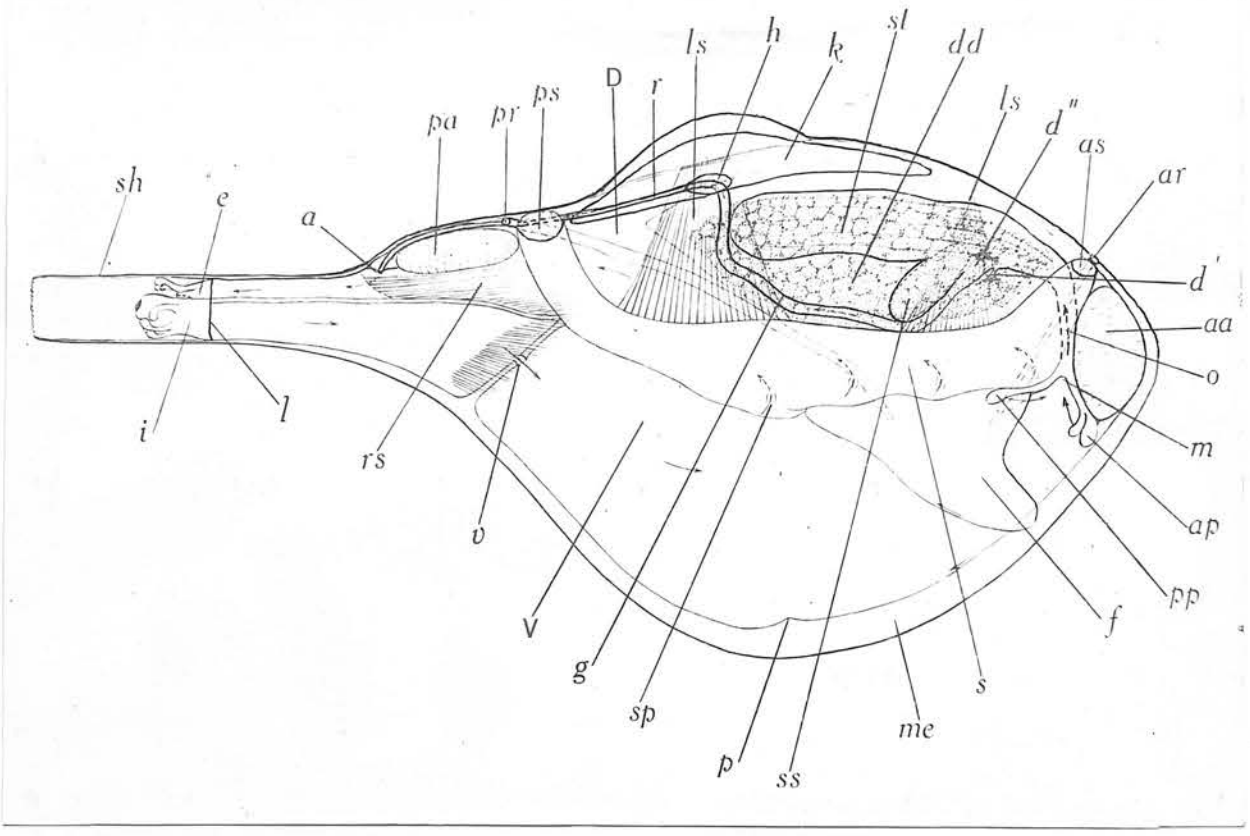
MARINE BIOLOGICAL ASSOCIATION OF THE UNITED KINGDOM, PLYMOUTH.

C. M. Yonge.

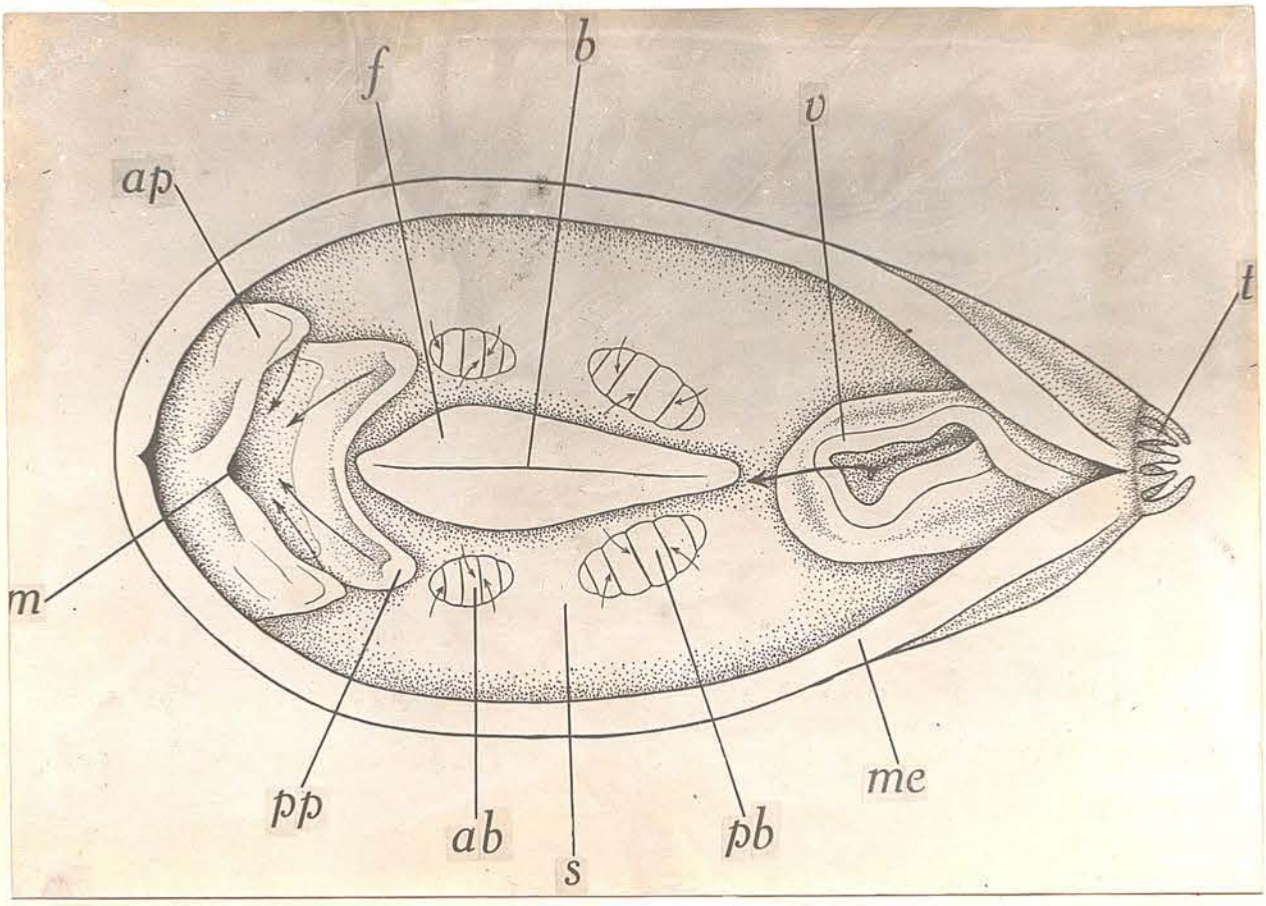
D. Sc. 1927

STRUCTURE AND FUNCTION OF THE ORGANS OF FEEDING AND DIGESTION IN THE SEPTIBRANCHS, CUSPIDARIA AND POROMYA.

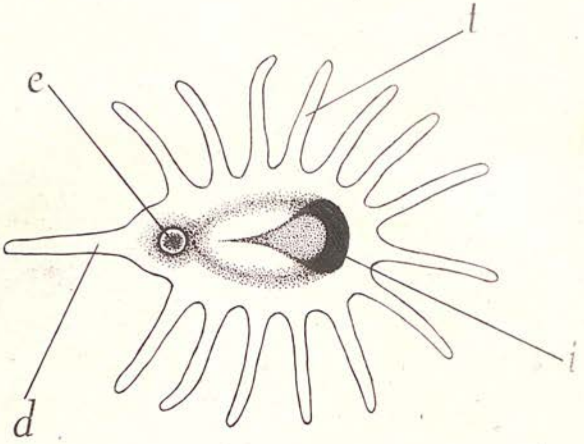
TEXT-FIGURES 1 - 7.



TEXT-FIG. 1. - Lateral view of *Cuspidaria rostrata* showing the anatomy of the feeding and digestive organs. × 7½.
a, anus; aa, anterior adductor; ap, anterior labial palps; ar, anterior retractor of foot; as, anterior septal muscle; d', anterior, right duct of digestive diverticula; d'', posterior, left duct of same; D, dorsal or supra-septal compartment of the mantle cavity; dd, digestive diverticula; e, exhalent siphon; f, foot; g, mid-gut; h, heart; i, inhalent siphon; k, kidney; l, line of attachment of siphons; ls, lateral septal muscles; m, mouth; me, mantle edge; o, oesophagus; p, point where mantle lobes unite; pa, posterior adductor; pp, posterior palps; pr, posterior retractor of foot; ps, posterior septal muscle; r, rectum; rs, retractor muscle of siphons; s, septum; sh, siphonal sheath; sp, septal pore; ss, style sac (style indicated by broken line); st, stomach; v, valve at junction of the inhalent siphon and the mantle cavity; V, ventral or infra-septal cavity.
Arrows indicate direction of water currents & food intake.

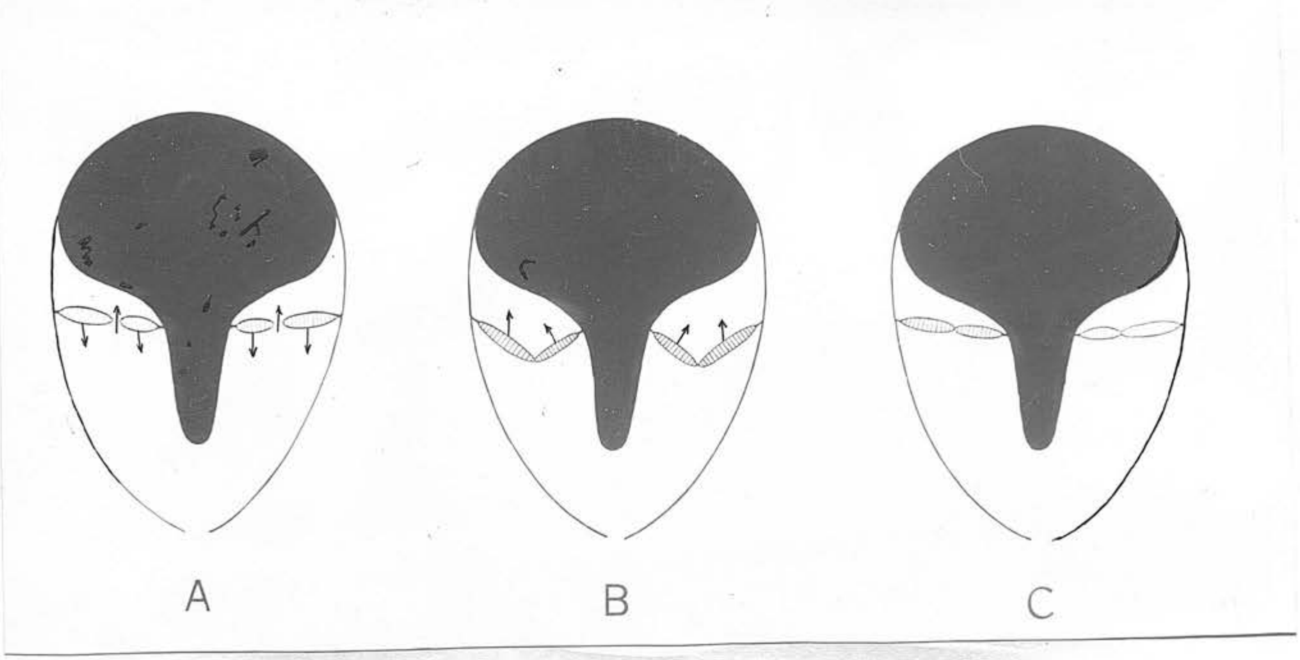


TEXT-FIG. 7. - Ventral view of Poromya granulata with mantle lobes drawn back to expose septum, drawn from life. × 22. ab, anterior branchial sieve; ap, anterior palps; b, byssus groove; f, foot; m, mouth; me, mantle edge; pb, posterior branchial sieve; pp, posterior palps; s, septum; t, tentacles surrounding siphonal openings; v, valve between inhalent siphon and infra-septal cavity. Large arrows indicate direction of food intake, small arrows the passage of the water current through the branchial sieves.

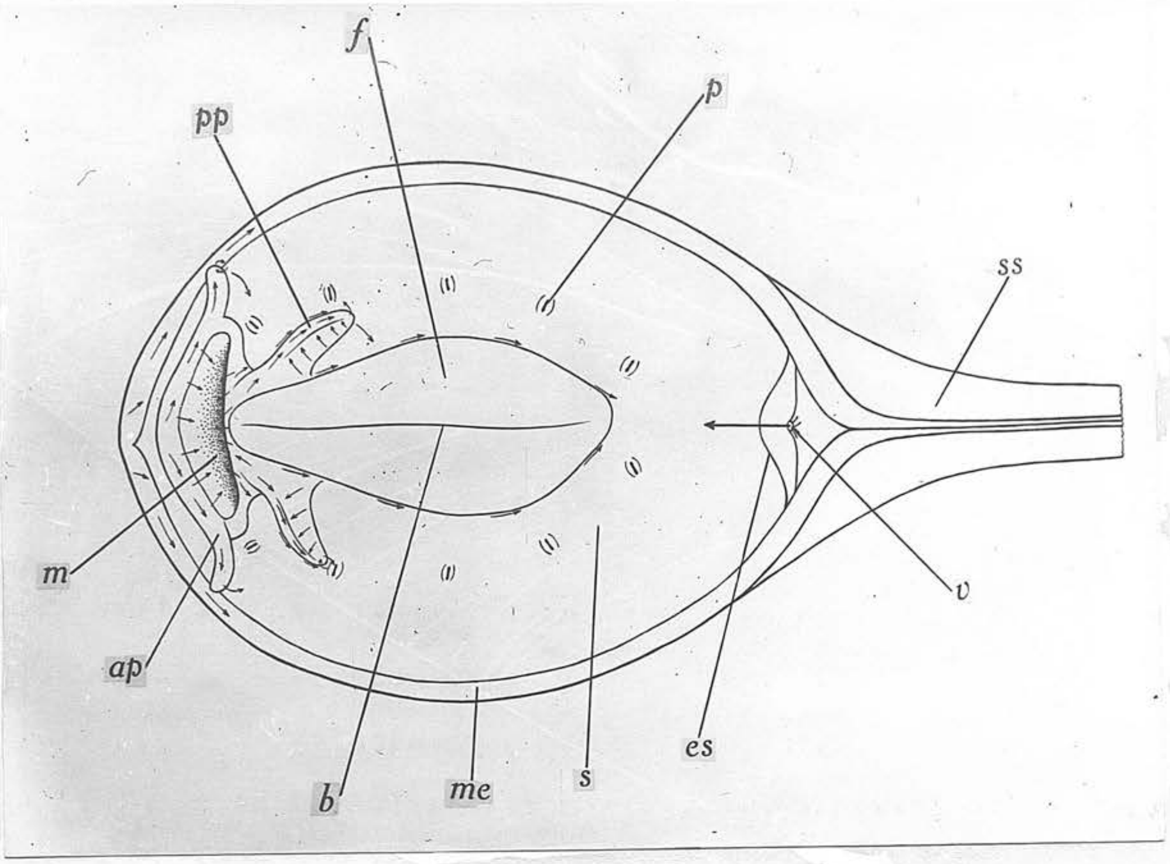


TEXT-FIG. 4. - Poromya granulata, siphons and surrounding tentacles fully extended, drawn from life. × 14.

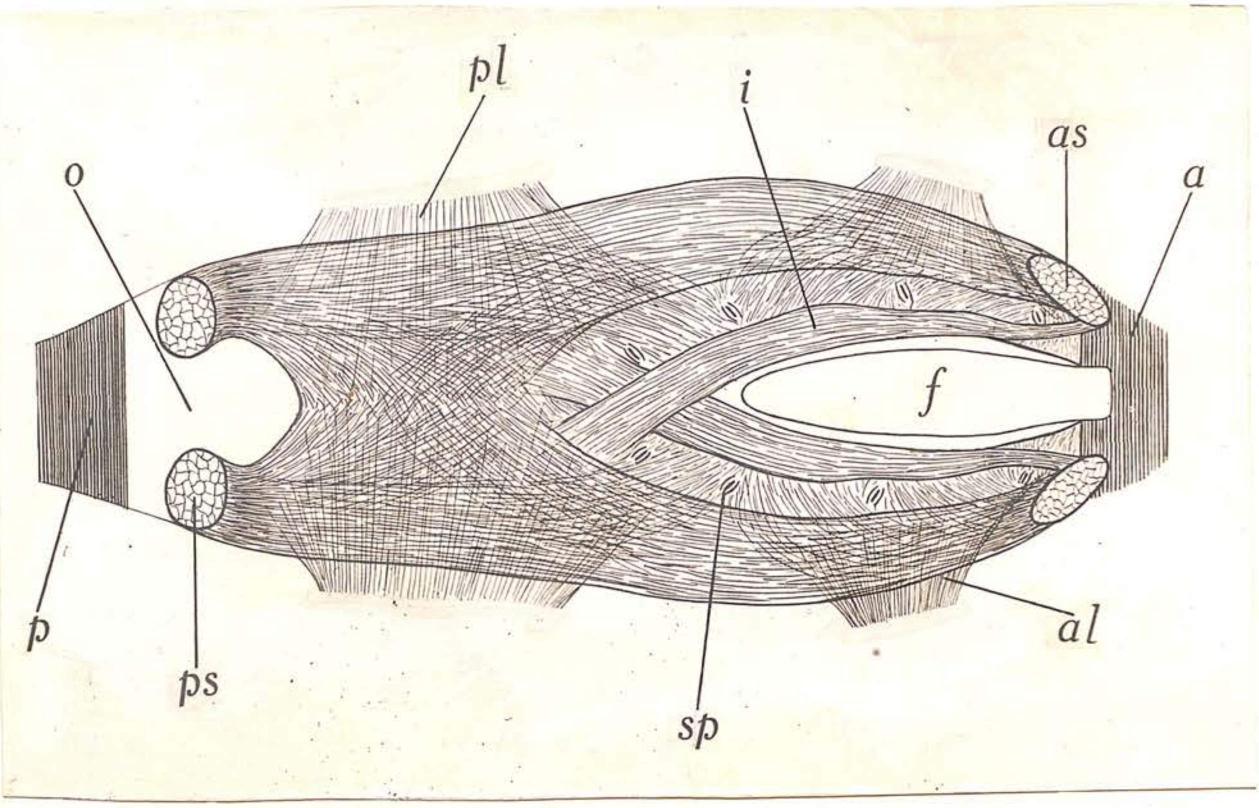
d, dorsal, unpaired tentacle; e, exhalent siphon; i, inhalent siphon; t, one of the fourteen paired tentacles.



TEXT-FIG. 5. - Diagram showing movements of septum. A, position of septum when at rest and preliminary to descending, current of water through pores, indicated by upward directed arrows, downward movement of septum indicated by arrows; B, position of septum at end of downward movement, pores closed, septum now moves upward as indicated by arrows; C, position at completion of upward movement, pores still shut.

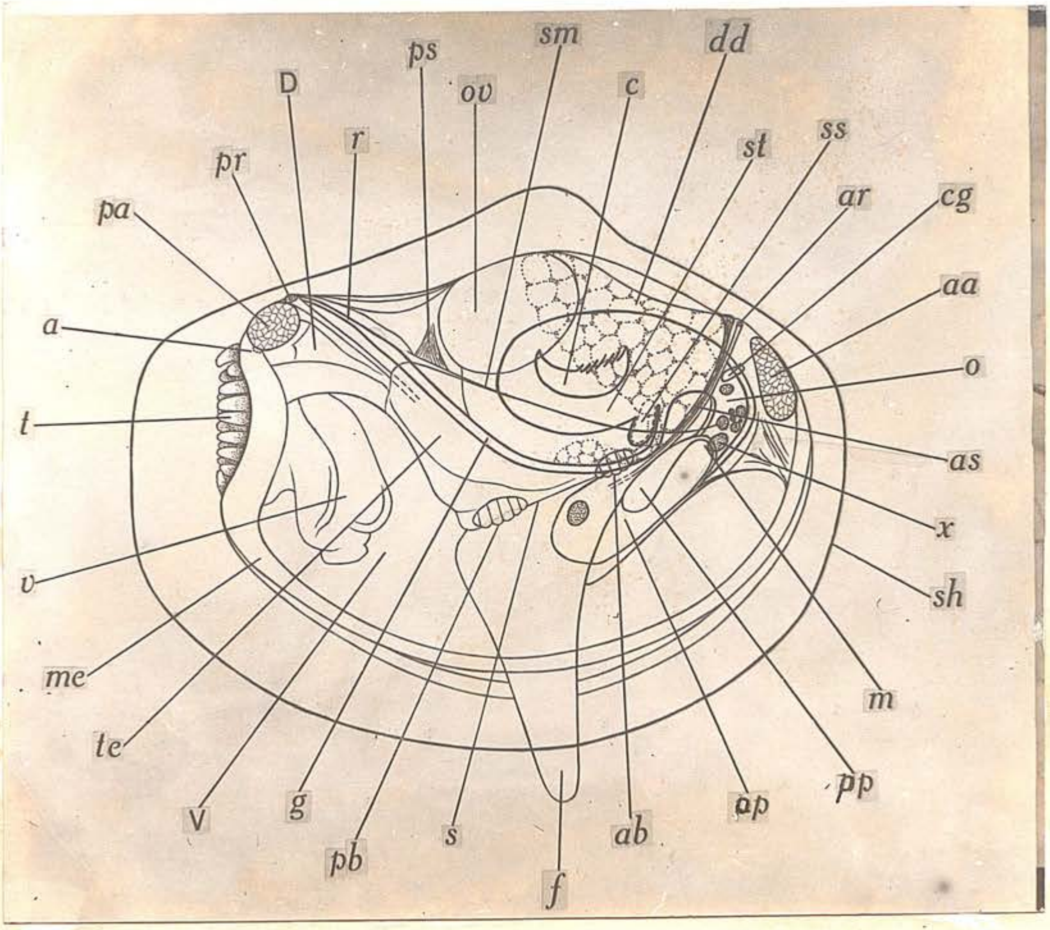


TEXT-FIG. 6. - Ventral view of *Cuspidaria cuspidata* with mantle lobes drawn back to expose septum, drawn from life. × 14. ap, anterior palps; b, byssus groove; es, posterior end of septum; f, foot; m, mouth; me, mantle edge; p, septal pore; pp, posterior palps; s, septum, ventral surface; ss, siphonal sheath; v, valve between inhalent siphon and infra-septal cavity. Large arrow indicates direction of main food and respiratory current, smaller arrows indicate direction of ciliary currents.



TEXT-FIG. 2. - Septum of *Cuspidaria rostrata*, dissected out and viewed from the dorsal aspect. × 10.

a, anterior adductor; al, anterior lateral septal muscle; as, anterior septal muscle; f, foot; i, inner longitudinal muscles from anterior septal muscle; o, opening leading to exhalent siphon; p, posterior adductor; pl, posterior lateral septal muscle; ps, posterior septal muscle; sp, septal pore.



TEXT-FIG. 3. - Lateral view of Poromya granulata, showing the anatomy of feeding and digestive organs. × 7½.

a, anus; aa, anterior adductor; ab, anterior branchial sieve; ap, anterior palps; ar, anterior retractor of foot; as, anterior septal muscle; c, crustacean in stomach; cg, cerebral ganglion; D, dorsal or supra-septal cavity; dd, digestive diverticula; f, foot; g, mid-gut; m, mouth; me, mantle edge; o, oesophagus; ov, ovary; pa, posterior adductor; pb, posterior branchial sieve; pp, posterior palps; pr, posterior retractor of foot; ps, posterior septal muscle; r, rectum; s, septum; sh, outline of shell; sm, lime of attachment of septum and mantle; ss, style-sac (style indicated by broken line); st, stomach; t, tentacles; te, testis; v, valve between inhalent siphon and infra-septal cavity; V, ventral or infra-septal cavity; x, sand grains between palps and in oesophagus.

Structure and Physiology of the Organs of Feeding and Digestion in *Ostrea edulis.*

By

C. M. Yonge, B.Sc., Ph.D.,
Temporary Assistant Naturalist at the Plymouth Laboratory.

With 42 Figures in the Text.

Reprinted from the Journal of the Marine Biological Association of the United Kingdom.
Vol. xiv., No. 2. August, 1926.

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CONTENTS.

1. INTRODUCTION.

THIS research is the outcome of a recommendation made by Dr. J. H. Orton in his report (1923) on the cause of the mortality of oysters during 1920 and 1921, in which he pointed out the necessity of our obtaining more precise information regarding the physiology of the oyster, both for its own sake and for its possible economic applications. I have endeavoured, therefore, to give as complete an account as possible of the structure and function of the food collecting and digestive organs in the oyster—larval, " spat," and adult—in the hope of so determining the optimum conditions for feeding and digestion, and, consequently, for growth and " fattening." In view of the fact that no complete account of the anatomy and histology of these organs exists, it has been necessary to devote considerable time to this aspect of the work, since a sound knowledge of the structure of any organ is essential if the function is to be determined. The research covers a great deal of ground, so that it has been impossible in the time available to investigate in detail every problem that has been encountered or to perform all the experiments that have suggested themselves, but no problem of the first importance has been neglected, while it is hoped in the near future to carry out further investigations into those aspects of the work which have been found the most important.

The work on the adult oysters was carried out at the Plymouth Laboratory, the oysters being obtained from the River Yealm, and the work on the larval and " spat " oysters at the Fisheries Experimental Station at Conway during July and August, 1925. I wish to express my gratitude for their kindness and help to the Director and members of the Staff, especially Dr. J. H. Orton, of the Plymouth Laboratory, and to Dr. Dodgson, Mr. H. P. Sherwood, and the other members of the Staff at Conway.

2. ANATOMY AND HISTOLOGY OF THE ALIMENTARY SYSTEM.

A. ADULT OYSTERS.

I. ANATOMY.

The arrangement of the food collecting and digestive organs in the oyster can best be described by reference to Fig. 1 in which an oyster is shown lying on the lower (left) shell valve with the right fold of the mantle cut away. The surface of the mantle (L.M.F.) is transversely ridged, and is bounded by a thickened margin bearing two rows of small tentacles. The mantle cavity is divided into inhalent (I.C.) and exhalent chambers (E.C.), the former being some four times the larger, and containing the gills (G.), which consist of four demibranchs, the inner ones being broader than the outer ones, the inner one on the left (under) side being the broadest of all. The outer demibranchs are attached directly to the mantle, the inner ones being attached to the mantle on the outer side and to one another on the inside. In the oyster the two pairs of demibranchs are not separated by a protruding foot or visceral mass. The gills extend in a semicircle from the junction between the right and left mantle folds, which forms the division between the inhalent and exhalent chambers (D.B.C.), to the labial palps (L.P.). The latter consist of triangular flaps attached by a broad base and arranged in two pairs, one on each side of the mouth (M.). The inner, opposing surfaces are ridged (see Fig. 2), the outer surfaces being smooth. The palps enclose the gills for a short distance, the outer and inner demibranchs of each side lying between the corresponding pairs of palps, the inner demibranchs arising slightly nearer the mouth than the outer, and immediately behind the most distal fold on the palp surface. Unlike the majority of Lamellibranchs, the inner and outer palps of the two sides are united to one another in the region of the mouth (M.), which lies in the middle line in the groove formed by the continuation of the grooves between the two sets of palps. The outer palps are united for about a quarter of their length, so that the mouth is entirely enclosed.

The mouth is a narrow horizontal slit and leads into a short œsophagus (O.) which has the the same shape in cross section and passes backwards and downwards into the stomach (S.). This is an irregular sac-shaped organ which is surrounded on all sides by the brown mass of the digestive

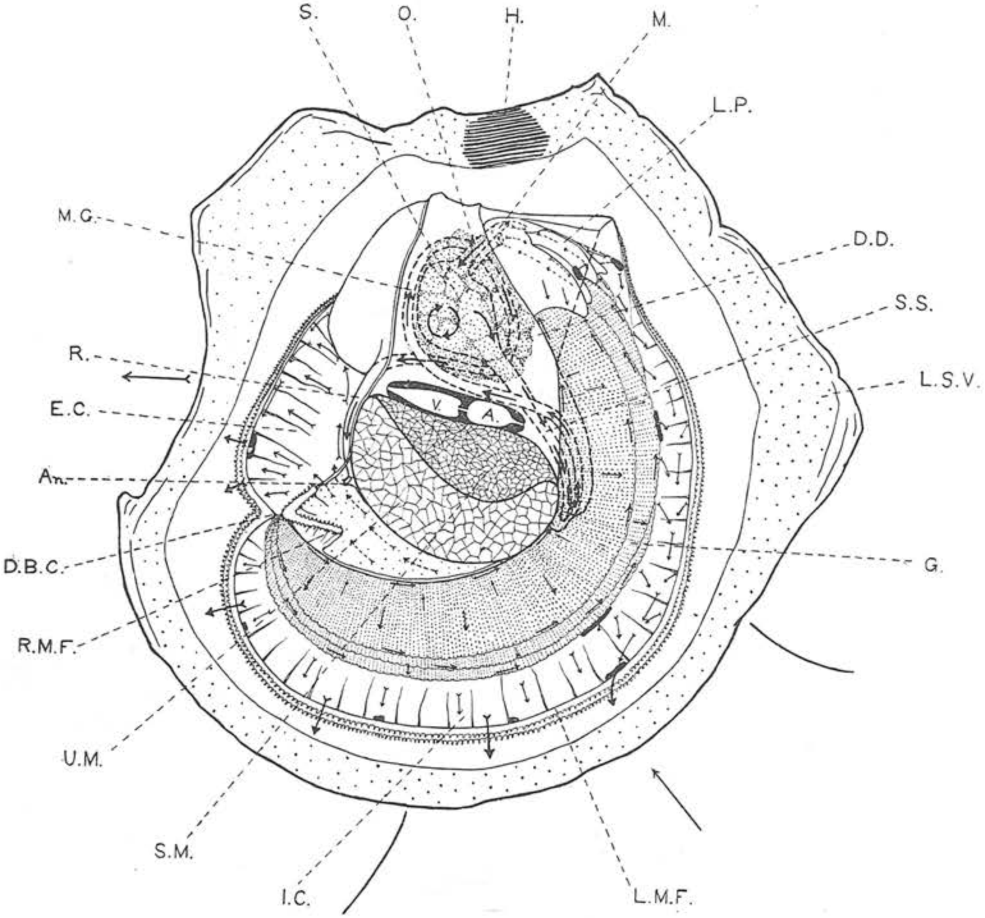

FIG. 1.—*Ostrea edulis*, right shell valve and mantle fold removed. × 1. A., auricle; An., anus; D.B.C., division between inhalent and exhalent chambers; D.D., digestive diverticula; E.C., exhalent chamber; G., gills; H., hinge; I.C., inhalent chamber; L.M.F., left mantle fold; L.P., labial palps; L.S.V., left shell valve; M., mouth; M.G., mid-gut; O., œsophagus; R., rectum; R.M.F., right mantle fold; S., stomach; S.M., adductor muscle, portion with striated fibres; S.S., style-sac; U.M., adductor muscle, portion with smooth fibres; V., ventricle. Large arrows external to shell denote direction of ingoing and outgoing currents, within shell plain arrows denote direction of ingoing currents and feathered arrows direction of outgoing currents, broken arrows (except in gut) denote currents on under surfaces.

diverticula (D.D.), while internally the walls are thrown into a series of ridges and folds so that the exact shape of the stomach in the living animal is difficult to determine when it is opened for inspection. In order to obtain a clear idea of the anatomy, casts of the stomach were made by injecting, by way of the œsophagus, a warm, concentrated solution of gelatin. This was allowed to cool and solidify, the tissues were then dissected away, and the cast hardened in formalin and stained lightly with hæmatoxylin. Gutheil (1912) used plaster for making casts of the stomach of Anodonta, but I have found the gelatin method much more satisfactory, and by its use have been able to demonstrate in detail the anatomy of the stomach—a much more complex and important organ in the Lamellibranchs than it has usually been considered—and its associated organs. Figs. 3 and 4 are drawings of a cast, the former from the ventral aspect and the latter from the dorsal aspect. The most conspicuous structure in the stomach is the long, grooved food sorting cæcum (F.C.), which extends backwards beneath the floor of the stomach, and is connected

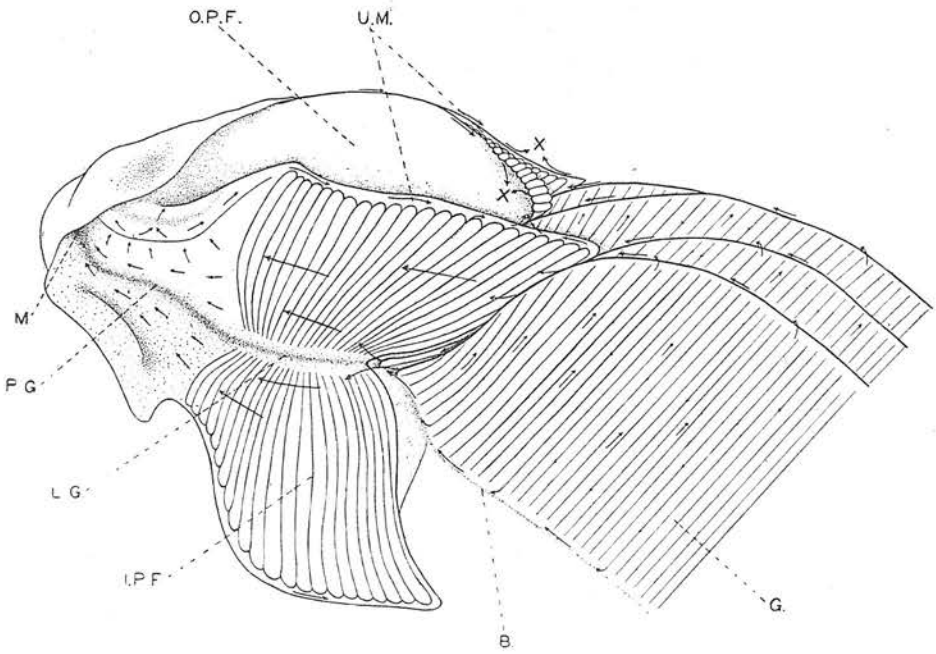

Fig. 2.—Junction of palps and gills, right palps opened out so as to expose inner, ridged surfaces. × 8. B., base of gill demibranch; G., gill; I.P.F., inner palp face; L.G., lateral oral groove; M., mouth; O.P.F., outer palp face; P.G., proximal oral groove; U.M., upper margin of palps; X., point where material is rejected from palps.

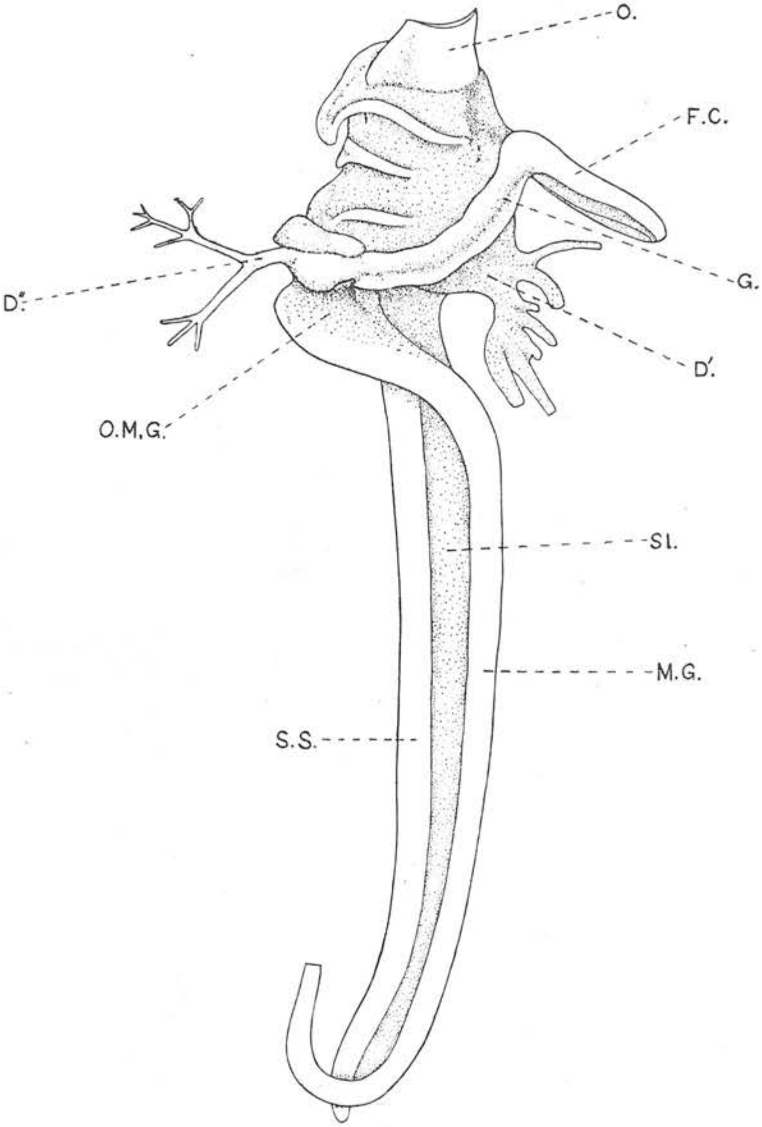

FIG. 3.—Gelatin cast of stomach with style-sac and first part of mid-gut and portion of œsophagus, from ventral aspect. × 4. D′., larger, left duct of digestive diverticula; D″., smaller, right duct of same; F.C., food sorting cæcum; G., ventral groove; M.G., mid-gut; O., œsophagus; O.M.G., opening of mid-gut; S.S., style-sac; Sl., slit connecting mid-gut and style-sac.

with the opening of the mid-gut (O.M.G.) by means of a deep groove (G.), which runs across the floor of the stomach. On opposite sides open the two ducts which lead into the digestive diverticula, that on the left side (D′.) being the larger and dividing into a greater number of smaller ducts than the one on the right (D″.). On the dorsal wall of the stomach is borne the gastric shield (G.S.), a cuticular structure of somewhat irregular shape (see Fig. 5) consisting of two broad lobes united by a narrow neck, the larger of the lobes being thin and smooth, while the smaller is thicker and bears a number of teeth, which are also shown in Fig. 4. It is against this shield that the crystalline style bears, and the dotted line in Fig. 4 shows the position of the style as it projects into the stomach from the style-sac (S.S.), and bears against the gastric shield on the opposite wall. The cavities of the style-sac and mid-gut are united by a narrow slit (Sl.), and pass downwards and slightly forwards from the stomach, as shown in Fig. 1.

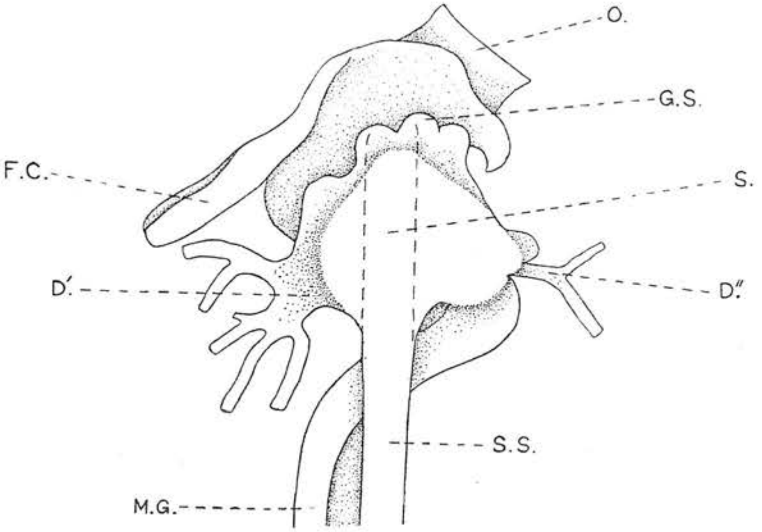

FIG. 4.—Stomach cast from dorsal aspect. × 4. G.S., gastric shield S., style. Other lettering as in Fig. 3.

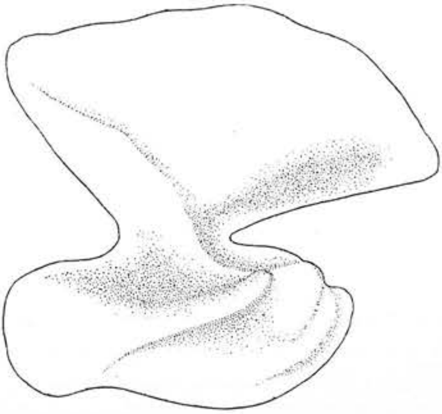

FIG. 5.—Gastric shield. × 20.

The style-sac is practically straight but the mid-gut, which opens into the stomach on the right side of the style-sac (Figs. 3 and 4), twists round to the left side immediately behind. At the distal end of the style-sac, the gut turns anteriorly and then completely back on its course, subsequently passing dorsal to the heart (Fig. 1, A. and V.) and encircling the stomach on the left side. Finally, it passes into the rectum (R.), which runs round the posterior margin of the adductor muscle (U.M.), and ends at the anus (A.), which lies at the tip of a small papilla on the posterior ventral surface of the muscle, and opens into the exhalent chamber.

II. HISTOLOGY.

Material for histological examination was fixed in Bouin's fluid or in Flemming's strong fluid, sections were cut 6μ thick, unless otherwise stated, and were stained with Delafield's hæmatoxylin and erythrosin; or with iron hæmatoxylin either with acid fuchsin as counterstain or with mucicarmine for the demonstration of mucus glands; or with alum carmine and picro-nigrosin.

(a) *Gills.*

An excellent account of the gills of *Ostrea edulis* has been given by Ridewood (1903), the substance of whose statements is as follows: "There are 9–12 filaments to the plica. The front of the principal filament has the form of a broad ridge. The filaments adjacent to the principal filament are slightly larger than usual, and have been called *transitional filaments* by Kellogg (1892). . . . The interlamellar junctions have the form of septa. At a short distance up, the interlamellar septa occur only in relation with alternate principal filaments, but the order is not absolutely regular. Higher up still each fourth septum only persists. The bars which run across the floor of the suprabranchial cavity from descending to ascending lamella are the thickened upper edges of alternate high septa. They recur at intervals of about eight plicæ. Most of the interfilamentar junctions are bands of tissue running horizontally round the inner surface of the plica, but each third or fourth in a vertical series extends across the plica as a horizontal septum. . . . The frontal and lateral cilia are normal. There are short cilia on the interlamellar edges of the principal filaments. No intrafilamentar septum is present. There is a fair amount of muscle in the interfilamentar junctions and in the inner edge of the horizontal septa. . . ."

Many of the characteristics of the gill of Ostrea given by Ridewood, and also other points which he does not emphasize but which are of importance functionally, are shown in Fig. 6, which represents a transverse section through a single lamella (i.e. one side only of a complete demibranch). A principal filament (P.F.) is figured with four filaments on either side, all being united by an interfilamentar junction (I.). (For the structure of the interlamellar junctions and the horizontal interfilamentar septa, reference must be made to Ridewood's figure.) The large size of the principal filament and the thickness of the chitinous supporting rods (C.R.) within it and the two transitional filaments (T.F.) one on either side of it are well marked. There are many strands of horizontal muscle (H.M.) in the interfilamentar junction and also a slight development (not mentioned by Ridewood) of vertical muscle (V.M.) in the principal filament. The abfrontal cilia (A.F.C.) noted by Ridewood are shown in the figure, and also the lateral (L.C.), frontal (F.C.), and laterofrontal (L.F.C.) cilia. The latter are not well developed in Ostrea and are difficult to distinguish in sections, but are easily seen in fresh material (see Fig. 21, p. 323). Mucus glands (M.G.) occur in the epithelium of the filaments, particularly in the frontal region. Wandering blood cells (P.) are present in large numbers within the filaments and the interfilamentar junctions, and are also frequently to be found actually between the cells of the epithelium. These cells, as will be shown later, are phagocytic, and will be referred to as phagocytes in the remainder of this account.

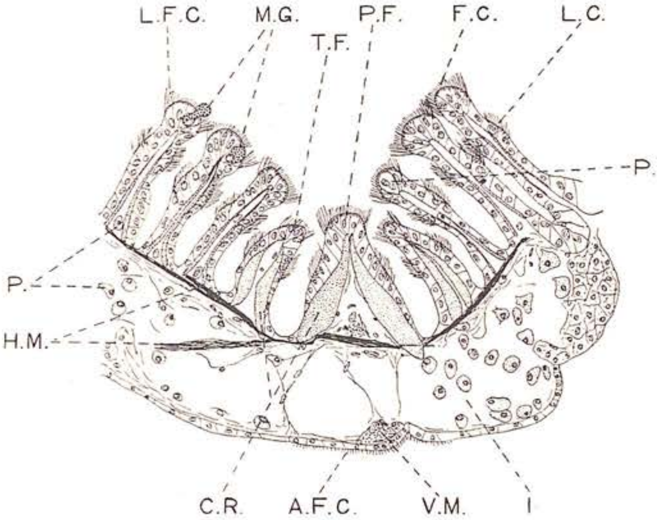

FIG. 6.—Transverse section single gill lamella through groove between plicæ. Delafield's hæmatoxylin and erythrosin. × 220. A.F.C., abfrontal cilia; C.R., chitinous supporting rod; F.C., frontal cilia; H.M., horizontal muscle; I., interfilamentar junction; L.C., lateral cilia; L.F.C., laterofrontal cilia; M.G., mucus glands; P., phagocytes; P.F., principal filament; T.F., transitional filament; V.M., vertical muscle.

Along the free, lower margins of the demibranchs and along their axes there are ciliated grooves.

(*b*) *Palps.*

The folds on the inner palp surfaces arise near the attached base of the palps, and run across the face to the upper free margin, gradually increasing in height and breadth. In cross section (Fig. 7) they are seen to bend forward slightly on the proximal side (i.e. in the direction of the mouth), a tendency which is most pronounced near the free margin.

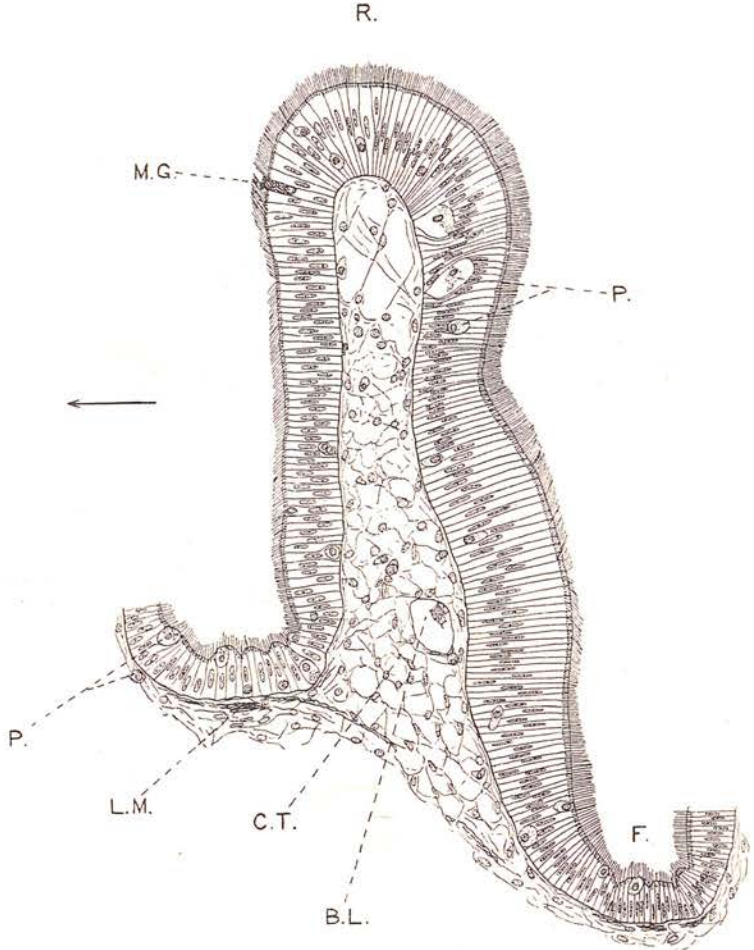

FIG. 7.—Transverse section through fold on inner palp face. Delafield's hæmatoxylin and erythrosin. × 330. B.L., blood lacuna; C.T., connective tissue; F., furrow between ridges; L.M., longitudinal muscle; M.G., mucus gland; P., phagocytes; R. summit of ridge. Arrow indicates direction of mouth.

The proximal wall of the folds is comparatively straight, but on the distal wall there is a well-developed longitudinal groove about one-third of the distance between the summit of the fold (R.) and the furrow (F.), which lies between adjacent folds. The epithelium of the folds is composed of long, regular cells with oval nuclei and bearing a thick covering of long cilia. These cilia, as can be seen by the directions in which they lie in the sections, do not all beat in the same direction. It is, however, impossible to distinguish all the different tracts except in the living tissue, an account of which is given in a later section. Unicellular mucus glands (M.G.) of the goblet type are present, almost exclusively near the summits of the folds. Siebert (1913) has also found sense cells in the epithelium of the palps in Anodonta. Between the epithelial cells are many phagocytes (P.), which are also present in the connective tissue and blood lacunæ (B.L.), some of them containing yellow or brown granules. The connective tissue is very open in character, consisting of a network of fine strands. There are longitudinal muscle fibres (L.M.) under the epithelium of the furrows, and running through the connective tissue at the base of the ridges. There are also occasional fibres running across to the smooth surface of the palp, and a feeble development of circular muscle immediately beneath the epithelium of the furrows. It is important to note that there are *no muscles within the folds* such as could cause it to contract downwards.

The epithelium of the smooth surface of the palps (Fig. 8) is very different. The cells are lower and more irregular, cilia are present but often difficult to distinguish in sections, so that some workers have denied their presence. I have often seen them in my sections of Ostrea, while experiments on the living palp demonstrate immediately their presence. Mucus glands of the usual type are extremely numerous. The contents of these cells may be granular, and stain darkly with iron hæmatoxylin or contain a mass of swollen granules or spheres which stain lightly with mucicarmine. Since intermediate stages between these two types are frequently found (this applies wherever mucus cells are found, from the mantle to the rectum), it seems probable that the granules represent an early

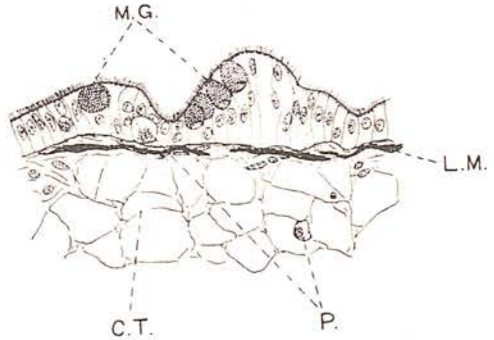

FIG. 8.—Transverse section epithelium of smooth, outer palp face. Delafield's hæmatoxylin and erythrosin. × 330. Lettering as in Fig. 7.

stage in the elaboration of the secretion. The glands invariably stain deeply with erythrosin, and have a great affinity for many stains. Beneath the basement membrane there is a well-developed layer of longitudinal muscle (L.M.). There is the usual network of connective tissue (C.T.) with darkly staining nuclei among which are many phagocytes (P.), which may also penetrate into the epithelium.

(c) *Mouth and Œsophagus.*

The epithelium of the mouth is a continuation of that of the grooves between the palps and consists of extremely long, thin cells, about four times the height of those on the folded surface of the palps. Long cilia are borne by the cells, mucus glands occur but not in large numbers, while phagocytes are present in great abundance.

The œsophagus (Fig. 9) is exceptionally large in the oyster and much compressed dorso-ventrally. The epithelium consists of narrow cells of much the same height as those of the mouth region, but with cilia of only about a third the length. Phagocytes are very numerous between the cells of the epithelium and also *free in the lumen* (P.), sometimes with ingested matter. Mucus glands are here very rare, but Gutheil (1912) has described and figured what he considers to be secretory cells in the œsophagus of *Anodonta cellensis* and similar cells can be distinguished in Ostrea. They stain more lightly and have rather more vacuolated protoplasm than the neighbouring cells, and have, in addition, no cilia. On the other hand, their nuclei are identical with those of the ciliated cells, and there is really very little evidence that they are secretory cells ; it seems more probable that they are damaged or degenerating epithelial cells. Particles are continually passing over the epithelium, which must suffer in the process, and it is quite common, moreover, to

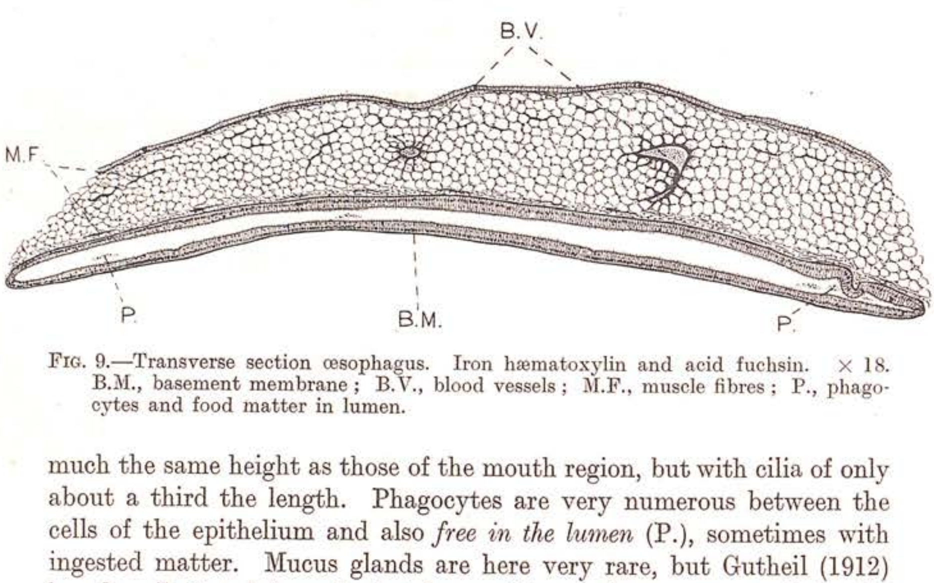

FIG. 9.—Transverse section œsophagus. Iron hæmatoxylin and acid fuchsin. × 18. B.M., basement membrane ; B.V., blood vessels ; M.F., muscle fibres ; P., phagocytes and food matter in lumen.

find dividing nuclei near the free surface of the epithelium. An exceptionally thick basement membrane (B.M.), through which phagocytes pass, surrounds the epithelium, and outside this there are thin strands of circular and longitudinal muscle fibres (M.F.). Muscle strands also occur in the vesicular connective tissue in which the œsophagus is embedded and which contains large blood-vessels (B.V.), in and out of which the phagocytes pass.

(*d*) *Stomach.*

The epithelium of the stomach is of two kinds, that composed of typical ciliated cells, which covers the greater part of the surface, and that which lies beneath the gastric shield. Fig. 10 represents a section through the junction between the two. The ciliated epithelium consists of narrow cells, a little higher than those of the œsophagus and possessing longer cilia. The border cuticle (B.C.) is particularly well developed here, consisting (as in all the ciliated cells) of a clear cuticular layer distal to the line of basal granules, from which the cilia arise. The distinct nature of this layer is not shown by the usual staining methods, but after staining with Prenant's three-colour process (iron hæmatoxylin, erythrosin, and light green) the border cuticle is stained by the light green and the cytoplasm by the erythrosin. Mucus glands (M.G.) are occasionally found; phagocytes (P.) are very abundant in the connective tissue, basement membrane, between the cells of the epithelium and free in the lumen.

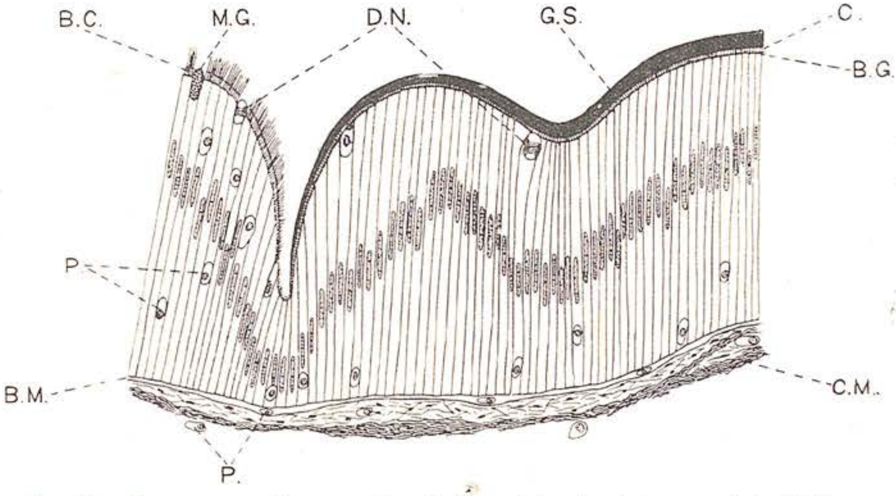

FIG. 10.—Transverse section stomach epithelium at junction between gastric shield area and ciliated epithelium. × 425. B.C., border cuticle; B.G., basal granules; B.M., basement membrane; C., cilia-like strands between edge of cells and gastric shield; C.M., circular muscle; D.N., dividing nuclei of epithelial cells; G.S., gastric shield: M.G., mucus gland; P. phagocytes.

Dividing nuclei (D.N.) of epithelial cells are frequently seen, the nuclei passing to the surface of the cells in the manner characteristic of the dividing nuclei of ciliated cells (see Ehrhard (1910), and particularly Gutheil (1911), who has described and figured in detail the process of mitosis). There is a fairly thick basement membrane (B.M.), and, beneath that, strands of muscle (C.M.) the whole being surrounded by vesicular connective tissue in which lie embedded the tubules of the digestive diverticula.

The epithelium which lies beneath the gastric shield resembles closely that of the rest of the stomach. Mucus glands are never present, and phagocytes, though invariably present, occasionally even in the substance of the gastric shield, are not so numerous. Dividing nuclei are frequent. The gastric shield (G.S.) in cross section appears as a homogeneous substance composed of indistinct horizontal strata. It stains vividly with light green, moderately deeply with erythrosin (except in Prenant's stain) and very lightly with mucicarmine. Gutheil considers that it is formed by droplets of secretion from the cells beneath, and this has been the general view with regard to its formation. In my sections, however, I have failed to find any evidence of secretion from the cells, while the substance of the shield is united to the epithelium by fine strands having the appearance of cilia (C.) and arising from basal granules (B.G.) at the edge of the cells, as shown in Fig. 10. It is possible in certain places to observe the continuation of the strands transversely through the whole substance of the shield, while, as we have seen, the shield takes up light green in the same way as the border cuticle. In view of these facts and also that the cells of the gastric shield area are in no way different from those of the rest of the epithelium with regard to either nucleus or cytoplasm, it seems very probable that the gastric shield is *not* a secretion, but is formed by the fusion of cilia, originally in response to the irritation caused by the head of the style. Nelson (1918) thinks the shield is probably in the nature of chondrin, which would appear to support this view.

(e) *Digestive Diverticula.*

These consist of a brownish mass of blind tubules which surround the stomach. They have been called " liver " and " hepatopancreas," but, as I have emphasized in a recent paper (1926) to which reference should be made for a detailed account of the structure and function of these organs, they are organs of assimilation and of intracellular digestion with none of the functions of a true liver or pancreas, and I suggested, therefore, that they are more suitably termed digestive diverticula.

They communicate with the stomach by way of two large ducts (Figs. 3 and 4, D′. D″.). These ducts are quite distinct in structure from the tubules with which they communicate. They are usually circular in cross section, though the lumen is irregular owing to the variation in height of the epithelium, which is similar to that of the stomach of which it is a direct continuation. Cilia are always present, the protoplasm is not vacuolated and stains darkly with erythrosin. Mucus glands are present and also phagocytes in large numbers, both in the epithelium and in the lumen. There is a layer of circular muscle beneath the basement membrane.

The tubules (Fig. 11) are quite different. Cilia are never present in sections nor can a border cuticle be distinguished as in the case of some Lamellibranchs, and the outline of the cells is frequently very irregular. The tubules are surrounded by a few strands of connective tissue (C.T.), but muscle is *never* present. The nuclei are very characteristic, being circular and possessing a large nucleolus. In cross section the lumen is usually tripartite or in the form of a cross, and in the crypts (C.) at the

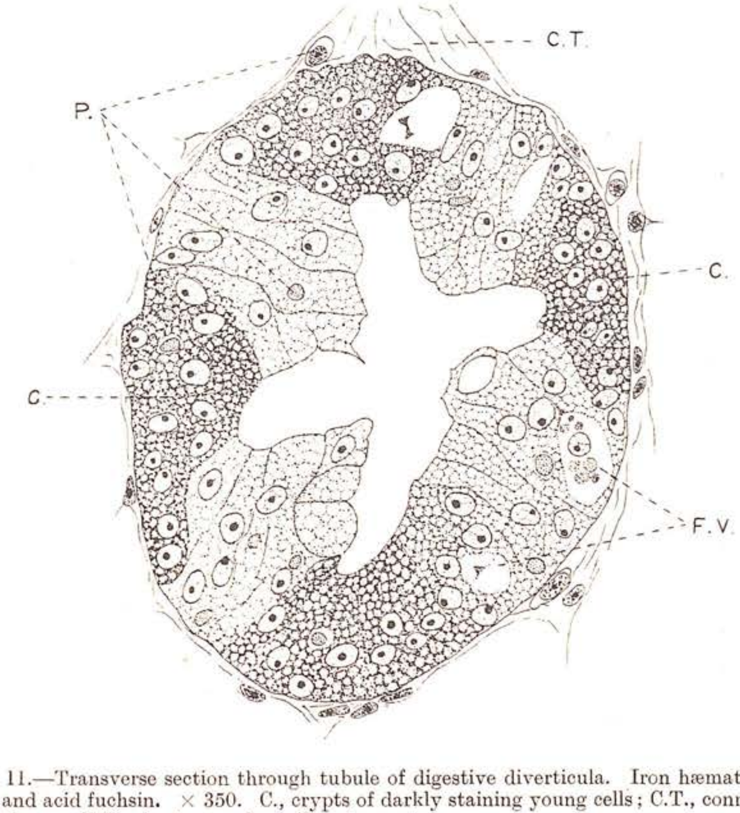

FIG. 11.—Transverse section through tubule of digestive diverticula. Iron hæmatoxylin and acid fuchsin. × 350. C., crypts of darkly staining young cells; C.T., connective tissue; F.V., food vacuoles; P., phagocytes.

end of the arms are low areas of darkly staining protoplasm with many nuclei, the outline of the cells being very indistinct. The remaining cells are larger, very vacuolated, and consequently more lightly staining. As I have pointed out (1926) there is every reason, " From the histological character, the distribution, and the behaviour of these small dark cells . . . for considering them young cells which, by dividing, are able to make good the loss resulting from the casting off of the old cells." Large vacuoles (F.V.), sometimes with ingested food material which stains with erythrosin, are frequently found in the older cells, while phagocytes occur everywhere. There is never any indication of secretion.

As already noted, cilia are never to be seen in sections (similar observations have been made on Ostrea by Carazzi (1896, 1897), MacMunn (1900), and Vonk (1924)), nor have I observed them in fresh material; but in many Lamellibranchs (though never possible to see more than a border cuticle in sections), it is possible to see long cilia beating in the tubules when fresh material is examined, as Potts (1923) and I (1926) have shown. As will be shown later, there is a constant stream of food particles passing into the diverticula and of rejected particles passing out, and as there is no system of circular and longitudinal muscles such as ensures a similar circulation in the Crustacea (in which the diverticula are organs of both assimilation and secretion), there is strong presumptive evidence that cilia are present in the tubules of *all* Lamellibranchs. In many cases, including Ostrea, these cilia appear to be retracted very readily, and so cannot be seen when the tissue is pressed out under a coverslip for examination.

The tubules are embedded in vesicular connective tissue, in which lie many phagocytes often containing included granules, which frequently, as MacMunn (1900) has described and figured, take the form of brown or yellow spheres, which often are blackened by osmic acid after fixation with Flemming. The nature of the pigment will be discussed in the section on Assimilation (p. 340).

(*f*) *Style-Sac.*

Except for a short diverticulum where it arises (see Fig. 3), the style-sac is united for its entire length with the mid-gut. The two cavities (Fig. 12) are separated by two typhlosoles which, however, are not so well marked as in such genera as Anodonta (Nelson, 1918) or Crepidula (Mackintosh, 1925). The epithelium of the gut is quite distinct from that of the style-sac, and will be described later. The epithelium of the style-sac (Fig. 13) is very characteristic, consisting of cells of medium height, very regularly arranged, with large oval nuclei and long, stout cilia all of the same length. The structure of the style-sac in *Crepidula fornicata* (which, although a Gastropod, has a style and style-bearing organs of exactly the same nature as those of the Lamellibranchs) has been investigated in detail by Mackintosh (1925). He has shown that the cilia are continued into the cell where they form an " internal fibrillar apparatus," the fibres of which are greatly thickened below the nucleus, so as to form " a bundle of thick rod-like bodies." I have observed the same arrangement in Ostrea (Fig. 13, I.F.), the fibres showing very clearly after staining with iron hæmatoxylin (though whether or no they really represent fibres in the living tissue cannot be stated). Mackintosh has also demonstrated the presence of a series of " intra-epithelial " canals, which appear in transverse sections near the base of the cells, and are filled with a very lightly staining, stringy substance. A similar state of affairs exists in Ostrea, the canals (I.E.C.) appearing to pass through and not between the cells, though it is difficult to be certain. Mackintosh has further shown that the larger canals extend longitudinally down the style-sac, and are connected with one another by smaller canals, and this appears also to be the case in Ostrea. Judging by their staining reactions, he is of the opinion that the contents are of the nature of connective tissue fibres, and considers that the function of the whole apparatus is to lend extra strength to the epithelium, which bears a considerable strain in revolving and pushing forward the style. The epithelium of the larger typhlosole (T′. Fig. 12), which corresponds to the *minor* typhlosole

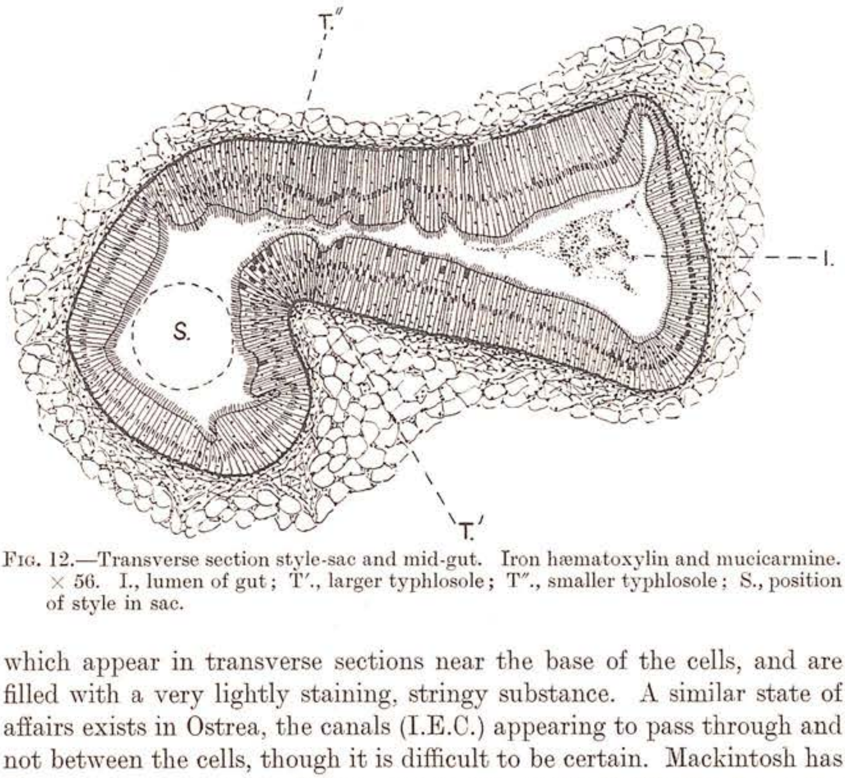

FIG. 12.—Transverse section style-sac and mid-gut. Iron hæmatoxylin and mucicarmine. × 56. I., lumen of gut; T′., larger typhlosole; T″., smaller typhlosole; S., position of style in sac.

of Anodonta and Crepidula, or the *right* typhlosole of Mya as described by Edmondson (1920), consists of long, very narrow cells with cilia a little shorter than those of the groove. Mucus glands are very numerous in this region and also occur in the other typhlosole (T″.)—which is covered with long cells which gradually merge into the epithelium of the mid-gut—but never in the epithelium of the style-sac. The intra-epithelial canals also occur in the typhlosoles, but in decreasing numbers as these merge into the epithelium of the gut. Phagocytes occur everywhere, though they are not so numerous in the epithelium of the style-sac as they are in that of the typhlosoles, in which they are exceptionally numerous. The whole is surrounded by a few strands of muscle, the typhlosoles being filled in with vesicular connective tissue of the usual type.

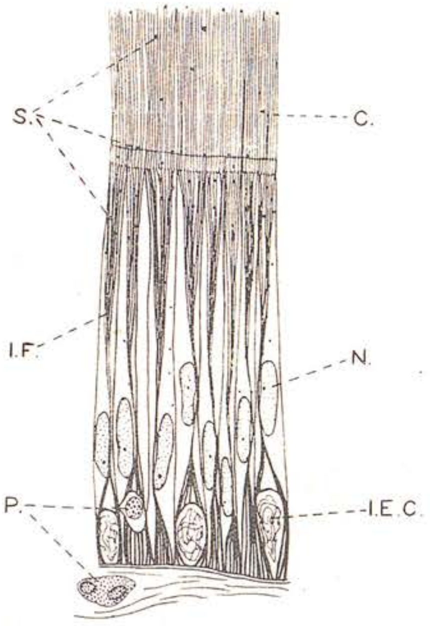

FIG. 13.—Transverse section epithelium of style-sac. Iron hæmatoxylin and acid fuchsin, secretion granules demonstrated by iron technique. × 900. C., long cilia of epithelium; I.E.C., intra-epithelial canals; I.F., internal fibrillar apparatus; N., nuclei of epithelial cells; P., phagocytes; S., droplets of secretion containing iron in solution.

It is very difficult to determine where and how the substance of the style is secreted. List (1902), Nelson (1918), Edmondson, and Mackintosh all think that it is secreted by the narrow cells of the minor typhlosole, but they have been unable to produce definite evidence. Gutheil describes and figures clear vesicular granules above the nuclei in the cells of the style-sac. In Ostrea, sections prepared for histological examination showed no sign of any secretion. It has been shown (1926) that the presence of minute droplets of secretion containing iron in solution can be demonstrated in the style-sac epithelium of *Mytilus edulis* four hours after a 0·5% solution of iron saccharate in sea-water has been injected by way of the foot. This method of demonstrating the presence of secretory cells has been employed with success for Crustacea, Insecta, and Gastropoda (for full details and literature see my papers (1924, 1926)). I have employed the same methods with Ostrea, injecting the same solution by way of the adductor muscle, afterwards washing the animals so as to prevent any of the fluid entering the mouth. The style-sac was fixed (by the methods described in the section on assimilation) two, four, and six hours later, and sections prepared which were treated so as to demonstrate the presence of iron by the Prussian blue method, the sections being stained with alum carmine. In the style-sac of the animal which had been fixed four hours after injection, it was easily possible to distinguish fine blue granules in the cytoplasm above the nuclei and in the process of being passed into the lumen. The position of the granules is indicated in Fig. 13 (the internal fibrillæ do not appear after staining with alum carmine, but were drawn from sections stained with iron hæmatoxylin). There was *no trace of similar granules in the epithelium of the gut*, nor could I determine their presence with certainty in the narrow cells of the larger typhlosole though they are present in the cells of the other typhlosole so long as they retain the character of the style-sac epithelium. In view of the presence of these granules, it seems probable that Gutheil is correct, and that the substance of the style is secreted by the cells of the groove and not of the larger typhlosole, and that it is then revolved by the cilia of the style-sac, so that, as Edmondson has shown in his experiments on the regeneration of the style in Mya, it comes to lie against the larger typhlosole the cilia of which have a different function, as will be described in the section on ciliary currents.

The style during life lies in the groove of the style-sac, as indicated by the broken circle in Fig. 12. It is a gelatinous rod, whose structure has been described too often for further detailed description to be necessary. In the oyster the central core is very fluid and flows freely to and fro, the outer portion being firmer and consisting of co-axial layers. The style is seldom white, usually yellowish or brown, but the colour depends on the nature of the food, as in all cases where the style-sac is in communication with the mid-gut. Spirochætes of the genus Cristispira are very numerous, particularly in the outer layers, and are able to move about freely in the substance of the style.

(*g*) *Mid-Gut.*

This region (Fig. 14) is characterised in cross section by the possession of a large typhlosole with a groove down the centre. The cells of the epithelium are invariably ciliated, mucus glands are present, but not in large numbers, while there is a complete absence of muscle around the epithelium, which is bounded by a broad basement membrane. Phagocytes are very plentiful both in and around the epithelium, and in the lumen, where they are to be seen lying among the food particles and mucus therein contained, particularly in the groove of the typhlosole.

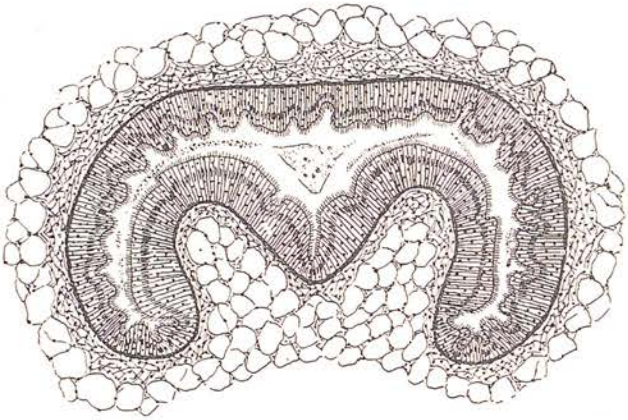

FIG. 14.—Transverse section mid-gut. Iron hæmatoxylin and acid fuchsin. Round dots in epithelium indicate phagocytes, dark masses indicate mucus glands. × 56.

(*h*) *Rectum.*

The rectum (Fig. 15) is practically circular in cross section, the lumen being larger than that of the mid-gut. The typhlosole is here thrown into more prominent folds, and the central groove is practically obliterated, owing to the coming together of the two halves of the typhlo-

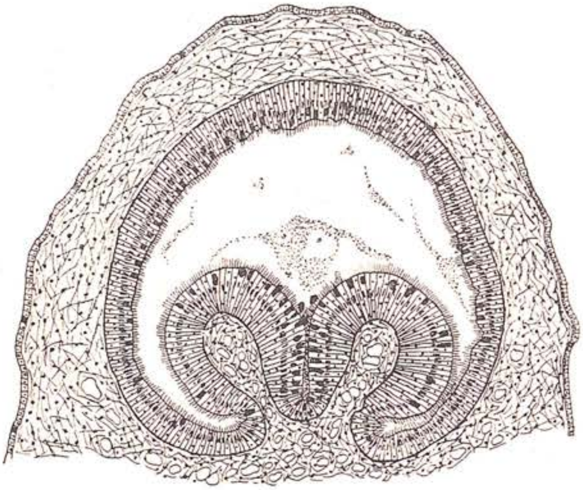

FIG. 15.—Transverse section rectum. Delafield's hæmatoxylin and erythrosin. Great numbers of mucus glands in epithelium. × 56.

sole. Mucus cells are extremely numerous, more so than in any other region of the alimentary canal (the same is true for *Mya arenaria* (Yonge (1923)). All the other cells of the epithelium are ciliated, phagocytes are very plentiful everywhere; there is no surrounding muscle, while the basement membrane is thinner than that of the mid-gut. The surrounding connective tissue is more compact than in any other region of the gut. In the lumen are found food particles, or excreta, mucus, and phagocytes.

(*i*) *The Phagocytes.*

As will have been noted from the foregoing account, one of the most striking features about the gills, palps, and entire alimentary tract is the universal presence of wandering phagocytic cells. They are always easy to distinguish because their nuclei, unlike those of the epithelial cells which are oval and lightly staining, are small, spherical and contain a great number of fine granules of chromatin, which stain darkly with hæmatoxylin. The cytoplasm of the phagocytes stains lightly with erythrosin. No less than seven different types of blood cells in the Lamellibranchs have been distinguished by de Bruyne (1896), but it is doubtful how many of these represent different stages in the same type. In this paper no attempt is made to divide the phagocytes into different types, although further work on the subject is contemplated.

The presence of these phagocytes is characteristic of the Lamellibranchs (with the possible exception of the Septibranchs), and attention has been drawn to their presence by many workers, although their great importance in the physiology of digestion in these animals has not always been recognised. Lankester (1886, 1893) seems to have been the first to note the presence of the phagocytes in the gills of green oysters; de Bruyne (1893, 1896) gave a long account of the wandering of phagocytic cells into the epithelium of the gills and mantle in a number of Lamellibranchs; Herdman and Boyce (1899) gave a full account of their activities, especially in connection with green leucocytosis in the American oyster; List (1902) noted their presence in and around the gut in the Mytilidæ; Gutheil (1912) gives a full account of their occurrence throughout the alimentary tract of Anodonta and in the connective tissue and blood-vessels, and he also observed them dividing amitotically in the region of the gut; Matthias (1914) observed the presence of great numbers of phagocytes in the ventral portion of the stomach of *Arca barbata;* Orton (1923) has noted their great numbers and widespread distribution throughout the tissues, and particularly round the gut, of *Ostrea edulis;* I have myself (1923, 1926) observed and figured them in the gut of Mya, and in connection with the digestive diverticula in the same animal and in Nucula, Cardium, and Teredo.

In the oyster they are abundant everywhere, and appear to pass freely through the tissues. Fig. 16 represents a blood-vessel from the region of the œsophagus (it is an enlarged drawing of the smaller blood-vessel shown in Fig. 9). In the lumen can be seen a mass of blood cells, which have probably come together as a result of fixation. Similar cells can be seen passing through the wall of the vessel, though it is impossible in this region to distinguish more than the characteristic nuclei ; the nuclei of the connective tissue which forms the wall of the blood-vessel are usually smaller, spindle-shaped, and stain intensely black. There can

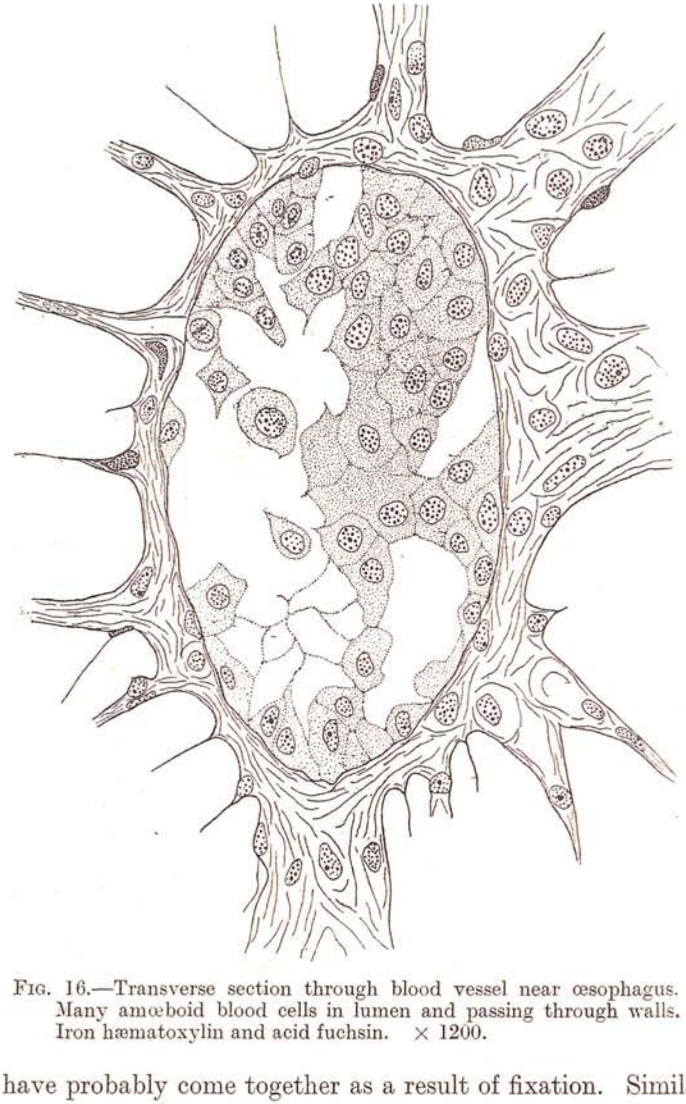

FIG. 16.—Transverse section through blood vessel near œsophagus. Many amœboid blood cells in lumen and passing through walls. Iron hæmatoxylin and acid fuchsin. × 1200.

be no doubt that the cells are amœboid, and have the power of wandering at will through the tissues and in and out of the lumens of the gut and of the blood-vessels. An account of the very important part they play in the assimilation of food will be given in the appropriate section.

B. LARVAL OYSTERS.

The development and structure of the larvæ of *Ostrea edulis* have been described in detail by Horst (1886), while Stafford (1913) has given an account of the developmental stages in the American oyster, *Ostrea virginica*, with a summary of the previous work on both species. Here it is necessary only to describe the alimentary organs of the veliger larvæ of *Ostrea edulis*. Fig. 17 represents such a larva, the dimensions of whose shell were 0·2×0·165 mm., drawn from life so as to show the alimentary organs. The velum (V.), which is protruded—when retracted the organs

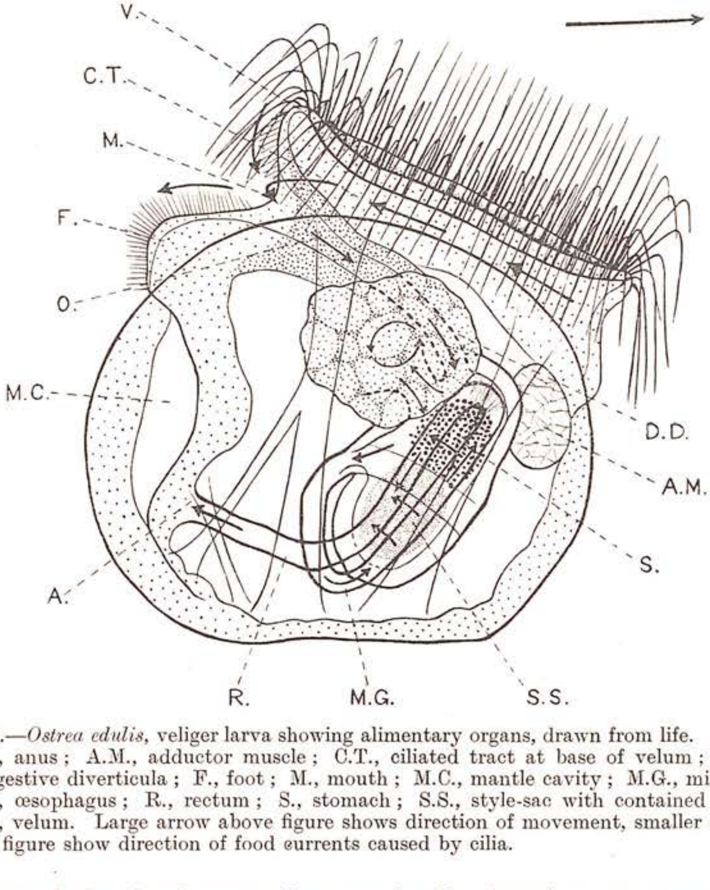

FIG. 17.—*Ostrea edulis*, veliger larva showing alimentary organs, drawn from life. × 330. A., anus; A.M., adductor muscle; C.T., ciliated tract at base of velum; D.D., digestive diverticula; F., foot; M., mouth; M.C., mantle cavity; M.G., mid-gut; O., œsophagus; R., rectum; S., stomach; S.S., style-sac with contained style; V., velum. Large arrow above figure shows direction of movement, smaller arrows in figure show direction of food currents caused by cilia.

are tightly packed together and difficult to distinguish—is crowned with extremely long cilia, while there are smaller cilia round the base. The mouth (M.) lies behind the velum, between it and the rudiments of the foot (F.). It is a wide, funnel-shaped orifice which leads into an œsophagus (O.), whose thick walls are pigmented. This passes forwards and downwards in the middle line and opens into the head of the stomach (S.), an oval-shaped organ divided by an annular thickening of the wall from the style-sac (S.S.). On the posterior wall of the stomach open the two simple lobes of the digestive diverticula (D.D.), which are arranged symmetrically one on either side, their more ventral portions overlapping the œsophagus. They are darkly pigmented and even at this stage have the structure of the adult diverticula (see Fig. 42, p. 353). The style-sac contains the style which, though difficult to distinguish normally, can easily be seen if the larvæ are placed for several hours in a very dilute solution of brom thymol blue in sea-water when the substance of the style stains a light yellow, and can be seen revolving rapidly in the stomach. It may be a single oval mass (as represented in Fig. 17), or be composed of from two to four rounded masses. The mid-gut (M.G.) begins on the posterior side of the stomach at the line of its junction with the style-sac, and passes dorsally and then ventrally, describing a loop on the right side of the stomach before turning backwards as the rectum (R.), which ends in the anus (A.) on the dorsal side of the mantle cavity (M.C.). The whole of the gut is lined with large and very active cilia (cilia cannot be seen in sections of the digestive diverticula, but there is evidence that they are present in the living tissue), though in the figure the only cilia shown are the group of extremely large ones on the antero-ventral wall of the stomach. The external dimensions of the various parts of the gut are : œsophagus, 0·02 mm. ; stomach, 0·046 mm. ; mid-gut, 0·012 mm. Sections of the larvæ do not demonstrate any points in the structure of the alimentary system, which cannot be seen in an examination of the living larvæ.

C. "SPAT" OYSTERS.

The structure of the food collecting and digestive organs in recently settled or "spat" oysters, though they quickly come to resemble those of the adult, show many interesting features. Unfortunately, 1925 proved a bad year for spat at Conway, and I was unable to obtain specimens in the act of settling, and so get stages in the metamorphosis from the larval to the adult structure, a process which takes place with great rapidity. The larvæ come to lie on the left valve cementing themselves firmly to the surface by means of a secretion from the byssus gland in the temporarily developed foot. A full account of the metamorphosis of the American oyster has been given by Stafford. Fig. 18 is a

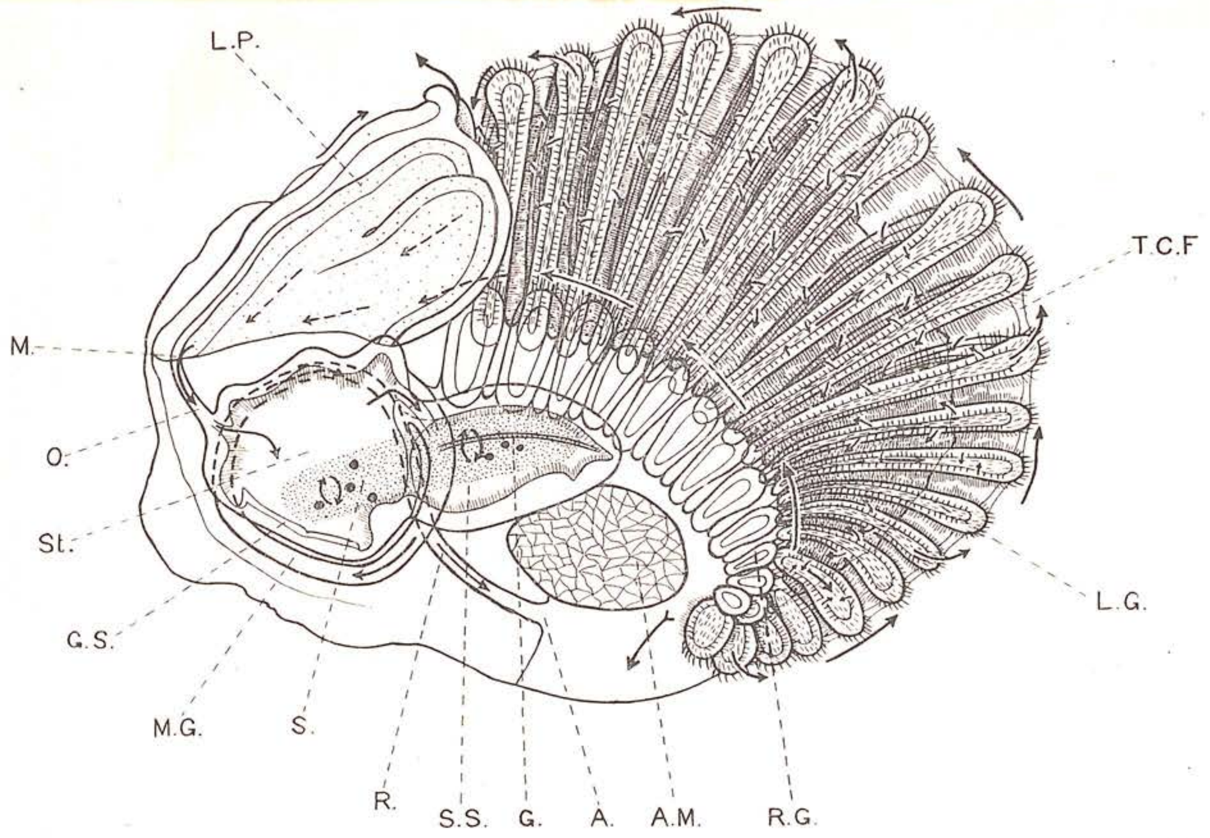

FIG. 18.—*Ostrea edulis*, "spat" shortly after settling, drawn from life after removal of shell (1·2 mm. deep), digestive diverticula not shown. × 155. A., anus; A.M., adductor muscle; G., groove down style-sac; G.S., gastric shield; L.G., left gill; L.P.; labial palps; M., mouth; M.G., mid-gut; O., œsophagus; R., rectum; R.G., right gill; S., style; S.S., style-sac; St., stomach; T.C.F., transparent connections between free ends of filaments. Arrows indicate direction of ciliary currents and movement of style.

drawing of the smallest settled oyster which I obtained, the shell (not figured) measured 1·2 mm. from the umbo to the margin and the body, after removal from the shell and consequent contraction of the mantle folds (i.e. as shown in the figure), 0·59×0·66 mm.

At this stage there is one simple gill on each side which represents the inner demibranch of the adult. There is a marked difference in the degree of development, the lower or left gill (L.G.) being much larger than the upper, right one (R.G.). Moreover, there are twenty filaments present on the left and only thirteen on the right. No firm lamella is formed, the filaments being united solely by thin strands of transparent tissue (T.C.F.) at their free extremities. The ascending and descending portions of the filaments are also unconnected. Lateral, frontal, and laterofrontal cilia are all to be distinguished on the filaments and also large cilia on the free extremities. The labial palps (L.P.) are much larger in proportion to the rest of the body than in the adult. The outer palps are completely united to form a hood which encloses the inner palps, which are united for about half their length. The mouth (M.) leads into a short œsophagus (O.), which opens into the large stomach (St.). Seen from the side this is a somewhat squarish organ with a well-developed gastric shield (G.S.) on the dorsal wall, against which bears the style (S.), which can readily be distinguished as a stout rod in which lie embedded diatoms and other particles. The wall of the stomach is covered with large cilia and so is that of the style-sac (S.S.), which forms a wide tubular diverticulum posterior to the stomach. Along one side of the sac is a narrow groove (G.). The stomach is surrounded by tubules of the digestive diverticula, though these have not been shown in Fig. 18 as they would have obscured the other organs ; they are best studied in sections. On the postero-ventral side of the stomach is the opening of the mid-gut (M.G.), still quite distinct from the style-sac. As in the adult, the gut describes a circle round the left side of the stomach before passing dorsally and backwards as the rectum (R.); the anus (A.) opens into the exhalent chamber on the dorsal side of the adductor muscle (A.M.).

Transverse sections through a slightly larger specimen—the shell was 2 mm. across—are shown in Figs. 19 and 20. The former represents a section through the middle of the stomach. Owing to the direction of the cut, the section has passed transversely through a number of the gill filaments and the disparity in numbers between the filaments of the two sides is again demonstrated. The stomach lumen is practically filled with the style, the dorsal walls—with the exception of the extreme dorsal end—being covered with the gastric shield, the remainder of the wall being thickly ciliated. On the ventral side is the opening of the mid-gut (O.M.G.) ; the gut has been cut twice (M.G.) in its course round the left side of the stomach. On the left wall of the stomach opens one of the ducts (O.D.) of the digestive diverticula, tubules of which (D.D.) are present on all sides of the stomach. Unlike the adult condition, however, the ducts have the same structure as the tubules—i.e. there are no ducts strictly speaking. The tubules are identical in structure with those of the adult, nests of darkly staining young cells lying between the more lightly staining, vacuolated and older cells. The dark masses in the stomach, the opening of the digestive diverticula, and in the lumen of the mid-gut are iron saccharate on which the animal had been fed one day before fixation.

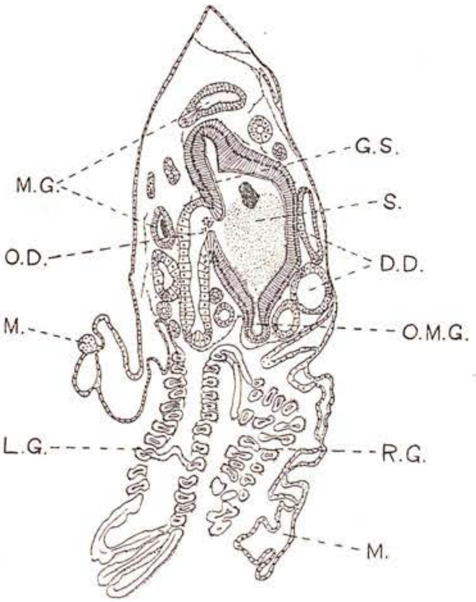

FIG. 19.—Transverse section through 2 mm. spat in region of stomach. Alum carmine. × 80. D.D., digestive diverticula; G.S., gastric shield; L.G., left gill; M., mantle; M.G., mid-gut; O.D., opening of digestive diverticula into stomach; O.M.G., opening of mid-gut into stomach; R.G., right gill; S., style.

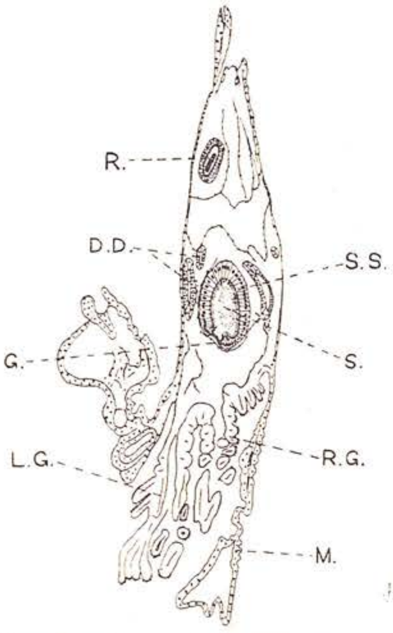

FIG. 20.—Section from same series as Fig. 19, more posterior. × 80. G., groove in style-sac; R., rectum; S.S., style-sac. Other lettering as in Fig. 19.

Fig. 20 represents a section from the same series as Fig. 19, but more posteriorly, the section passing transversely through the style-sac (S.S.), the structure of which is shown clearly. The epithelium consists of large cells, very clearly demarcated, containing large oval nuclei and covered with thick, long cilia. On the ventral side lies the groove (G.), which is formed of extremely low ciliated cells bounded on each side by a group of tall, narrow cells. It is along the line of this groove that the union of style-sac and mid-gut must later take place, and the areas of tall cells are, no doubt, identical with the cells of the future typhlosoles. The lumen of the sac is incompletely filled by the substance of the style (S.). In view of the fact that in Ostrea the style-sac and mid-gut are separate in the larvæ and early stages of the adult, it would be interesting to know whether in species such as *Mya arenaria* in which these structures are also separated in the adult, the separation represents a persistent embryonic condition or is secondary. The structure of the style-sac in the adult Mya would suggest that there has been union between the two and secondary separation. The other points of interest in Fig. 20 are the backward prolongations of the digestive diverticula (D.D.) on either side of the style-sac, and the rectum (R.) which here contains a mass of iron in the lumen.

3. FEEDING. THE COURSE OF THE CILIARY CURRENTS.

The course of the ciliary currents was followed in the intact tissues under the binocular microscope, and in small pieces of excised tissue under the high powers of the monocular microscope.

Carmine and carborundum powder of varying grades were employed to demonstrate the direction of the currents. The literature on this branch of the subject is extensive, and reference has been made to only the most important papers.

A. ADULT.

I. In the Mantle Cavity.

(*a*) *The Gills.*

Although in the oyster the mantle folds are not united except at the point of division between the inhalent and exhalent chambers, the food current is not drawn in along the whole of the inhalent chamber since, as described and figured by Orton (1912), the mantle folds are normally opposed except for the short distance on the ventral surface between the thick lines in Fig. 1. The ingoing current is caused by the action of the lateral cilia on the gills, a fact fully established by the work of Wallengren (1905) and Orton (1912). These cilia cause a strong current of water to pass between the gill filaments from the infrabranchial chamber into the suprabranchial chamber, which is in free communication with the exhalent chamber, as shown by the dotted arrows ventral to the adductor muscle in Fig. 1.

As a result of this current, any particles in suspension in the water will be carried into the inhalent chamber. As soon as the ingoing current has passed through the comparatively narrow inhalent aperture, its speed will be reduced and the largest particles in suspension will drop on to the mantle folds. This may be called the first selection of particles. Smaller particles remaining in suspension will be deposited on the surface of the gill which serves as a very efficient filter, the water passing between the filaments while the particles are stopped by the action of the laterofrontal cilia (Fig. 21, L.F.C.), which lie at the edges of the filaments, so that those of adjacent filaments interlock, while at the same time they beat across the surface of the filament, and so throw particles on to the frontal surface. Fig. 21, which represents several filaments pulled apart, shows these cilia very clearly and also the lateral cilia (L.C.) beneath. On account of their consecutive beat, these cilia appear to beat up the

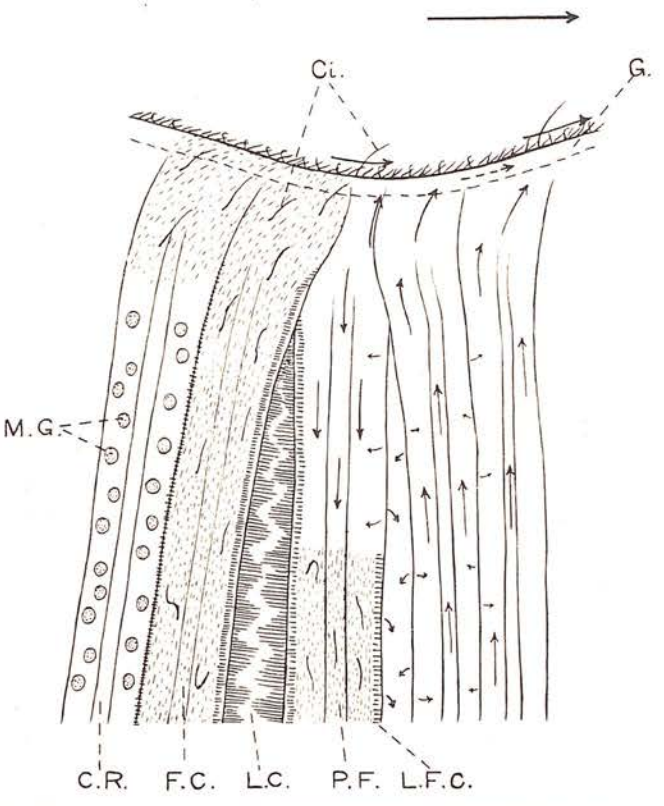

Fig. 21.—Semi-diagrammatic representation of five gill filaments and free margin of demibranch, several of the filaments being drawn apart to show cilia between. × 375. C.R., chitinous supporting rod in filament; Ci., cirri; G., ciliated groove at free margin; F.C., frontal cilia; L.C., lateral cilia; L.F.C., laterofrontal cilia; M.G., mucus glands; P.F., principal filament. Arrow above figure indicates direction of mouth, smaller arrows in figure show direction of beat of cilia.

side of one filament and down the side of the one opposite; but in reality the effective beat is inward into the interlamellar space which communicates with the suprabranchial chamber. The abfrontal cilia (see Fig. 6) no doubt assist in the formation of the current into the suprabranchial chamber. The frontal cilia (F.C.) are smaller than the laterofrontals, but here and there are especially large cilia, or cirri (Ci.) as they have been called by Wallengren who regards them as characteristic of the ciliated tracts along which food is carried. The frontal cilia are concerned solely with the transport of the particles which drop upon them or are thrown upon them by the laterofrontals, the contact of solid particles immediately causing the mucus glands (M.G.), with which the surface of the filaments is covered, to secrete and so entangle the particles with mucus. The beat of the frontal cilia on the principal filaments in the bottom of the grooves between the plicæ is the reverse of that on the other filaments. The former beat towards the base of the demibranch, the latter towards the free margin, as shown diagrammatically in Fig. 22. Conditions are the same on all four demibranchs. Kellogg (1915) has described a similar state of affairs in Pecten, but this difference in the beat of the cilia on two kinds of filaments is not usual in Lamellibranchs. Particles carried to the free margin are passed into the ciliated groove (G., Figs. 21 and 22), which runs along it and in which they are carried towards the palps and mouth, while particles taken to the base of the gills by the cilia of the principal filaments are also carried forward by the ciliated tracts present at the gill axes (see Figs. 1, 2, and 22).

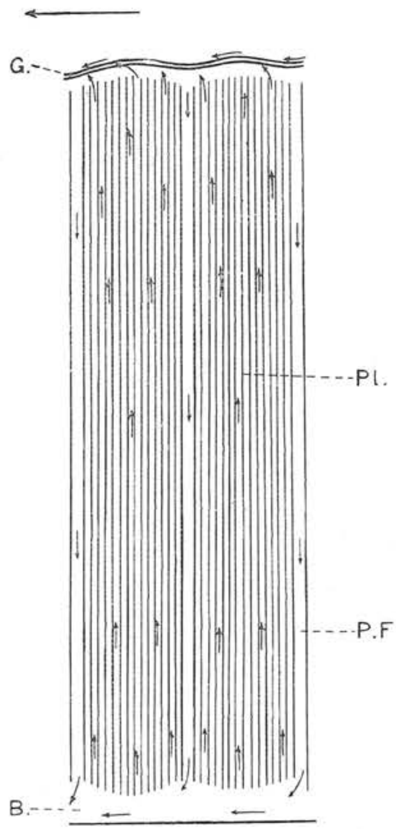

FIG. 22.—Diagrammatic figure of two plicæ and three principal filaments of gill lamella. ×10. B., base of gill, arrows show direction of current along gill axis; G., groove at free margin; P.F., principal filament; Pl., plica. Arrow above figure shows direction of mouth, smaller arrows direction of currents on face of gill.

It is the opinion of Kellogg that the arrangement of the ciliary currents on the gills is an adaptation which ensures that feeding shall take place only when very limited numbers of particles are present in the ingoing currents. These will tend to fall into the grooves and be carried by the cilia on the principal filaments to the base of the gill, and so direct to the palps. But when the water is heavily laden with silt, particles will fall on all parts of the gill, become embedded in a common mass of mucus, and *all* be dragged to the free margin of the gill under the action of the frontal cilia on the summits of the plicæ. Individual particles or thin strings of mucus in the ciliated groove are carried to the palps, as we have seen, but large particles or heavily laden mucus strings tend to fall out of the groove on to the mantle surface, from which they are expelled. Kellogg's observations have been confirmed; small particles alone are passed to the base of the gills, and from thence direct to the palps (except when they occur in such numbers that they accumulate in masses, are caught by the cilia on the plicæ and carried across to the free margin of the gill), while material in the grooves may or may not reach the palp according to its size. His deductions from these observations will be discussed in the section on the palps. There are thus *two selective mechanisms on the gills*, one on the surface of the filaments and one on the free margin, both of which act by selecting the smaller particles or masses for passage to the palps and mouth and reject the larger.

There is also a certain degree of muscular activity in the gills which has often been overlooked. Kellogg, however, with his accustomed keenness of observation, has noted (p. 674) that in Pecten "much material causes the gill grooves . . . to open wide, and then to close with so sudden a contraction that material is thrown out of them. Often this violent bending of filaments, which results in spreading open and then constricting the grooves, occurs in about a second of time. The whole demibranch, also, may present a wavy surface, and sway, fanwise, towards the mantle and inwards." Similar movements have been observed in the gills of Ostrea, the opening and sudden contraction of the grooves being of frequent occurrence. It has already been shown that horizontal muscles are present in the interfilamentar connections and also vertical muscles in the principal filaments, and it is the contraction of these muscles, presumably, which causes the movements of the gills. These types of movement, sudden contractions and bending of the filaments, result in excess of material being transferred from the grooves to the crests of the plicæ or from the surface of the gills to that of the mantle, and form yet another sorting mechanism, though of a less exact nature than the ciliary ones.

(*b*) *The Palps.*

The junction between the gills and palps is shown in Fig. 2 (p. 299), and on examination of this figure it will be seen that particles from the free margin of the gills are transferred to the middle of the inner palp face, whereas those from the gill axes (i.e. the smaller particles) pass into the groove between the palps, although, on account of the slight development of cilia in the grooves particles are passed on to the lower folds, as shown in the figure. In accordance with the terminology suggested by Kellogg, this groove will be called the lateral oral groove (L.G.), while the groove which leads from it to the mouth between the non-folded region of the palps will be known as the proximal oral groove (P.G.). There is a third, distal oral groove in Lamellibranchs in which the outer demibranchs do not extend so far forward as the inner, but this is practically absent in the oyster. Material passed on to the folded surface of the palps comes under the action of the long and very active cilia with which it is covered which, as will be described in detail shortly, conduct it either to the upper margin (U.M.) or across the palp folds in the direction of the mouth. There is a powerful backwardly directed current along the upper margin of the palps in which particles are carried back to a point marked X in Fig. 2 within a short distance of the tip, where it meets a forwardly directed current from the tip. A vortex is created in which particles are rolled into masses which, on attaining a certain size, fall off on to the mantle, directly from the left palps and by way of them in the case of the right palps.

The direction of the ciliary currents on the outer smooth surfaces of the palps is shown in Fig. 23. The cilia being shorter the currents are much weaker than those of the inner surfaces, and particles are carried diagonally backwards, those near the upper edge being transported into the upper marginal current on the inner face—and so finally rejected at X—while those in the central or lower areas are passed to the distal edge round which they are carried on to the folded surface, there to be either taken to the mouth or rejected as the case may be.

Passing now to a detailed examination of the inner, folded surface; Fig. 24 represents such a surface, the arrows showing the direction of the currents. The number of folds varies according to the age of the animal but this in no way affects their action. Each fold (as shown in the cross section in Fig. 7, p. 304) bends towards the mouth, overlapping to some extent the fold immediately proximal to it. In the middle of the exposed distal surface of each fold runs the longitudinal groove. There are no less than five distinct ciliated tracts on the exposed surface of the folds, details of which are shown in Fig. 25. Beginning with the most distal; there is a tract of cilia (*a*) which beats downward into the furrow between

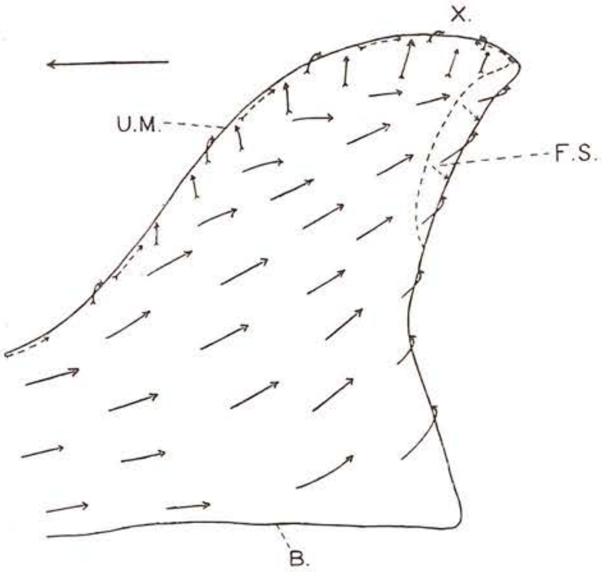

FIG. 23.—Smooth, outer surface of palp showing direction of ciliary currents. × 10. B., base of palp; F.S., folded, inner surface frequently exposed along dotted line; U.M., upper margin of palp; X., point where material rejected from palp. Large arrow shows direction of mouth.

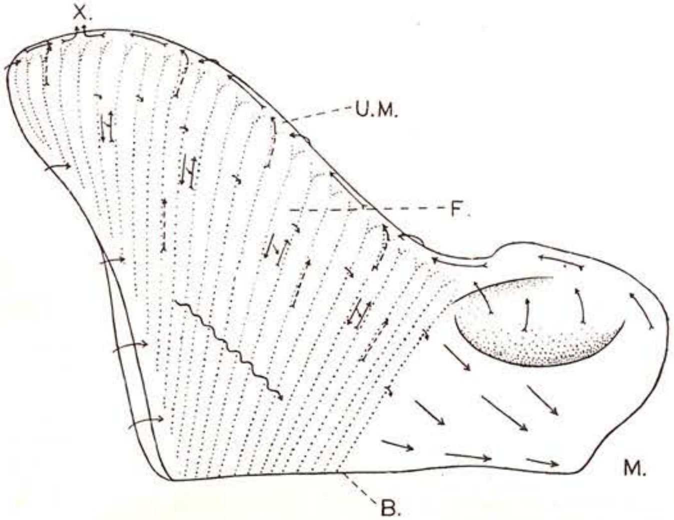

FIG. 24.—Folded, inner surface of palp showing direction of ciliary currents. × 10. B., base of palp; F., folds; M., position of mouth; U.M., upper margin; X., point where material rejected.

adjoining folds, but this region is largely covered by the adjacent overlapping fold ; next there is a narrow tract (*b*) within the longitudinal groove whose cilia beat in the direction of the base of the palp ; then a narrow tract (*c*) which directs particles diagonally across the palp towards the mouth ; then a tract (*d*) in which particles are carried to the upper margin of the palp ; and, finally, a tract of cilia (*e*) whose beat is directed at right angles to the line of the folds and towards the mouth. Moreover, in the furrows between the folds are tracts of cilia which lead, invariably, towards the upper margin (Siebert (1913) states that the cilia in the furrows in Anodonta beat in the opposite direction, but his findings have not been confirmed by other workers). The cilia on the proximal surface of the folds which are not exposed are difficult to observe, but appear in the main to beat into the furrows, and so are concerned with the rejection of particles. The path taken by particles carried on to the folded surface is the resultant of the action upon them of these different tracts of cilia, the interaction of which is very difficult to investigate. There can be no doubt, however, that the whole forms an extraordinarily efficient sorting mechanism. As the folds lie normally the effect of the five exposed ciliated tracts will be that light particles, such as carmine grains, are carried diagonally across the palp face, the individual particles being thrown lightly from fold to fold, largely by the action of the large cilia of tract (*e*), and following the somewhat serpentine course indicated by the long undulating arrow in Fig. 24. Large particles, such as carborundum, or smaller particles imbedded together in long mucus strings (which amounts to rather the same thing since the larger the particles the more mucus is secreted) tend to be drawn down within the furrows under the action of the cilia

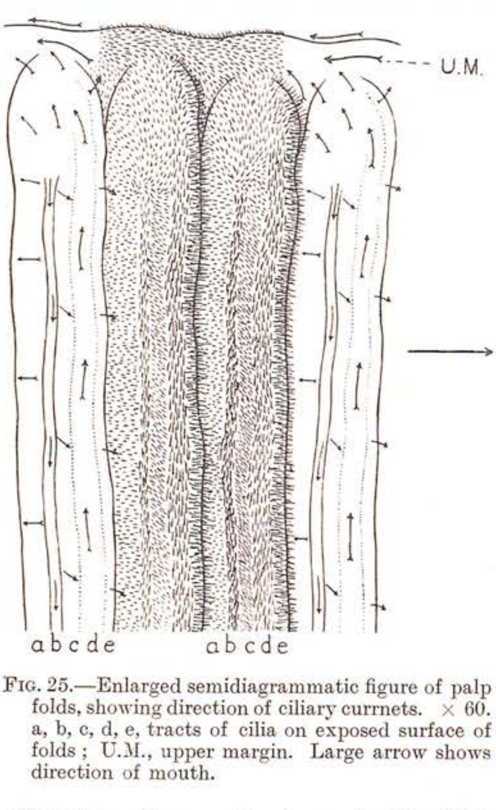

FIG. 25.—Enlarged semidiagrammatic figure of palp folds, showing direction of ciliary currnets. × 60. a, b, c, d, e, tracts of cilia on exposed surface of folds ; U.M., upper margin. Large arrow shows direction of mouth.

in tract (a), and so, finally, expelled. So strong are the cilia in the furrows that if any portion of a mucus string comes under their influence, the whole string is carried to the upper margin. It is difficult to be certain as to the true state of affairs when the opposing palps, as always happens in life, are working in conjunction; experimentally it is only possible to examine the working of one exposed surface. Though gravity may have some influence on the selection of particles or strings of mucus lying on the under surface, that, of course, cannot influence particles attached to the upper surface, though the larger particles will tend to fall on to the under surface. Undoubtedly the mucus is of great importance; the larger the strings or masses, the more they will come into direct contact with the cilia, and the more chance that some portion will be drawn into the furrows and removed. Kellogg thinks there is a muscular retraction of the proximal edge of the folds concerned which causes particles to fall into the furrows; but I have never seen any such action in the oyster.

There is, however, an immediate muscular reaction when large particles are placed on the palp surface, the entire palp curling back in the manner shown in the left palps in Fig. 2. This is caused, no doubt, by the thick layer of longitudinal muscle which lies beneath the epithelium of the smooth surface (see Fig. 8, p. 305). As a result, the inner surface becomes convex and the folds are drawn apart, thus exposing the furrows into which the majority of the material on the palp will fall and be removed. The palps may occasionally curl inwards—by a contraction of the muscles under the epithelium of the folded surface—so that the folds are puckered and spaces left through which particles can drop into the furrows. These muscular responses are of the first importance in the functioning of the palps as was first noted by Wallengren, who originally described the different tracts of cilia on the palp folds, but who considered that, as a result of their *individual* contraction, different tracts were brought into play, and in this way the direction taken by the particles was controlled. Kellogg has described a curling over of the ventral (upper) margin of the palp in Schizotherus, whereby material is drawn off directly from the palp surface on to the outgoing marginal tract. Such a movement has not been observed in the palps of Ostrea, which are not free from one another, as in Schizotherus, but are attached for a quarter of their length. Allen (1914, 1921) follows Wallengren's account, and ascribes selection to the action of the different tracts of cilia brought into play during different states of contraction and relaxation in the folds; he claims further (apparently owing to a faulty reading of Wallengren's paper) that by this means cilia are brought into action which led particles in the *opposite* direction to that of the mouth. Grave (1916) considers that there is a reversal of the beat of certain cilia (pointing to the similar conditions described by Parker for the sea anemone Metridium). I have never observed any sign of a reversal of cilia in the palps of any Lamellibranch, nor have Grave's opinions been supported by any more recent worker. Cobb (1918) has shown that the palps of Anodonta respond by muscular contractions to a variety of stimuli; mechanical, electrical, chemical, photic, and thermal. He also found that the detached palp reacts as effectively as one attached to the body (a fact also noted during these experiments on the palps of Ostrea), showing that "the palp contains within itself the neuromuscular organization necessary for all the responses described . . . and . . . possesses an autonomy even more complete than that of the vertebrate heart and comparable with what is shown by the tentacle of an actinian." Churchill (1924) has observed the muscular curling of the palps under normal feeding conditions in young, transparent fresh-water mussels. Nelson (1924) watched the feeding of spat oysters under similar conditions, and states that the rejection of particles is due to "reflex erection of the ridges of the palps which brings into play groups of cilia which beat away from the mouth." He does not state whether this erection is due to a general curling back of the palp surface, but describes the palps at this stage as consisting of "isolated filaments which are capable of independent movement." (This is certainly not the case in the spat of *Ostrea edulis*, where, as we have seen, the palps are more united than in the adult.) Nelson placed spat in 1/20 sat. magnesium sulphate, and states that the filaments of the palps lost the power to erect, with the result that masses of material passed over to the mouth and eventually blocked it. He concludes that feeding in the oyster is accomplished "through the delicate co-ordination of nervous, muscular, ciliary, and mucus secreting elements in which mechanical sorting of the materials plays the most important part"; an admirable summary of the state of affairs.

Herdman and Boyce (1899) have described in the oyster the presence of thin bands of muscle arising one on each side at the surface of the mantle near the anterior edge of the visceral mass and being inserted at the junction of the gills and palps, and have identified them with the protractor pedis muscle of other Lamellibranchs. They suggest that in the oyster they may function by pulling apart the inner and outer palps and gill demibranchs of each side, and so allowing food particles to reach the mouth more easily. It is difficult experimentally to prove this or to see its necessity since other Lamellibranchs function perfectly well without it, but, as they state, the opening of the shell will, by separating the points of attachment of the two muscles, cause "the opening up of the food avenues."

A considerable controversy has arisen around the question whether in the Lamellibranchs the selection of particles for swallowing is qualitative or quantitative. The view that there is a definite selection of particles, having food value has been upheld chiefly by Lotsy (1893), Allen (l.c.) and Grave (1916), but the majority of workers, including List (1902), Kellogg (l.c.), Yonge (1923), Nelson (1924), and Churchill (1924) have failed to find anything other than a purely mechanical selection having as its object the reduction of the quantity of matter passed to the mouth, large particles or many small particles embedded in mucus being rejected and smaller particles or mucus masses passed on to the mouth quite irrespective of their food value. This appears to be confirmed by examinations of stomach contents by Savage (1925), and the majority of previous investigators whose work he summarises. Churchill found that when fresh-water mussels were kept in suspensions of mixed organic and inorganic matter they took in a sample of everything small enough to enter the mouth. In some cases where the inorganic particles are the larger there may be—incidentally—a selection of particles having food value (as Nelson thinks is the case in spat oysters). Nothing but a purely mechanical or quantitative selection has been found in the oyster, and this has, I think, been made clear in the preceding account, but attention may again be drawn to the series of selective mechanisms which exist.*

1. The heaviest particles in the ingoing current drop on to the mantle and never reach the gills.
2. The smaller particles on the gills are carried by the cilia on the principal filaments to the base, the larger ones passing to the free margin.
3. The largest particles or mucus masses fall out of the groove on the free margin on to the mantle.
4. Muscular contractions in the gills cause material to be transferred from the grooves on to the crests of the plicæ, and from the surface of the gills to that of the mantle.
5. Material passed on to the inner face of the palps from the free margin of the gills is there most rigorously sorted, larger particles or masses being rejected and only the smallest crossing towards the mouth.
6. The smaller particles from the gill axes which pass into the lateral oral groove are not so rigorously sorted, since the folds at the base of the palps are lower and closer together and the effect of the curling back of the palp surface is much slighter.

Experiments with four grades of carborundum powder demonstrated the efficiency of these sorting mechanisms very clearly. The particles

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* Lamellibranchs, such as Syndosmya, Tellina or Gari, which have long, free siphons and are classified by Hunt (1925) as deposit feeders, may exercise a certain qualitative selection by means of the inhalent siphon which is fringed with sensory tentacles. Possibly the Protobranchs may do the same, though to a less extent, by means of the extrusible appendages of the outer pair of labial palps. In both cases, however, qualitative selection, if it occurs, takes place *outside* the mantle cavity.

were in all cases dropped lightly on the middle and posterior regions of the gills, and with the following results (the coarser grades being taken first) :—

Grade 120. Particles passed to the free margin of gill ; fall on to mantle before they can reach the palps.

Grade 220. All carried to free margin ; majority drop off, a few of the thinner mucus strings reach palps, there *all* rejected.

Grade F. All carried to free margin ; comparatively little falls off, *all* rejected by palps.

Grade FF. All carried to free margin ; very little falls off, great majority rejected by palps, a very little carried to mouth.

As already stated, Kellogg is of the opinion that Lamellibranchs can only feed in waters that are comparatively clear. This has been denied by Grave (1916), Nelson (1921)—who supplies the *definite evidence* that oysters can feed in waters bearing as high as 0·4 grams dry weight of suspended matter per litre—and Churchill (1924), and, I think, with reason. Certainly the more particles carried into the mantle cavity, the more wholesale is the rejection, but, as Churchill has shown for fresh-water mussels, although the main surface of the palp is concerned with the rejection of the large masses passed on from the marginal grooves on the demibranchs, the finer matter which enters by way of the lateral oral groove will find its way to the mouth. I place a similar interpretation on my experiments, although in the oyster the selective mechanisms, both on palps and gills, are more efficient than in the majority of Lamellibranchs—a correlation, no doubt, with the sessile mode of life and consequent danger of silting up—in which the frontal cilia of all gill filaments usually beat in the same direction, and food can pass to the mouth by way of the distal and lateral oral grooves without ever coming into contact with the folds on the palps ; *Mya arenaria* is a good example of this type of Lamellibranch. Even in the oyster, however, I have observed the passage of a certain amount of material from the gills to the palps under all conditions approaching the normal (if the gills are absolutely covered with a mass of particles these are all removed, whatever their individual size, but this would never occur in nature) ; carmine grains are carried to the mouth along the lateral oral groove while the rest of the palp surface is ridding itself of carborundum. It is not impossible, however, that Lamellibranchs, and especially such highly specialised species as the oyster, feed with the *maximum of efficiency* in waters that are comparatively clear ; they can, moreover, by frequent closing of the shell valves clear the water to some extent and prevent any too great accumulation of sediment within the inhalent chamber.

It remains to describe the passage of particles from proximal folds to the mouth, the course of which is shown in Fig. 2 (p. 299). The cilia in this region are short, and matter accumulates along a line parallel to the last fold and then passes slowly in the direction of the mouth. There is never an accumulation of material about the mouth, particles which do not pass deep in the proximal oral groove being caught by ciliated tracts which lead them upwards and then either distally on to the upper margin of the inner palp face, or over on to the outer face of the inner palps. In either case they are rejected finally. Material which reaches the mouth passes slowly into the œsophagus.

(*c*) *Removal of Material from the Mantle Surface.*

Material dropped on to the surface of the mantle is carried away by the ciliary tracts shown in Fig. 1 (p. 298). There are ciliary tracts in the anterior region of the mantle cavity which carry particles back to a point about the middle of the inhalent aperture where they accumulate, since the thickened ridge which bounds the mantle is not ciliated. The masses thus formed are expelled from time to time by sudden contractions of the valves. Nelson (1921) by very ingenious experiments has shown that ejections of this nature are most numerous when the water in which oysters are living is at its maximum turbidity. Along the posterior region of the inhalent chamber, and also in the exhalent chamber, matter passes directly to the edge of the mantle, there to accumulate and be expelled in the manner described.

II. IN THE GUT.

Mucus laden with particles passes slowly along the œsophagus, particularly in the grooves at the extremities of the lumen, as described by Yonk (1924), into the stomach. Fig. 26 represents the stomach and œsophagus opened out for examination of the ciliary currents. As a result of the position of the cut, the ventral wall of the stomach lies on the left side of the figure. The relative positions of the various parts is seen in Figs. 3 and 4, and by reference to these and to Fig. 26 some idea of the physiology of the stomach will be gained.

Particles entering the stomach will tend to pass into the food sorting cæcum (F.C.) either directly or by way of the ciliated tract (C.T.), which leads into it from the floor of the stomach. The cæcum, as shown in Figs. 3 and 4, is a long grooved diverticulum, which extends backwards under the floor of the stomach. Fig. 27 represents it opened out, the broken lines indicating the line of the cut. The ingoing ciliated tract (C.T.) is situated on a ridge, which passes down the right side of the cæcum to the extremity and then along the left side, terminating abruptly at a point level with the opening of the cæcum. Particles are carried very rapidly along this tract until they reach the point X, when they may be carried in either of two ways. If they are heavy (e.g. carborundum) they are rolled round and fall over into the groove on the right of the ridge, as shown by the arrows and dark mass in Fig. 27. The cilia in this groove conduct particles slowly round in the reverse direction to the cilia on the ridge and out of the cæcum into the deep ventral groove (G., Figs. 3, 4, 26, and 27), which runs across the floor of the stomach and is continued into the mid-gut, as shown in Fig. 26. On the other hand, light particles, such as carmine grains, not embedded in great masses of mucus, pass along the ciliated tract past the point X, and are wafted out of the left side of the cæcum in the direction indicated by the dotted arrows in Fig. 27, being ultimately carried to the region of the gastric shield, as shown in Fig. 26. The cæcum constitutes yet another sorting mechanism wherein larger particles are separated from smaller ones without any apparent regard to their food value, the larger ones being removed from the stomach by way of the mid-gut, and the smaller being retained in the stomach and passed towards the head of the style.

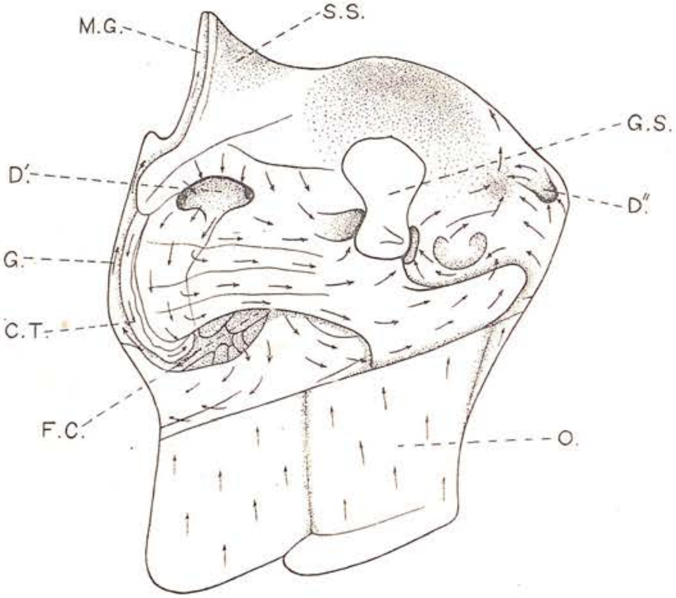

Fig. 26.—Stomach opened out to show direction of ciliary currents, cut made along right ventral surface. × 4. C.T., ciliated tract leading into food sorting cæcum ; D′., larger, left duct of digestive diverticula ; D″., smaller, right duct ; F.C., food sorting cæcum ; G., ventral groove leading from food sorting cæcum to mid-gut ; G.S., gastric shield ; M.G., mid-gut ; O., œsophagus ; S.S., style-sac.

Nelson (1918) has described a similar cæcum in Modiolus, and I have given an account of a food sorting area in the stomach of Mya (1923). In both of these cases the mechanism is more complicated than in Ostrea, presumably because in the latter the selective powers of the gills and palps are better developed, a fact testified to by the smaller size of the particles in the stomach of the oyster. The remaining cilia on the wall of the stomach either conduct particles towards the gastric shield, where they come under the action of the style, or else towards the ducts of the digestive diverticula (D′. and D″., Figs. 3, 4, and 26). These ducts are bounded on the one side by an overhanging wall over which the cilia beat *into* the opening, but on the other the opening lies flush with the epithelium of the stomach, and the cilia on this side lead particles *away* from the opening. There is thus a mechanism whereby particles enter the ducts on the one side and leave them on the other, which is essential if a circulation is to be maintained within the diverticula.

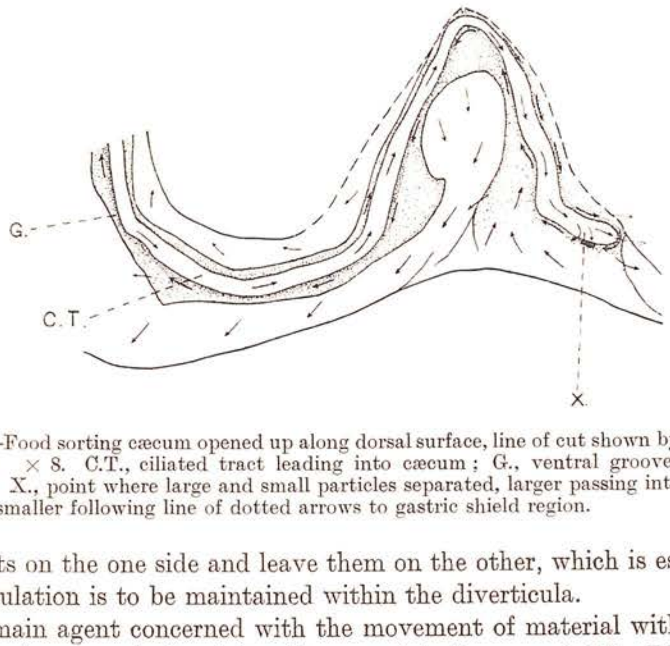

FIG. 27.—Food sorting cæcum opened up along dorsal surface, line of cut shown by broken lines. × 8. C.T., ciliated tract leading into cæcum; G., ventral groove leading out; X., point where large and small particles separated, larger passing into groove and smaller following line of dotted arrows to gastric shield region.

The main agent concerned with the movement of material within the stomach, however, is the style. It was originally suggested by List that the style was probably revolved by the action of the cilia in the style-sac, but it was left to Nelson (1918), as the result of careful opening of the stomach, to observe the actual revolution of the style in the stomach of Anodonta and Modiolus. He found that the maximum number of revolutions per minute in Anodonta at 11·5° C. was 11, and in Modiolus at 25° C. was 13. In both cases the direction of the movement was clockwise when viewed from the anterior end of the animal. It has never been possible to observe the movement in the adult oyster, in which the stomach is less exposed than in the majority of Lamellibranchs, but I have seen it in the larvæ and spat (as will be described later), while Churchill (1924) has observed it in young, transparent fresh-water mussels, and there can be no doubt, if only from the nature of the ciliation of the style-sac, that the style revolves in all Lamellibranchs. The head of the style is continually being dissolved away, and in the sticky mass become embedded particles and strings of mucus, and it may well be, as Orton (1923) has suggested, that material is in some cases drawn into the stomach as a result of the mucus strings being wound round the "shredded revolving head of the style like a capstan." As we have seen, muscle is practically absent from the gut of the oyster (in common with all Lamellibranchs except the Septibranchs), the place of peristalsis being taken by ciliary activity. One of the principal functions of the style, as Nelson (1918, 1925) has pointed out, is that of stirring and mixing particles in the stomach, an operation performed in many other animals by peristaltic contractions. Although, of necessity, the different activities of the stomach have been described separately, in life, of course, they are all proceeding simultaneously, food entering from the œsophagus, being sorted in the cæcum, being revolved in the head of the style, passing in and out of the ducts of the digestive diverticula, and being removed by way of the mid-gut all at the same time.

The disposition of the ciliary currents in the style-sac and first part of the mid-gut is shown in Fig. 28. Particles enter the mid-gut from the stomach by way of the ventral groove (G.) and pass quickly down it along the channels at the base of the typhlosoles (T′. and T″.). The cilia on the typhlosoles beat diagonally away from the stomach and into the gut. The groove of the style-sac is ridged transversely, and the beat

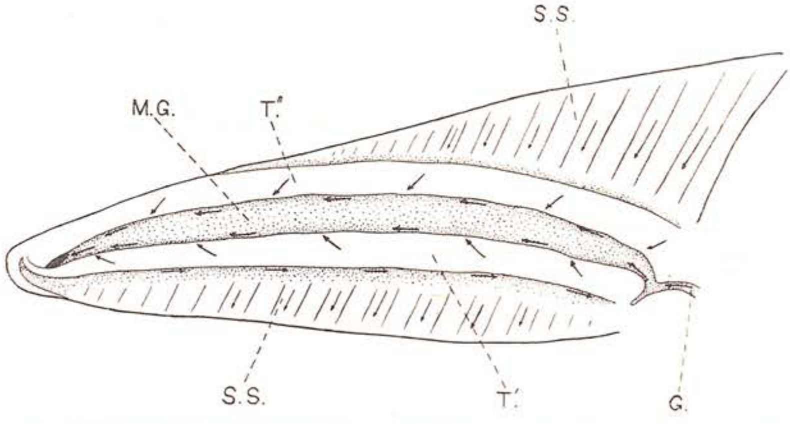

FIG. 28.—Style-sac opened along middle of surface so as to expose ciliary currents in style-sac and mid-gut. × 4. G., ventral groove in stomach; M.G., mid-gut; S.S., style-sac; T′., larger typhlosole; T″., smaller typhlosole.

of its large cilia is very difficult to determine ; particles placed upon them appear to get caught between the cilia, as they can be seen trembling with the movement of the cilia but are moved extremely slowly. Such movement as there is, however, is from right to left (looking at the style-sac from the stomach), i.e. in the direction which would revolve the style in a clockwise direction when seen from the same standpoint. There is a tract of cilia beating in the direction of the stomach on the side of the larger typhlosole (T′.), which is somewhat easier to demonstrate and is accompanied by the production of great quantities of mucus. The same disposition of cilia is found in the style-sac of Mya (Yonge (1923), and there is the same difficulty in demonstrating the direction of their beat. The style, presumably, is revolved by the first set of cilia and pushed forward by the other, and the difficulty of demonstrating the direction of beat may be due to the cilia not being adapted for the movement of small particles which rest lightly on them, but for the movement of a firm body which is pressed firmly against them. In spite of the presence of the ciliary currents leading from the style-sac into the gut over the face of the typhlosoles, a certain amount of material which has been carried down the gut gets caught up in the substance of the style, wrapped round it spirally as it revolves, and carried back to the stomach. This " retrieving function " of the style has been commented on by Nelson (1918, 1925), Allen (1921), and Orton (1923)—the latter having figured the spiral bands of mucus laden food strings wrapped round the style of the oyster—and is probably of some importance in Lamellibranchs, such as Ostrea, in which the style-sac and mid-gut are in communication.

Throughout the remainder of the gut material is passed slowly backwards under the influence of the cilia, and is finally ejected by way of the anus into the exhalent chamber (see Fig. 1), where it comes under the influence of the exhalent currents and of the cilia on the mantle surface and is removed from between the shell valves.

B. THE LARVÆ.

The arrows in Fig. 17 (p. 317) indicate the direction of the ciliary currents in the larvæ. If larvæ are placed in suspensions of carmine, indian ink or other fine particles these are thrown by the large cilia of the velum on to the ciliated tract (C.T.), which runs round the base of the velum, where they are embedded in mucus and carried back to the mouth. The velum, therefore, acts both as a swimming and as a food collecting organ. Not all the material passes into the mouth, any surplus being carried off by the cilia on the lobe which represents the rudiments of the foot (F.), so that a larva swimming through a thick suspension leaves behind it a trail of particles embedded in a long string of mucus. If the suspension is excessively thick the larvæ become embarrassed in their movements and turn repeatedly over and over in their efforts to free the cilia from the mass of particles which they automatically collect.

Material is passed into the stomach by way of the œsophagus and is there rotated, as indicated by the arrows in the figure, by the cluster of large cilia at the anterior end and also by the action of the smaller cilia which line the wall of the stomach. At the same time, the style, in which particles become embedded, is rotating in the style-sac. The direction of rotation appears to be constant for the individual, but to vary in the different larvæ, in some clockwise, in others anti-clockwise. Nelson, on the other hand, states that in the larvæ of *Ostrea virginica* the movement is always clockwise. The speed varies greatly, as few as 36 and as many as 90 revolutions per minute having been counted. Partly as a result of this movement, particles are thrown into the cavity of the digestive diverticula in which they can be seen in active movement, as shown by the curved arrows in Fig. 17. We may therefore assume that cilia are present in the cavity of the diverticula. Particles leave the stomach by the mid-gut, and are carried rapidly through the remainder of the alimentary tract and ejected at the anus. When larvæ were kept in heavy suspensions of carmine the gut became packed with a continuous red stream, and under these conditions the action of the cilia was practically inhibited, owing to the pressure of the enclosed mass ; movement became exceedingly slow and a certain amount of peristaltic activity was observed. The gut in the larvæ is, it may be noted, unlike that of the adult, free from the surrounding tissue. The fæces are rolled into a ball by the action of the cilia in the mantle cavity, and are then expelled.

C. THE SPAT.

All mechanisms concerned with the rejection of surplus matter are well developed in the spat. Thus the cilia of the mantle are larger and more active than those in the adult, while the palps are relatively of immense size and reject the great majority of particles passed on to them from the gills, which collect them in the usual manner as indicated by the arrows in Fig. 18 (p. 319). Fig. 29 shows the palps seen from the free end after they had been dissected out of a 1 mm. spat, the two inner palps (I.P.) being enclosed by the hood formed by the outer palps (O.P.). It is extremely difficult at this early stage in their development to distinguish the direction of all the ciliary currents on these small organs. No folds are present, although there is a groove on each of the palps along which the cilia beat in the direction of the free extremities of the palps, as in the furrows of the fully developed palp, and there are ciliated tracts leading in the same direction along the outer edges of the outer palps

Other tracts lead across the palps, but, after careful examination, only one tract—on the right inner palp—was distinguished in which the cilia beat towards the base. When particles are placed upon the palps only a minute proportion succeed in passing between the inner and outer palps of each side and so reaching the mouth, the majority are passed rapidly to the depression at the junction of the outer palps (see Figs. 18 and 29), where they are rolled into a large ball (M.), which finally falls on to the mantle surface. In experiments on whole spat the palps were found to be very active and to respond readily to stimulation by drawing back and upwards, probably by so doing exposing to their maximum the outgoing tracts.

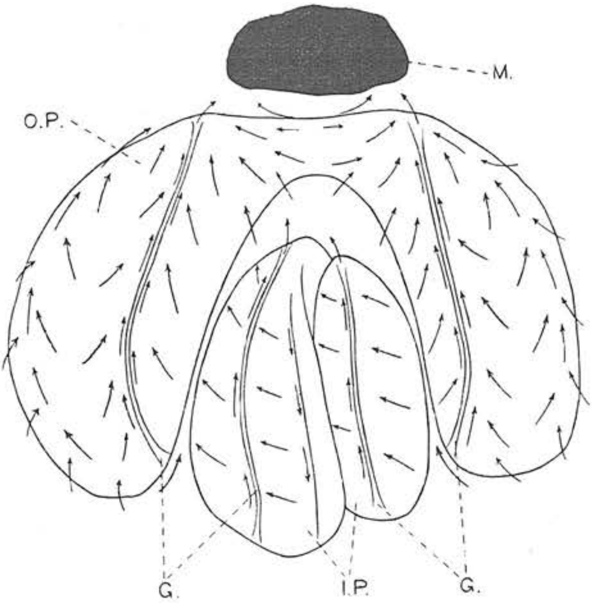

FIG. 29.—Palps from 1 mm. spat dissected out and drawn from free end, i.e. looking in direction of mouth. × 275. G., grooves on inner faces of palps; I.P., inner palps; M., mass of rejected material accumulated in depression at junction of outer palps; O.P., outer palp.

Particles which succeed in reaching the mouth are passed rapidly through the œsophagus into the stomach (see Fig. 18). There they are whirled round by the cilia and in the head of the style, which in spat of this size can be seen in rapid movement through the wall of the stomach. It consists of a somewhat irregular rod which bears against the gastric shield and revolves in a clockwise direction when viewed from the anterior, the speed observed varying between 60 and 70 revolutions per minute.

Embedded in its substance, especially near the head, are particles of all sizes, the largest observed being specimens of the spherical diatom Coscinodiscus having a diameter of about 23μ. These are shown in Fig. 18. It is difficult to observe the disposition and interior of the digestive diverticula in the spat, but movements were seen within them, while peristaltic movements were well marked in the mid-gut, especially in the region nearest the stomach, particles being moved by this means and by ciliary activity through the mid-gut and rectum and expelled at the anus, which opens in the exhalent chamber.

The great development of the organs concerned with the removal of surplus matter in the spat can readily be understood, since a small sessile organism of this nature is in constant danger of being smothered by falling silt unless this can speedily be removed from within the mantle cavity. The presence of peristaltic activity in the gut of both larvæ and spat seems to indicate that the absence of peristalsis in the adult is not primitive. Peristalsis is usually well developed in the Gastropods, which may represent, in this respect at any rate, the more primitive condition.

4. ASSIMILATION.

I. Literature and Methods.

Although in animals such as the Vertebrates, digestion precedes assimilation, this is the case only to a very limited extent in the Lamellibranchs, since food is ingested directly both by the phagocytes and the tubules of the digestive diverticula and digestion then takes place *intracellularly*. The only extracellular enzymes in the gut of Lamellibranchs are those set free by the dissolution of the head of the style. In this paper, therefore, an account of the process of assimilation is given before passing to a consideration of the digestive enzymes.

I have recently had occasion (1926) to review the literature dealing with assimilation in the digestive diverticula, so that it is unnecessary to discuss the matter in detail. As a result of a study of previous work and as the outcome of my own experiments, the conclusion was reached that the digestive diverticula are organs of absorption and of intracellular digestion, since they absorb soluble matter such as iron sulphate (Carazzi (1897) on Ostrea) or iron saccharate (Yonge (1926) on Nucula, Mya, and Teredo), and ingest solid matter such as Indian ink (List (1902) on Mytilus, Potts (1923) on Teredo, Vonk (1924) on Ostrea), carmine (List on Mytilus) or blood corpuscles from dogfish (Yonge (1926) on Teredo). Sigerfoos (1908) and Potts have further shown that the Teredinidæ ingest wood fragments in digestive diverticula specialised for that purpose. Matter which may be of use to the animal such as iron (Carazzi (1897), Yonge (1926)) or blood corpuscles (Yonge) is carried away in amœbocytes, but useless material such as Indian ink is rejected into the lumen of the diverticula shortly after ingestion and carried out of the body (List, Vonk).

Carazzi (1896, 1897) claims that iron is absorbed by the epithelial cells of the gills, palps, and œsophagus, and then carried to the digestive diverticula by way of the amœbocytes. Since, however, he kept his oysters for *four months* in a solution of iron sulphate in sea water so that they had time to become thoroughly permeated with iron, an entirely contrary interpretation may be placed on his results, namely, that the phagocytes become loaded with iron either from the digestive diverticula or by direct ingestion and then carry it to all the tissues. In the same way the Marennin from Navicula is taken in by the phagocytes and carried to all free surfaces of the oyster, so that the gills, palps, and gut are coloured green (for full details on the subject of green oysters see Lankester (1886), Herdman and Boyce (1899), Mitchell and Barney (1916), and other papers quoted by them). Gutheil (1912) found fat globules in the ciliated epithelium of the gut in Anodonta, except in the style-sac and the region of the gastric shield. He therefore concluded that the epithelium could absorb, although he carried out no controlled experiments by first starving and then feeding animals, but argued from the presence of fat in the epithelium of fresh animals. Churchill (1915, 1916) states that after keeping fresh-water mussels in very dilute solutions of soap, egg albumen, or starch stained with iodine, these substances are taken by the outer epithelial cells of the body, mantle, foot, gills, and palps, some being carried away by blood cells, which he observed on occasion between the epithelial cells. His experiments were in most cases kept up for a considerable number of days, and, though the same objection cannot be made to them as to those of Carazzi, since he plugged the mouth of many of his animals thus preventing the passage of food to the digestive diverticula, yet the presence of these substances in the epithelial cells did not necessarily mean that they had been absorbed directly by them. Canegallo (1924) kept Unio in soap solution and found that this was absorbed to a far greater extent by the epithelium of the intestine than of the gills, the fat being carried away by leucocytes. Ranson (1926) considers that molluscs can absorb organic matter in solution through any free surface as well as by the intestine. In my own work on Nucula, Cardium, Mya, and Teredo (1926) the absorption of iron saccharate was never observed except in the tubules of the digestive diverticula.

Large particles are taken in directly by phagocytes, to the universal presence of which attention has already been drawn. De Bruyne (1893, 1896) considered that they ingested damaged or degenerating epithelial cells particularly in the gills. Gutheil (1912) has described and figured in Anodonta the passage of phagocytes laden with material from between the epithelial cells through the basement membrane and into the connective tissue and blood vessels. Cuénot (1914) has observed phagocytosis in the blood cells of Lamellibranchs, as a result of the injection of Chinese ink. Canegallo (1924), by injecting olive oil stained with Sudan III into Unio, found that this was quickly taken in by leucocytes. I have described (1923) the presence of great numbers of these phagocytes in the gut of Mya, and shown that they may contain large, hard particles such as sand grains or the tests of diatoms, often in such numbers that the gut is coloured grey. After feeding Cardium and Mya with blood corpuscles of dogfish it was found (1926) that the corpuscles were ingested by phagocytes lying between the epithelial cells in the stomach and ducts of the digestive diverticula. They were carried into the connective tissue and there digested. Reference has already been made in this paper to the presence of phagocytes in all parts, and to the fact that they often contain green or brown granules, the colour being due to a pigment investigated by MacMunn (1900) and named by him Enterochlorophyll, on account of its close relationship to chlorophyll.

Oysters after appropriate periods of starvation in water which had been passed through filter cloth were fed with suspensions in sea-water of iron saccharate, of blood corpuscles from dogfish, of a pure culture of the diatom Nitzschia, and with an emulsion of olive oil stained with Nile blue sulphate. No experiments were carried out with Indian ink, the recent and conclusive work of Vonk (1924) on Ostrea having rendered them unnecessary. Animals were removed, and the various regions of the alimentary system fixed, at varying intervals after the commencement of feeding. After feeding with iron saccharate tissues were fixed in equal parts of 5% of ammonium sulphide in 95% alcohol and Bouin's fluid, sections being later treated for ten minutes with a 10% solution in water of potassium ferrocyanide, and then for a few minutes in a very dilute solution of HCl in order to demonstrate the presence of iron by the Prussian blue reaction, the sections being stained with alum carmine. After feeding with the other substances tissues were fixed either in Flemming's strong fluid or in Bouin. If by the former method, sections were stained with a saturated solution of safranin in 70% alcohol and later differentiated in clove oil saturated with orange G, the osmicated fat by this method standing out very clearly against the red nuclei and yellow cytoplasm. After fixation in Bouin sections were stained with Delafield's hæmatoxylin and erythrosin.

Larvæ and spat were fed on carmine and iron saccharate, and fixed respectively in Bouin and in the ammonium sulphide-alcohol Bouin mixture.

II. FEEDING EXPERIMENTS ON ADULTS.

(*a*) *With Iron Saccharate.*

This substance was taken in readily, a thick brown suspension in sea-water being rapidly cleared. Oysters opened within a few hours of feeding were found to have the stomach full of a brown mass of iron saccharate, a great deal of which was embedded in the head of the style. After sectioning, iron was found in the lumen of all parts of the gut up to two days after feeding (it was present in very great quantity in the rectum six hours after feeding), sometimes it was seen ingested in phagocytes lying free in the lumen and—very rarely—being carried by them in between the cells of the epithelium. *But in the epithelium of neither the gills nor the palps nor any part of the gut except the tubules of the digestive diverticula was it absorbed.* In the cells of the latter it is ingested freely, slight traces being present six hours after feeding, a maximum being reached from one to two days after feeding, very slight traces being found after three days and none after any longer period.

The typical conditions of absorption are shown in Fig. 30, which represents two cells from a digestive tubule two days after feeding with iron saccharate. The free surface of the cells is very irregular, and iron is taken into large vacuoles and accumulates in the form of irregularly round or oval masses. It is *never* absorbed in the form of fine granules or in a diffuse condition. Exactly the same conditions were found in Nucula, Mya, and Teredo, while List and Vonk found that Indian ink was taken into vacuoles in the diverticula of Mytilus and Ostrea in a similar manner. It is impossible, as Vonk has also noted, to distinguish a bounding membrane around the masses which appear to lie

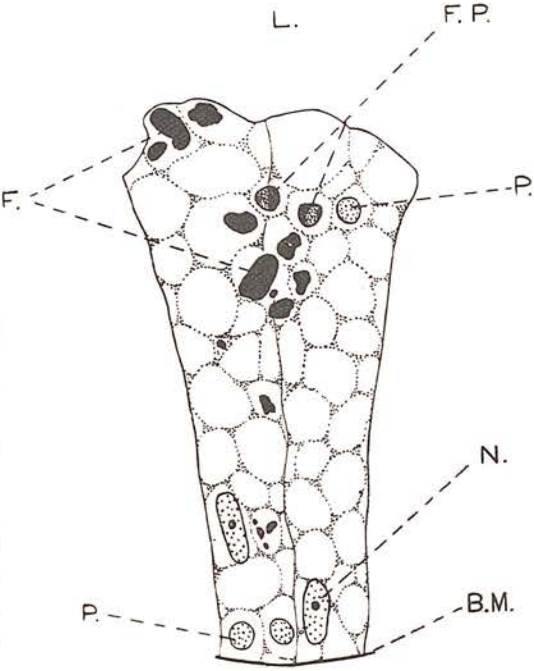

FIG. 30.—Two cells of digestive diverticula two days after feeding with iron saccharate. Iron technique. × 1350. B.M., basement membrane; F., masses of ingested iron; F.P., iron partly filling vacuoles; L., lumen; N., nucleus of cell; P., phagocytes.

free in cavities in the protoplasm, but the manner in which the iron first forms a ring (Fig. 30, F.P.) the interior of which is later filled up, seems to point to the presence of such a membrane. This manner of absorption is unlike that found in animals, such as Arthropods and Annelids, in which digestion is extracellular and only the soluble products of digestion are absorbed, and would appear to be an indication of the presence of intracellular digestion, as would also the irregular outline of the free surface of the cells.

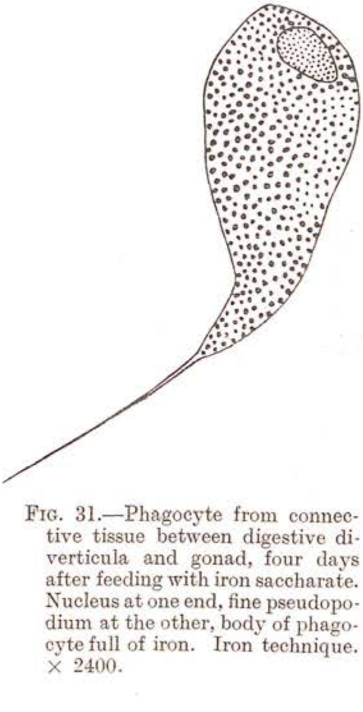
FIG. 31.—Phagocyte from connective tissue between digestive diverticula and gonad, four days after feeding with iron saccharate. Nucleus at one end, fine pseudopodium at the other, body of phagocyte full of iron. Iron technique. × 2400.

Phagocytes are almost invariably present in the cells in which iron is being ingested, they may or may not be present in the others. Usually only their nuclei (as in Fig. 30) can be distinguished, although occasionally the outline of the cells can be seen, particularly when they are full of iron which they have collected from the cells. Four days after feeding, though no trace of iron was found in the tubules, many phagocytes full of minute granules of iron were to be seen immediately round the tubules, in the connective tissue (e.g. the phagocyte in Fig. 31), and occasionally in the blood vessels and in the gonads (Carazzi considered that the final destination of the iron was the gonad). There was never any indication of rejection of iron into the lumen, in the manner described by List and Vonk after feeding with Indian ink.

(*b*) *With Blood Corpuscles.*

A quantity of fresh blood from a dogfish was added to the filtered sea-water in a large bell-jar in which a number of oysters had been starved. The corpuscles were taken in rapidly by the oysters. The stomach contents of an oyster opened three hours after the blood had been added consisted exclusively of mucus, blood corpuscles of dogfish, phagocytes of the oyster and a few ciliates and spirochætes. The style was intact. The great majority of the corpuscles were in perfect condition, the outline being smooth and the nucleus quite clear, some were lying free in the stomach, some entangled in mucus or in the substance of the head of the style, while others were in *process of being ingested by phagocytes*. This process is shown in Figs. 32 and 33; in the former a phagocyte is beginning to engulf a corpuscle, while in the latter one has already been ingested, and is lying in a vacuole within the phagocyte which is beginning to engulf a second corpuscle. The stomach contents of an animal opened six hours after feeding were a diffuse red, probably owing to the presence of free hæmaglobin, very few corpuscles could be distingished, and there were many fewer phagocytes free in the lumen, those present being often large, and containing the remnants of many corpuscles in an advanced state of digestion. Many other phagocytes contained no ingested matter. Phagocytes with ingested corpuscles could be distinguished passing into the epithelium of the stomach. Eighteen hours after feeding there was only a slight redness in the stomach, which contained very few corpuscles, the outline of which was often serrated.

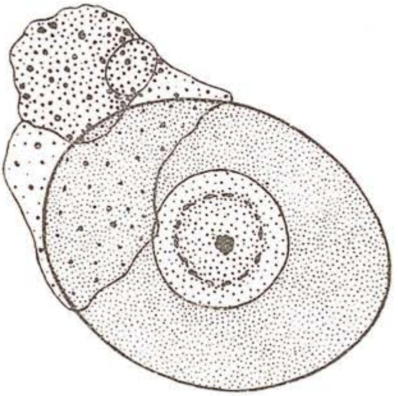

FIG. 32.—Phagocyte in stomach ingesting blood corpuscle three hours after feeding with blood from dogfish. Drawn from life. × 2400.

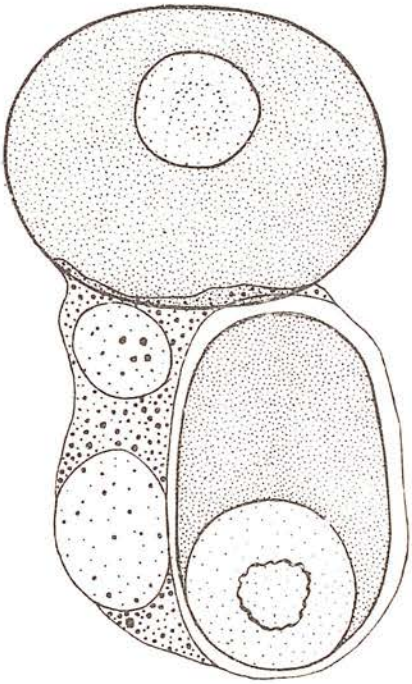

FIG. 33.—As above, phagocyte with one corpuscle ingested and beginning to ingest a second. Drawn from life. × 2400.

As a result of sectioning it was found that corpuscles are taken in between the cells of the epithelium in all regions by the phagocytes. This was most rare in the rectum, few corpuscles passing so far in the lumen, and in the digestive diverticula where, although corpuscles were occasionally found ingested in the cells, they only appeared to be digested with consequent formation of fat globules in the presence of phagocytes. Ingestion by phagocytes took place to a small extent in the gills, palps and œsophagus, to a greater extent in the mid-gut, but the principal centre of phagocytic activity was found to be the stomach and ducts of the digestive diverticula, immense numbers of phagocytes making their appearance in the lumen and epithelium in these regions. The course of phagocytic ingestion of corpuscles was followed in detail in the stomach epithelium.

It is very difficult to remove all traces of fat from oysters, even after prolonged starvation. Feeding experiments were carried out on animals which had been starved four and eleven weeks, and in both cases, though the quantity of fat was substantially less than in fresh animals, there

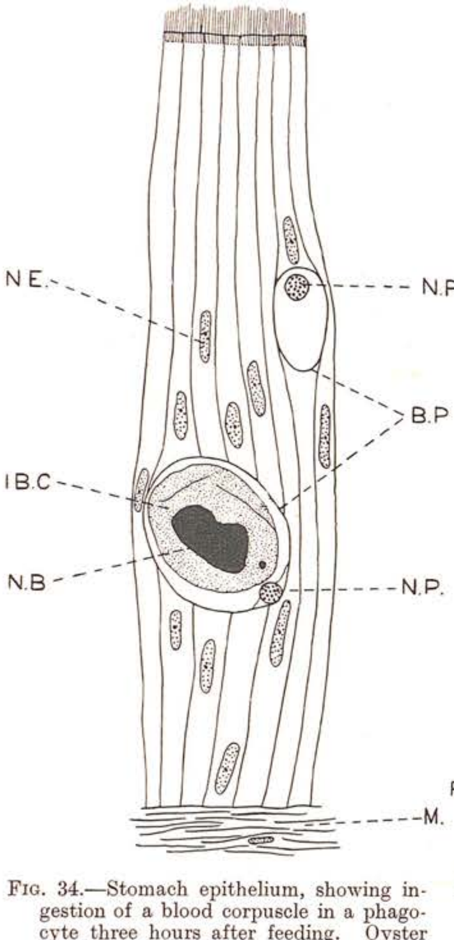

Fig. 34.—Stomach epithelium, showing ingestion of a blood corpuscle in a phagocyte three hours after feeding. Oyster starved for eleven weeks previously. Fixed strong Flemming, stained safranin and orange G. × 900. B.P., boundary of phagocyte; I.B.C., ingested blood corpuscle; M., muscle; N.B., nucleus of blood corpuscle; N.E., nucleus of epithelial cell; N.P., nucleus of phagocyte.

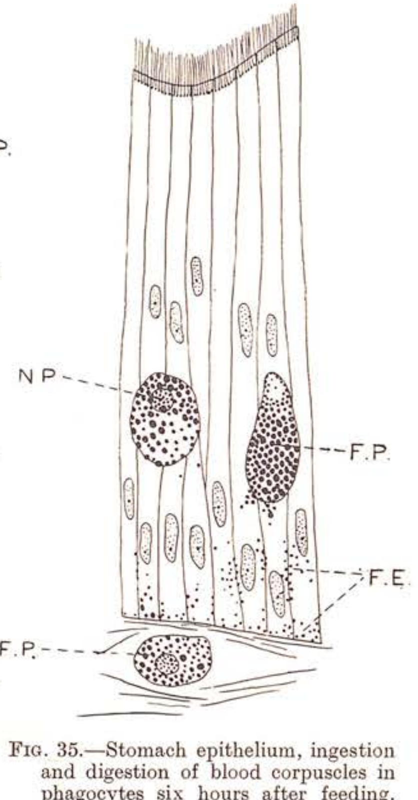

Fig. 35.—Stomach epithelium, ingestion and digestion of blood corpuscles in phagocytes six hours after feeding. Oyster starved for eleven weeks previously. Fixed Flemming, stained safranin and orange G. × 900. F.E., fat in epithelium; F.P., fat in phagocytes; N.P., nucleus of phagocyte.

was still a certain amount present, especially in the connective tissue, in the phagocytes and very occasionally at the base of the epithelial cells. Nevertheless, the difference in the fat content after feeding with blood corpuscles was quite unmistakable. Fig. 34 shows the ingestion of a corpuscle three hours after the commencement of feeding. The corpuscle lies in a phagocyte in the middle of the epithelium, the outline is uneven and the nucleus is degenerating. At this period there are few phagocytes in the epithelium, and there is practically no sign of fat in either the ingested corpuscles or in the epithelial cells. The condition

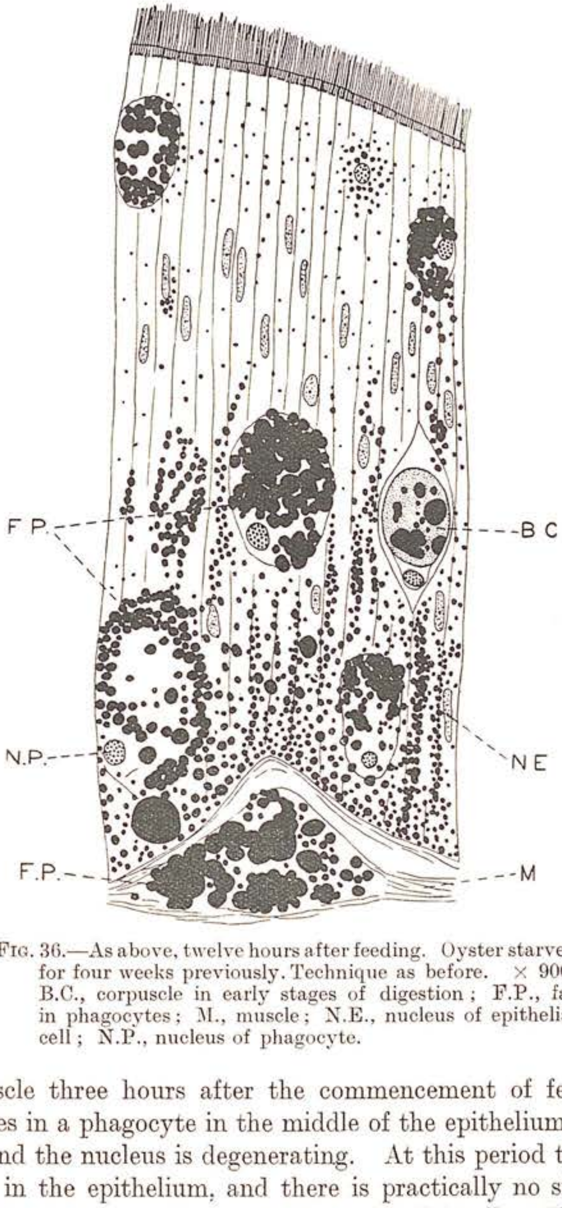

FIG. 36.—As above, twelve hours after feeding. Oyster starved for four weeks previously. Technique as before. × 900. B.C., corpuscle in early stages of digestion; F.P., fat in phagocytes; M., muscle; N.E., nucleus of epithelial cell; N.P., nucleus of phagocyte.

six hours after feeding is shown in Fig. 35. There are now many times more phagocytes in the epithelium than at the preceding period; the ingested corpuscles are difficult to distinguish, consisting now, as a result of the digestive action of the phagocytes, of a mass of fat globules. Two phagocytes laden with fat are shown in the epithelium in the figure and a third is seen passing through the circular muscle into the connective tissue. Fat is being passed from the phagocytes to the cells, in which it is accumulating near the base. Fig. 36 represents a portion of the epithelium twelve hours after feeding. Owing to the mass of fat globules it is difficult to distinguish the outline of the epithelial cells, of the phagocytes, and of the nuclei. Phagocytes are present in the epithelium in vast numbers; in the figure one phagocyte contains a corpuscle (B.C.) in the early stages of digestion, the other phagocytes containing great numbers of fat globules, which in some cases probably represent the products of digestion of two or more corpuscles. Fat has passed from the phagocytes to the cells, the whole epithelium appearing black with osmicated fat. Fat is also being transported into the connective tissue, though the nuclei and outline of the phagocyte or phagocytes which carry it are obscured by fat. There is a sharp distinction between the ciliated epithelium of the stomach and the epithelium of the gastric shield area, the latter containing no fat and few phagocytes, which never contain ingested corpuscles.

One day after feeding conditions were much the same as twelve hours after, but there was a still greater accumulation of fat in the phagocytes, in the epithelium, and in the vesicular connective tissue cells in which it is deposited by the phagocytes. It is never carried by them into the blood vessels. Conditions remain substantially the same two and three days after feeding. At the end of the latter period great quantities of fat were observed at the base of the cells of the gastric shield area, phagocytes were rare, and only at the base of the cells, and it is they, presumably, which carry the fat here from the ciliated epithelium, since there is no indication that phagocytes can pass through the substance of the gastric shield. Five days after feeding, though the connective tissue contains great quantities of fat, there are only slight traces in the epithelium, while the few phagocytes which contain fat are in most cases either at the base of the epithelium or in the basement membrane. Very similar conditions prevail six days after feeding, while after eight days there is a complete absence of fat in both epithelium and phagocytes in the ciliated areas of the stomach, but in the region of the gastric shield there is still abundance of fat near the base of the cells, though phagocytes are very rarely seen. There is a reduction in the amount of fat in the vesicular connective tissue. In an oyster fixed eleven days after feeding, however, there was no trace of fat in the epithelium of the gastric shield area, but a little, especially in the phagocytes, in the ciliated epithelium; there was a considerable reduction in the quantity of fat in the vesicular connective tissue. Fourteen days after feeding there was a considerable quantity of fat in the ciliated epithelium, phagocytes, and connective tissue. These individual variations are due probably to variations in the number of corpuscles taken in, not all the oysters having opened their shell valves for the same period, and to the degree to which they had been deprived of fat by starvation, which depends on the amount present previous to starvation. The same degree of phagocytic activity was observed in the ducts of the digestive diverticula; similar activity in the ducts has been described and figured (1926) for *Mya arenaria*.

(c) *With Olive Oil.*

An emulsion of olive oil stained red with Nile blue sulphate was injected by means of a pipette either into the mouth or mantle cavity of oysters, parts of whose shells had been drilled away so as to permit of the operation. The shell valves were then clamped, and the oysters placed in water with the drilled valve undermost, so as to prevent the light oil from floating out. The animals were examined after one day.

When opened the epithelium of the mantle, free surface of the visceral mass, gills, palps, and stomach was in many cases found to be coloured *blue* in patches, while under the microscope the gill mucus was seen to be full of phagocytes, most of them ingesting oil. Fig. 37 represents such a phagocyte. The large vacuoles (shown empty in the figure) are filled with unchanged oil, but the smaller vacuoles (black in the figure) are vividly blue, owing to the transformation of the neutral fat into fatty acids by the lipase of the phagocyte, with a consequent change in the colour of the stain. The use of Nile blue sulphate provides a very graphic demonstration of the digestion of fats. The blue colour of the epithelia was found to be due, when the tissues were cleared in glycerine, to the presence of great numbers of phagocytes, all laden with fat and fatty acids, both on the surface, in the epithelium, and in the deeper layers. The condition in the gill is shown in Fig. 38, in which

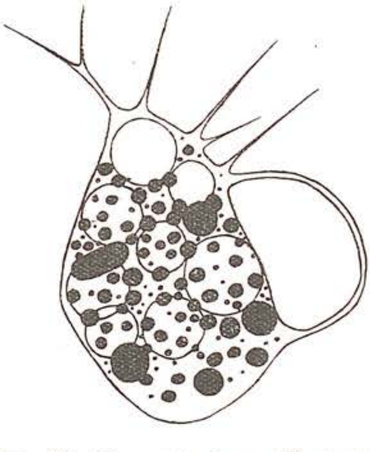

FIG. 37.—Phagocyte from gill mucus after ingestion of olive oil stained with Nile blue sulphate. Large vacuoles full of red oil, small vacuoles (shown black) containing blue stained fatty acid. Drawn from life. × 2700.

phagocytes are seen lying free on the surface of the gill, while others are passing into the tissue, and there are a line of them down the centre of the filament in the blood channel, most of them containing fat. Similar conditions prevail in the mantle, as represented in Fig. 39, the centre of the mantle tentacle being deep blue with darker spots denoting

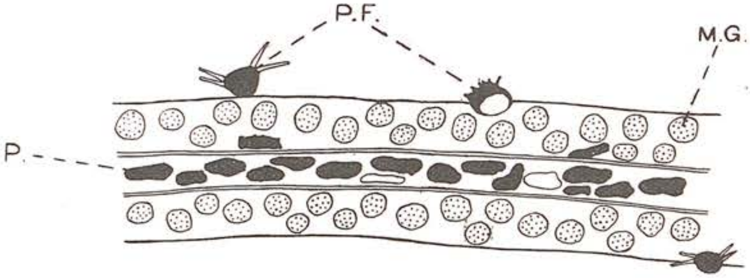

FIG. 38.—Portion of gill one day after feeding with olive oil stained Nile blue sulphate, cleared with glycerine. × 480. M.G., mucus glands; P., phagocytes with fat in centre of gill filament, others passing in; P.F., phagocytes free on surface of gill, full of fat and fatty acids.

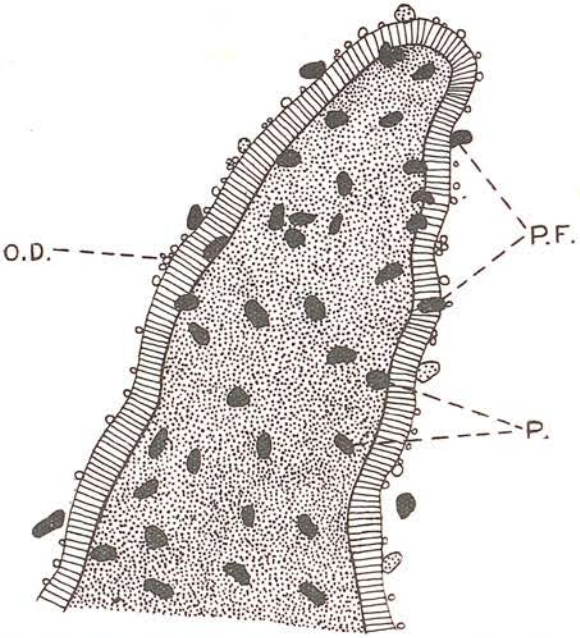

FIG. 39.—Tentacle from edge of mantle one day after feeding with olive oil stained Nile blue sulphate, cleared in glycerine. × 240. O.D., droplets of oil on surface of epithelium; P., phagocytes coloured blue owing to fatty acids, lying deep in tissues; P.F., phagocytes containing fat and fatty acids free on surface and passing through epithelium.

the presence of phagocytes near the surface. Other phagocytes are passing through the epithelium on the surface of which are more phagocytes and droplets of oil.

In the lumen of the stomach there were immense numbers of phagocytes, most of them with ingested oil. In certain cases they collected in great numbers round large droplets of oil, which had turned blue under the influence of their enzymes. *All oil droplets lying free in the stomach and not surrounded by phagocytes retained the red colour*—evidence of the absence of lipase in the stomach. Nelson (1918) also noted the absence of extracellular lipase in the stomach of other Lamellibranchs. Portions of the epithelium cleared in glycerine showed that phagocytes laden with oil were passing through it in large numbers.

(*d*) *With Nitzschia.*

Oysters which had been starved for three months were fed with a pure culture of Nitzschia, a quantity of which was added daily to the filtered sea-water. The oysters were observed to open their valves more widely than usual. One oyster was opened after seven days. In the stomach were many phagocytes ingesting Nitzschia, such as the one shown in Fig. 40, which has ingested three diatoms, and there were also very many free diatoms, while at the head of the style was a brown mass consisting exclusively of entangled diatoms. There were fewer phagocytes in the stomach than after feeding with blood corpuscles or oil. Many of the phagocytes contained green or yellow globules, the result probably of the ingestion of the brown chromatophores of the diatoms. Digestive diverticula pressed out and examined under a coverslip were largely colourless, except for the presence in some tubules of light green or brown vacuoles, which were not seen in the diverticula of starved animals. Substantially the same conditions were found after two weeks of feeding with Nitzschia.

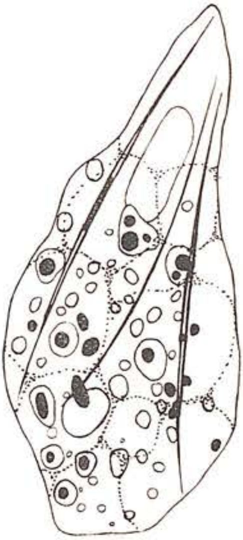
FIG. 40.—Phagocyte from stomach ingesting three Nitzschia. Drawn from life. × 2400.

Sections of the stomach and mid-gut, fixed in Flemming, showed many fat globules in the epithelium and great numbers of phagocytes. It was difficult to see ingested diatoms in the phagocytes, but in Fig. 41 is shown a portion of the edge of the stomach epithelium, in which lie two phagocytes, each containing an ingested diatom. As a result of the digestion of the diatoms, there is a quantity of fat in the phagocytes, and some has been passed into the cells of the epithelium. Conditions are thus essentially the same as after feeding with blood corpuscles. It was never possible to detect ingested diatoms in the digestive diverticula. Vonk after feeding starved oysters with plankton, never observed the presence of whole diatoms in the cells of the "liver," only numerous green inclusions of very irregular form, though occasionally green algæ appeared to be taken in entire.

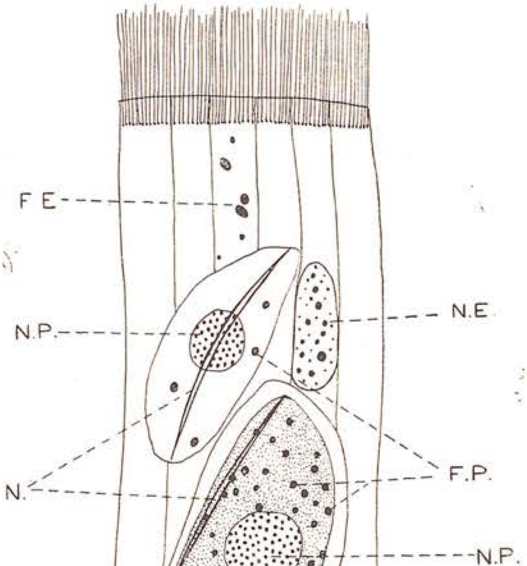

FIG. 41.—Edge of stomach epithelium, two phagocytes ingesting Nitzschia. × 2700. F.E., fat in epithelial cells; F.P., fat in phagocytes; N., Nitzschia; N.E., nucleus of epithelial cell; N.P., nucleus of phagocyte.

III. FEEDING EXPERIMENTS ON LARVÆ AND SPAT.

Larvæ placed in a suspension of iron saccharate in sea-water took it in in large amounts. A study of sections shows that it was assimilated *exclusively* in the cells of the digestive diverticula. Fig. 42 represents a transverse section through one of the two simple diverticula twenty-one hours after feeding with iron saccharate. This has been absorbed in large quantities and lies in discrete round masses in vacuoles in most of the cells. It is never in the form of fine granules or diffuse. It is being passed from the cells to phagocytes, two of which are seen in the connective tissue around the diverticula, both of them so packed with iron that only the nucleus, and that with difficulty, can be distinguished.

In the spat, iron was taken in exclusively by the cells of the digestive diverticula in the same manner as in the larvæ and adult, although iron was found in the lumen of all parts of the gut (see Figs. 19 and 20).

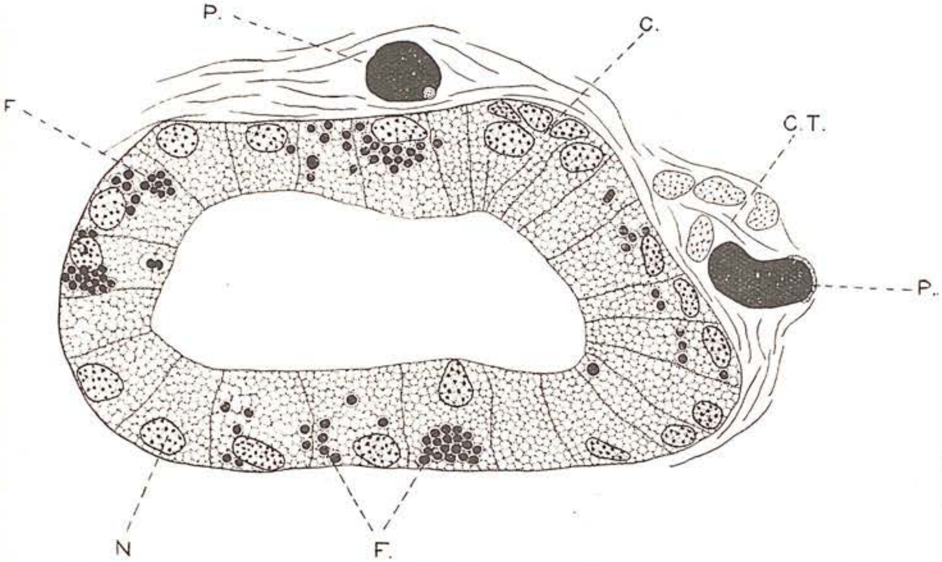

FIG. 42.—Transverse section through digestive diverticulum of one side in larval oyster. Fed on iron saccharate twenty-one hours before fixing. Iron technique. × 1800. C., crypt of young cells ; C.T., connective tissue ; F., iron lying in round vacuoles in cells ; N., nucleus of cell of diverticulum ; P., phagocytes laden with iron.

Carmine was also taken in by the spat in such quantity that in sections stained with Delafield's hæmatoxylin the lumen of the gut appeared as a uniform red. Carmine is ingested by the cells of the digestive diverticula in precisely the same manner as the iron saccharate, and in no other region of the gut.

IV. DISCUSSION OF RESULTS.

Soluble matter, such as iron saccharate, is absorbed exclusively in the cells of the digestive diverticula in larva, spat, and adult, being invariably taken into large vacuoles and carried away by leucocytes. Presumably, therefore, the products of extracellular digestion in the stomach due to the action of the digestive enzymes from the style are here absorbed. Fine particles, such as carmine grains or Indian ink (List and Yonk), are ingested by the cells of the digestive diverticula, being also taken into large vacuoles and being expelled later if of no food value. It may be assumed that the contents of the green or brown vacuoles, seen in the digestive diverticula of freshly fed animals (see Fig. 11), consist of finely divided vegetable matter which has been ingested by the cells and is in process of being digested intracellularly within the vacuoles. The presence of bright yellow or brown concretions, which alone remain in the diverticula after prolonged starvation, and which are also found in the lumen of the ducts and of the hinder portions of the gut represents in all probability the indigestible remnants of this intracellular digestion which is expelled in the same manner as the Indian ink. These concretions are best seen in Pecten (Yonge (1926)). It has already been shown that there is a mechanism for ensuring a circulation of particles in the tubules of the digestive diverticula. The presence of the enterochlorophyll described by MacMunn in the cells of the tubules and in the leucocytes in the connective tissue round about them, and in other parts will be the result of the decomposition of the ingested chlorophyll.

All larger particles, such as droplets of oil, blood corpuscles, or even such small diatoms as *Nitzschia closterium* forma *minutissima*, are ingested by the phagocytes, which abound everywhere in the mantle cavity and gut, but particularly in the stomach, ducts of the digestive diverticula and mid-gut. They very rarely pass into the tubules of the digestive diverticula, those that enter the ducts being there seized by phagocytes. Ingested matter is rapidly digested by the phagocytes, part of the products of digestion being passed into the cells of the epithelium, including that of the gastric shield area, and the remainder carried to the vesicular connective tissue cells, or Langer's vesicles, and there stored. *No evidence of any absorption in the epithelium of the gut or of any free surface in the mantle cavity, other than by the agency of phagocytes, was found*, and previous accounts of direct absorption by the ciliated epithelium on further investigation will probably be found to be the result of the action of phagocytes and the transference of material from them to the cells.

5. THE DIGESTIVE ENZYMES.

Digestive enzymes are present in the style and in the tissue of the digestive diverticula, the former are released into the stomach when the style dissolves and the latter remain in the tissues, where they act intracellularly. It is clear from the results of the experiments described in the last section that the phagocytes must also possess powerful digestive enzymes of various kinds. The enzymes were obtained by grinding up the styles or the excised tissue of the digestive diverticula with sand, and then extracting for two or three days with distilled water (the extracts being as efficacious as those prepared in sea-water and being easier to deal with), toluol being used as antiseptic. Except when otherwise stated, extracts of the style were always of a strength of 1% and extracts of the digestive diverticula 10%, and incubation took place at about 30° C. Rigorous controls consisting of boiled extracts were invariably set up. All experiments were confined to adult oysters.

I. THE STYLE.

The presence of digestive enzymes in the style was first discovered by Coupin (1900), who found an amylase and a weak invertase in the style of Cardium; this has been confirmed, amongst others, by Mitra (1901), who found amylase and glycogenase in Anodonta, Van Rynberk (1908), who found amylase and invertase in Mytilus, Nelson (1918), who found similar enzymes in Anodonta, and Yonge (1923), who found amylase and glycogenase in the style of Mya, and showed that the amylase had all the properties of a typical enzyme. More recently Berkeley (1923) has found an oxidase in the styles of several Lamellibranchs. Barrois (1889) gives a detailed chemical analysis of the styles of Cardium made for him by Lambling, who found that they consisted of 87·11% water, 12·03% solid organic matter, and 0·86% solid inorganic matter. The mass of the organic matter consisted of a globulin, though traces of a mucin or chondrin like substance were found. List also found the latter in the styles of Mytilus. Mitra (1901), in ignorance of the work of Barrois, made a thorough examination of the styles of Anodonta, with almost identical results. Mackintosh (1925) finds that the style of Crepidula consists largely of globulin with some mucus. Mitra thought that the style represented a mass of enzyme, but Nelson (1918) advances the more probable view that the enzymes are *adsorbed* on the surface of globules of albuminoid substance.

In view of the complete agreement of previous workers, I have not carried out a chemical examination of the style of Ostrea, there being no reason to doubt that it differs in any important degree from those which have been analysed.

(*a*) *Specificity.*

In common with previous workers, I have failed to find any trace of proteoclastic or lipoclastic enzymes in the style, experiments with calcified milk, methyl acetate, and phenol red milk, all giving negative results. No action was found on the glucosides, amygdalin and salicin, on pectin or on lactose, maltose, raffinose, cellulose, or sucrose (in spite of the contrary assertions of Coupin and Mitra with regard to the latter). Starch and glycogen, as in Mya, were the only substances acted on by the enzymes of the style, both being rapidly converted into reducing sugars, as shown by their action on Fehling's and Benedict's reagents. The properties of the amylase have been studied in detail.

(*b*) *Influence of Temperature on Amylase.*

The experiments shown in Table I were carried out to determine the optimum temperature for the working of the style amylase. The enzyme was destroyed after incubation, the contents of each tube filtered and made up to the original volume.

TABLE I.

OPTIMUM TEMPERATURE OF STYLE AMYLASE.

10 c.c. of extract with 10 c.c. of 1% starch solution in each experiment.

1. Extract of 1·14 gms. of style made in 70 c.c. toluol water. Experiments incubated for 4 hours.

Temperature.	Titrated with 10 c.c. Benedict.
16° C.	9·95 c.c. needed.
25° C.	9·7 ,,
30° C.	9·2 ,,
35° C.	9·05 ,,
40° C.	8·9 ,,
48° C.	8·9 ,,
55° C.	10·0 ,,

2. Extract of 0·93 gms. of style made in 50 c.c. toluol water. Incubated for 3 hours.

Temperature.	Titrated with 10 c.c. Benedict.
40° C.	15·05 c.c. needed.
43° C.	14·35 ,,
46° C.	14·7 ,,
49° C.	15·45 ,,
52° C.	16·25 ,,

These two experiments demonstrate that the optimum temperature lies at, or a little below, 43° C. The pH was 5·9 in both experiments.

Experiments were carried out to determine the temperature of destruction. The heating of 5 c.c. of enzyme extract for fifteen minutes at eight temperatures between 100° C. and 56° C. resulted in complete destruction of the enzyme, as shown by subsequent incubation for twenty hours at 30° C. with 1% starch solution. Heating at 55° C. and all lower temperatures resulted in some of the enzyme remaining active.

It appears that the enzyme is destroyed at 56° C. There was practically no action on starch at 0° C., the enzyme being inactivated, not destroyed. It is interesting to compare the above optimum temperature and temperature of destruction with those found for the style enzyme of Mya (1923), which were 32° C. and 51° C. respectively. The difference between the optima is very striking, and may reflect differences in the habitat of the two animals ; it is known that the oyster will breed and flourish in the Norwegian pools, where the temperature may rise as high as 90° F. (32° C.), but in neither animal does the optimum temperature represent anything approaching the temperature at which digestion must normally proceed.

(c) *Influence of pH.*

Table II shows the results of an experiment to determine the optimum pH for the working of the amylase.

TABLE II.

OPTIMUM PH OF STYLE AMYLASE.

Extract of 1·36 gms. of style made in 90 c.c. toluol water. 10 c.c. of extract and 10 c.c. of 1% starch solution in each experiment with acid or alkali, volume made up to 25 c.c. with water. All incubated for 6 hours at 32° C.; pH determined by Clark and Lubs' indicators.

	·01N HCl.	·01N NaOH.	Initial pH.	Titrated with 10 c.c. Benedict.
A.	3·0 c.c.	—	3·4	No reduction.
B.	0·5 c.c.	—	4·9	55·4 c.c. needed.
C.	0·3 c.c.	—	5·2	13·5 ,,
D.	—	—	5·9	9·1 ,,
E.	—	0·1 c.c.	6·2	9·7 ,,
F.	—	0·2 c.c.	6·6	10·15 ,,
G.	—	0·5 c.c.	7·3	11·6 ,,
H.	—	0·7 c.c.	7·6	13·05 ,,
I.	—	1·0 c.c.	9·3	21·0 ,,

The optimum is very sharply defined, and lies at about 5·9, i.e. at the pH produced by the dissolution of the style in water, on either side of this point, and particularly on the acid side, the efficiency of the enzyme being rapidly reduced.

(d) *Influence of Salts.*

In view of the fact that if the pancreatic amylase is dialysed it loses its power to act upon starch, as shown by Bierry, Giaja, and Henri (1906), and that the amylase from the liver is inactivated in the same manner (Starkenstein (1910, 1910a)), action being restored in the former case by the addition of the electro-negative chloride or bromide ions, and in the latter by the addition of sodium chloride, experiments were carried out to determine whether the amylase of the style is similarly dependent for its efficacy on the presence of electrolytes.

An extract of 0·75 gms. of style was made in 40 c.c. of toluol water. After three days the enzyme was precipitated by the addition of 200 c.c. of absolute alcohol, the precipitate being filtered off, thoroughly washed with absolute alcohol, dried, and then dissolved in 40 c.c. of glass-distilled water. The experiments in Table III were then carried out, the sea-water used in experiments B and C being made acid until the pH approximated to the optimum.

TABLE III.

ACTION OF PURIFIED ENZYME WITH AND WITHOUT SALTS FROM SEA-WATER.

10 c.c. extract with 10 c.c 1% starch solution in each experiment. Incubated for 5 hours at 32° C., enzyme destroyed and titrated.

	Added.	pH.	Titrated with 10 c.c. Benedict.*	
A.	20 c.c. distilled water	5·8	175	c.c. needed
B.	20 c.c. 100% sea-water	5·7	28·05	,,
C.	20 c.c. 200% sea-water	5·5	25·6	,,
D.	20 c.c. dis. water and 1 drop sea-water	5·8	72·75	,,

In the absence of the salts present in sea-water the enzyme is almost inactivated (A), action is restored to some extent by the addition of a trace of sea-water (D), and fully restored in a medium of 50% (B) or 100% (C) sea-water, action being slightly less in the former.

A series of dialysis experiments were then carried out, details of which are given in Tables IV, V, and VI.

TABLE IV.

ACTION OF DIALYSED EXTRACT.

0·75 gms. style extracted in 80 c.c. toluol water for 3 days, divided into two parts, A and B, each of 40 c.c. These dialysed in separate parchments for 3 days, surrounding fluid being changed daily, contents of each finally made up to 40 c.c. 10 c.c. extract with 10 c.c. 1% starch solution in each experiment. Incubated for 5 hours at 32° C., enzyme destroyed and titrated.

		Added.	pH.	Titrated with 10 c.c. Benedict.*	
A.	1.	10 c.c. distilled water	5·8	275	c.c. needed.
	2.	10 c.c. acidified sea-water	5·8	24·05	,,
	3.	10 c.c. surrounding fluid	5·8	230	,,
	4.	10 c.c. 1% NaCl	5·8	28·75	,,
B.	1.	10 c.c. distilled water	5·8	290	,,
	2.	10 c.c. 1% Na_2SO_4	5·8	290	,,
	3.	10 c.c. 1% NaBr	5·8	50	,,
	4.	10 c.c. 1% KCl	5·8	40·1	,,

* Or suitable aliquot part.

TABLE V.

ACTION OF DIALYSED EXTRACT.

0·45 gms. style extracted in 40 c.c. toluol water, dialysed 3 days, water changed 4 times. Experiments conducted as in Table IV.

		Added.	pH.	Titrated with 10 c.c. Benedict.*
C.	1.	10 c.c. distilled water	6·4	241·5 c.c. needed.
	2.	10 c.c. 1% Na_2CO_3	9·8	186·5 ,,
	3.	10 c.c. 1% KI	6·6	96·5 ,,
	4.	10 c.c. 1% $CaCl_2$	5·7	23·0 ,,

TABLE VI.

ACTION OF DIALYSED EXTRACT.

0·64 gms. style extracted in 60 c.c. toluol water, dialysed 4 days, water changed 4 times. Experiments conducted as in Table IV.

		Added.	pH.	Titrated with 10 c.c. Benedict.*
D.	1.	10 c.c. distilled water	6·6	270 c.c. needed.
	2.	10 c.c. 1% MgCl	5·8	46·5 ,,
	3.	10 c.c. 1% NaF	6·0	270 ,,
	4.	10 c.c. 1% $NaNO_3$	6·2	123·5 ,,
	5.	10 c.c. 1% K_2SO_4	6·1	300 ,,
	6.	10 c.c. 1% BaCl	5·8	40 ,,

An examination of the results of these four sets of experiments shows that the dialysed extract is almost without action on starch, but that action is restored to a slight degree on the addition of 10 c.c. of the water into which the salts had passed from out of the parchment (A3), while action was completely restored as before on the addition of sea-water (A2). Action was also restored in the presence of the chlorides of sodium (A4), potassium (B4), calcium (C4), magnesium (D2), and barium (D6), and in that of sodium bromide (B3). To a less extent it was restored in the presence of the iodide of potassium (C3), the nitrate of sodium (D4) and the carbonate of sodium (C2), in spite of the high pH in the last case. There was no increase in activity in the presence of the sulphates of sodium (B2) or potassium (D5), or in that of sodium fluoride (D3). The amylase of the style appears, therefore, to need for its action the presence of electro-negative ions—preferably those of chlorine or bromine—the identity of the electro-positive ion being immaterial. Conditions are the same as in the case of the amylase of the pancreas or of the liver in Vertebrates. Since the extracts of the style made up in distilled water have the same efficacy as those prepared in sea-water it appears that these ions are present in sufficient quantity in the substance of the style.

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* Or suitable aliquot part.

II. THE DIGESTIVE DIVERTICULA.

The presence of digestive enzymes in extracts of the digestive diverticula has been shown by Fredericq (1878), who found protease in Mya and Mytilus; Mitra (1901), who found amylase and invertase in Anodonta; Van Rynberk (1908), who found amylase in Mytilus; Dakin (1909), who found amylase, protease and lipase in Pecten; Heymann (1914), who found protease, lipase and a variety of sucroclastic enzymes in Ostrea; and Yonge (1923), who found in Mya sucroclastic enzymes which acted on starch, glycogen, sucrose, maltose, and lactose, also a protease acting in acid media and a lipase. Most of these workers considered that the digestive diverticula were secretory, and that these enzymes were discharged into the stomach. As shown in detail in a previous paper (1926) there is no evidence, histological or physiological, of any secretion in the diverticula which are organs of absorption and of intracellular digestion, the digestive enzymes acting on material ingested.

TABLE VII.

ACTION OF 10% EXTRACT OF DIGESTIVE DIVERTICULA ON CARBOHYDRATES, ETC.

10 c.c. extract with 10 c.c. of substrate, controls of boiled extract, incubated at 30° C.

No.	Substrate.	Time.	Experiment.	Control.
			Titrated with 10 c.c. Benedict.	
1.	1% starch	2 hrs.	4·3 c.c.	9·0 c.c.
2.	0·5 % glycogen	1 day	5·9 c.c.	9·0 c.c.
3.	5% sucrose	,,	4·8 c.c.	9·0 c.c.
4.	1% raffinose	3 days	6·8 c.c.	9·0 c.c.
5.	1% inulin	,,	8·2 c.c.	8·2 c.c.
6,	1% salicin	,,	4·2 c.c.	8·3 c.c.
7.	1% amygdalin	,,	4·2 c.c.*	8·1 c.c.
			1 c.c. boiled with 5 c.c. Barfoed's sol. 10 min.	
8.	2% maltose	1 day	Reduction	No reduction.
9.	2% lactose	,,	Reduction	No reduction.

* Smell of CN.

(a) *Sucroclastic Enzymes.*

Specificity.—Owing to the presence of reducing sugars in the extract of the digestive diverticula, it is necessary to estimate the sugar in both experiments and controls. In Table VII are shown the results of experiments on the simpler carbohydrates and glucosides. Starch, glycogen, sucrose, raffinose (to a slight degree), maltose, and lactose were all digested by the enzymes in the extract and also the two glucosides, salicin and amygdalin. Inulin was not digested. A series of longer experiments was set up to determine whether cellulose or pentosans are digested. Both of these are of great importance since cellulose must bulk large in the food of the oyster, while Petersen (1911), in his work on the food of oysters in the Limfjord, maintained that detritus was the principal source of food, and Boysen Jensen (1914) has shown that the main constituent of this detritus consists of pentosans. No experiments were made by him on the digestion of pentosans, although Heymann (1914), by somewhat questionable methods, found that pectin was digested by extracts of the

TABLE VIII.

ACTION OF 10% EXTRACT OF DIVERTICULA ON CELLULOSE, PENTOSANS, AND INULIN.

No.	Experiment.	Temp.	Time.	Titrated with 10 c.c. Benedict.
1.	A. 20 c.c. with 0·5 gm. sawdust.	32° C.	3 wks.	A. 3·2 c.c.
	B. Ditto boiled.	,,	,,	B. 5·2 c.c.
	C. 20 c.c. extract alone.	,,	,,	C. 3·2 c.c.
2.	A. 20 c.c. with 0·5 gm. sawdust.	,,	2 wks.	A. 2·55 c.c.
	B. Ditto boiled.	,,	,,	B. 3·2 c.c.
	C. 20 c.c. extract alone.	,,	,,	C. 2·55 c.c.
3.	A. 10 c.c. with 10 c.c. 1% pectin.	,,	15 days.	A. 5·0 c.c.
	B. Ditto boiled.	,,	,,	B. 7·0 c.c.
	C. 10 c.c. with 10 c.c. water.	,,	,,	C. 5·0 c.c.
4.	A. 20 c.c. with 10 c.c. 1% pectin.	,,	16 days.	A. 4·45 c.c.
	B. Ditto boiled.	,,	,,	B. 7·30 c.c.
	C. 20 c.c. with 10 c.c. water.	,,	,,	C. 4·5 c.c.
5.	A. 20 c.c. with 10 c.c. 5% gum arabic.	,,	2 wks.	A. 2·4 c.c.
	B. Ditto boiled.	,,	,,	B. 2·92 c.c.
	C. 20 c.c. with 10 c.c. water.	,,	,,	C. 2·4 c.c.
6.	A. 20 c.c. with 10 c.c. 5% gum arabic.	,,	3 wks.	A. 2·2 c.c.
	B. Ditto boiled.	,,	,,	B. 4·5 c.c.
	C. 20 c.c. with 10 c.c. water.	,,	,,	C. 2·6 c.c.
7.	A. 10 c.c. with 10 c.c. 2% inulin	,,	2 wks.	A. 5·85 c.c.
	B. Ditto boiled.	,,	,,	B. 9·8 c.c.
	C. 10 c.c. with 10 c.c. water.	,,	,,	C. 6·0 c.c.
8.	A. 20 c.c. with Ulva 3″×1″	,,	3 wks.	A. Ulva unchanged
	B. Ditto boiled.	,,	,,	B. Ulva unchanged.

" liver " of the oyster. The same author also maintaining that inulin is digested, a longer experiment was set up in order to confirm the results of the experiment in Table VII. In view of the autolysis which proceeds if tissue extracts are left for any long period, resulting in the formation of additional quantities of reducing sugars, two controls were necessary for these experiments, one with boiled extract and substrate and the other with unboiled extract without substrate. Sawdust was used for the experiments on cellulose, owing to the presence in it of hemicelluloses, which do not occur in filter paper. Table VIII gives the result of these experiments.

None of these substances were digested, the only increase in reducing sugar being due to autolysis. Cellulose in the form of sawdust or as the green alga, Ulva, was not digested even after three weeks incubation. It would have been surprising if it had since the power of digesting cellulose by means of an enzyme is rare, being confined, in the Mollusca, to certain of the herbivorous Pulmonates and Tectibranchs, which secrete an extracellular cellulase and, in the Lamellibranchs, to the specialised Teredinidæ, which digest wood intracellularly (for résumé of work on this subject see Yonge (1925a)). After incubations of two and three weeks there was no indication of the digestion of the pentosans, pectin and gum arabic. It is impossible to confirm the findings of Heymann, nor is confidence in his work strengthened by the negative results of the experiments here performed on inulin. The implications of these results on the theories of Petersen and Boysen Jensen will be discussed later.

Influence of Temperature on Amylase.—Similar experiments to those carried out on the style amylase were done on the amylase from the digestive diverticula. The experiments in Table IX were performed to determine the optimum temperature.

TABLE IX.

OPTIMUM TEMPERATURE OF AMYLASE.

10 c.c. 10% extract with 10 c.c. 1% starch solution, digests in left column incubated 2 hours, in right column 3 hours.

Temperature.	Titrated with 10 c.c. Benedict.	Temperature.	10 c.c. Benedict.
18·5° C.	7·75 c.c. needed.	40° C.	5·2 c.c. needed.
28° C.	6·8 ,,	43° C.	5·0 ,,
35° C.	6·4 ,,	46° C.	5·0 ,,
40° C.	6·3 ,,	49° C.	5·2 ,,
45° C.	6·25 ,,	52° C.	5·4 ,,
50° C.	6·8 ,,		
55° C.	8·0 ,,		
60° C.	9·45 ,,		

These experiments show that, at pH 5·5, the optimum temperature is 44·5° C., i.e. slightly higher than that of the style amylase, where the pH, however, was 5·9.

Experiments to determine the temperature of destruction showed that the heating of 5 c.c. of enzyme extract for fifteen minutes at four temperatures between 100° C. and 67° C. resulted in complete destruction of the enzyme as shown by subsequent incubation for twenty hours at 30° C. with 1% starch. The enzyme remained active after heating at 64° C. and all lower temperatures. The temperature of destruction therefore, at pH 5·5, lies between 64° C. and 67° C. This is considerably higher than that of the style amylase (56° C.); there, however, the pH was 5·9, and as Compton (1921 and previous papers therein quoted) has shown that temperature optima of enzyme actions are dependent, amongst other things, on pH, there is not rigorous proof that the two enzymes are distinct in their properties. The action of the amylase from the diverticula is practically inhibited at 0° C.

Influence of pH.—The experiment in Table X was carried out to determine the optimum pH for the action of the amylase.

TABLE X.

OPTIMUM PH OF AMYLASE FROM DIVERTICULA.

10 c.c. 10% extract and 10 c.c. 1% starch solution with acid or alkali, volume made up to 25 c.c. with water. Incubated for 2 hours at 30° C.

	HCl.	NaOH.	Initial pH.	Titrated with 10 c.c. Benedict.	
A.	5 c.c. ·1N	—	2·4	10·8 c.c. needed.	
B.	3 c.c. ·1N	—	3·2	9·6	,,
C.	1 c.c. ·1N	—	3·6	8·4	,,
D.	3 c.c. ·01N	—	4·0	7·45	,,
E.	2 c.c. ·01N	—	4·6	6·65	,,
F.	1 c.c. ·01N	—	5·0	6·1	,,
G.	—	—	5·5	5·8	,,
H.	—	1 c.c. ·01N	5·8	6·0	,,
I.	—	2 c.c. ·01N	6·2	6·03	,,
J.	—	3 c.c. ·01N	6·6	6·1	,,
K.	—	5 c.c. ·01N	7·0	6·45	,,
L.	—	0·8 c.c. ·1N	7·8	7·3	,,
M.	—	1 c.c. ·1N	8·6	8·0	,,
N.	—	2 c.c. ·1N	9·6	9·4	,,

The optimum lies at about pH 5·5, i.e. somewhat lower than that of the style (5·9). The optimum is not so sharply defined as in the case of the style enzyme, the efficacy of the enzyme not decreasing so rapidly on either side of that point.

Influence of Salts.—A number of experiments were conducted to determine the action of salts on the activity of the amylase, the results being given in Tables XI and XII.

TABLE XI.

ACTION OF PURIFIED ENZYME WITH AND WITHOUT SALTS FROM SEA-WATER.

15 gms. diverticula extracted in 60 c.c. toluol water, enzyme precipitated with alcohol and purified as in expts. on style. Ppt. dissolved in 40 c.c. glass distilled water. 10 c.c. extract with 10 c.c. 1% starch in each experiment, incubated for 5 hours at 32° C.

	Added.	pH.	Titrated with 10 c.c. Benedict.
A.	20 c.c. distilled water.	6·4	29·0 c.c. needed.
B.	20 c.c. 100% sea-water.*	5·8	17·4 ,,
C.	20 c.c. 200% sea-water.*	5·6	17·3 ,,
D.	20 c.c. dis. water and 1 drop sea-water.	6·4	24·4 ,,

TABLE XII.

ACTION OF DIALYSED EXTRACT.

50 c.c. 10% extract dialysed for 3 days, water changed 4 times. Experiments conducted as in Table XI.

	Added.	pH.	Titrated with 10 c.c. Benedict.
A.	10 c.c. distilled water.	6·6	38·8 c.c. needed.
B.	10 c.c. 1% NaCl.	5·8	23·25 ,,
C.	10 c.c. 1% NaBr.	9·6	28·2 ,,
D.	10 c.c. 1% $CaCl_2$.	5·8	22·65 ,,
E.	10 c.c. 1% KI.	6·0	31·75 ,,

Here again the enzyme requires for its working the presence of the salts in sea-water, only a trace of which has a considerable effect (Table XI, D). The action of the enzyme is definitely inhibited after dialysis. It is more difficult to purify the enzyme from the tissue extract than from the style and hence the greater activity of the dialysed enzyme in this case. Action was restored in the presence of the chlorides of sodium and calcium (Table XII, B and D) and of the bromide of sodium (C)—the reduced action in the last case being due to the high pH, owing to the presence

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* Acidified.

of impurities in the salt—and to a slighter extent in the presence of potassium iodide (E).

(*b*) *Lipoclastic Enzymes.*

The results of a series of experiments on the lipase in the digestive diverticula are shown in Table XIII.

TABLE XIII.

ACTION OF 10% EXTRACT OF DIGESTIVE DIVERTICULA ON FATS AND ESTERS.

Controls of boiled extract, incubation at 32° C.

				Acidity in terms of ·1N NaOH.	
No.	Extract.	Substrate.	Time.	Experiment.	Control.
1.	15 c.c.	30 drops olive oil emulsion	7 days	3·2 c.c.	2·5 c.c.
2.	25 c.c.	30 drops ,, ,,	14 ,,	2·5 c.c.	2·1 c.c.
3.	20 c.c.	30 drops ,, ,,	21 ,,	1·05 c.c.	0·85 c.c.
4.	10 c.c.	10 c.c. 5% methyl acetate	7 ,,	9·0 c.c.	2·5 c.c.
5.	10 c.c.	10 c.c. 10 % ,, ,,	14 ,,	17·35 c.c.	5·15 c.c.
6.	5 c.c.	5 c.c. boiled milk with 3 c.c. 2 % Na_2CO_3 and phenol red.	17 hrs.	Yellow.	Remains Red.
7.	5 c.c.	ditto with 1 c.c. Na_2CO_3	19 ,,	Yellow.	Remains Red.

The action on olive oil is very slight even after three weeks incubation; but there is considerable action on methyl acetate, and experiments with phenol red milk were all positive. Since fat is taken in freely by the phagocytes and there digested, very little appearing in the digestive diverticula, there is probably no necessity for the presence of a powerful lipase in the latter. Indeed, the slight lipolytic action of the extract may be due, in part at any rate, to the phagocytes in the tissue extracted and *not* to enzymes from the actual absorptive tubules.

(*c*) *Proteoclastic Enzymes.*

It is very difficult to test for the presence of proteoclastic enzymes in extracts of the diverticula on account of the weakness of their action. No digestive activity on coagulated egg albumen or congo red fibrin could be demonstrated. Satisfactory results were obtained by the method of Dernby (quoted by Bodansky and Rose). A 10% solution of gelatin was prepared and a series of experiments performed with extracts of the diverticula at different hydrogen ion concentrations. At stated intervals

5 c.c. of the digests were removed and the process of digestion determined by placing them in ice for fifteen minutes, and then observing the degree of liquefaction. The gelatin is liquefied as digestion proceeds, and fails to solidify to a greater or less extent dependent upon the degree to which digestion has proceeded. Dernby used the following scale of numbers to denote the approximate degree of digestion :—

0 = Completely solid.
1 = Solid, but small pieces may be torn off by strong shaking.
2 = Solid, but the surface moves somewhat when tubes are shaken.
3 = Soft.
4 = Half liquid.
5 = Almost liquid.
6 = Entirely liquid.

Table XIV shows the result of an experiment of this nature which confirmed the results of a previous experiment. There appear to be two optima, one at a pH of about 3·7 and the other at and above pH 9·0. There is *no* action at the normal pH of the tissue extract, while optimum conditions prevail at a degree of alkalinity which cannot be present

TABLE XIV.

DIGESTION OF GELATIN BY EXTRACT OF THE DIVERTICULA.

10 c.c. 15% extract with HCl or NaOH with 15 c.c. 10% gelatin with water = 30 c.c.

No.	HCl.	NaOH.	Initial pH.	Degree of liquefaction after incubation at 32° C. for :— 2 days.	3 days.	4 days.	5 days.
1	2·5 c.c. N	—	2·2	1–2	1–2	2	3
2	1·0 c.c. N	—	3·7	5	6	6	6
3	5·0 c.c. ·1N	—	4·2	2	3	4	6
4	2·5 c.c. ·1N	—	4·8	1–2	2	2	2
5	5·0 c.c. ·01N	—	5·4	1	1	1	1
6	—	—	5·8	0	0	0	0
7	—	0·7 c.c. ·1N	6·0	0	0	0	0
8	—	1·0 c.c. ·1N	6·4	0	0	0	0
9	—	2·0 c.c. ·1N	7·3	0–1	1	1–2	3
10	—	3·0 c.c. ·1N	8·6	2	2	3	6
11	—	4·0 c.c. ·1N	9·2	2–3	3	6	6
12	—	5·0 c.c. ·1N	9·8	3	3	6	6
13	—	1·0 c.c. N	10·2	3	3–4	6	6
14	—	2·0 c.c. N	10·8	6	6	6	6
15	—	3·0 c.c. N	11·3	6	6	6	6

normally in the tissues. It may be that we are dealing here with two enzymes, as Bodansky and Rose (1922) believe to be the explanation of similar double optima obtained in experiments of the same nature on certain Coelenterates. In the case of the oyster, one enzyme may come from the digestive diverticula and the other from the phagocytes ; Heymann, indeed, states that there are three proteases in the oyster : a trypsin, a " liver " pepsin, and a blood pepsin. He knew nothing, however, of the digestive powers of the phagocytes. It is useless to call one pepsin and the other trypsin, as it is possible at the optimum of either for the extract to act on peptone with the formation of amino acids, as proved by positive results of tests for tryptophane eighteen hours after the commencement of experiments. On the other hand, *after three weeks digestion with gelatin there is no indication of the presence of amino acids* in any medium. The extract coagulates calcified milk in four or five hours.

The important point in connection with this work is not whether there are two enzymes or one, but the *weakness* of the proteoclastic enzyme. Although albumenoses are split up with formation of amino acids, gelatin is not, while albumen and fibrin are not attacked. It takes two days for the digestion of gelatin to proceed to the stage it attained in one or two hours in the experiments of Bodansky and Rose on the Coelenterates, Physalia and Stomolophus. These animals are by nature carnivorous, whereas the oyster is not, and it is an interesting fact that in the Ascidian, *Ciona intestinalis*, which also feeds by ciliary currents and has a similar diet to the oyster, it was found (1925) that there is a similar weakness of proteoclastic enzymes, though in this case digestion is exclusively extracellular. Apparently there is a correlation between the nature of the food and the variety and strength of the digestive enzymes in animals. In Ciona, as in the Lamellibranchs, the sucroclastic enzymes are very powerful. In the omnivorous Crustacea both sucroclastic and proteoclastic enzymes are highly developed (Yonge (1924)).

III. STOMACH CONTENTS.

Digests with the stomach fluid show the presence of enzymes, presumably derived from the style, capable of quickly digesting starch and glycogen. Slight traces of reducing sugars were found after three days incubation with sucrose, maltose and amygdalin, but none after five days incubation with lactose. This action is far slighter than that of the extract of the digestive diverticula and can safely be attributed to the phagocytes, great numbers of which are always present in the stomach. To the same origin, no doubt, can be attributed the traces of lipase and protease. Phenol red milk made alkaline with 2 c.c. of 2% Na_2CO_3 is turned yellow in two hours by the action of stomach fluids and calcified milk is coagulated in the same time. These experiments were repeated with filtered and unfiltered fluid, since in the former the phagocytes would be absent. The experiments were otherwise identical in all respects and controls were set up. In the test for lipases the phenol red milk was turned yellow in two hours by the unfiltered fluid and in twelve hours by the filtered fluid ; in the test for protease the calcified milk was coagulated in twelve hours by the unfiltered and in forty hours by the filtered fluid, the control also coagulating after forty hours in the latter case. As we have seen there is *no action on olive oil* by enzymes free in the stomach, only by phagocytes. There is thus no evidence that the digestive diverticula secrete enzymes into the stomach, since the only enzymes of any power proceed from the style, the traces of other enzymes having their origin in the phagocytes. The lack of powerful digestive enzymes in the digestive tract is confirmed by the presence—noted by many workers—of living and apparently unprotected organisms, both plant and animal, in the mid-gut, rectum and fæces of the oyster and other Lamellibranchs. No naked organism, unless protected chemically like intestinal parasites, could survive the action of powerful enzymes.

IV. Gill Mucus.

Gorka (1916), in a paper which I have been unable to see, but which is quoted by Vonk, states that he found enzymes in the gill mucus of Anodonta and Unio capable of digesting polysaccharides, glucosides and fat, and in the mucus of the palps he also found a protease. A series of experiments on the gill mucus of Ostrea were carried out, the mucus being obtained by covering the gills with fine carborundum and collecting the mucus laden strings and extracting them in toluol water, later filtering off the carborundum. After four days incubation no trace of action on any carbohydrate or glucoside was found, nor did digests with phenol red milk or olive oil give positive results, although there was a slight increase in acidity after two weeks incubation with methyl acetate. Traces of tryptophane were found after two weeks incubation with peptone, while calcified milk was coagulated after three days. In both cases controls gave negative results. There appear therefore to be traces of lipase and protease in the mucus, but if that is examined under the microscope many phagocytes are seen which wander freely on the surface of the gill, as already described in the section on feeding with olive oil. There seems no doubt that the slight development of enzymatic action in these experiments, and probably in those of Gorka, is due to enzymes from these phagocytes.

V. OXIDASES.

It is most convenient here to refer to the presence of oxidases in the tissues. Berkeley (1923) has shown that extracts of the styles of *Saxidomus giganteus*, *Paphia staminea*, and *Mya arenaria* have a marked oxidising action on guaiacum, paraphenylendiamine, and pyrogallol in the absence of H_2O_2, and in its presence after boiling, and further that the oxidation of guaiacum takes place as rapidly in the absence of air. He suggests, in connection with his theory that the style is concerned with anærobic respiration (to which reference will be made later), that the substance is a complex of an oxidising agent and an enzyme which can convey oxygen to the tissues. He also found a slight action on guaiacum by extracts of the palps and traces by those of the mantle and " digestive gland," but none by those of the gills, gonad, or siphons.

In the oyster, extracts were made of the mantle, gills, palps, digestive diverticula, style, gonad, and muscle. Catalase was tested for by adding 2 c.c. of H_2O_2 to 5 c.c. of the extracts. There was a great evolution of oxygen, showing the presence of catalase, with the gonad and digestive diverticula, a medium evolution with the palps, gills, and muscle, but none with the style and mantle. Peroxidases were tested for with tincture of guaiacum, hydroquinone, and pyrogallol, in every case 5 c.c. of extract being used, and to it added 2 c.c. of H_2O_2 and twelve drops of freshly prepared guaiacum, 2% hydroquinone or 1% pyrogallol. With guaiacum oxidation was very slow, and after a day slight traces of activity were found only with the style, palps, and gills. After five hours hydroquinone was turned a decided green-brown colour with the style extract, a light yellowish brown with the gills, palps, mantle, and digestive diverticula, and pale yellow with the muscle and gonad. Pyrogallol after five minutes was turned dark red-brown with the style extract, a medium brown with the digestive diverticula and muscle and a light yellow with the other tissues. The action of minced tissue was also tested with the indophenol reagent in the absence of H_2O_2, the results, which are striking, being given below :—

1. Style—deep purple almost immediately.
2. Gill—deep purple in a few minutes.
3. Mantle—purple in four to five minutes.
4. Palps—light purple in ten minutes.
5. Dig. diverticula—light purple in fifteen minutes.
6. Gonad—light purple in fifteen minutes.
7. Muscle—light purple in twenty minutes.

The different reagents all give different results with the various tissue extracts, except in the case of the style which in *all cases* gives the most decided reaction, and clearly contains, since it can act in the absence of H_2O_2, a complete oxidase system. It is strange that action on guaiacum should be so much less with the styles of Ostrea than with those of Saxidomus in Berkeley's experiments. Time has not permitted further work on this subject, but the presence of this enzyme in the style may be of great importance in the metabolism of the Lamellibranchs.

6. HYDROGEN ION CONCENTRATION IN THE GUT AND PERMANENCE OF THE STYLE.

I. Hydrogen Ion Concentration.

Table XV shows the pH of the fluid in the mantle cavity and in all regions of the gut, and of the substance of the digestive diverticula and style. Clarke and Lubs' indicators were used for the estimations, drops of fluid, or fragments of tissue being mixed with the indicators on a white plate and the colours compared with those of the same indicators added to drops of standard buffer solutions; the usual corrections for salt error were made. The pH in twelve healthy animals all with firm, well-developed styles was determined, the range, mid-point of range and

Table XV

pH in Fresh Oysters.

No.	Mantle cavity.	Œsophagus.	Stomach.	Style.	Dig. div.	Mid-gut.	Rectum.
1.	7·0	6·0	5·5	5·2	5·8	5·6	6·0
2.	7·1	5·9	5·4	5·2	5·8	5·5	6·0
3.	6·8	5·8	5·6	5·2	5·7	5·6	5·9
4.	7·2	5·9	5·5	5·2	5·9	5·8	5·9
5.	6·8	5·8	5·6	5·2	5·8	5·8	5·8
6.	6·8	5·6	5·6	5·2	5·8	5·8	5·8
7.	6·8	5·9	5·5	5·2	5·7	5·8	6·0
8.	7·0	6·0	5·4	5·2	5·8	5·8	6·3
9.	6·8	5·8	5·4	5·2	5·6	5·9	5·8
10.	7·1	5·6	5·4	5·2	5·7	6·0	5·8
11.	7·0	5·8	5·6	5·2	5·8	5·7	5·9
12.	6·9	5·8	5·4	5·2	5·8	5·8	6·0
Range	6·8–7·2	5·6–6·0	5·4–5·6	5·2	5·6–5·9	5·5–6·0	5·8–6·3
Mid-point of range	7·0	5·8	5·5	5·2	5·75	5·75	6·05
Average	6·94	5·83	5·5	5·2	5·77	5·76	5·93

average of each set of values being given. The results agree with those recorded (Yonge (1925b)) for Pecten, Mya, and Ensis, the style, which had in all cases a pH of 5·2, being the most acid substance in the gut, while of the fluids that of the stomach with an average pH of 5·5 is the most acid, followed by that of the mid-gut, œsophagus, rectum, and mantle cavity in the order named. The tissue of the digestive diverticula had an average pH of 5·77. Similar results were obtained with oysters starved for twelve weeks, as shown in Table XVI, the figures being slightly higher, i.e. conditions less acid, in all cases. The style was present in five out of the six oysters. The digestive diverticula were in all cases very pale, but the pH remained practically the same as in the fresh oysters.

TABLE XVI.

pH IN STARVED OYSTERS.

No.	Mantle cavity.	Œsophagus.	Stomach.	Style.	Dig. div.	Mid-gut.	Rectum.
1.	7·0	5·7	5·5	5·4	5·8	5·8	6·0
2.	7·0	5·8	5·6	5·4	5·7	5·9	6·1
3.	6·8	5·8	5·65	5·4	5·8	5·8	5·9
4.	7·0	5·7	5·7	5·4	5·7	5·8	5·8
5.	7·0	5·8	5·6	5·4	5·9	5·8	6·0
6.	7·0	6·0	5·9	—	5·9	5·9	6·0
Average	6·97	5·8	5·66	5·4	5·8	5·83	5·95

It was shown in the paper cited above that the origin of the acidity of the gut lay in the style and *not*, as previously thought, in a secretion from the "liver." This provides, incidently, yet further evidence that the digestive diverticula do not secrete. By removing the style from Mya or inducing it to disappear from Mytilus by keeping animals out of water for four days or by placing them in boiled or deoxygenated water for six days, it was found that the pH of the stomach rose even though that of the mantle cavity fell on account of the accumulation of CO_2. Similar results were obtained with Crepidula kept out of water for two days, and with Tapes whose shell valves had been clamped together for seven days.

The last method has been found the most satisfactory, and in Table XVII are shown the results of a series of experiments with oysters which had been clamped for one, two, three, four, five, and six days. Twelve animals were used for each experiment, each, after clamping, being replaced in the tanks and so kept at normal temperature. In all case *the style was absent*, and, as a result of the accumulation of CO_2, the average pH in the mantle cavity fell from the normal average value of 6·94 to 6·7, 6·56, 6·53, 6·51, 6·44, and, finally, 6·41 respectively after from one to six days clamping, while during the same periods the pH of the stomach rose from a normal of 5·5 to 5·67, 5·7, 5·84, 5·9, 6·02, and 6·14. Thus while the pH in the mantle cavity dropped by 0·53, the pH in the stomach rose, on account of the absence of the style, due to decrease in the rate of secretion, by 0·64, so that it came near to that of the mantle cavity. This experiment, together with those cited above, leaves no doubt that the acidity of the gut is due to the dissolution in it of the style. It is important to note that the pH thus produced in the stomach approximates to the optimum pH for the working of the amylase of the style (5·9).

TABLE XVII.

pH IN CLAMPED OYSTERS.

No.	1	2	3	4	5	6	7	8	9	10	11	12	Average
Clamped 1 day.													
pH in mantle cavity .	6·7	6·6	6·6	6·8	6·8	6·8	6·7	6·6	6·6	6·7	6·7	6·8	6·7
pH in stomach .	5·7	5·7	5·6	5·7	5·6	5·7	5·6	5·7	5·8	5·6	5·7	5·7	5·67
Clamped 2 days.													
pH in mantle cavity .	6·6	6·7	6·6	6·6	6·5	6·6	6·6	6·4	6·4	6·6	6·6	6·5	6·56
pH in stomach .	5·6	5·7	5·8	5·7	5·6	5·7	5·8	5·6	5·8	5·7	5·7	5·6	5·7
Clamped 3 days.													
pH in mantle cavity .	6·6	6·4	6·5	6·6	6·5	6·4	6·6	6·5	6·6	6·7	6·5	6·5	6·53
pH in stomach .	6·0	5·8	5·9	5·8	5·8	5·8	6·0	5·8	5·6	5·9	5·9	5·8	5·84
Clamped 4 days.													
pH in mantle cavity .	6·6	6·4	6·6	6·5	6·4	6·6	6·5	6·6	6·6	6·5	6·4	6·4	6·51
pH in stomach .	6·1	5·8	5·9	5·8	5·7	6·0	5·8	6·0	5·9	6·0	5·9	5·9	5·9
Clamped 5 days.													
pH in mantle cavity .	6·5	6·3	6·6	6·5	6·3	6·6	6·3	6·4	6·4	6·5	6·4	6·5	6·44
pH in stomach .	6·1	5·8	6·0	5·9	6·0	6·1	6·0	6·0	6·0	6·0	6·1	6·2	6·02
Clamped 6 days.													
pH in mantle cavity .	6·5	6·4	6·6	6·5	6·7	6·3	6·3	6·4	6·4	6·1	6·5	6·2	6·41
pH in stomach .	6·3	6·2	6·4	6·1	6·2	6·2	6·1	6·1	6·0	6·0	6·1	6·0	6·14

II. PERMANENCE OF THE STYLE.

The view was advanced (1925b) and has recently been reasserted (1926a) that the style is dissolved by the fluid in the stomach, and is only maintained as a result of a balance between the rate of secretion and the rate of dissolution. The view that its presence is correlated with the presence of food has been disproved by the work of Orton (1923), Martin (1923), Berkeley (1923), and Yonge (1925b), all of whom showed that Lamellibranchs retain the style after long periods of starvation, provided they are kept perfectly healthy, whereas in the presence of abundant food the style may be absent in unhealthy animals. As shown in Table XVI, five of the six oysters starved for twelve weeks retained the style.

The style is dissolved and reformed at very different rates in different animals. After artificial extraction of the style of Mya, Edmondson (1920) found that it took seventy-four days completely to regenerate (though this may have been due in part to the injury caused by the operation), while in *Ostrea virginica* Nelson (1925) states that it is alternately formed and dissolved in a rhythmical fashion. The style is large and firm at flood tide when the animals are feeding actively, but at late ebb tide when " most of the sand has been sorted out and removed from the stomach and digestion is well under way the style may be reduced to a soft amorphous mass of jelly." A similar rhythm is shown in the production of other forms of digestive secretion, such as that of the salivary glands of Gastropods (Hirsch (1914), Krijgsman (1925)).

In *Ostrea edulis* the style is usually present as shown in Table XVIII. Out of fifteen healthy animals examined, all of which had been in the tanks for a week so as to provide time for recovery from the effects of the journey from the beds, in only two cases was the style absent, and this was not correlated with the colour of the digestive diverticula, paleness of which Orton (1923) thought might be connected with absence of the

TABLE XVIII.

CONDITION OF STYLE AND DIGESTIVE DIVERTICULA IN FRESH OYSTERS.

No.	Condition of Style.	Condition of Dig. Div.
1.	Large, firm.	Pale.
2.	,, ,,	Dark.
3.	Absent.	,,
4.	Large, firm.	,,
5.	Medium, soft.	,,
6.	Large, firm.	,,
7.	,, ,,	,,
8.	,, ,,	Pale.
9.	,, ,,	Dark.
10.	,, ,,	,,
11.	Absent.	,,
12.	Large, firm.	,,
13.	,, ,,	Pale.
14.	,, ,,	Dark.
15.	,, ,,	,,

style. All the animals appeared in good condition ; in those obviously in bad condition, with flabby watery tissues, the style is frequently absent or much reduced.

The style invariably disappears when oysters are kept out of water for any length of time. Table XIX shows the results of a series of experiments to test the speed at which the style was dissolved, thirty-six healthy oysters being kept out of water and opened six at a time at one-hour intervals. After one hour in only one case was the style absent, and the same conditions were found after two hours, although the styles were much reduced. After three hours only two animals possessed styles, while after four, five, and six hours in no case was a style present.

TABLE XIX.

CONDITIONS OF STYLE AFTER REMOVAL OF OYSTERS FROM WATER.

	Oysters out of water for :—					
	1 hour.	2 hours.	3 hours.	4 hours.	5 hours.	6 hours.
No.	Condition of style.	Condition of style.	Condition of style.	Condition of Style.	Condition of Style.	Condition of Style.
1.	Soft, $\frac{1}{2}$ size.	Firm, $\frac{3}{4}$ size.	Absent.	Absent.	Absent.	Absent.
2.	Absent.	Soft, $\frac{1}{2}$ size.	,,	,,	,,	,,
3.	Practically intact.	Absent.	Soft, $\frac{1}{4}$ size.	,,	,,	,,
4.	Intact.	Soft, $\frac{1}{4}$ size.	Absent.	,,	,,	,,
5.	,,	Practically intact.	,,	,,	,,	,,
6.	Firm, $\frac{3}{4}$ size.	,, ,,	Practically intact.	,,	,,	,,

It was found in the previous work on the subject (1925b) that styles were dissolved rapidly in alkaline or slightly acid media, but increasingly slowly as the pH was reduced until at a certain critical pH—probably corresponding to the isoelectric point of the globulin of the style—it ceased to be dissolved. This critical pH varied for the styles of different animals, being 4·4 for Ensis, 4·2 for Mya, and 3·6 for Pecten, Mytilus, and Crepidula. It was suggested that the differences might be due to the fact that in the former cases the style is lodged in a separate cæcum, and is a much firmer and more resistant body than in the other three in which it lies in free communication with the gut.

In Table XX are shown a similar series of experiments carried out on the styles of Ostrea, large, firm styles being placed in tubes containing 10 c.c. of standard buffer solutions, a little toluol being added to prevent decomposition. The styles were dissolved rapidly in pH between 10 and 2·6, more slowly at pH 2·3 and extremely slowly—it took fifteen days for a style 2·5 cm. long to be dissolved—in pH 1·9. Below this point dissolution was also very slow, though gradually increasing in speed down to pH 1·04, in which a style of 2·6 cm. took seven days to dissolve.

TABLE XX.

DISSOLUTION OF STYLE IN DIFFERENT PH.

pH	Length of style.	Time to dissolve.	pH.	Length of style.	Time to dissolve.
10·0	2·5 cm.	56 min.	2·6	2·6 cm.	90 min.
9·0	2·5 cm.	70 min.	2·3	3·0 cm.	22 hrs.
8·0	2·5 cm.	70 min.	1·9	2·5 cm.	15 days.
7·0	2·6 cm.	61 min.	1·65	2·4 cm.	13 days.
6·0	2·4 cm.	75 min.	1·42	2·8 cm.	13 days.
5·0	2·5 cm.	87 min.	1·25	2·4 cm.	9 days.
4·0	2·3 cm.	90 min.	1·14	3·1 cm.	7 days.
3·0	2·8 cm.	88 min.	1·04	2·6 cm.	7 days.

Unlike the other styles that of Ostrea is dissolved in all media, although the difference between the fifteen days needed for the process at pH 1·9 and the fifty-six minutes needed at pH 10 is very striking. Repeated experiments have confirmed these figures. The isoelectric point, 1·9, is much lower than the lowest, 3·6, recorded for the other molluscs examined, and as the style in Ostrea is exceptionally unstable, this gives additional evidence of the connection between the isoelectric point and the site of formation, and consequent firmness, of the style.

It is clear from the above experiments that the style must speedily be dissolved by the fluid in the stomach. It has been shown definitely that the presence of food is *not* necessary for the formation of the style, while Berkeley's theory that the style is a reserve of oxygen which is used in anærobic respiration cannot be substantiated in view of the fact that there is no correlation between the size of the style in different species and the nature of the habitat ; a criticism which has also been made by Nelson (1925). Moreover, in such animals as Siliqua, Schizothærus, Macoma (Edmondson (1920)), and Mya (Edmondson, Yonge (1923)), in which the style lies in a *separate cæcum* and so is protected from the action of the fluid in the gut, the style never dissolves even after death from starvation or from lack of oxygen. The style is continually being dissolved, and is only maintained by the continual secretion of new substance in the style-sac ; any lowering of the vital or metabolic activities of the animals is at once reflected in a reduction or stoppage in the rate of secretion, but the rate of dissolution remains constant and the style disappears. This is a purely physical reaction which cannot take place if the style is protected in a cæcum. The gradual reduction in secretion is indicated by the gradual rise in pH in the clamped animals. Absence of a style is, therefore, an indication of lowered metabolism, and it is noteworthy that Allen (1921) has found that the style is formed less readily in autumn and winter than in summer, and has proved by experiment that this is the direct result of the difference of temperature. Edmondson also states that the style of Mya is reformed more rapidly after excision in summer than in winter. Allen further notes that there is no rhythmical loss and renewal of the style in fresh-water Lamellibranchs as there is in marine, tidal species ; the result, clearly, of the equable conditions under which the former species live. Spärck (1925) considers " that absence of the crystalline style must be interpreted as an indication of something not quite normal, as regards the state of metabolism or nutrition." Adverse conditions of any kind will cause a lowering of metabolism, and this, in Lamellibranchs such as the oyster, will result in the partial or total dissolution of the style, the state of which presents a valuable index of the condition of the animal.

7. RESERVE FOOD MATERIALS.

It is fitting that some reference should be made to the nature and distribution of the reserve food materials. So much work has already been carried out on this subject (the most recent investigation is that by Russell (1923), which contains a summary and bibliography of previous work) that further research was considered unnecessary. As already noted, fat is stored in the oyster particularly in the vesicular connective tissue cells, or Langer's vesicles, and is also present in the epithelium of the gut and of the digestive diverticula. Traces were found in the connective tissue after three months starvation. Material fixed in Carnoy's fluid and treated with iodine shows the presence of masses of glycogen in the vesicular connective tissue, but never in the epithelium of the digestive diverticula or of the gut. These results are in complete accordance with those of previous workers both on the oyster and on other Lamellibranchs.

Quantitative estimations of the fat and glycogen in oysters made by the Government Chemist (Russell) and by previous workers show that the latter is much the more abundant (ranging between 21·34 and 40·04%, according to the analyses of the Government Chemist), while " fattening " of oysters is to be attributed, as pointed out by Mitchell (1916a), " to the accumulation of glycogen, which must be regarded as the chief storage substance for oysters." The same author (1916) has further found that oysters kept in a weak solution of glucose show an increase in the amount of glycogen in the tissues. There is a seasonal variation in the quantity of glycogen, which in the oyster, according to the estimations of the Government Chemist, is constantly high from July to January, the total carbohydrate and glycogen approximating closely, showing that practically all the carbohydrate is in the form of glycogen. It is to be assumed, as Russell points out, that " during this period the oyster accumulates reserve food substance in the form of glycogen." From February to April there is a fall in the glycogen content, although the total amount of carbohydrate remains constant, the former being presumably " broken down into an assimilative form which is then, in May and June (when the total carbohydrates fall), utilised in the formation of the sexual products " (Russell). There can be no doubt as to the primary importance of glycogen in the physiology of the oyster and all Lamellibranchs in which it seems to play the same part as does fat in the vertebrates. This throwing of the balance of metabolism on to the carbohydrate side is in close accordance with the results recorded on the nature of the digestive processes.

8. GENERAL DISCUSSION.

In the oyster the organs of feeding and digestion are specialised for dealing with small particles *exclusively*. The elaborate ciliary mechanisms in the mantle cavity with the accompanying secretion of mucus ensure the capture of fine particles in suspension, of which the selective mechanisms reject the larger particles or mucus laden masses and allow only the smaller ones to pass to the mouth. There is a reduction in the individual size and general bulk of the particles swallowed, but no indication of any selection of particles having definite food value. In the gut, cilia and mucus glands are also universally distributed, ciliary activity, either directly or by the agency of the style, having taken the place of the muscular peristalysis necessary for the passage of large particles through the gut. The style is clearly correlated, here as elsewhere, with the presence of cilia, mucus glands, and a finely divided, and principally vegetable food.

The purely mechanical process of feeding is confirmed by the results of investigations into the stomach contents of oysters and other Lamellibranchs. Thus Savage (1925) states that " the oyster appears to ingest anything suitable that it can capture, and no evidence was found to show that selection takes place." The work of Savage and previous investigators (quoted in detail by him) shows that in the stomach are found samples of all matter in suspension in the water in which the oysters live, and it is not surprising, therefore, to find that in the Limfjord, where there is a great development of Zostera and of detritus formed by its decomposition, the stomach contents of oysters should consist largely of detritus. This has led the Danish workers, notably Petersen (1911), Boysen Jensen (1914), Blegvad (1914), and Spärck (1925), to maintain that oysters are by nature detritus eaters. Recent American workers such as Nelson (1921), Churchill (1920), and Martin (1923) all consider that animate matter, and particularly diatoms, is of primary importance in the food of the oyster. Savage found that at Orford inanimate material provided the bulk of the stomach contents, animate matter never exceeding 10%. Hunt (1925), in his account of the stomach contents of Lamellibranchs, states that they consist of a mixture of micro-organisms and detritus. He is at variance with Blegvad in the latter's classification of Lamellibranchs as detritus feeders, adding, very aptly, that " When sand-grains are numerous in a stomach the proportion of detritus is correspondingly great, and the organisms present are largely bottom-living forms, but there is no reason to suppose that this preponderance of detritus signifies its value as food any more than the abundance of sand suggests the nutritive value of silica." Reviewing these results it is seen that the majority of workers have accepted the presence of material in the stomach of oysters or other Lamellibranchs as proof that it has been *deliberately swallowed and can be digested.* The Danish workers, in particular, do not appear to have studied either the mechanism of feeding or of digestion in Lamellibranchs.

Digestion is largely intracellular either in the tubules of the digestive diverticula or in the phagocytes. This is clearly correlated with the finely divided nature of the food, which is again sorted in the food cæcum in the stomach only the most minute particles entering the ducts and tubules of the digestive diverticula, the ramifications of the latter providing the large ingesting surface typical of the gut of animals which digest intracellularly. The larger particles in the gut are taken in directly by phagocytes. The only extracellular enzymes are those of the style which act exclusively on carbohydrates. This feeble development of extracellular digestion and particularly the complete absence of extracellular protease and lipase accounts for the passage of living organisms undamaged through the gut, their presence in the rectum and fæces having been noted by many authors, including Blegvad (1914), Coker, etc. (1921), Allen (1921), and Churchill and Lewis (1924). The two first of these, however, have drawn from the presence in the fæces of living diatoms, green algæ and other plankton organisms the *quite erroneous conclusion* that these are either useless or of secondary importance as food. Attention to this error has also been drawn by Nelson (1925). Sherwood (statement in Savage's paper) and Nelson (1921) have both noted the presence of living oyster larvæ in the fæces of the adults.

An examination of the enzymes shows that oysters are unable to digest everything which enters the stomach, whereas the contrary has been too often assumed. Thus there is no indication of digestive action on cellulose or pentosans by the enzymes of either the style or the digestive diverticula. Boysen Jensen (1914) found that pentosans were the only non-nitrogenous substances present in estimable quantities in the detritus of the Limfjord, but the only evidence he could produce as to digestion was that pentosans are digested by herbivorous mammals and that cellulose is digested by Helix, finally stating that, " We may then perhaps conclude that also bivalves are able to digest pentosan, and that the considerable amount of pentosan present in the sea bottom—besides other possible substances (hemicelluloses generally) plays an important part as non-nitrogenous nourishment for a great portion of the bottom fauna." The known facts of the comparative physiology of digestion indicate that conditions in Mammals and Gastropods have *no bearing whatever* on conditions in Lamellibranchs, in which the digestive processes are particularly characteristic, and of which the only members capable of digesting cellulose (and there is no evidence as yet that they can digest pentosans) are the highly specialised wood-boring Teredinidæ.

Like all Lamellibranchs, oysters are particularly adapted for the digestion of carbohydrates. The only extracellular enzymes are those which digest starch and glycogen, while extracts of the digestive diverticula reveal the presence of powerful sucroclastic enzymes capable of digesting a variety of carbohydrates. On the other hand, lipoclastic and proteoclastic enzymes are very weak, and fats and proteins are probably digested largely in the phagocytes. In close connection with this concentration on the digestion of carbohydrates is the storage of great quantities of glycogen which represent the principal reserve food material. There is a close parallel to these conditions in Ciona (Yonge (1925)), in which digestion is also concentrated on carbohydrates, and there are large reserves of glycogen particularly in large cells in the epithelium of the mid-gut. It is clearly this dependence on carbohydrates which has enabled the Teredinidæ to live on a diet consisting almost exclusively of the carbohydrates in wood.

It follows that the food of the oyster must consist of small organisms rich in carbohydrates, i.e. of microscopic plant life. The following table taken from the paper of Brandt (1900) shows the relative amounts of protein, chitin, fat, and carbohydrates in the ash-free dried substance of diatoms, peridinians, and copepods.

	Diatoms %	Peridinians %	Copepods %
Protein	28·7	13·7	65·1
Chitin	—	—	5·1
Fat	8·0	1·37	7·7
Carbohydrate	63·2	84·9	22·1

There is a much greater proportion of carbohydrates in the two former. Russell considers that growth is due to an increase in protein and "fattening" to an accumulation of carbohydrates; and the connection between "fattening" and the presence of large numbers of diatoms in the food has been noted by many workers, including Nelson (1921) and Savage. No doubt, in the spring, the abundance of algal spores provides ideal food, with their high carbohydrate content and delicate structure which renders them easy to assimilate. Martin (1923) has drawn attention to the importance of nannoplankton, especially small flagellates and peridinians, in the food of the oyster, and the structure and physiology of the digestive system supports this, since it is only organisms of this size which are ingested entire in the digestive diverticula. Only fragments of diatoms seem to be so ingested—whole diatoms are digested by the phagocytes—and it is only "detritus" of *this* nature, i.e. fragments of vegetable matter containing assimilative carbohydrates, which can be of use to the oyster.

It is clear from the results of this research that ideal conditions for "fattening," and incidently reproduction, in the oyster are found in the presence of abundant supplies of diatoms, peridinians, algal spores, and other microscopic vegetable matter. It is the quantity of *carbohydrate* which is important, the protein matter necessary for growth is probably always present in excess of the demands and powers of digestion of the oysters. Such conditions are provided artificially in the "claires" at Marennes and other places along the French coast. Immense numbers of diatoms and other microscopic organisms accumulate in them, and the speed with which the oysters "fatten" is proof positive of the fitness of the environment.

9. SUMMARY.

1. The anatomy and histology of the food collecting and alimentary organs of the adult oyster are described.
2. The anatomy of the stomach is investigated with the aid of gelatin casts and attention drawn to the food cæcum, the ventral groove, and the two ducts of the digestive diverticula.

3. Cilia and mucus glands are universal throughout the food collecting and alimentary organs.

4. There is evidence that the gastric shield is composed of fused cilia.

5. There is no evidence of secretion in the digestive diverticula.

6. The histology of the style-sac resembles that described by Mackintosh for Crepidula. There is evidence that secretion of the style takes place in the groove.

7. Phagocytes are everywhere numerous in the blood vessels, connective tissue and epithelia, and free in the gut and mantle cavity.

8. The alimentary organs of the larva are described.

9. The anatomy and histology of these organs in the "spat" is described, the palps are relatively large and the gills asymmetrical. The style-sac is distinct from the mid-gut.

10. The course of the ciliary currents on the gills and palps is described and the importance of the various selective mechanisms emphasized. Selection appears to be purely quantitative, large particles or mucus masses being rejected and smaller ones accepted.

11. Muscular activity is of great importance in the functioning of both gills and palps. Reversal of cilia has never been seen.

12. Rejected matter is removed from the mantle cavity.

13. Material is sorted in the food cæcum in the stomach, larger particles passing into the mid-gut and smaller ones towards the gastric shield and ducts of the digestive diverticula, within the tubules of which there is a constant circulation.

14. The rotation of the style assists in the stirring of matter in the stomach.

15. In the style-sac are cilia, which rotate the style and others which push it into the stomach.

16. In the larva the velum acts as a food collecting organ; the style lies in an extension of the stomach and rotates rapidly. Material passes freely into the digestive diverticula.

17. In the spat rejective mechanisms are highly developed. The style revolves at a speed of between sixty and seventy revolutions per minute.

18. The tubules of the digestive diverticula are the only place where soluble matter is absorbed, in adult, larvæ, or spat.

19. Fine particles are ingested and digested intracellularly in the tubules of the digestive diverticula, the products of digestion carried away by amœbocytes, and useless matter rejected into the lumen.

20. Larger particles are ingested and digested by phagocytes in all parts, the products of digestion being carried to the vesicular connective tissue cells and there stored.

21. Enzymes in the style digest starch and glycogen. The amylase, at pH 5·9, has an optimum temperature of 43° C., and is destroyed at

56° C. The optimum medium is pH 5·9. It is inactivated by purification with absolute alcohol or by dialysis, but action is restored on the addition of chlorides or bromides and to a less extent iodides, nitrates, and carbonates, but not with sulphates or fluorides.

22. Sucroclastic enzymes in the digestive diverticula act on starch, glycogen, sucrose, raffinose, maltose, lactose, salicin, and amygdalin, but not on inulin, cellulose, or pentosans.

23. The amylase, at pH 5·5, has an optimum temperature of 44·5° C., and is destroyed at between 64 and 67° C. It has an optimum pH of 5·5, and is inactivated after purification or dialysis, action being restored in the presence of chlorides or bromides.

24. There is a weak lipase and protease, the latter has two optima at pH 3·7 and at or above 9·0 ; its action is very slow.

25. The only enzymes free in the stomach are those from the style.

26. There is no evidence of any enzymes free in the gill mucus.

27. There is a powerful complete oxidase system in the style, and a catalase in the digestive diverticula and gonad, and traces in the palps, gills, and muscle.

28. The style is the most acid substance in the gut and the cause of the acidity of the gut.

29. The style is dissolved rapidly in fluid of pH 2·3 and above, but very slowly below that point. It is readily dissolved and reformed in the oyster, its presence depending on the maintenance of the balance between the rate of secretion and the rate of dissolution. Its condition is a valuable indication of the state of metabolism.

30. Glycogen and fat are stored, particularly in the vesicular connective tissue cells, the former furnishing the principal reserve food material.

31. The presence of abundant supplies of microscopic plant life rich in carbohydrates provides ideal food for the oyster, and represents optimum conditions for " fattening " and reproduction.

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[*Extracted from the* LINNEAN SOCIETY'S JOURNAL—ZOOLOGY,
vol. xxxvi., *December* 1926.]

Ciliary Feeding Mechanisms in the Thecosomatous Pteropods.

By C. M. YONGE, B.Sc., Ph.D., Temporary Assistant Naturalist at the Plymouth Laboratory. (From the Station Zoologique Russe, Villefranche-sur-Mer.) (Communicated by Dr. H. G. CANNON, F.L.S.)

(With 5 Text-figures.)

[Read 4th November, 1926.]

CONTENTS.

1. INTRODUCTION.

ALTHOUGH it has long been known, as a result of the investigations of Gegenbaur (1855), Boas (1885), Pelseneer (1888), Tesch (1904, 1913), and, above all, Meisenheimer (1905) that the Thecosomatous Pteropods feed by means of ciliary currents, yet the actual process of feeding has never been described and figured in detail, largely, I think, because the majority of the observations hitherto have been made on preserved material. During a short visit to the Station Zoologique Russe at Villefranche in February 1926, I took the opportunity presented by the great numbers of Pteropods then occurring in the plankton, of tracing out the exact course of the ciliary currents in four selected species. I also carried out a series of feeding experiments the results of which will be described in a later paper. No observations were made on the feeding processes of the Gymnosomatous Pteropods, which do not possess ciliary feeding mechanisms.

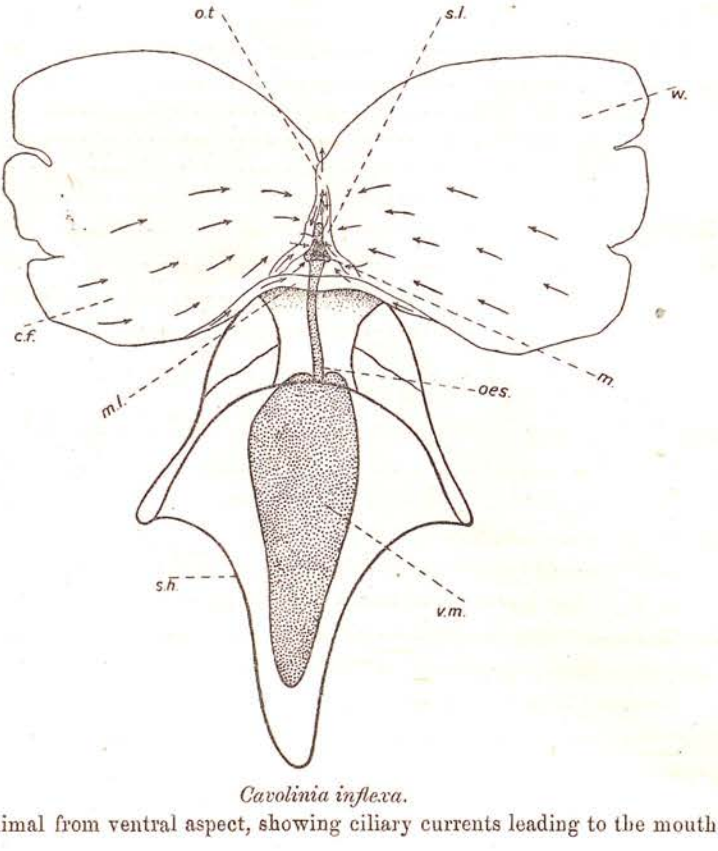
I wish to express my gratitude to Professor Davidoff and Dr. G. Trégouboff and their Assistants of the Laboratory at Villefranche for their great kindness and help, and also to the Carnegie Trust of the Universities of Scotland for providing me with a grant of money to defray the expenses of my visit to Villefranche.

2. CILIARY MECHANISMS.

The four species chosen for examination were : *Cavolinia inflexa*, *Creseis acicula*, *Cymbulia peronii*, and *Gleba* (*Tiedemannia*) *cordata*. They were selected as showing different stages in the development of the ciliary mechanisms. Although the genus *Creseis* is considered by the systematists to be more primitive than *Cavolinia*, yet in the disposition of the ciliary mechanisms, which are very similar in the two genera, *Creseis* appears the more specialized, and accordingly *Cavolinia* is here described first.

The course of the ciliary currents was followed under the low powers of the microscope by placing the animals in shallow glass dishes containing sea-water, and adding drops of suspensions in sea-water of carmine, Indian ink, or fine carborundum powder.

FIG. 1.



Cavolinia inflexa.
Whole animal from ventral aspect, showing ciliary currents leading to the mouth. × 7.

a. *Cavolinia inflexa.* (Fig. 1.)

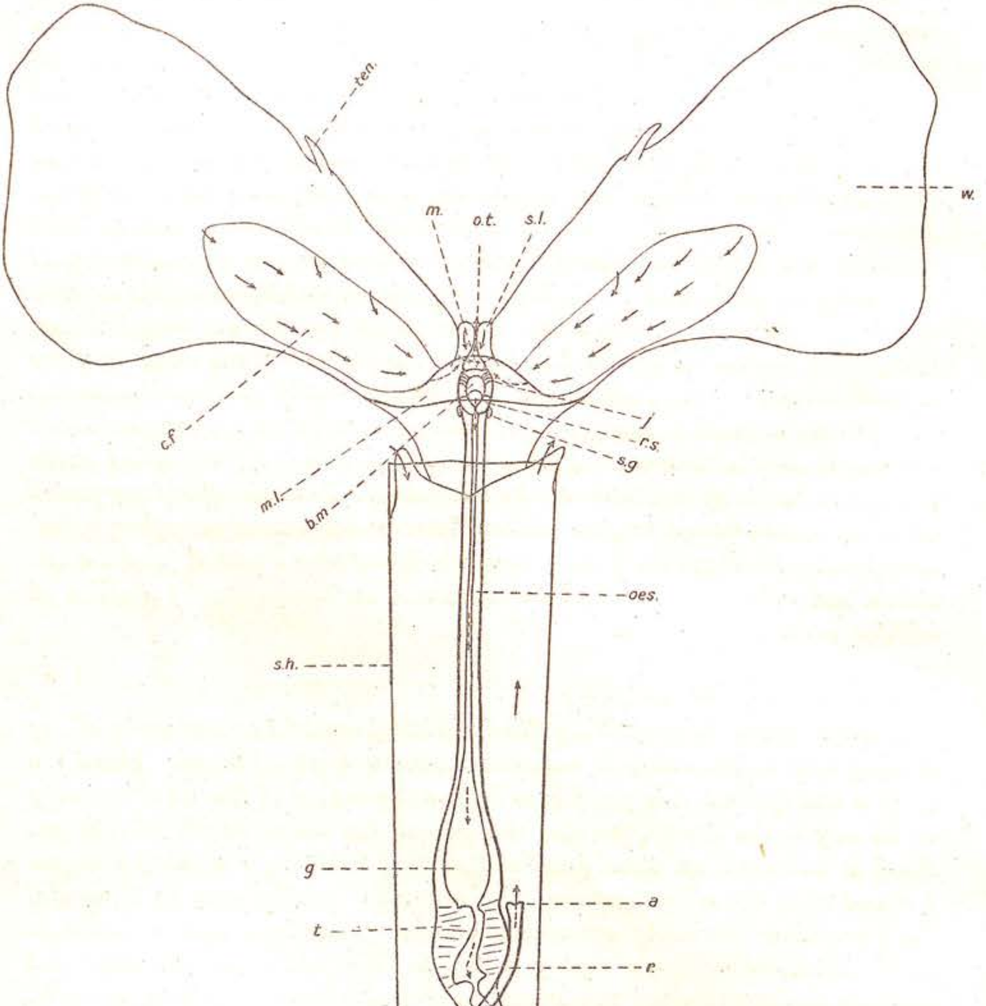
The ciliary mechanism in this species is the simplest and least specialized of the four species here described. There is a ciliated field (Wimperfeld) attached to the posterior margin of each of the wings, and approximately equal to them in size. There are numerous unicellular mucus glands between the ciliated cells. The beating of the cilia drives particles towards the mouth, which is enclosed in a triangle formed by three ridges representing, as Meisenheimer has shown, the unpaired middle lobe (*m.l.*) and two side lobes (*s.l.*) of the foot. Meisenheimer has further shown that the ciliated field is to be regarded as a lateral extension of the middle lobe of the foot; its epithelium is quite distinct from that of the wings, while, in common with the middle and side lobes, it is innervated from the pedal ganglion. The three ridges are all ciliated, and food particles pass on from them to the mouth, as shown by the direction of the arrows in fig. 1. They are contractile, and may be drawn together so that the mouth is covered and the particles gather into a ball at the summit of the contracted ridges, being later shaken off by the flapping of the wings. Even when they are not contracted, however, not all the particles necessarily pass into the mouth. If too much material is brought by the ciliary currents, it accumulates about the mouth and is then carried off by a tract of cilia (*o.t.*) which lies above the mouth in the groove between the side lobes. Particles which are passed on to the mouth do not proceed without interruption into the œsophagus, but are admitted first into the buccal mass, which contains a pair of jaws, a small radula and salivary glands, and are taken into the œsophagus by a series of definite swallowing actions.

b. *Creseis acicula.* (Fig. 2.)

This species, while resembling *Cavolinia* in all essentials, possesses a ciliary feeding mechanism which is somewhat more restricted in area. Since the body is transparent, it is possible to follow the course of the food, not only on its way to the mouth, but also throughout the entire length of the gut. Food is collected on clearly defined ciliated fields (*c.f.*) which lie superimposed upon the wings and are relatively much smaller than in *Cavolinia.* They are more obviously extensions of the middle lobe on the foot than in *Cavolinia*, as is shown clearly in fig. 2. The middle lobe is large and obscures the mouth when the animal is laid with the ventral side upwards. Food is passed from the ciliated fields to the mouth, which is bounded by the two side lobes. The three lobes do not contract together as in *Cavolinia*, but there is a well-defined outgoing tract in the same position as in that species for the rejection of surplus matter. Any abnormal surplus is removed by a violent flapping of the wings.

From the mouth the food passes into the globular buccal mass (*b.m.*), into which opens a pair of small salivary glands (*s.g.*), and which is furnished above with a pair of chitinous jaws (*j.*) and below, and more ventrally, with a radula sac (*r.s.*) containing a small radula which is made up of about ten transverse rows each consisting of three teeth (Meisenheimer). Food

FIG. 2.



Creseis acicula.

Anterior half of body from ventral aspect, showing ciliary currents leading to the mouth and the course of the food through the alimentary canal. Only the alimentary organs are shown. × 20.

proceeds into the œsophagus (*oes.*) as a result of a definite swallowing act, and there comes under the action of the cilia with which all parts of the gut (with the exception of the gizzard) are lined. It streams down the long œsophagus into the so-called stomach, a pear-shaped organ which, as Pelseneer (1888) has observed, is in reality, in this as in all other Thecosomata, "a masticatory gizzard with muscular walls, and exhibits four large symmetrical plates, a fifth posterior plate, and generally eight small anterior plates." The teeth (*t.*) are well developed, but since the food particles are invariably minute as a result of the mode of collection the mastication which they undergo appears quite unnecessary, and the invariable presence of these gastric teeth in the Thecosomata may be attributed to their descent from Tectibranchs such as *Scaphander*, with which, according to the classification proposed by Pelseneer (1888, 1906), they are closely allied. *Scaphander* swallows its prey—which usually consists of small bivalves—whole, "to be broken up by the calcareous plates of its powerful gizzard" (Hunt (1925)).

Behind the gizzard is a chamber into which open side by side the mid-gut and the digestive gland ("liver"); and into either of these openings food may pass. The digestive gland in *Creseis* is greatly modified owing to the needle-like shape of the body. It is slightly lobed immediately behind the gizzard, and it extends to the extreme tip of the long body as a single straight tube. It is usually yellow or brown in colour and composed of a single layer of large cells, the whole organ being so transparent that food particles can be seen within it being passed rapidly up and down as a result of rhythmical peristaltic movements. Although difficult to observe with certainty, cilia are probably present, but they are certainly not so regularly arranged or so numerous as in the remainder of the gut. When the digestive gland of a freshly caught animal is examined, the contained food appears as greenish-brown masses, obviously of a predominantly vegetable nature. It is known that in many Gastropods food particles pass into the cavity of the digestive gland where they are ingested and digested intracellularly, by absorptive cells (*e. g.*, the observations of Enriques (1901) on *Aplysia*, of von Bruel (1904) on *Caliphylla*, of Jordan (1918) on *Helix*, etc.). I do not intend to discuss the question of absorption in this paper, but observations on the movement of food in the gut of *Creseis* showed that particles are passed into the digestive gland, presented to the large—presumably ingesting—surface and then, if not taken in, passed back to the opening and into the mid-gut.

Opening into the alimentary canal about the junction of the digestive gland and the posterior end of the gizzard there is a small finger-shaped diverticulum (*d.*), which is ciliated but into which food does not pass. The nature and function of this organ will be discussed later. Particles which enter the mid-gut, either directly from the gizzard or by way of the digestive gland, pass rapidly to the exterior, coming under the combined influence of ciliary and peristaltic action. The mid-gut and rectum form a twisted loop so that the anus (*a.*) is situated at the left side of the stomach and points anteriorly. The fæces are discharged into the mantle cavity where, under the influence of the cilia which maintain a constant stream of water in the cavity, they are carried away (see the direction of the arrows in fig. 2).

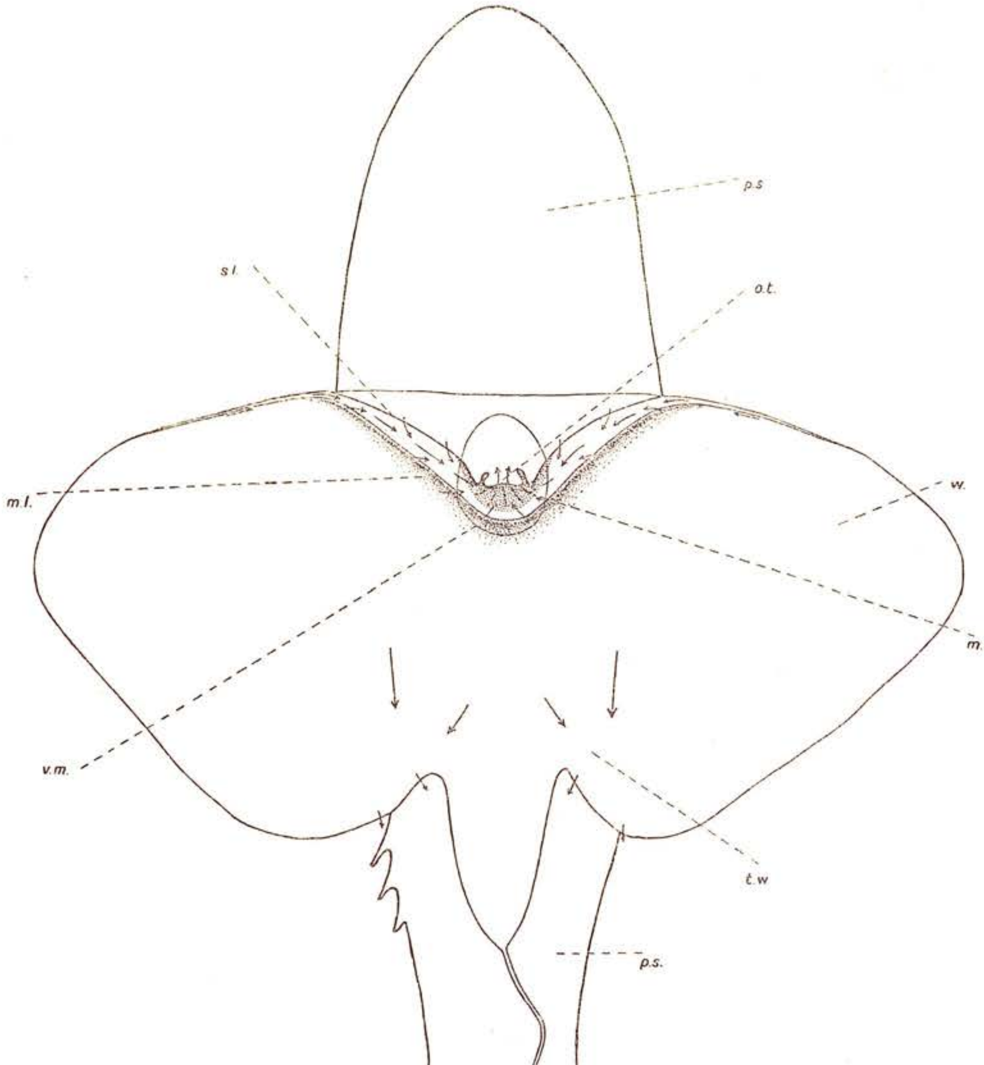
An attempt was made to obtain some indication of the pH in the gut of *Creseis* by placing living animals in sea-water lightly coloured with neutral red or brom thymol blue. No clear results were obtained with the former, but with brom thymol blue the œsophagus, gizzard and digestive gland all coloured yellow (pH probably about 6·0), and the latter part of the mid-gut and the rectum deep blue (pH between 7·5 and 8·0). This agrees very closely with the results obtained (Yonge (1925)) for *Aplysia*, a benthic Tectibranch, in which the fore- and mid-gut are acid having a pH between 5·8 and 6·8, and the rectum is alkaline having a pH of 8·3.

c. *Cymbulia peronii.* (Fig. 3.)

The ciliary mechanism is here greatly reduced, being formed exclusively by the middle and side lobes of the foot with no ciliated field extending from the former. The mouth (*m.*) lies in the middle line while on either side of it there extends a ciliated groove, the raised sides of which represent the lobes of the foot, the unpaired middle lobe forming the posterior side, and the two side lobes the anterior side. The grooves begin midway along the anterior margin of the wings as narrow ciliated tracts which widen and become raised up laterally as the mouth is approached. Particles which fall upon them are conducted to the bottom of the groove, where they come under the influence of a strong ciliary current leading straight to the mouth. This lies at the bottom of a funnel-shaped depression, the walls of which (like the alimentary tract within) are deeply pigmented. Food streams down into the mouth by way of the ciliary currents which line this depression, but whether it passes directly into the œsophagus or has to be swallowed it is impossible to say. There is a buccal mass in *Cymbulia* possessing jaws, radula, and salivary glands, but all of these are much less developed than in the two species already described.

Any excess of food is removed as before by an outgoing tract of cilia (*o.t.*) situated on the lobe which overlies the mouth anteriorly, separating the two side lobes of the foot, *i. e.*, occupying the same relative position as in *Cavolinia* and *Creseis*. Particles caught in this tract are led away from the mouth, rolled into a ball and, when large enough, shaken free. The greater part of the surface of the wings is, as usual, not ciliated, the surface being kept clean by continual flapping. There are, however, tracts of slowly moving cilia (*t.w.*) on either side of the middle line (*i. e.*, where flapping will have no effect) which lead foreign particles to the posterior margin of the wings, where cilia occur along the two short stretches on each side as delimited by the two sets of arrows shown in fig. 3.

FIG. 3.



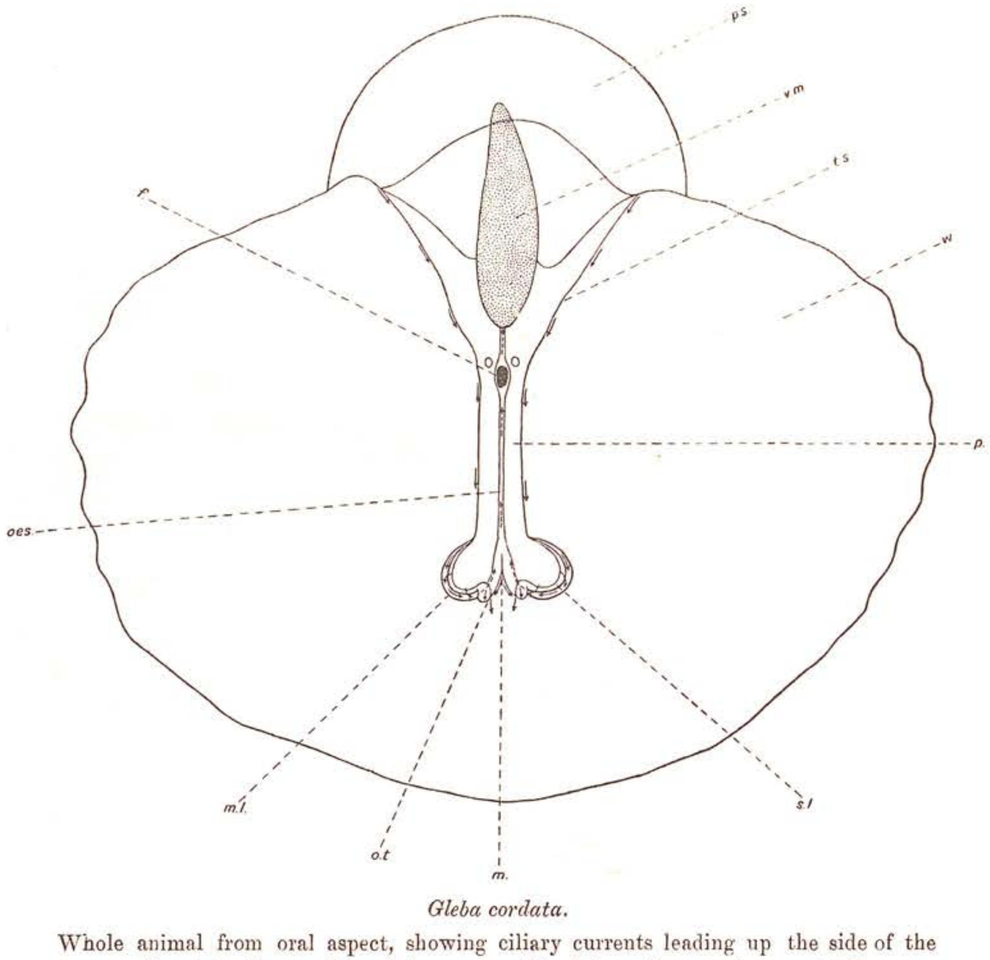
Cymbulia peronii.

Whole animal from oral aspect, showing ciliary currents leading to mouth and on the wings. × 2½.

d. *Gleba cordata.* (Figs. 4 & 5.)

In *Gleba*, although conditions are essentially the same as in *Cymbulia*, the rudimentary triangular proboscis developed in the latter has become drawn out into a long proboscis (fig. 4), attached by a broad base and extending backwards parallel to the surface of the wings. This is flattened from above downwards and has a pair of lateral rounded lobes at the tip.

FIG. 4.

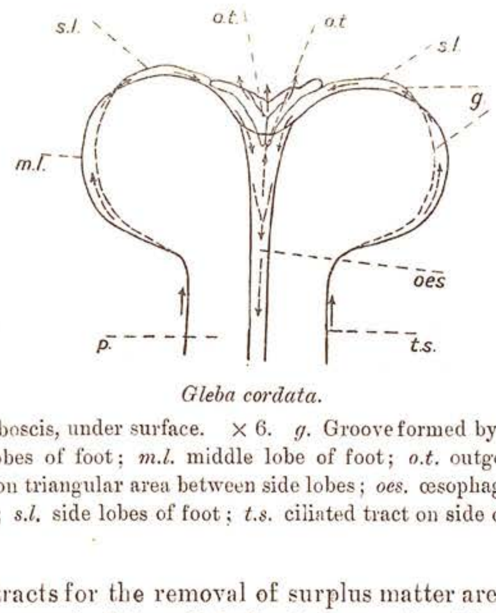


Gleba cordata.

Whole animal from oral aspect, showing ciliary currents leading up the side of the proboscis to the mouth, and the course of food down the œsophagus. × 2½.

Narrow ciliary tracts (*t.s.*) begin where the edges of the broad base are attached to the wings and run, one up either side of the proboscis, leading into grooves which bound the outer margin of the terminal lobes. As in *Cymbulia*, these grooves are formed by the lobes of the foot, the two side lobes (*s.l.*, fig. 5) forming the upper ridge, and the unpaired middle lobe (*m.l.*) the lower ridge. The mouth (*m.*) lies in a depression at the tip, and in the middle line, of the proboscis. Particles enter it from the grooves and then pass without interruption into the œsophagus, which can easily be seen through the transparent tissue of the proboscis. *There is no buccal mass, and hence no jaws, radula or salivary glands.* Material passes down the œsophagus under the combined influence of cilia and peristalsis, the particles often massing together into balls which extend the walls of the œsophagus (see *f.* in fig. 4). From the œsophagus, it proceeds to the gizzard and remainder of the alimentary canal which lie within the visceral mass (*v.m.*).

FIG. 5.



Gleba cordata.

Tip of proboscis, under surface. × 6. *g.* Groove formed by middle and side lobes of foot; *m.l.* middle lobe of foot; *o.t.* outgoing ciliated tracts on triangular area between side lobes; *oes.* œsophagus; *p.* proboscis; *s.l.* side lobes of foot; *t.s.* ciliated tract on side of proboscis.

The outgoing tracts for the removal of surplus matter are situated, as in the preceding species, on the lobe which lies between the side lobes of the foot. This can be seen in fig. 5, which represents the under surface of the proboscis. The middle lobe dips in the middle line exposing the triangular area lying between the side lobes. Particles pass down the grooves into the mouth, the two streams not uniting until they have passed a little way down the œsophagus (as shown by the union of the dotted arrows in the figure). The grooves are very narrow at the entrance to the mouth, so that if any large quantity of material passes along them it will overflow on to the triangular area, and so come under the influence of the outgoing tracts and be carried away. All rejected matter is rolled into a ball in the region between the two arrows at the tip of the proboscis in fig. 4, and finally shaken off. No cilia can be distinguished on any part of the wings in *Gleba*.

3. Discussion.

The species examined show four stages in the adaptation of the Thecosomatous Pteropods to ciliary feeding. In each case the ciliary feeding mechanism is more localized and more efficient—because it is more compact and interferes less with the movement of the wings—than in the one preceding. This is brought about by the increased specialization of the middle and side lobes of the foot, out of which the ciliary mechanisms are in all cases formed. At the same time, the buccal mass and its associated structures, radula, upper jaws and salivary glands, which the Thecosomata have inherited from their benthic, and probably carnivorous, ancestors, gradually diminish, being represented by slight vestiges, of doubtful functional value, in *Cymbulia,* and being entirely absent in *Gleba* (and also in the allied genus, *Corolla* (*Cymbuliopsis*) as noted by Pelseneer (1888) and later investigators). The gizzard, probably another structure handed down from carnivorous ancestors and clearly of little use to an animal which feeds by ciliary mechanisms, is retained throughout.

A further and most interesting point is the presence of a blind appendage opening into the stomach at or near the opening of the digestive gland, and shown in the figure of *Creseis* (it was originally described in this genus by Gegenbaur). Meisenheimer states that a similar organ is present in all the Thecosomata, and that it is lined by a ciliated epithelium and contains a hyaline, structureless secretion which completely fills the hinder portion of the sac but decreases in circumference as it approaches the opening, beyond which, however, it may project. The diverticulum is too small for the contained secretion to be large enough to be seen except in sections, but in Meisenheimer's figures it bears a close resemblance to the crystalline style of the Lamellibranchs and primitive Gastropods. Meisenheimer has noted this resemblance and, discussing the probable function, states : "Seiner physiologischen Function nach hat dieser Blindsack, der nach Johannes Müller peristaltische Bewegungen ausführen soll, unzweilelhaft eine Rolle bei der Verdauung zu spielen, dafür spricht schon der auffallende Verbrauch seines Sekretes nach der Mündung hin . . . . . . Ob diese Function in der Erzeugung eines besonderen verdauenden Sekretes besteht, oder ob auch hier das Sekret dazu dient, Fremdkörper und unverdauliche Hartteile der Nahrungsorganismen mit einer Hülle zum Schutze der zarten Darmwände zu umgeben, wie man es neuerdings für die Lamellibranchiaten angenommen hat, ist wohl schwer zu entscheiden." He rejects the older theory that it represents a bile secretion. The presence of a style—which contains an amylolytic enzyme and serves to whirl round food particles in the stomach (for review of recent work on the subject see Nelson (1925))—is always associated with a predominantly vegetable diet and, except in certain of the Gastropods, with ciliary feeding mechanisms (*e. g.*, in all the Lamellibranchs and in such Gastropods as *Crepidula* in which it is better developed than in any other members of that class ; see Orton (1912) and Mackintosh (1925)). It is very striking that a similar structure should have arisen in the only group among the higher Gastropods which has developed ciliary feeding mechanisms and is to a large extent vegetarian. Boas has given an account of the stomach contents of the Thecosomata. In species from the warmer seas, he found *Globigerina* and other Foraminifera and also Radiolarians ; in those from the colder seas many Dinoflagellates, while in both he found Diatoms, Coccospheres and Tintinnids.

In the Gymnosomatous Pteropods, which are carnivorous—their food consisting, according to Massy (1917), largely of Thecosomata—and do not possess ciliary feeding mechanisms, there is no development of a blind sac, while radula, jaws and salivary glands (all associated with a carnivorous diet) are retained throughout. In the Thecosomata, as in the Lamellibranchs, the secretion of the blind sac may quite possibly contain an amylolytic enzyme for the extracellular digestion of the starch present in the vegetable food ; the older theory that it serves to coat hard particles has been abandoned as a result of recent work. The Mollusca are a very homogeneous phylum, and its members tend to produce similar structures in response to similar stimuli. The peculiar nature and form of the style are probably to be attributed, as I have already pointed out (1923), to the universal presence of mucus glands and cilia in the alimentary tract of the Mollusca (with the exception of the Cephalopoda), the former assisting in the formation of the substance of the secretion and the latter rolling it into shape.

4. SUMMARY.

1. The ciliary feeding mechanisms of four species of Thecosomatous Pteropods, *Cavolinia inflexa*, *Creseis acicula*, *Cymbula peronii*, and *Gleba cordata*, have been studied.

2. The ciliary mechanism is in all cases formed by the unpaired middle lobe, and the two side lobes, of the foot, with the addition of tracts leading to them in the case of *Gleba* ; all food particles are conducted to the mouth.

3. There is a progressive reduction in the area occupied by the ciliary mechanism in the four species examined. In *Cavolinia* and *Creseis* the middle lobe is extended as a ciliated field, in *Cymbulia* the ciliary mechanism is composed of grooves leading to the mouth, one from the anterior margin of each of the wings, while in *Gleba* the mouth lies at the end of a proboscis, up the sides of which lead ciliated tracts, the grooves formed out of the lobes of the foot being confined to the rounded margin near the tip of the proboscis.

4. In all cases there is an outgoing tract of cilia for the rejection of surplus food situated on the small lobe which overhangs the mouth anteriorly and lies between the side lobes of the foot.

5. The restriction in area and increased specialization of the ciliary mechanisms is accompanied by a diminution and final disappearance (in *Gleba*) of the buccal mass and its associated structures, jaws, radula and salivary glands.

6. The course of the food through the alimentary canal has been followed in *Creseis*. The food, apparently mainly vegetable, is passed through by ciliary and peristaltic activity, being triturated in the gizzard and passed into the cavity of the digestive gland before being rejected by way of the mid-gut and rectum.

7. As a result of *intra vitam* staining with brom thymol blue in *Creseis*, the œsophagus, gizzard and digestive gland show a pH of about 6·0 and the latter part of the mid-gut and the rectum one of between 7·5 and 8·0.

8. A ciliated diverticulum is present in all species and opens about the junction of the digestive gland and gizzard. It contains a hyaline secretion strongly reminiscent of the crystalline style of the Lamellibranchs and certain Gastropods. It is suggested that in the Thecosomata, as in those animals, the style-like secretion may be correlated with the presence of ciliary feeding mechanisms which collect food principally of a vegetable nature, and may contain an amylolytic enzyme for the extracellular digestion of starch.

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6. REFERENCE LETTERING.

a.	anus.
b.m.	buccal mass.
c.f.	ciliated field.
d.	diverticulum.
d.g.	digestive gland.
f.	food mass.
g.	gizzard.
j.	jaws.
m.	mouth.
m.g.	mid-gut.
m.l.	middle lobe of foot.
o.t.	outgoing ciliated tracts.
oes.	œsophagus.
p.	proboscis.
ps.	pseudoconch.
r.	rectum.
r.s.	radula sac.
s.g.	salivary glands.
s.l.	side lobes of foot.
sh.	shell.
t.	tooth.
t.s.	ciliated tract on side of proboscis.
t.w.	ciliated tract on wings.
ten.	tentacle.
v.m.	visceral mass.
w.	wing.

STRUCTURE AND FUNCTION OF THE ORGANS OF FEEDING AND DIGESTION IN THE SEPTIBRANCHS, CUSPIDARIA AND POROMYA.

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CONTENTS.

1. INTRODUCTION.

Previous work on the structure and function of the alimentary system in the Lamellibranchs (YONGE (1923, 1925, 1926a, 1926b)) showed that the many peculiarities which they exhibit appear to be correlated with the highly developed ciliary feeding mechanisms on the gills and palps, as a result of the action of which only the smallest particles are passed into the oesophagus and stomach. This latter organ is concerned chiefly with sorting the particles, the larger ones being passed directly into the mid-gut and the smaller ones entering the ducts of the digestive diverticula ("liver" or "hepatopancreas") where they are digested intracellularly. The food is largely of a vegetable nature and the digestive processes are concerned especially with the disposal of carbohydrates. There are present, free in the lumen of the gut, in the epithelium and in the surrounding tissues, great numbers of phagocytes which actively ingest food particles. Their presence, also, appears to be correlated with the finely divided nature of the food and the fact that, but for the digestive action of these phagocytes, these food particles, unless sufficiently fine to enter the ducts of the digestive diverticula, can only be digested if composed of starch or glycogen. The only extracellular digestive enzymes in the gut of the Lamellibranchs, namely those set free by the dissolution in the stomach of the head of the crystalline style, act exclusively on these two carbohydrates.

Owing to their deep water habitat, the Septibranchs have been little studied but PELSENEER (1891, 1911) and PLATE (1897) have reported, on the evidence of the stomach contents, that they are carnivorous, while all investigators who have worked upon them have shown that the structure of both the food collecting and digestive organs in the Septibranchs are quite distinct from those of the other Lamellibranchs. Gills are absent, their place being taken by the muscular septum, the labial palps are very small and the gut is provided with a muscular coating of a thickness unknown in the other Lamellibranchs where the finely divided food is carried through the gut exclusively by ciliary activity.

Clearly, therefore, a study of the structure and function of the organs of feeding and digestion in the Septibranchs would have two valuable results; not only would it go far towards completing our knowledge of this aspect of the structure and physiology of the Lamellibranchia, but it might be expected - should the carnivorous habit be definitely established - to provide important confirmatory evidence that the peculiar nature of the gut and the digestive processes in those Lamellibranchs which feed by means of ciliary currents *is* due to the size and nature of the food particles.

For the purpose of observing living Septibranchs, carrying out feeding experiments and collecting material for histological examination, a period of four weeks was spent at the Biologiska Station, Trondhjem, Norway, and of one week at the Kristinebergs Zoologiska Station, Sweden. As a result entirely of the kindness and labours of Dr. O. NORDGAARD at Trondhjem and of Dr. M. AURIVILLIUS at Kristineberg, a number of living specimens of these rare animals was obtained, and I wish to record my gratitude to these gentlemen without whose help this research would have been impossible. I also desire to thank the Council of the Marine Biological Association of the United Kingdom, and the Development Commission for granting me the necessary leave of absence from the Plymouth Laboratory. The work has been completed at Plymouth and I have to thank the Director, Dr. E. J. ALLEN, F.R.S., for his unfailing interest in it, and other members of the Staff for their assistance on many points.

2. MATERIAL.

The Order Septibranchia (Pelseneer) is divided into three famillies, Poromyidae (Dall), Cetoconchidae (Ridewood), and Cuspidariidae (Fischer). No representatives of the second of these have ever been examined in the living condition; they are abyssal and have only been taken on deep-sea expeditions such as the "Challenger" (see PELSENEER (1888b)) and the "Siboga" (see PELSENEER (1911)). Of the Poromyidae, I obtained two living specimens of <u>Poromya granulata</u> which were dredged in the Trondhjem Fjord at depths of 150 and 200 metres. Since returning to Plymouth, I have received three further specimens of this species preserved in alcohol which were collected by Dr. M. AURIVILLIUS on an expedition to the Koster Islands in the Skager Rack and were sent on to me by Dr. N. Hj. ODHNER of the Riksmuseum, Stockholm, for whose kindness I am extremely grateful.

Living specimens of three species of Cuspidaria were obtained. Twelve *Cuspidaria obesa* were dredged at depths of between 100 and 300 metres in the Trondhjem Fjord. Unfortunately this species is so small that it is difficult to handle and observe, and most of my observations on living Cuspidaria were made on one specimen of *Cuspidaria rostrata* which was dredged at a depth of 250 metres at Trondhjem, and three specimens of *Cuspidaria cuspidata* dredged in the Gullmars Fjord in Sweden at depths of between 40 and 60 metres. I also received from Dr. O. NORDGAARD two preserved specimens of *Cuspidaria rostrata*, and since my return Dr. M. AURIVILLIUS has kindly sent me a number of preserved *Cuspidaria rostrata*, and several *C. obesa* and *C. cuspidata*, and one *C. costellata*. This preserved material has proved of great value in the histological and anatomical portions of the research.

3. ANATOMY AND HISTOLOGY OF THE ORGANS OF FEEDING AND DIGESTION.

Throughout this paper, for the sake of convenience, the conditions in the genus Cuspidaria, whose members represent the highest development of the Septibranchs, will be described before those in Poromya. It must not be forgotten, however, that, as shown by PELSENEER (1888a, 1888b, 1891, 1911) and as further emphasized in this paper, Poromya should logically be treated first as it represents a somewhat more primitive condition and shows more affinities to the typical Lamellibranchs - especially to the Anatinacea from which, according to PELSENEER, the Septibranchs probably sprang - than does the more highly specialized Cuspidaria.

(i). ANATOMY.

A. CUSPIDARIA.

Literature. - Although the absence of gills in Cuspidaria (Neaera) was first noted by DALL (1886b) and this author has described the shell and external characters of many species of the Cuspidariidae (1886a, 1889a, 1889b, 1894), the first adequate description of Cuspidaria was furnished by PELSENEER (1888b) who gave an account of C. curta, C. fragilissima and C. platensis from the "Challenger" material and C. rostrata obtained from Naples, later (1891) giving a more detailed description of the last species. He has since (1911) described the Cuspidariidae taken by the "Siboga" expedition. GROBBEN (1892) in his memoir on Cuspidaria cuspidata has provided the most detailed account of the morphology of the Cuspidariidae. A short description of the morphology of Cuspidaria obesa (unfortunately without figures) has been given by PLATE (1897). Finally RIDEWOOD (1903) in his work on the gills of Lamellibranchs gave some account of the septum and palps of Cuspidaria glacialis.

General Anatomy. - The observations here recorded on the anatomy of the Cuspidariidae are based largely on examinations of living and preserved specimens of the comparatively large species, Cuspidaria rostrata and C. cuspidata. The general anatomy can best be described by reference to text-fig. 1 which represents a lateral view of Cuspidaria rostrata. The animal is flask shaped, the siphons (i & e) lying in a long posterior extension of the shell. The inhalent siphon (i) is the larger and possesses four club-shaped tentacles which are attached on the ventral side to the base of the siphonal opening, which is large and muscular. The exhalent siphon (e) has a much narrower opening and is shorter, three tentacles, similar in structure to those of the inhalent siphon, are attached to its dorsal surface. In life, the siphons normally project from the shell but on stimulation, or after fixation, they are withdrawn within the siphonal sheath (sh), as shown in the figure. They are attached to this about half way along the siphonal extension, along the line marked 1.

(Insert text-fig. 1.)

Anterior to this the siphons are divided by a stout partition which terminates at its junction with the muscular septum (s) which divides the mantle cavity into ventral (V) and dorsal (D) chambers. At their base, the siphons are attached to the shell by a widely spreading series of muscle strands (rs) which, by their contraction, withdraw the siphons. The inhalent siphon is separated from the ventral mantle chamber by a sheet of tissue perforated by a round valve (v) near the centre. The mantle is excessively thin - resembling fine tissue paper in consistency - which is characteristic of the Septibranchs. Ventrally the mantle lobes are bounded by thickened ridges which are united in the posterior half of the mantle cavity, the point of attachment being indicated in the figure by the letter p. Projecting in the middle line through the anterior half of the septum is the foot (f) which is long and narrow and possesses a byssus groove on its posterior surface (see text-fig.6,b) associated with a gland in the body of the foot. The foot is capable of great extension and is withdrawn by the action of two retractor muscles which are attached to the mid dorsal region of the shell, an anterior retractor (ar) immediately posterior to the large anterior adductor muscle of the shell (aa) and a posterior retractor (pr) above the anterior part of the posterior adductor of the shell (pa). Of the adductor muscles the anterior is the larger and lies in the extreme anterior region of the body with its greatest ~~length~~ diameter vertical, while the posterior adductor is situated dorsal to the anterior region of the exhalent siphon, is more oval in cross section and is horizontally extended.

Anterior to the foot and projecting ventrally from the under surface of the septum are the labial palps. These consist of an anterior (ap) and a posterior (pp) pair, the latter being slightly the lafger. The anterior palps are attached for the greater part of their surface to the posterior ventral surface of the anterior adductor muscle, and form a veil round the anterior side of the mouth (m); the posterior pair are wedge-shaped and free, they extend posteriorly on either side of the foot.

The palps are not ridged as in the other Lamellibranchs and this, and especially their small size, has aroused comment from most observers, DALL (1886b) originally stating that they were completely absent, but his material~~, however,~~ was in bad condition. In later work (1888) he refers to the palps of the Cuspidariidae as obsolete, and in a further paper (1889b) states that the palps are absent in Myonera paucistriata (a member of the Cuspidariidae). PELSENEER (1888b, 1891) states that the posterior palps of Cuspidaria curta and C. fragilissima are absent. GROBBEN noted the small size of the palps in Cuspidaria cuspidata, and PLATE stated that palps are absent in C. obesa , my own observations on this species, however, have shown that, though the posterior palps are reduced to mere ciliated tracts, as described by PLATE, the anterior palps, though greatly reduced, are present. In Myonera dubia, PELSENEER (1911) states that the posterior palps project very little, but that in Cuspidaria (Pseudneaera) thaumasia they are large and extend for a considerable distance. I have found both pairs of palps comparatively well developed in Cuspidaria rostrata and C. cuspidata (see text-fig.6), but in both they contracted considerably after fixation - probably owing to their possession of relatively powerful muscles - and it is not impossible that they may be present in species in which they have been recorded as absent. That they retain some importance in feeding will be shown in a later section.

Septum. - The septum consists of an extremely thick muscular partition which divides the mantle cavity into two chambers, in the upper of which lies the visceral mass. It is slung longitudinally across the mantle cavity and is attached at either end by a pair of stout muscles to the dorsal region of the shell. The anterior septal muscles (as) are attached to the shell immediatey posterior to the anterior adductor and on either side of the anterior retractor muscle of the foot, and the posterior pair (ps) slightly anterior to the posterior adductor. These muscles are called septal retractors by PELSENEER but both DALL and GROBBEN prefer to call them simply septal muscles and, in view of the peculiar functioning of the septum, which will be described subsequently, I prefer the latter name. The septum (*C. rostrata*) is perforated by four pairs of pores (sp) which are symetrically arranged on either side of the middle line in the anterior two thirds of the exposed septal surface. The most anterior pair are slightly posterior to the mouth, and the hindermost pair a little distance behind the base of the foot. They lie nearer to the base of the foot than to the mantle, as is shown in text-fig. 2. Each consists of a narrow slit-like opening laterally extended and bounded by low lips. They provide the sole means of communication between the ventral and dorsal chambers of the mantle cavity (or infra- and supra-septal cavities as they will hereafter be called).

The arrangement of the muscles in the septum has been described by DALL (1889b) and in more detail by GROBBEN, and will

(Insert text-fig. 2.)

most easily be described by reference to text-fig. 2 which shows the arrangement of the septal muscles as seen from the dorsal aspect after the septum has been dissected out. At the attachment of the septum to the mantle on the outer, and to the sides of the foot on the inner, side, the tissues are thin and somewhat membraneous, but the body of the septum consists of thick muscular strands. In the outer regions these run longitudinally, bundles of fibres from the anterior septal muscle (as) passing backwards and meeting bundles from the posterior septal muscle (ps). Smaller bundles of longitudinally directed fibres (i) separate from the anterior septal muscles, pass downwards and then posteriorly along the side of the foot on the inner side of the pores, finally crossing one another posterior to the foot and becoming merged into the general mass of the septum. These fibres have a separate insertion nearer to the middle line than the main anterior septal muscle in *Cuspidaria cuspidata*, as described by GROBBEN, and also in *C. modesta*, *C. convexa*, *C. (Myonera) dubia* and in two other unidentified species from the "Siboga" collections (PELSENEER (1911)). Besides the longitudinally directed fibres, there are others which pass diagonally across the septum from the main longitudinal bundles, and the somewhat thinner region between the pores is largely composed of such muscles which have their origin in the anterior septal muscle, while posterior to the foot similar muscles pass across the centre of the septum and meet diagonally directed fibres from the posterior septal muscles. The two sets of muscles from each side unite and, together with the fibres of ~~from~~ the inner longitudinal bands from the anterior septal muscle, form a thick muscular sheet composed of closely interwoven fibres, as shown in text-fig. 2. An opening (o) is left between the posterior septal muscles whereby the supra-septal cavity is connected with the exhalent siphon.

The septum is also connected with the shell by means of numerous thin muscular strands which extend dorsally through the tissue of the mantle and are attached to the shell near the mid-dorsal line. These lateral septal muscles (text-fig. 1, ls) are arranged in two pairs in Cuspidaria rostrata, a smaller anterior pair (text-fig. 2, al) and a larger posterior pair (pl). The same condition is found in Cuspidaria mitis, C. strictirostris, C. corrugata and a further unnamed species from the 'Siboga" collections (PELSENEER (1911)). In C. cuspidata, however, the lateral septal muscles are continuous (see figures 1 and 2 in GROBBEN) and also in C. modesta (PELSENEER (1911)). In other species different conditions are found, there may be one pair of lateral muscles as in an unnamed species from the 'Siboga", four pairs as in C. fragilissima, or none as in C. (Myonera) dubia (PELSENEER (1911)). The fine isolated bundles forming these muscles extend down through the mantle until they reach the septum when they are continued transversely across its dorsal surface, and can be distinguised in sections as a thin layer immediately beneath the epithelium. As will be shown later, their structure is distinct from that of the main septal muscles.

Although the majority of the known species of the Cuspidariidae possess, like C. rostrata, four pairs of septal pores (see PELSENEER (1911) for details as to species), *C. cuspidata* ~~(see text-fig. 6)~~, *C. convexa* and *C. arctics var glacialis* all have five pairs. If reference be made to text-fig. 6 which represents *C. cuspidata* as seen from the ventral aspect with the mantle lobes drawn apart, the five pairs of pores will be seen. The size of the palps, which were drawn from life, is also clearly shown in the same figure.

Alimentary system. - Referring again to text-fig. 1, the mouth (m) lies in the middle line between the two pairs of palps and is a laterally extended opening of relatively large size, as is best seen in text-fig. 6. It leads into a short oesophagus (o) with folded walls which extends almost directly dorsally to open into the stomach (st). This latter organ is, for a Lamellibranch, of unusual size and shape. It is long and cylindrical, extending almost from end to end of the visceral mass in a longitudinal direction. Its walls are thrown into a series of prominent folds (see figure 7), the entire inner surface being covered with a thick cuticular lining. Surrounding it on all sides except the extreme dorsal surface are the brownish, blind-ended, tubules of the digestive diverticula (so-called liver or hepatopancreas), the whole consisting of somewhat asymetrical halves lying on either side of the stomach into which each opens by a separate duct (d', d''). Both of these open into the ventral region of the stomach, near the anterior end, the one on the right (d') being smaller and slightly anterior to the one on the left (d'') which opens on a line with the beginning of the mid-gut.

Both the style-sac (ss) and the mid-gut (g) open into the stomach near its anterior end and a little to the right of the mid-ventral line, the mid-gut being the more anterior of the two. The style-sac is a short oval cavity and contains a small cylindrical style as indicated by the broken line in text-fig.1. The style removed from a living specimen of Cuspidaria cuspidata was only 1.9 mm long and .74 mm broad, and projected but slightly into the lumen of the stomach. The lumina of the style-sac and the mid-gut are separated by a well-developed fold but remain connected by a narrow longitudinal slit. The mid-gut is both short and straight; after extending ventrally as far as the base of the style-sac, it is then directed posteriorly lying among the tubules of the digestive diverticula. Posterior to the stomach it turns abruptly upwards and leaves the visceral mass in the region below the umbo. It becomes merged here into the rectum (r) which at the beginning of its course traverses the heart (h) and later passes between the posterior septal muscles, over the posterior adductor and then turns downward to open at the anus (a) into the base of the exhalent siphon.

B. POROMYA.

Literature. - The anatomy of Poromya granulata and P. tornata was first described and figured by PELSENEER (1888b) who later (1891) gave a more detailed account of the former species. In 1911 the same author described eight species of Poromya from the "Siboga" collections. DALL (1886a, 1889a, 1889b) has described the shell and external anatomy of the body in a number of species of the Poromyidae. RIDEWOOD (1903) has provided an account of the structure of the septum and the branchial sieves in Poromya malespinae and P. oregonensis.

General Anatomy. - A lateral view of Poromya granulata is represented in text-fig. 3. The shell (sh) has no posterior siphonal prolongation as in the Cuspidariidae, the posterior margin being subtruncate and slightly gaping. The siphons are short - almost sessile - and the inhalent opening is much larger than the exhalent (see text-fig.4, i & e), both being surrounded by a common ring of long, slightly tapering tentacles (text-figs.3 & 4, d & t) consisting of an unpaired dorsal tentacle (text-fig.4, d) and seven pairs of tentacles round the lateral and ventral sides of the inhalent siphon. The opening of the inhalent siphon into the infraseptal cavity (V) is guarded by a large muscular valve (v). The surface of the mantle is excessively thin as in the Cuspidariidae, the ventral margins (me) alone are thick and are free from one another for the entire length of the body from the anterior adductor (aa) to the siphons. The foot (f) is long and thin and possesses a byssus groove on the posterior surface (see text-fig.7, b). It has two retractor muscles, an anterior (ar) and a posterior retractor (pr) which are attached to the shell in the same relative positions as in Cuspidaria rostrata. The palps are broader and larger than those of the Cuspidariidae, a fact which has been noted by all observers, the anterior pair

(Insert text-fig.3)

(ap) being especially long and, unlike the anterior palps of the Cuspidariidae, being free from the anterior adductor (see also text-fig. 7). The posterior pair (pp) are united to one another in the middle line and do not extend back on either side of the foot as in Cuspidaria. The degree to which the mouth (m) is guarded and obscured by the palps is seen best in text-fig. 7 which was drawn from life. The adductor muscles (aa & pa) occupy the same relative positions as in Cuspidaria rostrata but are smaller, and the posterior adductor is round and not oval in cross section. The visceral mass occupies the bulk of the supra-septal cavity (D), the dorsally situated ovary (ov) and the more posterior and ventral testis (te) being both well developed (like all the Septibranchs, Poromya is hermaphrodite). Lying above the oesophagus (o) are the cerebral ganglia (cg).

Septum. - The septum in Poromya is a much smaller and more delicate organ than in the Cuspidariidae. It is attached to the mantle on its outer sides, the right side being attached along the line marked sm in text-fig. 3. The two sides are united posterior to the foot but are closely apposed,and not united,to the base of the foot along the line marked s. The septal muscles are very much smaller than those of the Cuspidariidae and consist of two pairs, one anterior (as) and the other posterior (ps), which are attached to the shell a little distance posterior to the anterior ~~adductor~~ retractor and immediately posterior to the visceral mass respectively. The muscles run through the tissue of the mantle before becoming attached to the shell. There is no indication of lateral septal muscles but, as will be discussed later, there is evidence that the septal muscles in Poromya may correspond to the lateral septal muscles, and not to the septal muscles, of the Cuspidariidae.

There are no pores like those in the septum of the Cuspidariidae; instead there are a pair of anterior, and a pair of posterior, branchial sieves (ab, pb) which probably represent vestiges of the Lamellibranch gill. Each of these, in the words of RIDEWOOD (p. 272), "has the form of a shallow convex sieve, with the convexity directed downward and outward into the pallial cavity, and is attached all round its edge to the branchial septum by a thickened border". The anterior pair are on a level with the anterior border of the foot and each possesses five filaments, the posterior pair are situated opposite the hind end of the foot and have each six filaments. Both pairs are much nearer to the foot than to the mantle and lie somewhat obliquely. The slit-like openings between the filaments represent the sole means of communication between the infra- and the supra-septal cavities, for the edge of the septum, though not attached to the side of the foot, is too closely applied to it to permit the passage of water . Though all known species of the Poromyidae possess two pairs of branchial sieves, these vary in size and in the number of filaments in different species. PELSENEER (1911) has tabulated the different conditions found in the eight species collected by the "Siboga" and has shown hat the number of filaments in the anterior branchial sieve ay vary in number between five and eight, and in the posterior ne between five and eleven.

The conditions in the Cetoconchidae, according to PEL-ENEER (1888b) and RIDEWOOD, approximate more closely to those ound in the Poromyidae than in the Cuspidariidae, the septum eing thin and possessing three paired sets of openings conisting, in <u>Cetoconcha sarsi</u> (see RIDEWOOD fig. 60), of an anterior eries of five pores, a second series of five pores, and a postrior of three. In cross section, as shown by RIDEWOOD, the oundaries between the pores appear as shortened gill filaments s in the Poromyidae. Both the valve guarding the entrance to he infra-septal cavity and the palps of the Cetoconchidae are arge and resemble those of the Poromyidae and PELSENEER (1911), pparently) ith good reason, regards the Cetoconchidae, though somewhat ntermediate between the Poromyidae and the Cuspidariidae, as uch more nearly related to the former family, concluding (p. 78) "la nécessité d'une famille Cetoconchidae n'est nullement demontrée".

<u>Alimentary System</u> - The widely-open mouth (m) leads into a short and broad oesophagus (o) which is directed antero-dorsally, turning posteriorly to open into the large cylindrical stomach (st). This is not quite so long nor so regularly cylindrical as the stomach of the Cuspidariidae but resembles this in the possession of a thick cuticular lining. It is surrounded, except in the posterior region, by the brownish tubules of the digestive diverticula

(dd) which extend further forwards than in Cuspidaria and open by two short, wide ducts near the anterior end of the stomach. There is an even smaller style-sac (ss) than in Cuspidaria and the contained style does not project far into the lumen of the stomach. The sac is in communication on its anterior side with the mid-gut (g) by means of a fine longitudinal slit. The mid-gut is short; after passing beneath the style-sac, it extends posteriorly to the end of the visceral mass and then diagonally upwards merging into the narrower rectum (r) ~~before~~ which passes over the posterior adductor to open at the anus (a) which lies at the base of the exhalent siphon. The cleared specimen of *Poromya granulata* from which text-fig. 3 was drawn contained between its posterior palps and in the oesophagus large sand grains (x), and in the stomach a relatively large crustacean (c) which occupied the centre of the lumen.

(ii). HISTOLOGY.

A. CUSPIDARIA.

Mantle and Foot. - The thin mantle is bounded on both surfaces by a delicate pavement epithelium, as described in detail by GROBBEN. The thickened ventral edges possess on either side an epithelium of high, narrow cells, those on the outer and ventral surfaces being concerned, presumably, with the formation of the shell. The epithelium on the inner side is the only region of the mantle which is ciliated while there are present beneath the epithelium for the anterior two thirds of its course large goblet-shaped mucus glands. These glands, which stain darkly with muchaematein, occur in such numbers as to form a thick layer beneath the epithelium. They discharge their contents by way of narrow extensions which pass between the cells of the epithelium. GROBBEN has described them in C. cuspidata and PLATE in C. obesa, in my own sections I have found them in these two species and also in C. rostrata. The ciliated regions extend posteriorly to the region of the valve at the posterior end of the mantle cavity.

The surface of the foot is thrown into a series of fine ridges which are bounded by a columnar epithelium which, except near the base of the foot, is ciliated, mucus glands occuring in the tissue beneath. The interior of the foot is composed of plain muscle fibres passing in all directions amongst which ramify the extensions of the byssus gland, the ciliated duct of which opens on the posterior surface of the foot near the base.

Septum. - GROBBEN is the only worker who has described the fine histology of the septum in detail though his findings have been confirmed to some extent by PLATE. As shown in PL I fig.1, both dorsal and ventral surfaces are covered with a low pavement epithelium (d.e. + v.e.), especially thin on the former, no cilia can be distinguished in sections (though their presence on the dorsal surface was noted in living C. rostrata and C. cuspidata) only a fine border cuticle, while nuclei are infrequent and irregularly distributed. The interior of the septum is composed of a mass of interwoven muscle fibres which, as already noted and figured by GROBBEN in C. cuspidata and confirmed by PLATE in C. obesa, have a characteristic and unique structure. As shown in fig. 3, they consist of flat fibres which, in the case of fibres from the septum of C. rostrata, are about 13 μ wide and less than 2 μ thick. After staining teazed out fibres with iron haematoxylin, cross striations (st.) can be seen as dark bands somewhat narrower than the intervening lighter portions and about 1.5 μ apart. The fibres are of great length and multinucleate, the nuclei, as shown in fig. 3, n.s occuring at intervals and being situated in the centre of the fibres. They are long and narrow - about 11 μ long and 3 μ wide - and appear to lie in a lightly staining strip (c.a.) in the centre of the fibre, this area extending down the middle of the fibre for some distance beyond the extremities of the nuclei. The fibres are usually wavey and their linear appearance in cross section is shown in fig. 1 (the cross striations do not appear in this section which was stained with Delafield's haematoxylin and eosin), and in longitudinal section, with the striations indicated, in fig. 2. There is an almost complete absence of connective tissue strands, but there are many wandering cells (wc) amongst the muscle fibres. This type of muscle appears to be unique in the animal kingdom, it is certainly unique so far as the Lamellibranchs are concerned, and its peculiar structure may be correlated with the remarkable mode of functioning of the septum, particulars of which will be given later.

The lateral muscle fibres which run across the dorsal surface of the septum immediately beneath the epithelium, consist of plain muscle, roundish in cross section and are shown (l.sm.) in fig. 1. The striated muscle fibres are not present in the narrow membraneous strips which connect the septum to the mantle and to the foot, only a little unstriped muscle - probably derived from the lateral septal muscles being found between the epithelia in these areas. The septal pores are best studied in cross section (i.e. in longitudinal sections of the septum). They have been described by PELSENEER (1891) in *C. rostrata* but not in any histological detail, GROBBEN studied the pores of *C. cuspidata* very carefully and PLATE stated that he found similar conditions in *C. obesa*, RIDEWOOD'S material was too badly preserved for him to determine the structure of the pores. In my own sections, I have found essentially similar conditions in all three species examined. The conditions in *C. rostrata* will be described in detail, figs. 1 and 2 respectively representing longitudinal and horizontal sections through the septum of this species in the neighbourhood of pores. Near the pores the epithelium is raised, becoming columnar with well defined cells containing regularly arranged and prominent nuclei. As already noted by PELSENEER (1891) and GROBBEN, the inner or dorsal region of the pores is drawn out into the form of a valve (v.) with raised, dorsally directed lips, the whole, being sunk considerably below the dorsal surface of the septum (as shown clearly in fig. 1) in both *C. rostrata* and *C.*

cuspidata, in C. obesa, however, the valve is relatively larger and its dorsal extremity lies on a level with the upper surface of the septum. In all cases the under surface of the pores is flush with the surface of the septum. The pores are ciliated in two regions on their inner, opposed surfaces. There are prominent cilia, at least as long as the cells that bear them, in the extreme dorsal region (d.c) as shown in figs. 1 and 2. Beneath this there is an unciliated area, rather greater in extent than the upper, ciliated region, and below this again a second set of cilia (v.c), which extend as far as the ventral opening of the pores. These cilia are much shorter than those in the dorsal region and are difficult to see, especially in C. rostrata. They are more easily distinguished in C. obesa, while GROBBEN has noted and figured them in C. cuspidata.

Around the pores, and particularly in the valvular region, a well developed sphincter of plain muscle fibres is present beneath the epithelium (figs. 1 & 2, sp.), and can easily be identified in both transverse and horizontal sections, the fibres being quite distinct from those of the septal musculature and resembling those of the lateral muscles. The presence of this sphincter has not hitherto been described but is of some importance as will be emphasized later.

Palps. - A transverse section through one of the posterior palps of C. rostrata is shown in fig. 4. The inner surface (i.e.) is lined with a columnar epithelium possessing a uniform coating of cilia ~~and this~~ which is continued for a short distance round either edge of the palp. There are none of the prominent ridges and furrows present on the more compex palps of the typical Lamellibranchs (see YONGE (1926b) which contains references to previous literature). The outer surface (o.e.) bears no cilia and is bounded by a thin pavem~~m~~ent epithelium with ill-defined cell boundaries and few nuclei. There is a complete absence of mucus glands in both epithelia. Within the palp there is a considerable development of plain muscle (m.) running both transversely and longitudinally, the latter being best shown in longitudinal sections, and being most conspicuous near the base and extending towards the tip of the palp under both epithelia. There are also connective tissue strands and many wandering cells (w.c), but the latter are never found in the epithelium as is the case, for example, in Ostrea (YONGE (1926b)).

Mouth and Oesophagus. - The wide mouth is lined with a ciliated epithelium resembling that of the palps of which it forms a continuation. It is surrounded by a moderately thick layer of circular muscle fibres. The oesophagus, as shown in fig. 5, is roughly circular in cross section, with its walls, especially on the anterior and posterior sides, much folded longitudinally, many of the ridges (r.) being of considerable ~~length~~ height and projecting for some distance into the lumen. The columnar epithelium which lines the lumen is ciliated for the most part, cilia, however, are not present on the lateral walls in the distal region of the oesophagus, as indicated in fig. 5, the epithelium there being bounded solely by the thin border cuticle which is also present on the ciliated cells. Surrounding the oesophagus s an extremely thick layer of circular muscle (cm), as already bserved by PELSENEER (1891), GROBBEN and PLATE, a condition ever found in the typical Lamellibranchs, where the gut muscle s throughout very weakly developed. There are also, here and here, muscle strands (rm) which radiate out from the interior f the ridges and pass through the circular muscle layer.

tomach. - Longitudinal and transverse sections of the stomachs f *C. rostrata* and *C. cuspidata* respectively are shown in figs. and 7. The epithelium consists of extemely narrow ells which vary greatly in length so as to form a series of igh, longitudinal ridges (lr). Nuclei are small and wander-ng, phagocytic cells are only very rarely found in the epithelum. The cells are filled with fine yellowish brown granules, specially in the upper regions. There are no cilia in the tomach. At the junction with the oesophagus a thick, lamellat-d, cuticular layer is formed by the stomach epithelium and this s continued over the entire surface of the stomach as shown in fig. 6 (cu). The presence of this cuticle has been noted by both PELSENEER (1891) and GROBBEN, and it appears to be characteristic of the Septibranchs and to represent, very probably, an extension over the whole surface of the stomach of the smaller gastric shield (flèche tricuspide) which is found in all Fili-ranchs and Eulamellibranchs where it is situated on the wall of the stomach directly opposite to the opening of the style-sac. It serves to provide a firm surface against which the head of the crystalline style can bear as it revolves (see NELSON(1918)).

s previously noted (YONGE (1926b)), the gastric shield appears o be formed of the same material as the cilia or the border uticle; itis certainly not secreted in the usual manner. n Cuspidaria also there is no evidence that the epithelium f the stomach is composed of anything but modified ciliated ells and there is no evidence of secretion. As in Ostrea, here are fine transverse striations extending through the cuticle about ts junction with the epithelium, which have certainly the appear-nce of cilia. Probably, therefore, the stomach cuticle of he Septibranchs is merely an extension of the gastric shield f the other Lamellibranchs.

Surrounding the epithelium there is a well-developed ayer of circular muscle fibres (cm.), and fine fibres also pass etween the cells of the epithelium,especially in the centre of he ridges. The presence of these muscles, and the fact that he stomach in Cuspidaria is practically free from the surrounding tissues provide further important distinctions between the stomach of the Septibranchs and those of the other Lamellibranchs.

Digestive Diverticula. - The opening of the anterior and smaller duct of the digestive diverticula in *C. cuspidata* is shown in fig. 7(d). The actual duct is, when compared with that of a typical Lamellibranch such as Mytilus (LIST (1902)), Anodonta (GUTHEIL (1912)) or Ostrea (YONGE (1926b)), exceptionally short and wide approximating most nearly to the conditions found in the Teredinidae (SIGERFOOS (1908), POTTS (1923), YONGE (1926a)) where, on account of the elongated shape of the animals, the digestive diverticula are spread out in a thin sheet round the ventral surface of the stomach and their ducts, as a result, are short and wide. In the Cuspidariidae, as in the other Lamellibranchs, the ducts are lined by a ciliated epithelium; ~~[illegible]~~ neither phagocytes nor mucus glands are. ~~however~~. to be seen in this epithelium. The diverticula (t.) themselves are notable for their widely open lumina and the extent to which, especially in the regions nearest the ducts, they unite with one another to form a more compact structure than the separate acini characteristic of the majority of the Lamellibranchs. ~~It~~ They tend~~s~~ more to the condition found in some of the more highly organized Gastropods, such as Doris, where the digestive "gland" possesses a large central chamber into which secondary cavities open on all sides. In structure, the cells of the tubules of the digestive diverticula do not vary essentially from the conditions found in the other Lamellibranchs (for full details and literature on this subject see YONGE (1926a)). One type of cell only is present, groups of large, vacuolated cells which frequently contain inclusions of various sizes and usually of a brown or yellowish colour, being separated from one another by crypts of smaller, less vacuolated and darkly staining, cells, (fig. 13, o.c. & cp.) but the latter, as previously shown (1926a), represent nests of young cells destined to replace the older cells which in time are destroyed and cast into the lumen. As in the digestive diverticula of the other Lamellibranchs, there is no evidence of secretion by any of these cells. The nuclei are of the characteristic shape, namely large, round and with a prominent nucleolus, and are most numerous in the crypts of young cells. No evidence of the presence of cilia was found either in fresh material or in sections, nor any sign of a border cuticle. It is not impossible, however, that, as in other Lamellibranchs, long retractile cilia may be borne on these cells in the living condition (see POTTS and YONGE (1926a)). Around the tubules there is a thin bounding membrane but no muscle such as surrounds the ducts (see fig. 7). The area between the tubules is conspicuous for the almost compete absence of connective tissue strands, there are occasional muscle fibres and a certain number of wandering cells. This is very different from the conditions found in the majority of the other Lamellibranchs where the digestive diverticula are embedded in a firm matrix of connective tissue.

Style-sac. - The longitudinal section through the stomach of *C. rostrata* represented in fig. 6, shows the position and relative size of the style-sac.(s.s.) with its contained style (c.s.). The opening of the mid-gut anterior to it is only just indicated in the section (bg.) and, owing to the S-shaped form of the separating ridge (~~[illegible]~~), there is the appearance in longitudinal section of three cavities; the narrow cavity (c.g.) shown on the left of the style-sac in fig. 6 is in reality a portion of the connecting slit between the style-sac and the gut. The extreme basal region of the style-sac, as shown by horizontal sections, is separate from the mid-gut. The style-sac is lined with an epithelium of large, cubical cells (e.s.) with well-defined cell boundaries and large round nuclei which occupy the centre of the cells. The latter are covered a dense and very even coating of strong, bristle-like cilia, on the edges of this epithelium, where it passes into the typhlosoles which separate the lumina of the Style-sac and the Mid-gut, there are groups of tall, narrow cells. In every particular, therefore, the structure of the style-sac in Cuspidaria resembles that of the other Lamellibranchs which has been described in detail by NELSON (1918), EDMONDSON (1920) and YONGE (1923, 1926b) and other authors therein quoted. The epithelium of the separating ridge is ciliated and resembles that of the mid-gut.

The style itself is of the usual structure but is exceptionally short. It does not protrude far into the stomach, as is shown clearly in fig. 6, and clearly cannot act against the cuticular lining on the opposite wall of the stomach in the same way that the style in the typical Lamellibranchs acts against the gastric shield. The probable reasons for this will be discussed later, it may be mentioned here, however, that there is strong evidence that the style in the Septibranchs is largely a vestigial organ.

Mid-gut and Rectum. - For a short distance after its separation from the style-sac, the mid-gut possesses a prominent typhlosole (fig. 8, ty.) which represents the continuation of the ridge separating it from the style-sac. The epithelium consists of tall cylindrical cells with long cilia and oval, basally situated, nuclei. Here and there are groups of narrow, darkly staining, and probably young, cells (y.c.). Around the epithelium is a thin circular muscle layer (c.m.). There is a complete absence of mucus glands in the epithelium and phagocytic wandering cells are extremely rare. The typhlosole does not extend very far posteriorly and, for the greater part of its course, the mid-gut is a thin-walled, oval tube. In the region of the heart, as indicated in text-fig. 1, it merges into the rectum and the junction between the two is shown in fig. 9. The mid-gut is here much wider and is bounded by a thin, ciliated epithelium which contains occasional mucus glands (mg). The circular muscle layer is extremely thin in this region. The mid-gut (mg.) is united on its dorsal side to the rectum (r.) which has a characteristic structure. It is bounded by tall, narrow cells bearing long cilia and interspersed with many mucus glands (mg). It is surrounded by a comparatively thick circular muscle layer. After separating off from the mid-gut, it continues as a straight tube, circular in cross section and with a narrow lumen.

It is worthy of note that, with the exception of the peculiar mode of union between the mid-gut and rectum, and the absence of phagocytes from the epithelium, both mid-gut and rectum in Cuspidaria have essentially the same structure as in the other Lamellibranchs (e.g. Anodonta (GUTHEIL (1912)), Mya or Ostrea (YONGE (1923, 1926b)).

The structure of the gut in the three species of Cuspidaria examined is, in all essential details, identical.

B. POROMYA.

With the exception of the septum, the structure of the feeding and alimentary organs in Poromya granulata is little different from that found in Cuspidaria. The mantle is thin and in structure resembles that of Cuspidaria, the thickened ventral margins are bounded on their inner sufaces by a columnar epithelium which is ciliated but contains few mucus glands beneath it. The surface of the foot is covered with a ciliated epithelium except in the basal area. The septum, a portion of which is shown in longitudinal section in fig. 10, is bounded on either side by well-defined epithelia of cubical cells (d.e. & v.e.), neither of which show the presence of cilia in sections but possess a border cuticle ~~(de & ve)~~. The septum is much thinner than in Cuspidaria and the musculature is much slighter. The fibres run mainly longitudinally and are unstriped and roundish in cross section, in no part of the septum is there any indication of the presence of the striped muscle so characteristic of the septum of the Cuspidariidae.. As noted by RIDEWOOD in P. malespinae, the septum is thicker and more muscular in the region behind the posterior branchial sieve.

The structure of the branchial sieves in Poromya malespinae and P. oregonensis has been described by RIDEWOOD, and that of P. granulata in less detail by PELSENEER (1891).

A transverse section through one of the posterior branchial sieves is shown in fig. 10. The filaments show essentially the same structure as the gill filaments of the other Lamellibranchs. Thick rods of "chitin" (ch.) are present beneath the epithelium on the sides of the filaments, the interior of which is filled with strands of "chitin" and also other connective tissue, and wandering cells (w.c) are present both here and ~~also~~ in the meshes of the somewhat vacuolated "chitinous" supporting rods. In the dorsal region of the filaments (i.e. the morphologically interlamellar region) there are thick bands of longitudinal muscle (l.m.). There is no evidence of any interfilamentar junctions in Poromya granulata, nor were they found by RIDEWOOD in P. oregonensis, though this author noted their presence in P. malespinae as did PELSENEER (1888b) in P. tornata. Laterally the filaments are bounded by tall epithelial cells which carry long cilia (l.c.) which correspond to the lateral cilia of the typical filament. No frontal cilia can be distinguished in P. granulata, RIDEWOOD found them in P. malespinae but not in P. oregonensis, but small latero-frontal cilia may be present. If so they are quite different from the large straining laterofrontals found in the typical filament. The reasons for this modification of the ciliation of the filaments composing the branchial sieve will be discussed later.

A longitudinal section through the labial palps, mouth, oesophagus and stomach of P. granulata is shown in Fig. 11. As will be observed, they do not differ essentially from those of

Cuspidaria. The comparatively large palps (a.p. & p.p.) are ciliated on their inner surfaces only and contain numerous muscle strands, the mouth (m.) is large and leads into a wide, ciliated oesophagus (o.) which is surrounded by a thick layer of muscle (m.). The stomach (st.) is large and its ridged walls are covered with a high, columnar epithelium which contains numerous fine, yellowish, refractile inclusions. A thick cuticular layer (cu.) lines all regions of the stomach, which is surrounded by a thick layer of circular muscle fibres. Both tubules and ducts of the digestive diverticula resemble those of Cuspidaria. The style-sac is small and contains a small rounded style which does not project far into the stomach; the midgut is connected with the style-sac in the same manner, and has the same structure throughout, as in Cuspidaria, being ciliated, round in cross section in the region of the stomach and becoming oval before it passes into the rectum. The rectum is narrow, ciliated and contains many mucus glands.

4. THE PROCESS OF FEEDING.

(i). MODE OF LIFE.

Both Cuspidaria and Poromya live in mud into which they burrow. This process was followed in the laboratory by placing freshly caught animals in vessels containing sea water beneath which was a layer of mud. All three species of Cuspidaria, and Poromya granulata behaved in essentially the same manner. No previous observations appear to have been made on living

Septibranchs so that the observations recorded in this section probably represent an extension to our knowledge concerning the habits and feeding mechanisms of the Lamellibranchia.

Burrowing is performed largely by means of the foot which can be protruded from between the shell valves as a thin wedge which, when fully extended, is about the same length as the shorter axis of the shell. It can be directed either ventrally or anteriorly. The burrowing of *C. obesa* was carefully followed at Trondhjem. After being placed on its side on a layer of mud about one inch thick, the animal worked its way downwards until the anterior half of the body region (i.e. as apart from the siphonal extension) of the shell was buried. At the same time the siphons with their surrounding tentacles (all tinged red in life) were protruded. About once a minute a violent contraction of the shell valves was observed, a contraction which was apparently connected with movements of the entire animal whereby it was rotated slightly and at the same time pushed deeper into the mud. This movement was always accompanied by a sudden ejection of water through the *inhalent* siphon - a necessary safeguard if the septum is not to be severely strained or perhaps ruptured. The animals usually burrowed diagonally downwards and with considerable rapidity though in a series of jerks with appreciable intervals between them. At each movement the posterior end of the animal was raised to an almost vertical position and was then lowered again, the animal at the same time sinking deeper into the mud.

Finally it burrowed so deeply that the end of the siphonal extension of the shell was flush with the surface of the mud above which only the siphons projected, and, had not the previous movements of the animal been followed, it would have been difficult to distinguish these. The animals did not usually remain long in this position, but moved about on the surface of the mud which soon became channelled and pitted as a result of their movements and burrowings. However deeply the animals burrowed the siphons were never covered. Similar habits were observed in the case of <u>C. cuspidata</u> at Kristineberg.

Poromya protrudes its siphons and their surrounding tentacles more readily than does Cuspidaria. As already noted the latter are very long and, when extended, they lie backwardly directed over the posterior region of the shell covering some quarter of its surface, they may, however, erect themselves so that they stand out at right angles to the surface. They were often observed in movement. When placed on mud Poromya burrows into it in much the same manner as <u>C. obesa</u>, using its long, extensile foot. Water appears to be forced out of the shell anteriorly, a proceedure which may assist burrowing as the animal was observed in this manner to force away mud from in front of its shell. During burrowing, the animal was observed to erect itself, posterior end upwards, in the mud and then turn slowly round, sinking into the mud as it did so, finally resuming a horizontal position; It then proceeded to move along and downwards in the channel it had made. All the movements, as in Cuspidaria, were sudden with appreciable intervals between them. As a result of this process, first the anterior end and finally the entire shell becomes buried beneath the mud. Gradually the animal assumes a vertical position, anterior end downwards, with only the siphons exposed which lie flush with the surface of the mud, the two siphonal openings

(Insert text-fig.4)

pointing directly upwards (text-fig.4, i. & e.) and the tentacles (t) lying flat on the surface of the mud as shown in text-fig. 4.

(ii). FUNCTION OF THE SEPTUM.

The movements of the septum were very carefully followed with a view to determining the true function of this organ which has been a matter of dispute.

In the Septibranchs, unlike the other Lamellibranchs, there is no continuous current of water passing in through the inhalent, and out by way of the exhalent, siphon, even when these are fully extended and obvious~~l~~ly functioning. Instead there is an occasional widening of the opening of the inhalent siphon followed by a sudden intake of water while at the same time the exhalent siphon opens to its fullest extent, water being expelled through the opening with considerable force, a fact which can be forcibly demonstrated by introducing a suspension of carmine grains into the water around the exhalent siphon. The exhalent siphon in the Septibranchs has an exceptionally narrow opening, the lips of which are normally drawn together - a necessary precaution in view of the danger of small particles entering the siphon in the absence of a steady outflowing current. The inhalent and exhalent movements take place perfectly regularly in animals which are functioning normally with siphons fully extended. In *Cuspidaria obesa* they were observed to take place about six times per minute, and in *C. cuspidata* some four times a minute.

By carefully removing the shell valves from the two larger species of Cuspidaria, these sudden movements were found to be caused by the movements of the septum, the action of which did not appear to be interfered with when the shell was removed. Contary to what has hitherto been assumed from an examination of its anatomy, the septum when at rest, i.e. between the periodic movements, does not lie stretched to its fullest extent ventrally. On the contary, it is drawn up dorsally to the maximum degree, as shown in text-fig. 5 A. During rest the

(Insert text-fig.5)

pores are open and the cilia with which they are lined beat inwards so as to cause a small, but perceptible, current upwards from the infra- into the supra-septal cavity, as indicated by the arrows in the diagram. With the pores still open, the septum is lowered to its fullest extent when the pores are shut tightly, presumably by means of the sphincter of plain muscle. This condition is indicated diagramatically in text-fig.5B. The valve which guards the entrance to the infra-septal cavity probably prevents water from being expelled by way of the inhalent siphon during the downward movement of the septum, while the opening of the exhalent siphon remains shut so that water cannot be drawn through in the wrong direction. As a result, therefore, of the downward movement of the septum, water is transfered from the infra-septal cavity by way of the openings provided by the pores into the supra-septal cavity. The septum then drawn sharply upwards in the direction indicated by the arrows in text-fig. 5B with the pores still tightly shut - the pressure of the water against the dorsally directed valves preventing them from being forced open - until it regains its original position when it comes to rest, with the pores still shut, as indicated in text-fig. 5C. Finally the pores reopen and the slow flow of water through them is renewed. Exactly the same proceedure was observed in both C. rostrata and C. cuspidata.

The movements of the septum are invariably accompanied by the opening and extension of the siphons as already described, this taking place during the upward movement of the septum. The result of the septal movements is clearly to draw water and food matter into the infra-septal cavity, the water being later passed through the pores, slowly when the septum is at rest but quickly and in great quantities during its downward movements, and being expelled through the exhalent siphon. Thus, whatever the origin of the septum, ~~the~~ its function it is analogous with ~~that of~~ the Lamellibranch gill, ~~namely to~~ producing a current of water through the mantle cavity and ~~to~~ drawing in food. But, owing to the more powerful, though ntermittent, current produced by the septum, the food drawn in eed not - and does not - consist solely of fine particles arried in suspension by the water as in the ciliary feeding mellibranchs, but includes comparatively large particles or ll animals which may be sucked in unawares as they pass the nconspicuous siphons which are all that is exposed of the ried Septibranch.

In Poromya the action of the septum does not appear o be so regular. Occasionally - not at perfectly regular inter- ls and not more than once a minute - a sudden sharp expulsion f water was observed from the exhalent siphon, so powerful, ndeed, that if carmine grains were placed in the water they were hot away to a distance of about four or five centimetres. nfortunately, probably owing to the weakness of its musculature, e septum of Poromya did not function after the shell valves ad been removed for better observation. It proved impossible, herefore, to determine whether it acts in the same way as the eptum of Cuspidaria, a matter of importance in view of the dif- erent types of musculature in the septa of the two families. e cilia of the branchial sieves were observed in the living tate and seen to beat inwards, like those surrounding the pores f the Cuspidariidae, and so cause a current of water from the nfra- to the supra-septal cavity. The openings of the sieve an probably be closed by the contraction of the longitudinal uscles at the base of the filaments. The septum of Poromya is learly unfitted for the powerful and frequent movements displayed by that of

Cuspidaria; in structure it is too delicate while the branchial sieves are not adapted to stand the same pressure of water as the pores with their dorsally directed valves.

The peculiar state of affairs in the Cuspidariidae whereby the septum between its periods of activity is in its shortest condition *may* be connected with the peculiar type of muscle of which it is composed. The flat fibres are very long and wavey and it may be that on stimulation they straighten out and so extend the septum. This appears a more probable explanation than that the septum is in a state of tonus for the greater part of its existence. Physiological experiments - unfortunately impossible with the limited material and apparatus at my disposal - are needed to determine in what state the septum of Cuspidaria is actually relaxed, while the physiology of the septal muscle would undoubtedly repay further investigation. One thing only is clear, that the development of striped muscle is correlated with the need for a continuous series of comparatively sudden movements - a state of affairs which has led to the development of striped muscle in two other groups of Lamellibranchs, in the adductors of Pecten and the Teredinidae.

From morphological considerations, PELSENEER (1891) came to a conclusion as to the function of the septum which agrees fairly closely with my observations on the living animal. He states (p. 225) "Cette cloison, avec ses orifices, entretient assurément une active circulation d'eau sur la paroi intérieure manteau (dorsalement au septum, comme chez Poromya): la oison, en se contractant, ferme ses orifices et chasse l'eau r le siphon anal; lorsqu'elle se relâche, le siphon anal nt fermé, les orifices du septum s'ouvrent et l'eau entre dans chambre supraseptale, la valvule du siphon branchial pouvant pêcher qu'elle sorte par ce dernier".

GROBBEN agreed ~~largely~~ in the main with the above statement conering that so muscular an organ as the septum could not be ncerned with respiration but would be of great importance changing the water in the mantle cavity, as it is clearly apted for powerful movements, while in view of the cross riation of the muscle he thought it probable that very strong ntractions could be accomplished. He goes on to state (p. 13) at, "Doch möchte ich glauben, dass nur von Zeit zu Zeit ein lch ausgiebiger, durch Contraction des Septums bewirkter sserwechsel stattfindet, dass im Uebrigen, wenn sich das ier in Ruhe befindet, die wenngleich geringe Verbreitung von impern an den Spalten, sowie im Mantel und am Fuss für einen ngsamen Wasserwechsel sich als ausreichend erweist. Anderseits ird aber die geringe Ausdehnung von Wimperepithelien an den die antelhöhle begrenzenden Flächen wieder auf einen zeitweilig othwendigen ausgiebigeren Wasserwechsels durch Contraction des Septums hinweisen". In view of his lack of observations on living animals this statment is remarkably accurate.

PLATE did not think it probable that the movements of the septum could be intermittent with so enormously developed nd histologically so highly differentiated, a musculature. thought, moreover, that the cilia on the pores did not serve pass water through but merely acted as a sieving apparatus reventing the passage of food particles into the upper cavity. se opinions have not stood the test of experimental verification.

DALL had a very different opinion as to the function the septum. He considered (1889b, p.443) that the septal scles, "if not honologous with, at least perform the functions the siphonal retractors of ordinary Pelycopods, and in forms ke *Poromya mactroides*, where the usual retractors are present, e siphonal septum is destitute of musculature, or possesses it ly to an inferior degree". Later (p.445), refering to the ptal pores in Cuspidaria, he stated, "I suppose that they erve to admit fresh water to the upper chamber, which I believe o be utilized in some, if not all, instances as a marsupium. t is probable that, by suitable muscular contractions, the eptum will operate somewhat like the washer of a pump-valve, nd that the upper chamber can be filled or emptied of its contained water at will...... I do not regard it (the septum) as n any way homologous with the normal ctenidia". He supports his theory that the supra-septal cavity is a marsupium where the ova develop (as quite possibly - though quite incidentally - they do, for the eggs are large and yolky and the developing embryo will not require food for some time after hatching) by stating that in young specimens of various species of Cuspidaria and Poromya the septal pores or sieves are partially or completely ut, only opening completely when the animals attain sexual turity. It is clear, however, that if they were completely t the animals could neither feed nor respire since a through rent of water could not be maintained. There appears to o justification for DALL'S views as to the function of the ptum, his views with regard to its origin will be discussed ter. RIDEWOOD makes no comment on the function of the septum.

(iii). THE INTAKE OF FOOD.

In the Cuspidariidae, particles or small animals are wn in through the inhalent siphon as a result of the water rrent caused by the sudden upward movement of the septum. e four club-shaped tentacles which surround the inhalent siphon y perhaps assist in this, for they are freely movable and nd inwards, in a claw-like fashion, around the opening of the iphon beyond which they extend; but this was never experimentlly proved. Food passes through the valve leading into the fra-septal cavity, as indicated by the large arrow in text-fig.

(Insert text-fig.6)

6, and, as the animals always lie with the anterior end downwards, t will then fall down towards the mouth region. There are no cilia to guide it there such as are present on the gills of the ciliary feeding Lamellibranchs.

The palps probably serve to push the food into the mouth (though this was never experimentally demonstrated as it was in Poromya). Though they are small, especially the posterior pair which are absent in C. obesa, frequent movements were observed, as would be expected in view of their relatively well-developed musculature. In the majority of the Lamellibranchs, the two pairs of palps are closely applied to one another so that the mouth is obscured, but in Cuspidaria the large mouth is fully exposed and may extend~~s~~ considerably when food is swallowed, and ~~is~~ passed into the muscular oesophagus.

The cilia on the inner surfaces of the posterior palps (pp) beat in the directions indicated by the arrows in text-fig. 6. There is an outer lateral area on which the cilia beat towards the tip of the palp, the cilia on the remainder of the surface beating across it and carrying paticles into this backwardly-directed stream. On the anterior palps (ap), the cilia on the inner surfaces beat towards the tips of the palps. The cilia on the basal region of the palps, perhaps better described as the lips of the mouth, beat inwards as do those within the mouth and lining the oesophagus. As a result of the action of the cilia on the palps, small particles are carried away from the mouth, being passed from the posterior palps through the septal pores (as shown in text-fig.6) either directly into the second pair or by way of the foot. The cilia on the foot beat posteriorly and particles are carried to the hinder end where they appear to be drawn through the posterior pair of pores. As we have seen, there is a complete absence of cilia on the majority of the surface of the mantle, only the thickened marginal ridges (me) possessing them. These cilia eat posteriorly and carry fine particles to the hind end of he mantle cavity in the region beneath the valve. This iliary current corresponds to the "untere Rückströmung" originally described by STENTA (1903) and which has been shown to present invariably in the ventral region of the mantle in l Lamellibranchs (see especially KELLOGG (1915)). This rrent is always concerned with the cleansing of the mantle vity and the rejection of useless particles and it is note-rthy that it is the only ciliary current in the mantle cavity f the Septibranchs which clearly corresponds to a current found the other Lamellibranchs. Particles are massed together t the posterior end of the mantle cavity as the result of its tion and, as in other siphonate Lamellibranchs, are probably isposed of by sudden contractions of the shell valves which orce out water and suspended matter through the inhalent siphon.

Such cilia as are present in the infra-septal cavity, the mantle edges, on the foot, on the palps and round the ores, are therefore all concerned, not with feeding, but with he removal of fine particles from the mantle cavity. This leansing is obviously of great importance to animals which ive in mud and are consequently in constant danger of being logged with fine particles. Feeding is the result, exclusively, of the muscular action of the siphons, the septum, the palps and the anterior region of the gut (aided perhaps by cilia to a slight degree in the last instance).

In the supra-septal cavity there are, on the surface of the visceral mass, cilia which beat posteriorly and carry particles towards the exhalent siphon. In living specimens of Cuspidaria rostrata and C. cuspidata, moreover, a sparse ciliation was observed on the dorsal surface of the septum never on the ventral surface), as a result of the action of which particles were carried backwards. There are no cilia on the mantle surface. All cilia in the supra-septal cavity, therefore, serve to carry away particles and also, no doubt, assist the cilia of the septal pores in maintaining a slight circulation through the mantle cavity when the septum is at rest.

In Poromya, as shown in text-fig.7, conditions are

(Insert text-fig.7)

essentially the same. Owing to the fact that the inhalent siphon (see text-fig.4) has a wider opening, larger particles are drawn in than in Cuspidaria. When the animal is sunk in the mud and the siphons are functioning, the inhalent siphon is almost sessile and its dorso-ventrally compressed aperture is normally shut owing to the closing together of the rounded lips. The exhalent siphon is much smaller, is round and protrudes slightly as a roundish papilla, about 1 mm in diameter. Pieces of the gonad of Pecten about a millemetre across were placed on the inhalent siphon of a living Poromya. At first they were refused and pushed away by the surrounding tentacles, but on the second attempt they were drawn in slowly through the siphonal opening, being seized by the lips and slowly passed into the infra-septal cavity. A few moments later the inhalent siphon opened to its fullest extent and no sign of the food could be seen. A piece of coagulated blood, some 2 to 3 mm long and 1 mm wide, from Myxine was later fed to the same animal and was swallowed in a like manner.

It was observed that food was taken into the inhalent siphon by a series of movements clearly related to the contractions of the septum, or, if the food was not too large, by one sudden inrush. Both siphons were opened to their fullest extent, there was a sudden ejection of water through the exhalent siphon (showing that the septum had contracted) and at the same time matter was pulled into the inhalent siphon. After a series of these movements the larger food masses were finally taken completely into the mantle cavity. During the process of food intake, the lips of the inhalent siphonal opening were fully expanded and raised to a height of some two or three millemetres, i.e. above the exhalent siphon.

If too much food was taken in, then the surplus was frequently ejected - as a result of sudden contractions of the shell valves - but only if the food was still, at any rate partially, in the inhalent siphon and had not passed the valve leading into the infra-septal cavity.

As in the Cuspidariidae, the food falls down towards the mouth. There it is at once pushed into the mouth by the palps which are both larger and more active than those of Cuspidaria.

fter placing pieces of the gonad of Pecten upon them, both pairs f palps immediately curled inward, as indicated by the arrows n text-fig.7, and quickly pushed the food into the large mouth ich opened wide to receive and swallow it. There is thus t the slightest doubt concerning the muscular function of e palps in Poromya.

The only cilia whose presence could be identified n the living animal were those on the branchial sieves. ections show the presence of cilia on the palps, on the mantle ges and on the foot but these are evidently too small and heir action too feeble to be easily identified by placing armine upon them. The observations, moreover, had to be ade on one specimen only and without the aid of a binocular icroscope. In view of the similarity in the feeding habits nd the structure of the feeding organs in the two genera, there an be little reason to doubt that the cilia in the mantle cavity f Poromya serve the same function as those of Cuspidaria, amely to clear the mantle ~~mx~~ cavity of small particles.

(iv). PASSAGE OF FOOD THROUGH THE GUT.

Food is carried through the oesophagus largely by the peristaltic movemnets of its thick muscular layer. In Poromya, food was occasionally rejected through the mouth apparently by antiperistaltic movements.

In the stomach the food is broken up into small ragments. The stomach in the Septibranchs is a crushing izzard as its structure (see figs.6 & 7) plainly indicates. e powerful musculature serves to contract its walls violently that the ridges with their thick cuticle come together and ush up the large food masses which lie between them. It often oved difficult to section the stomach of both Poromya and spidaria owing to the mass of chitinous fragments and somees sand grains which filled the lumen. Occasionally, as own in text-fig.3, whole Crustacea were found in the stomach. e crushed up fragments must either be pushed into the wide, liated ducts of the digestive diverticula (fig.7) or into e opening of the mid-gut. It is necessary that particles ving food value should be passed into the former opening r in the digestive diverticula alone can they be digested, ereas the useless fragments of chitin, sand and the like ll need to be passed into the mid-gut. In the stomach of e ciliary feeding Lamellibranchs there is a highly efficient rting mechanism which disposes of the food particles, the aller ones passing into the ducts of the digestive diverticula r towards the gastric shield, and the larger ones being conucted straight into the mid-gut (see NELSON (1918), YONGE (1923, 1926b). In the stomach of the Septibranchs there is no such mechanism and it is not easy to see how such a separation takes place and exactly how food is separated from faecal matter. Within the tubules of the digestive diverticula it is quite possible that, as in other Lamellibranchs, a circulation is maintained by the action of long, retractile cilia which cannot be distinguish- after fixation and may be withdrawn when fresh material is press- out under a coverslip for examination. The presence of these cilia is rendered the more probable owing to the lack of a vascular network round the tubules such as is found in the Crustacea (see YONGE (1924) for details and literature) and serves, by its alternate contractions and relaxations, to produce a circulation through the tubules of the "hepatopancreas".

Material will be passed through the short mid-gut chiefly by ciliary action, for there is very little muscle and cilia are abundant (see fig. 8); the same is probably true for the rectum, though the more powerful encircling muscles in this region may aid in defaecation. Both of these regions of the gut, therefore, possess a similar function, as well as a similar structure, to that found in the other Lamellibranchs. The faeces are discharged into the posterior region of the supra-septal cavity and will be quickly ejected through the exhalent siphon.

5. THE NATURE OF THE FOOD.

Alone amongst the Lamellibranchia, the Septibranchia are carnivorous. PELSENEER (1891) originally came to this conclusion, stating (p.219) that, "*Poromya* est carnivore; la longeur de l'ouverture palléale antérieure, la largeur de la bouche et de l'oesophage, et la brièveté de l'intestin s'accordent

vec ce regime." Later (p.224) he writes, "Cuspidaria est franche-
nt carnivore. Dans l'estomac de C. rostrata, j'ai trouvé
lement un animal d'aspect déjà un peu défiguré, mais oculé et
evêtement de spicules. C'est là, avec Poromya, une except-
parmi les Lamellibranches; ce régime s'explique par l'habitat
es deux genres dans des eaux profondes où ne s'étend pas la
végétale. Les mouvements du septum musculaire aident pro-
blement à attirer la proie morte dans le manteau (qui est assez
vert), et la largeur de l'oesophage en facilite l'ingestion."

PLATE found the remains of Copepods and Annelids in
stomach of C. obesa, but continues by stating, "glaube aber
cht, dass die Cuspidarien sich hinsichtlich der Ernährung
gendwie von den übrigen Muscheln, die kurz als Planktonfresser
eichnet werden können, unterscheiden." Neither the extent
PLATE'S investigations (sections through a single specimen of
obesa) nor his knowledge of the feeding of the Cuspidariidae,
e of sufficient significance for much weight to be attached
the above statement.

PELSENEER (1911) in his account of the Cetoconcha
Silenia) in the "Siboga" collections - the only complete specimens
this rare genus as yet examined - states (p.79) that the
stomach contains "des débris de Crustacés", adding that Cetoconcha is thus, like the other Septibranchs, a carnivore.

My own investigations bear out fully PELSENEER'S
conclusions. The stomach contents of two living specimens of

C. cuspidata were examined at Kristineberg. One consisted of a Crustacean (probably, in the opinion of Dr. M. V. Lebour, an arly stage of a parastic Copepod) in almost perfect condition, ,2 mm long and with a carapace 1 mm wide, and also of the mpty shell of an Ostracod 1 mm long and 0.36 mm broad. The ther consisted chiefly of the remains of a Crustacean embedded in a mass of ~~fine~~ sand grains, the whole measuring some 0.9 mm in length and 0.45 mm in breadth. In neither stomach was there the slightest indication of that ~~fine~~ suspension of fine particles and organisms which invariably constitute the stomach contents of the ciliary feeding Lamellibranchs (see HUNT (1925) and SAVAGE (1925) for accounts of the stomach contents of Pecten opercularis and Ostrea edulis respectively).

The manner in which the sand grains were embedded in the food indicated the power of the gizzard and also suggests that sand grains may assist in the breaking up of the food. similar suggestion has been made in the case of the ciliary feeding Lamellibranchs which take in sand grains, but the almost complete absence of muscle in the gut, and the high development of the ciliary sorting mechanism in the stomach, of these animals provide conclusive evidence against this theory. The welding together of the food and the sand grains may be assisted by the substance of the style (for there are no mucus glands in the oesophagus or stomach) - indeed, in view of the almost total absence of finely divided or starchy foods, this appears to be the only function which the style can have.

In Poromya also, as shown in text-fig.3, Crustacea are taken whole into the stomach. In sections of both Poromya and the three species of Cuspidaria, the stomach was frequently found packed with fragments of animals, usually Crustacea, while the mid-gut contained fragments of chitin, spines, limbs, etc, all clearly of either Crustacean or Annelid origin. There was never any evidence of the presence of vegetable matter or fine plankton organisms in any part of the alimentary canal.

To what extent the Septibranchs depend on living or dead prey must remain uncertain. PELSENEER, as quoted above, suggests that the latter form the principal food, and, in view of the sluggish habits of the Septibranchs, this is quite possible. An active animal could doubtless easily escape them, especially since the Septibranchs have no means of actively seizing their prey, unless they chanced to swim too near to the aperture of the inhalent siphon and so were drawn in by the sudden and unexpected current. For the most part, ~~however,~~ we can imagine the Septibranchs moving about slowly through the mud and sucking in the small dead or dying animals which they ~~find~~ encounter. In deeper waters they will not have the opportunity, and neither there nor in shallower waters the ~~capacity~~ power, ~~to~~ of ~~take in~~ swallowing the diatoms, peridinians and other fine phytoplankton organisms which form the food of the great majority of the Lamellibranchs.

6. ASSIMILATION.

A number of feeding experiments were carried out, pecimens of Cuspidaria being placed in water containing, in spension, iron saccharate (ne of which passes into colloidal solution), Indian ink or the coagulated blood corpuscles various fish. Poromya was fed directly with pieces of he coagulated blood of Myxine and with pieces of the gonad Pecten, a second specimen being placed in a suspension iron saccharate in sea water. After suitable periods the imals were fixed in appropriate ways.

After feeding C. obesa with iron saccharate and reating in the usual manner (for details see YONGE (1926a)) fter periods of 6, 9 and 12 hours and one day, and subsequent ectioning, iron was found to be present in the mantle cavity here it was attached to all the ciliated areas, especially he foot and the margins of the mantle - i.e. clearly in process of being removed from the mantle cavity. It was also resent in the lumen of the stomach, the mid-gut and the rectum, ut it was never found in the epithelial cells of these regions. t was absorbed solely by the cells lining the tubules of the igestive diverticula, in the manner shown in fig. 12 which epresents the condition found subsequent to feeding for six hours. he iron saccharate is taken into large vacuoles (f.) within the ells and never appears in a diffuse or finely granular condition. Precisely the same state of affairs was found in Nucula, Mya, Teredo (YONGE (1926a)) and in Ostrea (YONGE (1926b)) and, as as pointed out in the former paper, there is reason to suppose hat this method of ingestion in large vacuoles is an indication f the presence of *intracellular* digestion. Iron saccharate absorbed in a diffuse or finely granular condition in animals nnelida or Arthropoda for example - in which digestion is clusively *extracellular*.

The same conditions were found in Poromya, an animal xed nine hours after it had been placed in a suspension of on saccharate showing the presence of iron lying on the cilia on e mantle edges; on the foot, on the palps and passing through e branchial sieves into the supra-septal cavity, (evidence that ese cilia serve the same function as those in Cuspidaria). was also found free in the lumen of the stomach and of the t, but it was absorbed *exclusively* in the cells of the tub-les of the digestive diverticula and there only in large vacuoles.

Specimens of *C. obesa* which had been placed in a spension of Indian ink and later fixed in Bouin, showed, in ctions, the presence of small quantities of indian ink lying the cilia in the mantle cavity and also being passed into e supra-septal cavity by way of the pores. A few particles re found in the stomach lying against the cuticle, but none the digestive diverticula.

Previous feeding experiments using the blood corpuscles f fish (YONGE (1926a, 1926b)) have shown that these are taken in reely by Lamellibranchs and are ingested. With the exception

f Teredo, however, in all the Lamellibranchs studied they were
gested by the phagocytes which abound in the epithelium, the
rrounding tissue and the lumen of the gut; especially were
ey so ingested in the stomach, the ducts of the digestive
verticula and the mid-gut. They were seized while still in
e lumen by these phagocytes which ingested them and then
rried them through the epithelium and into the connective
issue. Within the phagocytes they were slowly digested. Only
the case of Teredo where, as we have seen, the ducts of the
gestive diverticula are exceptionally short and wide, did
e blood corpuscles succeed in passing into the tubules of the
igestive diverticula where they are ingested by the cells.

In the Septibranchs, the histological examination
vealed the almost complete absence of these wandering phag-
ytic cells and the fate of the coagulated blood corpuscles with which they
re fed was, therefore, of the greatest interest. Specimens
f all three species of Cuspidaria were treated in this manner.
. obesa removed and fixed in Bouin after twelve hours of such feed-
ng showed the presence, after sectioning and staining with
iron haematoxylin and acid fuchsin, of blood corpuscles ingested
in the cells of the tubules of the digestive diverticula and
in no other region. The same conditions were found in *C.
rostrata* after similar treatment. In both of these experiments
the blood of cod was used.

Fig. 13 shows the appearance in cross section of a ngle tubule from the digestive diverticula of a <u>C. cuspidata</u> ich had been in a suspension in sea water of the blood of rasse for ten hours. The animal was fixed in Bouin and section figured was stained with Mann's Methyl-blue eosin bination. The effect is very striking, the ingested blood rpuscles staining a bright red while the cytoplasm colours e, the nuclei (n.t.) are blue except for the prominent nucleoli ich stain red. Great numbers of the blood corpuscles are gested, the great majority (b.c.i.) having already been carried wards the base of the cells, one, however, remains free in lumen (b.c.l.) while several others are in process of ingest- n (b.c.p.), apparently sinking into the protoplasm of the cells ther than being actively enclosed by it. Ingestion takes ace in the older, vacuolated cells (v.c.) and not in the crypts young, darkly staining cells (c.p.). In many cases the ingested od corpuscles can be seen lying within clearly defined vac- les. Although some of the ingested corpuscles lay against basement membrane (b.m.) of the tubules, in none of the sect- s was there any evidence of their being carried away by ndering phagocytic cells, as was observed in Teredo (YONGE (1926a)). rhaps this occurs later in digestion but lack of material and e danger of the animals dying if they were left for too long period after feeding, prevented any more prolonged feeding periments from being undertaken.

Blood corpuscles were found in small numbers in the umina of different regions of the gut, but <u>never</u> ingested in phagocytes.

Similar results were obtained in Poromya, blood corpuscles from the blood of Myxine being ingested exclusively in the tubules of the digestive diverticula. In this case, moreover, swallowed blood corpuscles were obtained from the stomach four hours after feeding as a result of antiperistaltic regurgitations from the stomach. They were examined and found to be undamaged - showing the lack of proteases and lipases in the stomach - and were in no case being ingested by phagocytes as was found to occur in the stomach lumen of <u>Ostrea edulis</u> three hours after the beginning of feeding (YONGE (1926b)). There were no phagocytes in the regurgitated fluid.

It will be observed that, while matter in colloidal solution, such as iron saccharate, or in coagulated masses, such as blood, is taken within the alimentary canal, the finely divided particles of Indian ink, or of iron saccharate in suspension, though they are drawn into the mantle cavity by the action of the septum, are almost entirely removed from it by the cleansing cilia and very little enters the gut, and comparatively large particles, like blood corpuscles, are ingested, the latter being, presumably, digested intracellularly. In the ciliary feeding Lamellibranchs this localization of the absorptive surface is compensated for by the presence of the phagocytes in the lumen and epithelium of all regions of the gut, but this is not the case in the Septibranchs.

The reasons why such comparatively large particles as phagocytes.

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As a result of these feeding experiments - though it is to be regreted that more could not be carried out - it can be stated definitely that the only absorptive surface in the gut of the Septibranchs, as in the other Lamellibranchs, is provided by the tubules of the digestive diverticula. There both soluble matter, such as iron saccharate, is absorbed, and comparatively large particles, like blood corpuscles, are ingested, the latter being, presumably, digested intracellularly. In the ciliary feeding Lamellibranchs this localization of the absorptive surface is compensated for by the presence of the phagocytes in the lumen and epithelium of all regions of the gut, but this is not the case in the Septibranchs.

The reasons why such comparatively large particles as lood corpuscles pass into the digestive diverticula of the Septibranchs ut not into those of the other Lamellibranchs (with the exeption of Teredo) is clearly due to the absence of phagocytes the gut and in the ducts of the diverticula which could gest them prior to their entrance into the tubules, and to he exceptionally short and wide ducts which lead from the tomach into the digestive diverticula.

As is well-known, the tissues of the Lamellibranchs re normally exceptionally rich in glycogen, a fact which has een recorded by many investigators (see especially RUSSELL 1923)), and there is no doubt as to the primary importance of his reserve food substance in the metabolism of these animals. n previous work on Ostrea (1926b) attention was drawn to this act and to the striking degree to which the digestive processes re specialized for dealing with carbohydrate food. In the eptibranchs, however, the food is <u>not</u> predominently carbohydrate, on the contary it must be largely protein, and the pecial digestive mechanism for dealing with carbohydrates provided in the style is much reduced. It would therefore appear robable that glycogen is not stored to any great extent in he Septibranchs. In order to obtain some evidence on this oint, one freshly caught specimen of <u>C. obesa</u> was fixed in Carnoy's fluid and sections prepared which were treated with the Langhans Iodene Method. <u>No</u> indication of the presence of glycogen was found in any of the sections. Thus we have evidence of an lteration in the metabolism of the Septibranchs consequent on their assumption of a carnivorous diet.

7. GENERAL DISCUSSION OF RESULTS.

This research is particularly interesting in its arings on the general problems of feeding and digestion in e Lamellibranchs. This class of the Mollusca possesses, on e gills and the palps and in the stomach, the most elaborate d most efficient ciliary feeding mechanism found in the tire animal kingdom. Associated with this are the many culiarities, both morphological and physiological, of the t, to which reference was made in the introductory section. t has been shown, I think conclusively, in the foregoing count that the Septibranchs are carnivorous and that feeding chanisms have been evolved for dealing with large food masses. e are dealing, therefore, with a striking example of the olution of function and the adaptation of feeding mechanisms, f ~~the~~ an alimentary system and of digestive processes all specialized for dealing with excessively fine food particles largely f a vegetable nature, for dealing with large masses of food nsisting chiefly of animal matter.

In place of the gills has evolved the muscular septum. his performs the same function in maintaining a circulation of ter through the mantle cavity, being assisted in this by the estiges of the gill ciliation in the lateral cilia on the ilaments of the branchial sieve in Poromya and in the cilia round the pores in Cuspidaria. But it also, by its sudden vements, draws in large masses of food which the continuous t slowly moving current created by the gill cilia could never ,. The large food masses introduced into the infra-septal ity in this manner are pushed into the mouth by the small, t very muscular, labial palps. The exceptionally highly veloped ciliary mechanism on the ridged palps of the other ellibranchs which acts by rigorously sorting the particles ssed on to it from the gills, rejecting the larger particles d passing the smaller ones into the mouth (for details see LLENGREN (1905) and YONGE (1923, 1926b) has been lost, the w remaining cilia being concerned exclusively with the rejectn of fine particles which might impede the working of the gut. t this ciliation is of importance is shown by the fact that ese ciliated tracts are retained even though the palps, as the case of the posterior pair in C. obesa, have been lost. similar rôle is played by the remaining cilia in the mantle vity, on the foot and on the ventral margins of the mantle. e survival of these cilia and no others is clearly correlated th the danger which both the Septibranchs and the other mellibranchs face in common, that of being silted up by fine rticles of mud or sand. Mucus glands, as universal as cilia the other Lamellibranchs, are confined to the ciliated regions the Septibranchs.

The foregut of the Septibranchs is totally unlike that f the Lamellibranchs which feed on fine particles. Although he oesophagus possesses cilia, these are clearly of little importnce, food being carried along by the peristaltic movements or thick surrounding muscle, so conspicuously absent in the ther Lamellibranchs. The stomach is even more highly spec- lized and acts as a crushing gizzard, for which function its ged walls, cuticular lining, surrounding muscles and freedom m the surrounding tissues, all combine to fit it. Clearly ery different structure from the complex ciliated organ of other Lamellibranchs, which is almost devoid of muscle and rves to sort out the finely divided food particles.

The crystalline style in the Septibranchs has no long- the great importance that it possesses in the other Lamelli- nchs. In the latter, by its rotation it assists in the move- t of the fine particles through the gut, and by the dissolut- of the head in the stomach it sets free carbohydrate split- g enzymes and also maintains the fluid in the stomach near optimum hydrogen ion concentration for the action of the yme (NELSON (1918, 1925), YONGE (1925, 1926b)). In the ptibranchs, owing to the contractions of the gizzard-like mach, the style can no longer project freely across the stom- and bear against the gastric shield on the opposite wall, the contary it barely projects out of the short style-sac in ich it is secreted; it would clearly be worn away by the traction of the stomach were it to project any further. e cuticular lining of the stomach probably represents an tension over the entire stomach of the gastric shield which vers only a small area in the stomachs of the other Lamellibranchs.

The shortness and exceptional width of the ducts ding into the tubules of the digestive diverticula is cor-lated, no doubt, with the comparatively large fragments which ll be forced into them by the squeezing action of the stomach. e wide lumina of the tubules, especially in the neighbour-d of the ducts, are to be attributed to the same cause.

The only regions of the gut which perform essentially e same function as in the other Lamellibranchs, the mid-gut d the rectum, show no structural modifications.

The absence of the wandering phagocytes which form so spicuous a feature in the gut of the ciliary feeding Lamelli-nchs is very striking and there can be no doubt that these ve developed owing to the necessity of dealing with ~~the larger~~ d particles too large to enter the ducts of the digestive verticula and which cannot, owing to their nature, be digested the amylase or the glycogenase from the style which repre-t the only extracellular enzymes present in the gut of the mellibranchs. In the Septibranchs where there are no particles this size to be dealt with (blood corpuscles being swallowed the form of coagulated masses and not individually), and, reover, where the epithelium of the stomach is covered with thick layer of cuticle, there is clearly no need for these agocytes. Furthermore, the widely open ducts of the digestive iverticula allow food particles of the order of magnitude nor-ally seized by phagocytes (e.g. red blood corpuscles) to enter the tubules where they are ingested.

It is a striking fact that the digestive processes, rt from the loss of the phagocytes, do not appear to have n modified in the Septibranchs. There is no evidence of elaboration of extracellular enzymes other than those in style, and these, on account of the carnivorous habit, t be of very little use to the animal. Indeed there is lose correlation, born out still further by the conditions nd in the Septibranchs, between the degree of develop~~e~~ment the style and a finely divided and largely vegetable food. s in the Gastropods the style is best developed in such nals as Crepidula (MACKINTOSH (1925)) which feed by cil-y mechanisms (ORTON (1912)) and is lost in the carnivorous cies, to be regained in the Thecosomatous Pteropods which, cending from carnivorous ancestors, have taken to a pelagic e and developed ciliary feeding mechanisms (YONGE (1926c)).

The tubules of the digestive diverticula resemble structure those of the other Lamellibranchs, which were estigated in detail in a former paper (1926a), and show no tological evidence of secretion, nor did the examination lood corpuscles which had been in the stomach for four rs ~~show~~ reveal any indication of the action of digestive enzymes. appears, therefore, that, though capable of modifying their ding mechanisms and the structure of their alimentary canal, e Septibranchs have been incapable of modifying their digestive rocesses. The Lamellibranchs have retained the power of tracellular digestion to a far greater extent than the other ge groups of the Mollusca, ~~a fact~~ which is clearly correlated h the fact that, in the Lamellibranchs alone, are fulfilled two essential conditions of intracellular digestion, namely maximum of ingesting surface (provided by the ramifications the tubules of the digestive diverticula) and the presentation this surface of fine particles capable of direct ingestion. latter is ensured by the rigorous sorting action of the liary mechanisms on the gills and the palps and in the stomach. the Septibranchs, the second of these conditions is absent it is only by the crude method of breaking up the large y in the stomach that small particles can be obtained for ssage into the digestive diverticula. In no other metazoan nivore, with the exception of certain of the Turbellarians, there this complete lack of a preliminary protein digestion. the Coelenterates, though digestion is largely intracellular, re is invariably a preliminary breaking down of the prey by ns of proteases into particles of a size suitable for direct estion. In the Turbellarians (see WESTBLAD (1923), WILLIER, (1925)), the gut cells (except in certain of the Rhabdocoels re extracellular digestion probably occurs) are amoeboid and ite to form syncytia during absorption when they take in water l swell out so that they surround the food which is usually ft, ~~and is~~ having been sucked in by the muscular probosis. In this ecialized manner is the large prey taken into the cells immediately and digested intracellularly. In the Septibranchs, ere are no modifications other than the crushing action of stomach and they must still rely upon exactly the same methods digestion (less the digestive action of the phagocytes) which served the Lamellibranchs which possess highly developed iary feeding mechanisms. It seems probable that they must, least, have developed a more powerful intracellular protease in the digest- diverticula than is found, for example, in Ostrea in which, in probably all similar Lamellibranchs, digestion is prim- ly concerned with carbohydrates.

The Septibranchs are a small group and show no signs increasing. It seems probable that this is due to their ure to develop methods of digestion suitable to a carnivore, to the comparative failure of their extemely interesting ing mechanism. They have achieved the remarkable feat of sforming a feeding mechanism and correlated alimentary tem and digestive processes, which together represent the est developemants of their kind in the animal kingdom dealing with finely divided food largely of a vegetable nat- into mechanisms for dealing with large food masses of al origin. It is not surprising, therefore, that the re- t has been largely in the nature of a makeshift.

The question of the origin of the Septibranchs is of the greatest interest. From the radically inferior nat- of their feeding and digestive mechanisms, they cannot have lved in the face of keen competition. All the evidence we ssess points to their having evolved in deep water. All

known Septibranchs are marine and inhabit considerable depths,
Cetoconchidae, in particular, being abyssal animals. The
specimens of Cetoconcha (Silenia) sarsi taken by the "Challen-
came from depths of 1950 and 2650 fathoms, and the single
imen of Poromya (Verticordia) tornata from 1850 fathoms.
seems not improbable that below a certain depth the ciliary
ing Lamellibranchs cannot exist owing to the lack of phyto-
kton. Animals which happened to pass into these deep waters
ld die unless it chanced that feeding mechanisms capable of
ing with comparatively large animal prey, either living or
, were evolved. In the case of the Septibranchs this
pened and, as a result, they spread downwards into the deep-
seas where the sparseness of the animal population and the
equent lack of serious competition allowed them to survive
pite of the inadequate nature of their organs of feeding
digestion. As they became more specialized and so more
ble of holding their own in the keen competition for food which
ists ~~resent~~ in the shallower seas, they worked their way back
shallower water. It is noteworthy that the most highly
ialized of the three families of the Septibranchia, the
idariidae, are found in the shallowest waters. The three
imens of C. cuspidata obtained in the Gullmars Fjord were
taken in depths of about 50 metres along with other Lamellibranchs.

The supposition that the Septibranchs are a compar-
ively recent group is born out by the paleontological evidence;
in ZITTEL'S text -book (1913) it is stated that the Cuspid-

idae range back to the Jurasic and the Poromyacidae only the Cretaceous. The smallness of the group at the present e points to their comparative failure, the probable reasons for ch have been outlined above.

The origin of the septum has been a matter of dispute, L (1888, 1889b, 1894, 1895) maintaining that it is pallial in gin or else an anterior prolongation of the septum dividing inhalent and exhalent siphons, while PELSENEER (1888a, 1889, 1, 1911) considers it to be branchial. In support of this w he states that the nervous supply comes from the branchial ve and not from the siphonal or pallial nerve, and concludes t the septum represents the inner demibranch only. PELSENEER received the support of GROBBEN who regards the anterior t of the septum, at least, as of branchial origin, but TE agrees with DALL since he found that the septum of _C._ _sa_ was innervated by a nerve leaving the cerebral ganglion e by side with the visceral commissure,and not by a branchial nch of the visceral nerve. PELSENEER (1911) thinks he is taken in this. RIDEWOOD does not ~~dis~~agree~~s~~ with DALL that the cularity of the septum is any reason against its being of nchial origin, but finds it hard to understand how it uld have developed such inportant attachments to the shell. o not intend to engage in this controversy which is not kely to be definitely settled until the embryology of the ptibranchs has been studied. There does, however, appear o be substantial reasons for agreeing with PELSENEER rather with DALL; the septum certainly performs the same function creating a current of water through the mantle cavity as do gills - a fact which DALL failed to realize - and it is ficult to see how it could have evolved except as a direct elopemnt from the gills.

The validity of the separate order Septibranchia ed by PELSENEER has been questioned by DALL, GROBBEN and WOOD, the last named summarizing the conflicting evidence adding (p.183), "The reduction of the branchial organs is ainly very remarkable, but there are greater differences een the three genera included in the Septibranchia than een a form like *Poromya malespinae*, on the one hand, and *icordia* on the other. The conditions found in *Poromya*, *oconcha*, and *Cuspidaria* may be considered to have evolved pendently, although following the same general trend. relations between these forms and the Verticordiidae being ious, it is proposed, in the absence of more accurate inform- n as to general anatomy, to place the three families, Poromyidae oconchidae, and Cuspidariidae after the Verticordiidae in a inal sub-order (Poromyacea) of the Synaptorhabda."

As PELSENEER (1911) points out, the taxonomic divisions establish are of relative value only since continuity is the of nature, and in his opinion the establishment of the order tibranchia is justified for they represent, "le stade final ne longue évolution dans un sens déterminé."

On the other hand, the very different structure of the tum in Poromya and Cuspidaria, particularly the development the striated musculature in the latter, does rather support opinion of RIDEWOOD that they may have evolved independently that the structural resemblences may therefore be due to vergence, the result of similar habitats and the necessity dealing with similar food. Like the Teredinidae, the ibranchs appear to be highly specialized animals adapted peculiar conditions, rather than the apex of the evolution the Lamellibranchs. But we need further evidence, especially ological, before these questions can be satisfactorily wered. For the time being, however, the order Septibranchia be conveniently employed to denote the three families two if, as PELSENEER suggests, the Cetoconchidae are to included under the Poromyidae) of carnivorous Lamellibranchs ch in water and feed by means of a muscular septum and whose alimentary em has been greatly modified as a result of their change abits and food.

8. SUMMARY.

Living and preserved specimens of the Septibranchs, Cuspidaria rostrata, uspidata, and C. obesa, and ~~of~~ Poromya granulata, have ~~b~~ n studied.

he siphons of Cuspidaria are long and are contained in a ional extension of the shell; the inhalent siphon has four ral tentacles and the exhalent siphon three dorsal tentacles. siphons of Poromya are short and surrounded by fifteen tentacles.

n both Cuspidaria and Poromya the entrance from the inhalent on into the mantle cavity is guarded by a valve, which is cially large in Poromya.

he mantle is extremely thin, it is bordered ventrally by a kened ridge which is the only region to possess cilia and s glands.

The foot is long and extensile and is ciliated except near base, it possesses a byssus gland.

he septum divides the mantle chamber ~~cavity~~ into infra-septal and ra-septal cavities.

In Cuspidaria it is exceptionally thick, and is attached to shell by large anterior and posterior septal muscles and by licate lateral muscles the arrangement of which varies in the fferent species. The mass of the septum consists of longit- inal bundles of flat, striated, multinucleate muscle fibres ich cross over one another posterior to the foot. The teral muscles are smooth and pass transversely across the rsal surface of the septum.

The septum of Poromya is more delicate. It is attached to shell by a pair of anterior and a pair of posterior septal scles, and is composed of plain muscle fibres.

The septum of Cuspidaria is perforated by narrow, slit-like res, either four or five according to the species, which e dorsally directed valves. They are bounded by a columnar ithelium which is ciliated in two regions, and are surrounded a sphincter of plain muscle.

The septum of Poromya is perforated by a pair of anterior a pair of posterior branchial sieves, the former possessing e and the latter six filaments. These resemble ordinary l filaments , lateral, but not frontal, cilia being present *P. granulata*; longitudinal muscles occur at their bases.

The palps are small in Cuspidaria, the posterior pair being sent in *C. obesa*, but are larger in Poromya. They are ciliated their inner surfaces, are smooth and very muscular.

The mouth and the oesophagus are large, both are ciliated d surrounded by a thick layer of muscle.

The stomach is large and cylindrical, the walls are ridged d covered throughout with a thick cuticle which probably reents an extension of the gastric shield. It is surrounded thick layer of muscle and is free from the surrounding tissues.

The ciliated ducts of the digestive diverticula are exceptally short and wide. The tubules have the same structure in the digestive diverticula of the other Lamellibranchs.

The style-sac is short and contains a small, oval style h does not project far into the stomach.

The short mid-gut is ciliated and possesses little muscle. rectum is narrow, ciliated, contains mucus glands and is rounded by muscle. The anus opens at the base of the lent siphon.

There is a almost complete absence of the wandering phagocytic cells d in the gut of the ciliary feeding Lamellibranchs.

The conditions in Cetoconcha appear to resemble those in mya.

Both Cuspidaria and Poromya live in mud into which they burrow.

The septum in Cuspidaria makes regular movements, first desding and then drawing sharply upwards. Between movements is in its shortest condition. As a result of the movements r and are drawn into the mantle cavity. In Poromya the septum ears to act in a similar manner though less frequently.

The cilia on the septal pores and branchial sieves and in supra-septal cavity serve to maintain a slow current of r through the mantle cavity when the septum is at rest.

The cilia in the infra-septal cavity - on the palps, the t and on the mantle edges - serve to remove fine particles the mantle cavity.

Food is pushed into the mouth by the muscular palps.

Food is passed through the oesophagus by peristalsis largely, is crushed up in the gizzard-like stomach, the fragments being sed either into the ducts of the digestive diverticula or the mid-gut through which they are passed by ciliary action.

The Septibranchs are carnivorous, feeding on small animals, her dead or alive, usually Crustacea or Annelida.

The tubules of the digestive diverticula provide the only rbing surface in the gut, they are prgans of absorption intracellular digestion. There is no evidence that they rete.

Fine particles, such as Indian ink, if taken into the mantle ity are almost all removed by the cleansing action of the ia and do not enter the gut.

There is no evidence of any storage of glycogen in <u>C. obesa</u>.

The Septibranchs have adapted feeding mechanisms and an entary system specialized for dealing with fine particles, the disposal of large masses of food.

The crystalline style in the Septibranchs is small and ably vestigial, for it is concerned essentially with the port through the gut of fine particles and with the digestion carbohydrates.

The absence of wandering phagocytic cells is to be attributed the absence in the food of particles small enough for them to st, and also to the ease with which particles can enter the stive diverticula.

The digestive processes do not otherwise appear to differ those of the ~~other~~ remaining Lamellibranchs. Although carnivores, Septibranchs have developed no preliminary extracellular stion of protein.

The Septibranchs are a small and unsuccessful group which ably evolved in deep water where the majority of them still live.

The origin of the septum is disputed, but the balance of evidence is in favour of its being branchial.

The order Septibranchia, established by PELSENEER, is probab- alid, though Cuspidaria and Poromya may resemble each other the result of convergence and not of a common origin.

The conditions found in the carnivorous Septibranchs provide able confirmatory evidence that the peculiar nature of the gut of the digestive processes in the other Lamellibranchs are ~~due~~ to the finely divided food collected by their elaborate ciliary feeding mechanisms.

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10. DESCRIPTION OF PLATES.

List of Reference Letters.

= anterior palp.
i.= ingested blood corpuscles.
l.= blood coupuscle in lumen.
p.= blood corpuscle in process of being ingested.
= beginning of mid-gut.
= basement membrane.
= clear area in which lies nucleus of striated fibre.
= connecting groove between style-sac and mid-gut.
= circular muscle.
= crystalline style.
"chitinous" supporting rod in filament of branchial sieve.
crypts of young cells in tubules of digestive diverticula.
cuticle.
duct of digestive diverticula.
= dorsal ciliated tract round septal pore.
= dorsal epithelium of septum.
= epithelium of style-sac.
iron in vacuoles in tubule cells.
mid-gut.
infra-septal cavity.
= epithelium of inner surface of palps.
wide lumina of digestive diverticula.
= lateral cilia.
= longitudinal muscles.
= longitudinal ridges in stomach.
m.= lateral septal muscles.
mouth.
= mucus gland.
= muscle strands.
c.= nucleus of ingested blood corpuscle.
= nucleus of striated fibre.
= nucleus of tubule cell.
oesophagus.
= older, vacuolated cells of tubules.
= epithelium of outer surface of palps.
= posterior palp~~s~~.
rectum.
= radiating muscle fibres.
= longitudinal ridges in oesophagus.
supra-septal cavity.
= septal muscle.
= style-sac.
sphincter of plain muscle round septal pore.
striation in muscle fibre.

,= stomach.
= tubule of digestive diverticula.
,= typhlosole.
= valve on dorsal side of septal pore.
0.= ventral ciliated tract round septal pore.
e.= ventral epithelium of septum.
,= vacuole in tubule cell.
0.= wandering cell.
0.= young, darkly staining cells in mid-gut.

Plate I

g. 1. Cuspidaria rostrata. - Longitudinal section through the ptum cutting a septal pore transversely. Fixed Bouin, stained lafield's haematoxylin and eosin. *6 μ. × 150.*

g. 2. Cuspidaria rostrata. - Horizontal section through the ptum passing somewhat obliquely through a septal pore in e dorsal region. Fixed Bouin, stained iron haematoxylin and id fuchsin. *6 μ. × 150.*

g. 3. Cuspidaria rostrata. - Portion of a teazed out muscle bre from the septum. Fixed alcohol, stained iron haematoxylin. *× 500*

g. 4. Cuspidaria rostrata. - Transverse section through a sterior palp, about the middle. Fixed Bouin, stained lafield's haematoxylin and eosin. *6 μ. × 130.*

g. 5. Cuspidaria cuspidata. - Transverse section through the sophagus immediately anterior to the stomach. Fixed Bouin, ained iron haematoxylin and acid fuchsin. *6 μ. × 60.*

g. 6. Cuspidaria rostrata. - Longitudinal section through the omach and style-sac, showing also the beginning of the mid-gut d the connecting groove between it and the style-sac. Fixed uin, stained Delafield's haematoxylin and eosin. *6 μ. × 40.*

g. 7. *Cuspidaria cuspidata.* - Transverse section through the mach passing through the opening of the anterior and smaller ct of the digestive diverticula. The shortness of the duct d the wide lumina of the tubules into which it opens are both own. Fixed Bouin, stained iron haematoxylin and acid chsin. 6 μ. × 40.

Plate II

g. 8. *Cuspidaria cuspidata.* - Transverse section through the d-gut immediately posterior to its separation from the style- o, showing the presence of the typhlosole. Fixed Bouin, ined iron haematoxylin and acid fuchsin. 6 μ. × 110

g. 9. *Cuspidaria cuspidata.* - Transverse section through the mid- t in the region of its junction with the rectum to which it united dorsally. Fixed Bouin, stained Mann's methyl blue d eosin. 6 μ. × 110.

g. 10. *Poromya granulata.* - Longitudinal section through the ptum cutting one of the posterior branchial sieves at right gles. The filaments are shown in transverse section and eir resemblence to the gill filaments of the other Lamellibranchs shown. Fixed alcohol, stained Delafield's haematoxylin d eosin. 6 μ. × ~~27~~ 60.

g. 11. *Poromya granulata.* - Longitudinal section through the lps, mouth, oesophagus and stomach, showing their mutual relat- ships and the wide lumina of the oesophagus and stomach. ed Bouin, stained Mann's methyl blue and eosin. 6 μ. × 33.

Fig. 12. *Cuspidaria obesa*. - Section through four cells from a tubule of the digestive diverticula fixed after 12 hours of feeding with a suspension of iron saccharate. Fixed equal parts Bouin and 5% ammonium sulphide in absolute alcohol, iron treated by Prussian blue method, sections stained with alum carmine. 6μ. × 1140.

Fig. 13. *Cuspidaria cuspidata*. - Transverse section through a single tubule of the digestive diverticula fixed after 10 hours of feeding with blood from a Wrasse. The structure of the tubule is shown, also the presence of blood corpuscles, one free in the lumen, others in process of being ingested and many actually ingested within the cells. Fixed Bouin, stained Mann's methyl blue and eosin. 6μ. × 380.

The Sect.

PHILOSOPHICAL TRANSACTIONS

OF THE

ROYAL SOCIETY OF LONDON.

SERIES B, VOL. 216, Pp. 221–263.

[PLATES 12–14.]

STRUCTURE AND FUNCTION OF THE ORGANS OF FEEDING AND DIGESTION IN THE SEPTIBRANCHS, CUSPIDARIA AND POROMYA.

BY

C. M. YONGE, D.Sc., PH.D. (EDIN.),
BALFOUR STUDENT IN THE UNIVERSITY OF CAMBRIDGE.

B 434. 7.2.28

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IV. *Structure and Function of the Organs of Feeding and Digestion in the Septibranchs*, Cuspidaria *and* Poromya.*

By C. M. Yonge, *D.Sc., Ph.D. (Edin.), Balfour Student in the University of Cambridge.*

Communicated by Dr. E. J. Allen, *F.R.S.*

(Received May 28,—Read June 30, 1927.)

(Plates 12, 13, 14.)

Contents.

1. Introduction.

Previous work on the structure and function of the alimentary system in the Lamellibranchs (Yonge (1923, 1925, 1926a, 1926b)) showed that the many peculiarities which they exhibit appear to be correlated with the highly developed ciliary feeding mechanisms on the gills and palps, as a result of the action of which only the smallest particles are passed into the œsophagus and stomach. This latter organ is concerned chiefly with sorting the particles, the larger ones being passed directly into the mid-gut and the smaller ones entering the ducts of the digestive diverticula (" liver " or " hepatopancreas "), where they are digested intracellularly. The food is largely of a vegetable nature and the digestive processes are concerned especially with the disposal of carbohydrates. There are present, free in the lumen of the gut, in the epithelium and in

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* This paper formed part of a thesis submitted for the degree of Doctor of Science at the University of Edinburgh.

[Published February 7, 1928.

the surrounding tissues, great numbers of phagocytes which actively ingest food particles. Their presence, also, appears to be correlated with the finely divided nature of the food and the fact that, but for the digestive action of these phagocytes, particles of food, unless sufficiently fine to enter the ducts of the digestive diverticula, can only be digested if composed of starch or glycogen. The only extracellular digestive enzymes in the gut of the Lamellibranchs, namely, those set free by the dissolution in the stomach of the head of the crystalline style, act exclusively on these two carbohydrates.

Owing to their deep water habitat, the Septibranchs have been little studied, but PELSENEER (1891, 1911) and PLATE (1897) have reported, on the evidence of the stomach contents, that they are carnivorous, while all investigators who have worked upon them have shown that in structure both the food collecting and digestive organs of the Septibranchs are quite distinct from those of the other Lamellibranchs. Gills are absent, their place being taken by the muscular septum, the labial palps are very small and the gut is provided with a muscular coating of a thickness unknown in the other Lamellibranchs, where the finely divided food is carried through the gut exclusively by ciliary activity, and so muscle for peristalsis is unnecessary.

Clearly, therefore, a study of the structure and function of the organs of feeding and digestion in the Septibranchs would have two valuable results; not only would it go far towards completing our knowledge of this aspect of the structure and physiology of the Lamellibranchia, but it might be expected—should the carnivorous habit be definitely established—to provide important confirmatory evidence that the peculiar nature of the gut and the digestive processes in those Lamellibranchs which feed by means of ciliary currents *is* due to the size and nature of the food particles.

For the purpose of observing living Septibranchs, carrying out feeding experiments and collecting material for histological examination, a period of four weeks was spent at the Biologiska Station, Trondhjem, Norway, and of one week at the Kristinebergs Zoologiska Station, Sweden. As a result entirely of the kindness and labours of Dr. O. NORDGAARD at Trondhjem and of Dr. M. AURIVILLIUS at Kristineberg, a number of living specimens of these rare animals was obtained, and I wish to record my gratitude to these gentlemen, without whose help this research would have been impossible. I also desire to thank the Council of the Marine Biological Association of the United Kingdom and the Development Commission for granting me the necessary leave of absence from the Plymouth Laboratory.

The work was completed at the Plymouth Laboratory while I was Temporary Assistant Naturalist, and I have to thank the Director, Dr. E. J. ALLEN, F.R.S., for his unfailing interest in it, and other members of the staff for their assistance on many points.

2. MATERIAL.

The Order Septibranchia (PELSENEER) is divided into three families, Poromyidæ (DALL), Cetoconchidæ (RIDEWOOD), and Cuspidariidæ (FISCHER). No representatives of the second of these have ever been examined in the living condition; they are abyssal and have only been taken on deep-sea expeditions, such as the "Challenger" (see PELSENEER (1888B)) and the "Siboga" (see PELSENEER (1911)). Of the Poromyidæ, I obtained two living specimens of *Poromya granulata* which were dredged in the Trondhjem Fjord at depths of 150 and 200 metres. After returning to Plymouth, I received three further specimens of this species preserved in alcohol which were collected by Dr. M. AURIVILLIUS on an expedition to the Koster Islands in the Skager Rack, and were sent on to me by Dr. N. HJ. ODHNER of the Riksmuseum, Stockholm, for whose kindness I am extremely grateful.

Living specimens of three species of Cuspidaria were obtained. Twelve *Cuspidaria obesa* were dredged at depths of between 100 and 300 metres in the Trondhjem Fjord. Unfortunately this species is so small that it is difficult to handle and observe, and most of my observations on living Cuspidaria were made on one specimen of *Cuspidaria rostrata*, which was dredged at a depth of 250 metres at Trondhjem, and three specimens of *Cuspidaria cuspidata*, dredged in the Gullmars Fjord in Sweden at depths of between 40 and 60 metres. I also received from Dr. O. NORDGAARD two preserved specimens of *Cuspidaria rostrata*, and since my return Dr. M. AURIVILLIUS has kindly sent me a number of preserved *Cuspidaria rostrata*, and several *C. obesa* and *C. cuspidata*, and one *C. costellata*. This preserved material has proved of great value in the histological and anatomical portions of the research.

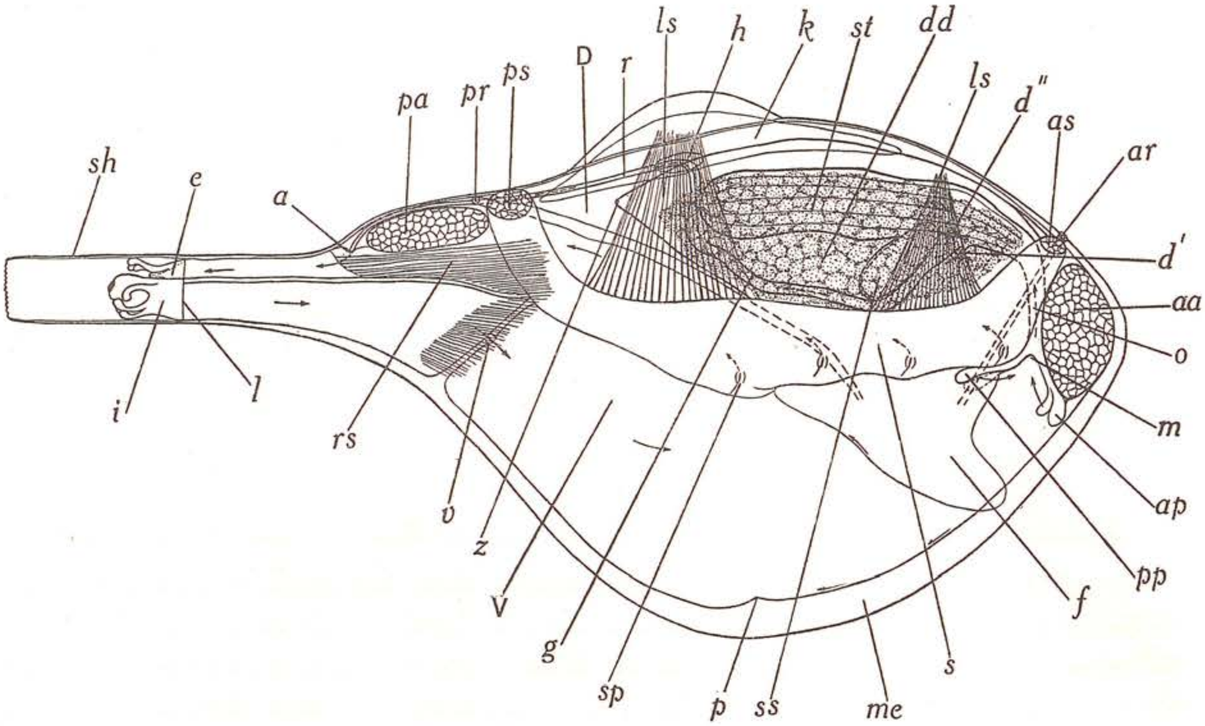
3. ANATOMY AND HISTOLOGY OF THE ORGANS OF FEEDING AND DIGESTION.

Throughout this paper, for the sake of convenience, the conditions in the genus Cuspidaria, whose members represent the highest development of the Septibranchs, will be described before those in Poromya. It must not be forgotten, however, that, as shown by PELSENEER (1888A, 1888B, 1891, 1911) and as further emphasised in this paper, Poromya should logically be treated first as it represents a somewhat more primitive condition and shows more affinities to the typical Lamellibranchs—especially to the Anatinacea, from which, according to PELSENEER, the Septibranchs probably sprang—than does the more highly specialised Cuspidaria.

(i) *Anatomy*. A.—*Cuspidaria*.

Literature.—Although the absence of gills in Cuspidaria (Neæra) was first noted by DALL (1886B) and this author has described the shell and external characters of many species of the Cuspidariidæ (1889A, 1889B, 1894), the first adequate description of Cuspidaria was furnished by PELSENEER (1888B), who gave an account of *C. curta*, *C. fragilissima* and *C. platensis* from the "Challenger" material and *C. rostrata* obtained from Naples, later (1891) giving a more detailed description of the last species. He has since (1911) described the Cuspidariidæ taken by the "Siboga" expedition. GROBBEN (1892) in his memoir on *Cuspidaria cuspidata* has provided the most detailed account of the morphology of the Cuspidariidæ. A short description of the morphology of *Cuspidaria* *obesa* (unfortunately without figures) has been given by PLATE (1897). Finally, RIDEWOOD (1903) in his work on the gills of Lamellibranchs gave some account of the septum and palps of *Cuspidaria glacialis*.

General Anatomy.—The observations here recorded on the anatomy of the Cuspidariidæ are based largely on examinations of living and preserved specimens of the comparatively large species, *Cuspidaria rostrata* and *C. cuspidata*. The general anatomy can best be described by reference to text-fig. 1, which represents a lateral view of *Cuspidaria rostrata*.



TEXT-FIG. 1.—Lateral view of *Cuspidaria rostrata* showing the anatomy of the feeding and digestive organs. × 6. *a.*, anus ; *a.a.*, anterior adductor ; *a.p.*, anterior labial palps ; *a.r.*, anterior retractor of foot ; *a.s.*, anterior septal muscle ; *d'.*, anterior, right duct of digestive diverticula ; *d''.*, posterior, left duct of same ; *D.*, dorsal or supra-septal compartment of the mantle cavity ; *d.d.*, digestive diverticula ; *e.*, exhalant siphon ; *f.*, foot ; *g.*, mid-gut ; *h.*, heart ; *i.*, inhalant siphon ; *k.*, kidney ; *l.*, line of attachment of siphons ; *l.s.*, lateral septal muscles ; *m.*, mouth ; *m.e.*, mantle edge ; *o.*, œsophagus ; *p.*, point where mantle lobes unite ; *p.a.*, posterior adductor ; *p.p.*, posterior palps ; *p.r.*, posterior retractor of foot ; *p.s.*, posterior septal muscle ; *r.*, rectum ; *r.s.*, retractor muscle of siphons ; *s.*, septum ; *sh.*, siphonal sheath ; *s.p.*, septal pore ; *s.s.*, style-sac (style indicated by broken line) ; *st.*, stomach ; *v.*, valve at junction of the inhalant siphon and the mantle cavity ; *V.*, ventral or infra-septal cavity ; *z.*, posterior end of visceral mass. Arrows indicate direction of water current and food intake.

The animal is flask-shaped, the siphons (*i.* and *e.*) lying in a long posterior extension of the shell. The inhalant siphon (*i.*) is the larger and possesses four club-shaped tentacles which are attached on the ventral side to the base of the siphonal opening, which is large and muscular. The exhalant siphon (*e.*) has a much narrower opening and is shorter, three tentacles, similar in structure to those of the inhalant siphon, are attached to its dorsal surface. In life, the siphons normally project from the shell, but on stimulation, or after fixation, they are withdrawn within the siphonal sheath (*sh.*), as shown in the figure. They are attached to this about half-way along the siphonal extension, along the line marked *l.* Anterior to this the siphons are divided by a stout partition, which terminates at its junction with the muscular septum (*s.*) which divides the mantle cavity into ventral (*V.*) and dorsal (*D.*) chambers. At their base, the siphons are attached to the shell by a widely spreading series of muscle strands (*r.s.*) which, by their contraction, withdraw the siphons. The inhalant siphon is separated from the ventral mantle chamber by a sheet of tissue perforated by a round valve (*v.*) near the centre. The mantle is excessively thin—resembling fine tissue paper in consistency—which is characteristic of the Septibranchs. Ventrally the mantle lobes are bounded by thickened ridges which are united in the posterior half of the mantle cavity, the point of attachment being indicated in the figure by the letter *p.* Projecting in the middle line through the anterior half of the septum is the foot (*f.*), which is long and narrow and possesses a byssus groove on its posterior surface (see text-fig. 6, *b*) associated with a gland in the body of the foot. The foot is capable of great extension and is withdrawn by the action of two retractor muscles which are attached to the mid-dorsal region of the shell, an anterior retractor (*a.r.*) immediately posterior to the large anterior adductor muscle of the shell (*a.a.*), and a posterior retractor (*p.r.*) above the anterior part of the posterior adductor of the shell (*p.a.*). Of the adductor muscles the anterior is the larger and lies in the extreme anterior region of the body with its greatest diameter vertical, while the posterior adductor is situated dorsal to the anterior region of the exhalant siphon, is more oval in cross-section, and is horizontally extended.

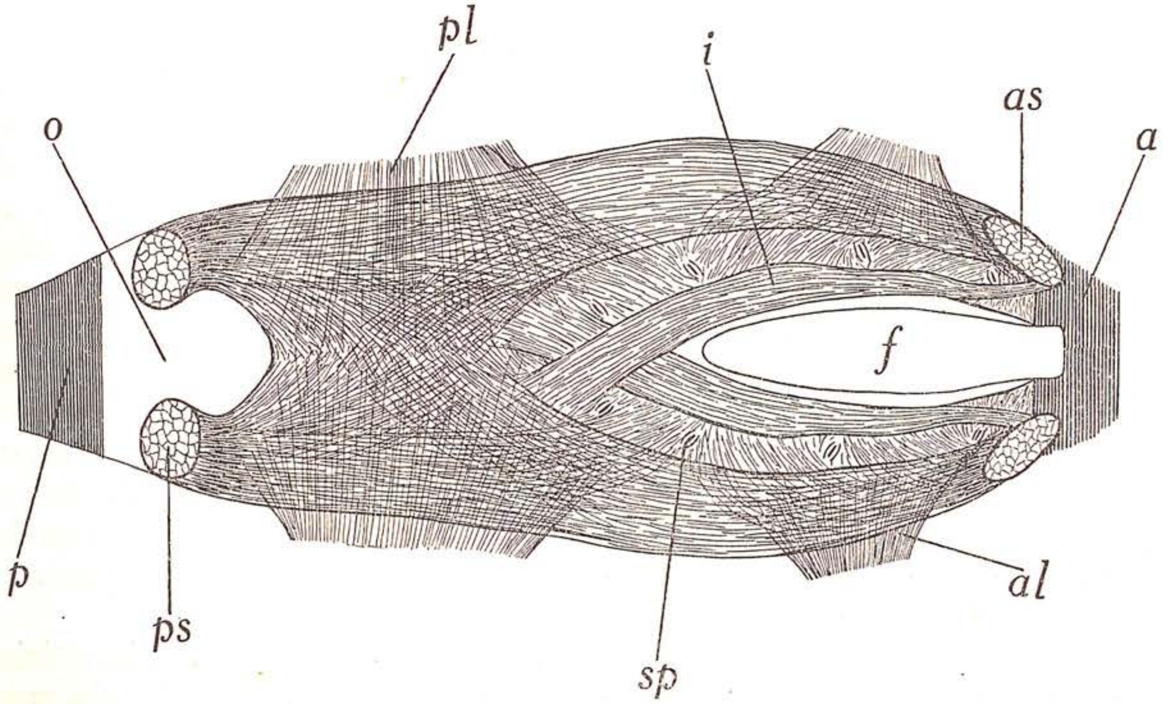
Anterior to the foot and projecting ventrally from the under surface of the septum are the labial palps. These consist of an anterior (*a.p.*) and a posterior (*p.p.*) pair, the latter being slightly the larger. The anterior palps are attached for the greater part of their surface to the posterior ventral surface of the anterior adductor muscle, and form a veil in front of the mouth (*m.*) ; the posterior pair are wedge-shaped and free, they extend posteriorly on either side of the foot. The palps are not ridged as in the other Lamellibranchs, and this, and especially their small size, has aroused comment from most observers, DALL (1886B) originally stating that they were completely absent, but his material was in bad condition. In later work (1888) he refers to the palps of the Cuspidariidæ as obsolete, and in a further paper (1889B) states that the palps are absent in *Myonera paucistriata* (a member of the Cuspidariidæ). PELSENEER (1888B, 1891) states that the posterior palps of *Cuspidaria curta* and *C. fragilissima* are absent. GROBBEN noted the small size of the palps in *Cuspidaria cuspidata*, and PLATE stated that palps are absent in *C. obesa*. My own observations on this species, however, have shown that, though the posterior palps are reduced to mere ciliated tracts, as described by PLATE, the anterior palps, though greatly reduced, are present. In *Myonera dubia*, PELSENEER (1911) states that the posterior palps project very little, but that in *Cuspidaria*

(*Pseudnecœra*) *thaumasia* they are large and extend for a considerable distance. I have found both pairs of palps comparatively well developed in *Cuspidaria rostrata* and *C. cuspidata* (see text-fig. 6), but in both they contracted considerably after fixation—probably owing to their possession of relatively powerful muscles—and it is not impossible that they may be present in species in which they have been recorded as absent. That they retain some importance in feeding will be shown in a later section.

Septum.—The septum consists of an extremely thick muscular partition which divides the mantle cavity into two chambers, in the upper of which lies the visceral mass. It is slung longitudinally across the mantle cavity and is attached at either end by a pair of stout muscles to the dorsal region of the shell. The anterior septal muscles (*a.s.*) are attached to the shell immediately posterior to the anterior adductor and on either side of the anterior retractor muscle of the foot, and the posterior pair (*p.s.*) slightly anterior to the posterior adductor. These muscles are called septal retractors by PELSENEER, but both DALL and GROBBEN prefer to call them simply septal muscles, and, in view of the peculiar functioning of the septum, which will be described subsequently, I prefer the latter name. The septum of *C. rostrata* is perforated by four pairs of pores (*s.p.*) which are symmetrically arranged on either side of the middle line in the anterior two-thirds of the exposed septal surface. The most anterior pair are slightly posterior to the mouth, and the hindermost pair a little distance behind the base of the foot. They lie nearer to the base of the foot than to the mantle, as is shown in text-fig. 2. Each consists of a narrow slit-like opening, laterally extended and bounded by low lips. They provide the sole means of communication between the ventral and dorsal chambers of the mantle cavity (or infra- and supra-septal cavities, as they will hereafter be called).

The arrangement of the muscles in the septum has been described by DALL (1889B) and in more detail by GROBBEN, and will most easily be understood by reference to text-fig. 2, which shows the arrangement of the septal muscles as seen from the dorsal aspect after the septum has been dissected out. At the attachment of the septum to the mantle on the outer, and to the sides of the foot on the inner, side, the tissues are thin and somewhat membranous, but the body of the septum consists of thick muscular strands. In the outer regions these run longitudinally, bundles of fibres from the anterior septal muscle (*a.s.*) passing backwards and meeting bundles from the posterior septal muscle (*p.s.*). Smaller bundles of longitudinally directed fibres (*i.*) separate from the anterior septal muscles, pass downwards and then posteriorly along the side of the foot on the inner side of the pores, finally crossing one another posterior to the foot and becoming merged into the general mass of the septum. These fibres have a separate insertion nearer to the middle line than the main anterior septal muscle in *Cuspidaria cuspidata* as described by GROBBEN, and also in *C. modesta*, *C. convexa*, *C.* (*Myonera*) *dubia*, and in two other unidentified species from the "Siboga" collections (PELSENEER (1911)). Besides the longitudinally directed fibres, there are others which pass diagonally across the septum from the main longitudinal bundles, and the somewhat thinner region between the pores is largely composed of such muscles, which have their origin in the anterior septal muscle, while posterior to the foot similar muscles pass across the centre of the septum and meet diagonally directed fibres from the posterior septal muscles. The two sets of muscles from each side unite and, together with the fibres of the inner longitudinal bands from the anterior septal muscle, form a thick muscular sheet composed of closely interwoven fibres, as shown in text-fig. 2. An opening (*o.*) is left between the posterior septal muscles whereby the supra-septal cavity is connected with the cavity of the exhalant siphon.

The septum is also connected with the shell by means of numerous thin muscular strands which extend dorsally through the tissue of the mantle and are attached to the shell near the mid-dorsal line. These lateral septal muscles (text-fig. 1, *l.s.*) are arranged in two



TEXT-FIG. 2.—Septum of *Cuspidaria rostrata* dissected out and viewed from the dorsal aspect. × 10. *a.*, anterior adductor ; *a.l.*, anterior lateral septal muscle ; *a.s.*, anterior septal muscle ; *f.*, foot ; *i.*, inner longitudinal muscles from anterior septal muscle ; *o.*, opening leading to exhalant siphon ; *p.*, posterior adductor ; *p.l.*, posterior lateral septal muscle ; *p.s.*, posterior septal muscle ; *s.p.*, septal pore.

pairs in *Cuspidaria rostrata*, a smaller anterior pair (text-fig. 2, *a.l.*) and a larger posterior pair (*p.l.*). The same condition is found in *Cuspidaria mitis*, *C. strictirostris*, *C. corrugata*, and a further unnamed species from the "Siboga" collections (PELSENEER (1911)). In *C. cuspidata*, however, the lateral septal muscles are continuous (see figs. 1 and 2 in GROBBEN) and also in *C. modesta* (PELSENEER (1911)). In other species different conditions are found; there may be one pair of lateral muscles as in an unnamed species from the "Siboga," four pairs as in *C. fragilissima*, or none as in *C.* (*Myonera*) *dubia* (Pelseneer (1911)). The fine isolated bundles forming these muscles extend down through the mantle until they reach the septum, when they are continued transversely across its dorsal surface, and can be distinguished in sections as a thin layer immediately beneath the epithelium. As will be shown later, their structure is distinct from that of the main septal muscles.

Although the majority of the known species of the Cuspidariidæ possess, like *C. rostrata*, four pairs of septal pores (see Pelseneer (1911) for details as to species), *C. cuspidata*, *C. convexa* and *C. arctica* var. *glacialis* all have five pairs. If reference be made to text-fig. 6, which represents *C. cuspidata* as seen from the ventral aspect with the mantle lobes drawn apart, the five pairs of pores will be seen. The size of the palps, which were drawn from life, is also clearly shown in the same figure.

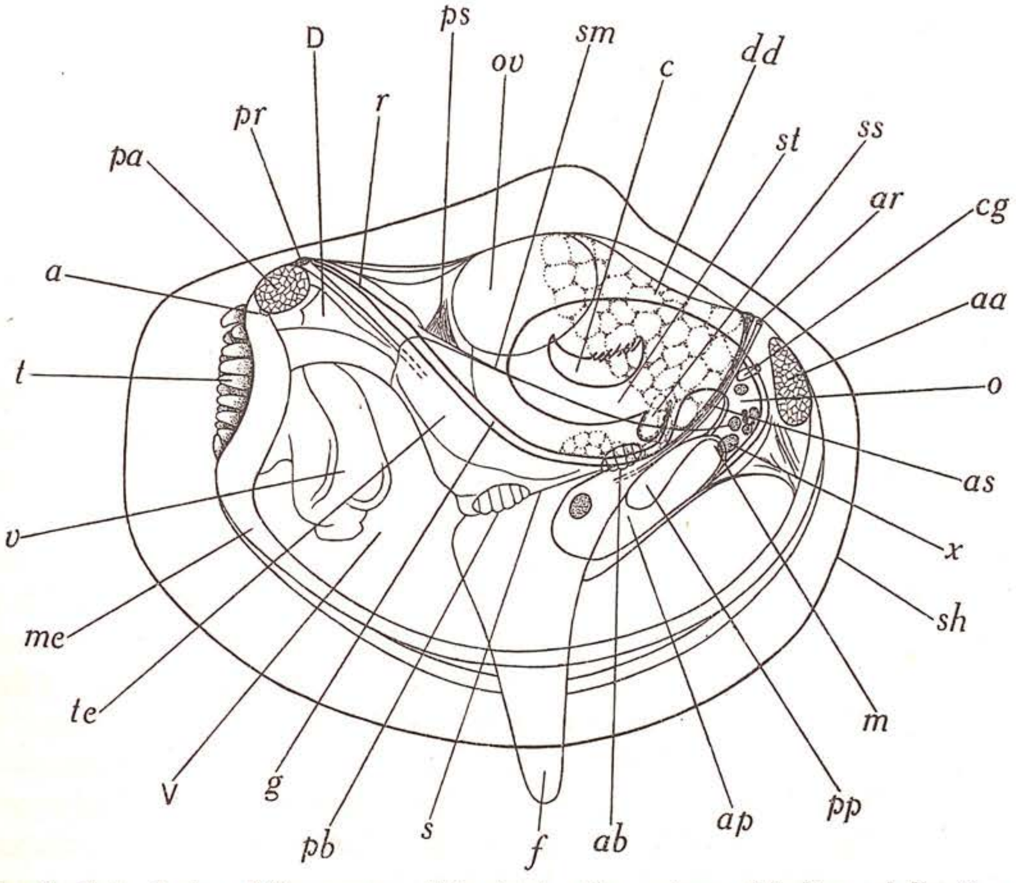
Alimentary System.—Referring again to text-fig. 1, the mouth (*m.*) lies in the middle line between the two pairs of palps and is a laterally extended opening of relatively large size, as is best seen in text-fig. 6. It leads into a short œsophagus (*o.*) with folded walls which extends almost directly dorsally to open into the stomach (*st.*). This latter organ is, for a Lamellibranch, of unusual size and shape. It is long and cylindrical, extending almost from end to end of the visceral mass in a longitudinal direction. Its walls are thrown into a series of prominent folds (see fig. 7), the entire inner surface being covered with a thick cuticular lining. Surrounding it on all sides except the extreme dorsal surface are the brownish, blind-ended tubules of the digestive diverticula (so-called liver or hepatopancreas), the whole consisting of somewhat asymmetrical halves lying on either side of the stomach, into which each opens by a separate duct (*d'*., *d''*.). Both of these open into the ventral region of the stomach near the anterior end, that on the right (*d'*.) being smaller and slightly anterior to that on the left (*d''*.), which opens on a line with the beginning of the mid-gut.

Both the style-sac (*s.s.*) and the mid-gut (*g.*) open into the stomach near its anterior end and a little to the right of the mid-ventral line, the mid-gut being the more anterior of the two. The style-sac is a short oval cavity and contains a small cylindrical style indicated by the broken line in text-fig. 1. The style removed from a living specimen of *Cuspidaria cuspidata* was only 1·9 mm. long and 0·74 mm. broad, and projected but slightly into the lumen of the stomach. The lumina of the style-sac and the mid-gut are separated by a well-developed fold, but remain connected by a narrow longitudinal slit. The mid-gut is both short and straight; after extending ventrally as far as the base of the style-sac, it is then directed posteriorly, lying among the tubules of the digestive diverticula. Posterior to the stomach it turns abruptly upwards and leaves the visceral mass in the region below the umbo. It becomes merged here into the rectum (*r.*), which at the beginning of its course traverses the heart (*h.*) and later passes between the posterior septal muscles, over the posterior adductor, and then turns downward to open at the anus (*a.*) into the base of the exhalant siphon.

B.—*Poromya*.

Literature.—The anatomy of *Poromya granulata* and *P. tornata* was first described and figured by Pelseneer (1888b), who later (1891) gave a more detailed account of the former species. In 1911 the same author described eight species of Poromya from the "Siboga" collections. Dall (1886a, 1889a, 1889b) has described the shell and external anatomy of the body in a number of species of the Poromyidæ. Ridewood (1903) has provided an account of the structure of the septum and the branchial sieves in *Poromya malespinæ* and *P. oregonensis*.

General Anatomy.—A lateral view of *Poromya granulata* is represented in text-fig. 3. The shell (*sh.*) has no posterior siphonal prolongation as in the Cuspidariidæ, the posterior



Text-Fig. 3.—Lateral view of *Poromya granulata*, showing the anatomy of feeding and digestive organs, × 10. *a.*, anus; *a.a.*, anterior adductor; *a.b.*, anterior branchial sieve; *a.p.*, anterior palps; *a.r.*, anterior retractor of foot; *a.s.*, anterior septal muscle; *c.*, crustacean in stomach; *c.g.*, cerebral ganglion; *D.*, dorsal or supra-septal cavity; *d.d.*, digestive diverticula; *f.*, foot; *g.*, mid-gut; *m.*, mouth; *m.e.*, mantle edge; *o.*, œsophagus; *ov.*, ovary; *p.a.*, posterior adductor; *p.b.*, posterior branchial sieve; *p.p.*, posterior palps; *p.r.*, posterior retractor of foot; *p.s.*, posterior septal muscle; *r.*, rectum; *s.*, septum; *sh.*, outline of shell; *s.m.*, line of attachment of septum and mantle; *s.s.*, style-sac (style indicated by broken line); *st.*, stomach; *t.*, tentacles; *te.*, testis; *v.*, valve between inhalant siphon and infra-septal cavity; *V.*, ventral or infra-septal cavity; *x.*, sand grains between palps and in œsophagus.

margin being subtruncate and slightly gaping. The siphons are short—almost sessile—and the inhalant opening is much larger than the exhalant (see text-fig. 4, *i.* and *e.*), both being surrounded by a common ring of long, slightly tapering tentacles (text-figs. 3 and 4, *d.* and *t.*) consisting of an unpaired dorsal tentacle (text-fig. 4, *d.*) and seven pairs of tentacles round the lateral and ventral margins of the inhalant siphon. The opening of the inhalant siphon into the infra-septal cavity (*V.*) is guarded by a large muscular valve (*v.*). The surface of the mantle is excessively thin as in the Cuspidariidæ, the ventral margins (*me.*) alone are thick and are free from one another for the entire length of the body from the anterior adductor (*a.a.*) to the siphons. The foot (*f.*) is long and thin and possesses a byssus groove on the posterior surface (see text-fig. 7, *b.*). It has two retractor muscles, an anterior (*a.r.*) and a posterior retractor (*p.r.*) which are attached to the shell in the same relative positions as in *Cuspidaria rostrata.* The palps are broader and larger than those of the Cuspidariidæ, a fact which has been noted by all observers, the anterior pair (*a.p.*) being especially long and, unlike the anterior palps of the Cuspidariidæ, being free from the anterior adductor (see also text-fig. 7). The posterior pair (*p.p.*) are united to one another in the middle line and do not extend back on either side of the foot as in Cuspidaria. The degree to which the mouth (*m.*) is guarded and obscured by the palps is seen best in text-fig. 7 which was drawn from life. The adductor muscles (*a.a.* and *p.a.*) occupy the same relative positions as in *Cuspidaria rostrata* but are smaller, and the posterior adductor is round and not oval in cross-section. The visceral mass occupies the bulk of the supra-septal cavity (*D.*), the dorsally situated ovary (*ov.*) and the more posterior and ventral testis (*te.*) being both well developed (like all the Septibranchs, Poromya is hermaphrodite). Lying above the œsophagus (*o.*) are the cerebral ganglia (*c.g.*).

Septum.—The septum in Poromya is a much smaller and more delicate organ than in the Cuspidariidæ. It is attached to the mantle on its outer sides, the right side being attached along the line marked *s.m.* in text-fig. 3. The two sides are united posterior to the foot, but are closely apposed, and not united, to the base of the foot along the line marked *s.* The septal muscles are very much smaller than those of the Cuspidariidæ and consist of two pairs, one anterior (*a.s.*) and the other posterior(*p.s.*), which are attached to the shell a little distance posterior to the anterior retractor and immediately posterior to the visceral mass respectively. The muscles run through the tissue of the mantle before becoming attached to the shell. There is no indication of lateral septal muscles, but, as will be discussed later, there is evidence that the septal muscles in Poromya may correspond to the *lateral* septal muscles, and not to the septal muscles, of the Cuspidariidæ.

There are no pores like those in the septum of the Cuspidariidæ ; instead there are a pair of anterior, and a pair of posterior, branchial sieves (*a.b.*, *p.b.*) which probably represent vestiges of the Lamellibranch gill. Each of these, in the words of RIDEWOOD (p. 272), " has the form of a shallow convex sieve, with the convexity directed downward and outward into the pallial cavity, and is attached all round its edge to the branchial septum by a thickened border." The anterior pair are on a level with the anterior border of the foot and each possesses five filaments, the posterior pair are situated opposite the hind end of the foot and have each six filaments. Both pairs are much nearer to the foot than to the mantle and lie somewhat obliquely. The slit-like openings between the filaments represent the sole means of communication between the infra- and the supra-septal cavities, for the edge of the septum, though not attached to the side of the foot, is too closely applied to it to permit the passage of water. Though all known species of the Poromyidæ possess two pairs of branchial sieves, these vary in size and in the number of filaments in different species. PELSENEER (1911) has tabulated the different conditions found in the eight species collected by the "Siboga" and has shown that the number of filaments in the anterior branchial sieve may vary in number between five and eight, and in the posterior one between five and eleven.

The conditions in the Cetoconchidæ, according to PELSENEER (1888B) and RIDEWOOD, approximate more closely to those found in the Poromyidæ than in the Cuspidariidæ, the septum being thin and possessing three paired sets of openings, consisting, in *Cetoconcha sarsi* (see RIDEWOOD, fig. 60), of an anterior series of five pores, a second series of five pores, and a posterior of three. In cross-section, as shown by RIDEWOOD, the boundaries between the pores appear as shortened gill filaments as in the Poromyidæ. Both the valve guarding the entrance to the infra-septal cavity and the palps of the Cetoconchidæ are large and resemble those of the Poromyidæ, and PELSENEER (1911), apparently with good reason, regards the Cetoconchidæ, though somewhat intermediate between the Poromyidæ and the Cuspidariidæ, as much more nearly related to the former family, concluding (p. 78) "la nécessité d'une famille Cetoconchidæ n'est nullement démontrée."

Alimentary System.—The widely open mouth (*m.*) leads into a short and broad œsophagus (*o.*), which is directed antero-dorsally, turning posteriorly to open into the large cylindrical stomach (*st.*). This is not quite so long nor so regularly cylindrical as the stomach of the Cuspidariidæ, but resembles that in the possession of ridged walls with a thick cuticular lining. It is surrounded except in the posterior region by the brownish tubules of the digestive diverticula (*d.d.*) which extend farther forwards than in Cuspidaria and open by two short, wide ducts near the anterior end of the stomach. There is an even smaller style-sac (*s.s.*) than in Cuspidaria and the contained style does not project far into the lumen of the stomach. The sac is in communication anteriorly with the mid-gut (*g.*) by means of a fine longitudinal slit. The mid-gut is short; after passing beneath the style-sac, it extends posteriorly to the end of the visceral mass and then diagonally upwards, merging into the narrower rectum (*r.*), which passes over the posterior adductor to open at the anus (*a.*) which lies at the base of the exhalant siphon. The cleared specimen of *Poromya granulata* from which text-fig. 3 was drawn contained between its posterior palps and in the œsophagus large sand grains (*x.*), and in the stomach a relatively large crustacean (*c.*), which occupied the centre of the lumen.

(ii) *Histology.* A.—*Cuspidaria.*

Mantle and Foot.—The thin mantle is bounded on both surfaces by a delicate pavement epithelium, as described in detail by GROBBEN. The thickened ventral edges possess on either side an epithelium of high narrow cells, those on the outer and ventral surfaces being concerned, presumably, with the formation of the shell. The epithelium on the inner side is the only region of the mantle which is ciliated, while there are present beneath the epithelium for the anterior two-thirds of its course large goblet-shaped mucous glands. These glands, which stain darkly with muchæmatein, occur in such numbers as to form a thick layer beneath the epithelium. They discharge their contents by way of fine extensions, which pass between the cells of the epithelium. GROBBEN has described them in *C. cuspidata*, and PLATE in *C. obesa*; in my own sections I have found them in these two species and also in *C. rostrata*. The ciliated regions extend posteriorly to the region of the valve at the posterior end of the mantle cavity.

The surface of the foot is thrown into a series of fine ridges which are bounded by a columnar epithelium which, except near the base of the foot, is ciliated, mucous glands occurring in the tissue beneath. The interior of the foot is composed of plain muscle fibres passing in all directions, amongst which ramify the extensions of the byssus gland, the ciliated duct of which opens on the posterior surface of the foot near the base.

Septum.—GROBBEN is the only worker who has described the fine histology of the septum in detail, though his findings have been confirmed to some extent by PLATE. As shown in fig. 1, both dorsal and ventral surfaces are covered with a low pavement epithelium (*d.e.* and *v.e.*), especially thin on the former; no cilia can be distinguished in sections (though their presence on the dorsal surface was noted in living *C. rostrata* and *C. cuspidata*), but a fine border cuticle is present. Nuclei are infrequent and irregularly distributed. The interior of the septum is composed of a mass of interwoven muscle fibres which, as already noted and figured by GROBBEN in *C. cuspidata* and confirmed by PLATE in *C. obesa*, have a characteristic and unique structure. As shown in fig. 3, they consist of flat fibres which, in the case of fibres from the septum of *C. rostrata*, are about 13 μ wide and less than 2 μ thick. After staining teazed-out fibres with iron hæmatoxylin, cross striations (*sr.*) can be seen, as dark bands somewhat narrower than the intervening lighter portions and about 1·5 μ apart. The fibres are of great length, the nuclei, as shown in fig. 3 (*n.s.*), being situated in the centre of the fibres. They are long and narrow—about 11 μ long and 3 μ wide—and appear to lie in a lightly staining strip (*a.*) in the centre of the fibre, this area extending down the middle of the fibre for some distance beyond the extremities of the nuclei. The fibres are usually wavy and their linear appearance in cross-section is shown in fig. 1 (the cross striations do not appear in this section, which was stained with Delafield's hæmatoxylin and eosin), and in horizontal section, with the striations indicated, in fig. 2. There is an almost complete absence of connective-tissue strands, but there are many wandering cells (*w.c.*) amongst the muscle fibres. This type of muscle appears to be unique in the animal kingdom; it is certainly unique so far as the Lamellibranchs are concerned, and its peculiar structure may be correlated with the remarkable mode of functioning of the septum, particulars of which will be given later.

The lateral muscle fibres which run across the dorsal surface of the septum, immediately beneath the epithelium, consist of plain muscle, roundish in cross-section and are shown (*l.s.m.*) in fig. 1. The striated muscle fibres are not present in the narrow membranous strips which connect the septum to the mantle and to the foot, only a little unstriped muscle—probably derived from the lateral septal muscles—being found between the epithelia in these areas. The septal pores are best studied in cross-section (*i.e.*, in longitudinal sections of the septum). They have been described by PELSENEER (1891) in *C. rostrata*, but not in any histological detail. GROBBEN studied the pores of *C. cuspidata* very carefully and PLATE stated that he found similar conditions in *C. obesa*. RIDEWOOD's material was too badly preserved for him to determine the structure of the pores. In my own sections I have found essentially similar conditions in all three species examined. The conditions in *C. rostrata* will be described in detail, figs. 1 and 2 respectively, representing longitudinal and horizontal sections through the septum of this species in the neighbourhood of pores. Near the pores the epithelium is raised, becoming columnar with well-defined cells containing regularly arranged and prominent nuclei. As already noted by PELSENEER (1891) and GROBBEN, the inner or dorsal region of the pores is drawn out into the form of a valve (*v.*) with raised dorsally directed lips, the whole being sunk considerably below the dorsal surface of the septum (as shown clearly in fig. 1) in both *C. rostrata* and *C. cuspidata*. In *C. obesa*, however, the valve is relatively larger and its dorsal extremity lies on a level with the upper surface of the septum. In all cases the under surface of the pores is flush with the surface of the septum. The pores are ciliated in two regions on their inner apposed surfaces. There are prominent cilia, at least as long as the cells that bear them, in the extreme dorsal region (*d.c.*), as shown in figs. 1 and 2. Beneath this there is an unciliated area, rather greater in extent than the upper ciliated region, and below this again a second set of cilia (*v.c.*), which extend as far as the central opening of the pores. These cilia are much shorter than those in the dorsal region and are difficult to see, especially in *C. rostrata*. They are more easily distinguished in *C. obesa*, while GROBBEN has noted and figured them in *C. cuspidata*. Around the pores, and particularly in the valvular region, a well-developed sphincter of plain muscle fibres is present beneath the epithelium (figs. 1 and 2, *sp.*), and can easily be identified in both transverse and horizontal sections, the fibres being quite distinct from those of the septal musculature and resembling those of the lateral muscles. The presence of this sphincter has not hitherto been noted but is of some importance, as will be emphasised later.

Palps.—A transverse section through one of the posterior palps of *C. rostrata* is shown in fig. 4. The inner surface (*i.e.*) is lined with a columnar epithelium possessing a uniform coating of cilia, and this is continued for a short distance round either edge of the palp. There are none of the prominent ridges and furrows present on the more complex palps of the typical Lamellibranchs (see YONGE (1926B), which contains references to previous literature). The outer surface (*o.e.*) bears no cilia and is bounded by a thin pavement epithelium with ill-defined cell boundaries and few nuclei. There is a complete absence of mucous glands in both epithelia. Within the palp there is a considerable development of plain muscle (*mu.*) running both transversely and longitudinally, the latter being best shown in longitudinal sections, and being most conspicuous near the base and extending towards the tip of the palp under both epithelia. There are also connective-tissue strands and many wandering cells (*w.c.*), but the latter are never found in the epithelium, as is the case, for example, in Ostrea (YONGE (1926B)).

Mouth and Œsophagus.—The wide mouth is lined with a ciliated epithelium resembling that of the palps of which it forms a continuation. It is surrounded by a moderately thick layer of circular muscle fibres. The œsophagus, as shown in fig. 5, is roughly circular in cross-section, with its walls, especially on the anterior and posterior walls, much folded longitudinally, many of the ridges (*r.o.*) being of considerable height and projecting for some distance into the lumen. The columnar epithelium which lines the lumen is ciliated for the most part. Cilia, however, are not present on the lateral walls in the distal region of the œsophagus, as indicated in fig. 5, the epithelium there being bounded solely by the thin border cuticle, which is also present on the ciliated cells. Surrounding the œsophagus is an extremely thick layer of circular muscle (*c.m.*), as already observed by PELSENEER (1891), GROBBEN and PLATE, a condition never found in the typical Lamellibranchs, where the musculature of the gut throughout is very poorly developed. There are also, here and there, muscle strands (*r.m.*) which radiate out from the interior of the ridges and pass through the circular muscle layer.

Stomach.—Longitudinal and transverse sections of the stomachs of *C. rostrata* and *C. cuspidata* respectively are shown in figs. 6 and 7. The epithelium consists of extremely narrow cells which vary greatly in length so as to form a series of high, longitudinal ridges (*l.r.*). Nuclei are small, and wandering, phagocytic cells are only very rarely found in the epithelium. The cells are filled with fine yellowish-brown granules, especially in the upper regions. There are no cilia in the stomach. At the junction with the œsophagus a thick, lamellated, cuticular layer is formed by the stomach epithelium and this is continued over the surface entire of the stomach, as shown in fig. 6 (*cu.*). The presence of this cuticle has been noted by both PELSENEER (1891) and GROBBEN, and it appears to be characteristic of the Septibranchs and to represent, very probably, an extension over the whole surface of the stomach of the smaller gastric shield (flèche tricuspide), which is found in all Filibranchs and Eulamellibranchs, where it is situated on the wall of the stomach directly opposite the opening of the style-sac. It provides a firm surface against which the head of the crystalline style can bear as it revolves (see NELSON (1918)). As previously noted (YONGE (1926B)), the gastric shield appears to be formed of the same material as the cilia or the border cuticle ; it is certainly not secreted in the usual manner. In Cuspidaria also there is no evidence that the epithelium of the stomach is composed of anything but modified ciliated cells, and there is no evidence of secretion, while, as in Ostrea, there are fine transverse striations having the appearance of cilia extending through the cuticle about its junction with the epithelium. Probably, therefore, the stomach cuticle of the Septibranchs is merely an extension of the gastric shield of the other Lamellibranchs.

Surrounding the epithelium there is a well-developed layer of circular muscle fibres (*c.m.*), and fine fibres also pass between the cells of the epithelium, especially in the centre of the ridges. The presence of these muscles, and the fact that the stomach in Cuspidaria is practically free from the surrounding tissues, provide further important distinctions between the stomach of the Septibranchs and those of the other Lamellibranchs.

Digestive Diverticula.—The opening of the anterior and smaller duct of the digestive diverticula in *C. cuspidata* is shown in fig. 7 (*d.*). The actual duct is, when compared with that of a typical Lamellibranch such as Mytilus (LIST (1902)), Anodonta (GUTHEIL (1912)), Mya or Ostrea (YONGE (1923, 1926B)), exceptionally short and wide, approximating most nearly to the conditions found in the Teredinidæ (SIGERFOOS (1908), POTTS (1923), YONGE (1926A)), where, on account of the elongated shape of the animals, the digestive diverticula are spread out in a thin sheet round the ventral surface of the stomach, and their ducts, as a result, are short and wide. In the Cuspidariidæ, as in the other Lamellibranchs, the ducts are lined by a ciliated epithelium ; but neither phagocytes nor mucous glands are to be seen in this epithelium. The diverticula (*t.*) themselves are notable for their widely open lumina (*l.*) and the extent to which, especially in the regions nearest the ducts, they unite with one another to form a more compact structure than the separate acini characteristic of the majority of the Lamellibranchs. They tend more to the condition found in some of the more highly organised Gastropods, such as Doris, where the digestive " gland " possesses a large central chamber into which secondary cavities open on all sides. In structure, the cells of the tubules of the digestive diverticula do not vary essentially from the conditions found in the other Lamellibranchs (for full details and literature on this subject, see YONGE (1926A)). One kind of cell only is present, groups of large vacuolated cells, which frequently contain brown or yellowish-coloured inclusions of various sizes, being separated from one another by crypts of smaller, less vacuolated and darkly staining, cells (fig. 13, *o.c.* and *cp.*), but the latter, as previously shown (1926A), represent nests of young cells destined to replace the older cells which in time are destroyed and cast into the lumen. As in the digestive diverticula of the other Lamellibranchs, there is no evidence of secretion by any of these cells. The nuclei are of the characteristic shape, namely large, round and with a prominent nucleolus, and are most numerous in the crypts of young cells. No evidence of the presence of cilia was found either in fresh material or in sections, nor any sign of a border cuticle. It is not impossible, however, that, as in other Lamellibranchs, long retractile cilia may be borne on these cells in the living condition (see POTTS (*loc. cit.*) and YONGE (1926A)). Around the tubules there is a thin bounding membrane, but no muscle such as surrounds the ducts (see fig. 7). The area between the tubules is conspicuous for the almost complete absence of connective-tissue strands, although there are occasional muscle fibres and a certain number of wandering cells. This is very different from the conditions found in the majority of the Lamellibranchs, where the digestive diverticula are embedded in a firm matrix of connective tissue.

Style-Sac.—The longitudinal section through the stomach of *C. rostrata*, represented in fig. 6, shows the position and relative size of the style-sac (*s.s.*) with its contained style (*c.s.*). The opening of the mid-gut anterior to it is only just indicated in the section (*b.g.*), and, owing to the S-shaped form of the separating ridge, there is the appearance in longitudinal section of three cavities; the narrow cavity (*c.g.*) shown on the left of the style-sac in fig. 6 is in reality a portion of the connecting slit between the style-sac and the gut. The extreme basal region of the style-sac, as shown by horizontal sections, is separate from the mid-gut. The style-sac is lined with an epithelium of large, cubical cells (*e.s.*) with well-defined cell boundaries and large round nuclei which occupy the centre of the cells. The latter are covered by a dense and very even coating of strong, bristle-like cilia; on the edges of this epithelium, where it passes into the typhlosoles which separate the lumina of the style-sac and the mid-gut, there are groups of tall narrow cells. In every particular, therefore, the structure of the style-sac in Cuspidaria resembles that of the other Lamellibranchs, which has been described in detail by NELSON (1918), EDMONDSON (1920) and YONGE (1923, 1926B) and other authors therein quoted. The epithelium of the separating ridge is ciliated and resembles that of the mid-gut.

The style itself is of the usual structure but is exceptionally short. It does not protrude far into the stomach, as is shown clearly in fig. 6, and clearly cannot act against the cuticular lining on the opposite wall of the stomach in the same way that the style in the typical Lamellibranchs acts against the gastric shield. The probable reasons for this will be discussed later; it may be mentioned here, however, that there is strong evidence that the style in the Septibranchs is a vestigial organ.

Mid-Gut and Rectum.—For a short distance after its separation from the style-sac, the mid-gut possesses a prominent typhlosole (fig. 8, *ty.*). The epithelium consists of tall cylindrical cells with long cilia and oval, basally situated, nuclei. Here and there are groups of narrow, darkly staining, and probably young, cells (*y.c.*). Around the epithelium is a thin circular muscle layer (*c.m.*). There is a complete absence of mucous glands in the epithelium, and phagocytic wandering cells are extremely rare. The typhlosole does not extend very far posteriorly and, for the greater part of its course, the mid-gut is a thin-walled oval tube. In the region of the heart, as indicated in text-fig. 1, it merges into the rectum, and the junction between the two is shown in fig. 9. The mid-gut is here much wider and is bounded by a thin ciliated epithelium which contains occasional mucous glands (*m.g.*). The circular muscle layer is extremely thin in this region. The mid-gut (*g.*) is united on its dorsal side to the rectum (*r.*), which has a characteristic structure, being bounded by tall, narrow cells bearing long cilia and interspersed with many mucous glands (*m.g.*), and surrounded by a comparatively thick circular muscle layer. After separating off from the mid-gut, it continues as a straight tube, circular in cross-section and with a narrow lumen.

It is worthy of note that, with the exception of the peculiar mode of union between the mid-gut and rectum, and the absence of phagocytes from the epithelium, both mid-gut and rectum in Cuspidaria have essentially the same structure as in the other Lamellibranchs—*e.g.*, Anodonta (GUTHEIL (1912)), Arca (MATTHIAS (1914)), Mya or Ostrea (YONGE (1923, 1926B)).

The structure of the gut in the three species of Cuspidaria examined is, in all essential details, identical.

B.—*Poromya.*

With the exception of the septum, the structure of the feeding and alimentary organs in *Poromya granulata* is little different from that found in Cuspidaria. The mantle is thin and in structure resembles that of Cuspidaria, the thickened ventral margins are bounded on their inner surfaces by a columnar epithelium which is ciliated but contains few mucous glands beneath it. The surface of the foot is covered with a ciliated epithelium except in the basal area. The septum, a portion of which is shown in longitudinal section in fig. 10, is bounded on either side by well-defined epithelia of cubical cells (*d.e.* and *v.e.*), neither of which show the presence of cilia in sections but possess a border cuticle. The septum is much thinner than in Cuspidaria and the musculature is much slighter. The fibres run mainly longitudinally and are *unstriped* and roundish in cross-section ; in no part of the septum is there any indication of the presence of the striped muscle so characteristic of the septum of the Cuspidariidæ. Although it is impossible to be certain without embryological evidence, it may be that the septal muscles in Poromya are homologous with the lateral septal muscles in Cuspidaria, and that the septal muscles in the latter represent a separate development. As noted by RIDEWOOD in *P. malespinæ,* the septum is thicker and more muscular in the region behind the posterior branchial sieve.

The structure of the branchial sieves in *Poromya malespinæ* and *P. oregonensis* has been described by RIDEWOOD, and that of *P. granulata* in less detail by PELSENEER (1891). A transverse section through one of the posterior branchial sieves is shown in fig. 10. The filaments show essentially the same structure as the gill filaments of the other Lamellibranchs. Thick rods of " chitin " (*ch.*) are present beneath the epithelium on the sides of the filaments, the interior of which is filled with strands of " chitin " and also other connective tissue, and wandering cells (*w.c.*) are present both here and in the meshes of the somewhat vacuolated " chitinous " supporting rods. In the dorsal region of the filaments (*i.e.*, morphologically the interlamellar region) there are thick bands of longitudinal muscle (*l.m.*). There is no evidence of any interfilamentar junctions in *Poromya granulata,* nor were they found by RIDEWOOD in *P. oregonensis,* though this author noted their presence in *P. malespinæ,* as did PELSENEER (1888B) in *P. tornata.* Laterally the filaments are bounded by tall epithelial cells which carry long cilia (*l.c.*) which correspond to the lateral cilia of the typical filament. No frontal cilia can be distinguished in *P. granulata*. RIDEWOOD found them in *P. malespinæ* but not in *P. oregonensis*, but small latero-frontal cilia may be present. If so, they are quite different from the large straining latero-frontals found in the typical filament. The reasons for this modification of the ciliation of the filaments composing the branchial sieve will be discussed later.

A longitudinal section through the labial palps, mouth, œsophagus and stomach of *P. granulata* is shown in fig. 11. As will be observed, they do not differ essentially from those of Cuspidaria. The comparatively large palps (*a.p.* and *p.p.*) are ciliated on their inner surfaces only and contain numerous muscle strands; the mouth (*m.*) is large and leads into a wide ciliated œsophagus (*o.*), which is surrounded by a thick layer of muscle (*c.m.*). The stomach (*st.*) is large and its ridged walls are covered with a high columnar epithelium, which contains numerous fine, yellowish, refractile inclusions. A thick cuticular layer (*cu.*) lines all regions of the stomach, which is surrounded by a thick layer of circular muscle fibres. The structure of both ducts and tubules of the digestive diverticula resembles that of Cuspidaria. The style-sac is small and contains a small rounded style which does not project far into the stomach; the mid-gut is connected with the style-sac in the same manner, and has throughout the same structure as in Cuspidaria, being ciliated, round in cross-section in the region of the stomach, and becoming oval before it passes into the rectum. The rectum is narrow, ciliated and contains many mucous glands.

4. THE PROCESS OF FEEDING.

(i) *Mode of Life.*

Both Cuspidaria and Poromya live in mud into which they burrow. This process was followed in the laboratory by placing freshly caught animals in vessels containing sea water beneath which was a layer of mud. All three species of Cuspidaria and *Poromya granulata* behaved in essentially the same manner. No previous observations appear to have been made on *living* Septibranchs, so that the observations recorded in this section probably represent an extension to our knowledge concerning the habits and feeding mechanisms of the Lamellibranchia.

Burrowing is performed largely by means of the foot, which can be protruded from between the shell valves as a thin wedge which, when fully extended, is about the same length as the shorter axis of the shell. It can be directed either ventrally or anteriorly. The burrowing of *C. obesa* was carefully followed at Trondhjem. After being placed on its side on a layer of mud about 1 inch thick, the animal worked its way downwards until the anterior half of the body region (*i.e.*, as apart from the siphonal extension) of the shell was buried. At the same time the siphons with their surrounding tentacles (all tinged red in life) were protruded. About once a minute a violent contraction of the shell valves was observed, a contraction which was apparently connected with movements of the entire animal, whereby it was rotated slightly and at the same time pushed deeper into the mud. This movement was always accompanied by a sudden ejection of water through the *inhalant* siphon—a necessary safeguard if the septum is not to be severely strained or perhaps ruptured. The animals usually burrowed diagonally downwards and with considerable rapidity, though in a series of jerks with appreciable intervals between them. At each movement the posterior end of the animal was raised to an almost vertical position and was then lowered again, the animal at the same time sinking deeper into the mud.

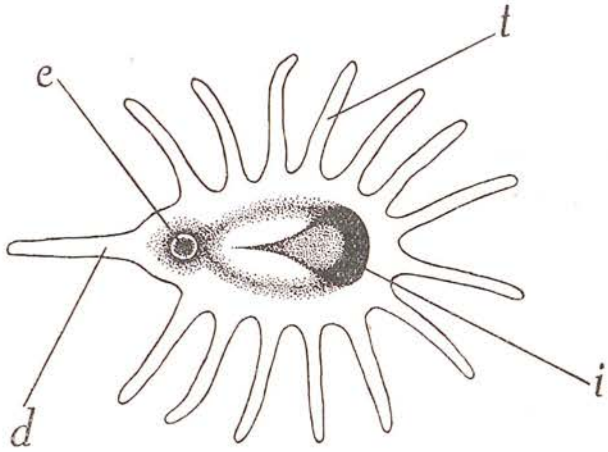
Finally, it burrowed so deeply that the end of the siphonal extension of the shell was flush with the surface of the mud, above which only the siphons projected, and, had not the previous movements of the animal been followed, it would have been difficult to distinguish these. The animals did not usually remain long in this position, but moved about on the surface of the mud, which soon became channelled and pitted as a result of their movements and burrowings. However deeply the animals burrowed the siphons were never covered. Similar habits were observed in the case of *C. cuspidata* at Kristineberg.

Poromya protrudes its siphons and their surrounding tentacles more readily than does Cuspidaria. As already noted, the latter are very long and, when extended, they lie backwardly directed over the posterior region of the shell covering some quarter of its surface; they may, however, erect themselves so that they stand out at right angles to the surface. They were often observed in movement. When placed on mud, Poromya burrows into it in much the same manner as *C. obesa,* using its long, extensile foot. Water appears to be forced out of the shell anteriorly, a procedure which may assist burrowing, as the animal was observed in this manner to force away mud from in front of its shell. During burrowing, the animal was observed to erect itself, posterior end upwards, in the mud and then turn slowly round, sinking into the mud as it did so, finally resuming a horizontal position. It then proceeded to move along and downwards in the channel it had made. All the movements, as in Cuspidaria, were sudden with appreciable intervals between them. As a result of this process, first the anterior end and finally the entire shell became buried beneath the mud. Gradually the animal assumed a vertical position, anterior end downwards, with only the siphons exposed, which lay flush with the surface of the mud, the two siphonal openings pointing directly upwards (text-fig. 4, *i.* and *e.*) and the tentacles (*t.*) lying flat on the surface of the mud, as shown in text-fig. 4.

(ii) *Function of the Septum.*

The movements of the septum were carefully followed with a view to determining the true function of this organ, which has been a matter of dispute.

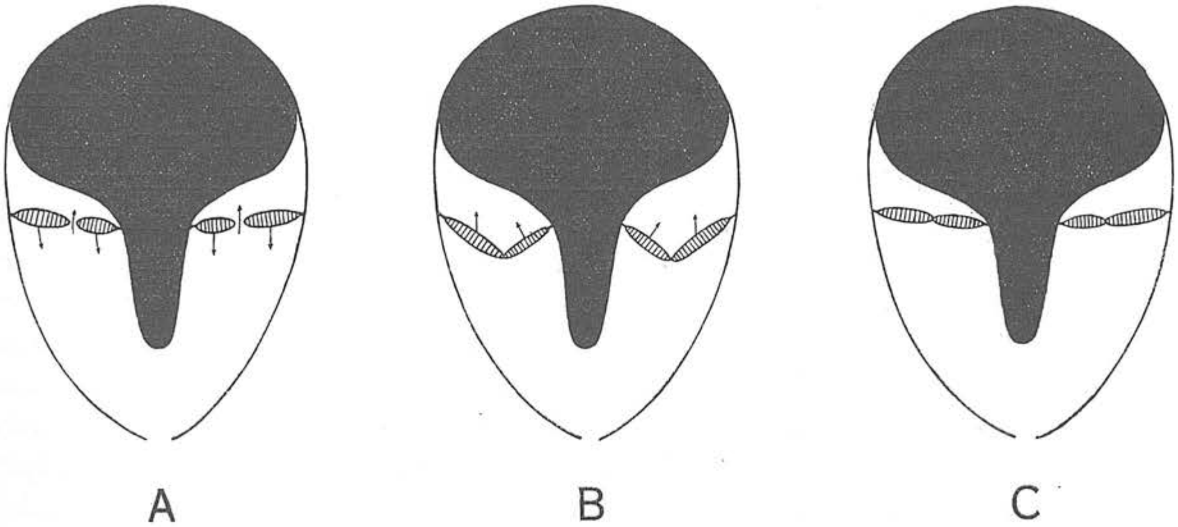
In the Septibranchs, unlike the other Lamellibranchs, there is no continuous current of water passing in through the inhalant, and out by way of the exhalant, siphon, even when these are fully extended and obviously functioning. Instead, there is an occasional widening of the opening of the inhalant siphon followed by a sudden intake of water, while at the same time the exhalant siphon opens to its fullest extent, water being expelled through the opening with considerable force, a fact which can be clearly demonstrated by introducing a suspension of carmine grains into the water around the exhalant siphon. The exhalant siphon in the Septibranchs has an exceptionally narrow opening, the lips of which are normally drawn together—a necessary precaution in view of the danger of small particles entering the siphon in the absence of a steady outflowing current. The inhalant and exhalant movements take place perfectly regularly in animals which are functioning normally with siphons fully extended. In *Cuspidaria obesa* they were observed to take place about six times per minute, and in *C. cuspidata* some four times a minute.



TEXT-FIG. 4.—*Poromya granulata*, siphons and surrounding tentacles fully extended, drawn from life. × 14. *d.*, dorsal, unpaired tentacle ; *e.*, exhalant siphon ; *i.*, inhalant siphon ; *t.*, one of the fourteen paired tentacles.

By carefully removing the shell valves from the two larger species of Cuspidaria, these sudden movements were found to be caused by the movements of the septum, the action of which did not appear to be interfered with when the shell was removed. Contrary to what has hitherto been assumed from an examination of its anatomy, the septum when at rest, *i.e.*, between the periodic movements, does not lie stretched to its fullest extent ventrally. On the contrary, it is drawn up dorsally to the maximum degree, as shown in text-fig. 5, A. During rest the pores are open and the cilia with which they are lined beat inwards so as to cause a small, but perceptible, current upwards from the infra- into the supra-septal cavity, as indicated by the arrows in the diagram. With the pores still open, the septum is lowered to its fullest extent, when the pores are shut tightly, presumably by means of the sphincter of plain muscle. This condition is indicated diagrammatically in text-fig. 5, B. The valve which guards the entrance to the infra-septal cavity probably prevents water and food from being expelled by way of the inhalant siphon during the downward movement of the septum, while the opening of the exhalant siphon remains shut so that water cannot be drawn through in the wrong direction. As a result, therefore, of the downward movement of the septum, water is transferred from the infra-septal cavity by way of the openings provided by the pores into the supra-septal cavity. The septum is then drawn sharply upwards in the direction indicated by the arrows in text-fig. 5, B, with the pores still tightly shut—the pressure of the water against the dorsally directed valves preventing them from being forced open—until it regains its original position, when it comes to rest, with the pores still shut, as indicated in text-fig. 5, C. Finally, the pores reopen and the slow flow of water through them is renewed. Exactly the same procedure was observed in both *C. rostrata* and *C. cuspidata*.

The movements of the septum are invariably accompanied by the opening and extension of the siphons as already described, this taking place during the upward movement of the septum. The result of the septal movements is clearly to draw water and food matter into the infra-septal cavity, the water being later passed through the pores, slowly when the septum is at rest but quickly and in great quantities during its downward movements, and being expelled through the exhalant siphon. Thus, whatever the origin of the septum, in function it is analogous with the Lamellibranch gill, producing a current of water through the mantle cavity and drawing in food. But, owing to the more powerful, though intermittent, current produced by the septum, the food drawn in need not—and does not—consist solely of fine particles carried in suspension by the water, as in the ciliary feeding Lamellibranchs, but includes comparatively large particles or small animals which may be sucked in unawares as they pass the inconspicuous siphons, which are all that is exposed of the buried Septibranch.



TEXT-FIG. 5.—Diagram showing movements of septum. A, position of septum when at rest and preliminary to descending, current of water through pores indicated by upward directed arrows, downward movement of septum indicated by arrows; B, position of septum at end of downward movement, pores closed; septum now moves upward as indicated by arrows; C, position at completion of upward movement, pores still shut.

In Poromya the action of the septum does not appear to be so regular. Occasionally—not at perfectly regular intervals and not more than once a minute—a sudden sharp expulsion of water from the exhalant siphon was observed, so powerful, indeed, that if carmine grains were placed in the water they were shot away to a distance of about 4 or 5 cm. Unfortunately, probably owing to the weakness of its musculature, the septum of Poromya did not function after the shell valves had been removed for better observation. It proved impossible, therefore, to determine whether it acts in the same way as the septum of Cuspidaria, a matter of importance in view of the different types of musculature in the septa of the two families. The cilia of the branchial sieves were observed in the living state and seen to beat inwards, like those surrounding the pores of the Cuspidariidæ, and so cause a current of water from the infra- to the supra-septal cavity. The openings of the sieve can probably be closed by the contraction of the longitudinal muscles at the base of the filaments. The septum of Poromya is clearly unfitted for the powerful and frequent movements displayed by that of Cuspidaria ; in structure it is too delicate, while the branchial sieves are not adapted to stand the same pressure of water as the pores with their dorsally directed valves.

The peculiar state of affairs in the Cuspidariidæ, whereby the septum between its periods of activity is in its shortest condition, *may* be connected with the peculiar type of muscle of which it is composed. The flat fibres are very long and wavy, and it may be that on stimulation they straighten out and so extend the septum. This appears a more probable explanation than that the septum is in a state of tonus for the greater part of its existence. Physiological experiments—unfortunately impossible with the limited material and apparatus at my disposal—are needed to determine in what state the septum of Cuspidaria is actually relaxed, while the physiology of the septal muscle would undoubtedly repay further investigation. One thing only is clear, that the development of striped muscle is correlated with the need for a continuous series of comparatively sudden movements—a state of affairs which has led to the development of striped muscle in the adductors of members of the Pectinacea and the Ostræacea, which constantly close the shell valves for the rejection of foreign particles or for swimming.

From morphological considerations, PELSENEER (1891) came to a conclusion as to the function of the septum which agrees fairly closely with my observations on the living animal. He states (p. 225), " Cette cloison, avec ses orifices, entretient assurément une active circulation d'eau sur la paroi intérieure du manteau (dorsalement au septum, comme chez *Poromya*) : la cloison, en se contractant, ferme ses orifices et chasse l'eau par le siphon anal ; lorsqu'elle se relâche, le siphon anal étant fermé, les orifices du septum s'ouvrent et l'eau entre dans la chambre supraseptale, la valvule du siphon branchial pouvant empêcher qu'elle sorte par ce dernier."

GROBBEN agreed in the main with the above statement, considering that so muscular an organ as the septum could not be concerned with respiration, but would be of great importance in changing the water in the mantle cavity, as it is clearly adapted for powerful movements, while in view of the cross striation of the muscle he thought it probable that very strong contractions could be accomplished. He goes on to state (p. 113) that, " Doch möchte ich glauben, dass nur von Zeit zu Zeit ein solch ausgiebiger, durch Contraction des Septums bewirkter Wasserwechsel stattfindet, dass im Uebrigen, wenn sich das Thier in Ruhe befindet, die wenngleich geringe Verbreitung von Wimpern an den Spalten, sowie im Mantel und am Fuss für einen langsamen Wasserwechsel sich als ausreichend erweist. Anderseits wird aber die geringe Ausdehnung von Wimperepithelien an den die Mantelhöhle begrenzenden Flächen wieder auf einen zeitweilig nothwendigen ausgiebigeren Wasserwechsel durch Contraction des Septums hinweisen." In view of his lack of observations on living animals this statement is remarkably accurate.

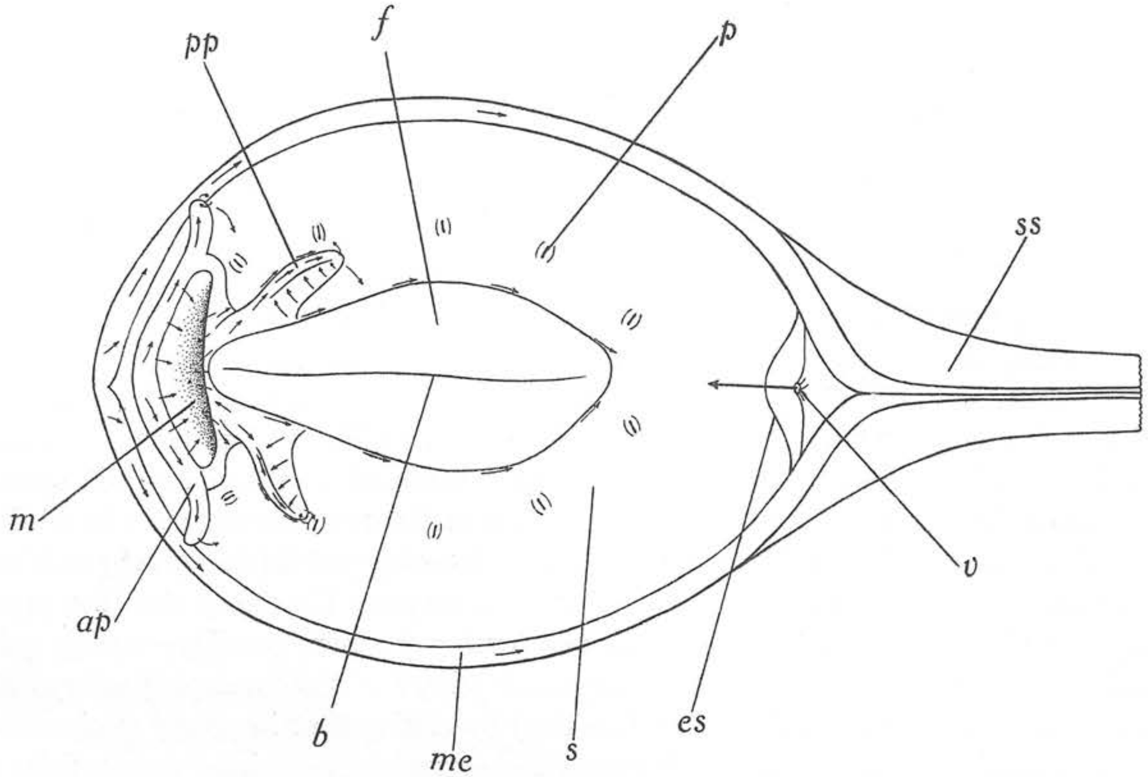
PLATE did not think it probable that the movements of the septum could be intermittent, with a musculature so enormously developed and histologically so highly differentiated. He thought, moreover, that the cilia on the pores did not serve to pass water through, but merely acted as a sieving apparatus preventing the passage of food particles into the upper cavity. These opinions have not stood the test of experimental verification.

DALL had a very different opinion as to the function of the septum. He considered (1889B, p. 443) that the septal muscles, "if not homologous with, at least perform the functions of, the siphonal retractors of ordinary Pelecypods, and in forms like *Poromya mactroides*, where the usual retractors are present, the siphonal septum is destitute of muscularity, or possesses it only to an inferior degree." Later (p. 445), referring to the septal pores in Cuspidaria, he stated, "I suppose that they serve to admit fresh water to the upper chamber, which I believe to be utilised in some, if not all, instances as a marsupium. It is probable that, by suitable muscular contractions, the septum will operate somewhat like the washer of a pump-valve, and that the upper chamber can be filled or emptied of its contained water at will. . . . I do not regard it (the septum) as in any way homologous with the normal ctenidia." He supports his theory that the supra-septal cavity is a marsupium where the ova develop (as quite possibly—though quite incidentally—they do, for the eggs are large and yolky and the developing embryo will not require food for some time after hatching) by stating that in young specimens of various species of Cuspidaria and Poromya the septal pores or sieves are partially or completely shut, only opening completely when the animals attain sexual maturity. It is clear, however, that if they were completely shut the animals could neither feed nor respire, since a through current of water could not be maintained. There appears to be no justification for DALL'S views as to the function of the septum ; his views with regard to its origin will be discussed later. RIDEWOOD makes no comment on the function of the septum.

(iii) *The Intake of Food.*

In the Cuspidariidæ, particles or small animals are drawn in through the inhalant siphon as a result of the water current caused by the sudden upward movement of the septum. The four club-shaped tentacles which surround the inhalant siphon may perhaps assist in this, for they are freely movable and bend inwards, in a claw-like fashion, around the opening of the siphon beyond which they extend ; but this was never experimentally proved. Food passes through the valve leading into the infra-septal cavity, as indicated by the large arrow in text-fig. 6, and, as the animals always lie with the anterior end downwards, it will then fall down towards the mouth region. There are no cilia to guide it there such as are present on the gills of the ciliary feeding Lamellibranchs.

The palps probably serve to push the food into the mouth (though this was never experimentally demonstrated as it was in Poromya). Though they are small, especially the posterior pair which are absent in *C. obesa*, frequent movements were observed, as would be expected in view of their relatively well-developed musculature. In the majority of the Lamellibranchs, the two pairs of palps are closely applied to one another so that the mouth is obscured, but in Cuspidaria the large mouth is fully exposed and may extend considerably when food is swallowed and passed into the muscular œsophagus.



TEXT-FIG. 6.—Ventral view of *Cuspidaria cuspidata* with mantle lobes drawn back to expose septum, drawn from life. × 15. *a.p.*, anterior palps; *b*, byssus groove; *e.s.*, posterior end of septum; *f.*, foot; *m.*, mouth; *m.e.*, mantle edge; *p.*, septal pore; *p.p.*, posterior palps; *s.*, ventral surface of septum; *s.s.*, siphonal sheath; *v.*, valve between inhalant siphon and infra-septal cavity. Large arrow indicates direction of main food and respiratory current, smaller arrows indicate direction of ciliary currents.

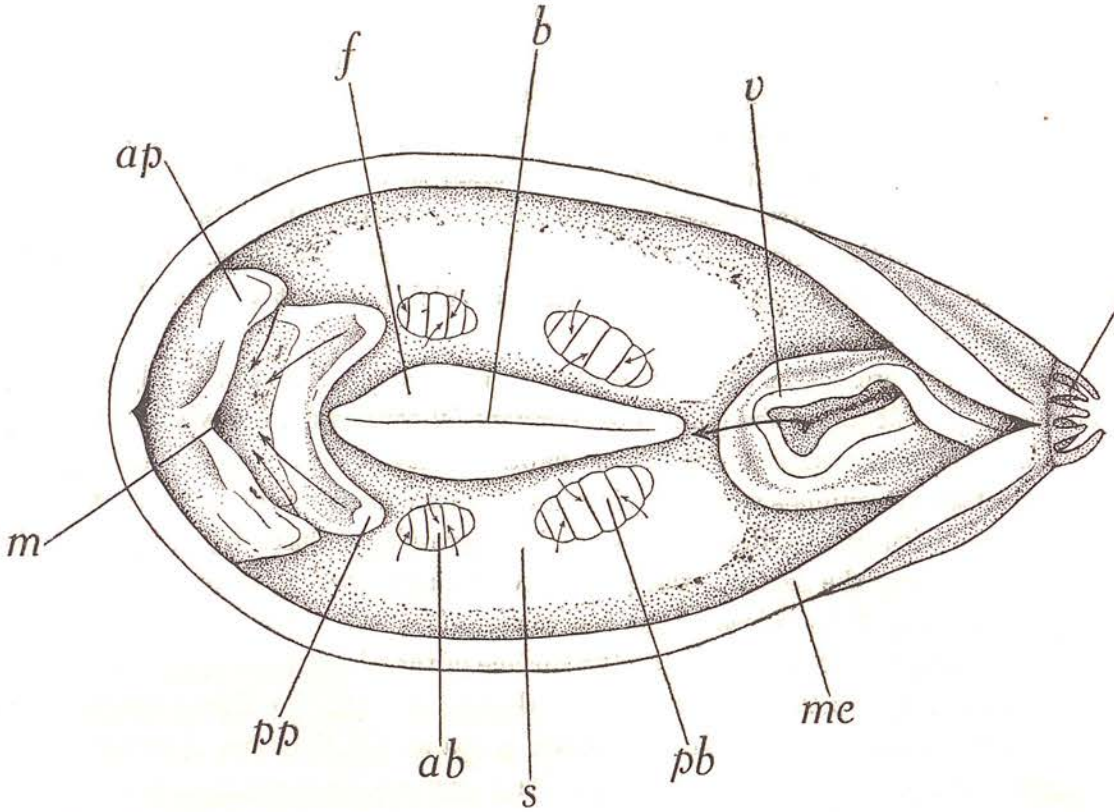
The cilia on the inner surfaces of the posterior palps (*p.p.*) beat in the directions indicated by the arrows in text-fig. 6. There is an outer lateral area on which the cilia beat towards the tip of the palp, the cilia on the remainder of the surface beating across it and carrying particles into this backwardly directed stream. On the anterior palps (*a.p.*), the cilia on the inner surfaces beat towards the tips of the palps. The cilia on the basal region of the palps, perhaps better described as the lips of the mouth, beat inwards, as do those within the mouth and lining the œsophagus. As a result of the action of the cilia on the palps, small particles are carried *away* from the mouth, being passed from the palps through the septal pores (as shown in text-fig. 6) or else in the case of the posterior palps, posteriorly by way of the foot. The cilia on the foot beat posteriorly and particles are carried to the hinder end, where they appear to be drawn through the posterior pair of pores. As we have seen, cilia are absent on the greater part of the surface of the mantle, only the thickened marginal ridges (*m.e.*) possessing them. These cilia beat posteriorly and carry fine particles to the hind end of the mantle cavity in the region beneath the valve. This ciliary current corresponds to the " untere Rückströmung " originally described by STENTA (1903) and which has been shown invariably to be present in the ventral region of the mantle in all Lamellibranchs (see especially KELLOGG (1915)). This current is always concerned with the cleansing of the mantle cavity and the rejection of useless particles, and it is noteworthy that it is the only ciliary current in the mantle cavity of the Septibranchs which clearly corresponds to a current found in the other Lamellibranchs. Particles are massed together at the posterior end of the mantle cavity as the result of its action and, as in other siphonate Lamellibranchs, are probably disposed of by sudden contractions of the shell valves, which force out water and suspended matter through the *inhalant* siphon.

Such cilia as are present in the infra-septal cavity, *i.e.*, on the mantle edges, on the foot, on the palps and round the pores, are therefore all concerned, not with feeding, but with the removal of fine particles from the mantle cavity. This cleansing is obviously of great importance to animals which live in mud and are consequently in constant danger of being clogged with fine particles. Feeding is the result, exclusively, of the *muscular* action of the siphons, the septum, the palps and the anterior region of the gut (aided perhaps by cilia to a slight degree in the last instance).

In the supra-septal cavity there are, on the surface of the visceral mass, cilia which beat posteriorly and carry particles towards the exhalant siphon. In living specimens of *Cuspidaria rostrata* and *C. cuspidata*, moreover, a sparse ciliation was observed on the dorsal surface of the septum (never on the ventral surface), as a result of the action of which particles were carried backwards. There are no cilia on the mantle surface. All cilia in the supra-septal cavity, therefore, serve to carry away particles and also, no doubt, assist the cilia of the septal pores in maintaining a slight circulation through the mantle cavity when the septum is at rest.

In Poromya, as shown in text-fig. 7, conditions are essentially the same. Owing to the fact that the inhalant siphon (see text-fig. 4) has a wider opening, larger particles are drawn in than in Cuspidaria. When the animal is sunk in the mud and the siphons are functioning, the inhalant siphon does not project above the surface and its dorso-ventrally compressed aperture is normally shut, owing to the coming together of the rounded lips. The exhalant siphon is much smaller, is round and protrudes slightly as a roundish papilla, about 1 mm. in diameter. Pieces of the gonad of Pecten about a millimetre across were placed on the inhalant siphon of a living Poromya. At first they were refused and pushed away by the surrounding tentacles, but on the second attempt they were drawn in slowly through the siphonal opening, being seized by the lips and slowly passed into the infra-septal cavity. A few moments later the inhalant siphon opened to its fullest extent and no sign of the food could be seen. A piece of coagulated blood, some 2 to 3 mm. long and 1 mm. wide, from Myxine was later fed to the same animal and was similarly taken in.

It was observed that food was taken into the inhalant siphon by a series of movements clearly related to the movements of the septum, or, if the food was not too large, by one sudden inrush. Both siphons were opened to their fullest extent, there was a sudden ejection of water through the exhalant siphon (showing that the septum had contracted) and at the same time matter was pulled into the inhalant siphon. After a series of these movements the larger food masses were finally taken completely into the mantle cavity. During the process of food intake, the lips of the inhalant siphonal opening were fully expanded and raised to a height of some 2 or 3 mm., *i.e.*, above the exhalant siphon.



TEXT-FIG. 7.—Ventral view of *Poromya granulata* with mantle lobes drawn back to expose septum, drawn from life. × 20. *a.b.*, anterior branchial sieve ; *a.p.*, anterior palps ; *b.*, byssus groove ; *f.*, foot ; *m.*, mouth ; *m.e.*, mantle edge ; *p.b.*, posterior branchial sieve ; *p.p.*, posterior palps ; *s.*, septum ; *t.*, tentacles surrounding siphonal openings ; *v.*, valve between inhalant siphon and infra-septal cavity. Large arrows indicate direction of food intake, small arrows the passage of the water current through the branchial sieves.

If too much food was taken in, then the surplus was frequently ejected—as a result of sudden contractions of the shell valves—but only if the food was still, at any rate partially, in the inhalant siphon and had not passed the valve leading into the infra-septal cavity.

As in the Cuspidariidæ, the food falls down towards the mouth. There it is at once pushed into the mouth by the palps, which are both larger and more active than those of Cuspidaria. After placing pieces of the gonad of Pecten upon them, both pairs of palps immediately curled inward, as indicated by the arrows in text-fig. 7, and quickly pushed the food into the large mouth, which opened wide to receive and swallow it. There is thus not the slightest doubt concerning the muscular function of the palps in Poromya.

The only cilia whose presence could be identified in the *living* animal were those on the branchial sieves, and it is significant that the frontal cilia, concerned with food collection in the other Lamellibranchs, have been lost, while the lateral cilia, concerned with the creation of the water current, are alone retained. Sections show the presence of cilia on the palps, on the mantle edges and on the foot, but these are evidently too small and their action too feeble to be easily identified by placing carmine upon them. The observations, moreover, had to be made on one specimen only and without the aid of a binocular microscope. In view of the similarity in the feeding habits and the structure of the feeding organs in the two genera, there can be little reason to doubt that the cilia in the mantle cavity of Poromya serve the same function as those of Cuspidaria, namely, to clear the mantle cavity of small particles, and to maintain a slight water current when the septum is at rest.

(iv) *Passage of Food through the Gut.*

Food is carried through the œsophagus largely by the peristaltic movements of its thick muscular layer. In Poromya, food was occasionally rejected through the mouth, apparently by antiperistaltic movements.

In the stomach the food is broken up into small fragments. The stomach in the Septibranchs is a crushing gizzard, as its structure (see figs. 6 and 7) plainly indicates. The powerful musculature serves to contract its walls violently so that the ridges with their thick cuticle come together and crush up the large food masses which lie between them. It often proved difficult to section the stomach of both Poromya and Cuspidaria owing to the mass of chitinous fragments and sometimes sand grains which filled the lumen. Occasionally, as shown in text-fig. 3, whole Crustacea were found in the stomach. The crushed-up fragments must either be pushed into the wide ciliated ducts of the digestive diverticula (fig. 7) or into the opening of the mid-gut. It is necessary that particles having food value should be passed into the former opening, for in the digestive diverticula alone can they be digested, whereas the useless fragments of chitin, sand, and the like will need to be passed into the mid-gut. In the stomach of the ciliary feeding Lamellibranchs there is a highly efficient sorting mechanism (see NELSON (1918), YONGE (1923, 1926B)), but in the stomach of the Septibranchs there is no such mechanism, and it is not easy to see how such a separation takes place and exactly how food is separated from fæcal matter. Within the tubules of the digestive diverticula it is quite possible that, as in other Lamellibranchs, a circulation is maintained by the action of long, retractile cilia which cannot be distinguished after fixation and may be withdrawn when fresh material is pressed out under a coverslip for examination. The presence of these cilia is rendered the more probable owing to the lack of a muscular network round the tubules, such as is found in the Crustacea (see YONGE (1924) for details and literature), and serves, by its alternate contractions and relaxations, to produce a circulation through the tubules of the " hepatopancreas."

Material is probably passed through the short mid-gut chiefly by ciliary action, for there is very little muscle and cilia are abundant (see fig. 8) ; the same is probably true for the rectum, though the more powerful encircling muscles in this region may aid in defæcation. Both of these regions of the gut, therefore, possess a similar function, as well as a similar structure, to that found in the other Lamellibranchs. The fæces are discharged into the posterior region of the supra-septal cavity and will be quickly ejected through the exhalant siphon.

5. THE NATURE OF THE FOOD.

Alone amongst the Lamellibranchia, the Septibranchia are carnivorous. PELSENEER (1891) originally came to this conclusion, stating (p. 219) that " *Poromya* est carnivore ; la longueur de l'ouverture palléale antérieure, la largeur de la bouche et de l'œsophage, et la brieveté de l'intestin s'accordent avec ce régime." Later (p. 224) he writes, " *Cuspidaria* est franchement *carnivore*. Dans l'estomac de *C. rostrata*, j'ai trouvé seulement un animal d'aspect déjà un peu défiguré, mais oculé et à revêtement de spicules. C'est là, avec *Poromya*, une exception parmi les Lamellibranches ; ce régime s'explique par l'habitat de ces deux genres dans des eaux profondes où ne s'étend pas la vie végétale. Les mouvements du septum musculaire aident probablement à attirer la proie *morte* dans le manteau (qui est assex ouvert), et la largeur de l'œsophage en facilite l'ingestion."

PLATE found the remains of Copepods and Annelids in the stomach of *C. obesa*, but continues by stating " Ich . . . glaube aber nicht, dass die Cuspidarien sich hinsichtlich der Ernährung irgendwie von den übrigen Muscheln, die kurz als Planktonfresser bezeichnet werden können, unterscheiden." Neither the extent of PLATE's investigations (sections through a single specimen of *C. obesa*) nor his knowledge of the feeding of the Cuspidariidæ are of sufficient significance for much weight to be attached to the above statement.

PELSENEER (1911) in his account of the Cetoconcha (Silenia) in the " Siboga " collections —the only complete specimens of this rare genus as yet examined—states (p. 79) that the stomach contains " des débris de Crustacés " adding that Cetoconcha is thus, like the other Septibranchs, a carnivore.

My own investigations bear out fully PELSENEER's conclusions. The stomach contents of two living specimens of *C. cuspidata* were examined at Kristineberg. One consisted of a Crustacean (probably, in the opinion of Dr. M. V. LEBOUR, an early stage of a parasitic Copepod) in almost perfect condition, 2·2 mm. long and with a carapace 1 mm. wide, and also of the empty shell of an Ostracod 1 mm. long and 0·36 mm. broad. The other consisted chiefly of the remains of a Crustacean embedded in a mass of sand grains, the whole measuring some 0·9 mm. in length and 0·45 mm. in breadth. In neither stomach was there the slightest indication of that suspension of fine particles and plankton which invariably constitute the stomach contents of the ciliary feeding Lamellibranchs (see HUNT (1925) and SAVAGE (1925) for accounts of the stomach contents of *Pecten opercularis* and *Ostrea edulis* respectively).

The manner in which the sand grains were embedded in the food indicates the power of the gizzard and also suggests that the presence of sand grains may assist in the breaking up of the food. A similar suggestion has been made in the case of the ciliary feeding Lamellibranchs, which take in sand grains, but the almost complete absence of muscle in the gut, and the high development of the ciliary sorting mechanism in the stomach, of these animals provide conclusive evidence against this theory. The welding together of the food and the sand grains *may* be assisted by the substance of the style (for there are no mucous glands in the œsophagus or stomach)—indeed, in view of the almost total absence of finely divided or starchy foods, this appears to be the only function which the style can perform.

In Poromya also, as shown in text-fig. 3, Crustacea are taken whole into the stomach. In sections of both Poromya and the three species of Cuspidaria, the stomach was frequently found packed with fragments of animals, usually Crustacea, while the midgut contained fragments of chitin, spines, limbs, etc., all clearly of either Crustacean or Annelid origin. There was never any evidence of the presence of vegetable matter or fine plankton organisms in any part of the alimentary canal.

To what extent the Septibranchs depend on living or dead prey must remain uncertain. PELSENEER, as quoted above, suggests that the latter form the principal food, and, in view of the sluggish habits of the Septibranchs, this is quite possible. An active animal could doubtless easily escape them, especially since the Septibranchs have no means of actively seizing their prey, unless it chanced to swim too near to the aperture of the inhalant siphon and so was drawn in by the sudden and unexpected current. For the most part we can imagine the Septibranchs moving about slowly through the mud and sucking in the small dead or dying animals which they encounter. In deeper waters they will not have the opportunity, and neither there nor in shallower waters the power, of swallowing the diatoms, peridinians and other fine phytoplankton organisms which form the food of the great majority of the Lamellibranchs.

6. ASSIMILATION.

A number of feeding experiments were carried out, specimens of Cuspidaria being placed in water containing, in suspension, iron saccharate (some of which passes into colloidal solution), Indian ink or the coagulated blood of various fish. Poromya was fed directly with pieces of the coagulated blood of Myxine and with pieces of the gonad of Pecten, a second specimen being placed in a suspension of iron saccharate in sea water. After suitable periods the animals were fixed in appropriate ways.

After feeding *C. obesa* with iron saccharate and treating in the usual manner (for details see YONGE (1926A)) after periods of 6, 9 and 12 hours and one day, and subsequent sectioning, iron was found to be present in the mantle cavity, where it was attached to all the ciliated areas, especially the foot and the margins of the mantle, *i.e.*, clearly in process of being removed from the mantle cavity. It was also present in the lumen of the stomach, the mid-gut and the rectum, but it was never found in the epithelial cells of these regions. It was absorbed solely by the cells lining the tubules of the digestive diverticula, in the manner shown in fig. 12, which represents the condition found subsequent to feeding for 6 hours. The iron saccharate is taken into large vacuoles (*f.*) within the cells and never appears in a diffuse or finely granular condition. Precisely the same state of affairs was found in Nucula, Mya, Teredo (YONGE (1926A)) and in Ostrea (YONGE (1926B)), and, as was pointed out in the former paper, there is reason to suppose that this method of ingestion in large vacuoles is an indication of the presence of *intracellular* digestion. Iron saccharate is absorbed in a diffuse or finely granular condition in animals—Annelida or Arthropoda, for example—in which digestion is exclusively *extracellular*.

The same conditions were found in Poromya, an animal fixed 9 hours after it had been placed in a suspension of iron saccharate showing the presence of iron lying on the cilia, on the mantle edges, on the foot, on the palps, and passing through the branchial sieves into the supra-septal cavity (evidence that these cilia serve the same function as those in Cuspidaria). It was also found free in the lumen of the stomach and of the gut, but it was absorbed *exclusively* in the cells of the tubules of the digestive diverticula, and there only in large vacuoles.

Specimens of *C. obesa* which had been placed in a suspension of Indian ink and later fixed in Bouin, showed, in sections, the presence of small quantities of Indian ink lying on the cilia in the mantle cavity, and also being passed into the supra-septal cavity by way of the pores. A few particles were found in the stomach lying against the cuticle, but none in the digestive diverticula.

Previous feeding experiments using the blood corpuscles of fish (YONGE (1926A, 1926B)) have shown that these are taken in freely by Lamellibranchs and are ingested. With the exception of Teredo, however, in all the Lamellibranchs studied they were ingested by the phagocytes which abound in the epithelium, the surrounding tissue and the lumen of the gut; especially were they so ingested in the stomach, the ducts of the digestive diverticula and the mid-gut. They were seized while still in the lumen by these phagocytes, which ingested them and then carried them through the epithelium and into the connective tissue. Within the phagocytes they are slowly digested. Only in the case of Teredo, where, as we have seen, the ducts of the digestive diverticula are exceptionally short and wide, did the blood corpuscles succeed in passing into the tubules of the digestive diverticula, where they are ingested by the cells.

In the Septibranchs, histological examination revealed the almost complete absence of these wandering phagocytic cells, and the fate of the coagulated blood corpuscles with which they were fed was, therefore, of the greatest interest. Specimens of all three species of Cuspidaria were treated in this manner. *C. obesa* removed and fixed in Bouin after 12 hours of such feeding showed the presence, after sectioning and staining with iron hæmatoxylin and acid fuchsin, of blood corpuscles ingested in the cells of the tubules of the digestive diverticula and in no other region. The same conditions were found in *C. rostrata* after similar treatment. In both of these experiments the blood of cod was used.

Fig. 13 shows the appearance in cross-section of a single tubule from the digestive diverticula of a *C. cuspidata* which had been in a suspension in sea water of the coagulated blood of a wrasse for 10 hours. The animal was fixed in Bouin and the section figured was stained with Mann's methyl-blue eosin combination. The effect is very striking, the ingested blood corpuscles staining a bright red while the cytoplasm colours blue; the nuclei (*n.t.*) are blue except for the prominent nucleoli, which stain red. Great numbers of the blood corpuscles are ingested, the great majority (*b.c.i.*) having already been carried towards the base of the cells; one, however, remains free in the lumen (*b.c.l.*) while several others are in process of ingestion (*b.c.p.*), apparently sinking into the protoplasm of the cells rather than being actively enclosed by it. Ingestion takes place in the older, vacuolated cells (*o.c.*) and not in the crypts of young, darkly staining cells (*cp.*). In many cases the ingested blood corpuscles can be seen lying within clearly defined vacuoles. Although some of the ingested corpuscles lay against the basement membrane (*b.m.*) of the tubules, in none of the sections was there any evidence of their being carried away by wandering phagocytic cells, as was observed in Teredo (YONGE (1926A)). Perhaps this occurs later in digestion, but lack of material and the danger of the animals dying if they were left for too long a period after feeding, prevented any more prolonged feeding experiments from being undertaken.

Blood corpuscles were found in small numbers in the lumina of different regions of the gut, but *never* ingested in phagocytes.

Similar results were obtained in Poromya, blood corpuscles from the blood of Myxine being ingested exclusively in the tubules of the digestive diverticula. In this case, moreover, swallowed blood corpuscles were obtained from the stomach 4 hours after feeding, as a result of antiperistaltic regurgitations from the stomach. They were examined and found to be undamaged—showing the lack of proteases and lipases in the stomach—and were in no case being ingested by phagocytes, as was found to occur in the stomach lumen of *Ostrea edulis* 3 hours after the beginning of feeding (YONGE (1926B)). There were no phagocytes in the regurgitated fluid.

It will be observed that, while matter in colloidal solution, such as iron saccharate, or in coagulated masses, such as blood, is taken within the alimentary canal, the finely divided particles of Indian ink, or of iron saccharate in suspension, though they are drawn into the mantle cavity by the action of the septum, are almost entirely removed from it by the cleansing cilia and very little enters the gut.

As a result of these feeding experiments—though it is to be regretted that more could not be carried out—it can be stated definitely that the only absorptive surface in the gut of the Septibranchs, as in the other Lamellibranchs, is provided by the tubules of the digestive diverticula. There both soluble matter, such as iron saccharate, is absorbed, and comparatively large particles, like blood corpuscles, are ingested, the latter being, presumably, digested intracellularly. In the ciliary feeding Lamellibranchs this localisation of the absorptive surface is compensated for by the presence of the phagocytes in the lumen and epithelium of all regions of the gut, but this is not the case in the Septibranchs.

The reason why such comparatively large particles as blood corpuscles pass into the digestive diverticula of the Septibranchs but not into those of the other Lamellibranchs (with the exception of Teredo) is clearly due to the absence of phagocytes in the gut and in the ducts of the diverticula, which could ingest them prior to their entrance into the tubules, and to the exceptionally short and wide ducts which lead from the stomach into the digestive diverticula.

As is well known, the tissues of the Lamellibranchs are normally exceptionally rich in glycogen, a fact which has been recorded by many investigators (see especially RUSSELL (1923)), and there is no doubt as to the primary importance of this reserve food substance in the metabolism of these animals. In previous work on Ostrea (1926B) attention was drawn to this fact and to the striking degree to which the digestive processes are specialised for dealing with carbohydrate food. In the Septibranchs, however, the food is not predominantly carbohydrate ; on the contrary, it must be largely protein, and the special digestive mechanism for dealing with carbohydrates provided in the style is much reduced. It would, therefore, appear probable that glycogen is not stored to any great extent in the Septibranchs. In order to obtain some evidence on this point, one freshly caught specimen of *C. obesa* was fixed in Carnoy's fluid and sections prepared which were treated with the Langhan's iodine method. No indication of the presence of glycogen was found in any of the sections. Thus we have evidence of an alteration in the metabolism of the Septibranchs consequent on their assumption of a carnivorous diet.

7. GENERAL DISCUSSION OF RESULTS.

This research is particularly interesting in its bearings on the general problems of feeding and digestion in the Lamellibranchia. This class of the Mollusca possesses, on the gills and the palps and in the stomach, the most elaborate and most efficient ciliary feeding mechanism found in the entire animal kingdom. Associated with this are the many peculiarities, both morphological and physiological, of the gut, to which reference was made in the introductory section. It has been shown, I think conclusively, in the foregoing account that the Septibranchs are carnivorous and that feeding mechanisms, an alimentary system and digestive processes, have been evolved for dealing with large food masses, thus providing a striking example of the evolution of function.

In place of the gills has evolved the muscular septum. This performs the same function in maintaining a circulation of water through the mantle cavity, being assisted in this by the vestiges of the gill ciliation in the lateral cilia, on the filaments of the branchial sieve in Poromya, and in the cilia around the pores in Cuspidaria. But it also, by its sudden movements, draws in large masses of food, which the continuous, but slowly moving, current created by the gill cilia could never do. The large food masses introduced into the infra-septal cavity in this manner are pushed into the mouth by the small, but very muscular, labial palps. The exceptionally highly developed ciliary mechanism on the ridged palps of the other Lamellibranchs, which acts by rigorously sorting the particles passed on to it from the gills, rejecting the larger particles and passing the smaller ones into the mouth (for details see WALLENGREN (1905) and YONGE (1923, 1926B)), has been lost, the few remaining cilia being concerned exclusively with the rejection of fine particles which might impede the working of the gut. That this ciliation is of importance is shown by the fact that these ciliated tracts are retained, even though the palps, as in the case of the posterior pair in *C. obesa*, have been lost. A similar rôle is played by the remaining cilia in the mantle cavity, on the foot and on the ventral margins of the mantle. The survival of these cilia and no others is clearly correlated with the danger which both the Septibranchs and the other Lamellibranchs face in common, that of being silted up by fine particles of mud or sand. Mucous glands, as universal as cilia in the other Lamellibranchs, are confined to the ciliated regions in the Septibranchs.

The foregut of the Septibranchs is *totally unlike* that of the Lamellibranchs which feed on fine particles. Although the œsophagus possesses cilia, these are clearly of little importance, food being carried along by the peristaltic movements of the thick surrounding muscle, so conspicuously absent in the other Lamellibranchs. The stomach is even more highly specialised and acts as a crushing gizzard, for which function its ridged walls, cuticular lining, surrounding muscles and freedom from the surrounding tissues, all combine to fit it—clearly a very different structure from the complex ciliated organ of the other Lamellibranchs, which is almost devoid of muscle.

The crystalline style in the Septibranchs has no longer the great importance that it possesses in the other Lamellibranchs. In the latter, by its rotation it assists in the movement of the fine particles through the gut, and by the dissolution of the head in the stomach it sets free carbohydate-splitting enzymes (NELSON (1918, 1925)), and also maintains the fluid in the stomach near the optimum hydrogen-ion concentration for the action of the enzymes (YONGE (1925, 1926B)). In the Septibranchs, owing to the contractions of the gizzard-like stomach, the style can no longer project freely across the stomach and bear against the gastric shield on the opposite wall; on the contrary, it barely projects out of the short style-sac in which it is secreted; it would clearly be worn away by the contraction of the stomach were it to project any farther. The cuticular lining of the stomach probably represents an extension over the entire stomach of the gastric shield, which covers only a small area in the stomachs of the other Lamellibranchs.

The shortness and exceptional width of the ducts leading into the tubules of the digestive diverticula are correlated, no doubt, with the comparatively large fragments forced into them by the squeezing action of the stomach. The wide lumina of the tubules, especially in the neighbourhood of the ducts, are to be attributed to the same cause.

The only regions of the gut which perform essentially the same function as in the other Lamellibranchs, the mid-gut and the rectum, show no structural modifications.

The absence of the wandering phagocytes which form so conspicuous a feature in the gut of the ciliary feeding Lamellibranchs is very striking, and there can be no doubt that these have developed owing to the necessity of dealing with food particles too large to enter the ducts of the digestive diverticula, and which cannot, owing to their nature, be digested by the amylase or the glycogenase from the style, which represent the only extracellular enzymes present in the gut of the Lamellibranchs. In the Septibranchs, where there are no particles of this size to be dealt with (the blood corpuscles were swallowed in the form of coagulated masses, and not individually), and, moreover, where the epithelium of the stomach is covered with a thick layer of cuticle, there is clearly no scope for the action of these phagocytes. Furthermore, the widely open ducts of the digestive diverticula allow food particles of the order of magnitude normally seized by phagocytes (*e.g.*, red blood corpuscles) to enter the tubules where they are ingested.

There is no evidence of any elaboration of extracellular enzymes other than those in the style, and these, on account of the carnivorous habit, must be of very little use to the animal. Indeed, there is a close correlation, borne out still further by the conditions found in the Septibranchs, between the degree of development of the style and a finely divided and largely vegetable food. Thus in the Gastropods the style is best developed in such animals as Crepidula (MACKINTOSH (1925)), which feed by ciliary mechanisms (ORTON (1912)), and is lost in the carnivorous species, to be regained in the Thecosomatous Pteropods which, descending from carnivorous ancestors, have taken to a pelagic life and developed ciliary feeding mechanisms (YONGE (1926C)).

The tubules of the digestive diverticula, like those of the other Lamellibranchs (YONGE (1926A)), show no histological evidence of secretion, nor did the examination of blood corpuscles which had been in the stomach for four hours indicate any action by digestive enzymes. It appears, therefore, that, though capable of modifying their feeding mechanisms and the structure of their alimentary canal, *the Septibranchs have been incapable of modifying their digestive processes*. The Lamellibranchs have retained the power of intracellular digestion to a far greater extent than the other large groups of the Mollusca, which is clearly correlated with the fact that in the Lamellibranchs alone are fulfilled the two essential conditions of intracellular digestion, namely, the maximum of ingesting surface (in the ramifications of the tubules of the digestive diverticula) and the presentation to this of fine particles which can be directly ingested, the latter being ensured by the rigorous sorting action of the ciliary mechanisms on the gills and the palps and in the stomach. In the Septibranchs the second of these conditions is absent, and it is only by the crude method of breaking up the large prey in the stomach that small particles for passage into the diverticula can be obtained. In no other metazoan carnivore, with the exception of certain of the Turbellarians (see WESTBLAD (1923), WILLIER, etc. (1925)), where the gut cells are amœboid and unite to form syncytia during absorption, when they take in water and swell out so that they surround the soft food which they ingest intracellularly, is there this complete lack of a preliminary protein digestion. In the Cœlenterates, though digestion is largely intracellular, there is invariably a preliminary breaking down of the prey by means of an extracellular protease. In the Septibranchs, there are no modifications other than the crushing action of the stomach, and they must still rely upon exactly the same methods of digestion (less the digestive action of the phagocytes) which have served the Lamellibranchs, which possess highly developed ciliary feeding mechanisms. It seems probable that they must, at least, have developed a more powerful intracellular protease in the digestive diverticula than is found, for example, in Ostrea, in which, as in probably all similar Lamellibranchs, digestion is primarily concerned with carbohydrates.

The Septibranchs are a small group. It seems probable that this is due to their failure to develop methods of digestion suitable to a carnivore, and to the comparative failure of their extremely interesting feeding mechanism. They have achieved the remarkable feat of transforming a feeding mechanism and correlated alimentary system and digestive processes, which together represent the highest developments of their kind in the animal kingdom for dealing with finely divided food, largely of a vegetable nature, into mechanisms for dealing with large food masses of animal origin. It is not surprising, therefore, that the result has been largely in the nature of a makeshift.

The question of the origin of the Septibranchs is one of the greatest interest. It follows from the preceding statements that they cannot have evolved in the face of keen competition. The evidence we possess points to their having evolved in deep water. All the known Septibranchs are marine and inhabit considerable depths, the Cetoconchidæ, in particular, being abyssal animals. The two specimens of *Cetoconcha* (*Silenia*) *sarsi* taken by the "Challenger" came from depths of 1,950 and 2,650 fathoms, and the single specimen of *Poromya* (*Verticordia*) *tornata* from 1,850 fathoms. It seems not improbable that in the greatest depths the ciliary feeding Lamellibranchs cannot exist owing to the lack of phytoplankton. Animals which happened to pass into these deep waters would die, unless it chanced that feeding mechanisms capable of dealing with comparatively large animal prey, either living or dead, were evolved. In the case of the Septibranchs this happened, and, as a result, they spread downwards into the abyssal regions where the sparseness of the animal population and the consequent lack of serious competition allowed them to survive in spite of the inadequate nature of their organs of feeding and digestion. As they became more specialised and so more capable of surviving the keen competition for food which exists in the shallower seas, they worked their way back into shallower water. It is noteworthy that the most highly specialised of the three families of the Septibranchia, the Cuspidariidæ, are found in the shallowest waters. The three specimens of *C. cuspidata* obtained in the Gullmars Fjord were all taken in depths of about 50 metres along with many other Lamellibranchs.

The supposition that the Septibranchs are a comparatively recent group is borne out by the paleontological evidence; thus in ZITTEL's text-book (1913) it is stated that the Cuspidariidæ range back to the Jurassic and the Poromyacidæ only to the Cretaceous. The smallness of the group at the present time points to their comparative failure.

The origin of the septum has been a matter of dispute, DALL (1888, 1889B, 1894, 1895) maintaining that it is pallial in origin or else an anterior prolongation of the septum dividing the inhalant and exhalant siphons, while PELSENEER (1888A, 1889, 1891, 1911) considers it to be branchial. In support of this view he states that the nervous supply comes from the branchial nerve and not from the siphonal or pallial nerve, and concludes that the septum represents the inner demibranch only. PELSENEER has received the support of GROBBEN, who regards the anterior part of the septum, at least, as of branchial origin; but PLATE agrees with DALL, since he found that the septum of *C. obesa* was innervated by a nerve leaving the cerebral ganglion side by side with the visceral commissure and not by a branchial branch of the visceral nerve. PELSENEER (1911) thinks he is mistaken in this. RIDEWOOD does not agree with DALL that the muscularity of the septum is evidence against its being of branchial origin, but finds it difficult to understand how it could have developed such important attachments to the shell. I do not intend to engage in this controversy, which is not likely to be definitely settled until the embryology of the Septibranchs has been studied. There do, however, appear to be substantial reasons for agreeing with PELSENEER rather than with DALL; the septum certainly performs the same function in creating a current of water through the mantle cavity as do the gills—a fact which DALL failed to realise—and it is difficult to see how it could have evolved except as a direct development from the gills.

The validity of the separate order Septibranchia formed by PELSENEER has been questioned by DALL, GROBBEN and RIDEWOOD, the last-named summarising the conflicting evidence and adding (p. 183), " The reduction of the branchial organs is certainly very remarkable, but there are greater differences between the three genera included in the Septibranchia than between a form like *Poromya malespinæ*, on the one hand, and *Verticordia* on the other. The conditions found in *Poromya*, *Cetoconcha*, and *Cuspidaria* may be considered to have evolved independently, although following the same general trend. The relations between these forms and the Verticordiidæ being obvious, it is proposed, in the absence of more accurate information as to general anatomy, to place the three families, Poromyidæ, Cetoconchidæ and Cuspidariidæ after the Verticordiidæ, in a terminal sub-order (Poromyacea) of the Synaptorhabda."

As PELSENEER (1911) points out, the taxonomic divisions we establish are of relative value only, since continuity is the law of nature, and in his opinion the establishment of the order Septibranchia is justified, for they represent, " le stade final d'une longue évolution dans un sens déterminé."

On the other hand, the very different structure of the septum in Poromya and Cuspidaria, particularly the development of the striated musculature in the latter, does rather support the opinion of RIDEWOOD that they may have evolved independently and that the structural resemblances may therefore be due to convergence, the result of similar habitats and the necessity for dealing with similar food. Like the Teredinidæ, the Septibranchs appear to be highly specialised animals, adapted to peculiar conditions, rather than the apex of the evolution of the Lamellibranchs. But we need further evidence, especially embryological, before these questions can be satisfactorily answered. For the time being, however, the order Septibranchia may be conveniently employed to denote the three families (or two, if, as PELSENEER suggests, the Cetoconchidæ are to be included under the Poromyidæ) of carnivorous Lamellibranchs which draw in water and food by means of a muscular septum, and whose alimentary system has been greatly modified as a result of their change of habits and food.

8. SUMMARY.

1. Living and preserved specimens of the Septibranchs, *Cuspidaria rostrata*, *C. cuspidata*, and *C. obesa*, and *Poromya granulata*, have been studied for the purpose of investigating the structure and functions of the organs of feeding and digestion.

2. In Cuspidaria the septum is extremely thick, and is attached to the shell by large anterior and posterior septal muscles and by delicate lateral muscles the arrangement of which varies in the different species. The mass of the septum consists of longitudinal bundles of flat, striated, muscle fibres which cross over one another posterior to the foot. The lateral muscles are smooth and pass transversely across the dorsal surface of the septum. The septum is perforated by narrow, slit-like pores, either four or five according to the species, which have dorsally directed valves. They are bounded by a columnar epithelium which is ciliated in two regions, and are surrounded by a sphincter of plain muscle.

3. The septum of Poromya is more delicate. It is attached to the shell by a pair of anterior and a pair of posterior septal muscles, and is composed of plain muscle fibres. It is perforated by a pair of anterior, and a pair of posterior, branchial sieves. In *P. granulata* the former possess five and the latter six filaments. These resemble ordinary gill filaments, lateral, but not frontal, cilia being present in *P. granulata*; longitudinal muscles occur at their bases.

4. The palps are small in Cuspidaria, the posterior pair being absent in *C. obesa*, but are larger in Poromya. They are ciliated on their inner surfaces, are smooth and very muscular.

5. The mouth and the œsophagus are large, both are ciliated and surrounded by a thick layer of muscle.

6. The stomach is large and cylindrical, the walls are ridged and covered throughout

with a thick cuticle which probably represents an extension of the gastric shield. It is surrounded by a thick layer of muscle and is free from the surrounding tissues.

7. The ciliated ducts of the digestive diverticula are exceptionally short and wide. The tubules have the same structure as in the digestive diverticula of the other Lamellibranchs. The style-sac is short and contains a small oval style which does not project far into the stomach.

8. The short mid-gut is ciliated and possesses little muscle. The rectum is narrow, ciliated, contains mucous glands and is surrounded by muscle. The anus opens at the base of the exhalant siphon.

9. There is an almost complete absence of the wandering phagocytic cells found in the gut of the ciliary feeding Lamellibranchs.

10. Both Cuspidaria and Poromya live in mud into which they burrow.

11. The septum in Cuspidaria makes regular movements, first descending and then drawing sharply upwards. Between movements it is in its shortest condition. As a result of the movements, water and food are drawn into the mantle cavity. In Poromya the septum appears to act in a similar manner, though less frequently.

12. The cilia on the septal pores and branchial sieves and in the supra-septal cavity serve to maintain a slow current of water through the mantle cavity when the septum is at rest. The cilia in the infra-septal cavity—on the palps, the foot and on the mantle edges—remove fine particles from the mantle cavity.

13. Food is pushed into the mouth by the muscular palps, being then passed through the œsophagus, largely by peristalsis, and crushed up in the gizzard-like stomach, the fragments being passed either into the ducts of the digestive diverticula or into the mid-gut, through which they are passed by ciliary action.

14. The Septibranchs are carnivorous, feeding on small animals either dead or alive, usually Crustacea or Annelida.

15. The tubules of the digestive diverticula provide the only absorbing surface in the gut, they are organs of absorption and intracellular digestion. There is no evidence that they secrete.

16. Fine particles, such as Indian ink, if taken into the mantle cavity are almost all removed by the cleansing action of the cilia and few enter the gut.

17. There is no evidence of any storage of glycogen in *C. obesa*.

18. The Septibranchs have converted feeding mechanisms, and an alimentary system specialised for dealing with fine particles, into an apparatus for the disposal of large food masses.

19. The crystalline style in the Septibranchs is small and, since in the other Lamellibranchs it is concerned essentially with the movement through the gut of fine particles and with the digestion of carbohydrates, is probably vestigial.

20. The absence of wandering phagocytic cells is to be attributed to the absence in the food of particles small enough for them to ingest, and also to the ease with which particles can enter the digestive diverticula.

21. The digestive processes do not otherwise appear to differ from those of the remaining Lamellibranchs. Although carnivores, the Septibranchs have not developed a preliminary extracellular digestion of protein.

22. The Septibranchs are a small and unsuccessful group, which probably evolved in deep water where the majority of them still live. The origin of the septum is disputed, but the balance of the evidence is in favour of its being branchial.

23. The order Septibranchia, established by PELSENEER, is probably valid, though Cuspidaria and Poromya may resemble each other as the result of convergence and not of a common origin.

24. The conditions found in the carnivorous Septibranchs provide valuable confirmatory evidence that the peculiar nature of the gut and of the digestive processes in the other Lamellibranchs is due to the finely divided food collected by their elaborate ciliary feeding mechanisms.

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10. Description of Plates.

List of Reference Letters.

a. = clear area in which lies nucleus of striated fibre.
a.p. = anterior palp.
b.c.i. = ingested blood corpuscles.
b.c.l. = blood corpuscle in lumen.
b.c.p. = blood corpuscle in process of being ingested.
b.g. = beginning of mid-gut.
b.m. = basement membrane.
c.g. = connecting groove between style-sac and mid-gut.
c.m. = circular muscle.
c.s. = crystalline style.
ch. = "chitinous" supporting rod in filament of branchial sieve.
cp. = crypts of young cells in tubules of digestive diverticula.
cu. = cuticle.
d. = duct of digestive diverticula.
d.c. = dorsal ciliated tract round septal pore.
d.e. = dorsal epithelium of septum.
e.s. = epithelium of style-sac.
f. = iron in vacuoles in tubule cells.
g. = mid-gut.
I. = infra-septal cavity.

i.e. = epithelium of inner surface of palps.
l. = wide lumina of digestive diverticula.
l.c. = lateral cilia.
l.m. = longitudinal muscles.
l.r. = longitudinal ridges in stomach.
l.s.m. = lateral septal muscles.
m. = mouth.
m.g. = mucous gland.
mu. = muscle strands.
n.b.c. = nucleus of ingested blood corpuscle.
n.s. = nucleus of striated fibre.
n.t. = nucleus of tubule cell.
o. = œsophagus.
o.c. = older, vacuolated cells of tubules.
o.e. = epithelium of outer surface of palps.
p.p. = posterior palp.
r. = rectum.
r.m. = radiating muscle fibres.
r.o. = longitudinal ridges in œsophagus.
S. = supra-septal cavity.
s.m. = septal muscle.
s.s. = style-sac.
sp. = sphincter of plain muscle round septal pore.
sr. = striation in muscle fibre.
st. = stomach.
t. = tubule of digestive diverticula.
ty. = typhlosole.
v. = valve on dorsal side of septal pore.
v.c. = ventral ciliated tract round septal pore.
v.e. = ventral epithelium of septum.
va. = vacuole in tubule cell.
w.c. = wandering cell.
y.c. = young, darkly staining cells in mid-gut.

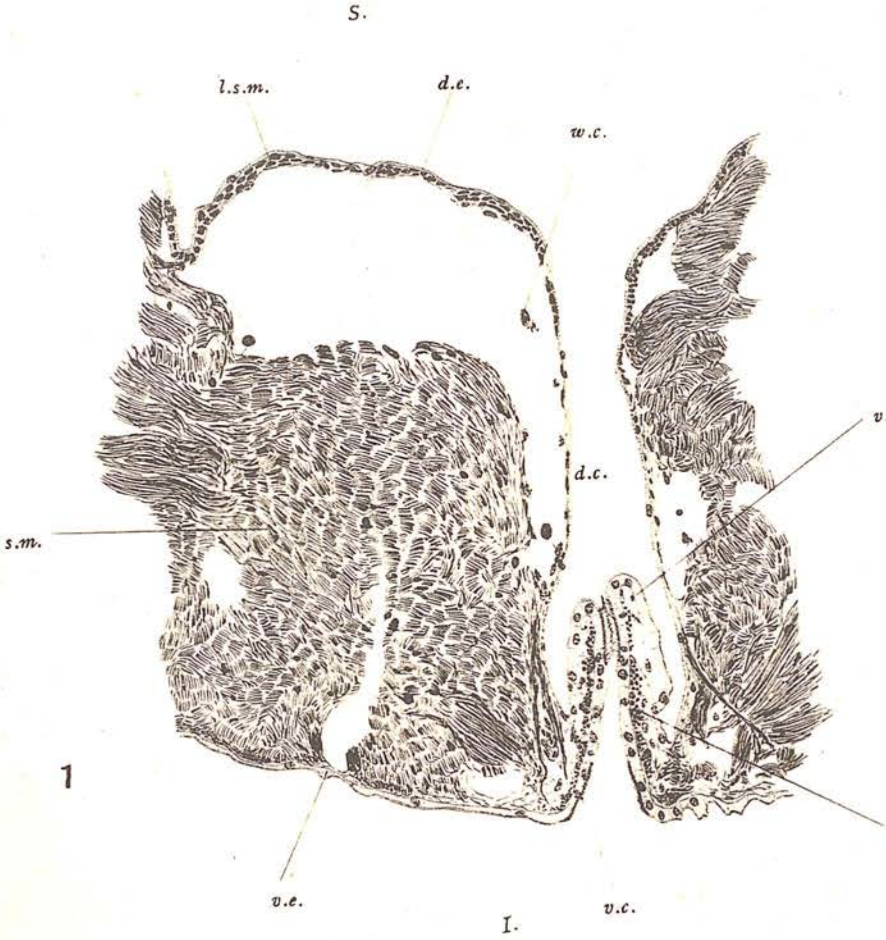
PLATE 12.

FIG. 1. *Cuspidaria rostrata.*—Longitudinal section through the septum cutting a septal pore transversely, Fixed Bouin, stained Delafield's hæmatoxylin and eosin. 6 μ × 200.

FIG. 2. *Cuspidaria rostrata.*—Horizontal section through the septum passing somewhat obliquely through a septal pore in the dorsal region. Fixed Bouin, stained iron hæmatoxylin and acid fuchsin. 6 μ × 200.

FIG. 3. *Cuspidaria rostrata.*—Portion of a teazed-out muscle fibre from the septum. Fixed alcohol. stained iron hæmatoxylin. × 666.

FIG. 4. *Cuspidaria rostrata.*—Transverse section through a posterior palp, about the middle. Fixed Bouin, stained Delafield's hæmatoxylin and eosin. 6 μ × 200.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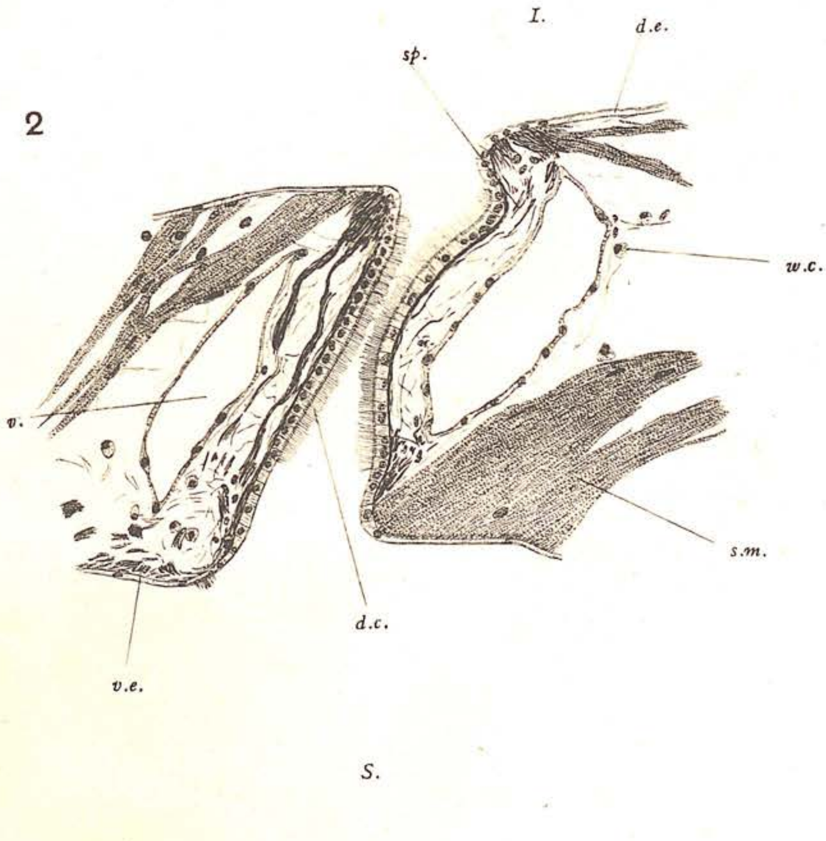
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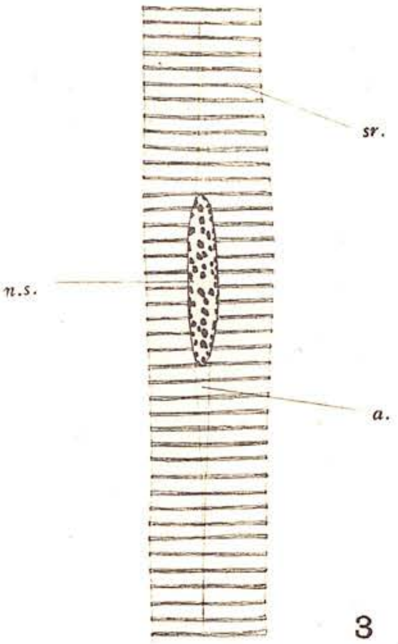
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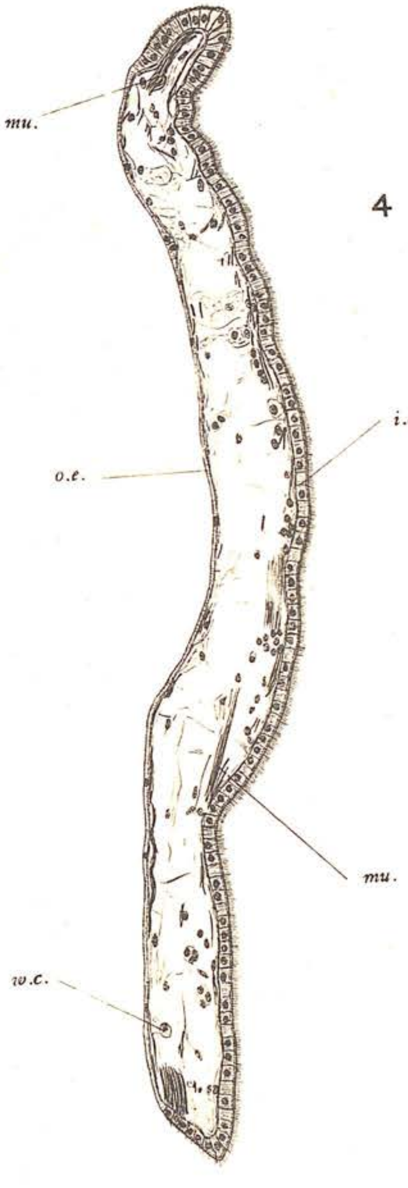
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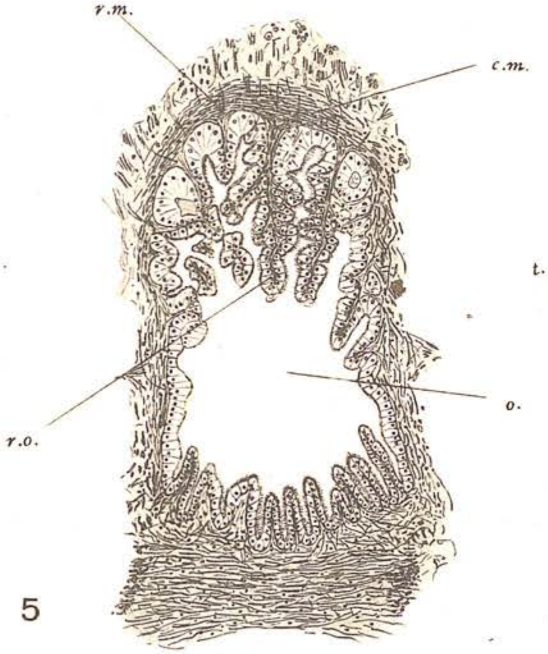
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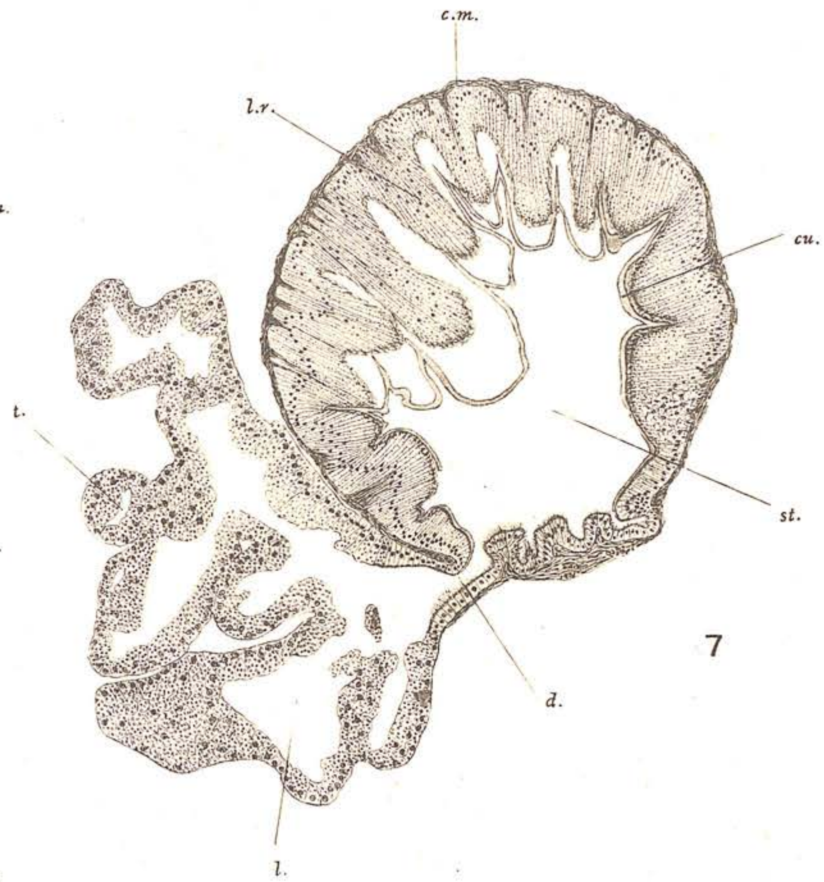
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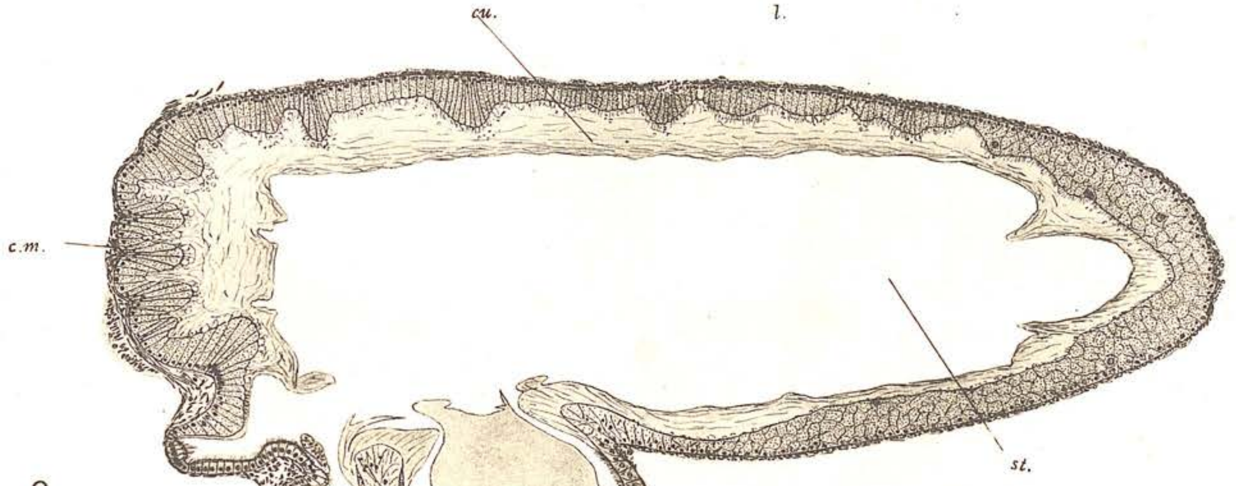
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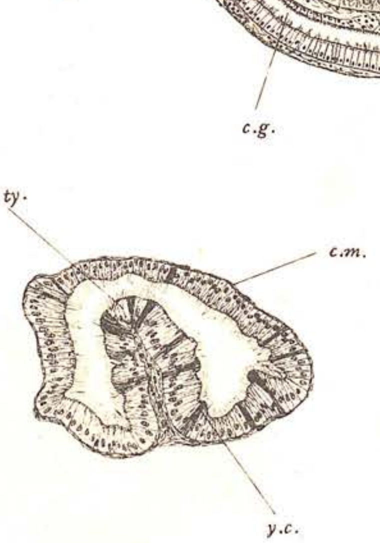
6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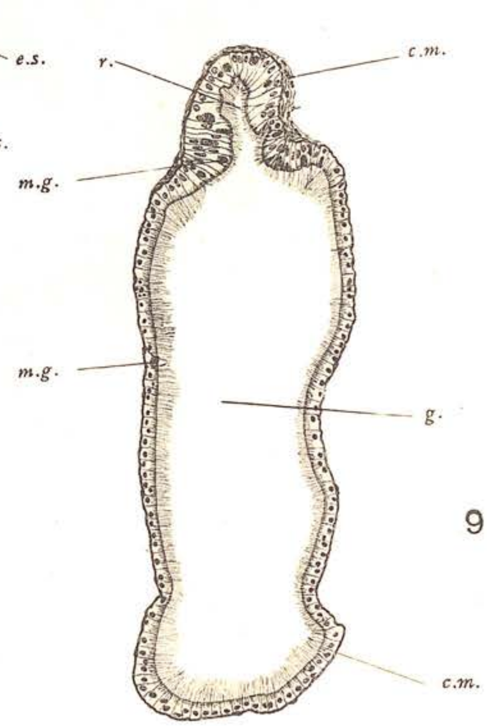
8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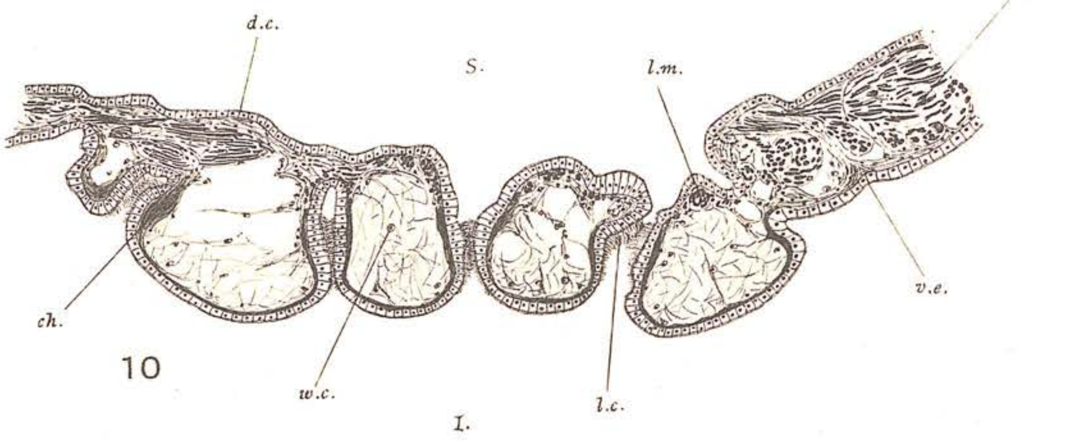
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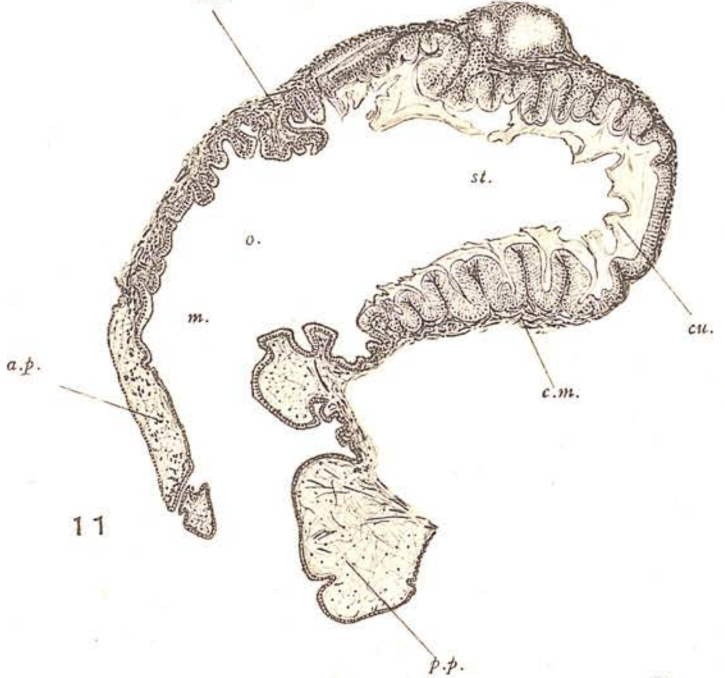
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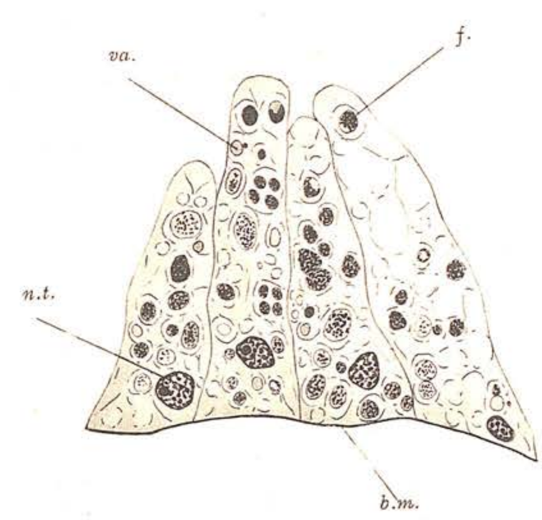
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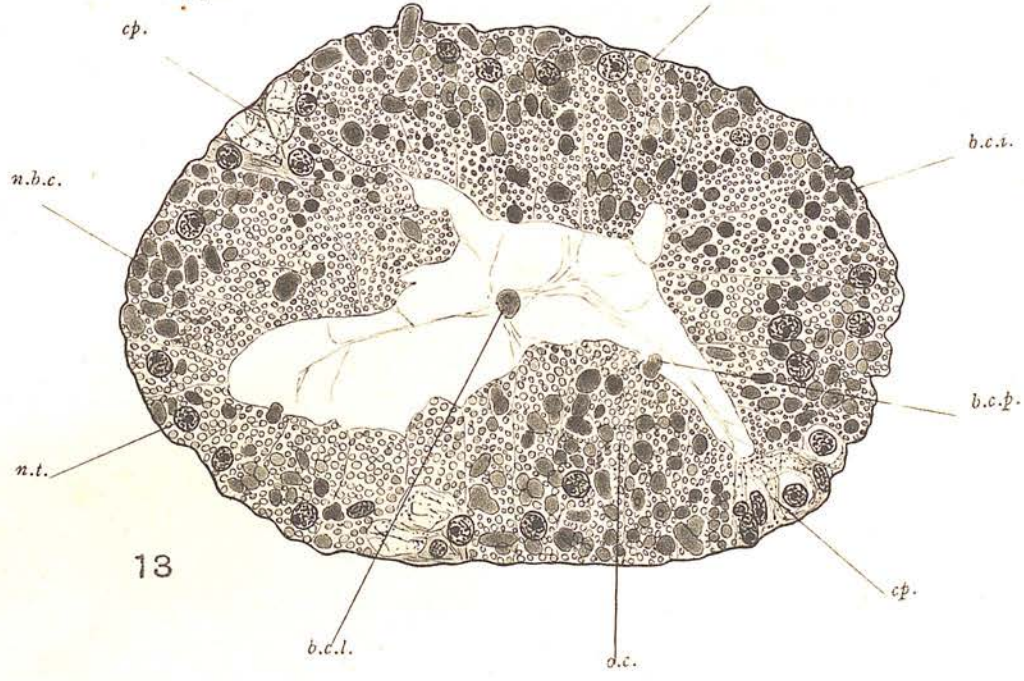
b.m.
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n.b.c.
b.c.p.
n.t.
cp.
b.c.l.
o.c.

13

PLATE 13.

FIG. 5. *Cuspidaria cuspidata.*—Transverse section through the œsophagus immediately anterior to the stomach. Fixed Bouin, stained iron hæmatoxylin and acid fuchsin. 6 μ × 76.

FIG. 6. *Cuspidaria rostrata.*—Longitudinal section through the stomach and style-sac, showing also the beginning of the mid-gut and the connecting groove between it and the style-sac. Fixed Bouin, stained Delafield's hæmatoxylin and eosin. 6 μ × 76.

FIG. 7.—*Cuspidaria cuspidata.*—Transverse section through the stomach passing through the opening of the anterior and smaller duct of the digestive diverticula. The shortness of the duct and the wide lumina of the tubules into which it opens are both shown. Fixed Bouin, stained iron hæmatoxylin and acid fuchsin. 6 μ × 76.

FIG. 8. *Cuspidaria cuspidata.*—Transverse section through the mid-gut immediately posterior to its separation from the style-sac, showing the presence of the typhlosole. Fixed Bouin, stained iron hæmatoxylin and acid fuchsin. 6 μ × 112.

FIG. 9. *Cuspidaria cuspidata.*—Transverse section through the mid-gut in the region of its junction with the rectum to which it is united dorsally. Fixed Bouin, stained Mann's methyl blue and eosin. 6 μ × 112.

PLATE 14.

FIG. 10. *Poromya granulata.*—Longitudinal section through the septum cutting one of the posterior branchial sieves at right angles. The filaments are shown in transverse section and their resemblance to the gill filaments of the other Lamellibranchs is shown. Fixed alcohol, stained Delafield's hæmatoxylin and eosin. 6 μ × 100.

FIG. 11. *Poromya granulata.*—Longitudinal section through the palps, mouth, œsophagus and stomach, showing their mutual relationships and the wide lumen of the œsophagus and stomach. Fixed Bouin, stained Mann's methyl blue and eosin. 6 μ × 34.

FIG. 12. *Cuspidaria obesa.*—Section through four cells from a tubule of the digestive diverticula fixed after 12 hours of feeding with a suspension of iron saccharate. Fixed equal parts Bouin and 5 per cent. ammonium sulphide in absolute alcohol, iron treated with the Prussian blue method, sections stained with alum carmine. 6 μ × 865.

FIG. 13. *Cuspidaria cuspidata.*—Transverse section through a single tubule of the digestive diverticula fixed after 10 hours of feeding with blood from a Wrasse. The structure of the tubule is shown, also the presence of blood corpuscles, free in the lumen, in process of ingestion and actually ingested within the cells. Fixed Bouin, stained Mann's methyl blue and eosin. 6 μ × 572.

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THE DIGESTIVE DIVERTICULA IN THE LAMELLIBRANCHS.

BY

C. M. YONGE, B.Sc., Ph.D.

[With Two Plates.]

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(MS. received February 8, 1926. Read March 8, 1926. Issued separately August 11, 1926.)

CONTENTS.

1. Introduction.

Because of the superficial resemblance of the digestive diverticula of the Lamellibranchs, and of many other Invertebrates, to the liver of the Vertebrates, and the discovery in them of glycogen by Bernard (1855), they became known as the "liver." Weber (1880) later introduced the name hepatopancreas as a result of his discovery of the secretory powers of the diverticula in the Crustacea. In spite of the fact that none of the constituents of bile has ever been discovered in the Invertebrates, and that the digestive diverticula are in no way analogous to the liver of the Vertebrates, as Jordan (1912) has shown in his review of the subject, the terms "liver" and "hepatopancreas," as well as the less questionable designation "digestive gland," are still generally used. Moreover, no attempt is made to distinguish between these organs in the different groups of Invertebrates although both their structure and function in, for example, the Lamellibranchs, Gastropods, Cephalopods, and Crustacea are totally different. In some cases they constitute a digestive gland; in others, including the Lamellibranchs, as I hope to show in this paper, their function is that of assimilation, and so they are most suitably designated digestive diverticula.

It is necessary, in order properly to determine the nature of any organ, to study both structure and physiology, since it is to the physiological assumptions of the morphologist and the morphological assumptions of the physiologist that the misconceptions of the past are due. In this research, therefore, I have not only examined the structure of the diverticula in a large number of species, but I have studied their physiology from as many aspects as possible, in the hope of determining definitely their nature.

This research was carried out at the Plymouth Laboratory during the winter of 1924–25, while I was holding a Carnegie Research Scholarship in Zoology of the University of Edinburgh. I wish to acknowledge my indebtedness to the British Association, the University of London, and the Royal Microscopical Society for granting me the use of their tables for various periods, to the Director and the Staff of the Laboratory for their kindness and help, and to Professor Ashworth for help in the preparation of this paper for publication.

---

* The Carnegie Trust for the Universities of Scotland has made a grant to the author towards the cost of the plates, which is gratefully acknowledged.

2. METHODS AND LIST OF SPECIES EXAMINED.

FRENZEL (1885, 1886, 1893) is the only investigator who has carried out a comparative study of the digestive diverticula in the Lamellibranchs, but, as he was unable in the majority of cases to fix his material satisfactorily, most of his observations were made on isolated cells from fresh material. Fixation is in some cases very difficult, and many fixatives had to be tried before satisfactory results were obtained. I have indicated, therefore, the fixative employed after the names of the 34 species examined in the list given below.

Sections were stained with Delafield's hæmatoxylin and erythrosin, or with iron hæmatoxylin, sometimes with acid fuchsin as counterstain.

The structure of the digestive diverticula has been examined in the following species:—

- Order PROTOBRANCHIA.
  - *Nucula nitida* (Bouin).
  - *Nucula radiata* (Bouin).
- Order FILIBRANCHIA.
  - *Anomia ephippium* (corr. sublimate in sea water).
  - *Arca tetragona* (corr. sublimate in sea water).
  - *Barbatia lactea* (corr. sublimate in sea water).
  - *Glycimeris glycimeris* (corr. sublimate in sea water).
  - *Mytilus edulis* (equal parts Bouin and absolute alcohol).
  - *Modiola modiolus* (equal parts Bouin and absolute alcohol).
  - *Modiolaria marmorata* (Bouin-Duboscq).
  - *Pecten maximus* (corr. sublimate in sea water).
  - *Pecten opercularis* (corr. sublimate in sea water).
- Order EULAMELLIBRANCHIA.
  - *Lima loscombi* (Bouin).
  - *Ostrea edulis* (Bouin).
  - *Astarte sulcata* (Bouin).
  - *Kellya suborbicularis* (corr. sublimate in sea water).
  - *Tellina crassa* (Bouin-Duboscq).
  - *Donax vittatus* (corr. sublimate in sea water).
  - *Spisula solida* (Bouin).
  - *Venus fasciata* (Bouin-Duboscq).
  - *Dosinia exoleta* (Bouin).
  - *Tapes pullastra* (corr. sublimate in sea water).
  - *Cardium edule* (equal parts Bouin and absolute alcohol).
  - *Cardium norvegicum* (20% formalin).
  - *Gari tellinella* (Bouin).
  - *Mya arenaria* (Bouin).
  - *Lutraria oblonga* (Bouin).
  - *Solecurtus antiquatus* (Bouin).
  - *Ensis siliqua* (Bouin).
  - *Saxicava rugosa* (Bouin).
  - *Gastrochæna dubia* (Bouin).
  - *Pholas dactylus* (corr. sublimate in sea-water).
  - *Pholadidea loscombiana* (Bouin-Duboscq).
  - *Xylophaga dorsalis* (Bouin-Duboscq).
  - *Teredo norvegica* (Bouin or Flemming).

I have been unable, unfortunately, to obtain good material of the Septibranchs in which, since alone amongst the Lamellibranchs they are carnivorous, different conditions may prevail. Owing to the kindness of Mr G. C. ROBSON, I was able to section a species of Cuspidaria from the British Museum, but, though the remainder of the alimentary canal was well preserved, the structure of the digestive diverticula could not be determined.

3. STRUCTURE.

The digestive diverticula form a darkly-coloured mass which surrounds the greater part of the stomach. They consist of blind tubules which unite with one another, and are in free communication with the stomach by way of ducts whose structure is distinct from that of the tubules.

The ducts are usually circular in cross section, although the outline of the lumen is undulating owing to variation in the height of the epithelium (see figs. 1 and 2). This epithelium resembles that of the stomach, of which it is a prolongation, and consists of tall, ciliated cells containing oval nuclei. It is surrounded by a thin layer of circular muscle. The protoplasm is not vacuolated, but in some species contains numerous highly refractile green, brown, or yellow granules near the free surface of the cells. This is particularly the case in Nucula, and I have also observed it in Arca, Glycimeris, Modiola, and Saxicava. The nature of these granules is not clear, but as these cells neither absorb nor secrete they are probably an excretion which accumulates in the same way as Marennin in green oysters. As in the gut, mucus cells may occur between the cells of the epithelium, and so may phagocytes, which are sometimes present in great numbers.

The junction between the epithelium of the ducts and that of the tubules may be sharply defined, as in Nucula and all the Eulamellibranchs examined, or may be gradual as in Mytilus (as described and figured by LIST (1902)) and the other Filibranchs examined, where the junctions in cross section often consist of two portions, the epithelium of the one being that typical of the ducts, while the other resembles that of the tubules.

The tubules are either round or oval in cross section (compare figs. 7 and 10), and are not surrounded by muscle, but at most by a few strands of connective tissue. They may be so numerous that they are packed tightly together with very little connective tissue between them, while in other species they may be spaced out with a corresponding increase in the amount of connective tissue, which may be "vesicular," as noted by MACMUNN (1900) in Ostrea, and is exceptionally well developed in Gastrochæna. In this tissue lie blood lacunæ and many wandering cells; strands of muscle are sometimes present, especially in Arca. The epithelium of the tubules is variable in height; the nuclei are very characteristic, being round, with a prominent nucleolus in the centre.

In sections, cilia can never be distinguished in the tubules, although in Nucula and all the Filibranchs examined the free edge of the cells is bounded by a fine cuticle (see figs. 4 and 6). This is particularly well marked in Glycimeris, where it has sometimes the appearance of very fine cilia. LIST has described and figured it in the Mytilidæ. I have never observed it in my sections of any of the Eulamellibranchs, while CARAZZI (1896, 1897) and VONK (1924) failed to find it in Ostrea, and GUTHEIL (1912) in Anodonta. In fresh material, on the other hand, FRENZEL (1886) states that the cells are covered with a "gleichmässig überziehenden Saum, welcher . . . einen niedrigen Deckel bildenden Härchen . . . zusammengesetzt sind." POTTS (1923) found in Teredo that the cells of the tubules specialised for the ingestion of wood had long cilia "beating with a rather languid motion, and easily retractile, so that, when ordinary reagents are used for fixation of material, it is impossible to demonstrate them in sections." On the projections which occur in this epithelium he found slender pseudopodia but no cilia. In the unspecialised region (which resembles that found exclusively in the other Lamellibranchs) he states that the cells have a border of retractile cilia, which he also observed in Pholas and Xylophaga.

I have examined tubules from the majority of the species sectioned, pressing them out under cover-slips, and observing them under high power. In most cases it was impossible to determine whether cilia were present or not, but in addition to the three cases in which Potts observed them, I have seen them in *Spisula truncata*, *Spisula solida*, *Dosinia exoleta*, *Cardium echinatum*, *Gari tellinella*, and *Pholadidea loscombiana*. In Spisula the cilia can be distinguished with exceptional ease, and can be seen beating actively in all the tubules. The beat is usually very languid, varying as a rule between fifty and one hundred and fifty to the minute. Although it is difficult to decide the length of the cilia, some idea of it can be obtained from the fact that the length of beat may be about 15μ. As will be shown later, particles both enter and leave the tubules in all cases, which implies the presence of cilia, although in some species they may be retracted more readily than in others, especially when pressed out for examination.

According to the character of its protoplasm—the nuclei are identical in all the cells—the epithelium of the tubules may be divided into two regions, in one of which the protoplasm is extremely vacuolated and lightly-staining, and in the other less vacuolated and darkly-staining. The vacuolated cells are the more numerous and are always larger, although they vary greatly according to the size and contents of their vacuoles. These, particularly if the tissue has been fixed shortly after the animal has been taken from the sea, are often filled with green, brown, or yellow masses of varying size and shape. In *Pecten maximus* and *Pecten opercularis* the vacuoles and inclusions, which consist of a great number of minute brown spheres, are both exceptionally large, as shown in fig. 4. Frenzel has described the colour, size, and properties of these inclusions, and figured them in colour, for all the species of Lamellibranchs which he examined, regarding them as characteristic of the different species. List disagrees with him, and points out that they cannot be a characteristic sign of a species since they are not constant, their nature depending wholly upon the food of the animal. In animals which have been starved the cells have few or no inclusions. At the same time, the size of the vacuoles certainly varies in different species, being much larger, for instance, in Pecten, Gari, Solecurtus, and Saxicava—where whole tubules may consist of a bounding membrane surrounding a number of great vacuoles (with or without contents), both nuclei and cell outlines being absent—than in the other species I have examined.

In the Mollusca generally, Frenzel (1885, 1886, 1893) found three kinds of cell in the digestive diverticula—granule-cells (Körnerzellen), ferment-cells (Keulenzellen), and lime-cells (Kalkzellen). The last of these he never found in the Lamellibranchs he examined, the granule-cells in every case but one, and with them ferment-cells in the following genera only: Pecten, Mactra, Capsa, Donax, Solecurtus, Lima, Cardium, Cyprina, Petricola, Tellina, Scrobicularia, Mya, and Gastrochæna, and also in *Venus gallina* and *Venus verrucosa*, although in *Venus decussata* he found ferment-cells exclusively. He admits that the morphological development of the ferment-cells in the Lamellibranchs is "insignificant," and his sole criteria as to their presence seems to have been the size and intensity of colour of the included masses. I have examined species of ten out of the fourteen genera in which he found two kinds of cell, and I can find no evidence whatever of their presence; there is one type of cell only. In the Opisthobranch or Pulmonate Gastropods, where both granule- and ferment-cells are present, there is never any doubt as to their identity, for in each both nucleus and protoplasm are characteristic. In the Lamellibranchs the only variation is in the quantity of matter included in the cells.

The smaller, darkly-staining cells are always present. They are found scattered irregularly in small groups round the lumen in Nucula and all the Filibranchs examined (see figs. 4 and 5). They are often low, and lie between large vacuolated cells which meet above them and shut them off from the lumen. In the remaining Lamellibranchs the lumen of the tubules is not regular, as in the species just considered, but is elliptical, tripartite, or in the form of a cross, with crypts (using the term employed by GUTHEIL) at the extremities of the two, three, or four arms respectively, in which lie groups of these dark cells. The arrangement in Mya, in which there are two crypts, and in Teredo, in which there are three or four, are shown in figs. 7 and 10. The same regular arrangement has been described and figured in Anodonta by GUTHEIL.

These cells have been considered ferment-cells by some workers—for no other reason, apparently, than that they are slightly different from the other cells—but all the evidence points to their being young cells. They are most numerous at the blind end of the tubules, decreasing in number as these widen. This is conspicuously the case in Nucula, where they are often absent in the wider tubules (fig. 6), though the same condition may be found in many species. FRENZEL thought that the older cells might be replaced by a multiplication of young cells, while LÖNNBERG (quoted by LIST) found that the cells of the tubules in *Mytilus edulis* divide mitotically. LIST, who describes and figures these cells in the Mytilidæ with great care, found division stages in them occasionally, and also noted the ejection of parts of the older cells and the degenerate appearance of their nuclei, and so came to the conclusion that the dark cells (Ersatzzellen as he called them) were nests of young cells. GUTHEIL found mitosis not infrequently in the crypts in Anodonta, and observed that it was commonest when signs of degeneration were most pronounced. I have examined sections of the digestive diverticula in *Mya arenaria* stained with iron hæmatoxylin, in order to determine whether division takes place in the crypts. I have found it frequently in sections of animals which had been starved by keeping them in filtered sea water for a month. In these the older cells are often to be seen either free in the lumen or in the process of being expelled from the epithelium, many cells coming together in spherical masses, and then passing into the lumen in that condition. Mitotic figures are frequent and always in the crypts. Figs. 8 and 9 represent two such cases, one during division and the other immediately after it. In all cases (as was also observed by GUTHEIL) the nuclei come near the lumen before dividing, and the chromosomes are large and granular. I have never seen mitosis in sections of animals which had recently been fed, but it is quite common to find either the whole or parts of the old cells being cast off.

From the histological character, the distribution, and the behaviour of these small dark cells there seems, therefore, every justification for considering them young cells which, by dividing, are able to make good the loss resulting from the casting off of the old cells. A similar process goes on in the gut of the Crustacea and Insecta.

The epithelium of the digestive diverticula in all the Lamellibranchs examined, with the exception of *Teredo norvegica*, consists of one type of cell only. In the Teredinidæ, as SIGERFOOS (1908) and POTTS have shown, the digestive diverticula are of two kinds, the one resembling in every respect that found in the other Lamellibranchs, and the other consisting of wide, excessively thin-walled tubules, the epithelium of which is made up of a single layer of cells whose boundaries are either absent or very indefinite.

4. FUNCTION.

(*a*) *Historical Summary.*—The earlier investigators (for full details and bibliography, see LIST) all considered the digestive diverticula formed a "liver" which secreted bile and digestive enzymes. FRENZEL (1886) states, with regard to the Mollusca generally (he failed to realise the different conditions that prevail in the various classes), "dass die Mitteldarmdrüse derselben, gerade wie die der Crustaceen, eine Verdauungsdrüse ist, d. h. dass sie ein Secret bildet und ausscheidet, welches zur Verdauung der in den Darmcanal aufgenommenen Speisen verwendet wird." SAINT-HILAIRE (1893) was the first to show that the digestive diverticula in the Mollusca serve as organs of absorption. He found that the vacuolated or granule cells in the Prosobranchs, Opisthobranchs, and Pteropods among the Gastropods, and in the Cephalopods, are not ferment-cells but absorptive cells. CARAZZI (1896, 1897), working on the green oysters of Marennes, and later on oysters fed with iron sulphate, came to the conclusion that the "liver" in the Lamellibranchs is an organ concerned with assimilation. According to him, Marennin and iron are taken up by the epithelial cells of the gills, palps, and gut, and then transported by amœbocytes to the "liver," where they are assimilated and stored, some of the iron being later passed on to the gonad. He did not, however, exclude the possibility of the tubules being also to some extent secretory, although he considered the ducts the chief source of digestive enzymes.

As LIST has pointed out, the value of CARAZZI'S results is greatly lessened by his experimental methods. He kept oysters for four months in three litres of sea water, to which had been added 20 grams of a 10 per cent. solution of iron sulphate in distilled water, and then placed them in clean sea water for one or two weeks before fixing them. The animals had time to get thoroughly permeated with iron, which was found both in the epithelium of the gills, palps, and gut, and also in the "liver"; but there was no more reason for assuming that it had been absorbed by the former and passed on to the latter than that the reverse had occurred.

No such objection can be made to the experiments of LIST. He added Indian ink to the water in which a number of Mytilus were kept, and found that after a short time, sometimes only two hours, the particles were taken in by the granule-cells in the digestive diverticula. In sections, he found ink in the lumen of the ducts and tubules, and particles passing through the "Cuticularsaum" into the granule-cells, where they become concentrated in vacuoles, at first a few dotted round the wall of the vacuole, and later in such numbers as to form a solid black mass. When the animals ceased to be fed, the ink was quickly cast out, entire "Körnerballen" being ejected into the lumen and passing through the gut to the exterior. LIST also found that carmine was taken in in the same manner, though, as he notes, this is always dissolved to some extent, together with powdered litmus (which indicated by its colour that some of the vacuoles were acid and others alkaline) and iron. He concludes finally that the colour of the "liver" at any time depends entirely upon the food, and that it is primarily an organ of assimilation.

ENRIQUES (1901), who worked at the same time as LIST, agreed with FRENZEL that the cells in the tubules of Ostrea were of only one type, but he considered them to be ferment-cells, not granule-cells, since he was unable to identify within them ingested chloroplasts such as he had found in the granule-cells in many Gastropods, and since the spectroscopic examination of a solution in alcohol of the brown inclusions gave no indication of chlorophyll. He admitted, however, that his oysters had been out of the sea for two or three days. He did not agree with CARAZZI that secretion takes place in the ducts, considering the mucus cells their only secreting elements, the function of the ducts being purely that of transport. Although the cells of the tubules may absorb, their main function, according to ENRIQUES, is the secretion of digestive enzymes.

In *Anodonta cellensis*, GUTHEIL states that the tubules are composed of one type of cell, which he regards as secretory. Like ENRIQUES, he noted the presence of great numbers of yellow or brown balls in the cells, from which they could be pressed out in teased material. He made no physiological experiments, but noted that the brown spheres remained at the basal end of the cells until they attained a certain size, when they moved to the surface of the cell and passed out—as enzymes, in his opinion. He could not follow in any detail the process of secretion, and attributed the loss of colour after the animals had been starved to a shrinkage in the amount of secretion. He also decided that the same cells could absorb since he found within them fine droplets of fat.

POTTS found that of the two regions of the "liver" in Teredo, the one with the wide thin-walled tubules, which he calls "digestive," is specialised for the intracellular digestion of wood, fragments of which are taken in both by the cells of the epithelium and by free cells in the lumen; and the other, described as "excretory," and which resembles the digestive diverticula of the other Lamellibranchs, contains "large quantities of highly refringent, resistant granules whose chemical nature is not known but which are probably excretory." He found that particles of Indian ink were taken in by the cells of these tubules.

In my own work on *Mya arenaria* (1923) I was unable to carry out feeding experiments, and accepted the presence of digestive enzymes in extracts of the "hepatopancreas," as I called it, as evidence that it is an organ of secretion (a safe assumption in many groups of animals but not in the Mollusca). Enzymes capable of digesting the carbohydrates—starch, glycogen, sucrose, maltose and lactose—were found, also a protease acting in acid media, and a lipase. Digestive enzymes have also been found in extracts of the digestive diverticula by, amongst others, FREDERICQ (1878), who found a protease in Mya and Mytilus; MITRA (1901), who found amylase and invertase in Anodonta; VAN RYNBERK (1908), who found amylase in Mytilus; DAKIN (1909), who found amylase, protease, and lipase in Pecten; and HEYMANN (1914), who found protease, lipase, and a number of carbohydrate-splitting enzymes in Ostrea.

Finally, VONK (1924) fed *Ostrea edulis* with Indian ink and carmine, and found that these were taken in as round masses in the cells of the tubules—exactly as LIST had found in Mytilus. Only very occasionally could he see a distinct membrane round the vacuoles, and he never observed particles being passed on to the amœbocytes as described by CARAZZI. He also fed oysters on plankton for three to five days, and compared them with oysters which had been starved for two or three weeks. In the former, diatoms were numerous throughout the gut, while "Im Gegensatz zu ungefütterten oder mit Farbstoff genährten Tieren zeigten nun die Leberzellen dieser Austern zahlreiche grüne Einschlüsse von sehr unregelmässiger Form." He never found whole diatoms in the cells of the tubules, though some green algæ appeared to be taken in whole. The green colour of the inclusions in sections he accounts for by quoting MOLISCH to the effect that the brown pigment of diatoms is extracted by cold alcohol, leaving a green pigment. VONK concludes that the oyster most probably assimilates food by phagocytosis in the cells of the tubules, adding that this agrees with the complete lack of protease in the stomach.

(*b*) *Feeding Experiments.*—I have carried out feeding experiments so as to determine where and how absorption takes places. For this purpose I used suspensions in sea water of iron saccharate (Ferrum Oxydatum Saccharatum) and of blood corpuscles of the dogfish. Animals were placed in these suspensions (which were quickly cleared by their ciliary activities) and fixed after definite periods; those fed on the iron compound in a mixture of 5 per cent. ammonium sulphide in 95 per cent. alcohol to which was added, immediately before use, an equal quantity of Bouin's fluid. This use of Bouin is my own modification of the usual method of fixing for iron; I find that it gives a much better fixation, while iron can be demonstrated just as well. Animals fed on blood corpuscles were fixed in Flemming, or in any fixative which had previously been found suitable. Sections were cut 6μ or 8μ thick. Iron was demonstrated by placing the slides for a few minutes in 10 per cent. potassium ferrocyanide and then in very dilute HCl, which converts it into Prussian blue; alum carmine was used to stain the sections and gives very beautiful results. Sections of animals fed with blood were stained with iron hæmatoxylin and acid fuchsin or by Arnold's method (for details see *Arch. Zellforsch.*, III, 1909, p. 434) after fixation in Flemming, or with Delafield's hæmatoxylin and erythrosin after other fixatives.

A number of animals were fed with iron, the best results being obtained in Nucula, Mya, and Teredo, an account of which will be given. The animals were starved previous to feeding, —Nucula for two weeks, Mya for a month, and Teredo for one or two days (if kept long out of wood Teredo dies).

In Nucula iron-feeding gives most striking results. Iron is taken into the lumen of the gut in great quantity—so that the lumen appears as a solid sheet of blue in the sections—but it is absorbed exclusively in the cells of the tubules, the junction of which with the ducts being vividly marked by the entire absence of blue in the epithelium of the ducts. Fig. 5 represents a portion of the epithelium of a tubule fixed six hours after feeding. Iron is already being absorbed in large quantities. The border cuticle cannot be seen and the free edges of the cells are very irregular, being extended in the form of pseudopodia (in some cases these extensions attain great length and are very attenuated). The iron is taken up in small vacuoles, those near the lumen being only partially filled with iron and having a lightly-coloured and granular appearance, while those in the more basal region of the cells are larger, and so packed with iron that they exhibit a uniform deep blue. Absorption takes place almost exclusively in the older cells and always in discrete round vacuoles; there is never any general absorption of tiny granules of iron throughout the cytoplasm, nor any diffuse blueness in it. A certain amount of absorption takes place in the young cells, but the vacuoles are more irregular. Fig. 6 represents an entire transverse section of a tubule two days after feeding. In this case all the vacuoles are packed with iron, and are uniformly blue. The vacuoles are extremely plentiful, the majority being crowded in the basal end of the cells, where they seem to be embedded in the cytoplasm, those nearer the lumen lying in open spaces in the protoplasmic network. The free edge of the cells, the absorption of iron having ceased, is regular in outline, and the border cuticle can easily be distinguished. Sections of the digestive diverticula three to five days after feeding show much the same conditions, but a certain amount of iron is being taken over by the amœbocytes, which are numerous between the tubules, although they are not so plentiful in the walls and lumen of the gut as in the higher Lamellibranchs. There is no sign of any rejection of iron into the lumen of the tubules. No attempt has been made to follow the course of the iron further.

A tubule of the digestive diverticula in Mya, one day after feeding with iron, is represented in fig. 7. The stomach of the animal was full of a thick brown suspension of the iron compound, and a certain amount of this can also be seen in the lumen of the tubule. It is also being ingested by one of the cells, which projects beyond the others, not, apparently, either as fine particles or in solution, but as a solid mass which is enclosed directly by the protoplasm. It is difficult, however, to be absolutely certain on this point. Further within the cells it is present in vacuoles, neither so large and so numerous nor so regular in shape as in Nucula, but never as scattered particles or diffuse. Where the vacuoles are not quite full the iron is massed round the margin in the same way as the Indian ink in LIST's experiments on Mytilus. Amœbocytes have entered two of the cells which contain iron, but none are present in any of the cells free from iron. I have never found iron in the young cells. In no other part of the gut was iron assimilated.

In Teredo, one day after feeding, iron was present in the lumen of the gut and of both portions of the digestive diverticula; but to a much greater extent in the unspecialised portion. As shown in fig. 10, it is taken in by the cells of these tubules, appearing as somewhat irregular masses within large vacuoles. It is found very occasionally in the cells of the specialised portion, and in the free cells which are present in the lumen, and always in a rather diffuse condition. Most iron is present in the amœbocytes—which occur in very great numbers between the tubules of the unspecialised region, and are usually laden with fat globules and other food—to which it is apparently almost immediately passed by the cells of the tubules. In the figure the amœbocytes represented are so full of iron that only the nucleus—and that with difficulty—can be distinguished from the mass of blue.

Cardium edule, *Mya arenaria*, and *Teredo norvegica* gave the clearest results after feeding with blood corpuscles. The corpuscles were taken into the gut freely, so that the stomach was full of them within a short time. In the case of Cardium and Mya, however, they were all ingested by the amœbocytes, which are everywhere present in and beneath the epithelium of the gut (including, of course, the ducts of the diverticula), and also free in the lumen. The corpuscles entered the ducts in large numbers, but were there seized by these phagocytes and taken into the wall of the ducts, passing between the cells of the epithelium. Sections of a specimen of Cardium, which had been fixed two days after feeding, and stained with Delafield's hæmatoxylin and with just enough erythrosin to colour the corpuscles and nothing else, showed the presence of great numbers of corpuscles all within phagocytes, sometimes in the connective tissue, but usually between the cells of the ducts, which could everywhere be readily distinguished on account of the red colour of the corpuscles. Never, however, did they succeed in reaching the tubules.

Exactly the same condition is found in Mya. Figs. 1, 2, and 3 represent three stages in the transport of the ingested corpuscles, the animal having been fixed six hours after feeding. In fig. 1 two corpuscles are shown ingested by phagocytes lying between the cells in the epithelium of one of the ducts. Fig. 2 represents a phagocyte containing a corpuscle in the act of passing through the circular muscle which surrounds the duct, while in fig. 3 is shown a corpuscle ingested by a phagocyte, which was lying in the connective tissue between the ducts and tubules. Animals fixed with Flemming's strong fluid from four to six days after feeding showed later stages in the digestion of corpuscles by phagocytes, the corpuscles being irregular and entirely without structure, and surrounded by numbers of fat globules.

Characteristic of the Lamellibranchs are the large numbers and great activities of these phagocytes, and this has been commented on by the majority of the investigators of this class. I have given an account (1923) of the presence of these phagocytes in Mya, and have shown that they often contain large hard particles, such as sand grains and the tests of diatoms, so that the surface of the gut is often difficult to cut in sections, and has a dark grey colour. The gut of Ensis, and other Lamellibranchs in which the sorting mechanism on the gills and palps allows relatively large hard particles to enter the gut, has the same appearance.

In Teredo, as shown in fig. 11, which is drawn from a specimen three days after feeding with blood, corpuscles were actually ingested by the cells of the tubules. The digestive diverticula in the Teredinidæ are spread out in a thin sheet round the ventral surface of the stomach, and the ducts are short and wide. As already noted, the phagocytes are most numerous between the tubules of the unspecialised portion, and they were often found with contained corpuscles (amongst other things), a typical case being shown in fig. 12. The corpuscles are taken in by the cells of the unspecialised tubules (see fig. 11), and lie in vacuoles within them, but they are often seized by phagocytes which remove them from the cells. I have never found corpuscles in the diverticula specialised for wood ingestion.

It is interesting, at this point, to note that in the Nudibranch *Archidoris tuberculata* I have observed that blood corpuscles are taken in by the absorptive cells in the digestive gland (which in the Nudibranchs contains both secretory and absorptive cells) in very great numbers and there digested. There is a wide opening from the stomach into this organ, while phagocytes are not found in the epithelium or in the lumen of the gut in the Gastropods, so that the corpuscles were never prevented from entering the digestive gland.

From the results of the experiments here described, and of those of Carazzi, List, Potts, and Vonk, there can be no doubt that the cells of the digestive diverticula in the Lamellibranchs absorb. The epithelium of the gut, and of the ducts leading into the diverticula, despite the contrary assertions of Carazzi, has no power of absorption (although the phagocytes everywhere present between its cells take in solid particles), but is concerned purely with transport, as is shown by the universal presence of cilia (with the solitary exception of the area which secretes the gastric shield in the stomach) and mucus glands.

All the evidence points to the intracellular digestion of food particles in the cells of the diverticula. Insoluble particles of Indian ink are ingested, while in the case of Teredo, entire blood corpuscles are taken in by the cells of the unspecialised tubules, and fragments of wood by the cells of the tubules specialised for that purpose. The cells of the tubules in Mya and Cardium have no opportunity to absorb corpuscles, owing to the prior seizure of the latter by phagocytes. The presence of vast numbers of green and brown globules in the cells of the tubules in the case of animals taken directly from the sea, which disappear when the animals have been starved for some weeks (as I have observed in many cases), so that the tissue becomes finally almost colourless, with only a few orange or yellow concretions here and there—the indigestible remnants of intracellular digestion in all probability—is additional evidence. I have been able to confirm the statement of Vonk that the globules reappear when starved animals are fed on diatoms, their natural food. The manner in which iron is absorbed is also strongly indicative of intracellular digestion ; instead of being taken in a more or less diffuse state, or in numerous, very minute vacuoles, as in true absorption—for example, in the gut of insects, as described by Steudel (1913), or in the salivary glands of Murex, as shown by Hirsch (1924), in both of which intracellular digestion does not take place—it is always found within large discrete vacuoles. Whether it is taken into the cells in solution or as solid matter (and in Mya, as figured, it appears to be ingested as a solid mass), the fact that, like the Indian ink in List's experiments on Mytilus, it invariably becomes aggregated in these large vacuoles is, I think, an indication of intracellular digestion. Moreover, the free surface of the cells which absorb the liquid products of digestion is never extended or drawn out into pseudopodia, as in the digestive diverticula of the Lamellibranchs.

Lastly, there is the question of the presence of a great number of digestive enzymes (to which reference has already been made) in extracts of the diverticula. If it can be proved that the cells do not secrete, then the presence in them of these enzymes can only be accounted for on the assumption that they constitute an organ of intracellular digestion. There is obviously no need for digestive enzymes in a tissue which absorbs the soluble products of extracellular digestion—glucose, amino-acids, fatty acids and glycerol.

(*c*) *The Question of Secretion.*—Since there is only one type of cell in the diverticula, and this certainly absorbs, it must perform a double function if secretion occurs. This, of course, is not impossible; thus HIRSCH (1924) has shown that the salivary glands of Murex both secrete and absorb. Histological examination of the cells gives no support to the view that they secrete; ENRIQUES and GUTHEIL, both of whom thought that secretion takes place, described and figured typical digestive vacuoles, and the same is true of FRENZEL. GUTHEIL's explanation of the loss of colour in a starved Anodonta as being due to a reduction in secretion is unsatisfactory; both HIRSCH (1915) and KRIJGSMAN (1925) have demonstrated that in the Gastropods the secretory cells contain secretion during periods of starvation.

If it could be proved that certain enzymes were present in the tissue of the diverticula and were never found in the stomach, that would provide conclusive evidence that secretion does not take place. There are, however, complications. In the first place, amylase and glycogenase are always present in the stomach as a result of the dissolution of the head of the style and the release of the contained enzymes, while the invariable presence of great numbers of phagocytes in the lumen of the stomach complicates tests for lipase and protease. The phagocytes must contain both these enzymes, since they will take in and digest blood corpuscles on which the animal has been fed, and also droplets of neutral olive oil stained red with Nile-blue sulphate, which turn blue shortly after ingestion owing to the digestion of the fat and the consequent formation of fatty acids which give a blue colour with the stain. Experiments carried out with the stomach fluid from the larger Lamellibranchs, *Pecten maximus*, *Cardium norvegicum*, *Dosinia exoleta*, *Ostrea edulis* and *Mya arenaria*, showed that, though fibrin and egg albumen stained with carmine or Congo red were not digested, and quantitative tests for lipase with olive oil and methyl acetate gave inconclusive results, yet positive results were given by the most delicate tests for protease—the coagulation of calcified milk, and for lipase—the turning yellow of milk which had been made alkaline with sodium carbonate and coloured pink with phenol red. Control experiments invariably gave negative results. This slight activity is probably due entirely to the enzymes from the phagocytes, and it is not necessary to postulate the presence of a secretion from the digestive diverticula. HEYMANN (1914) found protease in the blood of Ostrea, probably from the same source.

The acidity of the stomach contents has usually been regarded as the result of a secretion from the "liver." I have shown in a recent paper (1925), however, that this acidity is produced by the dissolution of the crystalline style, which is invariably the most acid substance in the alimentary system. If the style is extracted or induced in various ways to disappear, the hydrogen-ion concentration in the stomach falls considerably, until it approximates to that of the mantle cavity, and is much lower than that of the tissue of the diverticula. I have recently confirmed and extended these experiments on *Ostrea edulis*. Here again there is no evidence of any secretion from the diverticula.

By injecting into the tissues some form of iron solution or colouring matter which can later be identified in sections, it is possible in many Invertebrates to detect these substances later in the secreting cells of the digestive glands. This has been shown to be the case in Crustacea by CUÉNOT (1895), JORDAN (1904), and myself (1924); in Insecta by STEUDEL (1913), and in Gastropoda by CUÉNOT (1892, 1900), and myself (unpublished work). CUÉNOT considered the cells in which these substances were found to be invariably excretory (they are, of course, also found in the true excretory organs), but JORDAN has shown that this is not the case. Substances in solution in the blood-stream pass into the secreting cells, together with the material needed for the elaboration of ferments, and so far from being quickly excreted, JORDAN found iron in the secretory cells of Astacus thirty-six days after it had been injected. Moreover, the "excreted" material is immediately taken up by the absorptive cells which surround the secretory cells in the digestive gland of the Crustacea and higher Gastropoda, such as the Tectibranchs and Nudibranchs, as I also have observed in many cases. CUÉNOT (1900) injected various colouring matters into fifteen species of Lamellibranchs, but found no "excretory" cells in the "liver"; excretion took place exclusively in the nephridia and pericardial glands. I have injected a 0·5 per cent. suspension of iron saccharate in sea water by way of the foot, muscle, or edge of the mantle (afterwards washing the animals thoroughly to prevent any of the fluid entering the mouth), into *Glycimeris glycimeris*, *Mytilus edulis*, *Pecten maximus*, *Ostrea edulis*, *Cardium norvegicum* and *Mya arenaria*, fixing the digestive diverticula in the usual manner from two to six hours later. In no case was there any trace of iron in the cells, although it was often found in the blood lacunæ and in the amœbocytes. Yet when Gastropods such as Doris or Scaphander were treated in the same way the secretory cells were coloured blue. Similarly, when pilocarpine was injected there was no change in the activity of the cells such as might be expected if they secreted.

On the other hand, iron was found in the epithelium of the style-sac four hours after injection in the case of Mytilus, as shown in fig. 13. Extremely minute granules were present immediately above the nuclei and also nearer the surface of the cells and in the lumen. In Pecten, although iron was never identified in the style-sac with certainty, there was a great increase in the number of fine colourless granules after pilocarpine had been injected.

There is thus no evidence of any secretion of digestive enzymes save in the epithelium of the style-sac.

5. GENERAL DISCUSSION.

Histological examination has revealed the presence of one type of cell only in the digestive diverticula of the Lamellibranchs. The results of feeding experiments by previous workers and by myself show that these cells are capable of assimilating both soluble and insoluble particles, both of which are taken into large vacuoles, which probably contain digestive enzymes, where they are digested intracellularly. There is no evidence that any of the cells can secrete.

Among the Metazoa, intracellular digestion is known to occur in the Porifera, Cœlenterata, Turbellaria, to some extent in the Echinoidea, and in the Mollusca (for full details and bibliography see HIRSCH (1925)).* In the latter it is not found in the highly evolved Cephalopods, while in the Gastropods (as I hope to show in a later paper) there is a transformation of the digestive diverticula from purely absorptive to absorptive and secretory organs.

In the Lamellibranchs there is no such development in the function of the diverticula, the explanation for this lying in the similarity of food and feeding mechanisms throughout the

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* Although in the Arthropoda generally digestion is exclusively extracellular, there are two interesting cases of intracellular digestion in parasitic species. In the tick, Ornithodoros, according to CHRISTOPHERS (1906), blood corpuscles sucked from the host are digested intracellularly both in the large epithelial cells of the alimentary sac and in free cells, the origin of which he was unable to determine. REICHENOW (1918) found that in the mite, Liponyssus, the large cells of the gut are amœboid and ingest corpuscles from the blood of the host, digesting them intracellularly. After becoming gorged with food, these cells are detached and fall into the lumen of the gut.

In the Brachiopods, the feeding processes of which are closely analogous to those of the Lamellibranchs, intracellular digestion probably occurs. ASHWORTH (1915) describes the structure of the "liver" in the larvæ of Lingula and Pelagodiscus as being quite distinct from that of the remainder of the gut, no cilia are to be seen in sections of the "liver," while the cells are highly vacuolated and occasionally contain, in Lingula, ingested unicellular algæ. Other observers (for details, see JORDAN (1913)) have also noted the passage of food into the cavity of the "liver." Professor ASHWORTH has kindly permitted me to examine his sections, and certainly from the presence of the ingested algæ and the general structure of the "liver," I think there is good evidence that intracellular digestion takes place in the Brachiopods in much the same manner as in the Lamellibranchs.

class; the fact that, in the face of this similarity, FRENZEL found different conditions in the diverticula of two species of the same genus, Venus, is sufficient to throw doubt on his conclusions. All the Lamellibranchs—with the exception of the carnivorous Septibranchs, which must be excluded from any generalisation here made, and to some extent the Teredinidæ, which will be discussed later—obtain their food by means of ciliary currents on the gills and palps, which select only the smallest particles for subsequent entrance into the gut. In the stomach there is a second selection, large particles being passed directly into the mid-gut and smaller particles being conducted to the opening of the ducts leading into the digestive diverticula. NELSON (1918) has described the selective mechanism in the stomach of *Modiola modiolus*, and I have described a similar one in *Mya arenaria*, and have observed its presence in many other species. There is at the same time a certain extracellular digestion of carbohydrates in the stomach by the enzymes of the style.

For intracellular digestion, it is essential that only very small particles should be presented to the ingesting surface, which should be as extensive as possible (*e.g.*, the increase in surface provided by the mesenteries in Actinians, by the ramifications of the gut in many Turbellarians, and by the large number of flagellated chambers in the sponges). Both of these conditions are fulfilled in the Lamellibranchs; none but the very finest particles survive the rigorous selection of the various sorting mechanisms, and the action of the enzymes from the style, and pass into the digestive diverticula, which are composed of a great number of ramifying tubules which present a large surface. A continuous circulation is maintained in these tubules by the action of the long retractile cilia, so that food particles are brought in and the indigestible remnants of intracellular digestion removed. The fact that the two operations take place (as LIST experimentally demonstrated) implies the presence of cilia, even though they can never be seen in sections, and only in certain cases in fresh material. There is no system of longitudinal and circular muscles such as ensures a similar circulation in the Crustacea (for details and literature on this point see my paper on Nephrops (1924)). The presence of retractile cilia in cells which digest intracellularly has also been observed in the Cœlenterata by GREENWOOD (1888) and others. The glucose formed by the action of the style enzymes on carbohydrates in the food will also be absorbed by the cells of the tubules.

The process of digestion would seem to be as follows: Particles are taken into the vacuoles and there acted upon by enzymes. Material which is of use to the animal, such as iron, is then passed on to amœbocytes or stored (the connective tissue round the tubules is often rich in glycogen), while indigestible substances, like Indian ink, which is never passed on to the amœbocytes, are expelled. In Pecten (fig. 4) yellow or brown globules of excretion are massed together in large cavities in the older cells, and are found in the same condition after expulsion from the cells in the lumen of the tubules, ducts, mid-gut and rectum. The brown colour of this excretion is due to the presence of ingested chlorophyll and the products of its decomposition, which accounts for the "entero-chlorophyll" found by MACMUNN (1900) and others.

The Teredinidæ, besides possessing the usual ciliary mechanisms, though to a reduced extent, feed by swallowing the fragments of wood scraped off by the specialised shell valves, and it is very significant that the adaptation which enables them to digest the wood takes the form of tubules specialised for its intracellular digestion, and not the elaboration of an extracellular cellulase, as in such Gastropods as Helix or Aplysia which are also able to digest cellulose.

Correlated, no doubt, with the retention of intracellular digestion throughout the Lamellibranchs, is the utilisation of phagocytes for the direct ingestion of larger particles than those which can enter the digestive diverticula (whole diatoms are never found in the latter but are frequently to be seen in phagocytes). They are certainly less numerous in Nucula than in the higher Lamellibranchs, while in the Gastropods, where extracellular digestion is better developed, phagocytes do not occur in the gut.

6. SUMMARY.

1. The structure of the digestive diverticula in thirty-four species of marine Lamellibranchs has been studied.

2. The diverticula consist of blind tubules which open into the stomach by way of ciliated ducts, the epithelium of which resembles in structure and function that of the remainder of the gut.

3. There is only one type of cell in the tubules. There are darkly-staining young cells, the nuclei of which divide mitotically, but when older the cells are very vacuolated and contain great numbers of coloured granules which disappear after starvation.

4. In the Teredinidæ there are tubules specialised for the digestion of wood; the condition in the carnivorous Septibranchs has not been examined.

5. A border cuticle can be seen in sections of the tubules in Nucula and the Filibranchs, but not in the Eulamellibranchs. In fresh material long retractile cilia can be distinguished in a number of species and are probably present in all cases.

6. After feeding with iron saccharate in suspension, this is found later lying within large vacuoles in the cells of the tubules, being afterwards passed on to the amœbocytes.

7. Blood corpuscles from the dogfish are taken into the gut freely, but are ingested by phagocytes before they reach the tubules, except in the case of Teredo, where they are taken in by the cells of the unspecialised tubules.

8. The manner in which particles are taken in, and the presence of digestive enzymes in extracts of the diverticula point to the presence of intracellular digestion.

9. There is no histological evidence that the cells of the tubules secrete. The presence of enzymes in the stomach can be accounted for by the dissolution of the crystalline style and the occurrence of great numbers of phagocytes free in the lumen; the acidity of the gut is due to the dissolution of the style; injections of iron and pilocarpine fail to demonstrate the presence of secretory cells elsewhere than in the epithelium of the style-sac.

10. The diverticula provide the extensive surface characteristic of the alimentary systems of animals which possess intracellular digestion, while, as a result of the action of the various sorting mechanisms, only the very smallest particles are presented to the ingesting surface.

11. The digestive diverticula of the Lamellibranchs possess none of the functions of a liver or of a pancreas, but are organs of absorption and of intracellular digestion.

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8. DESCRIPTION OF THE PLATES.

List of Reference Letters.

B.C.	Border cuticle.
B.M.	Basement membrane.
B.P.	Boundary of phagocyte.
C.	Cilia.
C.M.	Circular muscle.
Cp.	Crypt of young cells.
C.T.	Connective tissue.
D.N.	Dividing nucleus of young cell.

F.I.	Iron in process of ingestion.
F.L.	Iron in lumen of tubule.
F.V.	Iron in vacuoles.
F.V.P.	Vacuoles partially full of iron.
Ft.	Fat globules.
I.B.C.	Ingested blood corpuscles.
I.M.	Ingested matter in vacuoles.
I.M.P.	Ingested matter in phagocytes.
L.	Lumen.
N.A.D.	Nuclei of young cells immediately after division.
N.B.	Nucleus of ingested blood corpuscle.
N.D.	Nucleus of epithelial cell of duct.
N.P.	Nucleus of phagocyte.
N.S.	Nucleus of epithelial cell of style-sac.
N.T.	Nucleus of cell of tubule.
Nu.	Large nucleolus of nucleus of tubule cell.
O.C.	Old, vacuolated cells of tubules.
P.	Phagocyte.
P.F.	Phagocyte containing ingested iron.
S.	Secretion of style-sac epithelium containing injected iron.
Y.C.	Young, darkly-staining cells of tubules.
Y.M.	Yellow concretions.

PLATE I.

Fig. 1. *Mya arenaria.*—Transverse section through a portion of a duct leading into the digestive tubules, six hours after feeding with blood from a dog-fish. Two blood corpuscles are shown lying within phagocytes between the epithelial cells. The nucleus of one of the phagocytes does not appear in the section. Fixed Bouin, stained Delafield's hæmatoxylin and erythrosin. 6μ. (× 1200.)

Fig. 2. *Mya arenaria.*—Another section in which a phagocyte with an ingested corpuscle is shown passing out of the epithelium through the circular muscle which surrounds the duct. 6μ. (× 1200).

Fig. 3. *Mya arenaria.*—Same as above. A phagocyte with an ingested blood corpuscle observed in the connective tissue between the ducts and tubules. (× 1200.)

Fig. 4. *Pecten opercularis*—Transverse section through a portion of a digestive tubule from a fresh animal, showing the border cuticle, the irregular arrangement of the nests of young cells, and the accumulation of yellow concretions in old cells without nuclei. Fixed corr. sublimate in sea water, stained Delafield's hæmatoxylin and erythrosin. 6μ. (× 1200.)

Fig. 5. *Nucula* sp.—Transverse section through part of a tubule six hours after feeding with iron saccharate. This is being absorbed, vacuoles near the base being full of it, while those near the lumen are only partially full. The free surface of the cells is irregular and there is no sign of the border cuticle. Fixed and stained by the methods described in the text, p. 710. 8μ. (× 1200.)

Fig. 6. *Nucula* sp.—Transverse section through an entire tubule two days after feeding with iron. Absorption has ceased, all the vacuoles are full of iron, the free surface of the cells is regular, and the border cuticle can be seen. Technique as on p. 710. 8μ. (× 1200.)

PLATE II.

Fig. 7. *Mya arenaria.*—Transverse section through an entire tubule one day after feeding with iron. This can be seen in the lumen, in the process of being taken into the cells, and lying in vacuoles within them. The crypts of young, darkly-staining cells with numerous nuclei are shown. Technique as on p. 710. 6μ. (× 1200.)

Fig. 8. *Mya arenaria.*—Transverse section through a crypt of young cells from an animal which had been starved for five weeks. One of the nuclei has migrated near the lumen and is dividing. Fixed strong Flemming, stained iron hæmatoxylin and acid fuchsin. 6μ. (× 1800.)

Fig. 9. *Mya arenaria.*—A similar section, showing the last stage in the division of a nucleus in a crypt. Fixed strong Flemming, stained iron hæmatoxylin. 6μ. (× 1200.)

Fig. 10. *Teredo norvegica.*—Transverse section through an unspecialised tubule one day after feeding with iron, which is lying in large vacuoles in the older cells and within the phagocytes which lie between the tubules. There are three crypts of young cells. 6μ. (× 1200.)

Fig. 11. *Teredo norvegica.*—Two cells from a digestive tubule three days after feeding with blood. An ingested corpuscle is shown lying within a vacuole in one of the cells. Fixed strong Flemming, stained Arnold's method. 6μ. (× 1200.)

Fig. 12. *Teredo norvegica.*—Phagocyte from between the tubules three days after feeding with blood; it contains a large quantity of ingested matter, including a blood corpuscle. Technique as above. (× 1200.)

Fig. 13. *Mytilus edulis.*—Transverse section through the epithelium in the middle of the groove which bears the style, four hours after injection with a suspension of iron saccharate. Minute droplets of secretion containing iron in solution are being produced and passed out of the cells. 6μ. (× 1200.)

Dr C. M. YONGE on "The Digestive Diverticula in the Lamellibranchs."—PLATE I.

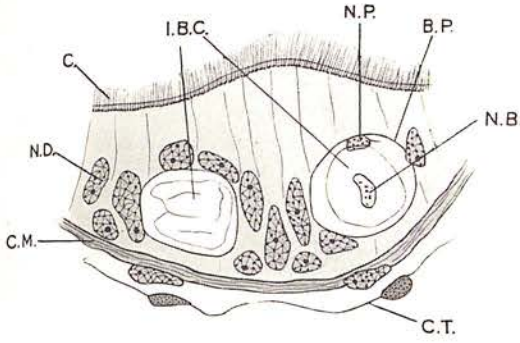

FIG. 1.

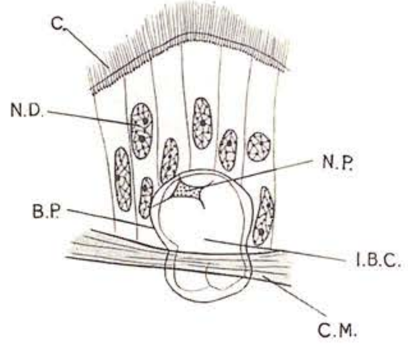

FIG. 2.

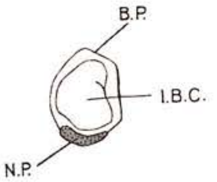

FIG. 3.

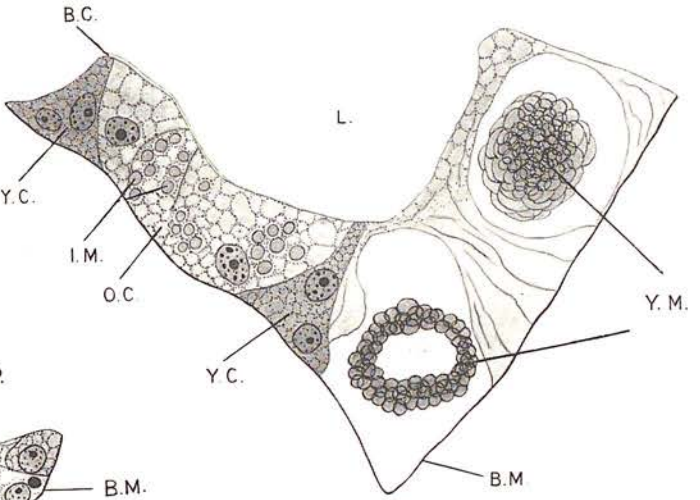

FIG. 4.

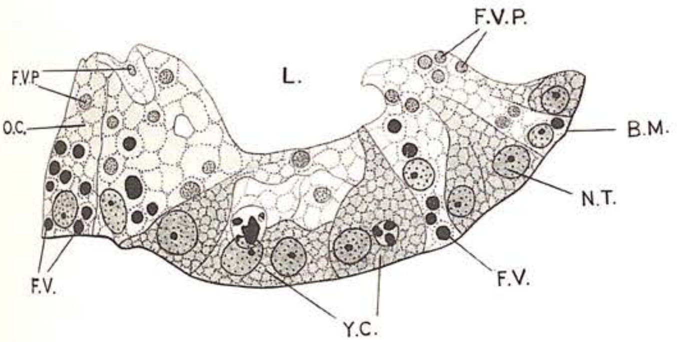

FIG. 5.

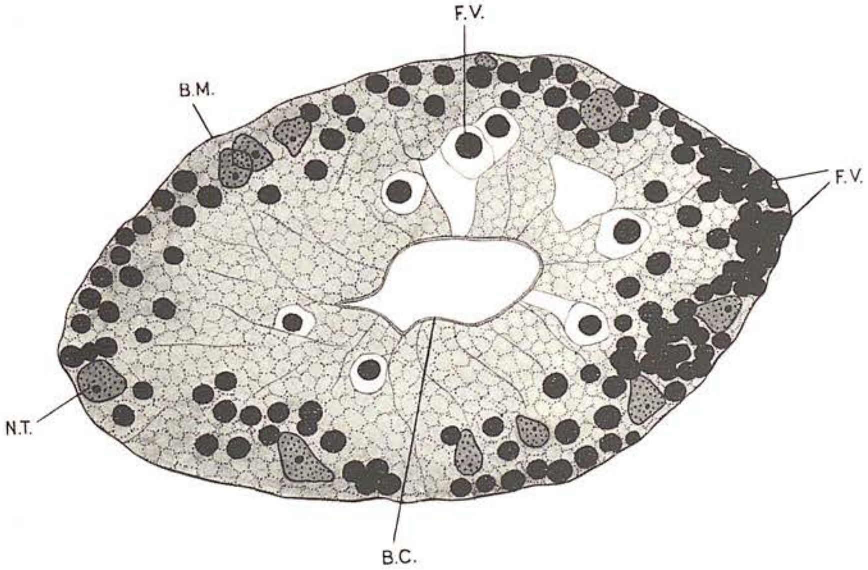

FIG. 6.

C. M. Yonge, del.

Dr C. M. Yonge on "The Digestive Diverticula in the Lamellibranchs."—Plate II.

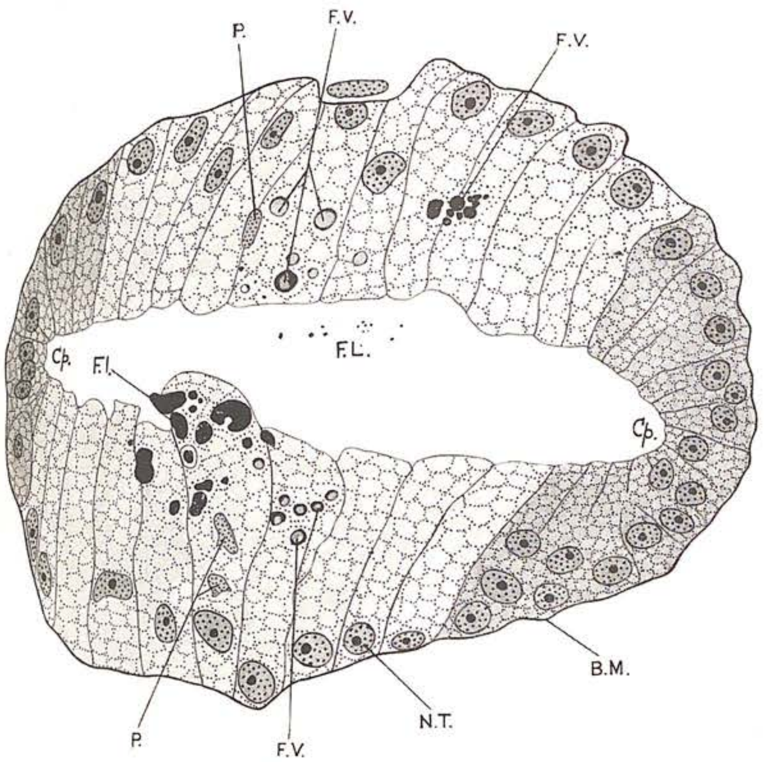

Fig. 7.

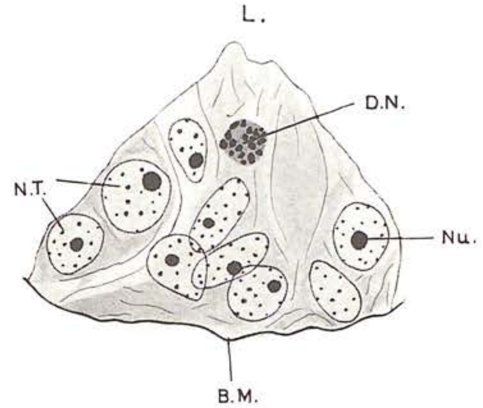

Fig. 8.

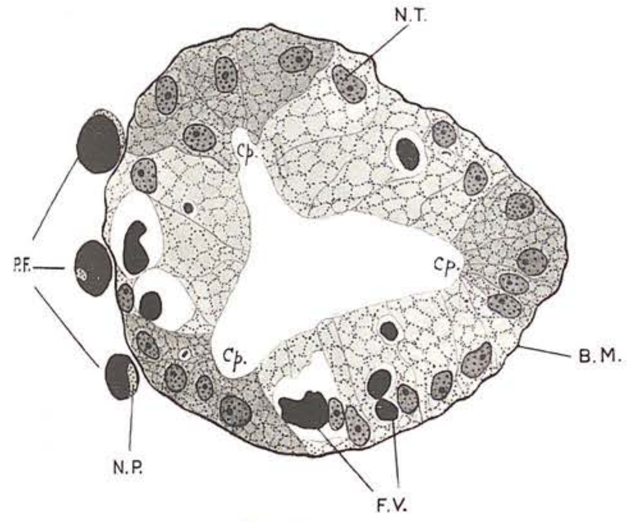

Fig. 10.

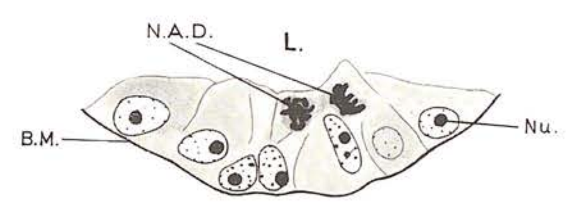

Fig. 9.

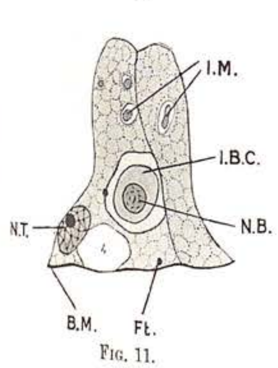

Fig. 11.

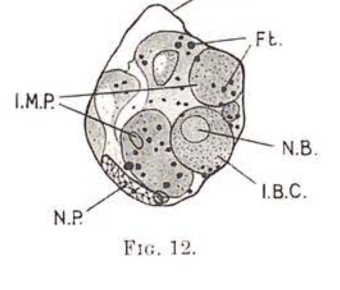

Fig. 12.

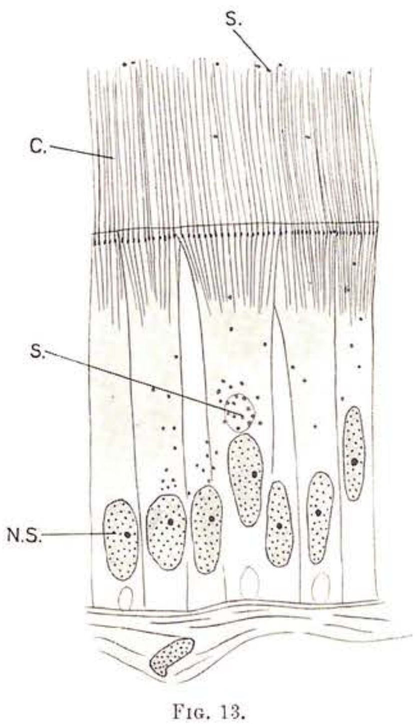

Fig. 13.

C. M. Yonge, del.

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OF THE

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VOL. LIV—PART III—(No. 15).

THE DIGESTIVE DIVERTICULA IN THE LAMELLIBRANCHS.

BY

C. M. YONGE, B.Sc., Ph.D.

[With Two Plates.]

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By C. M. Yonge, B.Sc., Ph.D., Temporary Assistant Naturalist at the Plymouth Laboratory. *Communicated by* Professor J. H. Ashworth, F.R.S. (With Two Plates.)*

(MS. received February 8, 1926. Read March 8, 1926. Issued separately August 11, 1926.)

CONTENTS.

1. Introduction.

Because of the superficial resemblance of the digestive diverticula of the Lamellibranchs, and of many other Invertebrates, to the liver of the Vertebrates, and the discovery in them of glycogen by Bernard (1855), they became known as the "liver." Weber (1880) later introduced the name hepatopancreas as a result of his discovery of the secretory powers of the diverticula in the Crustacea. In spite of the fact that none of the constituents of bile has ever been discovered in the Invertebrates, and that the digestive diverticula are in no way analogous to the liver of the Vertebrates, as Jordan (1912) has shown in his review of the subject, the terms "liver" and "hepatopancreas," as well as the less questionable designation "digestive gland," are still generally used. Moreover, no attempt is made to distinguish between these organs in the different groups of Invertebrates although both their structure and function in, for example, the Lamellibranchs, Gastropods, Cephalopods, and Crustacea are totally different. In some cases they constitute a digestive gland; in others, including the Lamellibranchs, as I hope to show in this paper, their function is that of assimilation, and so they are most suitably designated digestive diverticula.

It is necessary, in order properly to determine the nature of any organ, to study both structure and physiology, since it is to the physiological assumptions of the morphologist and the morphological assumptions of the physiologist that the misconceptions of the past are due. In this research, therefore, I have not only examined the structure of the diverticula in a large number of species, but I have studied their physiology from as many aspects as possible, in the hope of determining definitely their nature.

This research was carried out at the Plymouth Laboratory during the winter of 1924–25, while I was holding a Carnegie Research Scholarship in Zoology of the University of Edinburgh. I wish to acknowledge my indebtedness to the British Association, the University of London, and the Royal Microscopical Society for granting me the use of their tables for various periods, to the Director and the Staff of the Laboratory for their kindness and help, and to Professor Ashworth for help in the preparation of this paper for publication.

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* The Carnegie Trust for the Universities of Scotland has made a grant to the author towards the cost of the plates, which is gratefully acknowledged.

2. METHODS AND LIST OF SPECIES EXAMINED.

FRENZEL (1885, 1886, 1893) is the only investigator who has carried out a comparative study of the digestive diverticula in the Lamellibranchs, but, as he was unable in the majority of cases to fix his material satisfactorily, most of his observations were made on isolated cells from fresh material. Fixation is in some cases very difficult, and many fixatives had to be tried before satisfactory results were obtained. I have indicated, therefore, the fixative employed after the names of the 34 species examined in the list given below.

Sections were stained with Delafield's hæmatoxylin and erythrosin, or with iron hæmatoxylin, sometimes with acid fuchsin as counterstain.

The structure of the digestive diverticula has been examined in the following species:—

Order PROTOBRANCHIA.
- *Nucula nitida* (Bouin).
- *Nucula radiata* (Bouin).

Order FILIBRANCHIA.
- *Anomia ephippium* (corr. sublimate in sea water).
- *Arca tetragona* (corr. sublimate in sea water).
- *Barbatia lactea* (corr. sublimate in sea water).
- *Glycimeris glycimeris* (corr. sublimate in sea water).
- *Mytilus edulis* (equal parts Bouin and absolute alcohol).
- *Modiola modiolus* (equal parts Bouin and absolute alcohol).
- *Modiolaria marmorata* (Bouin-Duboscq).
- *Pecten maximus* (corr. sublimate in sea water).
- *Pecten opercularis* (corr. sublimate in sea water).

Order EULAMELLIBRANCHIA.
- *Lima loscombi* (Bouin).
- *Ostrea edulis* (Bouin).
- *Astarte sulcata* (Bouin).
- *Kellya suborbicularis* (corr. sublimate in sea water).
- *Tellina crassa* (Bouin-Duboscq).
- *Donax vittatus* (corr. sublimate in sea water).
- *Spisula solida* (Bouin).
- *Venus fasciata* (Bouin-Duboscq).
- *Dosinia exoleta* (Bouin).
- *Tapes pullastra* (corr. sublimate in sea water).
- *Cardium edule* (equal parts Bouin and absolute alcohol).
- *Cardium norvegicum* (20% formalin).
- *Gari tellinella* (Bouin).
- *Mya arenaria* (Bouin).
- *Lutraria oblonga* (Bouin).
- *Solecurtus antiquatus* (Bouin).
- *Ensis siliqua* (Bouin).
- *Saxicava rugosa* (Bouin).
- *Gastrochæna dubia* (Bouin).
- *Pholas dactylus* (corr. sublimate in sea-water).
- *Pholadidea loscombiana* (Bouin-Duboscq).
- *Xylophaga dorsalis* (Bouin-Duboscq).
- *Teredo norvegica* (Bouin or Flemming).

I have been unable, unfortunately, to obtain good material of the Septibranchs in which, since alone amongst the Lamellibranchs they are carnivorous, different conditions may prevail. Owing to the kindness of Mr G. C. ROBSON, I was able to section a species of Cuspidaria from the British Museum, but, though the remainder of the alimentary canal was well preserved, the structure of the digestive diverticula could not be determined.

3. STRUCTURE.

The digestive diverticula form a darkly-coloured mass which surrounds the greater part of the stomach. They consist of blind tubules which unite with one another, and are in free communication with the stomach by way of ducts whose structure is distinct from that of the tubules.

The ducts are usually circular in cross section, although the outline of the lumen is undulating owing to variation in the height of the epithelium (see figs. 1 and 2). This epithelium resembles that of the stomach, of which it is a prolongation, and consists of tall, ciliated cells containing oval nuclei. It is surrounded by a thin layer of circular muscle. The protoplasm is not vacuolated, but in some species contains numerous highly refractile green, brown, or yellow granules near the free surface of the cells. This is particularly the case in Nucula, and I have also observed it in Arca, Glycimeris, Modiola, and Saxicava. The nature of these granules is not clear, but as these cells neither absorb nor secrete they are probably an excretion which accumulates in the same way as Marennin in green oysters. As in the gut, mucus cells may occur between the cells of the epithelium, and so may phagocytes, which are sometimes present in great numbers.

The junction between the epithelium of the ducts and that of the tubules may be sharply defined, as in Nucula and all the Eulamellibranchs examined, or may be gradual as in Mytilus (as described and figured by LIST (1902)) and the other Filibranchs examined, where the junctions in cross section often consist of two portions, the epithelium of the one being that typical of the ducts, while the other resembles that of the tubules.

The tubules are either round or oval in cross section (compare figs. 7 and 10), and are not surrounded by muscle, but at most by a few strands of connective tissue. They may be so numerous that they are packed tightly together with very little connective tissue between them, while in other species they may be spaced out with a corresponding increase in the amount of connective tissue, which may be "vesicular," as noted by MACMUNN (1900) in Ostrea, and is exceptionally well developed in Gastrochæna. In this tissue lie blood lacunæ and many wandering cells; strands of muscle are sometimes present, especially in Arca. The epithelium of the tubules is variable in height; the nuclei are very characteristic, being round, with a prominent nucleolus in the centre.

In sections, cilia can never be distinguished in the tubules, although in Nucula and all the Filibranchs examined the free edge of the cells is bounded by a fine cuticle (see figs. 4 and 6). This is particularly well marked in Glycimeris, where it has sometimes the appearance of very fine cilia. LIST has described and figured it in the Mytilidæ. I have never observed it in my sections of any of the Eulamellibranchs, while CARAZZI (1896, 1897) and VONK (1924) failed to find it in Ostrea, and GUTHEIL (1912) in Anodonta. In fresh material, on the other hand, FRENZEL (1886) states that the cells are covered with a "gleichmässig überziehenden Saum, welcher . . . einen niedrigen Deckel bildenden Härchen . . . zusammengesetzt sind." POTTS (1923) found in Teredo that the cells of the tubules specialised for the ingestion of wood had long cilia "beating with a rather languid motion, and easily retractile, so that, when ordinary reagents are used for fixation of material, it is impossible to demonstrate them in sections." On the projections which occur in this epithelium he found slender pseudopodia but no cilia. In the unspecialised region (which resembles that found exclusively in the other Lamellibranchs) he states that the cells have a border of retractile cilia, which he also observed in Pholas and Xylophaga.

I have examined tubules from the majority of the species sectioned, pressing them out under cover-slips, and observing them under high power. In most cases it was impossible to determine whether cilia were present or not, but in addition to the three cases in which POTTS observed them, I have seen them in *Spisula truncata*, *Spisula solida*, *Dosinia exoleta*, *Cardium echinatum*, *Gari tellinella*, and *Pholadidea loscombiana*. In Spisula the cilia can be distinguished with exceptional ease, and can be seen beating actively in all the tubules. The beat is usually very languid, varying as a rule between fifty and one hundred and fifty to the minute. Although it is difficult to decide the length of the cilia, some idea of it can be obtained from the fact that the length of beat may be about 15μ. As will be shown later, particles both enter and leave the tubules in all cases, which implies the presence of cilia, although in some species they may be retracted more readily than in others, especially when pressed out for examination.

According to the character of its protoplasm—the nuclei are identical in all the cells—the epithelium of the tubules may be divided into two regions, in one of which the protoplasm is extremely vacuolated and lightly-staining, and in the other less vacuolated and darkly-staining. The vacuolated cells are the more numerous and are always larger, although they vary greatly according to the size and contents of their vacuoles. These, particularly if the tissue has been fixed shortly after the animal has been taken from the sea, are often filled with green, brown, or yellow masses of varying size and shape. In *Pecten maximus* and *Pecten opercularis* the vacuoles and inclusions, which consist of a great number of minute brown spheres, are both exceptionally large, as shown in fig. 4. FRENZEL has described the colour, size, and properties of these inclusions, and figured them in colour, for all the species of Lamellibranchs which he examined, regarding them as characteristic of the different species. LIST disagrees with him, and points out that they cannot be a characteristic sign of a species since they are not constant, their nature depending wholly upon the food of the animal. In animals which have been starved the cells have few or no inclusions. At the same time, the size of the vacuoles certainly varies in different species, being much larger, for instance, in Pecten, Gari, Solecurtus, and Saxicava—where whole tubules may consist of a bounding membrane surrounding a number of great vacuoles (with or without contents), both nuclei and cell outlines being absent—than in the other species I have examined.

In the Mollusca generally, FRENZEL (1885, 1886, 1893) found three kinds of cell in the digestive diverticula—granule-cells (Körnerzellen), ferment-cells (Keulenzellen), and lime-cells (Kalkzellen). The last of these he never found in the Lamellibranchs he examined, the granule-cells in every case but one, and with them ferment-cells in the following genera only: Pecten, Mactra, Capsa, Donax, Solecurtus, Lima, Cardium, Cyprina, Petricola, Tellina, Scrobicularia, Mya, and Gastrochæna, and also in *Venus gallina* and *Venus verrucosa*, although in *Venus decussata* he found ferment-cells exclusively. He admits that the morphological development of the ferment-cells in the Lamellibranchs is "insignificant," and his sole criteria as to their presence seems to have been the size and intensity of colour of the included masses. I have examined species of ten out of the fourteen genera in which he found two kinds of cell, and I can find no evidence whatever of their presence; there is one type of cell only. In the Opisthobranch or Pulmonate Gastropods, where both granule- and ferment-cells are present, there is never any doubt as to their identity, for in each both nucleus and protoplasm are characteristic. In the Lamellibranchs the only variation is in the quantity of matter included in the cells.

The smaller, darkly-staining cells are always present. They are found scattered irregularly in small groups round the lumen in Nucula and all the Filibranchs examined (see figs. 4 and 5). They are often low, and lie between large vacuolated cells which meet above them and shut them off from the lumen. In the remaining Lamellibranchs the lumen of the tubules is not regular, as in the species just considered, but is elliptical, tripartite, or in the form of a cross, with crypts (using the term employed by GUTHEIL) at the extremities of the two, three, or four arms respectively, in which lie groups of these dark cells. The arrangement in Mya, in which there are two crypts, and in Teredo, in which there are three or four, are shown in figs. 7 and 10. The same regular arrangement has been described and figured in Anodonta by GUTHEIL.

These cells have been considered ferment-cells by some workers—for no other reason, apparently, than that they are slightly different from the other cells—but all the evidence points to their being young cells. They are most numerous at the blind end of the tubules, decreasing in number as these widen. This is conspicuously the case in Nucula, where they are often absent in the wider tubules (fig. 6), though the same condition may be found in many species. FRENZEL thought that the older cells might be replaced by a multiplication of young cells, while LÖNNBERG (quoted by LIST) found that the cells of the tubules in *Mytilus edulis* divide mitotically. LIST, who describes and figures these cells in the Mytilidæ with great care, found division stages in them occasionally, and also noted the ejection of parts of the older cells and the degenerate appearance of their nuclei, and so came to the conclusion that the dark cells (Ersatzzellen as he called them) were nests of young cells. GUTHEIL found mitosis not infrequently in the crypts in Anodonta, and observed that it was commonest when signs of degeneration were most pronounced. I have examined sections of the digestive diverticula in *Mya arenaria* stained with iron hæmatoxylin, in order to determine whether division takes place in the crypts. I have found it frequently in sections of animals which had been starved by keeping them in filtered sea water for a month. In these the older cells are often to be seen either free in the lumen or in the process of being expelled from the epithelium, many cells coming together in spherical masses, and then passing into the lumen in that condition. Mitotic figures are frequent and always in the crypts. Figs. 8 and 9 represent two such cases, one during division and the other immediately after it. In all cases (as was also observed by GUTHEIL) the nuclei come near the lumen before dividing, and the chromosomes are large and granular. I have never seen mitosis in sections of animals which had recently been fed, but it is quite common to find either the whole or parts of the old cells being cast off.

From the histological character, the distribution, and the behaviour of these small dark cells there seems, therefore, every justification for considering them young cells which, by dividing, are able to make good the loss resulting from the casting off of the old cells. A similar process goes on in the gut of the Crustacea and Insecta.

The epithelium of the digestive diverticula in all the Lamellibranchs examined, with the exception of *Teredo norvegica*, consists of one type of cell only. In the Teredinidæ, as SIGERFOOS (1908) and POTTS have shown, the digestive diverticula are of two kinds, the one resembling in every respect that found in the other Lamellibranchs, and the other consisting of wide, excessively thin-walled tubules, the epithelium of which is made up of a single layer of cells whose boundaries are either absent or very indefinite.

4. FUNCTION.

(*a*) *Historical Summary.*—The earlier investigators (for full details and bibliography, see LIST) all considered the digestive diverticula formed a "liver" which secreted bile and digestive enzymes. Frenzel (1886) states, with regard to the Mollusca generally (he failed to realise the different conditions that prevail in the various classes), "dass die Mitteldarmdrüse derselben, gerade wie die der Crustaceen, eine Verdauungsdrüse ist, d. h. dass sie ein Secret bildet und ausscheidet, welches zur Verdauung der in den Darmcanal aufgenommenen Speisen verwendet wird." Saint-Hilaire (1893) was the first to show that the digestive diverticula in the Mollusca serve as organs of absorption. He found that the vacuolated or granule cells in the Prosobranchs, Opisthobranchs, and Pteropods among the Gastropods, and in the Cephalopods, are not ferment-cells but absorptive cells. Carazzi (1896, 1897), working on the green oysters of Marennes, and later on oysters fed with iron sulphate, came to the conclusion that the "liver" in the Lamellibranchs is an organ concerned with assimilation. According to him, Marennin and iron are taken up by the epithelial cells of the gills, palps, and gut, and then transported by amœbocytes to the "liver," where they are assimilated and stored, some of the iron being later passed on to the gonad. He did not, however, exclude the possibility of the tubules being also to some extent secretory, although he considered the ducts the chief source of digestive enzymes.

As List has pointed out, the value of Carazzi's results is greatly lessened by his experimental methods. He kept oysters for four months in three litres of sea water, to which had been added 20 grams of a 10 per cent. solution of iron sulphate in distilled water, and then placed them in clean sea water for one or two weeks before fixing them. The animals had time to get thoroughly permeated with iron, which was found both in the epithelium of the gills, palps, and gut, and also in the "liver"; but there was no more reason for assuming that it had been absorbed by the former and passed on to the latter than that the reverse had occurred.

No such objection can be made to the experiments of List. He added Indian ink to the water in which a number of Mytilus were kept, and found that after a short time, sometimes only two hours, the particles were taken in by the granule-cells in the digestive diverticula. In sections, he found ink in the lumen of the ducts and tubules, and particles passing through the "Cuticularsaum" into the granule-cells, where they become concentrated in vacuoles, at first a few dotted round the wall of the vacuole, and later in such numbers as to form a solid black mass. When the animals ceased to be fed, the ink was quickly cast out, entire "Körnerballen" being ejected into the lumen and passing through the gut to the exterior. List also found that carmine was taken in in the same manner, though, as he notes, this is always dissolved to some extent, together with powdered litmus (which indicated by its colour that some of the vacuoles were acid and others alkaline) and iron. He concludes finally that the colour of the "liver" at any time depends entirely upon the food, and that it is primarily an organ of assimilation.

Enriques (1901), who worked at the same time as List, agreed with Frenzel that the cells in the tubules of Ostrea were of only one type, but he considered them to be ferment-cells, not granule-cells, since he was unable to identify within them ingested chloroplasts such as he had found in the granule-cells in many Gastropods, and since the spectroscopic examination of a solution in alcohol of the brown inclusions gave no indication of chlorophyll. He admitted, however, that his oysters had been out of the sea for two or three days. He did not agree with Carazzi that secretion takes place in the ducts, considering the mucus cells their only secreting elements, the function of the ducts being purely that of transport. Although the cells of the tubules may absorb, their main function, according to Enriques, is the secretion of digestive enzymes.

In *Anodonta cellensis*, Gutheil states that the tubules are composed of one type of cell, which he regards as secretory. Like Enriques, he noted the presence of great numbers of yellow or brown balls in the cells, from which they could be pressed out in teased material. He made no physiological experiments, but noted that the brown spheres remained at the basal end of the cells until they attained a certain size, when they moved to the surface of the cell and passed out—as enzymes, in his opinion. He could not follow in any detail the process of secretion, and attributed the loss of colour after the animals had been starved to a shrinkage in the amount of secretion. He also decided that the same cells could absorb since he found within them fine droplets of fat.

Potts found that of the two regions of the "liver" in Teredo, the one with the wide thin-walled tubules, which he calls "digestive," is specialised for the intracellular digestion of wood, fragments of which are taken in both by the cells of the epithelium and by free cells in the lumen; and the other, described as "excretory," and which resembles the digestive diverticula of the other Lamellibranchs, contains "large quantities of highly refringent, resistant granules whose chemical nature is not known but which are probably excretory." He found that particles of Indian ink were taken in by the cells of these tubules.

In my own work on *Mya arenaria* (1923) I was unable to carry out feeding experiments, and accepted the presence of digestive enzymes in extracts of the "hepatopancreas," as I called it, as evidence that it is an organ of secretion (a safe assumption in many groups of animals but not in the Mollusca). Enzymes capable of digesting the carbohydrates—starch, glycogen, sucrose, maltose and lactose—were found, also a protease acting in acid media, and a lipase. Digestive enzymes have also been found in extracts of the digestive diverticula by, amongst others, Fredericq (1878), who found a protease in Mya and Mytilus; Mitra (1901), who found amylase and invertase in Anodonta; Van Rynberk (1908), who found amylase in Mytilus; Dakin (1909), who found amylase, protease, and lipase in Pecten; and Heymann (1914), who found protease, lipase, and a number of carbohydrate-splitting enzymes in Ostrea.

Finally, Vonk (1924) fed *Ostrea edulis* with Indian ink and carmine, and found that these were taken in as round masses in the cells of the tubules—exactly as List had found in Mytilus. Only very occasionally could he see a distinct membrane round the vacuoles, and he never observed particles being passed on to the amœbocytes as described by Carazzi. He also fed oysters on plankton for three to five days, and compared them with oysters which had been starved for two or three weeks. In the former, diatoms were numerous throughout the gut, while "Im Gegensatz zu ungefütterten oder mit Farbstoff genährten Tieren zeigten nun die Leberzellen dieser Austern zahlreiche grüne Einschlüsse von sehr unregelmässiger Form." He never found whole diatoms in the cells of the tubules, though some green algæ appeared to be taken in whole. The green colour of the inclusions in sections he accounts for by quoting Molisch to the effect that the brown pigment of diatoms is extracted by cold alcohol, leaving a green pigment. Vonk concludes that the oyster most probably assimilates food by phagocytosis in the cells of the tubules, adding that this agrees with the complete lack of protease in the stomach.

(*b*) *Feeding Experiments.*—I have carried out feeding experiments so as to determine where and how absorption takes places. For this purpose I used suspensions in sea water of iron saccharate (Ferrum Oxydatum Saccharatum) and of blood corpuscles of the dogfish. Animals were placed in these suspensions (which were quickly cleared by their ciliary activities) and fixed after definite periods; those fed on the iron compound in a mixture of 5 per cent. ammonium sulphide in 95 per cent. alcohol to which was added, immediately before use, an equal quantity of Bouin's fluid. This use of Bouin is my own modification of the usual method of fixing for iron; I find that it gives a much better fixation, while iron can be demonstrated just as well. Animals fed on blood corpuscles were fixed in Flemming, or in any fixative which had previously been found suitable. Sections were cut 6μ or 8μ thick. Iron was demonstrated by placing the slides for a few minutes in 10 per cent. potassium ferrocyanide and then in very dilute HCl, which converts it into Prussian blue; alum carmine was used to stain the sections and gives very beautiful results. Sections of animals fed with blood were stained with iron hæmatoxylin and acid fuchsin or by Arnold's method (for details see *Arch. Zellforsch.*, III, 1909, p. 434) after fixation in Flemming, or with Delafield's hæmatoxylin and erythrosin after other fixatives.

A number of animals were fed with iron, the best results being obtained in Nucula, Mya, and Teredo, an account of which will be given. The animals were starved previous to feeding, —Nucula for two weeks, Mya for a month, and Teredo for one or two days (if kept long out of wood Teredo dies).

In Nucula iron-feeding gives most striking results. Iron is taken into the lumen of the gut in great quantity—so that the lumen appears as a solid sheet of blue in the sections—but it is absorbed exclusively in the cells of the tubules, the junction of which with the ducts being vividly marked by the entire absence of blue in the epithelium of the ducts. Fig. 5 represents a portion of the epithelium of a tubule fixed six hours after feeding. Iron is already being absorbed in large quantities. The border cuticle cannot be seen and the free edges of the cells are very irregular, being extended in the form of pseudopodia (in some cases these extensions attain great length and are very attenuated). The iron is taken up in small vacuoles, those near the lumen being only partially filled with iron and having a lightly-coloured and granular appearance, while those in the more basal region of the cells are larger, and so packed with iron that they exhibit a uniform deep blue. Absorption takes place almost exclusively in the older cells and always in discrete round vacuoles; there is never any general absorption of tiny granules of iron throughout the cytoplasm, nor any diffuse blueness in it. A certain amount of absorption takes place in the young cells, but the vacuoles are more irregular. Fig. 6 represents an entire transverse section of a tubule two days after feeding. In this case all the vacuoles are packed with iron, and are uniformly blue. The vacuoles are extremely plentiful, the majority being crowded in the basal end of the cells, where they seem to be embedded in the cytoplasm, those nearer the lumen lying in open spaces in the protoplasmic network. The free edge of the cells, the absorption of iron having ceased, is regular in outline, and the border cuticle can easily be distinguished. Sections of the digestive diverticula three to five days after feeding show much the same conditions, but a certain amount of iron is being taken over by the amœbocytes, which are numerous between the tubules, although they are not so plentiful in the walls and lumen of the gut as in the higher Lamellibranchs. There is no sign of any rejection of iron into the lumen of the tubules. No attempt has been made to follow the course of the iron further.

A tubule of the digestive diverticula in Mya, one day after feeding with iron, is represented in fig. 7. The stomach of the animal was full of a thick brown suspension of the iron compound, and a certain amount of this can also be seen in the lumen of the tubule. It is also being ingested by one of the cells, which projects beyond the others, not, apparently, either as fine particles or in solution, but as a solid mass which is enclosed directly by the protoplasm. It is difficult, however, to be absolutely certain on this point. Further within the cells it is present in vacuoles, neither so large and so numerous nor so regular in shape as in Nucula, but never as scattered particles or diffuse. Where the vacuoles are not quite full the iron is massed round the margin in the same way as the Indian ink in LIST's experiments on Mytilus. Amœbocytes have entered two of the cells which contain iron, but none are present in any of the cells free from iron. I have never found iron in the young cells. In no other part of the gut was iron assimilated.

In Teredo, one day after feeding, iron was present in the lumen of the gut and of both portions of the digestive diverticula; but to a much greater extent in the unspecialised portion. As shown in fig. 10, it is taken in by the cells of these tubules, appearing as somewhat irregular masses within large vacuoles. It is found very occasionally in the cells of the specialised portion, and in the free cells which are present in the lumen, and always in a rather diffuse condition. Most iron is present in the amœbocytes—which occur in very great numbers between the tubules of the unspecialised region, and are usually laden with fat globules and other food—to which it is apparently almost immediately passed by the cells of the tubules. In the figure the amœbocytes represented are so full of iron that only the nucleus—and that with difficulty—can be distinguished from the mass of blue.

Cardium edule, *Mya arenaria*, and *Teredo norvegica* gave the clearest results after feeding with blood corpuscles. The corpuscles were taken into the gut freely, so that the stomach was full of them within a short time. In the case of Cardium and Mya, however, they were all ingested by the amœbocytes, which are everywhere present in and beneath the epithelium of the gut (including, of course, the ducts of the diverticula), and also free in the lumen. The corpuscles entered the ducts in large numbers, but were there seized by these phagocytes and taken into the wall of the ducts, passing between the cells of the epithelium. Sections of a specimen of Cardium, which had been fixed two days after feeding, and stained with Delafield's hæmatoxylin and with just enough erythrosin to colour the corpuscles and nothing else, showed the presence of great numbers of corpuscles all within phagocytes, sometimes in the connective tissue, but usually between the cells of the ducts, which could everywhere be readily distinguished on account of the red colour of the corpuscles. Never, however, did they succeed in reaching the tubules.

Exactly the same condition is found in Mya. Figs. 1, 2, and 3 represent three stages in the transport of the ingested corpuscles, the animal having been fixed six hours after feeding. In fig. 1 two corpuscles are shown ingested by phagocytes lying between the cells in the epithelium of one of the ducts. Fig. 2 represents a phagocyte containing a corpuscle in the act of passing through the circular muscle which surrounds the duct, while in fig. 3 is shown a corpuscle ingested by a phagocyte, which was lying in the connective tissue between the ducts and tubules. Animals fixed with Flemming's strong fluid from four to six days after feeding showed later stages in the digestion of corpuscles by phagocytes, the corpuscles being irregular and entirely without structure, and surrounded by numbers of fat globules.

Characteristic of the Lamellibranchs are the large numbers and great activities of these phagocytes, and this has been commented on by the majority of the investigators of this class. I have given an account (1923) of the presence of these phagocytes in Mya, and have shown that they often contain large hard particles, such as sand grains and the tests of diatoms, so that the surface of the gut is often difficult to cut in sections, and has a dark grey colour. The gut of Ensis, and other Lamellibranchs in which the sorting mechanism on the gills and palps allows relatively large hard particles to enter the gut, has the same appearance.

In Teredo, as shown in fig. 11, which is drawn from a specimen three days after feeding with blood, corpuscles were actually ingested by the cells of the tubules. The digestive diverticula in the Teredinidæ are spread out in a thin sheet round the ventral surface of the stomach, and the ducts are short and wide. As already noted, the phagocytes are most numerous between the tubules of the unspecialised portion, and they were often found with contained corpuscles (amongst other things), a typical case being shown in fig. 12. The corpuscles are taken in by the cells of the unspecialised tubules (see fig. 11), and lie in vacuoles within them, but they are often seized by phagocytes which remove them from the cells. I have never found corpuscles in the diverticula specialised for wood ingestion.

It is interesting, at this point, to note that in the Nudibranch *Archidoris tuberculata* I have observed that blood corpuscles are taken in by the absorptive cells in the digestive gland (which in the Nudibranchs contains both secretory and absorptive cells) in very great numbers and there digested. There is a wide opening from the stomach into this organ, while phagocytes are not found in the epithelium or in the lumen of the gut in the Gastropods, so that the corpuscles were never prevented from entering the digestive gland.

From the results of the experiments here described, and of those of Carazzi, List, Potts, and Vonk, there can be no doubt that the cells of the digestive diverticula in the Lamellibranchs absorb. The epithelium of the gut, and of the ducts leading into the diverticula, despite the contrary assertions of Carazzi, has no power of absorption (although the phagocytes everywhere present between its cells take in solid particles), but is concerned purely with transport, as is shown by the universal presence of cilia (with the solitary exception of the area which secretes the gastric shield in the stomach) and mucus glands.

All the evidence points to the intracellular digestion of food particles in the cells of the diverticula. Insoluble particles of Indian ink are ingested, while in the case of Teredo, entire blood corpuscles are taken in by the cells of the unspecialised tubules, and fragments of wood by the cells of the tubules specialised for that purpose. The cells of the tubules in Mya and Cardium have no opportunity to absorb corpuscles, owing to the prior seizure of the latter by phagocytes. The presence of vast numbers of green and brown globules in the cells of the tubules in the case of animals taken directly from the sea, which disappear when the animals have been starved for some weeks (as I have observed in many cases), so that the tissue becomes finally almost colourless, with only a few orange or yellow concretions here and there—the indigestible remnants of intracellular digestion in all probability—is additional evidence. I have been able to confirm the statement of Vonk that the globules reappear when starved animals are fed on diatoms, their natural food. The manner in which iron is absorbed is also strongly indicative of intracellular digestion; instead of being taken in a more or less diffuse state, or in numerous, very minute vacuoles, as in true absorption—for example, in the gut of insects, as described by Steudel (1913), or in the salivary glands of Murex, as shown by Hirsch (1924), in both of which intracellular digestion does not take place—it is always found within large discrete vacuoles. Whether it is taken into the cells in solution or as solid matter (and in Mya, as figured, it appears to be ingested as a solid mass), the fact that, like the Indian ink in List's experiments on Mytilus, it invariably becomes aggregated in these large vacuoles is, I think, an indication of intracellular digestion. Moreover, the free surface of the cells which absorb the liquid products of digestion is never extended or drawn out into pseudopodia, as in the digestive diverticula of the Lamellibranchs.

Lastly, there is the question of the presence of a great number of digestive enzymes (to which reference has already been made) in extracts of the diverticula. If it can be proved that the cells do not secrete, then the presence in them of these enzymes can only be accounted for on the assumption that they constitute an organ of intracellular digestion. There is obviously no need for digestive enzymes in a tissue which absorbs the soluble products of extracellular digestion—glucose, amino-acids, fatty acids and glycerol.

(*c*) *The Question of Secretion.*—Since there is only one type of cell in the diverticula, and this certainly absorbs, it must perform a double function if secretion occurs. This, of course, is not impossible; thus HIRSCH (1924) has shown that the salivary glands of Murex both secrete and absorb. Histological examination of the cells gives no support to the view that they secrete; ENRIQUES and GUTHEIL, both of whom thought that secretion takes place, described and figured typical digestive vacuoles, and the same is true of FRENZEL. GUTHEIL'S explanation of the loss of colour in a starved Anodonta as being due to a reduction in secretion is unsatisfactory; both HIRSCH (1915) and KRIJGSMAN (1925) have demonstrated that in the Gastropods the secretory cells contain secretion during periods of starvation.

If it could be proved that certain enzymes were present in the tissue of the diverticula and were never found in the stomach, that would provide conclusive evidence that secretion does not take place. There are, however, complications. In the first place, amylase and glycogenase are always present in the stomach as a result of the dissolution of the head of the style and the release of the contained enzymes, while the invariable presence of great numbers of phagocytes in the lumen of the stomach complicates tests for lipase and protease. The phagocytes must contain both these enzymes, since they will take in and digest blood corpuscles on which the animal has been fed, and also droplets of neutral olive oil stained red with Nile-blue sulphate, which turn blue shortly after ingestion owing to the digestion of the fat and the consequent formation of fatty acids which give a blue colour with the stain. Experiments carried out with the stomach fluid from the larger Lamellibranchs, *Pecten maximus*, *Cardium norvegicum*, *Dosinia exoleta*, *Ostrea edulis* and *Mya arenaria*, showed that, though fibrin and egg albumen stained with carmine or Congo red were not digested, and quantitative tests for lipase with olive oil and methyl acetate gave inconclusive results, yet positive results were given by the most delicate tests for protease—the coagulation of calcified milk, and for lipase—the turning yellow of milk which had been made alkaline with sodium carbonate and coloured pink with phenol red. Control experiments invariably gave negative results. This slight activity is probably due entirely to the enzymes from the phagocytes, and it is not necessary to postulate the presence of a secretion from the digestive diverticula. HEYMANN (1914) found protease in the blood of Ostrea, probably from the same source.

The acidity of the stomach contents has usually been regarded as the result of a secretion from the "liver." I have shown in a recent paper (1925), however, that this acidity is produced by the dissolution of the crystalline style, which is invariably the most acid substance in the alimentary system. If the style is extracted or induced in various ways to disappear, the hydrogen-ion concentration in the stomach falls considerably, until it approximates to that of the mantle cavity, and is much lower than that of the tissue of the diverticula. I have recently confirmed and extended these experiments on *Ostrea edulis*. Here again there is no evidence of any secretion from the diverticula.

By injecting into the tissues some form of iron solution or colouring matter which can later be identified in sections, it is possible in many Invertebrates to detect these substances later in the secreting cells of the digestive glands. This has been shown to be the case in Crustacea by CUÉNOT (1895), JORDAN (1904), and myself (1924); in Insecta by STEUDEL (1913), and in Gastropoda by CUÉNOT (1892, 1900), and myself (unpublished work). CUÉNOT considered the cells in which these substances were found to be invariably excretory (they are, of course, also found in the true excretory organs), but JORDAN has shown that this is not the case. Substances in solution in the blood-stream pass into the secreting cells, together with the material needed for the elaboration of ferments, and so far from being quickly excreted, JORDAN found iron in the secretory cells of Astacus thirty-six days after it had been injected. Moreover, the "excreted" material is immediately taken up by the absorptive cells which surround the secretory cells in the digestive gland of the Crustacea and higher Gastropoda, such as the Tectibranchs and Nudibranchs, as I also have observed in many cases. Cuénot (1900) injected various colouring matters into fifteen species of Lamellibranchs, but found no "excretory" cells in the "liver"; excretion took place exclusively in the nephridia and pericardial glands. I have injected a 0·5 per cent. suspension of iron saccharate in sea water by way of the foot, muscle, or edge of the mantle (afterwards washing the animals thoroughly to prevent any of the fluid entering the mouth), into *Glycimeris glycimeris*, *Mytilus edulis*, *Pecten maximus*, *Ostrea edulis*, *Cardium norvegicum* and *Mya arenaria*, fixing the digestive diverticula in the usual manner from two to six hours later. In no case was there any trace of iron in the cells, although it was often found in the blood lacunæ and in the amœbocytes. Yet when Gastropods such as Doris or Scaphander were treated in the same way the secretory cells were coloured blue. Similarly, when pilocarpine was injected there was no change in the activity of the cells such as might be expected if they secreted.

On the other hand, iron was found in the epithelium of the style-sac four hours after injection in the case of Mytilus, as shown in fig. 13. Extremely minute granules were present immediately above the nuclei and also nearer the surface of the cells and in the lumen. In Pecten, although iron was never identified in the style-sac with certainty, there was a great increase in the number of fine colourless granules after pilocarpine had been injected.

There is thus no evidence of any secretion of digestive enzymes save in the epithelium of the style-sac.

5. General Discussion.

Histological examination has revealed the presence of one type of cell only in the digestive diverticula of the Lamellibranchs. The results of feeding experiments by previous workers and by myself show that these cells are capable of assimilating both soluble and insoluble particles, both of which are taken into large vacuoles, which probably contain digestive enzymes, where they are digested intracellularly. There is no evidence that any of the cells can secrete.

Among the Metazoa, intracellular digestion is known to occur in the Porifera, Cœlenterata, Turbellaria, to some extent in the Echinoidea, and in the Mollusca (for full details and bibliography see Hirsch (1925)).* In the latter it is not found in the highly evolved Cephalopods, while in the Gastropods (as I hope to show in a later paper) there is a transformation of the digestive diverticula from purely absorptive to absorptive and secretory organs.

In the Lamellibranchs there is no such development in the function of the diverticula, the explanation for this lying in the similarity of food and feeding mechanisms throughout the

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* Although in the Arthropoda generally digestion is exclusively extracellular, there are two interesting cases of intracellular digestion in parasitic species. In the tick, Ornithodoros, according to Christophers (1906), blood corpuscles sucked from the host are digested intracellularly both in the large epithelial cells of the alimentary sac and in free cells, the origin of which he was unable to determine. Reichenow (1918) found that in the mite, Liponyssus, the large cells of the gut are amœboid and ingest corpuscles from the blood of the host, digesting them intracellularly. After becoming gorged with food, these cells are detached and fall into the lumen of the gut.

In the Brachiopods, the feeding processes of which are closely analogous to those of the Lamellibranchs, intracellular digestion probably occurs. Ashworth (1915) describes the structure of the "liver" in the larvæ of Lingula and Pelagodiscus as being quite distinct from that of the remainder of the gut, no cilia are to be seen in sections of the "liver," while the cells are highly vacuolated and occasionally contain, in Lingula, ingested unicellular algæ. Other observers (for details, see Jordan (1913)) have also noted the passage of food into the cavity of the "liver." Professor Ashworth has kindly permitted me to examine his sections, and certainly from the presence of the ingested algæ and the general structure of the "liver," I think there is good evidence that intracellular digestion takes place in the Brachiopods in much the same manner as in the Lamellibranchs.

class; the fact that, in the face of this similarity, FRENZEL found different conditions in the diverticula of two species of the same genus, Venus, is sufficient to throw doubt on his conclusions. All the Lamellibranchs—with the exception of the carnivorous Septibranchs, which must be excluded from any generalisation here made, and to some extent the Teredinidæ, which will be discussed later—obtain their food by means of ciliary currents on the gills and palps, which select only the smallest particles for subsequent entrance into the gut. In the stomach there is a second selection, large particles being passed directly into the mid-gut and smaller particles being conducted to the opening of the ducts leading into the digestive diverticula. NELSON (1918) has described the selective mechanism in the stomach of *Modiola modiolus*, and I have described a similar one in *Mya arenaria*, and have observed its presence in many other species. There is at the same time a certain extracellular digestion of carbohydrates in the stomach by the enzymes of the style.

For intracellular digestion, it is essential that only very small particles should be presented to the ingesting surface, which should be as extensive as possible (*e.g.*, the increase in surface provided by the mesenteries in Actinians, by the ramifications of the gut in many Turbellarians, and by the large number of flagellated chambers in the sponges). Both of these conditions are fulfilled in the Lamellibranchs; none but the very finest particles survive the rigorous selection of the various sorting mechanisms, and the action of the enzymes from the style, and pass into the digestive diverticula, which are composed of a great number of ramifying tubules which present a large surface. A continuous circulation is maintained in these tubules by the action of the long retractile cilia, so that food particles are brought in and the indigestible remnants of intracellular digestion removed. The fact that the two operations take place (as LIST experimentally demonstrated) implies the presence of cilia, even though they can never be seen in sections, and only in certain cases in fresh material. There is no system of longitudinal and circular muscles such as ensures a similar circulation in the Crustacea (for details and literature on this point see my paper on Nephrops (1924)). The presence of retractile cilia in cells which digest intracellularly has also been observed in the Cœlenterata by GREENWOOD (1888) and others. The glucose formed by the action of the style enzymes on carbohydrates in the food will also be absorbed by the cells of the tubules.

The process of digestion would seem to be as follows: Particles are taken into the vacuoles and there acted upon by enzymes. Material which is of use to the animal, such as iron, is then passed on to amœbocytes or stored (the connective tissue round the tubules is often rich in glycogen), while indigestible substances, like Indian ink, which is never passed on to the amœbocytes, are expelled. In Pecten (fig. 4) yellow or brown globules of excretion are massed together in large cavities in the older cells, and are found in the same condition after expulsion from the cells in the lumen of the tubules, ducts, mid-gut and rectum. The brown colour of this excretion is due to the presence of ingested chlorophyll and the products of its decomposition, which accounts for the "entero-chlorophyll" found by MACMUNN (1900) and others.

The Teredinidæ, besides possessing the usual ciliary mechanisms, though to a reduced extent, feed by swallowing the fragments of wood scraped off by the specialised shell valves, and it is very significant that the adaptation which enables them to digest the wood takes the form of tubules specialised for its intracellular digestion, and not the elaboration of an extracellular cellulase, as in such Gastropods as Helix or Aplysia which are also able to digest cellulose.

Correlated, no doubt, with the retention of intracellular digestion throughout the Lamellibranchs, is the utilisation of phagocytes for the direct ingestion of larger particles than those which can enter the digestive diverticula (whole diatoms are never found in the latter but are frequently to be seen in phagocytes). They are certainly less numerous in Nucula than in the higher Lamellibranchs, while in the Gastropods, where extracellular digestion is better developed, phagocytes do not occur in the gut.

6. SUMMARY.

1. The structure of the digestive diverticula in thirty-four species of marine Lamellibranchs has been studied.

2. The diverticula consist of blind tubules which open into the stomach by way of ciliated ducts, the epithelium of which resembles in structure and function that of the remainder of the gut.

3. There is only one type of cell in the tubules. There are darkly-staining young cells, the nuclei of which divide mitotically, but when older the cells are very vacuolated and contain great numbers of coloured granules which disappear after starvation.

4. In the Teredinidæ there are tubules specialised for the digestion of wood; the condition in the carnivorous Septibranchs has not been examined.

5. A border cuticle can be seen in sections of the tubules in Nucula and the Filibranchs, but not in the Eulamellibranchs. In fresh material long retractile cilia can be distinguished in a number of species and are probably present in all cases.

6. After feeding with iron saccharate in suspension, this is found later lying within large vacuoles in the cells of the tubules, being afterwards passed on to the amœbocytes.

7. Blood corpuscles from the dogfish are taken into the gut freely, but are ingested by phagocytes before they reach the tubules, except in the case of Teredo, where they are taken in by the cells of the unspecialised tubules.

8. The manner in which particles are taken in, and the presence of digestive enzymes in extracts of the diverticula point to the presence of intracellular digestion.

9. There is no histological evidence that the cells of the tubules secrete. The presence of enzymes in the stomach can be accounted for by the dissolution of the crystalline style and the occurrence of great numbers of phagocytes free in the lumen; the acidity of the gut is due to the dissolution of the style; injections of iron and pilocarpine fail to demonstrate the presence of secretory cells elsewhere than in the epithelium of the style-sac.

10. The diverticula provide the extensive surface characteristic of the alimentary systems of animals which possess intracellular digestion, while, as a result of the action of the various sorting mechanisms, only the very smallest particles are presented to the ingesting surface.

11. The digestive diverticula of the Lamellibranchs possess none of the functions of a liver or of a pancreas, but are organs of absorption and of intracellular digestion.

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8. DESCRIPTION OF THE PLATES.

List of Reference Letters.

B.C.	Border cuticle.
B.M.	Basement membrane.
B.P.	Boundary of phagocyte.
C.	Cilia.
C.M.	Circular muscle.
Cp.	Crypt of young cells.
C.T.	Connective tissue.
D.N.	Dividing nucleus of young cell.

F.I.	Iron in process of ingestion.
F.L.	Iron in lumen of tubule.
F.V.	Iron in vacuoles.
F.V.P.	Vacuoles partially full of iron.
Ft.	Fat globules.
I.B.C.	Ingested blood corpuscles.
I.M.	Ingested matter in vacuoles.
I.M.P.	Ingested matter in phagocytes.
L.	Lumen.
N.A.D.	Nuclei of young cells immediately after division.
N.B.	Nucleus of ingested blood corpuscle.
N.D.	Nucleus of epithelial cell of duct.
N.P.	Nucleus of phagocyte.
N.S.	Nucleus of epithelial cell of style-sac.
N.T.	Nucleus of cell of tubule.
Nu.	Large nucleolus of nucleus of tubule cell.
O.C.	Old, vacuolated cells of tubules.
P.	Phagocyte.
P.F.	Phagocyte containing ingested iron.
S.	Secretion of style-sac epithelium containing injected iron.
Y.C.	Young, darkly-staining cells of tubules.
Y.M.	Yellow concretions.

PLATE I.

Fig. 1. *Mya arenaria.*—Transverse section through a portion of a duct leading into the digestive tubules, six hours after feeding with blood from a dog-fish. Two blood corpuscles are shown lying within phagocytes between the epithelial cells. The nucleus of one of the phagocytes does not appear in the section. Fixed Bouin, stained Delafield's hæmatoxylin and erythrosin. 6μ. (× 1200.)

Fig. 2. *Mya arenaria.*—Another section in which a phagocyte with an ingested corpuscle is shown passing out of the epithelium through the circular muscle which surrounds the duct. 6μ. (× 1200).

Fig. 3. *Mya arenaria.*—Same as above. A phagocyte with an ingested blood corpuscle observed in the connective tissue between the ducts and tubules. (× 1200.)

Fig. 4. *Pecten opercularis*—Transverse section through a portion of a digestive tubule from a fresh animal, showing the border cuticle, the irregular arrangement of the nests of young cells, and the accumulation of yellow concretions in old cells without nuclei. Fixed corr. sublimate in sea water, stained Delafield's hæmatoxylin and erythrosin. 6μ. (× 1200.)

Fig. 5. *Nucula* sp.—Transverse section through part of a tubule six hours after feeding with iron saccharate. This is being absorbed, vacuoles near the base being full of it, while those near the lumen are only partially full. The free surface of the cells is irregular and there is no sign of the border cuticle. Fixed and stained by the methods described in the text, p. 710. 8μ. (× 1200.)

Fig. 6. *Nucula* sp.—Transverse section through an entire tubule two days after feeding with iron. Absorption has ceased, all the vacuoles are full of iron, the free surface of the cells is regular, and the border cuticle can be seen. Technique as on p. 710. 8μ. (× 1200.)

PLATE II.

Fig. 7. *Mya arenaria.*—Transverse section through an entire tubule one day after feeding with iron. This can be seen in the lumen, in the process of being taken into the cells, and lying in vacuoles within them. The crypts of young, darkly-staining cells with numerous nuclei are shown. Technique as on p. 710. 6μ. (× 1200.)

Fig. 8. *Mya arenaria.*—Transverse section through a crypt of young cells from an animal which had been starved for five weeks. One of the nuclei has migrated near the lumen and is dividing. Fixed strong Flemming, stained iron hæmatoxylin and acid fuchsin. 6μ. (× 1800.)

Fig. 9. *Mya arenaria.*—A similar section, showing the last stage in the division of a nucleus in a crypt. Fixed strong Flemming, stained iron hæmatoxylin. 6μ. (× 1200.)

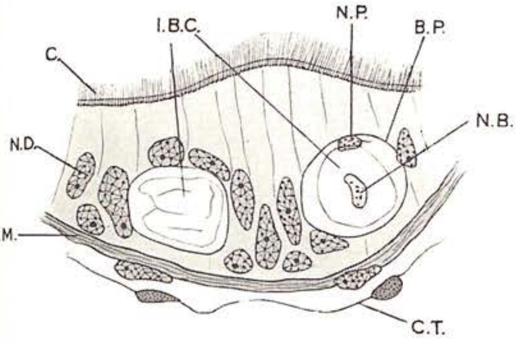
Fig. 10. *Teredo norvegica.*—Transverse section through an unspecialised tubule one day after feeding with iron, which is lying in large vacuoles in the older cells and within the phagocytes which lie between the tubules. There are three crypts of young cells. 6μ. (× 1200.)

Fig. 11. *Teredo norvegica.*—Two cells from a digestive tubule three days after feeding with blood. An ingested corpuscle is shown lying within a vacuole in one of the cells. Fixed strong Flemming, stained Arnold's method. 6μ. (× 1200.)

Fig. 12. *Teredo norvegica.*—Phagocyte from between the tubules three days after feeding with blood; it contains a large quantity of ingested matter, including a blood corpuscle. Technique as above. (× 1200.)

Fig. 13. *Mytilus edulis.*—Transverse section through the epithelium in the middle of the groove which bears the style, four hours after injection with a suspension of iron saccharate. Minute droplets of secretion containing iron in solution are being produced and passed out of the cells. 6μ. (× 1200.)

Dr C. M. YONGE on "The Digestive Diverticula in the Lamellibranchs."—PLATE I.



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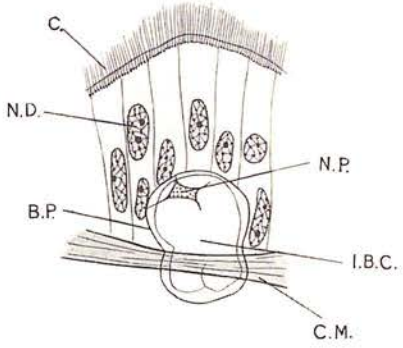

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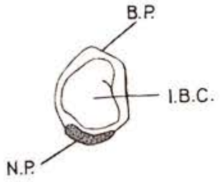

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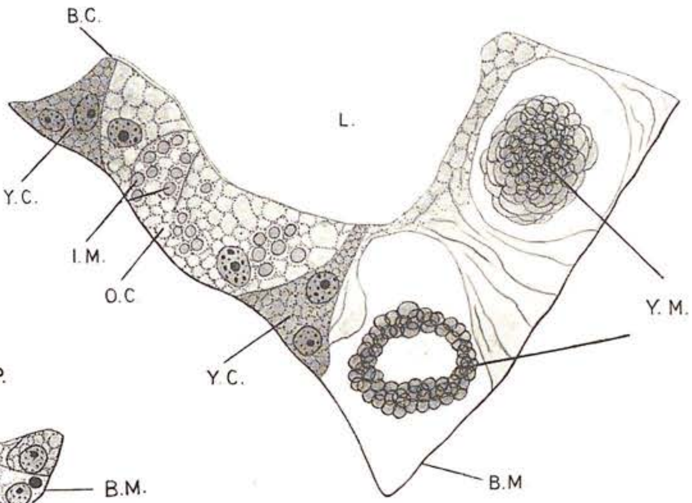

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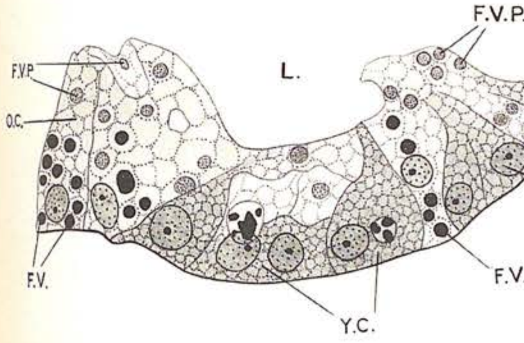

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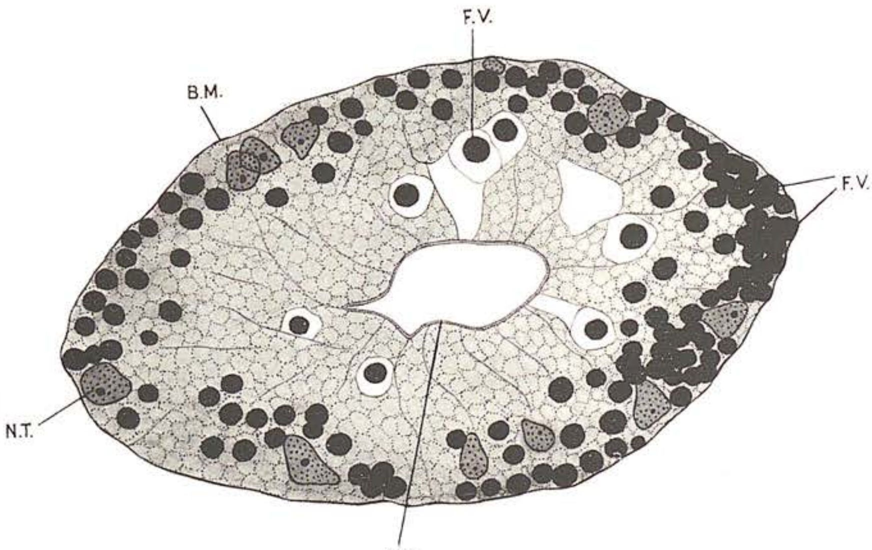

FIG. 6.

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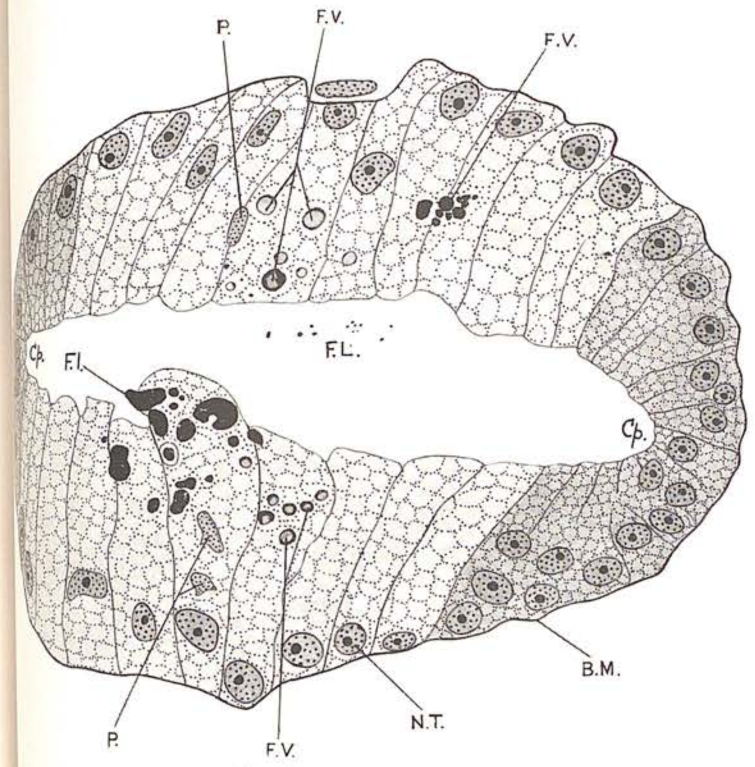
Dr C. M. YONGE on "The Digestive Diverticula in the Lamellibranchs."—PLATE II.



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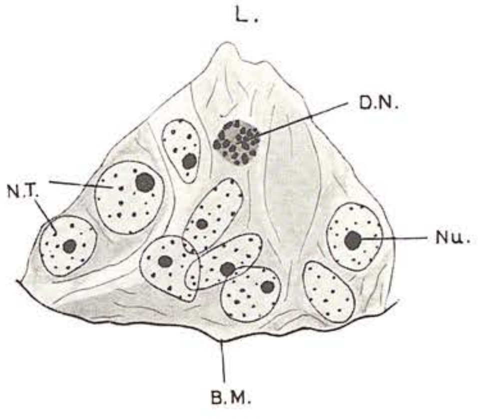

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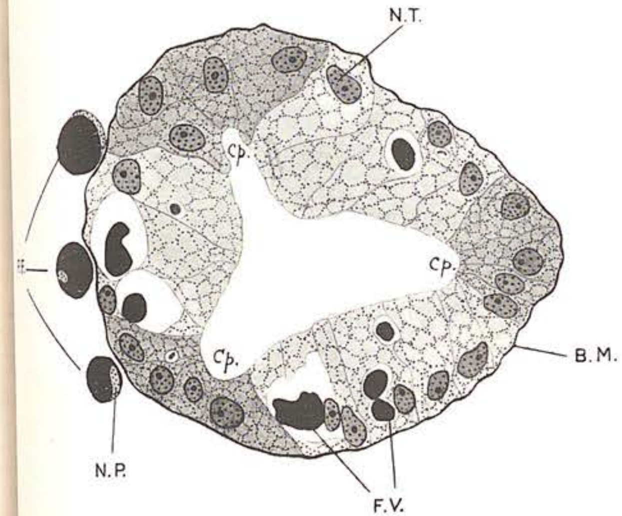

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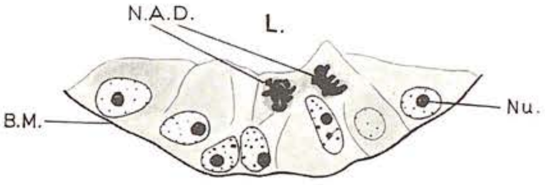

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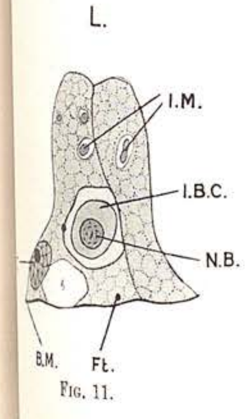

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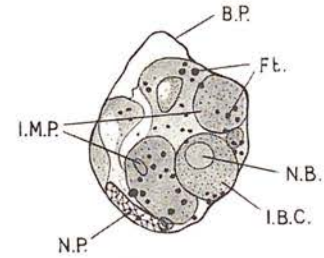

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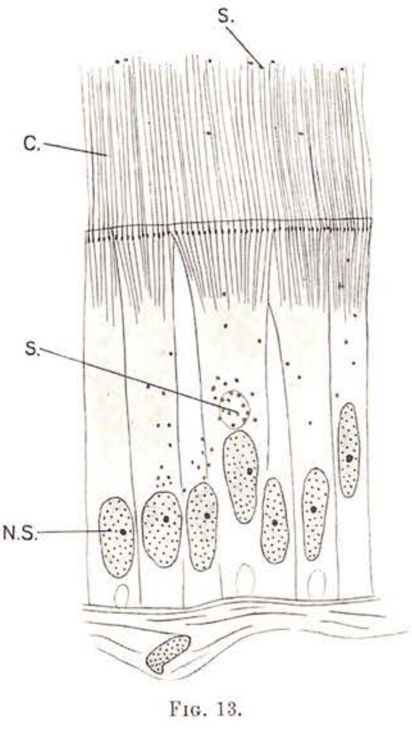

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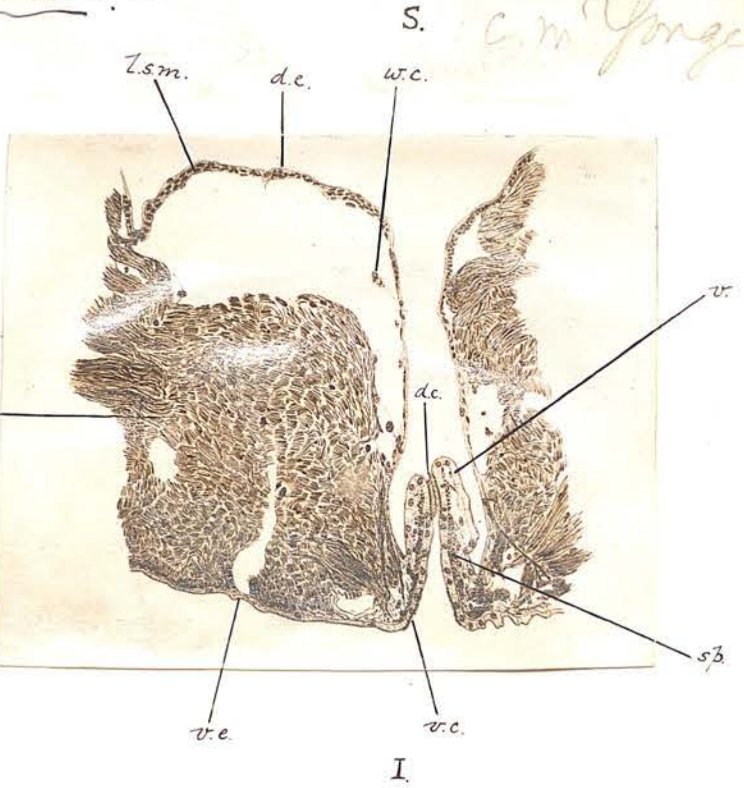
Structure Physiology &c of the Septibranchs. &c

C. M. Yonge 1927 D.Sc

Th. Scot



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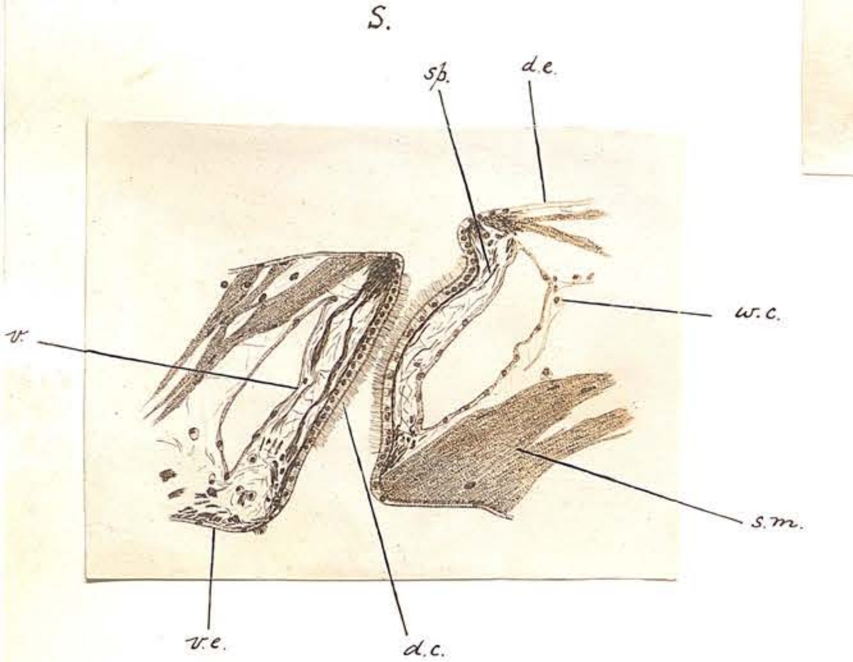

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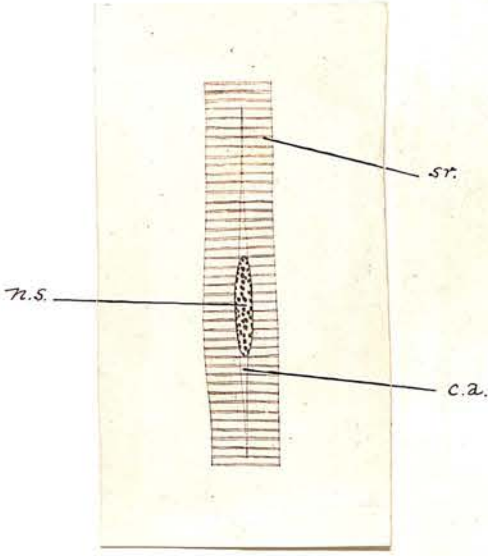

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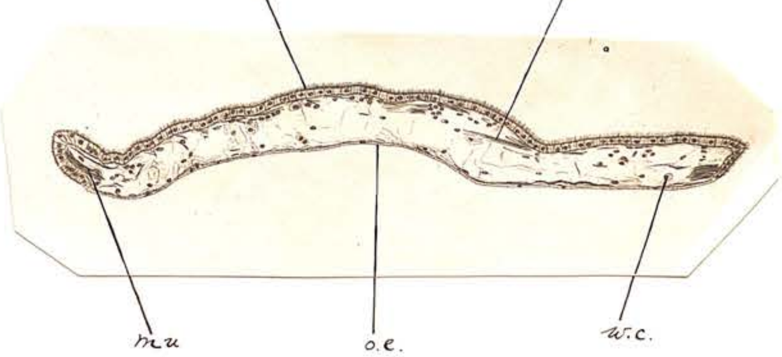

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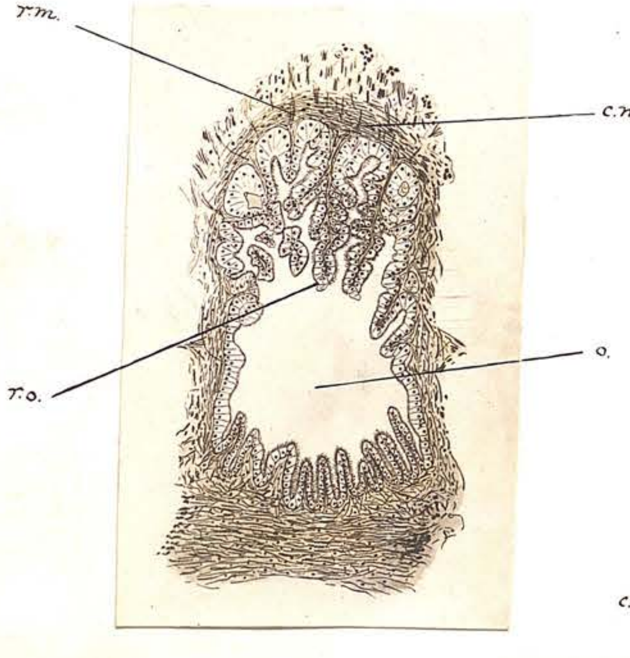

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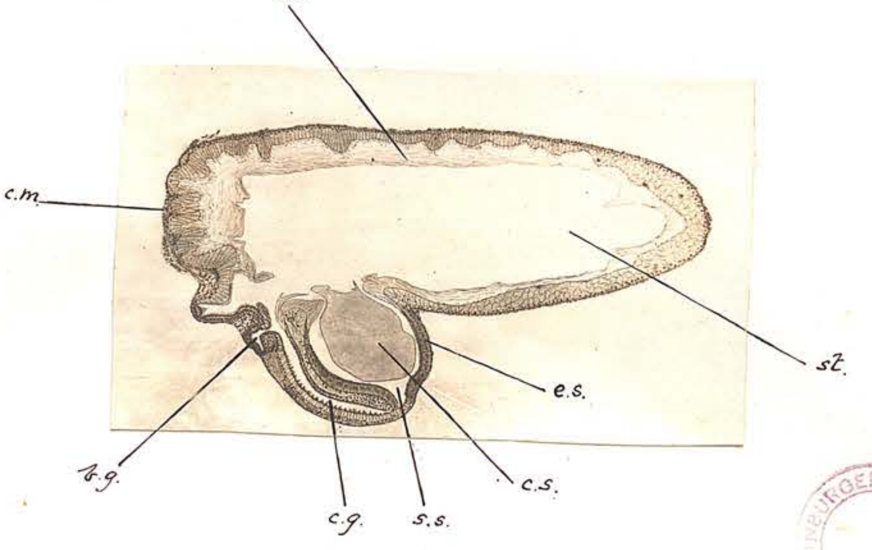

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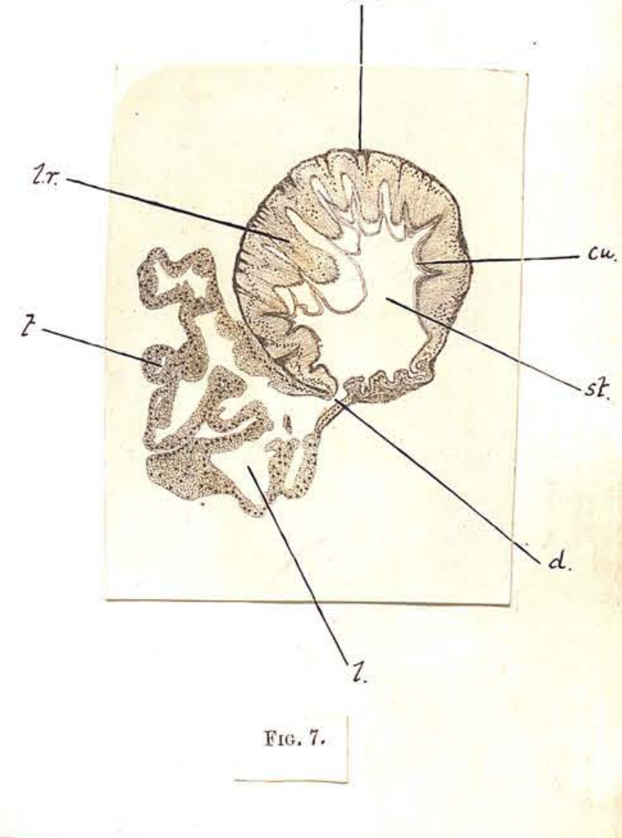


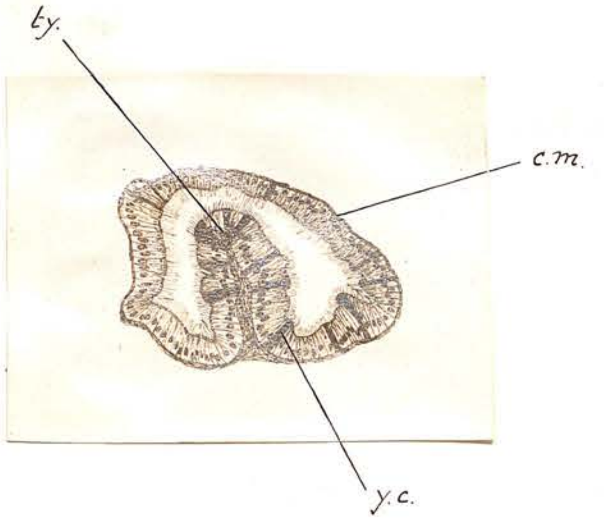
FIG. 7.

C. M. Yonge, del.

Structure Function &c of the Septibranchs &c.

C. M. Yonge, 1927 DSc

Th. Scot



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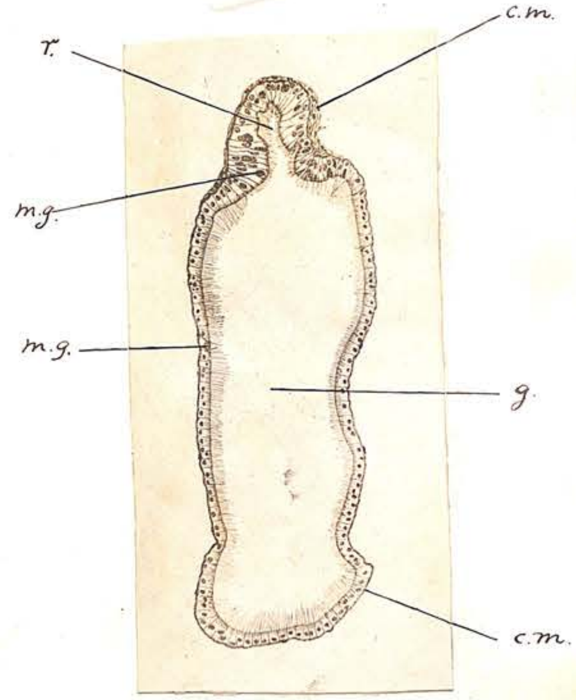

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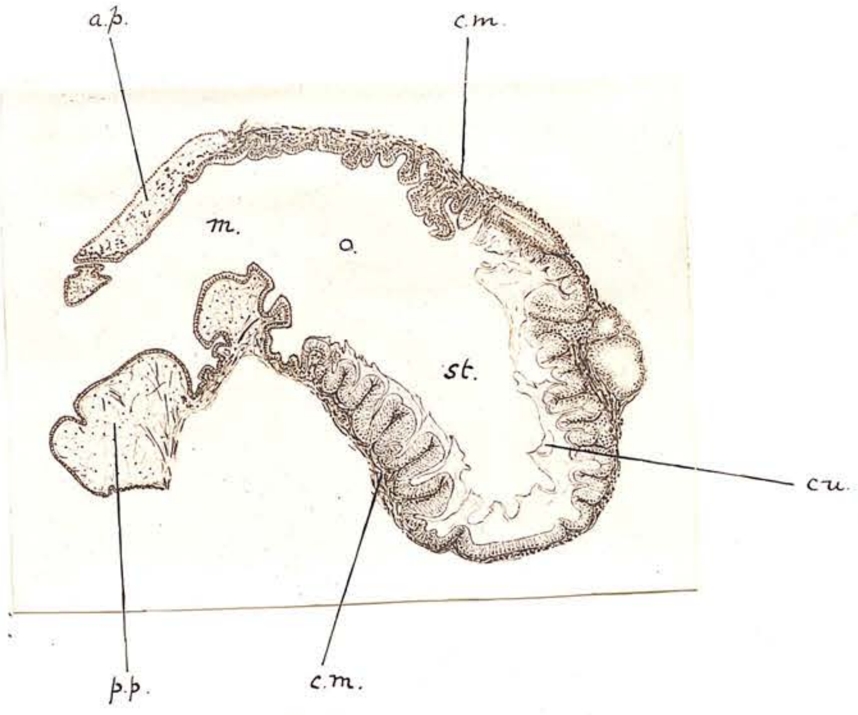

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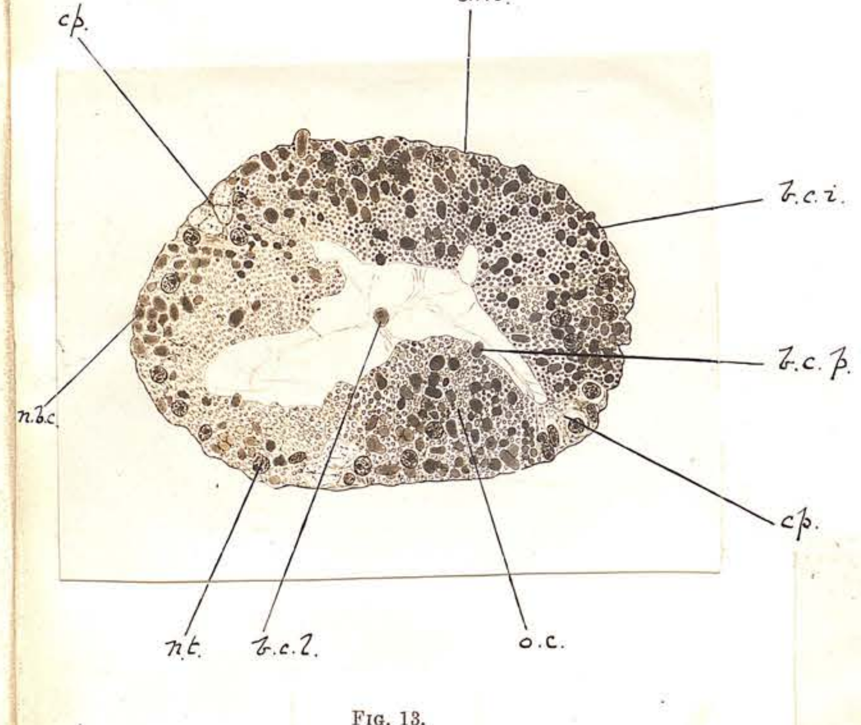

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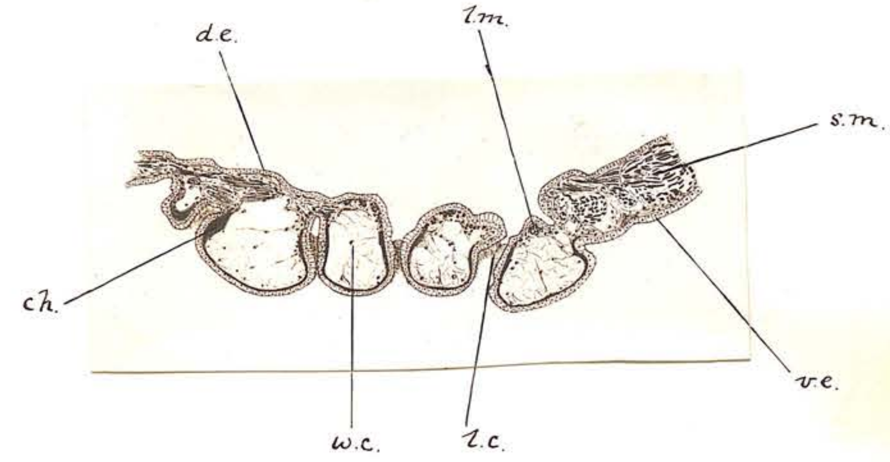

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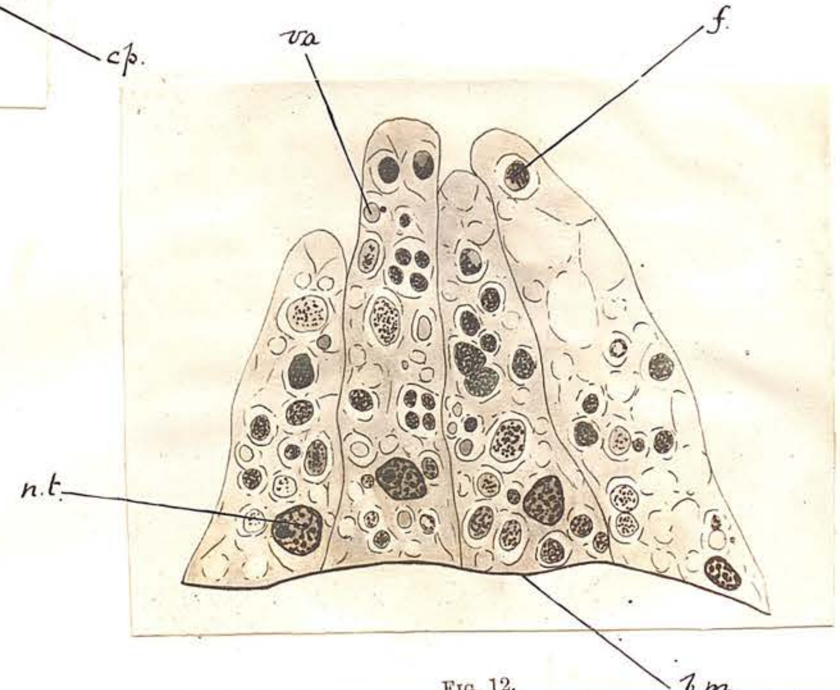

C. M. Yonge, del.

FIG. 12.