The Structure and Function of the Alimentary Canal of Aplysia Punctata.¹

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With 14 Text-figures.

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I. INTRODUCTION.

The species here described is Aplysia punctata Cuvier.

The fullest accounts of the morphology and physiology of the alimentary canal of Aplysia are given by Zuccardi (1890), Mazzarelli (1893), Enriques (1901), and Eales (1921). The monographs of Mazzarelli and Eales contain full reference to earlier literature. With the exception of the section of the paper by Enriques devoted to the structure of the glandular epithelium of the digestive diverticula, these accounts are all singularly lacking in detail and describe a uniformity of histological struc-

¹ Owing to Dr. H. H. Howells's absence on active service, this paper, which represents the substance of the thesis he presented for the degree of Doctor of Philosophy, has been prepared for publication by Prof. C. M. Yonge.
ture which is not confirmed by critical examination. Moreover, the interpretation of the functions of the regions of the gut is misleading. Reference will be made later in this paper to other work which has been carried out on special problems relating to digestion in Aplysia.

The Opisthobranchs are very specialized in regard to their food and feeding mechanisms. Unlike Philine, Scaphander, Haminaea, and Actaeon (Fretter, 1939), Aplysia is strictly herbivorous. An attempt has been made to correlate the feeding mechanisms, mechanical action of the gut and the nature and distribution of the enzymes, with the food of the animal.

The research was conducted in the Department of Zoology of the University of Bristol and in the Laboratory of the Marine Biological Association at Plymouth. I am indebted to the University of Bristol for the use of their table at Plymouth and to the Colston Research Fund of the University which defrayed certain expenses. I also wish to thank Professor C. M. Yonge who suggested this research and offered much assistance and criticism.

II. Methods.

The particular difficulty of obtaining suitable fixation of the alimentary canal of Aplysia has already been commented upon by MacMunn (1899). The difficulty is made the more acute in the case of the glandular epithelium of the digestive diverticula owing to the extreme fragility of the cells which rupture even during the most careful excision.

Fixation of small pieces of the gut with Flemming (with acetic) preserved most of the cytoplasmic detail which could be seen in living cells, while the chrome-osmic mixture of Champy gave almost equally valuable results. Adequate fixation of larger pieces of the gut was obtained with Helly's modification of Zenker's fluid and Ciaccio. Heidenhain's 'susa' and Bouin were less satisfactory, differentiation of the cells being rendered difficult by a partial solution of the cytoplasmic inclusions, while destruction of the glandular epithelium of the digestive gland was almost complete.

Sections from 4 to 10μ thick were stained with Heidenhain's iron-alum haematoxylin, followed by eosin, erythrosin or light
green. For general purposes Heidenhain's 'azan' proved a most useful stain, offering consistent differentiation of the cytoplasmic granules and clearly revealing the muscle fibres within the sub-epithelial connective tissue. Mayer's mucicarmine counterstained with orange G was used for the identification of mucous glands.

Fixation in neutral formalin followed by staining with purpurin was employed for the detection of calcium deposits in the cells of the digestive diverticula. Flemming without acetic and Ciaecio's fluid were used to indicate the presence of fats and lipoids, Carnoy's fluid and absolute alcohol for that of glycogen.

The sites of absorption and secretion were determined with the aid of soluble iron lactate introduced into the lumen of the gut and the blood stream respectively. Aplysia could not be induced to feed on the salt which was therefore forcibly pipetted into the mouth. The presence of iron in the tissues was revealed by fixation in a mixture of equal parts of 5 per cent. ammonium sulphide in 95 per cent. alcohol and Bouin, followed by treatment of the sections with solutions of potassium ferrocyanide (10 per cent.) and HCl (1 per cent.). The sections were counterstained in eosin or orange G.

III. Anatomy and Histology.

According to Guiart (1901) the buccal mass, oesophagus, and crop together comprise the foregut; the gizzard, stomach, and intestine the midgut; and the rectum the hindgut. He does not, however, state the evidence on which he bases this subdivision. The early development of Aplysia has been described and figured by Saunders and Poole (1910) who state that 'the intestine grows out as a tube-like evagination from the right posterior portion of the stomach. The anus is formed at once and there is but a very slight ectodermal invagination—the oesophagus is long and narrow, and almost entirely endodermal.' Unfortunately they were unable to carry the larvae beyond the free-swimming veliger stage. Later stages in the development of Philine aperta are described by Brown (1924) but, apart from the buccal mass and salivary glands which are ectodermal, he gives no account of the embryonic origin of regions of the gut.
It is therefore impossible to make any subdivision of the gut which has morphological significance, and for purposes of description it is here divided into the following regions, distinguished according to function: buccal mass, lodging the odontophore and into which opens a pair of salivary glands, oesophagus and crop; gizzard; filter chamber (corresponding to the 'second triturating stomach' of Zucardi (1890), Mazzarelli (1893), and Enriques (1901), and the 'second portion of the gizzard' of Eales (1921)); stomach, bearing the openings to the digestive gland and caecum; and the coiled intestine bearing anteriorly the opening to the stomach and leading posteriorly to the rectum and anus which is situated on the posterior face of the siphonal fold of the mantle. It must be emphasized that this nomenclature does not imply either homology or identity of function of these regions with those similarly named even in closely related tectibranchs.

The gut is lined throughout by a simple columnar epithelium. This is ciliated in the oesophagus and crop, stomach, intestine, and rectum. In the buccal mass, gizzard, and filter chamber it bears a secretion which, tested by the modified Van Wisselingh-Brunswick tests of Campbell (1929), proves to be chitin.

Mouth and Buccal Mass.

The narrow slit-shaped mouth lies at the base of a shallow buccal funnel (Text-fig. 1, bf) formed by the expanded bases of the anterior tentacles (te1). The funnel is interrupted ventrally where it is separated from the foot by the shallow gutter of the opening of the pedal gland (pg). The walls of the funnel carry a number of folds which extend inwards towards the mouth and are paler in colour than the general body surface. The epithelium of the folds is deeper (20μ) than that covering the general body surface and, except towards the base of the funnel, possesses an even dense carpet of cilia 7μ long and arising from distinct basal granules. Yellowish brown pigment granules lie within the cytoplasm towards the distal extremity of the cell. The epithelium is richly supplied with mucous glands of two types. Most numerous are the flask-shaped gland cells (Text-fig. 2, mc), lying in a deep layer within the subepithelial con-
TEXT-FIG. 1.
Sagittal section through the head region of *Aplysia*. The cut surfaces have been left blank. The body cavity is shown in black. × 6. ac, anterior constriction of crop; bc, buccal commissure; bf, buccal funnel; cc, cerebral commissure; dfc, dorsal food channel; dlf, dorso-lateral fold; j, jaw; lsg, left salivary gland; m, membrane; pc, pedal commissure; pg, pedal gland; r, radula; ra, radular artery; rs, radula sac; sa, aperture of salivary gland; te₁ and te₂, anterior and posterior tentacles; yt, yellow tissue.
nective tissue, and discharging on to the surface by a coiled duct (dmc) running between the chitinogenous cells and terminating in a small dilatation near the surface of the epithelium. Cells of this type occur in large numbers beneath the epithelium of the pedal sole. Here, in the buccal funnel, they undoubtedly lubri-

cate the passage of food towards the mouth. The gland cells of the second type (Text-fig. 4, mc) are situated in the epithelium and are of the same height as the ciliated cells, with an expanded deeper portion causing lateral constriction of the neighbouring cells and with a narrow distal extremity. They are, in the nomenclature of Hirsch (1931), polyphasic: the act of secretion does not end the life of the cell. The nuclei of both types (nmc) are large and rounded or irregular in shape, and contain a prominent nucleolus and chromatin staining heavily with iron-alum haematoxylin. The secretion is contained in vacuoles within a finely granular cytoplasm.
Towards the region of the mouth the ciliated cells give way to chitinogenous cells which are devoid of basal granules (Text-fig. 2, chc). The funnel is here lined by a thin chitinous cuticle continuous with the substance of the ‘jaws’ (Text-fig. 1, j). The epithelium is here a little taller (23μ) and the intracellular fibrillae are strongly developed connecting from the base of the chitin, through the cytoplasm of the cell, to the basement membrane. Beneath the jaws the fibrillae reach their maximum development and are distinguishable in the region of the oval nucleus, about one-third of the length of the cell from the base. The upper portion of the cytoplasm bears a few refringent granules, pale yellowish orange in life, and staining black with iron-alum haematoxylin after fixation in Ciaccio’s fluid. They are probably of a lipoid nature. The jaws are local exaggerations of the chitin supporting the rim of the mouth and strengthened by a number of dark brown-coloured rods of harder chitin (the ‘stick cells’ of Eales) packed closely side by side, and with their free tips slightly bent towards the buccal cavity. The rods are interrupted at the dorsal and ventral corners of the mouth, giving the appearance of two distinct laterally disposed jaws. Behind the jaws the greater development of the cytoplasmic granules obscures the intracellular fibrillae. Mucous cells of the first type are crowded in a wide layer beneath the basement membrane and open into the buccal cavity through minute pores in the chitin.

The buccal mass lies immediately behind the mouth and in front of the nerve collar. At rest it is pear-shaped (Text-fig. 3); the narrower anterior region tapers towards the mouth opening, the larger posterior portion being more rounded. A low ridge runs along the mid-dorsal surface from a point immediately behind the mouth to the oesophagus (o) which leaves the bulb on the posterio-dorsal side. The ridge overlies the dorsal food channel in the roof of the buccal cavity (Text-fig. 1, dfc). The tip of the radula sac (Text-fig. 3, rs) is visible externally as a low rounded prominence, slightly less opaque than the adjacent muscles, situated mid-ventrally. A shallow transverse groove (Text-fig. 3, lgr) separates the anterior and posterior regions laterally, being interrupted dorsally by the median ridge and
ventrally by a depression immediately anterior to the radula sac which receives the radular artery (Text-fig. 1 and 3 b, ra).

The pulley-like odontophore arises from the floor of the posterior cavity and bulges into the cavity filling it almost completely. Dorsally, the odontophore is divided longitudinally
by a median groove which is shallow anteriorly but deepens rapidly into the radula sac. The radula (Text-fig. 1, r) is situated on the sides of the groove, arising from paired depressions at the base of the sac. New teeth are formed here. They are soft and colourless and as they move forwards by the growth of the odontophore mature to a yellow and finally dark red colour. The worn teeth at the anterior edge of the radula are covered by a tough white membrane (Text-fig. 1, m) which protects the wall of the buccal cavity when the odontophore is thrust forwards to bring the functional teeth against the jaws.

The food channel runs the entire length of the roof of the buccal cavity. When the buccal cavity is at rest the channel is enclosed by a pair of longitudinal folds (Text-fig. 1, dlf) formed by a greater development of the underlying connective tissue and closely approximated along their median edges. A number of small colourless denticles project from the cuticle of the crests of the folds bounding the anterior half of the channel. At the posterior end of the cavity the folds extend ventrally to meet the ventral side of the oesophageal opening so that communication with the oesophagus is only possible by way of the channel.

The buccal cavity is lined throughout by a thin chitinous cuticle, cilia being absent. The chitinous layer is finely striated vertically with a broader horizontal banding which may represent periodicity of secretion (Text-fig. 2, ch). In common with the radula membrane and the newly formed soft teeth at the base of the radula sac it stains pink with eosin and erythrosin, and a bright clear blue with ‘azan’. It stains feebly or not at all with haematoxylin. On the other hand the substance of the ‘stick cells’, mature radula teeth, and denticles of the dorso-lateral folds stain intensely with haematoxylin and a brilliant red with ‘azan’. The changes which ensue in the hardening of chitin are therefore accompanied by well defined changes in staining properties. Similarly, Sollas (1907) observed an increasing affinity for haematoxylin during the maturation of the radula teeth of Helix aspersa.

The walls of the buccal cavity in contact with the sides of the odontophore consist of a spongy yellow tissue (Text-fig. 1, yt) containing gland cells the secretion of which lubricates the sides
of the odontophore. The cells are of two kinds clearly distinguishable in their staining reactions and cytoplasmic structure.

![Image](image_url)

**Text-fig. 4.**

A, section of a fold of the yellow tissue on the lateral walls of the buccal mass. ×500. B, epithelial cells from the same region. ×1500. *mc*, mucous gland; *nchc*, nucleus of chitinogenous cell; *nsc*, nucleus of secreting cell; *sc*, secreting cell; *sgr*, secretion granule. Other lettering as before.

Mucous cells of the intra-epithelial type already described (Text-fig. 4 B, *mc*) occur in large numbers. The deeper portions
of the chitinogenous cells are typically much constricted to accommodate the width of these cells which is sometimes as great as 20μ. Outnumbering these are the secretory cells (sc), similar in shape to the mucous cells but with rounded nuclei and irregularly shaped secretion masses (the largest 5μ across) occurring singly or in clumps. The granules (sgr) stain red and blue with 'azan', the red coloration being limited to granules in the neighbourhood of the nucleus (which lies near the basal end of the cell) and being progressively lost by the granules towards the distal end of the cell. The change in staining reaction possibly accompanies the elaboration of the secretion mass. Fretter (1939) has described cells of an apparently similar kind in Philine, Scaphander, and Haminaea. From their distribution in these tectibranchs it would seem certain that they produce a lubricating secretion.

The musculature of the buccal mass (Text-fig. 3 A, B, C) is well developed, the following intrinsic and extrinsic muscles respectively co-operating in its movements:

I. A thin layer of muscle originating at the mouth region and radiating posteriorly over the surface of the anterior portion to its insertion in the lateral groove.

II. A thin superficial band encircling the posterior region. It arises dorso-laterally from the groove and passes ventrally to cover the tip of the radula sac. Some of the fibres connect across the mid-dorsal line roofing the buccal gutter. The band forms the entire thickness of the wall dorsal to the attachment of the odontophore on each side.

III. Well-developed circular muscles lying beneath I and some 20 times thicker than the latter. They form a sphincter around the mouth and the anterior portion of the buccal mass. The muscles are attached to ligaments on the mid-dorsal and mid-ventral lines.

IV. A thick mass of muscle originating in the groove and diving beneath II to be inserted into the sides of the odontophore.

V. Paired fan-shaped muscles originating from the groove ventro-laterally and inserted into the sides of the radula sac. They lie beneath IV.
I. A thick mass of muscle running predominantly in a transverse direction between the tissue constituting the so-called ‘cartilages’ embedded in the halves of the radula pulley. There are two pairs of extrinsic muscles ($E^1$ and $E^2$). They originate in the grooves and pass forwards and outwards to their insertion in the body wall around the mouth. Their fibres are continuous with those of the superficial intrinsic muscles $I^2$.

Salivary Glands.

A pair of salivary glands (averaging 3 cm. in length, 2 mm. in width, and 0.5 mm. in thickness) open on to the lateral walls of the buccal mass below the folds of the buccal gutter (Text-fig. 1, sa) and discharge their secretion over the surface of the odontophore. The glands are attached posteriorly to the anterior end of the gizzard. A central channel some 0.14 mm. in diameter runs the entire length of each gland. It communicates by lateral openings with the acini, but some 3 mm. short of its opening into the buccal mass it becomes a non-secreting ciliated duct with a round lumen and a layer of circular muscles some 0.2 mm. thick (Text-fig. 3 a and c, dsg). A thin layer of connective tissue with scattered muscle fibres underlies the glandular epithelium of the acini. Secreting cells of two kinds occur together with small groups of ciliated cells. The epithelium varies considerably in height and in the relative numbers of the three cell types in different parts of the gland. In the acini, where the epithelium is some 45 μ deep, the gland cells are most abundant. One type (Text-fig. 5, me), with a round heavily staining nucleus and vacuolated finely granular cytoplasm staining blue with ‘azan’ and a pale pink with mucicarmine, probably secretes mucus which is poured out in masses. These extend for some distance between the cilia before finally breaking free. The secreting cell of the second type (se) is typically more nearly cylindrical in shape and has a large nucleus containing a prominent nucleolus staining orange with ‘azan’. The vacuolated cytoplasm stains pink with ‘azan’ and is thickly packed during life with pale yellow droplets, some highly refractile, and non-refractile granules. These are dissolved during fixation. Ni (1933) observed the disappearance of these granules.
and droplets from the acini of the gland following secretion induced by electrical stimulation. The salivary secretion (at least as obtained under experimental conditions) is heavily charged with droplets which, in view of the presence of a strong amylase and a protease in extracts of the gland, are most probably enzymatic in nature. The ciliated cells (cic) occur tightly wedged between the glandular cells. They bear long cilia arising from small basal granules. The epithelium of the central duct

TEXT-FIG. 5.

Portion of a transverse section through an acinus of the salivary glands fixed in Ciaceto, stained iron haematoxylin and erythrosin. The connective tissue has been drawn from sections stained 'azan'. ×1000. bg, basal granules of cilia; c, cilia; cic, ciliated cell; mu, mass of secretion issuing from mucous gland. Other lettering as before.
of the gland is somewhat shallower (36μ) and larger groups of ciliated cells occur between the secreting and mucous cells. In the short non-secreting portion of the duct the cells are much shorter (12μ) forming an almost cubical epithelium and bearing long cilia (10μ).

Oesophagus and Crop.

The oesophagus and crop form a structural unit without morphological differentiation. Viewed from the dorsal side they form an S-shaped tube, the smaller, anterior loop bending towards the floor and the larger posterior loop towards the roof of the cavity. Two shallow annular constrictions situated approximately one-quarter and one-half its length from the buccal mass divide the tube into three dilatations, each increasing in size posteriorly, and with wide connecting passages. The constrictions are never completely obliterated by the dilatation of the crop, even when the animal is fully extended. Eales describes the presence of a constriction at the point of junction of the crop and gizzard. This is better described as a sudden change in diameter between the thinner distensible walls of the crop and the thicker, more rigid, walls of the gizzard, a change which is most marked after a meal.

The epithelium of the oesophagus and crop is longitudinally folded owing to variation in thickness of the underlying connective tissue. Some twelve folds are present at the narrower anterior end of the tube and are continuous in direction with folds originating in the dorsal food channel. They increase in number within the dilatations of the posterior crop and are complicated by a secondary longitudinal folding of the epithelium. These smaller folds alone can be seen when the gut is fully distended, the primary folds being obliterated. The epithelium closely resembles that of the buccal cavity and dorsal food channel. The nuclei of the cells occur within the basal third of the cytoplasm the upper parts of which are packed during life with the yellowish orange refractile granules, accompanied by a few larger granules (Text-fig. 6, lq) which are dissolved by Ciaccio but precipitated by chrome-osmic fixation. A thin layer of cuticle (ch), identical in staining properties with the chitin of
ALIMENTARY CANAL OF APYLSIA

the buccal mass, lines the surface of the epithelium, but a fine carpet of threads arising from basal granules (bg) at the surface of the cell passes through the cuticle and apparently consists of cilia (c). A cuticle in this position has been identified in the oesophagus of larval Actaeon by Mazzarelli (1906) and in the adult by Fretter (1939). It protects the surface of the epithelium from coarse particles in the food. The cilia are extremely weak, being unable to move the smallest particles. Their activity must be quite subsidiary to that of the muscles in the functioning of

TEXT-FIG. 6.

Part of a transverse section through the wall of the crop. ×3000.

bm, basement membrane; icm, inner circular muscles; lg, granules of a lipoid or fatty nature; lm, longitudinal muscles; nmc, nucleus of mucous gland; ocm, outer circular muscles.

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the oesophagus and crop. Examination of living tissue proves that they are not universally present in the epithelium. Mucous cells are very sparse, and in structure intermediate between the two types already distinguished in the epithelium of the buccal cavity. The enormous nucleus (Text-fig. 6, \textit{nmc}), approaching 20\ \mu\text{m} in diameter, lies towards the base of the flask-shaped cell which bulges the basement membrane (\textit{bm}). Mucus is discharged through a narrow duct opening by way of a minute pore in the cuticle. There is a layer of muscles (\textit{icm}) attached to the basement membrane, and this probably assists in folding when this portion of the gut is contracted. An outer layer of circular muscle fibres (\textit{ocm}), running in well defined bands, is separated from the inner circular muscles by connective tissue through which anastomose fine strands of longitudinal muscle fibres (\textit{lm}).

\textbf{Gizzard and Filter Chamber.}

The outer circular muscles are best developed in the thick wall of the gizzard where longitudinal muscles are absent. The inner surface of the gizzard is lined with chitin, and bears some 4 or 5 alternating rows of teeth (about 50 to 60 in all) which represent local thickenings of the chitin. Each tooth is pyramidal in shape and secreted by a rhomboidal area of epithelium which is raised above the general level of the surrounding tissue. The anterior faces of each of the larger teeth have a greater area than the posterior faces, the apex of each tooth being posteriorly directed (Text-fig. 7). The anterior faces possess furrows (Text-fig. 7, \textit{ag}) into which fit the edges of the pair of teeth lying on each side and in front. The teeth thus fit very closely and on contraction of the gizzard their points meet across the lumen except for those of the anterior two rows which are reduced in size. These fulfil a particular role in the activity of the gizzard. The points of the larger teeth (Text-fig. 7 \textit{a}) are continually being worn down, the loss being made good by a secretion of new chitin at the base. The points of the teeth of the posterior row (Text-fig. 7 \textit{b}) are not worn down because they make no contact with the teeth of other rows, and as a result they become greatly elongated and recurved.

The musculature of the walls of the filter chamber closely
resembles that of the crop. Here there are some 24 loosely arranged long acicular teeth (Text-figs. 9 and 10, d) each arising from a small circular base.

The epithelium of the gizzard and filter chamber is composed entirely of chitinogenous cells identical with those lining the buccal cavity. An epithelium of a similar kind has been described for the gizzard of Cymbuliaperonii (Howells, 1936) and beneath the jaws of Haminaeahydatis (Fretter, 1939). The appearance of 'basal granules' at the surface of the cells, reported in Cymbulia, is here seen, with better fixation and using critical illumination, to be due to the presence of minute papillae of cytoplasm around each of the fibrillae as these leave the cell to become embedded in the substance of the teeth. The extra-cellular fibrillae hence form an anchorage for the secretion. But it is possible that their appearance may be due to a separation of the epithelium from the secretion mass during fixation. They were visible after fixation by all the methods employed. Whether the intra-cellular fibrillae of the chitinogenous cell are
homologous with the fibrillae of the ciliated cell is also a question which cannot easily be answered.

**Stomach and Caecum.**

From its junction with the filter chamber the intestine describes a single loop within the posterior body cavity. Its anterior portion (Text-fig. 8, ai) lies only partially embedded in the digestive gland, the wall on the right side being visible at the surface of the visceral mass. This portion, the ‘intestino valvolare’ of Enriques, bears on its left side a large opening to the stomach (Text-fig. 9, os) guarded by two folds of epithelium.

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**TEXT-FIG. 8.**

Dorsal view of the alimentary canal posterior to the gizzard. The digestive diverticula have been dissected away to show the stomach and caecum. × c. 5. ai, anterior intestine; ca, caecum; fc, filter chamber; i, intestine; re, rectum; s, stomach bearing cut ends of the digestive diverticula.
(adf and vf) formed by the great development of the sub-
epithelial connective tissue on the antero-dorsal and ventral 
sides. No special musculature is developed in connexion with 
these folds. In their natural position (as seen through the trans-
parent walls of the intestine) they completely obscure the open-

ANTERIOR INTESTINE OPENED BY A LONGITUDINAL INCISION ALONG THE RIGHT 
SIDE. THE ARROWS INDICATE THE DIRECTION OF CILIARY CURRENTS. × 6. 
ADF, ANTERO-DORSAL INTESTINAL FOLD; D, TOOTH OF THE FILTER CHAMBER; 
F, FAECAL ROD; OS, INTESTINAL OPENING OF STOMACH; T1 AND T2, TERMINAL 
DILATATIONS OF THE MAJOR AND MINOR TYPHLOSOLES; VF, VENTRAL 
INTESTINAL FOLD. OTHER LETTERING AS BEFORE.

The so-called stomach (Text-figs. 8 and 10, s) represents 
anatomically a dilatation of the combined ducts of the digestive 
diverticula behind their opening into the intestine. It is com-
pletely embedded in the tissue of the digestive diverticula. 
Large openings (Text-fig. 10, d′−d‴′) lead to the ducts of the
diverticula which divide almost immediately into narrower ducts, the number and position of which is subject to some variation. The walls of the ducts are longitudinally folded, the folds converging on to the opening of the caecum on the posterior surface of the stomach (ic). From its junction with the stomach the caecum (Text-fig. 8, ca) passes through the tissue of the diverticula, its distal end appearing on the right posterior surface.
The alimentary canal of Aplysia consists of the visceral mass. Its cavity is incompletely divided longitudinally by two typhlosoles of unequal size (Text-figs. 10 and 11, t₁ and t₂) which extend beyond the opening of the caecum across the posterior ventral wall of the stomach to terminate in dilatations between the distal ends of the intestinal folds. The folds entering the caecum from the ducts converge on the channel of the left side (here termed the incurrent channel (Text-figs. 10 and 11, ic) in view of its function) and are continuous with the longitudinal foldings of its wall. The channel of the right side (excurrent channel) is smooth-walled. It is prolonged into a groove (Text-fig. 10, ec) separated from the cavity of the stomach by the extensions of the typhlosoles and it ends in the intestine. The typhlosoles terminate a short distance from the distal end of the caecum, thus affording a communication between the right and left channels.

The epithelium of the stomach is similar to that of the ducts of the diverticula and the incurrent channel of the caecum. It is a typical ciliated epithelium richly supplied with intraepithelial mucous gland cells of the normal type and varying in height (from 12 to 35μ) with the folding of the wall. Ribbons of ciliated epithelium continue beyond the ends of the ducts into the glandular areas of the diverticula as previously observed in Cymbulia (Howells, 1936) and Philine (Fretter, 1939).

A different epithelium lines the excurrent channel of the caecum (Text-fig. 11). The cells are taller (95μ) and narrower and consist of mingled gland cells (Text-fig. 12, gc) and ciliated cells. The two occur in approximately equal numbers but the gland cells are much larger (see Text-fig. 12) and occupy the greater part of the epithelium. The nuclei of the ciliated cells (ncc) are long and narrow while those of the gland cells (ngc) are rounded and occupy a lower level. In sections in which the mucous gland cells of the incurrent channel are stained a brilliant red with mucicarmine the secretion of the gland cells of the excurrent channel stains only faintly pink, while in sections stained with 'azan' the pale blue of these contrasts with the intense blue of the mucous gland cells. The secretion is therefore not mucus but is probably a substance which imparts the firm surface to the faecal rod. Droplets of the secretion occur
abundantly between the cilia at the surface of the epithelium. Clear circular areas (iec) show up distinctly within the denser cytoplasm beneath the nuclei of the gland cells. They are too minute for their staining reactions to be ascertained with cer-

**Text-fig. 11.**
Transverse section of caecum. × 75. Lettering as before.

tainty. They are probably intra-epithelial canals which occur commonly in the gut of molluscs where extra strength is required in the epithelium, e.g. in the style-sacs of Crepidula (Mackintosh, 1925) and Ostrea (Yonge, 1926a), and in the caecum to the mid-gut of Cymbulia (Howells, 1936). A thin layer of muscle fibres occurs in the connective tissue layer beneath the epithelium of the stomach, caecum, and ducts of the digestive diverticula.

**Digestive Diverticula.**

The glandular epithelium of the digestive diverticula shows marked changes of appearance according to the phase of activity of its cells. Four types of cell may be distinguished. Most
numerous are those rising to a maximum height of 75\( \mu \) above the basement membrane, and with rounded ends projecting above the general level of the epithelium (Text-fig. 13, \textit{abc}). The cytoplasm contains numerous small round granules showing internal granulation. The granules in the neighbourhood of the nucleus are coloured green in life (\textit{gg}) and are slightly smaller than the brown granules (\textit{brg}) which are crowded towards the free surface of the cell. The granules are coloured vivid green and red respectively after treatment with \textit{‘azan’}. The brilliant green coloration is probably due to the action of the hot acetic acid in the azocarmine solution. MacMunn (1899) obtained a similar coloration by heating in 33 per cent. HCl. The green granules...
in the living cell were mistaken for chloroplasts by Enriques, but Hörstadius (1933) has observed their formation from a diffuse green pigment scattered throughout the cell immediately after a meal and probably derived from the breakdown of chlorophyll. The cells have received the names of ‘cellule absorbenti chlorofilliche’ (Enriques), and ‘Resorptionszellen’ (Biedermann and Moritz, 1899). But Hörstadius has proved conclusively that these cells are incapable of phagocytic ingestion. Animals fed experimentally with blood of Scyllium in the course of this research failed to take up the erythrocytes while Philine similarly fed showed an abundance of corpuscles within the ingesting cells of the gland. Vesicles charged with brown granules may be found at various stages of separation from the surface of these cells. The vesicles may break down later in the gut to liberate the granules which are found, together with unbroken vesicles, in the detritus bound in mucous strings on

![Text-Fig. 13.](image-url)

Part of a transverse section through a tubule of the digestive gland. Fixed Flemming without acetic, stained iron haematoxylin. The cytoplasmic inclusions of the large cell are drawn from living tissue. × 835. abc, absorptive cell; brg, brown granules; c₄, cell of the fourth type; cr, orange-coloured crystal; ed, olive-green excretion droplet; exc, excretory cell; gg, green granule; ncₑ, nucleus of cell of the fourth type. Other lettering as before.
the wall of the stomach. Large orange-coloured crystals (cr) of hexagonal shape and unknown constitution occur occasionally in these cells. That these cells absorb and excrete is therefore apparent. Whether they perform a secretory function in addition has not been determined.

Secretion is the major activity of the cells of the second type (sc) which occur tightly wedged between the absorptive cells. The cytoplasm contains globular secretion masses staining black with iron-alum haematoxylin after fixation in Bouin. Enriques reports the disappearance of these globules during digestion and their accumulation during starvation. Cells identical in appearance have been identified in *Cymbulia* (Howells, 1936) where they were found to take up iron lactate from the blood-stream.

The cells of the third type (exc) are cone-shaped with a broad attachment to the basement membrane. They reach a maximum height of approximately 40 μ. The cytoplasm of the growing cell is charged with globules which collect to form a single large droplet (ec), olive-green in colour and surrounded by a thin layer of clear fluid within a vacuole some 25 μ in diameter, lying towards the distal extremity of the cell. The droplet consists of a fluid of high surface tension which holds together when liberated into the lumen of the gut by the rupture of the cell. The cell is monophasic. The fact that the droplets are found intact in the faecal rod within the caecum argues against the opinion expressed by Barfurth (1883) and by MacMunn (1899) that they are enzymatic in nature, and favours the view that they represent excrement.

The cells of the fourth type (c4) are very large and tightly packed with colourless refractile spherules separated by thin layers of cytoplasm containing minute yellowish brown granules. The spherules are not dissolved by fixation with Ciacco’s fluid, but do not resist chrome-osmic fixation. They stain a light clear blue with ‘azan’. In material fixed in neutral formalin a slight coloration with purpurin suggests that they contain a little calcium salt, but fixation in this reagent is so unsatisfactory that the preparations are almost valueless. Enriques reports (a) the disappearance of the spherules during fasting, the cells being completely emptied after 10 days’ starvation, (b) their
solubility in water, and (c) the presence of similar spherules in the cells of the diverticula of Cephalopoda. Enriques suggests that they are associated with the metabolism and storage of carbohydrate, presumably a pentosan, which has been identified in extracts of the digestive diverticula by Röhmman (1899) and Botazzi (1901).

All four types of cell occur throughout the glandular epithelium, the cells of the fourth type occurring in greatest number towards the distal extremities of the tubules. The tubules are closely united by a thin layer of connective tissue containing scattered muscle fibres.

Intestine.

Posteriorly to the opening of the stomach the intestine (Text-fig. 8, i) travels just beneath the surface of the visceral mass to reappear on the dorsal side. From this point it forms a single loop around the anterior end of the mass, lying in a groove on its surface. Its walls are a transparent yellowish green in colour and provided with a thin layer of connective tissue and muscle fibres, predominantly circular in arrangement. A flat strip of epithelium occupying approximately one-fifth of the circumference runs the entire length of the tube. The remainder of the wall is longitudinally folded. The epithelium is ciliated and columnar. Over the intestinal valves it reaches an average depth of 80μ and bears a fringe of cilia 8μ long. The oval nuclei lie at various levels in the epithelium about the centre of the cell. Mucous cells (Text-fig. 14, mc) of the normal type occur in the epithelium. In the intestine posterior to the valves the ciliated cells are rather shorter (Text-fig. 14, cic), and a second type of gland cell makes its appearance (sc) in approximately equal number to the mucous cells. The nuclei of these gland cells are situated near the basement membrane, while the secretion granules (sgr), staining brightly red with ‘azan’, lie within the cytoplasm towards the distal ends of the cells. When discharged the granules swell into thin-walled vesicles (sv) with a fine granular structure. They are carried away by the cilia and added to the faecal mass, probably aiding the binding of the loose matrix of mucus and undigested food particles into the
solid faeces. What may be designated basal cells (bac) occur occasionally at the base of the epithelium. They have not been observed in contact with the surface of the epithelium. They are characterized by the possession of large nuclei each with a prominent nucleolus. Their function is obscure.

**Rectum.**

The rectum (Text-fig. 8, r) is some 6 to 8 mm. long. It leaves the visceral mass and extends dorsally within the connective
tissue of the body wall to its opening at the anus on the posterior face of the siphonal fold of the mantle. It is differentiated from the intestine by its smaller diameter, the absence of gland cells other than mucous cells in its epithelium, and the greater development of the circular muscles in its wall which form a sphincter around the anus.

IV. HYDROGEN ION CONCENTRATION.

The pH of different regions of the digestive tract and its associated glands is given below, the results obtained agreeing closely with those obtained by Yonge (1925). Fluid was obtained from the salivary glands after they had been washed rapidly in distilled water and teased out in a watch glass. Measured quantities of fluid were taken and added to indicators on a white tile, the colours so obtained being compared with similar quantities of buffer solutions with indicators. The usual corrections have been made for the salt error. The figures represent the average results obtained from an examination of six recently fed individuals. A range of 0-4 was obtained in the filter chamber, but elsewhere the figures agreed within 0-3.

<table>
<thead>
<tr>
<th>Region</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Buccal mass</td>
<td>6-2</td>
</tr>
<tr>
<td>Salivary glands</td>
<td>6-0</td>
</tr>
<tr>
<td>Oesophagus and crop</td>
<td>4-8</td>
</tr>
<tr>
<td>Gizzard</td>
<td>4-9</td>
</tr>
<tr>
<td>Filter chamber and anterior intestine</td>
<td>5-6</td>
</tr>
<tr>
<td>Stomach</td>
<td>5-5</td>
</tr>
<tr>
<td>Digestive diverticula</td>
<td>5-9</td>
</tr>
<tr>
<td>Caecum</td>
<td>7-2</td>
</tr>
<tr>
<td>Posterior intestine</td>
<td>7-6</td>
</tr>
<tr>
<td>Rectum</td>
<td>8-2</td>
</tr>
</tbody>
</table>

V. DIGESTIVE ENZYMES.

A number of investigations have already been made into the nature of the digestive enzymes of Aplysia. In 1899 Röhmam examined the gut contents microscopically and noted the dissolution of starch in the crop and the absence of this carbohydrate from the faeces. Botazzi (1901) obtained digestion of starch in vitro with crop fluid and extracts of the digestive diverticula. He also concluded, from the breaking up of the chloroplasts in the gut, that a protease is present capable of
digesting the protein present in the chloroplasts. Enriques (1901) repeated the microscopical investigation in a number of molluscs and concluded that in *Aplysia* the gut contains in addition to an amylase and a protease, a cellulase which breaks down the cellulose walls of the algal cells to liberate the chloroplasts. Unfortunately, Enriques not only mistook the starch grains for chloroplasts in the cells of *Ulva*, but also the greenish brown excretion masses from the diverticula for the chloroplasts in the gut fluid. The presence of a cellulase has not yet, as far as is known, been demonstrated experimentally in *Aplysia*. The presence of an amygdaloclastic enzyme has been demonstrated by Giaja (1909) and of a saccharase by Bierry (quoted by Vonk, 1937). Krüger (1929) confirms the presence of an esterase in *A. depilans*, and Hörstadius (1933) a protease capable of digesting agar.

The nature of the secretions of the salivary glands and of the diverticula was tested experimentally and compared with the composition of the gut fluid. Extracts were made of the glands by grinding the tissues (carefully separated from the adjacent viscera) with clean sand. The extracts were then made up to the required strength with distilled water, bacterial action being prevented by the addition of toluol.

The optimum pH of the activity of the enzymes was determined at 30° C. The mixtures of extract and substrate were buffered with the solutions of McIlvaine and of Atkins and Pantin. Reducing sugars were quantitatively estimated by the method of Hagedorn and Jensen (as modified by Boyland, 1928) and the products of protein digestion by the Sorensen formol-titration method. An estimate of the action of the lipase was obtained by titration to pH 9 with N/100 NaOH using thymol blue as an indicator.

A strong amylase was found in extracts of the salivary glands and of the digestive diverticula. The optimum pH for the activity of the enzyme from the former source is at 5-6, and from the latter at 5-8, suggesting activity in the crop where a strong amylase is to be found with maximum activity at pH 5-6. Enzymes hydrolysing sucrose, lactose, and maltose are all active in the same region of the gut, being secreted by the digestive
diverticula. A glycogenase is active in extracts of the glands, but its absence from the lumen of the gut suggests that it is a tissue enzyme. The conclusion is made the more likely by the normal absence of this carbohydrate from the food.

Early experiments failed to demonstrate the presence of a cellulase in the gut fluid or in extracts of the gut glands. The action of 10 per cent. extracts on finely teased Whatman filter paper (no. 40) even after 14 days’ incubation failed to produce a detectable amount of reducing sugars. Using a high concentration of substrate, however, and a mixture of crop juice and buffer solution in equal proportions, a weak action on filter paper could be obtained after incubation for 30 days, its optimum pH being at 5.8.

Karrer and his co-workers, studying the digestion of cellulose by Helix found that for action on cellulose, cotton powder, cotton wool, filter paper, and various types of artificial silk, an undiluted or even concentrated digestive juice had to be employed (for literature see Yonge, 1938). But when the crop juice of Helix was submitted to the same experimental treatment as that used for Aplysia, an action many times stronger was observed. The results were confirmed by an examination of the crop contents containing fragments of Ulva after incubation in vitro with a little toluol for 40 days. The cell walls were intact, and the chloroplasts, although turned brown by the action of the acid and collected together against the cell wall within the dead protoplasts, were still distinct. The polygonal cells were, however, more rounded in shape, small spaces having appeared between them, possibly due to the weak action of the cellulase assisted by a more active digestion of an intercellular substance. In this connexion the identification of a pectinase in the diverticula and crop is of particular interest. The source of the cellulase is difficult to trace; no such enzyme could be detected in extracts of the gut glands, possibly due to the fact that the enzymes were not sufficiently concentrated in these extracts, although it is interesting to note in this connexion that Yonge (1932) was unable to locate the source of the strong cellulase in the gut of Pterocera. The possibility of the existence of a kinase from a separate source is suggested.
The lipase in the lumen of the gut is no doubt secreted by the digestive diverticula where an enzyme occurs with an optimum pH identical with that of the enzyme in the crop (pH 5-6), and capable of digesting olive oil, ricinus oil, and esters. The esterase action is strongest, ricinus oil and especially olive oil being digested with greater difficulty. These oils are present as larger globules which present small surface area to the action of the enzyme.

A protease was identified in all regions of the gut, including the salivary glands, capable of attacking gelatin. Action on calcified milk was fairly rapid with extracts from the diverticula and crop fluid, the enzymes present from these sources digesting fibrin, casein, and peptone. The protease was most active between pH 2-8 and 3-4 and also between 8-4 and 9-4. Sharp optima were not found in experimental investigations of the protease.

VI. Mode of Feeding.

Aplysia was fed on a variety of weeds including species of Ulva, Chylocladia, Nitophyllum, Polysiphonia, Rhodomela, and Zostera. Starved animals will feed on their own egg cordons which they are, however, unable to digest. The small molluscs, annelids, and echinoderms occasionally to be found in the contents of the crop have been swallowed together with the weed to which they were attached and do not form a normal constituent of the food.

The anterior portion of the foot assists in feeding. It firmly grasps the weed, while the latter is explored by the walls of the buccal funnel. The walls are freely movable, and when they meet with a free end of the weed, they manoeuvre it into the mouth. If no free end is encountered the weed is firmly gripped by the jaws, while the walls of the funnel proceed to shape the weed into a form capable of being passed through the mouth.

Contraction of the superficial intrinsic muscles $I_1$ and $I_2$ and the dorsal extrinsic muscles $E_1$ pulls the posterior portion of the buccal mass forwards. During this movement the organ loses its pear shape to become almost spherical and the posterior extremity rotates forwards and upwards. A more pronounced forward rotation of the odontophore occurs, operated by the nos. 331, 332.
contraction of the basal mass of muscle $I^6$ together with that of the muscles $I^4$ attached to the sides of the radula membrane. The latter cause a simultaneous divergence of the radular halves, the divergence being widest in front and spreading backwards towards the radula sac at the completion of the motion. The functional teeth of the radula are now firmly pressed against the jaws with their points raised owing to the increased curvature of the membrane to which they are secured. After a slight pause the contraction of the sphincter $I^3$ and of the ventral extrinsic muscles $E^2$ together with the relaxation of those muscles affecting the forward movement, returns the odontophore to its former position with a strong thrust. The movement is aided by contraction of the muscles $I^5$ attached to the radula sac. At the onset of the return movement the radular halves converge about the weed, but at the conclusion of the movement they lie apart in their position of rest. The weed is thus conveyed towards the roof of the buccal cavity where it receives the secretion from the salivary glands and is taken up by the lateral folds of the dorsal food channel which firmly grasp the weed with the aid of the denticles.

These movements draw in some 3 mm. of weed at each backward thrust of the odontophore. During these operations the mouth is not completely closed. After some 2 cm. of weed have been taken in, a vigorous contraction of the sphincter during the return motion of the odontophore causes the jaws to tighten round the weed which is thus torn by the radula teeth. *Aplysia* is able in this way to feed comparatively rapidly. Large pieces of weed are taken into the crop.

VII. Physiology of the Gut.

Strong peristaltic waves of contraction originating at the anterior end of the food channel pass backwards to the neighbourhood of the second constriction, so propelling the weed into the dilatations of the crop. Here it meets with digestive juices regurgitated from the stomach, and with smaller pieces of weed which this fluid has flushed back into the crop from the gizzard. The posterior portion of the crop undergoes peristaltic contractions timed apparently independently of those of the anterior...
region. These contractions force the weed against the teeth of the gizzard. The smaller teeth of the anterior rows grip the weed and 'stoke' it backwards into the mill formed by the succeeding larger teeth. Their sharp tips diverge during dilatation of the gizzard and swing backwards as they converge on to the food mass during contraction of the gizzard wall. They thus perform an essentially similar function to that played by the three groups of hard plates in the posterior crop of the larval Bulla hydatis (Berrill, 1930). The weed is compressed between the larger teeth as they approach one another and finally broken up towards the end of contraction when the surfaces of the teeth move reciprocally by their slight rotation along a transverse axis.

The muscular action of the walls of the stomach and of the ducts of the digestive diverticula, acting together, drives the fluid secretion of the alveoli of the gland across the intestinal folds (Text-fig. 9, adf and vf) into the anterior regions of the gut. Although the folds are very closely approximated, their surfaces are not in actual contact, so that fluid, together with the small droplets and granules of excrement which have escaped entanglement in the mucous strings on the walls of the ducts, pass unhindered from the stomach forward as far as the crop. The term 'valve' for the intestinal folds is unsuitable, suggesting an alternation of movements which have not been observed. Dilation of the stomach and ducts of the digestive diverticula results in a passage of fluid from the crop through the gizzard and filter chamber. These pulsations are normally regular and continuous, and the observed movement of small air bubbles experimentally introduced into the gut demonstrates their vigour. The forward streaming of the digestive juices during contraction is strong enough to dislodge even large pieces of weed from the gizzard and carry them forwards again into the crop. On the other hand when expansion of the gizzard coincides with expansion of the stomach, pieces of weed some 2–3 mm. across are frequently drawn through the gizzard and filter chamber together with food in a finely divided and fluid state.

The passage of material from the crop to the intestine is therefore slow. The presence of enzymes from the salivary
glands and the digestive diverticula permit the digestion in the crop of substances liberated from the plant cells by the rupture of their walls in the gizzard.

A separation of particulate from fluid food is effected by ciliary currents operating in the anterior intestine. Text-figure 9 illustrates the direction of these currents as followed by the aid of particles of weed taken from the crop and experimentally introduced into this region. Currents on the folds convey the larger particles away from the opening to the stomach towards the bases of the folds. Here they come under the influence of currents which convey pieces of weed directly from the filter chamber posteriorly into the intestine. The gut fluid, on the other hand, is drawn into the stomach through a ‘filter’ of cilia at the approximated edges of the folds.

Cilia in the ducts of the digestive diverticula carry excretory granules and droplets away from the alveoli into the stomach. Here cilia on the crests of the folds (Text-fig. 10) beat obliquely into the grooves in which this material is carried, in long mucous strings, into the caecal opening on the left side. Here the thick, untwisted bunch of strings are conveyed by way of the incurrent channel (Text-fig. 10, ic) towards the distal extremity of the caecum. They receive at the same time a generous coating of mucus. At the end of the caecum the strings bend sharply round and enter the excurrent channel. Here they are rotated in a clockwise direction and receive a layer of ‘cement’ from the gland cells (Text-fig. 12, gc) as they move back towards the stomach. It is possible also that the viscosity of the mucus is increased owing to the lower hydrogen ion concentration in this channel (Yonge, 1935).

A compact rod with a smooth surface thus issues from the caecum and is conveyed between the typhlosoles across the posterior wall of the stomach into the intestine (see arrows in Text-fig. 10). Here, under the influence of the cilia on the flat longitudinal tract, it becomes spirally coiled, at the same time becoming embedded in the looser packing of mucus and undigested weed short-circuited from the filter chamber. The completed faecal mass is finally consolidated and cemented by the secretion of the glands in the intestine, while its passage
through the tube is lubricated by a plentiful supply of mucus. The whole mass is propelled towards the rectum by the combined action of the cilia and muscles. The operation is probably assisted by the higher viscosity of the mucus due to the low hydrogen ion concentration in the posterior part of the intestine and rectum. A string of faecal pellets is ejected from the anus by the strong muscular activity of its walls, the constrictions separating the pellets being formed by contractions of the anal sphincter. After a meal of Ulva the faeces are a strong green in colour due to the presence of fragments of undigested weed within the matrix enclosing the spiral rod. Pieces of weed some 3 mm. across, composed of cells unaltered by their passage through the gut, can easily be identified. The spiral rod, on the other hand, is a dark brown in colour and so compacted that the small yellowish green fluid droplets and even smaller pink, yellow, red, and green granules and greyish vesicles which can be seen in the stomach are no longer distinguishable. In the faeces of animals starved for 3 days it forms the only constituent and uncoils at the anus. It should be emphasized that the spiral rod is almost exclusively excretory and quite distinct in origin from the undigested food residue in the surrounding matrix.

The study of the structure and function of the caecum in Aplysia has led to a reconsideration of views previously expressed (Howells, 1936) as to the nature of the caecum in the Thecosomatous Pteropods. This structure was originally noted by Souleyet (1852), while Meisenheimer (1905) showed that it was universally present in this group and commented on its resemblance to the style-sac in the Lamellibranchia. He further suggested that the rod-shaped mass it contains might have the same function as the crystalline style. This was further emphasized by Yonge (1926b) who described the ciliary feeding mechanisms in a variety of these animals and showed that the food is essentially similar to that of Lamellibranchs. Histological examination of the caecum in Cymbulia peronii (Howells, 1936) revealed the great similarity between the epithelium of the caecum and that of the style-sac. But examination of the caecum in Aplysia has revealed a similar structure and anatomical relations, while the function is clear. It is there-
fore concluded that the caecum in the closely allied Thecosomatous Pteropods is not a style-sac but an organ concerned with the consolidation and moulding of the faecal mass. It is interesting to note in this connexion that in the Protobranchia Yonge (1939) has recently shown that the ventral region of the stomach is similar in histological structure to the style-sac of the other Lamellibranchia and of certain Gastropoda, and it is also similar to the caecum in these Opisthobranchia. This region in the Protobranchia secretes mucus in which the indigestible particles are entangled and is responsible for the preliminary moulding of the faecal mass. It does not secrete an amylase. It is suggested by Yonge that the style-sac with its contained style evolved from a caecum concerned with the secretion of mucus for the consolidation of the faeces. Acceptance of this view would have the additional advantage of explaining the similarity in histological structure between the caecum in Aplysia and in the Thecosomatous Pteropods and the style-sac.

VIII. DISCUSSION.

Perhaps the most outstanding feature of the alimentary canal of Aplysia is the relatively enormous size of the anterior regions in which food is mixed with the secretions of the digestive glands and digestion occurs. The so-called stomach of Aplysia is reduced, representing morphologically no more than the combined ducts of the digestive diverticula immediately behind their opening into the intestine. But the anterior gut, comprising the oesophagus, crop, gizzard, and filter chamber, consists of a series of large dilatations possessing great freedom of movement within the anterior body cavity. A constant forward and backward motion of their contents is maintained by the muscular action of the gut wall aided by the co-ordinated pulsations of the walls of the stomach and the digestive diverticula behind. No distinction can be drawn, either morphological or functional, between the oesophagus and crop when the animal is actively feeding. The entire length of the gut between the buccal mass and the gizzard is equally distensible but, owing to the backward direction of the waves of muscular movement of the gut wall, the anterior part of the
tube is emptied more quickly. This then collapses to a narrow diameter, thus simulating a purely conducting tube which has been termed 'oesophagus' by earlier workers. The elaboration of the anterior gut is probably secondary. This is in marked contrast to conditions in the primitive tectibranch Actaeon in which it is present as a straight narrow tube, without differentiation, between the buccal mass and the stomach, which is produced into an extensive backwardly directed caecum on the left side of the visceral mass. According to Fretter (1939), the stomach and caecum of Actaeon are probably of considerable importance in digestion, the food here undergoing similar treatment to that received by the food in the anterior gut of more specialized tectibranchs, i.e. trituration and admixture with the gastric fluid.

No successive action of enzymes from different sources of the alimentary canal is possible in Aplysia. All the enzymes act on the food in the same region of the gut. The fore-gut glands pour their secretion on to the food as it passes over the odontophore. The secretion contains, in addition to the mucus which is a normal product of these glands in molluscs, a weak protease and a strong amylase. The food and salivary secretion is immediately conveyed into the crop where it meets with a strong amylase, sucrase, lactase, maltase, pectinase, and proteases, together with a weak cellulase, secreted by the digestive diverticula and regurgitated by the rhythmic contractions of the tubules of the gland and of the walls of the stomach.

It is surprising that an exclusively herbivorous mollusc should possess a cellulase which, acting alone, is not strong enough to liberate the contents of the cells of the weed upon which the animal feeds. The action is many times weaker than that observed for the crop contents of Helix under the same experimental conditions. The triturating action of the gizzard of Aplysia is, however, very efficient and is almost entirely responsible for the exposure of the contents of the plant cells to the action of the enzymes. The food receives only very slight trituration in the buccal mass. The weed is torn into pieces of comparatively large size (often 1.5 cm. long) when a contraction of the oral sphincter coincides with a backward thrust of the
odontophore. The chief action of the radula is that of a conveyor belt, rapidly passing food from the mouth to the roof of the buccal cavity where it is immediately seized by the sharp denticles on the longitudinal ridges bounding the muscular buccal gutter. The importance of a rapid feeding mechanism to an animal which has to deal with a comparatively large quantity of food and which is confined to an environment in which feeding is often made impossible by the strong action of tidal currents is evident.

In marked contrast with that of Actaeon, the caecum of Aplysia is concerned solely with the cementing into a compact faecal mass of the material excreted from cells in the digestive diverticula. A similar structure occurs in closely allied genera, e.g. Aclesia, and in the Thecosomatous Pteropods, in all of which there is a similar need for avoiding the fouling of ciliary mechanisms lying in the path of the faeces after they are voided from the anus. In other tectibranchs (e.g. Philine, Sca- phander, Gastropteron, and Actaeon) a spiral pallial caecum (the ‘caecum glandulaire’ of Pelseneer (1894) and the ‘hypobranchial gland’ of Brown (1934)), lies near the anus. It is lined by mucus-secreting cells and strips of strongly ciliated epithelium which draw a vigorous current of water over the anus and into the caecum. The current is thence expelled through the exhalant aperture at the posterior end of the mantle cavity. In this way material voided by the anus is rapidly conveyed away from the mantle cavity. Nothing corresponding with this pallial caecum is present in the mantle cavity of Aplysia and the Thecosomatous Pteropods. The respiratory current in Aplysia is created by the cilia on the etenidium and is sluggish in comparison with that of the tectibranchs cited above. The faecal pellets remain in the region of the anus for a considerable time before eventually falling clear of the mantle cavity. In the Thecosomatous Pteropods the faeces are voided into the reduced mantle cavity on the right side of the visceral mass. They then pass forwards and leave the body in the immediate neighbourhood of the ciliary feeding tracts.
IX. SUMMARY.

1. The anatomy and histology of the alimentary canal, process of feeding, and physiology of digestion in *Aplysia punctata* have been investigated.

2. The food undergoes little trituration in the buccal cavity. The mode of action of the jaws and odontophore is adapted to the rapid intake of vegetable food.

3. The oesophagus and crop together form an anatomical and physiological unit.

4. Trituration occurs in the gizzard. The teeth are adapted to the trituration of plant material; this is of particular importance owing to the weak action of the cellulase.

5. Coarser particles of weed are retained by the teeth of the filter chamber and returned to the gizzard during the forward movement of the gut fluid.

6. The ciliary currents in the anterior intestine ensure that only food in a finely divided or fluid state is admitted to the stomach. Medium and larger sized particles are carried straight into the intestine.

7. Ciliary currents in the stomach are concerned with the removal of material rejected from the tubules of the digestive diverticula. This material is consolidated, cemented, and moulded into a faecal rod within the caecum, and conveyed by ciliary action to the intestine.

8. The intestine is concerned with the further consolidation and moulding of the complete faecal mass, and its propulsion (by combined ciliary and muscular action) to the rectum.

9. Mucus is secreted throughout the gut with the exception of the regions of the jaws, gizzard, and filter chamber. Enzymes are secreted in the salivary glands (amylase and protease) and in the digestive diverticula (carbohydrases, lipase, and proteases). Glands probably secreting a lubricant (other than mucus) occur in the epithelium of the lateral walls of the buccal cavity, and others, secreting a cementing substance, in the caecum and intestine.

10. Absorptive cells occupy the greater part of the epithelium of the digestive diverticula. They occur together with secretory, excretory, and storage cells.
11. Digestion occurs within the oesophagus and crop, gizzard, filter chamber, anterior intestine, stomach, and tubules of the digestive diverticula. The hydrogen ion concentration is here suitable for the action of the enzymes, and the gut fluid is kept in motion by the muscular activity of the walls.

12. A high pH exists in the lumen of the caecum, posterior intestine, and rectum, probably assisting in the consolidation of the faecal mass by increasing the viscosity of the mucus.

13. The presence of a highly efficient mechanism for the formation of the faeces is probably correlated with the poorly developed cleansing mechanism in the mantle cavity.

References.


Biedermann, W., and Moritz, P., 1899.—“Function der sogenannter Leber der Mollusken”, ‘Arch. ges. Physiol.’, 75.


Eales, N. B., 1921.—‘Aplysia.’ L.M.B.C. Memoir, No. XXIV.


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MacMunn, C. A., 1899.—"Gastric Gland of Mollusca and Decapod Crustacea", 'Phil. Trans.', B, 193.


— 1906.—"Larve libere degli Opisthobranchi", 'Arch. zool. Ital.', 2.


Sollas, I. B. J., 1907.—"Molluscan Radula, its Chemical Composition and Development", ibid., 51.


— 1926 a.—"Structure and Physiol. of Organs of Feeding and Digestion in Ostrea edulis", ibid., 14.


