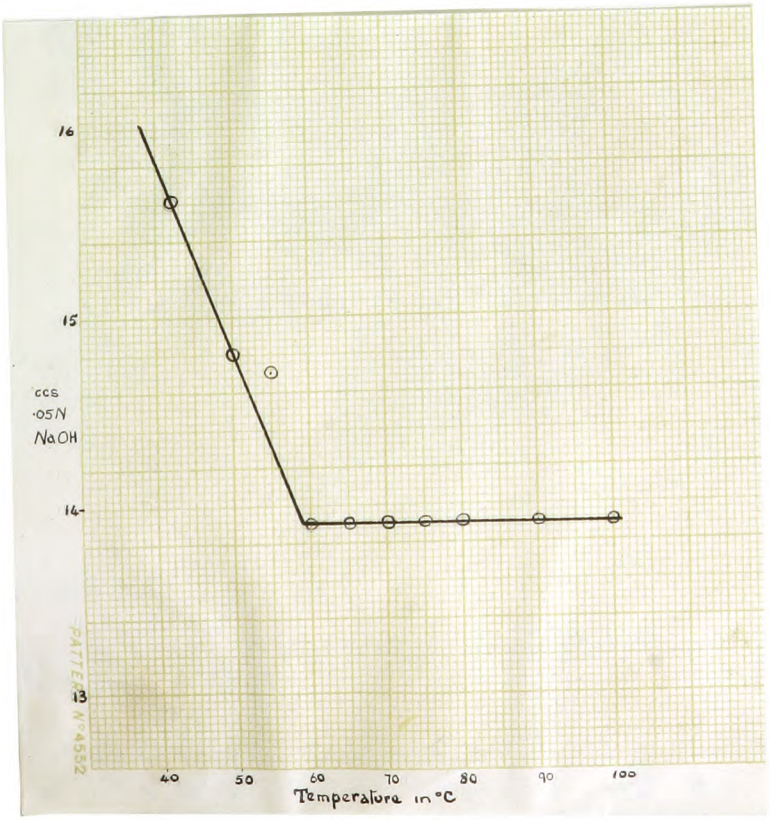
The Temperature of Destruction of Lipase.

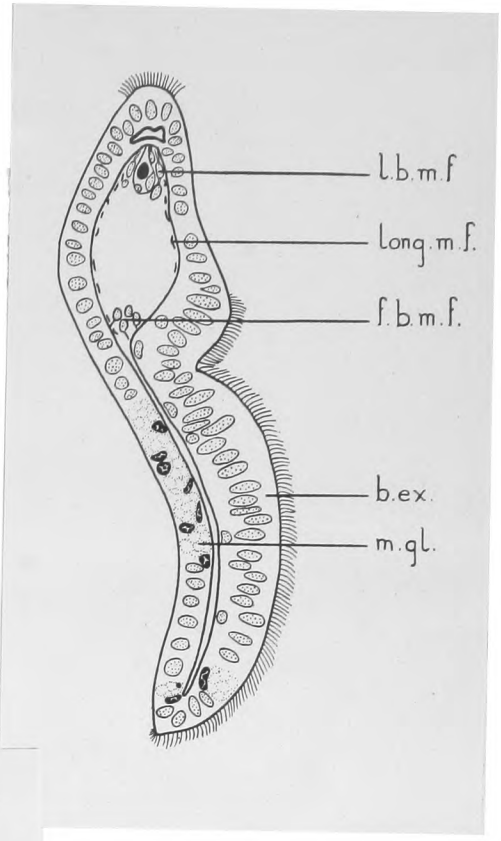
0.5cc. Ethyl butyrate + 2cc. 2% Enzyme extract.

The enzyme extract was heated to various temperatures for 15 minutes before setting up the experiment.

pH of Experiment = 6.4.
Duration of Experiment = 10 hours.
Temperature of Experiment = 30°C.

Temperature	cc. N/20 NaOH. for 2.5cc.	For 10 cc.
100	3.46	13.9
80	3.46	13.9
75	3.46	13.9
70	3.46	13.9
60	3.46	13.9
55	3.67	14.7
50	3.7	14.8
42	3.9	15.6

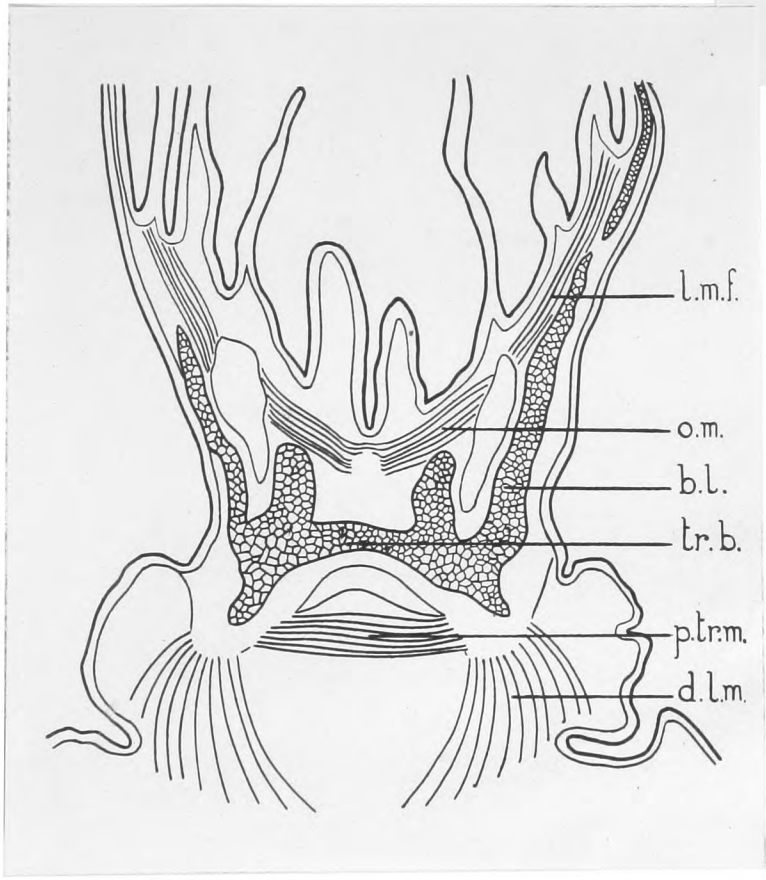




Text-figure 1.

Transverse section through the base of a pinnule to shew the musculature. x 450.

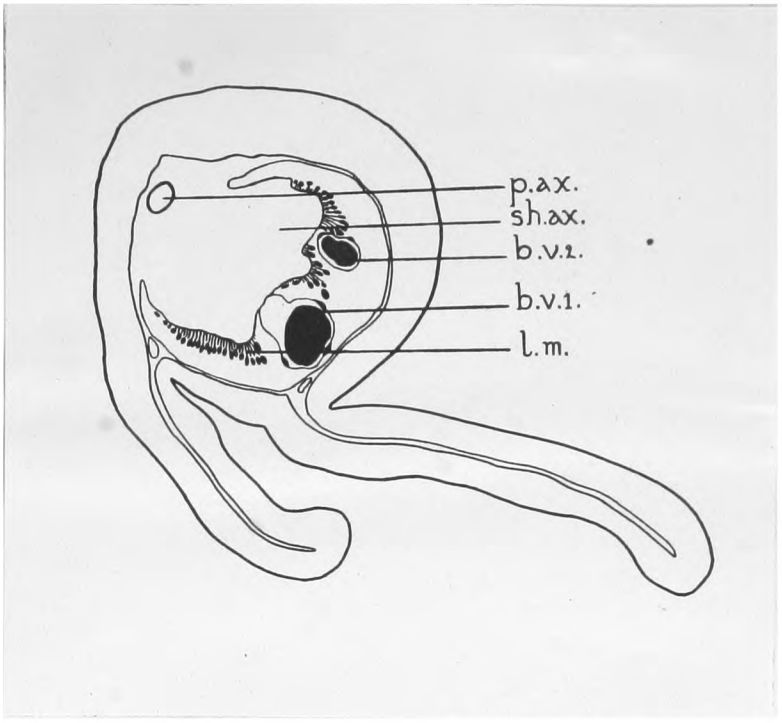
b. ex. basal expansion.
f. b. m. f. frontal basal muscle fibres.
l. b. m. f. lateral basal muscle fibres.
long. m. f. longitudinal muscle fibre.
m. gl. mucus gland.



Text-figure 2.

Longitudinal section through the branchial region to shew the musculature. x 30.

b. l. basal lamella. d. l. m. dorsal longitudinal muscles. L. m. f. longitudinal muscles of filaments. o. m. oblique muscles. tr. b. transverse bar. p. tr. m. posterior transverse muscle.



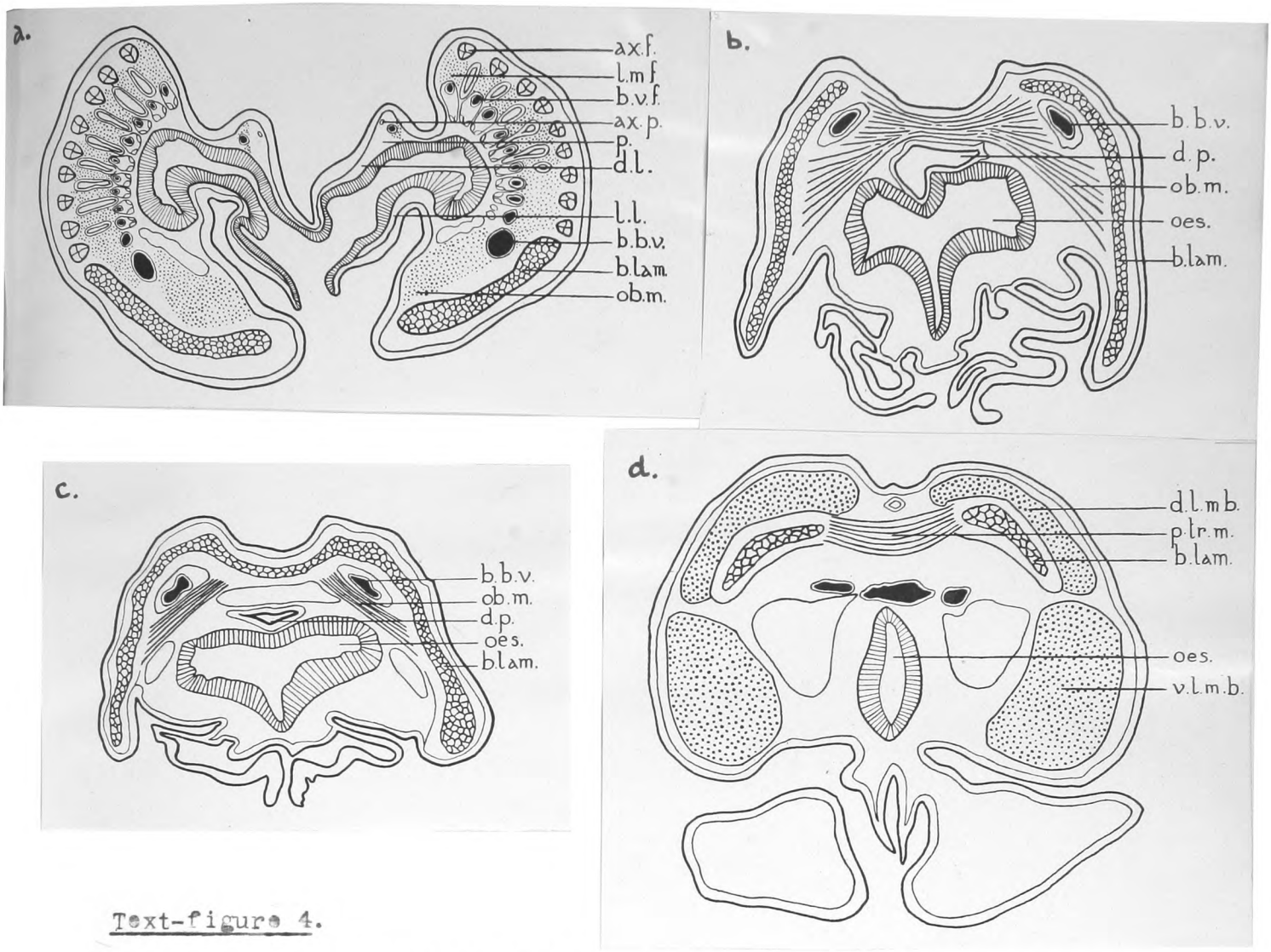
Text-figure 3.

Transverse section through the left palp to show the internal structure. x 166.

b. v. 1. blood vessel of palp. b. v. 2. abnormal 2nd. vessel. l. m. longitudinal muscles. p. ax. supporting axis of palp. sh. ax. sheath of axis.

Key to lettering of text-figure 4.

ax. f. supporting axis of filament. ax. p. supporting axis of palp. b. b. v. branchial blood vessel. b. lam. basal lamellla. b. v. f. blood vessel of filament. d. l. dorsal lip. d. l. m. b. dorsal longitudinal muscle bundle. d. p. dorsal pit. l. l. lateral lip. l. m. f. longitudinal muscles of filament. oes. oesophagus. ob. m. oblique muscles. p. palp. p. tr. m. posterior transverse muscle. v. l. m. b. ventral longitudinal muscle bundle.



Text-figure 4.

Four transverse sections through the branchial region to show the musculature. x 30.

a) A section through the extreme base of the gill filaments showing the bases of the longitudinal muscle bundle of the filaments and the beginnings of the oblique muscle bands.

b) A section through the branchial crown immediately anterior to the transverse bar of the internal supporting structure, showing the oblique muscles passing along the inside of the basal lamellae, and forming a transverse band across the mid-dorsal line.

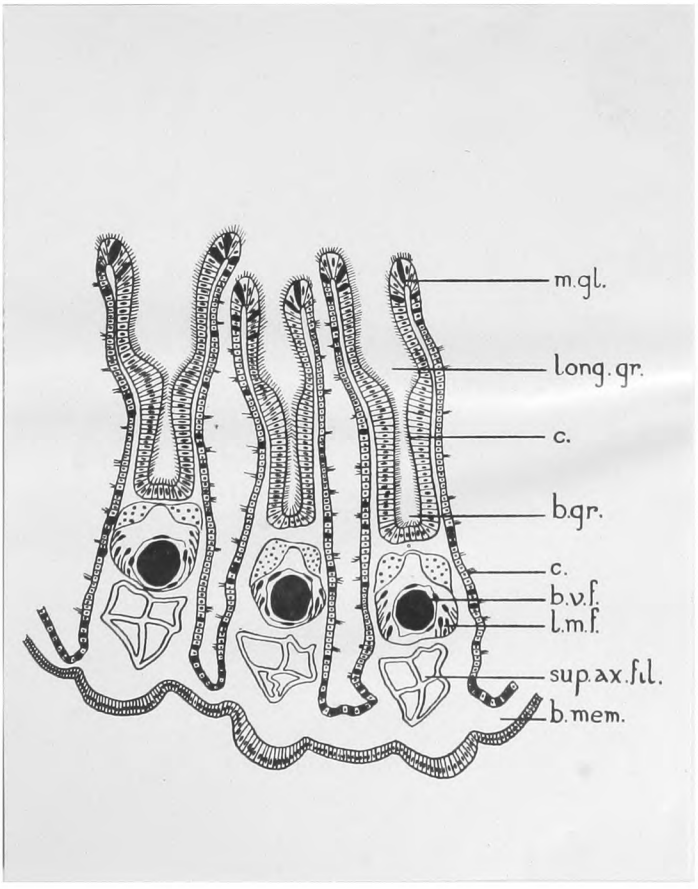
c) A section through the transverse bar, showing the oblique muscles running across the dorso-lateral corners of the basal lamellae.

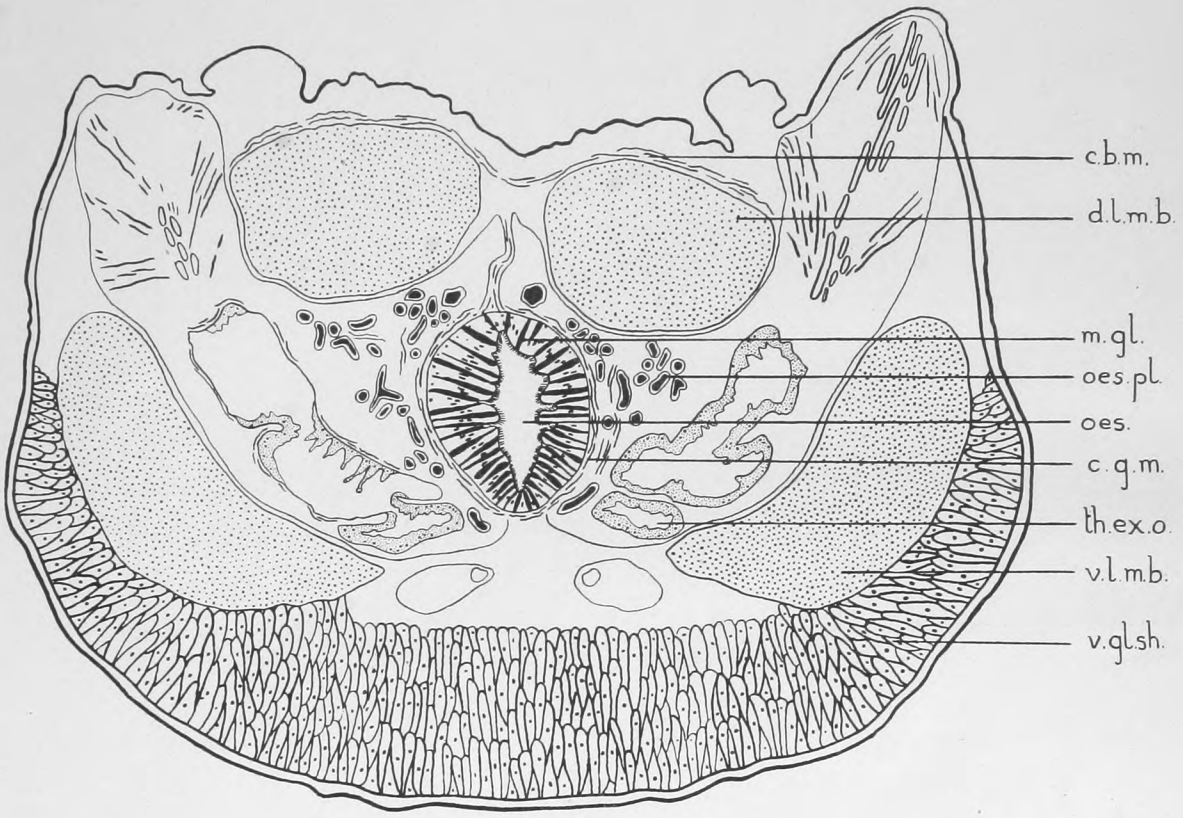
d) A section through the branchial crown posterior to the transverse bar, showing the transverse muscle band joining the posterior projections of the basal lamellae and the dorsal and ventral longitudinal muscle bundles of the body.

Text-figure 5.

A transverse section through the bases of three filaments to show the distribution of mucous glands on the basal folds. x 110.

b. gr. basal groove. b. v. f. blood vessel of filament. b. mem. basal membrane. c. cilia. long. gr. longitudinal groove. l. m. f. longitudinal muscles of filament. m. gl. mucous gland. sup. ax. f. supporting axis of filament.

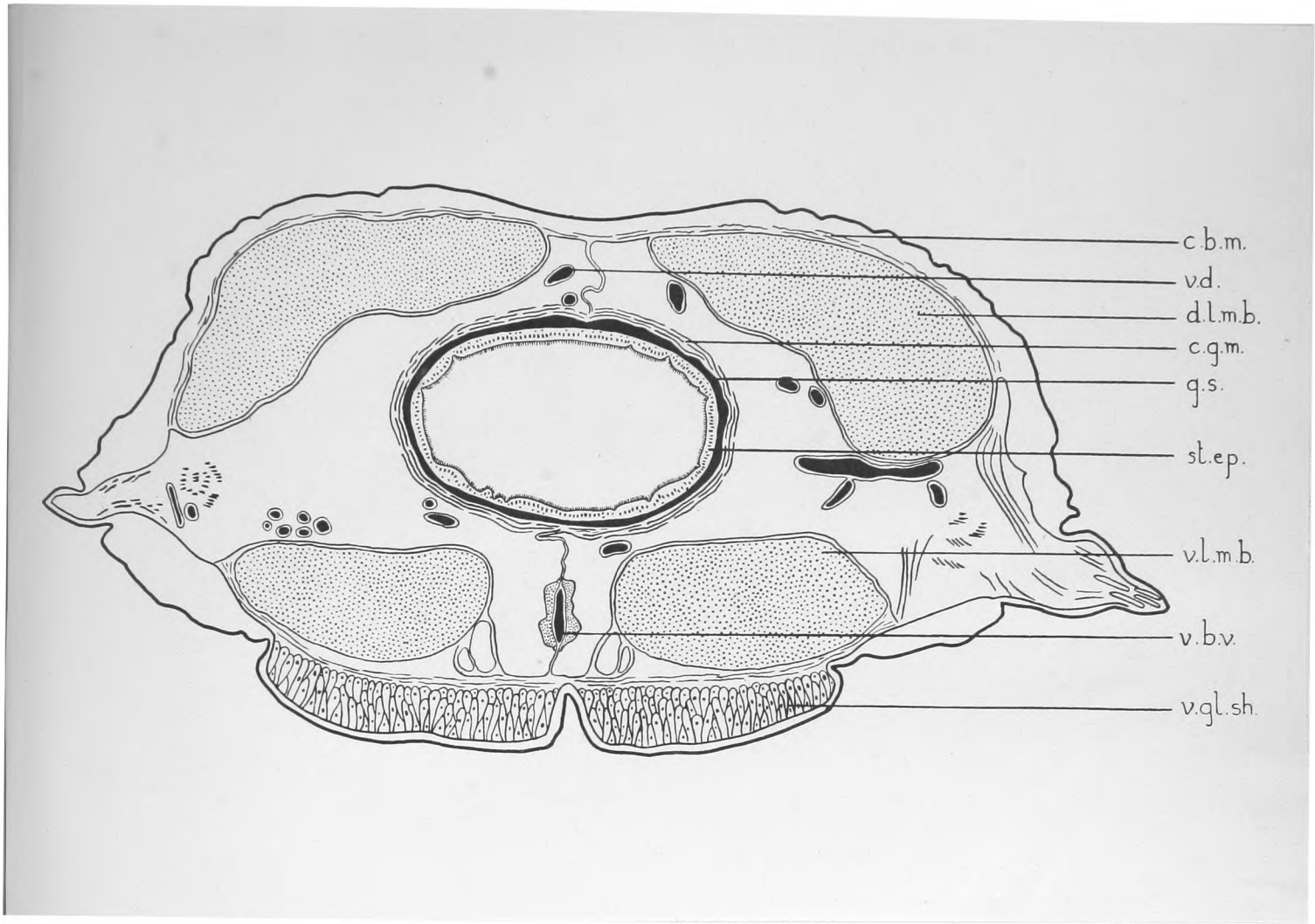




Text-figure 6.

A transverse section through the first body segment, to show the anatomy of the thorax and the relationship of the oesophagus to it. x 36.

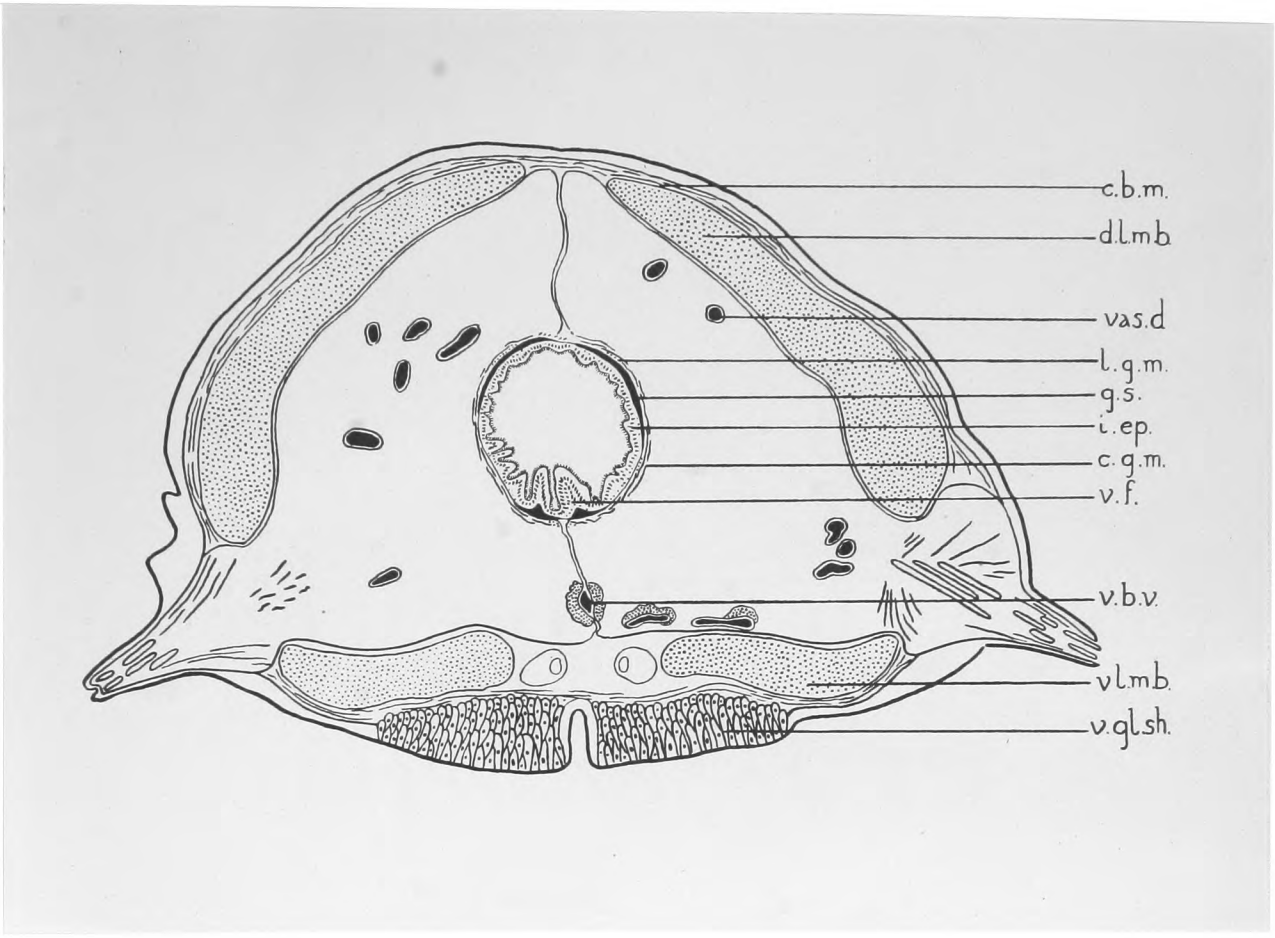
c. b. m. circular body muscles. c. g. m. circular gut muscles. d. l. m. b. dorsal longitudinal muscle bundles. m. gl. mucous glands. oes. oesophagus. oes. pl. oesophageal plexus. th. ex. o. thoracic excretory organ. v. gl. sh. ventral gland shield. v. l. m. b. ventral longitudinal muscle bundle.



Text-figure 7.

A transverse section through the anterior part of the abdominal region, to show the anatomy and the relationship of the stomach to it. x 36.

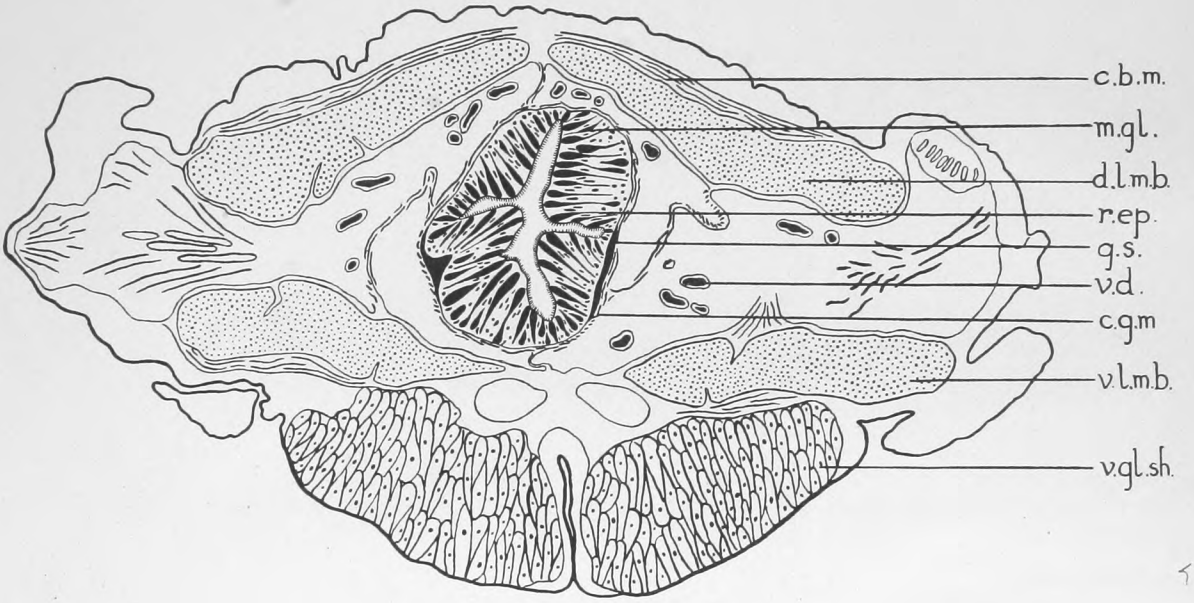
c. b. m. circular body muscles. c. g. m. circular gut muscles. d. l. m. b dorsal longitudinal muscle bundles. g. s. gut sinus. st. ep. stomach epithelium. v. b. v. ventral blood vessel. v. d. vascular diverticula v. gl. sh. ventral gland shield. v. l. m. b. ventral longitudinal muscle bundle.



Text-figure 8.

A transverse section through the region of the intestine. x 36.

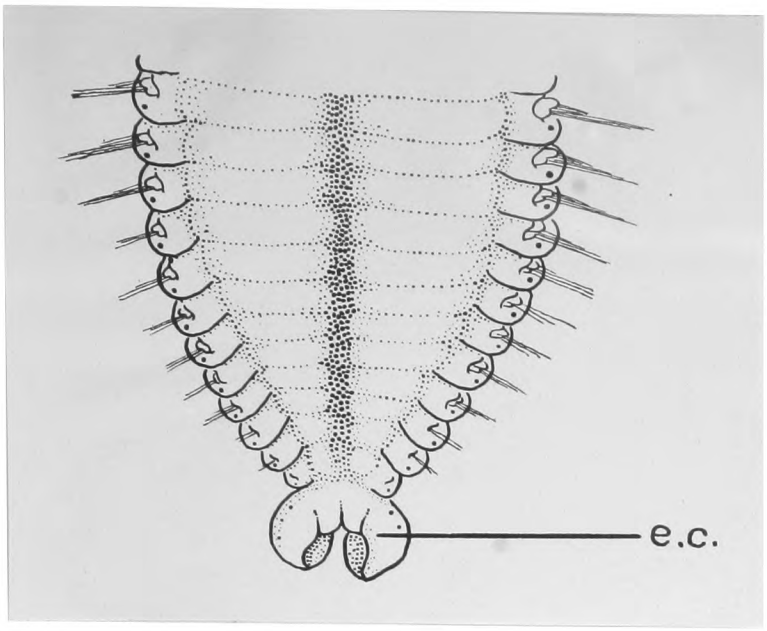
c. b. m. circular body muscles. c. g. m. circular gut muscles.
d. l. m. b. dorsal longitudinal muscle bundles. g. s. gut sinus.
i. ep. intestinal epithelium. l. g. m. longitudinal gut muscles.
v. b. v. ventral blood vessel. vas. d. vascular diverticulum.
v. f. ventral fold. v. gl. sh. ventral gland shield. v. l. m. b. ventral longitudinal muscle bundle.

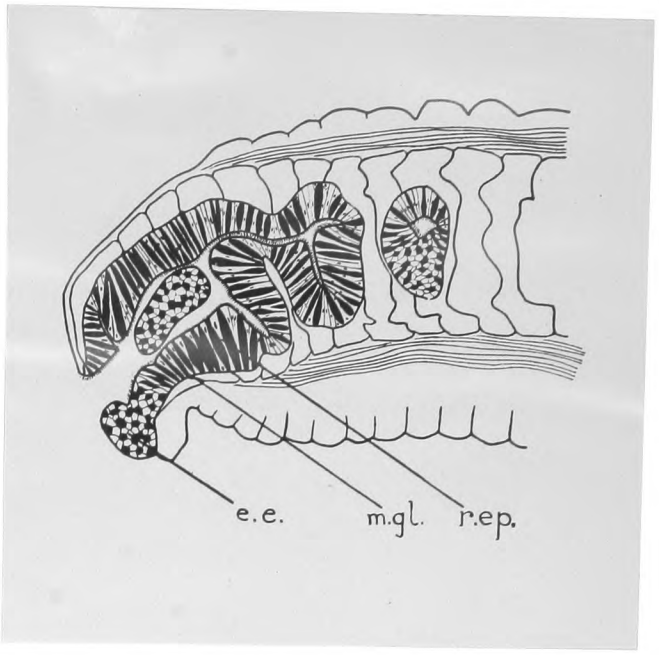


Text-figure 9.

A transverse section through the region of the rectum. x 56.

c. b. m. circular body muscles. c. g. m. circular gut muscles. d. l. m. b. dorsal longitudinal muscle bundles. g. s. gut sinus. m. gl. mucous gland. r. ep. rectal epithelium. v. d. vascular diverticulum. v. gl. sh. ventral gland shield. v. l. m. b. ventral longitudinal muscle bundle.





Text-figure 10.

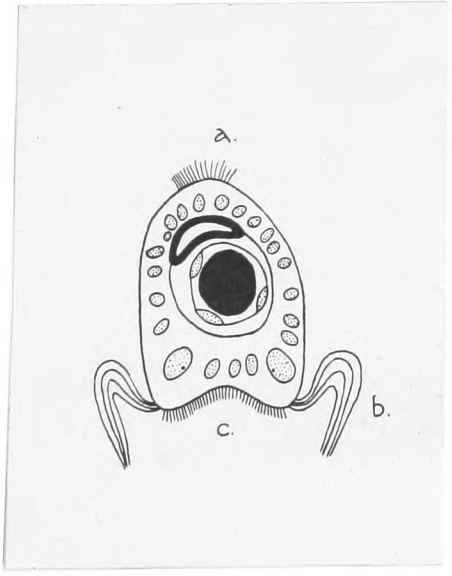
A dorsal view of the posterior end of a worm, showing the endodermal evagination.

e. c. endodermal cushion.

Text-figure 11.

A longitudinal section through the anus, to show the endodermal evagination and the development of mucus glands. x 25.

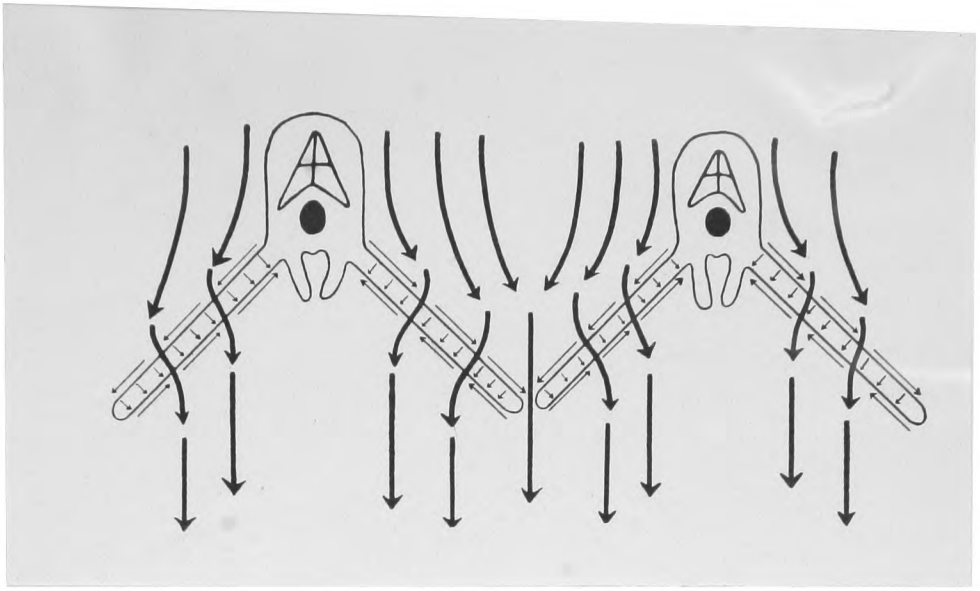
e. e. ectodermal evagination. m. gl. mucus glands. r. ep. rectal epithelium.



Text-figure 12.

A transverse section through a pinnule, to show the ciliation. x 500.

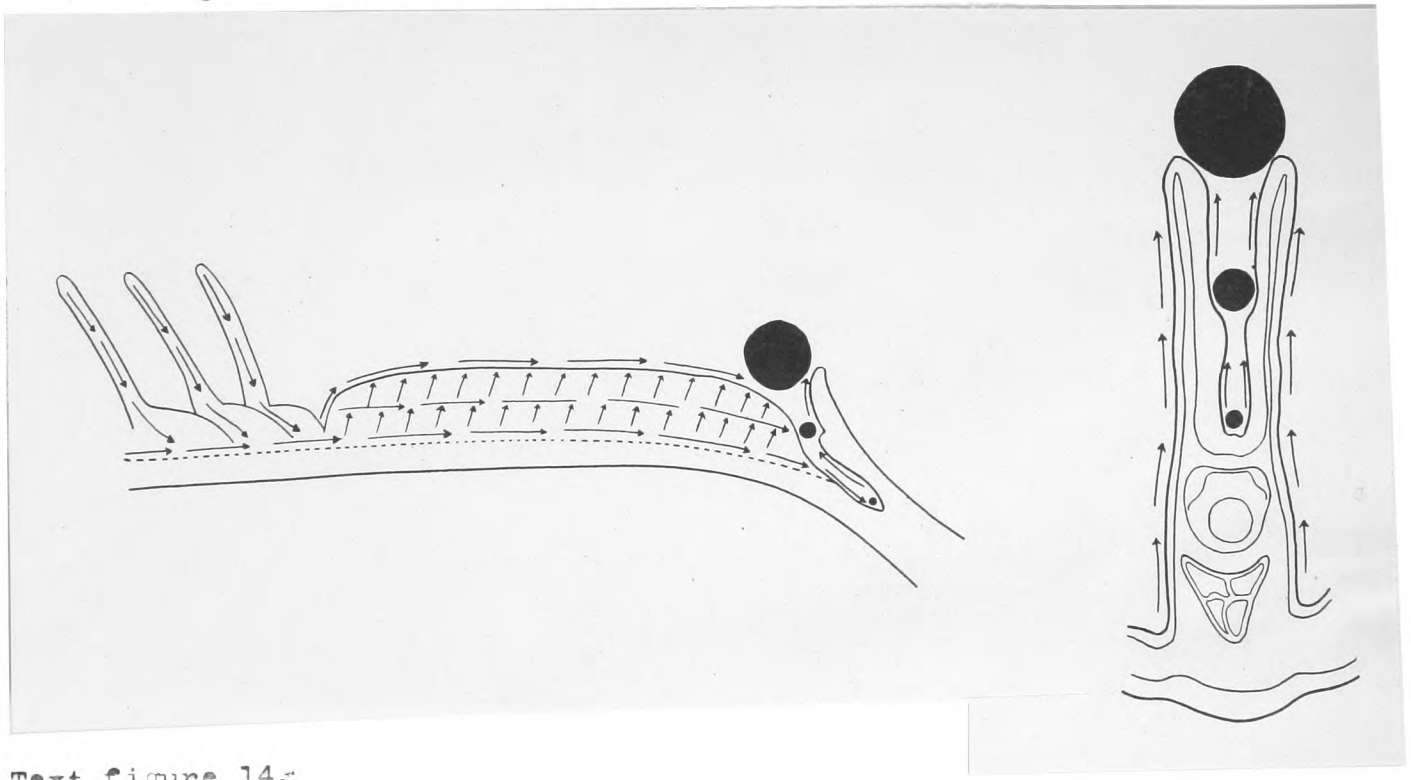
a. abfrontal cilia. b. latero-frontal cilia. c. frontal cilia.



Text-figure 13.

A diagrammatic section of two gill-filaments, to show the direction of flow of the water entering the branchial funnel, and the direction of beat of the cilia which cause the current.

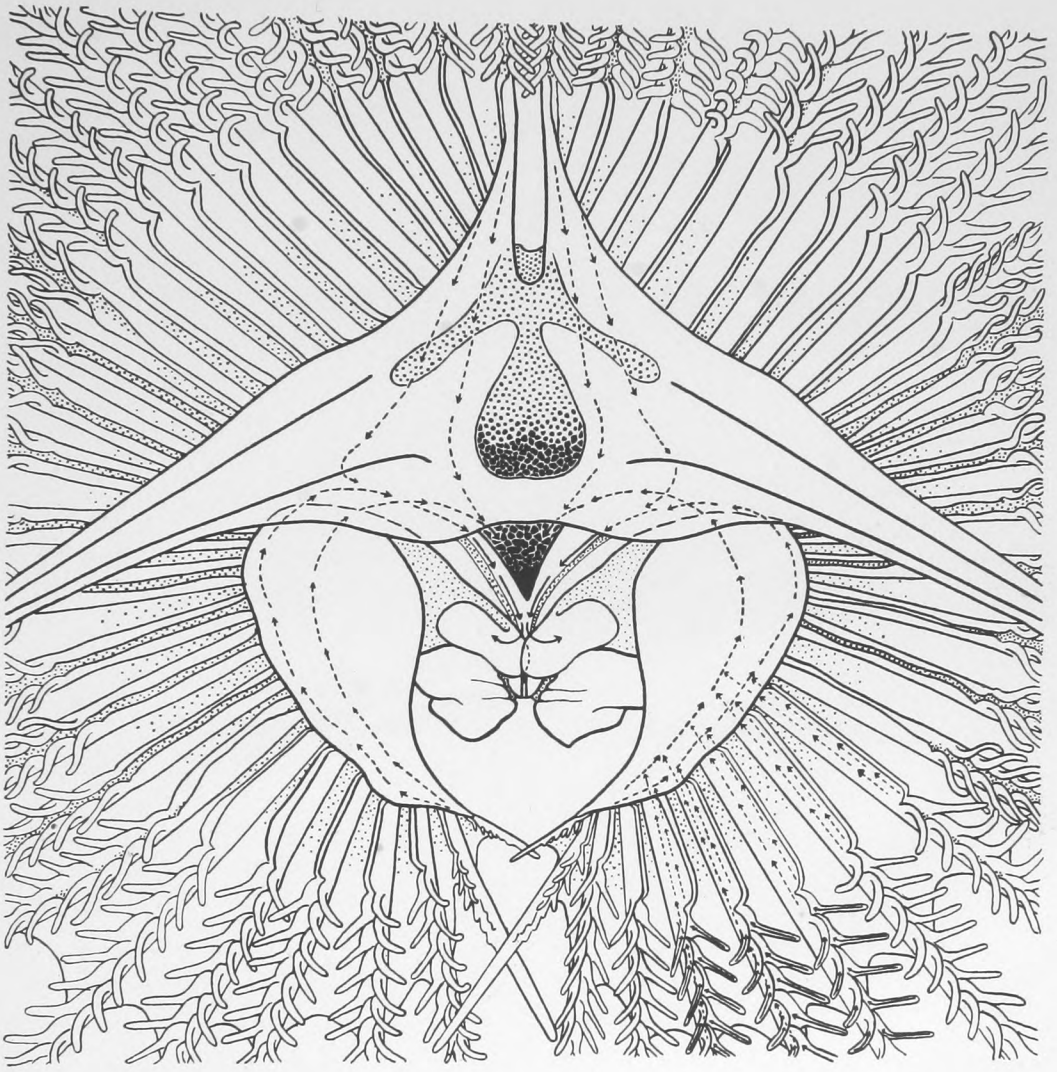
The small arrows indicate the direction of beat of the cilia.
The large arrows indicate the direction of flow of the water.



Text-figure 14.

Two diagrammatic representations of the base of a filament to illustrate the sorting mechanism.

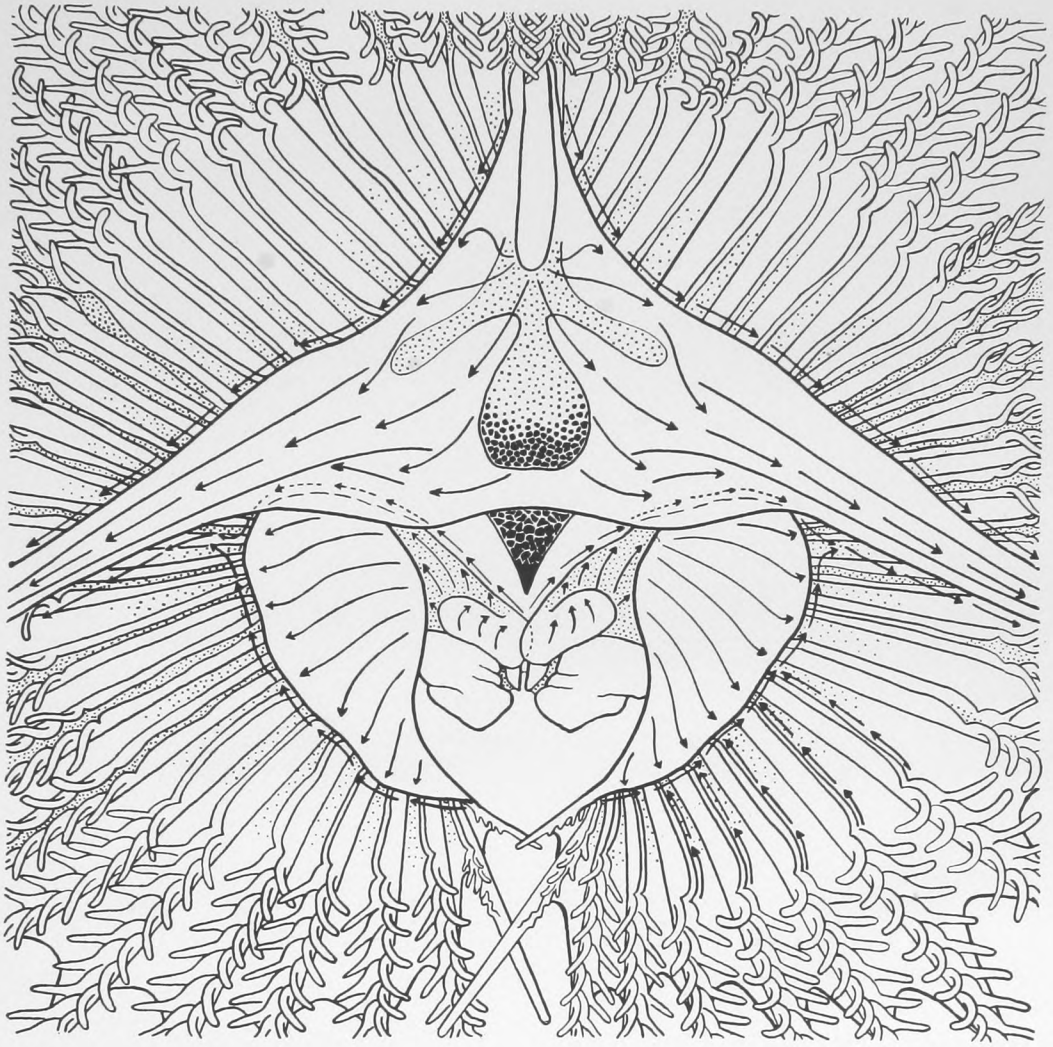
a. The lateral lip and the base of a gill filament with one basal fold removed to show the ciliated tracts and the relative sizes of particles passing along them.
b. A transverse section through a pair of basal folds to show the position of the longitudinal tracts and the relative sizes of particles passing along them.



Text-figure 15.

A terminal view of the branchial crown of Sabella with the filaments fully spread, to show the collecting tracts of the filaments and lips. x 6.

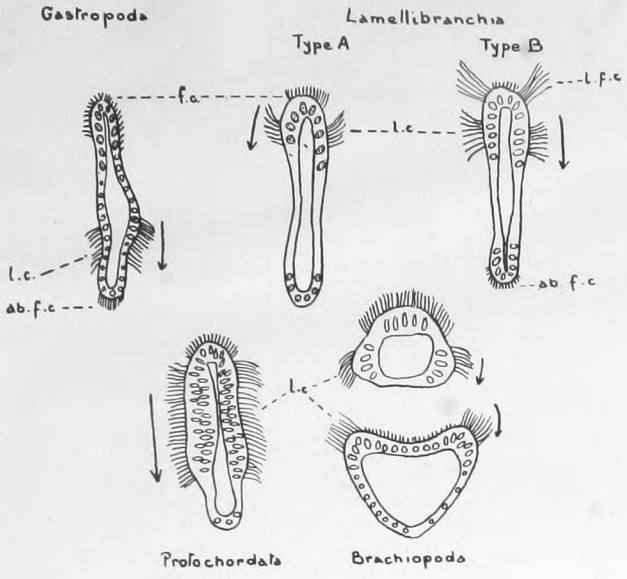
The arrows indicate the path taken by particles passing to the mouth or to the ventral sacs.



Text-figure 16.

A terminal view of the branchial crown of Sabella with the filaments fully spread, to show the rejection tracts of the filaments, palps and lips. x 6.

The arrows indicate the path of particles passing to the tips of the palps.



Text-figure 17.

A series of transverse sections of the gill-filaments of members of the Gastropoda, Lamellibranchia, Protochordata and Brachiopoda, illustrating the essential similarity of the ciliation of the filaments in all these groups.
(After ORTON .)

ab. f. c. abfrontal cilia.
f. c. frontal cilia.
l. c. lateral cilia.
l. f. c. lateral frontal cilia.

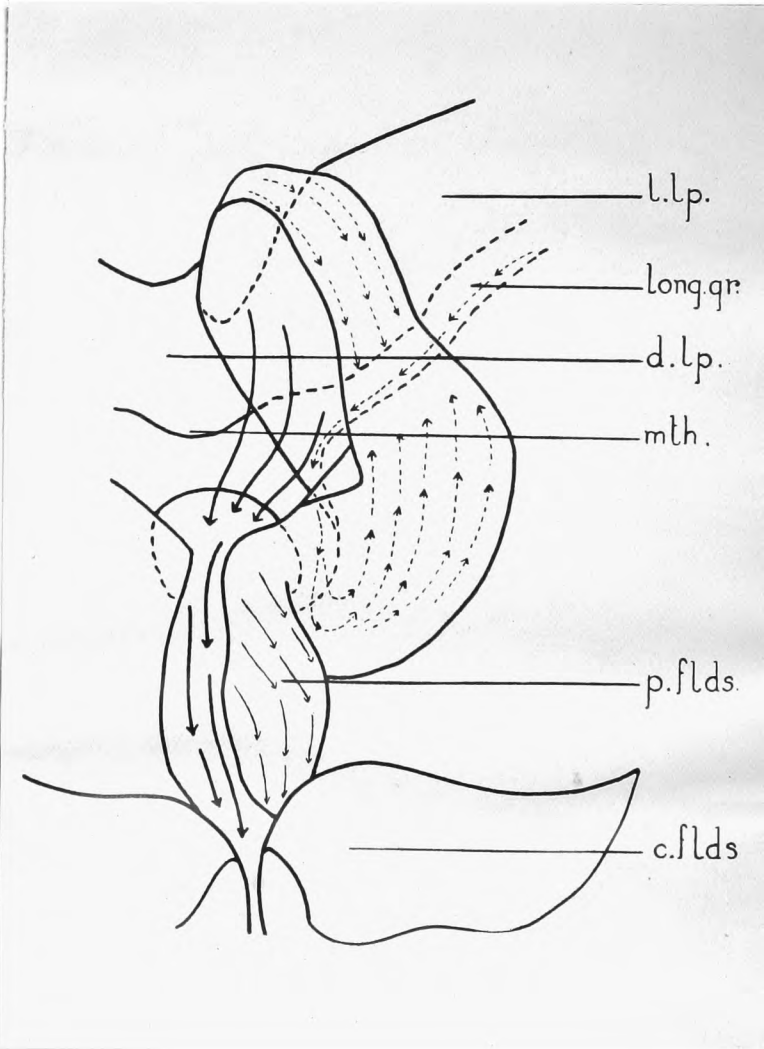
Text-figure 18.

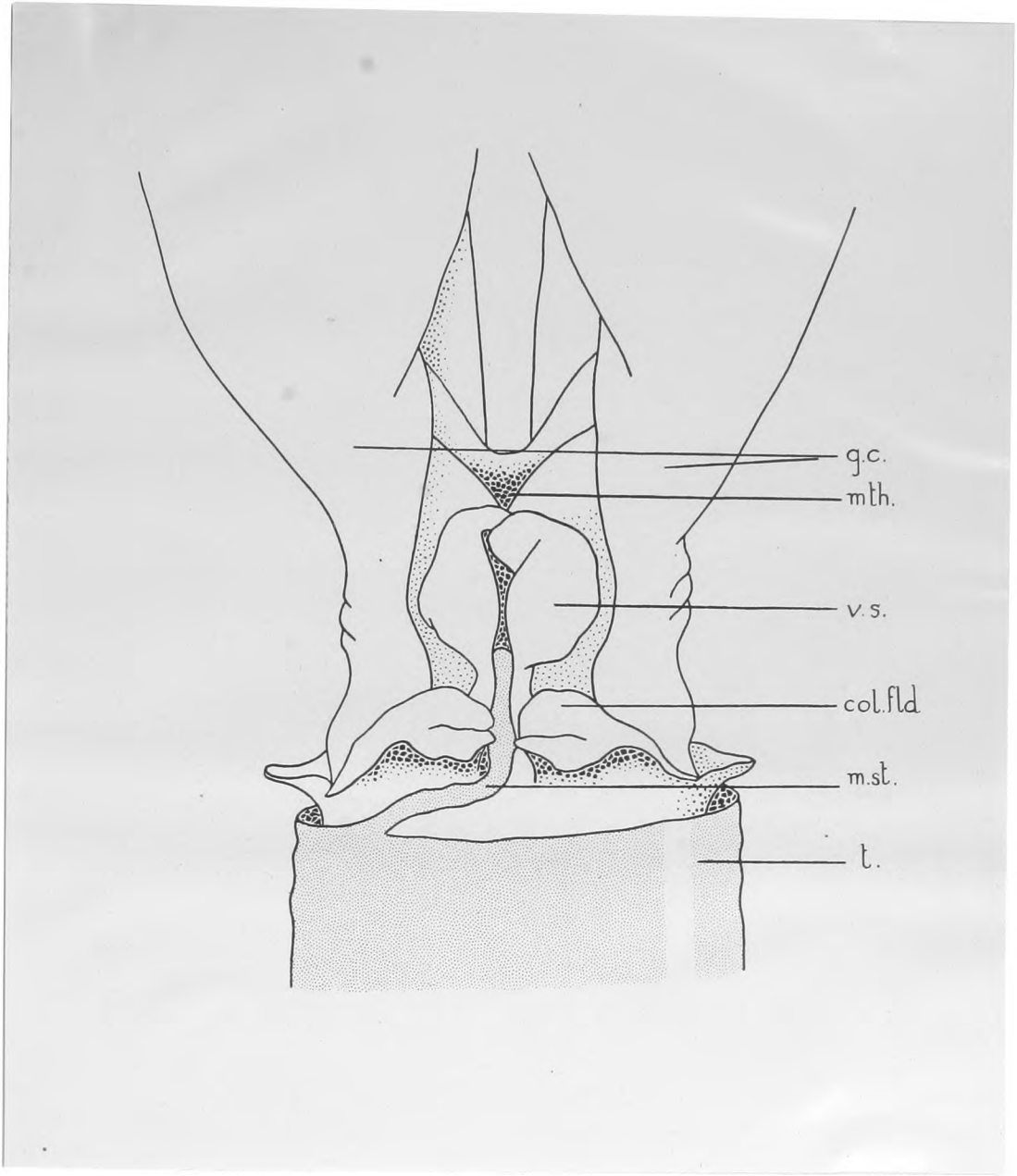
A diagrammatic representation of a ventral sac to show the paths taken by particles entering and leaving it.

c. fld. collar fold.
d. lp. dorsal lip.
l. lp. lateral lip.
long. gr. longitudinal groove.
mth. mouth.
p. flds. parallel folds.

The broken arrows show the path of particles entering the sacs.
The thick arrows show the path of particles leaving the sac.

The thin arrows show the direction of beat of the cilia between the parallel folds.

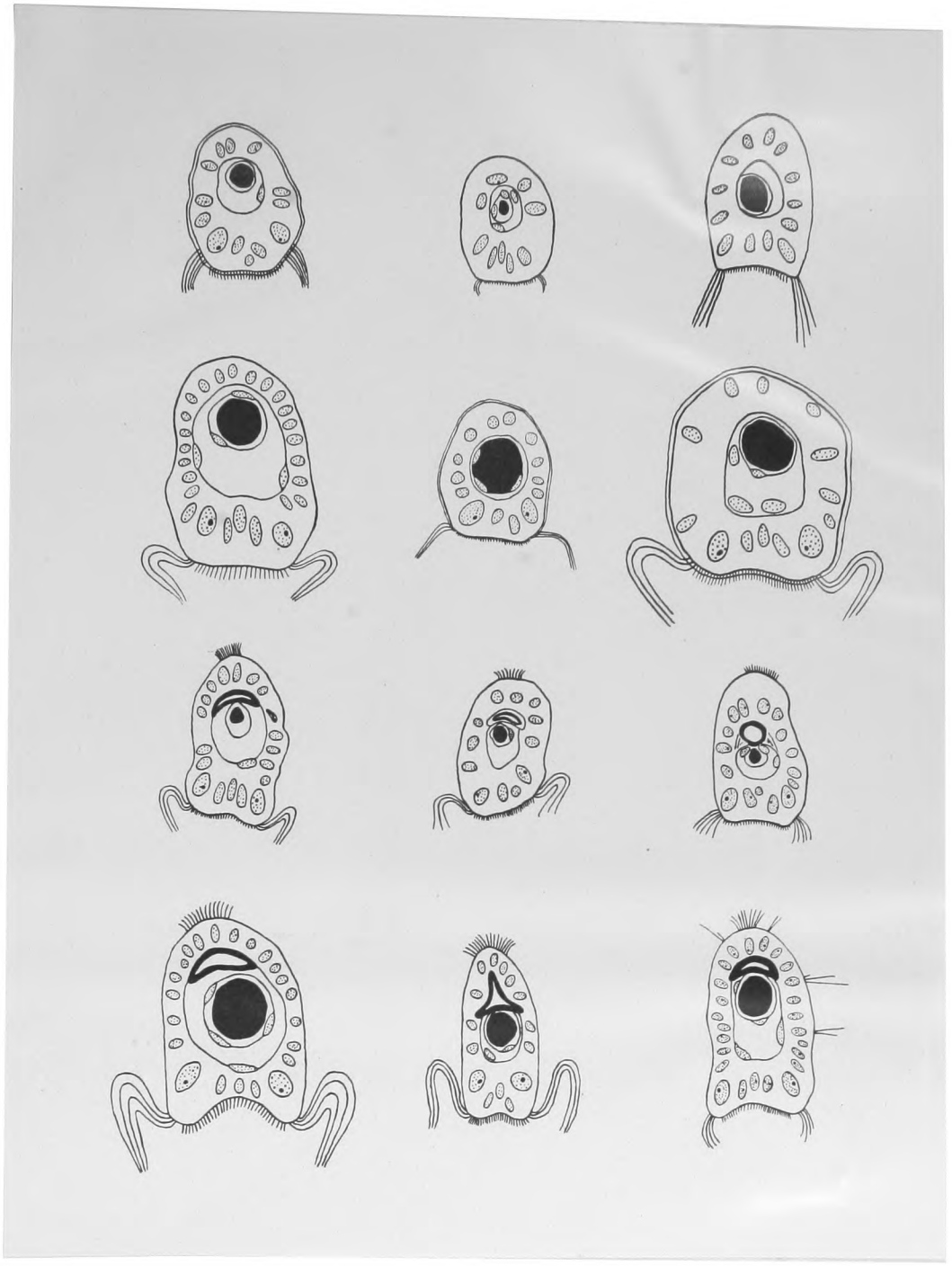




Text-figure 19.

A ventral view of a worm in the act of tube-building, to show the formation of the mucus and sand string and the method of applying it to the edge of the tube. x12.

col. fld. collar fold. g. c. gill crown. m. st. mucous string. mth. mouth. t. tube. v. s. ventral sac.



Text-figure 20.

A series of transverse sections of the gill pinnules of various members of the Sabellidae and Serpulidae, to show the ciliation. x 500

Serpulids. a.) Hydroides norvegica. b,) Filograna implexa.
c.) Spirorbis borealis. d.) Serpula vermicularis.
e.) Pomatoceros triquetor. f.) Protula tubularia.

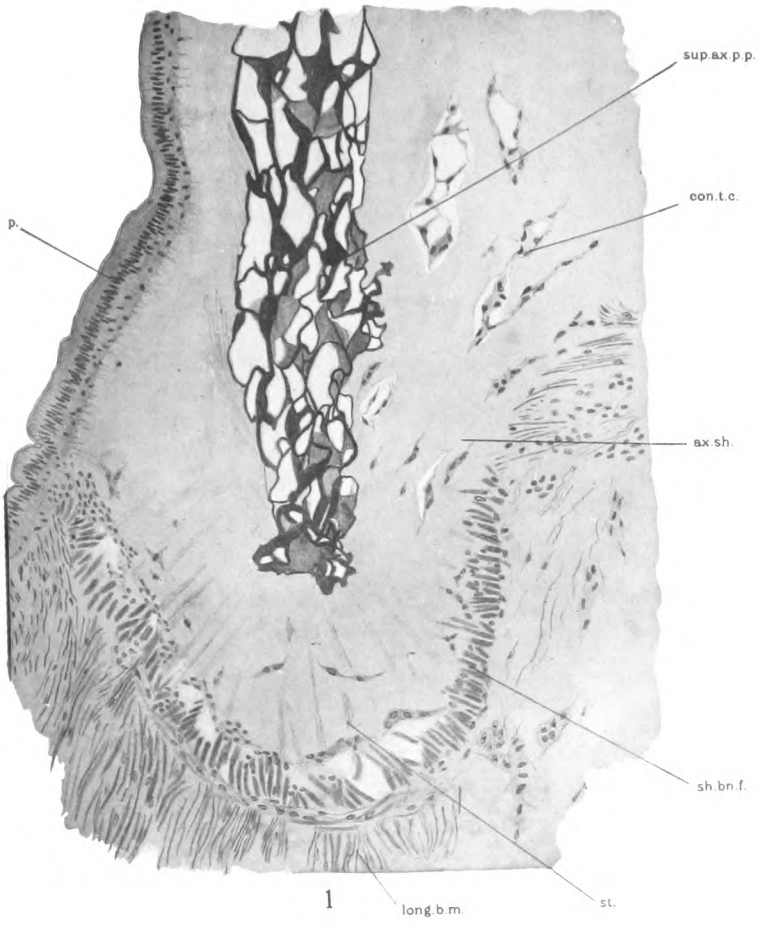
Sabellids. g.) Bispira voluticornis. h.) Myxicola infandibulum.
i.) Potamilla reniformis. j.) Sabella pavonina.
k.) Dasychone bombyx. l.) Branchiomma vesiculosum.

PLATE I.

Figure 1.

Figure 2.

Dr. E. A. T. Nicol: "*Sabella pavonina*." —Plate II.



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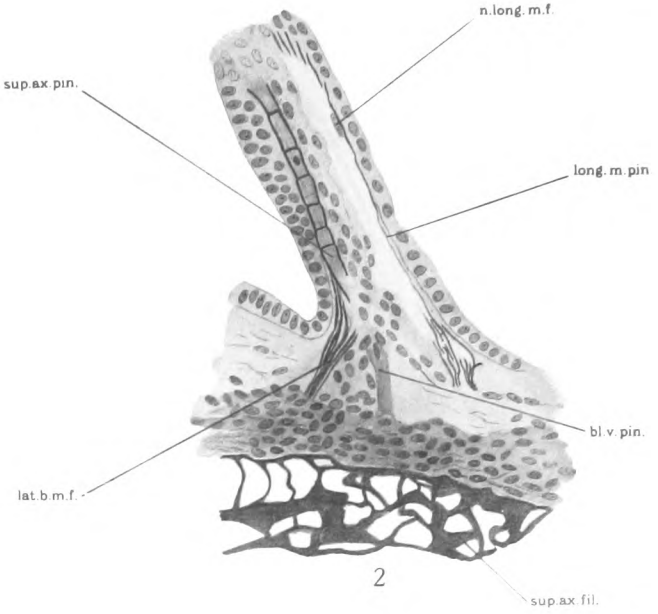

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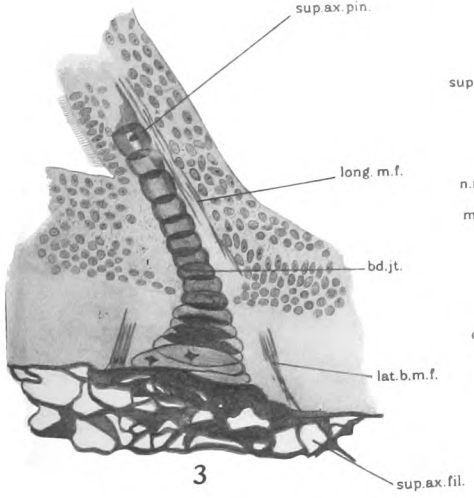

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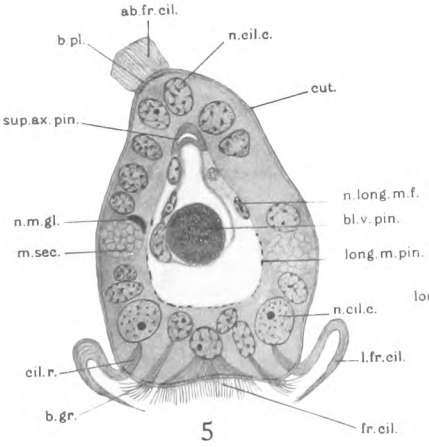

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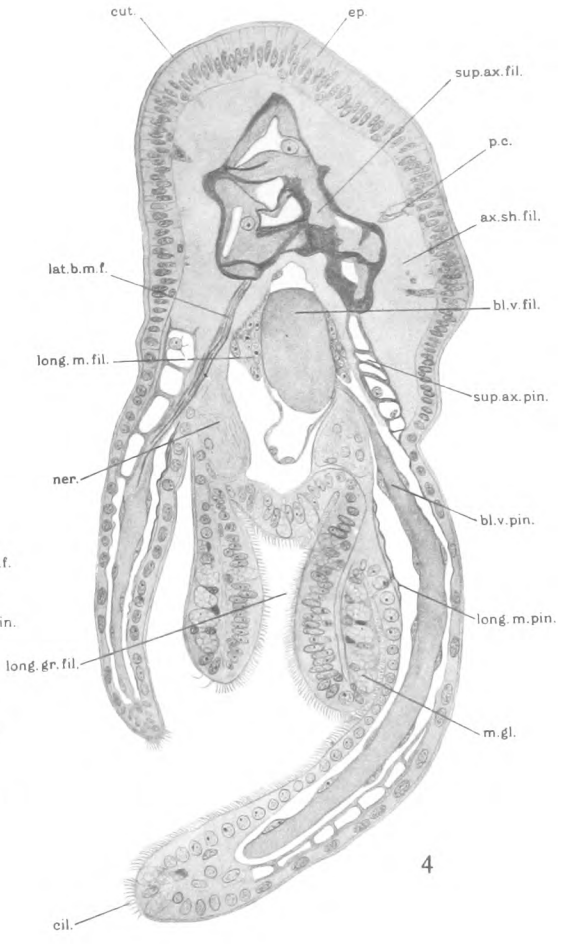

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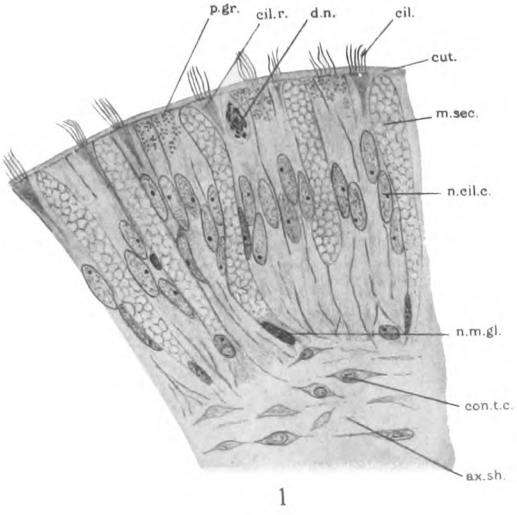
Dr. E. A. T. Nicol: "*Sabella pavonina*." —Plate III.



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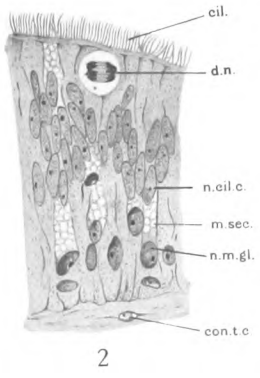

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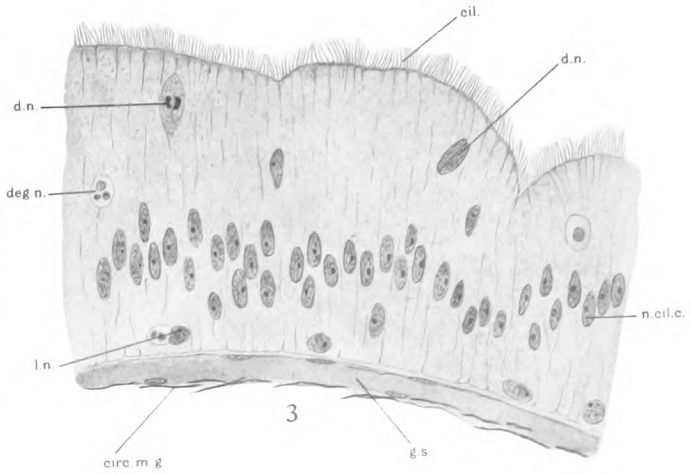

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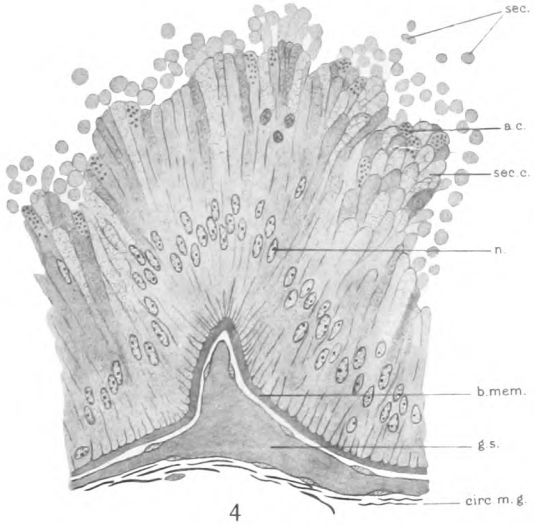

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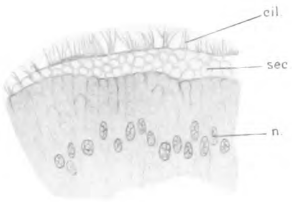

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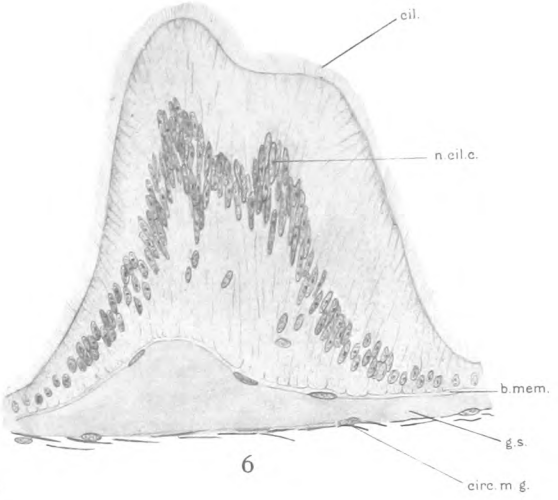

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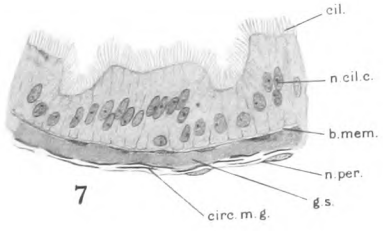

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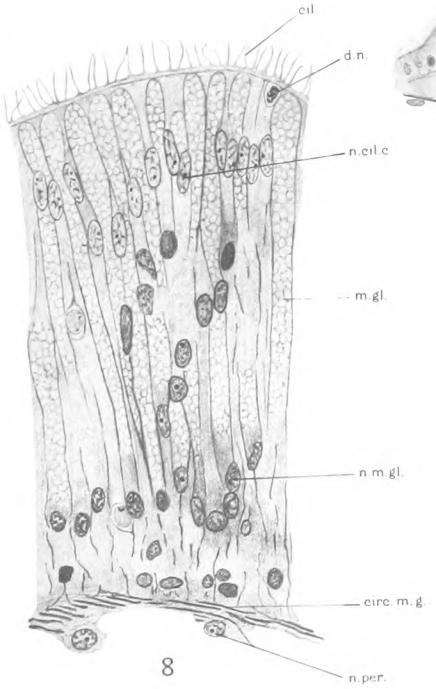

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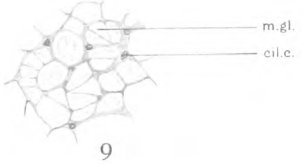

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