HISTOLOGY OF THE DIGESTIVE TRACT OF SACCObRANCHUS FOSSILIS AND MACRONES VITTATUS.

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This paper deals with the histology of the digestive tract of two Siluroid fishes, *Saccobranchus fossilis* and *Macrones vittatus*. The paper is based on studies of sections with details of gross anatomy from fresh material. Particular attention is given to the epithelium of the different regions of the digestive tract, since they exhibit many variations.

*Bouin’s fluid* was used exclusively for fixation. The usual method of paraffin-wax embedding was employed for cutting sections. The stains used were *Hæmalum* and *hæmatoxylin* with *eosin* as a cytoplasmic stain. In some cases Mallory’s triple and Pascini’s stains were used.

The work was undertaken at the suggestion of Prof. C. R. Narayan Rao, and carried out under his direction. I am much indebted to him for his suggestions and encouragement shown during the course of the work. I am thankful to Mr. A. Narayan Rao, for his guidance and to Asst. Prof. B. R. Seshachar, and Mr. L. S. Ramaswamy, for the supply of required materials.
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Historical.

It is quite impossible in a short historical account to do justice to the work that has been carried out on the structure of the digestive tract of fishes. Agassiz and Vogt in 1845 worked on the stomach of the trouts. Later, in 1861, Valatour worked on Teleost fishes.

During the current century, the results of four prominent researchers are on record; those of Greene on King Salmon (1912), of Ben Dawes on the alimentary tract of Plaice (1929), a detailed paper by Irving, H. Blake on the histology of the digestive tract of the Sea Bass (1930), and a full account on the digestive tract of Minnow (1931), by Mary Dora Rogick. The literature is indeed limited on this subject from the viewpoint of modern technique employed in histological investigation.

General Morphological Notes.

The alimentary tract of Saccobranchus fossilis is not a uniform straight tube throughout, but is thrown into a large number of folds. It is only partially differentiated into regions of which the following can be recognised in addition to buccal cavity and pharynx: oesophagus, stomach and intestine. The buccal cavity and pharynx can be seen when that part of the digestive tube is cut open. The buccal cavity is narrow in front and becomes wide posteriorly. It extends from the lips up to the first pair of gill-slits. The pharyngeal cavity includes the branchial region, as well as the region of the pharyngeal teeth. It is wider in front and narrows down posteriorly. The oesophagus is in the form of a short tube, of a greater calibre in front and where it joins the stomach it becomes narrow. There is a slight external indication of the passage of oesophagus into the stomach, but if it is cut open, the line of demarcation is well marked off, the stomach folds appear distinctly different from those of oesophagus.

The stomach is a U-shaped organ and its greatest diameter is at the middle of its length, posterior to which it becomes more slender especially near the pyloric sphincter. A part of the sphincter projects into the lumen of the intestine.

The intestine is much convoluted (except the terminal portion—the rectal—which follows a straight course to the anus) and is held in position by the mesentery.
The pneumatic duct comes and joins the posterior part of the oesophagus. The bile and the pancreatic ducts enter the anterior part of the intestine just near the pyloric region of the stomach.

The digestive tract is supplied with pure blood from a branch of the dorsal aorta. The hepatic portal vein is found distributed in the mesentery of the intestine and stomach. From the stomach the hepatic vein joins the liver. This part is innervated by a branch of the vagus.

Although the lengths of the different regions of the alimentary tract are generally subject to considerable variation, the following carefully made measurements of the series in a single fish, 18.5 cm. long, will convey some idea of their order.

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<td>Length of the whole tract coiled from lips to anus</td>
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<tr>
<td>Lips to the posterior margin of pharyngeal teeth</td>
<td>2.1</td>
</tr>
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<td>Length of the oesophagus</td>
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</tr>
<tr>
<td>Anterior end of stomach to pyloric sphincter</td>
<td>1.0</td>
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<td>3.8</td>
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1. **Lips.**

The lip consists peripherally of a stratified epithelium and beneath this a sub-epithelial connective tissue. The stratified epithelium has mucous cells and taste buds towards its free surface and closely packed undifferentiated columnar cells towards the sub-epithelial connective tissue. A basement membrane and a stratum compactum are not found though the compactly arranged connective tissue fibres below the undifferentiated cells stimulate the presence of a stratum compactum (Plate VII, Fig. 1 A).

**Epithelium.**—The mucous cells are either elongated or oval and they are arranged with their long axis perpendicular to the surface of the epithelium. Those that open to the exterior are goblet-shaped. They exhibit a reticular appearance and the meshes are filled with a granular substance. Each mucous cell has a basal nucleus which is spherical usually or flattened occasionally and consists of a single heavily stained nucleolus with some lightly stained chromatin granules. The mucous cells are derived from the undifferentiated cells and as such the different stages could be made out throughout the thickness of the epithelium (Plate VII, Fig. 1 B).

Taste buds which occupy the whole thickness of the epithelium are located on the summits of the connective tissue papillae. They are spindle shaped and consist of elongated cells with their nuclei situated more towards their base than towards their centre. The nuclei are oval in form and
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contain heavily stained chromatin granules. The nucleolus cannot be made out. From the structure of the nucleus it can be inferred that the taste buds are composed of modified undifferentiated cells of the epithelium. The free surface of the taste bud is generally sunk giving the appearance of a gustatory pore (Plate VII, Fig. 1 B).

The undifferentiated cells are columnar towards their bases and taper into points towards their distal ends. The nuclei are generally oval in shape while some are spherical. Each nucleus consists of chromatin granules which react differently to one and the same stain. In some the nucleoli can be made out with difficulty.

Sub-epithelial connective tissue.—The sub-epithelial connective tissue could be divided into a compactly arranged region beneath the epithelium and a loosely arranged mesh-work of fibres which are vascularised and innervated. There are pigment bodies here and there (Plate VII, Fig. 1 B).

2. Buccal Cavity.

The buccal wall consists of a stratified epithelium of about ten to twelve cells thick and sub-epithelial connective tissue beneath it. The epithelium is composed of mucous cells and taste buds towards its free surface and undifferentiated cells towards the base. Besides these, there are certain big cells conspicuous by their one or more nuclei situated here and there in the thickness of the epithelium (giant cells). There are certain bodies of variable shapes which take up dark stain with hæmatoxylin and are found in the basal region of the epithelium (Plate VIII).

Epithelium.—The mucus cells are oval in shape and a majority of them open to the buccal cavity. When they do not do so, they are spherical in appearance. The cytoplasm of these cells is reticulate in structure. The nucleus which is found usually at the base of each cell is either spherical or flattened. Each nucleus has a single conspicuous nucleolus (Plate VIII, Fig. 2 B).

The taste buds are very like those found in the lips. The connective tissue papille on which the taste buds are situated are not as conspicuous and elevated as in the lips. The gustatory pore is prominent. The free ends of the cells are heavily stained and on examination with a high power of the microscope reveal highly refracting granules comparable to the hairlets of the same organ in mammals.

Some of the undifferentiated cells are columnar while others are roughly spherical. Their cell outlines cannot be made out very distinctly. The nuclei of these cells are of two types. Some are lightly stained, bigger in size, with a conspicuous nucleolus, while others are heavily stained, smaller
in size, sometimes with one nucleolus, which can be made out with some difficulty (Plate VIII, Fig. 2 B).

The cytoplasm of the big cells found in the thickness of the epithelium is finely granular and contain from one to four nuclei; usually these cells contain a clearer region in the centre which is probably the nuclear area after the disappearance of the nuclear membrane. The carefully made measurements of two typical cells, one with four nuclei and another with a single nucleus, are given below. The former measures 29 microns along its long axis and 25 microns along its short axis. The diameter of the clear space is 12 microns. The diameter of each nucleus is about 2 to 3 microns. The latter measures 30 microns along its long axis and 16 microns along its short axis, while the diameter of the single nucleus is 4 microns. From the above data it can be inferred that these cells are dividing. The cell cytoplasm does not divide with the division of the nucleus but is delayed till another division of the daughter nuclei takes place. The size of the cell is in conformity with this view. Later the cytoplasm divides, each part getting its share of nucleus. The structure of the daughter cells and their nuclei are very like that of the undifferentiated cells of the spherical type with a smaller heavily stained nucleus. From the similarity of the structure of these two types it can be inferred that the former are derived from the latter. In fact, the similarity between these nuclei and those found at the base of the mucous cells reveal the view that those large cells divide and their daughter cells gradually metamorphose themselves to form mucus cells.

Sub-epithelial connective tissue.—This region of the buccal wall can be divided into two regions as in the lips. The compactly arranged connective tissue fibres differ from the same structure of the lips by the presence of nuclei which is in all probability that of connective tissue cells though cells as such cannot be made out. The remaining part of the connective tissue differs from that of the lips in having a very loose mesh-work with blood vessels and capillaries.

3. Pharynx.

The pharyngeal wall can be structurally divided into anterior and posterior regions. The former comprises the branchial region and the latter forms the pharyngeal dental portion. The anterior part is characterised by the absence of musculature and the epithelium is not thrown into folds; on the other hand, the posterior part is thrown into folds and the musculature is complicated by the inclusion of oblique muscles. The posterior part is also marked by the presence of teeth, the structure of which is dealt with under a separate heading.
(a) *Anterior pharyngeal region.*—The pharyngeal wall consists of a stratified epithelium and beneath it the sub-epithelial connective tissue (Plate IX).

*Epithelium.*—The epithelium of this region, in regard to details of histological structure, is very like that of the buccal epithelium. It is thrown into a few folds. The summit of the folds sometimes contains a taste bud. The mucous cells are found at the base of the crypts; in some specimens they are found arranged in a single row peripherally as seen in the illustration (Plate IX).

*Sub-epithelial connective tissue.*—This region can be differentiated into two parts. That part which is next to the epithelium consists of a closer network and is well vascularised. Beneath this is areolar connective tissue of a very loose texture. The interstices of the mesh-work is probably filled up by fat cells.

(b) *Posterior pharyngeal region.*—The pharyngeal wall in this region has stratified epithelium, sub-epithelial connective tissue and muscularis (Plate X).

*Epithelium.*—The epithelium is composed of mucous cells, taste buds and undifferentiated cells which are actively dividing.

The mucous cells are generally arranged superficially in one or two layers and are located in the side walls of the crypts. Those that are found near the surface are generally bigger than those lying beneath them. The cells that open into the pharyngeal lumen are either vase or goblet-shaped. On a minute examination, their interior reveals a reticulate structure. Sometimes the contents occur in a frothy condition lying on the free surface of the epithelium. Hence the reticulate structure of the cell must be the sectional view of mucus. The nucleus is found at the base and in some cells it is stained heavily. The distal part of the nucleus, which is applied to the base of the mucous cell, is like that of a shallow cup and the opposite end is drawn out into a tapering point. The mucous cells of the second layer are either spherical or oval with a basal nucleus. The clear spaces of these cells are in all probability in the nature of vacuoles which reach an enormous size as the quantity of mucus in them increases. When they are full of mucus, their distal ends reach the surface and burst discharging the contents into the lumen (Plate X).

The structure of the taste buds occurring in this region is similar to that of the same organs in buccal epithelium. They are however few in number.

The undifferentiated cells occupy the remaining space of the epithelium. They vary in size and shape. Some of them are columnar and others are
cubical. A minute observation of the nuclei of these cells reveals the fact that they are in different stages of division. Two types of nuclei can be made out. One of the types takes heavier stain and these are generally nuclei of the daughter cells; while the other type takes a lighter stain and are generally nuclei of bigger cells which are in an active state of division. The cells by dividing increase the thickness of the epithelium as well as the surface; hence the folded nature of the epithelium.

Sub-epithelial connective tissue.—This region of the pharyngeal wall is very like that of the anterior region of the pharynx in containing a compactly arranged connective tissue next to the epithelium and a loose areolar connective tissue beneath it. The latter contains in its meshes longitudinal muscle bundles. Some fat cells could be made out here and there in this region. Both the regions are well vascularised and innervated.

Muscularis.—The muscle bundles form two coats in this region. The longitudinal muscle bundles which are found in the areolar connective tissue forms the inner coat of musculature. The transversely disposed muscle bundles occupy fairly a quarter of the thickness of the pharyngeal wall and form the outermost coat. The muscle bundles are of the striated type.

(c) The structure of the pharyngeal dental region.—The epithelium in this region is very much like that of the preceding region but for the fact that it is not much folded. The mucous cells are not found in abundance. At the base of the areolar connective tissue there seems to be a bundle of muscle fibres arranged obliquely for the movement of the pharyngeal teeth. The latter are elevated from the general level and look like convex discs. The arrangement of muscle bundles is such that the set or sets act as a whole.

The development of the secondary pharyngeal tooth-germs.—The development of secondary tooth-germs is very interesting to study. The epithelium of this region sinks down in the sub-epithelial connective tissue to form solid cords, thus making the base of the epithelium look like a festoon. The cells at the tip of the cords cut out a knob of cells which arrange themselves to form hollow spheres. For some time they retain the connection with the epithelium and later on they sink into the connective tissue which finally surrounds them in this region. In sections they appear circular. The wall of the hollow sphere consists of two tiers of cells concentrically arranged. They are cubical or columnar and the latter seem mostly to be derived from the former, by division. Later the inner tier of cells gives rise to others which fill in the hollow space, to form the central cells. At this time the sphere is solid. A little later some transparent structureless substance is formed between the central cells and the inner layer of the sphere. This forms the substance
of the tooth. The sphere elongates towards the pharyngeal lumen and as it does so, the tooth substance becomes conical and later becomes elongated. The tip pierces its investing layer of cells and projects a short distance in the pharyngeal cavity. Meanwhile the base becomes slightly swollen out before it spreads out in the sub-epithelial connective tissue tangentially to form a firm support; it constricts again to form a narrow neck. The central core of cells remains for some time unaltered and ultimately disappears. The worn out teeth are replaced by freshly formed secondary ones (Plate XI).

4. Oesophagus.

The oesophageal wall consists of a stratified epithelium, sub-epithelial connective tissue, muscularis and serosa.

Epithelium.—The epithelium is composed of mucous cells and undifferentiated cells. Taste buds are of very rare occurrence. The epithelium differs in its structure as it passes from the anterior to the posterior region. The epithelium of the anterior region is thicker than that of the posterior part. The folds of the anterior portion which are longitudinal and uninterrupted are blunt towards their tip and are of uniform size. The crypts are narrow. In the posterior region the epithelium is also thrown into folds, and bear sharp free edges which meeting together almost obliterate the lumen of the oesophagus. These folds branch mostly towards one side.

The mucous cells of the anterior region resemble to a great extent those of the pharynx and are found at the sides and bottom of the crypts. Most of the cells are greatly elongated and contain a basal nucleus which is either flattened or tapers into a point. A big mucous cell measures 47 microns along its long axis and 18 microns along its short axis. The cell cytoplasm is reticular in appearance. These cells mark the transition between the pharynx and oesophagus proper (Plate XII).

In the posterior region the epithelium consists of a greater number of mucous cells than in any other region. They are of very big size and look like sacs containing mucus in them. These cells are mostly distributed in one or two layers. A majority of them open into the oesophageal cavity. The mucous cells have nuclei with distinct nucleoli (Plate XIII).

The actively dividing undifferentiated cells are found towards the anterior part of the oesophagus. Different stages of dividing nuclei could be made out. Some of the nuclei are big and take up a light stain while others are small and take up a heavy stain. Few cells contain chromatin material without a distinct nuclear membrane. Some of the big cells are just like those found in the buccal epithelium. A few of the undifferentiated cells form a group and their cell outlines cannot be made out but chromatin
granules could be discerned in groups. They seem to contain some greenish yellow bodies.

In the thickness of the epithelium a few nuclei could be seen which are not well stained and they have no nuclear membrane. Some of the nuclei do not possess nucleoli.

Taste buds are of rare occurrence. A few structures simulating these bodies are found sunk below the surface of the epithelium communicating with the oesophageal cavity by a narrow passage leading from the gustatory pore.

Sub-epithelial connective tissue.—This region consists of connective tissue fibres loosely arranged so as to form a mesh-work. It is well vascularised and innervated. Some nuclei are found here and there. This tissue not only forms a central core for the folds but also forms a layer all round the epithelium. In the posterior region, the connective tissue fibres are so closely set that it does not appear like a mesh-work, but it looks like a connective tissue sheet studded with nuclei.

Muscularis.—The musculature can be divided into an inner longitudinal layer and an outer circular coat. The cut ends of longitudinal muscle bundles are found in the meshes of the sub-epithelial connective tissue. They gradually decrease in number posteriorly. The circular muscle fibres are transversely disposed and occupy a major part of the thickness of the wall of the oesophagus. The muscle fibres are of the striated variety.

Serosa.—The serosa is a conspicuous layer consisting of connective tissue fibres and cells, blood vessels and nerves, covered externally by flattened peritoneal cells. This coat of the oesophagus is external to circular muscle fibres and is continuous with the connective tissue found in this region.

The pneumatic duct joins the posterior part of the oesophagus. It is internally lined by a single layer of columnar epithelial cells. The circular muscle fibres of this duct are continuous with the circular muscle fibres of the oesophagus.

It will be of interest to consider the structure of the oesophagus just before it joins the stomach. The epithelium is gradually transformed from the mucous type to the single layered columnar epithelium of the stomach. This transformation is seen at the tips and sides of the oesophageal folds. The basal nuclei of the mucous cells are converted into the nuclei of the columnar cells. Some of these columnar cells are engaged in secretion. In this region the extraordinarily reduced longitudinal muscle bundles are a feature of interest to be noted (Plate XIV).
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5. Stomach.

This part of the digestive tract can be structurally divided into an anterior cardiac portion and a posterior pyloric region.

Cardiac region of the stomach.—The cardiac stomach wall is composed of gastric epithelium, tunica propria, glands, connective tissue layer, muscularis and serosa (Plate XV).

Epithelium.—The epithelium is thrown into a number of gastric folds. Each fold is supported by connective tissue fibres. The cells forming the epithelium are roughly columnar and vary in shape according to their position as well as at different stages of digestion.

The cells covering the tips of the gastric folds can be correctly described as trumpet-shaped, when they are not actively engaged in secretion. These are elongated cells whose free surfaces are wide while their bases are produced into filaments which join the tunica propria. The cell cytoplasm is finely granular and possesses a big ellipsoidal or spherical nucleus which is found either in the centre or the distal third of the cell. The nucleus contains a deeply staining nucleolus and some chromatin granules (Plate XVI).

The cells described above present a different picture altogether when they are actively engaged in secretion. The first stage of activity is manifested by the appearance of a transparent, tiny globule of fluid secreted by the cell at the free surface. This gives a characteristic appearance to the epithelium, since the distal parts of these cells take a lighter stain. The second stage of activity is marked by the growth of the secreted product till it assumes a spherical shape. At this stage the cell at its distal end presents the appearance of a cup. Subsequently, the secreted product is expelled into the gastric lumen. Probably, these cells are engaged in secreting a fluid which acts on the food-stuffs.

The cells lining the crypts may be appropriately described as columnar. The nucleus is situated generally in the basal third of the cell and exhibits the same characters as mentioned above. In an inactive condition, the cell cytoplasm is finely granular and while they are active, the distal third of the cell stains very lightly and at the free surface the secreted product accumulates.

The cells found at the bottom of the crypts are roughly cubical or rectangular and their bases are slightly wider than their distal surfaces. Their nuclei are more centrally placed. The cells of this region are also, to a certain extent, concerned in the secretory activity.

The formation of simple, tubular glands from the gastric epithelium will be described in the section dealing with glands.
**Tunica propria.**—The tunica propria is a term applied for that part of the connective tissue found between the gastric epithelium and glands. In fact, it is a part of the sub-epithelial connective tissue which has been isolated from the rest by the peculiar way by which the glands are derived from the gastric epithelium. This region consists of connective tissue fibres and in their meshes are found a good number of capillaries. There are many nuclei with a variety of shapes seen in this region, of which the oval or elongate type is common.

**Glandular region.**—This region is divided into compartments or blocks by the connective tissue septa found at regular intervals which connect the tunica propria on the one hand and the connective tissue found beneath the glands on the other hand. Elsewhere the two are separated by the glands.

The gland cells are usually arranged in such a manner that they generally form simple tubes placed at right angles to the surface, separated from one another by connective tissue septa. This simple arrangement is disturbed in some places by branching. Some of these glands open at the bottom of the crypts. A tangential section reveals the cut-ends of the glands which are either circular or oval in outline and are formed from four to six cells, sometimes with a lumen in the centre and at times without it. Each tube is isolated from the adjacent ones by septa which consist of connective tissue fibres and blood capillaries. Some connective tissue cells of a triangular type could be seen with fibres proceeding from three corners with a central nucleus.

The cells composing the glands can be classified into groups according to their position and structure.

The cells towards the epithelium are roughly cubical in shape and the cell outlines are distinct. The surface of the cells towards the gland lumen is smaller than that of the opposite side. The nucleus is of the spherical type and takes a heavy stain with a well-stained nucleolus containing some chromatin granules. The cytoplasm exhibits a fine reticular appearance.

The cells forming the basal region of the glands exhibit the same structure as above except for the cytoplasm which is coarsely granular, and the granules are quite conspicuous by their number and size. These granules are zymogen granules, since they are concerned with the production of the enzymes.

It is very interesting to study as to how the glands are formed by the epithelium. Some of the sections when examined present the following structure:—
Just beneath the epithelium under a particular focus a curved row of nuclei is seen which gives the appearance of a hollow invagination of the epithelium being formed. If the focus is changed so that the underlying layers of the sections might be viewed, a tangential view of the cells which presents a honey comb appearance can be seen. From this it is inferred that a hollow invagination of the epithelium is taking place. The cells at the bottom and the sides of the pits so formed differ in structure from the cells of the epithelium. When this sinking is taking place, it is covered automatically by a coat of connective tissue. The invagination proceeds deeper down and the lumen narrows. The cells at the bottom of the tube become highly granular. Thus the glands and their connective tissue covering are derived from the modification of the epithelial cells, and the sub-epithelial connective tissue respectively.

Connective tissue region.—This region not only forms the central core of the stomach folds but also forms a circular layer internal to circular muscle fibres. The correct idea of this statement could be grasped by considering the nature of the stomach folds. These folds are distinct from the epithelial folds. If the aggregate of the epithelium, tunica propria and the glandular regions is considered as forming a compound layer, the stomach folds are formed from the folding of this compound layer and the connective tissue forms the central core of these folds. A large number of nuclei could be made out in this region and the majority of these nuclei are ovate or elongate in shape, take a heavy stain and consist of chromatin granules. The cut ends of a few longitudinal muscle bundles are visible: probably these are the remnants of the longitudinal muscle bundles of the oesophagus. This is not characteristic of the stomach and is found only in the transitional region (Plate XV).

Muscularis.—The musculature consists of a thick internal circular muscle coat and a thin external longitudinal muscle layer. The muscle fibres of the stomach are of the non-striated type except at the region where the oesophagus passes into the stomach.

Serosa.—The serosa is of considerable thickness in this region and its structure is very like that of the oesophagus. At different regions of the stomach wall, the serosa is directly connected with the connective tissue layer by connective tissue fibres.

Pyloric region of the stomach.—This part of the stomach presents a strikingly different appearance from that of the cardiac region. The stomach wall is not thrown into folds but the gastric epithelium presents the feature of folds and crypts. The structure of the columnar cells of the
epithelium is very like that of the cardiac part of the stomach. The absence of the glandular region is conspicuous. The sub-epithelial connective tissue is very like that of the oesophagus. In the posterior region the circular muscle fibres increase in thickness to form the sphincter which projects into the lumen of the anterior part of the intestine for a short distance. The longitudinal muscle fibres and serosa are similar to those of the cardiac part of the stomach (Plate XVII).

6. Intestine.

The intestinal wall is composed of a columnar epithelium, sub-epithelial connective tissue, muscularis and serosa (Plate XII).

Epithelium.—It is characterised by the presence of columnar cells and is thrown into a number of folds which occasionally branch. In addition to this there are certain mucous producing cells of the goblet type which are modified columnar cells. There is still another type of cell, the wandering cell or the leucocyte.

The cytoplasm of the columnar cells is finely granular in appearance. The nucleus occupies the basal third of the cell and takes a moderately good stain and contains many chromatin granules besides a well-stained nucleolus. Towards the free surface of the cells a vertically striated plate-like structure could be made out, the top plate. The columnar cells at the tips of the folds, especially at the anterior region of the intestine, presents a different picture when they are actively engaged in absorption. They increase in size and their cytoplasm exhibits a coarsely granular appearance. The nucleus takes a lighter stain. In this active region the top plate cannot be made out. Though the columnar epithelium is one cell layer in thickness, yet it shows three to four rows of nuclei in a section which is 6 microns in thickness.

The goblet type of cells are of rare occurrence and they are of two types; they differ in staining reactions. Thus one type of cell does not take stain. Both the types are derived from the modified columnar epithelial cells. Such of those that open to the exterior are found near the surface, while others are found deeper down. The cells of the other type, though they resemble the above-mentioned one with respect to their distribution, yet differ in their staining reactions. These cells which take a heavy stain are studded with coarse granules. Some cells of this type appear like tubes with their nuclei basally situated. The free surface is at a higher level than the top plate and the edge flanks all round, thus furnishing the appearance of a trumpet. These cells are of very rare occurrence. As to how these cells differ in function from the above-mentioned type is not certain (Plate XIX).
The wandering cells or the leucocytes do not belong to the epithelium proper. They are immigrants and hence they are found in the interstitial spaces at the basal part of the epithelium. The cell outline is roughly spherical and the cytoplasmic area is transparent containing a very heavily staining nucleus: near the base of the epithelium, these cells are found in greater number than near the periphery. By the similarity of the structure of cells found both at the base and at the peripheral regions, it could be inferred that the cells wander from the basal to the peripheral regions.

Sub-epithelial connective tissue.—This tissue not only forms the central core of the folds but also forms a thin layer internal to circular muscle fibres. This is richly vascularised and innervated. Very often in sections a clear space appears in this tissue near the tip of the folds, probably these spaces function as the lacteals of mammals. Oval or elongate nuclei with chromatin granules can be discerned in this region. In the meshes of the connective tissue near the base of each fold a big blood vessel with its external muscle coat and an internal endothecium can be made out.

Muscularis.—The muscle fibres are of the smooth non-striated type. These are arranged to form an internal circular layer and an external longitudinal layer which is a comparatively thinner layer than the former. The circular muscle layer varies in thickness in one and the same section at different regions.

Serosa.—This layer is thickest in this region of the alimentary tract and in its composition it is very like that found covering the stomach. In some sections, the sub-epithelial connective tissue penetrates the musculature and establishes its connection with the serosa, since it is from this layer it receives its vascular supply.

The bile and the pancreatic ducts join the anterior part of the intestine, near the pyloric region of the stomach, at one and the same place. These ducts open in a strange manner. They enter as such through the muscularis and like one of the folds reach the central lumen where it opens. The tube is internally lined by columnar epithelial cells with connective sheaths surrounding them.

Conclusion.

The most striking histological features of the digestive tract of Sacco-branchus fossilis are the following:—

1. Taste buds roughly resembling those of the mammals in structure are present in the lips, buccal epithelium and pharynx in great numbers and a few are present in the oesophageal region.
2. In the buccal epithelium and in the anterior part of the pharynx there are giant cells, conspicuous by their one or more nuclei. These cells are dividing cells and no mention is made of them by any of the previous authors.

3. The anterior region of the pharynx is separated from the posterior part, for reasons mentioned in the paper.

4. No part of the free surface of the posterior region of the oesophagus, is free from mucous cells. External longitudinal muscle bundles are absent in the oesophagus.

5. The pneumatic duct comes and joins the posterior part of the oesophagus, while the bile and the pancreatic ducts open into the anterior part of the intestine just near the pyloric end of the stomach.

6. The stomach is divisible into cardiac and pyloric regions. The former is conspicuous by the presence of the glands while the latter is devoid of them.

7. There is no pyloric valve, nevertheless, the same object is achieved by the presence of the pyloric sphincter. There is no intestino-rectal valve.

Histology of the Digestive Tract of Macrones vittatus.

Macrones vittatus and Saccobranchus fossilis resemble each other to a great extent regarding histological details of their digestive tracts, since both of them are allied species. To avoid unnecessary repetitions, only those regions of the alimentary canal which exhibit structural differences are dealt with.

General Morphological notes.—The alimentary tract of Macrones vittatus is not a uniform tube throughout and the intestine is not greatly coiled. The short nature of the intestine indicates the fact that it must be carnivorous. As in Saccobranchus, the digestive tract may be externally differentiated into different regions. The pneumatic duct opens into the posterior region of the oesophagus.

Lips.—The epithelium of the lip is strikingly different from that of Saccobranchus, and comprises of undifferentiated and mucous cells. The cell outlines of the undifferentiated cells cannot be made out. The nuclei of these cells situated towards the free surface of the epithelium are spherical in shape each with a single nucleolus. The nuclei of the remaining undifferentiated cells are elongated in a radial direction; they take a heavy stain and each one of them contains a single nucleolus with some chromatin granules. The undifferentiated cells towards the base of the epithelium
are columnar in shape. The mucous cells are situated peripherally and are of the spherical type, with a basal nucleus.

Taste buds are few in number; they are unlike those found in Saccobranchus. Pigment bodies are of rare occurrence (Plate XX).

**Buccal cavity.**—The epithelium of this region can be differentiated from the same region of Saccobranchus by the rare occurrence of the taste buds. The superficially situated mucous cells are spherical in shape. The cell outlines of the undifferentiated cells cannot be made out; their nuclei are spherical and take a heavy stain. A few giant cells are found. The presence of a thick layer of stratum compactum beneath the epithelium is another important feature of this region (Plate XXI).

**Pharynx.**—The anterior pharynx is characterised by the presence of a distinct stratum compactum and by the absence of musculature. The stratified epithelium of this region is strikingly different from that of the same region of Saccobranchus. The epithelium consists of undifferentiated cells and conspicuous cells. The undifferentiated cells are of various sizes and shapes and are found in different stages of division. Their nuclei take a very heavy stain; the cytoplasm of the cells is finely granular. The conspicuous (giant) cells are superficially situated, covered by a single layer of cells towards the free surface. Their nuclei can be seen in different stages of division. Mucous cells are of very rare occurrence. The stratum compactum is present in the form of a thick, clear, wavy, uniformly staining band of fibres.

The posterior pharyngeal region is marked by a distinct muscularis which is complicated by the addition of oblique muscle bundles. The stratum compactum is absent. The epithelium of this region is about seven to eight cells thick and has mucous cells, undifferentiated cells, conspicuous cells and taste buds (Plate XXII).

The mucous cells are superficially situated and most of them open to the pharyngeal cavity. They are of spherical shape, and their cytoplasm exhibits a reticular structure. Each mucous cell has a flattened basal nucleus.

The undifferentiated cells are disposed in layers. The cells of the middle layers are roughly cubical, while the cells of the basal layers are columnar and are actively dividing. The nuclei are well stained and are found in various divisional stages.

The conspicuous cells are very like those described for the preceding region. From the similarity of shape between these cells and that of mucous cells, it may be inferred that they are in the process of being converted into mucous cells.
A few taste buds are present and are unlike those found in *Saccobranchus*. They are situated deeper down in the thickness of the epithelium on slightly raised areas of the sub-epithelial connective tissue and are of spherical type. In a majority of cases, they are covered over by cells of the superficial layer of the epithelium, while in a few cases they communicate with the pharyngeal cavity by a gustatory pore.

The rest of the digestive tract of *Macrones* does not show any striking structural differences which call for comment.

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**LIST OF ILLUSTRATIONS.**

(*Saccobranchus fossilis*).

**Plate VII.**

**Fig. 1.** A. Cross-section of the lip.
B. A part of the lip section highly magnified.

**Plate VIII.**

**Fig. 2.** A. Cross-section of the buccal epithelium.
B. A part of the buccal epithelium highly magnified.

**Plate IX.**

**Fig. 3.** A. A part of the cross-section of anterior pharynx.
B. A part of anterior pharynx highly magnified.

**Plate X.**

**Fig. 4.** A part of posterior pharynx highly magnified.

**Plate XI.**

**Fig. 5.** A. Cross-section in the region of the pharyngeal teeth.
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**Plate XII.**

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**Plate XIII.**

**Fig. 7.** A. Cross-section of the posterior part of the oesophagus.
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FIG. 10.
FIG. 12.
Fig. 14.
Fig. 15.
Histology of the Digestive Tract of S. fossilis & M. vittatus

Plate XIV.

Fig. 8. Section showing the transition between the œsophagus and stomach, highly magnified.

Plate XV.

Fig. 9. Cross-section of a part of the wall of the stomach.

Plate XVI.

Fig. 10. Two villi of the stomach with the gland cells highly magnified.

Plate XVII.

Fig. 11. Cross-section of the sphincter of the pyloric end of the stomach.

Plate XVIII.

Fig. 12. Cross-section of the intestine.

Plate XIX.

Fig. 13. Few of the villi of the intestine highly magnified (Macrones vittatus).

Plate XX.

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Plate XXI.

Fig. 15. Cross-section of the buccal epithelium.

Plate XXII.

Fig. 16. A part of the cross-section of the wall of the pharynx.

Key to Lettering.

B. V.—Blood vessel.
B. ep.—Blood capillaries.
C. M.—Circular muscle.
Ct. f.—Connective tissue fibres.
Ep.—Epithelium.
G. c.—Goblet cell.
G. Ep.—Gastric epithelium.
G. p.—Gustatory pore.
Gl. c.—Giant cells.
Gl. 1.—Gland lumen.
Gl. c.—Gland cells.
Gl.—Gland.
H. s. c.—Hollow sphere of cells.
I. c.—Investing cells.
I. ep.—Intestinal epithelium.
L. m.—Longitudinal muscle.
M. c.—Mucous cells.
M. b.—Muscle bundles.
N.—Nucleus.
P. b.—Pigment bodies.
S.—Serosa.
S. s. c.—Solid sphere of cells.
S. e. ct.—Sub-epithelial connective tissue.
St. c.—Stratum compactum.
T. b.—Taste bud.
T. p.—Top plate.
T. pr.—Tunica propria.
T. s.—Tooth substance.
U. c.—Undifferentiated cells.
W. c.—Wandering cells.
Z. g.—Zymogen granules.