THE ALIMENTARY TRACT OF THE COMMON BUMBLEBEE.

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INTRODUCTION.

The insects as a class offer more opposition to man than does any other class of animals. Indeed, the order Hymenopetera is the only group which is truly beneficial to man. It includes the ants, all the bees, both polonizing and honey-making, and all the parasitic wasps which keep in check other insect pests. Since the group is one of man's greatest allies, a knowledge of them is of importance.

For the present study a representative type, the common bumblebee, *Bremus pennsylvanicus* was taken. This is a medium-sized species with a black head, a black band between the wings, and black underparts. The outer border of the tibia is concave. Only male specimens were used in this work.

All the specimens were fixed in Carl's Fixitive and were preserved in 70% alcohol. Following this, both gross dissection and micro dissection were carried out.

1. *Gross dissection.* This was done by completely removing the dorsal wall of the insect, including the head. The tract is held in place by muscles, trachea, and by the tissue composing the air sacs.

2. *Micro Dissection.* The entire alimentary tract, including the oesophagus and rectum, was removed and imbedded in paraffin. The section was pinned out on cardboard during clearing to insure all parts being on the same level. Sections were then cut eight microns in thickness and stained in Delafield's haematoxylin and eosin. Cross sections were also made of the parts desired.

Drawings of the muscular network of the canal were made from unstained mounts, so the nuclei were not drawn.

I wish to acknowledge my indebtedness to Dr. C. H. Kennedy, of the Ohio State University, for his assistance and criticisms in the preparation of this paper.

Gross Anatomy of the Tract.

I. Mouth-parts.
II. Fore Gut.
  1. Pharynx.
  2. Oesophagus.
  3. Honey Stomach.
  4. Proventriculus.
  5. Oesophageal Valve.
  6. Salivary Glands.
III. Mid Gut.
  1. Stomach.
IV. Hind Gut.
  1. Malpighian Tubes.
  2. Pyloric Valve.
  3. Intestine.
  4. Colon.
  5. Rectum.

THE MOUTH-PARTS.

The appendages of the head comprising the mouth-parts are practically external. The ventral part of the head has no chitinous floor of its own, but is closed by the bundle of mouth-parts fitting tightly against the opening. When extended, the mouth-parts are twice the length of the head, and are more or less heavily constructed.

They are composed of the following parts:

(1) The Hypopharynx, which is a long cylindrical tube covered with yellow spines. These are arranged in rows running spirally around the tube. The mouth is at the apex of the tube, on the ventral surface. (Fig. 2).

(2) The Labium, which is represented by the palpi only, extending out toward the end of the hypopharynx, is composed of three visible segments, the basal large, and the others very small.

(3) The Maxillæ are well represented by the long laciniæ which extend to the apex of the labial palpi.

(4) The Mandibles are short and extend only to the base of the hypopharynx.

All of these parts are capable of being folded into a cylindrical-shaped organ, which bends in the center and folds back under the head when not in use.

THE FORE GUT

The fore gut is ectodermal in origin, having been formed by the invagination of the fore part of the embryo. It is about a half inch in length, reaching from the mouth to the fore part of the mid gut. It is thin, membranous, and almost transparent its entire length, except for the proventriculus and oesophageal valve. (Fig. 1).

On leaving the proboscis, the tract bends foreward and upward into the fore part of the head. It passes along the

upper part of the head toward the back, where it suddenly bends and proceeds down through the two lobes of the brain, and then straight back through the thorax into the abdomen, where it ends at the junction of the first and second segments. It is cylindrical and relatively small for most of its length until it reaches the abdomen, where it is greatly dilated, forming the honey stomach.

The Pharynx resembles the oesophagus in general appearance, but is more dilated and irregular. It is several times the diameter of the oesophagus, at its anterior end, but narrows at its posterior border where it empties into the oesophagus. It is not clearly differentiated from the oesophagus anywhere along its course, except in size and possibly in having a thicker covering of muscles.

The Oesophagus is a long tube extending from pharynx to the honey stomach. Its diameter is constant throughout the entire length. Like the pharynx, it is practically transparent and has a waxy appearance.

The Honey Stomach is formed by the greatly dilated posterior end of the oesophagus. It is about six or eight times the diameter of the oesophagus. It also has the same structure and appearance as the pharynx and oesophagus. (Fig. 1).

The Histology of the Fore Gut is as follows:

(1) A cuticula of chitin on the inner surface.
(2) An epithelial layer of hypodermal cells.
(3) A basement membrane, secreted by the hypodermal cells.
(4) A band of longitudinal muscle fibers.
(5) A band of circular muscle fibers.

The three parts of the fore gut already mentioned are alike in structure, (See Figs. 3, 4 and 5, Plate I). The chitinous cuticle is the most prominent layer, and is about four times as thick as the others combined. It is not solid but is made up of a very thin and greatly convoluted sheet of chitin. Under this chitinous layer is an epithelium of very thin flat cells. These are more or less indistinct and in sections have the appearance of a number of nuclei connected by threads. The basement membrane is not apparent in this portion of the fore gut. The longitudinal musclar layer is also very poorly developed. It is represented by a few widely scattered bundles of tissue. The circular muscles are also poorly developed, being represented by a few scattered strands.

The Proventriculus, (Fig. 1, Plate II), is a fleshy tube-like continuation of the posterior part of the honey stomach. In junction with the oesophageal valve it forms a valve-like door for the fore part of the stomach. Its anterior end is closed by four triangular-shaped lobes of tissue, which lean inward when food is passing through. Their inner surface is covered with chitinous spines, which are long at the apex of the lobes and which become shorter as they extend downward along the wall of the proventriculus. They are directed posteriorly into the gut, and probably serve to prevent the food from being forced back out into the oesophagus. The entire inner surface is covered with chitin, which is in the form of a relatively smooth sheet. The epithelial layer is very well developed, being made up of a single layer of oblong cells packed closely together. The longitudinal muscles are very well defined, forming about one third the total thickness of the wall. They run continously from one end to the other. Around the whole is an enormously developed layer of circular muscles. The outer membrane is not apparent. This is the only part of the entire gut where circular muscles are even moderately well developed. It evidently acts as a force pump for the entire system.

The Oesophageal Valve defines the posterior limit of the fore gut, which is merely a continuation of the proventriculus into the mid gut. It is conical in shape and tapers toward its posterior end, where a thick tuft of convoluted chitin protrudes from the interior. The chitinous layer is thin and not so well developed at the anterior end, but becomes thicker and heavier at the apex. The epithelial cells are not clearly differentiated from the muscles, but are present nevertheless in a scattered layer. A basement membrane is not apparent but the layer of longitudinal muscles is very well defined. It is heavy at the base but gradually branches off and disappears at the apex. The circular muscles are very poorly differentiated, being represented by a few scattered bundles. Surrounding the whole is a fairly well defined sheathing membrane.

In the oesophagus the chitin layer is the most prominent, while the other layers are relatively unimportant. In the proventriculus, the circular muscles are most prominent with the longitudinal ones next. In the oesophageal valve the longitudinal muscles are by far the most important.

The Salivary Glands belong embryonically to the fore gut. There are three main glands, two of which are cephalic, and the other thoracic, (Fig. 8, Plate I). They are all paired, one gland lying on either side of the median line. The supercerebral gland lies against the dorsal wall of the head, and is the smallest of the three. A duct leads downward and forward, and enters the pharynx in the fore part of the head. The post-cerebral glands lie back of the brain in the posterior part of the head. The frontal gland is merely the fore part of the post-cerebral gland. A duct leads from them inward and enters a main duct in the center of the head, which empties into the hypopharynx. The thoracic glands are large, and lie about the oesophagus, extending about half way back through the thorax. A duct leads from them forward and empties into the duct from the post-cerebral glands. All of the glands are well developed and occupy a large part of their respective body cavities.

The fore gut appears to be a conductor only. Other than the salivary glands, there appear to be no cells for secretion in this gut. Food is merely carried from the mouth to the stomach by this gut, and with the exception of the salivary fluid, is not affected by it.

THE MID GUT.

The stomach comprises about one-fourth of the entire length of the alimentary canal. (Fig. 1, Plate I and Figs. 1 to 5, Plate II). In diameter it is about four times the size of either the fore or hind guts. It is entodermal in origin, being formed by a proliferation of rings of tissue from the free ends of the embryonic stomodeum and proctodeum. Its most conspicuous layer is that of the digestive epithelium. The cells are arranged in circular folds, there being approximately one hundred and forty folds from the oesophageal valve to the pyloric valve. The epithelium is somewhat columnar, but not strikingly so. The cells are rounded and present a diagrammatic regularity as they fold up and down, forming in longitudinal sections papillæ-like projections into the gut. This type of gut has been formed from a gut having a straight, flat epithelium. Pressure applied to the ends would force the epithelium to lap back and forth accordian-like, into folds extending circularly about the stomach.

Outside this layer of cells is a fairly well defined basement membrane, which is in contact with each cell in the fold. It therefore undulates in keeping with the epithelial layer.

Between the folds and at their base are scattered bundles of muscle fibres. These are circular muscles, and have been squeezed down between the walls of cells by the folding action of the gut.

On the outside is a thin layer of longitudinal muscles composed of bundles of longitudinal muscles connected by strands of lateral fibres, the whole forming a lattice-like network. Due to the scarcity of these strands, the external wall of the stomach appears corrugated. This layer may not be functional as a muscular layer, but rather as a covering. There is no apparent sheath-like layer beyond this. (Fig. 7, Plate I).

The area about the oesophageal valve is smaller in diameter than the rest of the gut, probably because of the fact that food rarely finds its way into this cavity, being emptied farther out into the gut at the end of the valve. The cells in this region are small and are of a dense type of protoplasm. The nuclei evidently are of a weaker structure, since they appear coarsely granular when stained. The cells appear to be non-functional as far as secretion is concerned. (Figs. 2 and 4, Plate II).

The portion of the stomach behind the opening of the valve presents an entirely different view. In this portion all of the cells, and especially those at the ends of the folds, are quite large. The nuclei are apparently very dense, for they stain evenly and very darkly It is not an uncommon thing to find cells here which are six or eight times the size of those about the oesophageal valve. Evidently this is the source of secretion in the gut. The secretion is holocrene in this type of gut. The cell forms the digestive enzyme within itself until a certain quantity is collected and then the cell bursts open, liberating the enzyme into the gut. The old tissue is detached and the newer cells behind it move forward and take its place. At the base of the fold is a group of small cells called a nidus. From this nucleus of cells new cells are formed which move out and take the place of the cells which have completed secretion. In this way there is a constant change of cells as secretion progresses. (Figs. 2 and 5, Plate II).

At the anterior end of the mid gut is a circular ring of cells which surround the base of the oesophageal valve and which secrete a thin membrane extending back into the gut. This is called the peritrophic membrane, and extends the entire length of the mid gut. At the apex of the valve there are several elongate folds of the stomach wall, which extend into the gut

almost to the valve. At this point the peritrophic membrane becomes thickened, but whether these folds have anything to do with secretion is not clear. The membrane is secreted only at the anterior end of the gut and is carried along to the other end by continued secretion.

THE HIND GUT.

The hind gut comprises about one-half the length of the alimentary tract. It is small in diameter and rather muscular for most of its course, but becomes translucent and thin at the colon and rectum. There are five main parts to the hind gut. (Fig. 1, Plate I, Figs. 1 to 5, Plate III).

The Malpighian Tubes. At the junction of the mid gut with the hind gut, is a series of small tubes branching off in all directions, called the Malpighian tubes. There are approximately one hundred and twenty-five to one hundred and fifty tubes in all. They are arranged in three parallel, circular rows about the gut, and are rather small in diameter. They weave in and out among the folds of the gut and serve to hold it in a compact mass in the center of the abdomen. They are probably urinary in function, emptying their contents into the hind gut. (Figs. 1, 4 and 5, Plate III).

Within each tube is a small canal. Next is a layer of cells forming an epithelium, which is relatively thick and forms the true body of the tube. The cells are somewhat flat, being about twice as broad as deep. Surrounding the whole is a thin membrane of connective tissue.

The Pyloric Valve is a ring of elongated cells extending down into the hind gut at its anterior end, just posterior to the Malpighian tubes. The epithelial layer of the gut has merely bulged out into the cavity, and the cells have become elongate.

The Histology of the Hind Gut is as follows:

(1) A cuticula of chitin on the inner surface.
(2) An epithelial layer of hypodermal cells.
(3) A basement membrane.
(4) A layer of circular muscles.
(5) A thin layer of longitudinal muscles.
(6) A layer of circular muscles.

The gut as a whole is ectodermal in origin, being formed by an invagination at the posterior end of the embryo.

The Five Parts of The Gut are as follows:

The Malpighian Tubes. These are tubes formed by the epithelium and basement membrane. They do not possess the other layers.

The Pyloric Valve. The general characteristics of this valve have been described above. Its histology is identical with that of the intestine, except that the epithelial cells are two or three times as long as those in the intestine.

The Intestine. The chitinous layer is thin and relatively smooth. It lies compactly against the tips of the cells and is not folded in any way. The epithelium is of the columnal type, with nuclei at the basal ends of the cells. The cells are rounded at each end and are about three times as long as broad. There is no very definite basement membrane. The three layers of muscles are not easily differentiated. The circular muscles are well developed, but the longitudinal muscles appear only as short strands connecting each circular bundle with the next. The inner and outer layers of circular muscles are well defined. They fit so closely together that they appear as one layer. This is due to the fact that the strands of the outer layer have fallen down between those of the inner. The two layers form a lattice-like network, with the main strands running circularly about the gut. At intervals between these circular bundles, there will appear a longitudinal bundle of muscles. There is no apparent membrane around the whole. (Fig. 6, Plate I).

There are five longitudinal folds of the epithelium extending into the intestinal cavity. These extend from the Pyloric valve to the rectum. They are produced by convolutions of the epithelial layer. (Fig. 2, Plate III).

The Colon. This is a large sac-like structure at the posterior end of the intestine, and into which it empties. It is thin, translucent, and waxy in appearance. In diameter it is four or five times the size of the intestine. The chitinous lining is greatly wrinkled and convoluted, while the epithelium and muscle layers are thin and serve only as a covering. It is similar in structure to the oesophagus and honey stomach. The muscular layers are very thin and indistinct, but the longitudinal layer seems to be the most prominent. The natural position of the colon is against the dorsal surface of the body wall.

The Rectum. The colon leads back posteriorly under a dorsal anal sclerite, where it becomes very narrow and enters the rectum. The rectum broadens out and has its entire dorsal surface attached to the sclerite above it. It is held in place also by a thin chitinous plate which entirely covers it below and is attached on either side to the sclerite above. The anal opening is merely an opening in the articular membrane at the end of this dorsal sclerite, beyond the rectum. The rectum itself is not constricted at its opening but opens with its entire diameter.

The rectum is more chitinous than any other part of the gut. Its epithelial layer and muscles form only a thin covering. No rectal glands were found. Perhaps they do not occur in the male bee, though they are so very conspicuous in other Hymenoptera.

SUMMARY.

The alimentary tract as a whole is about twice as long as the body of the insect. The oesophagus is straight and leads back to the stomach in a direct line. The stomach and intestine are coiled upon themselves and are bound together by the mass of malpighian tubes. The fore gut is thin and practically transparent, except for the proventriculus and oesophageal valve. The mid gut is thick and corrugated, and is composed mostly of epithelial tissue. The hind gut is small and opaque except for the colon and rectum, which are somewhat transparent.

The entire system is rather simple and unspecialized. In each part of the canal there is but one prominent layer, which seems to have been evolved toward carrying on the entire function of that specific part of the gut. The other layers are often more or less discontinuous and vestigeal.

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EXPLANATION OF PLATES.

PLATE I.

Fig. 1. A dorsal view of the alimentary tract. Oe.—Oesophagus; H. S.—Honey stomach; S.—Stomach; Int.—Intestine; Rec.—Colon and rectum.

Fig. 2. The mouth-parts (Mandibles not shown). Hyp.—Hypopharynx; La.—Lacinia; La. P.—Labial Palp.

Fig. 3. Cross section of the oesophagus.

Fig. 4. Cross section of the honey stomach. C.—Chitin.

Fig. 5. Section of wall of sesophagus. C.—Chitin; Ep.—Epithelial cells; C. M.—Circular muscles.

Fig. 6. Muscular network around Intestine. C. M.—Circular muscle; Int.—Intestine.

Fig. 7. Muscular network of stomach. L. M.—Longitudinal muscle.

Fig. 8. The salivary glands. Hyp.—Hypopharynx; S. D.—Salivary duct; Ph.—Pharynx; F. Gl.—Frontal or post-cerebral glands; Pc. Gl.—Post-cerebral Glands; T. G.—Thoracic Glands; Sc. Gl.—Super-cerebral glands; Oe.—Oesophagus.

PLATE II.

Fig. 1. Longitudinal section of the proventriculus. L. M.—Longitudinal muscles; Sp.—Spine; Pvts.—Inner canal of proventriculus; Hy. Ep.—Hypodermal epithelium; C.—Chitin; Ho. St.—Honey stomach; M. G.—Mid gut; Es. V.—Oesophageal valve.

Fig. 2. Longitudinal section of oesophageal valve. Pvts.—Proventriculus; Oe. V.—Oesophageal valve; St.—Stomach.

Fig. 3. Diagramatic sketch of one-half of stomach, showing arrangement of the inner folds.

Fig. 4. A section of two of the folds in the fore part of the stomach lying about the oesophageal valve. C. M.—Circular muscle; C. Mar.—Ciliated margin of cells.

Fig. 5. A section of two of the folds of the stomach beyond the oesophageal valve. N.—Nidus; C. M.—Circular muscles; C. Mar.—Ciliated margin of cells.

PLATE III.

Fig. 1. Longitudinal section of pyloric valve. Int.—Intestine; Ep.—Epithelium; C.—Chitin; C. M.—Circular muscles; V.—Valve proper; M. T.—Malpighian tubes; St.—Stomach.

Fig. 2. Cross section of intestine. Ep.—Epithelium; L. M.—Longitudinal muscles; C. M.—Circular muscle.

Fig. 3. Longitudinal section of junction of intestine and colon. Int.—Intestine; Ep.—Epithelium; Rec.—Colon or rectum.

Fig. 4. Cross section of Malpighian tube.

Fig. 5. Longitudinal section of Malpighian tube.

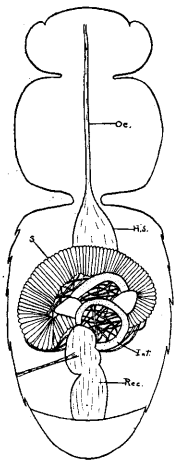
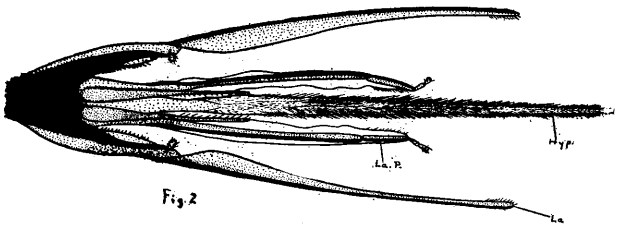


Fig. 1



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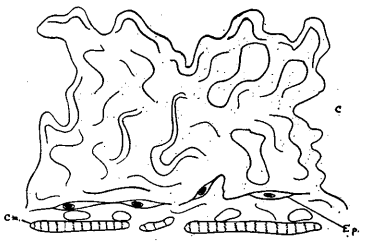

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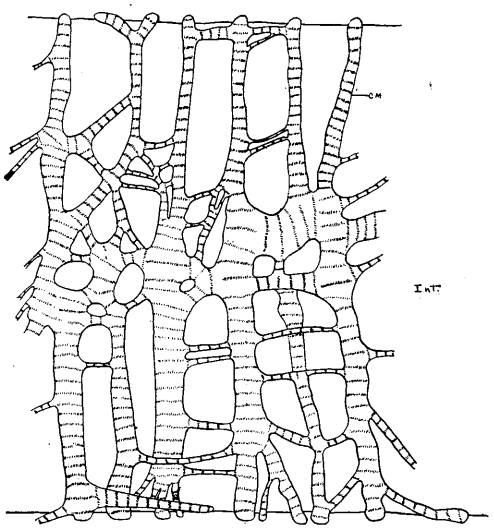

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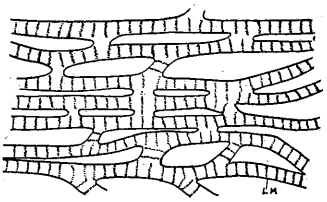

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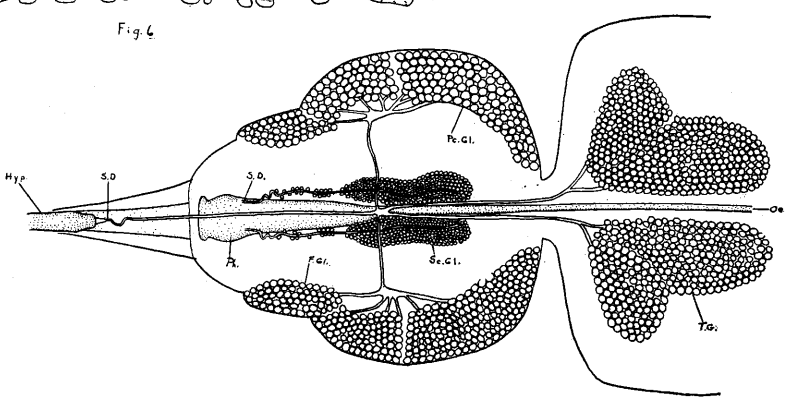

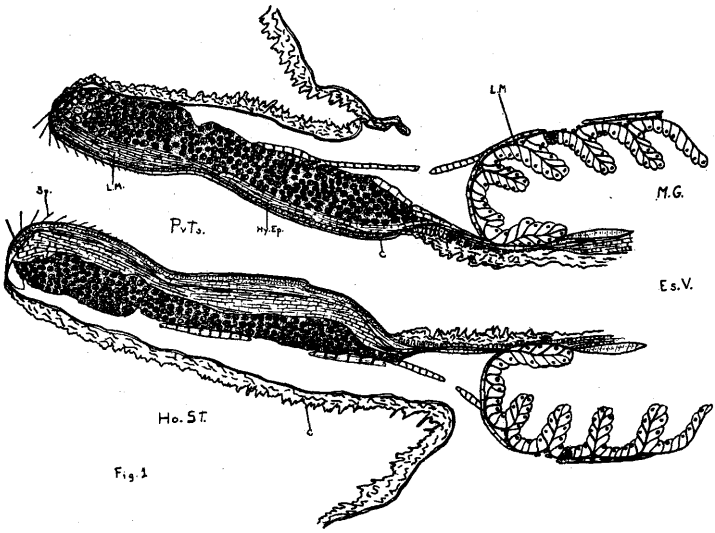

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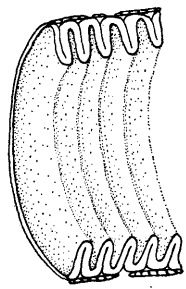

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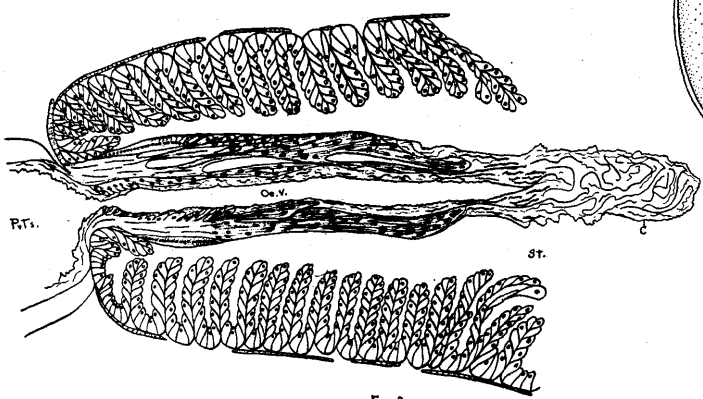

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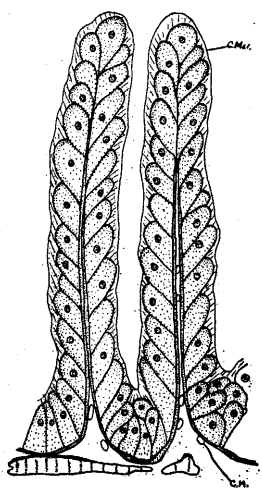

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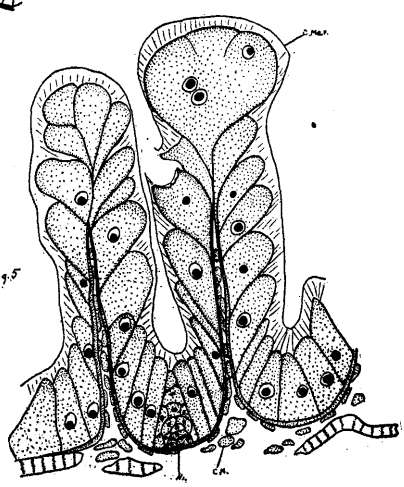

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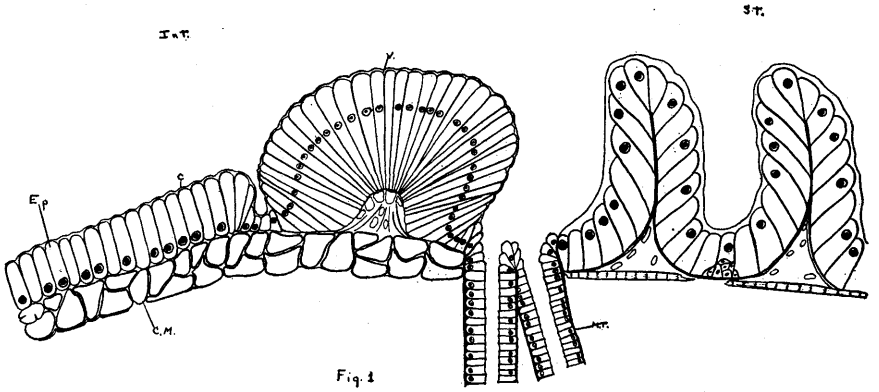

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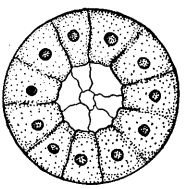

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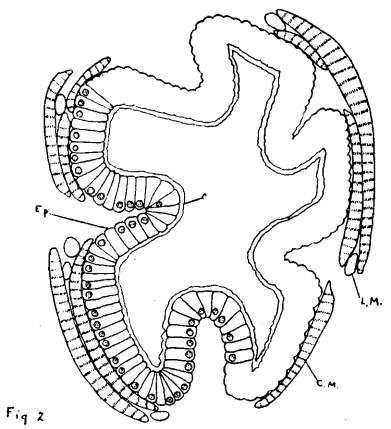

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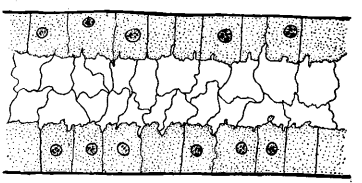

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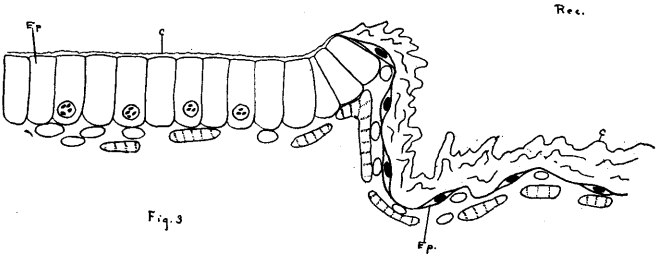

Fig. 3