THE MORPHOLOGY OF THE ALIMENTARY TRACT OF THE BLISTER BEETLE, EPICAUTA PENNSYLVANICA, DEG.

(COLEOPTERA: MELOIDAE)

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INTRODUCTION

In central Ohio the black blister beetle, *Epicauta pennsylvanica*, Deg., is found in abundance in September feeding on the pollen of goldenrod (Solidago). This member of the Meloidae is wholly black, ranging in length from 7 to 13 mm.

METHODS

Specimens collected were placed in Kahle's fixative immediately after being killed with potassium cyanide. Twenty-four hours later they were transferred to seventy per cent alcohol. Borax-carmine was used as an *in toto* stain before embedding in paraffin. Serial sections were stained in haemalum (one part to two parts alcohol) for seventeen minutes, and in Fast Green for thirty seconds. Difficulty was experienced in getting good sections of large structures. This was thought to be due to the hardening effect of the higher alcohols. A Dioxan technique was tried, hoping to toughen the material and make it more elastic. This method, however, removed the *in toto* stain and was abandoned.

ACKNOWLEDGMENTS

The author is grateful for the criticisms and advice of Dr. C. H. Kennedy, who supervised the work, and whose "Methods for the Study of the Internal Anatomy of Insects" was used as a manual of technique. Many valuable suggestions were also given by Dr. P. E. Schaefer.

THE GROSS ANATOMY

The morphology of the alimentary tract (Plate I, Fig. 1) of *E. pennsylvanica* Deg., is relatively simple. It has three main divisions: The fore-intestine (stomadaeum), the mid-intestine (mesenteron), and the hind-intestine (proctodaeum). Of these the stomodaeum and the proctodaeum are of ectodermal origin since they are formed by anterior and posterior invaginations respectively of the external germ layer. The mesenteron originates from the endoderm.

The fore-intestine is straight and simply constructed. It extends through the thorax and first abdominal segment. The mid-intestine is much larger in diameter and occupies the greater part of the abdominal cavity. It extends from the anterior of the first to the middle of the seventh abdominal segment. The hind-intestine is about one-half the diameter of, and approximately one and one-third times the length of the mid-gut.

The Fore-Intestine

There is no distinct pharynx, oesophagus, and proventriculus in the fore-intestine. The oesophagus is narrow anteriorly, gradually increasing in diameter until it empties into the mid-gut. The comparative size of the anterior, middle and posterior regions of the oesophagus may be noted in Plate II, Figures 1, 2 and 3. The gradual enlargement of the oesophagus is the only semblance of a proventriculus or gizzard. A lack of a definite chamber of mastication is typical of pollen feeding insects. The fore-intestine extends into the mid-intestine forming a pronounced oesophageal valve (Plate III, Fig. 5). There is no external indication of this valve.

The Mid-Intestine

The mid-intestine is larger in diameter than any other part of the alimentary tract, tapering at either end where it joins the fore-intestine and hind-intestine respectively. Externally the mid-gut appears folded or wrinkled transversely. This wrinkled appearance is due to the infolding of the thickened epithelial tissue.

The Hind-Intestine

There are three definitely differentiated regions forming the hind-intestine. These regions are the ileum, the colon, and the rectum. Just posterior to the mesenteron the ileum bends forward dorsally, extending anteriorly about one-half the length of the mid-intestine. The colon begins at the posterior bend of the ileum in its position over the mesenteron. The colon enlarges toward the rectum, where it constricts abruptly. This constriction is more pronounced dorsally. The rectum is about two-thirds the diameter of the colon at their point of union. Anterior to the anal opening the rectum enlarges slightly.

Malpighian Tubules

Six Malpighian tubules enter the alimentary tract at the point where the mid-intestine and hind-intestine meet. These tubules make many convolutions throughout the body cavity of the beetle, eventually entering under the connective tissue which covers the colon. The exact point at which the tubules enter under this tissue was not determined definitely, but it is in the bend of the hind-intestine where the ileum and colon meet. The tubules are found in numerous short bendings along the entire length of the colon, ending abruptly at the rectal constriction.

THE HISTOLOGY OF THE ALIMENTARY TRACT

The Fore-Intestine

Just as there is no morphological differentiation of the fore-intestine, so also there is no histological separation into a pharynx, oesophagus, and proventriculus. The wall of the fore-intestine is made up of the following five regions listed successively from interior to exterior: (1) a chitinous inner lining, or intima; (2) a thin epithelium; (3) longitudinal muscles; (4) circular muscles; and (5) a membrane of connective tissue covering the whole fore-intestine.

The intima is apparently composed of two layers. This is evident from the fact that a definite inner part of it stains much deeper with Fast Green than does the outer part. Within this intima there are six or seven deep longitudinal infoldings which extend the entire length of the fore-intestine. The folds increase in size toward the mesenteron, and as many as three or four smaller infoldings may occur between the larger ones at the region where the fore-intestine and mid-gut meet (Plate II, Fig. 4). The intima is modified on the interior surface and assumes a serrate appearance. In some specimens these serrations were further modified forming definite spines.

The epithelium of the fore-intestine is a single layer of elongated and flattened cells. This tissue follows the outer surface and the infoldings of the intima.

Although the longitudinal muscles occur around the entire circumference of the stomodaeal wall, they are massed for the most part at the base of, and in the infoldings of the intima and epithelium.

The next outer histological region of the fore-intestine is composed of circular muscles, which vary in the number of layers from one to three.

As the oesophagus enlarges posteriorly the wall becomes thinner. The longitudinal muscles are fewer, and the circular muscles limited in number.

There is no external indication of an oesophageal valve. It can, however, be readily demonstrated by pulling the oesophagus forward from the mesenteron. This action will pull from within the mesenteron an extension of the oesophagus. This extension of the oesophagus into, and for a distance of one-third the length of the mesenteron, is the oesophageal valve (Plate III, Fig. 5). Just at the point of entry of the oesophagus into the mid-gut, gross dissection reveals six splinter-like fingers of chitin. These chitinous structures are light brown in color, and run along the longitudinal axis of the alimentary tract almost to the end of the extension of the oesophagus into the mesenteron. A microscopical examination of a cross section shows these chitinous fingers to be located on the interior surface of the intima (Plate III, Fig. 6). These pieces of chitin remain unstained in mounted serial sections, and are not united at any point but are attached to, or embedded in, the layer of intima. R. T. Everly, in his study of the Margined Blister Beetle, found only four such structures. He also found that they were attached anteriorly only and were free and separate posteriorly.

The inner surface of the intima of the oesophageal valve of the Margined Blister Beetle, according to Everly, is definitely more modified than the anterior oesophagus. He found the same true of the pyloric valve region. No such definite differentiation is to be found between the anterior intima of the oesophagus of *E. pennsylvanica* and the intima of the oesophageal valve, or between the intima of the pyloric valve and that of the remainder of the hind-intestine.

In the region where the oesophagus and mesenteron unite fatty tissue is part of the wall of the alimentary tract. Circular muscles surround the valve under and posterior to this fatty tissue. There is a definite ring of these muscles which probably act in constricting and closing the alimentary passage. The epithelium of the oesophagus is continuous, extending into the valve well towards the end of the extension. This epithelium also is continuous anteriorly from this point around the outside of the ring of circular muscles, eventually uniting with the anterior epithelium of the mesenteron. Before it unites with the mesenteric epithelium, the epithelium of the oesophageal valve evaginates into the crypt of the first fold of the mid-gut epithelium. This forms a collar-like structure of intima and epithelium around the oesophageal extension.

The Mid-Intestine

The mid-gut is composed of epithelium, a basement membrane, circular muscles, and longitudinal muscles. There is also a peritrophic membrane. There is, however, no cuticula in the mid-intestine. This division of the alimentary tract has a thick wall due to (1) the gradual transition of the epithelium from the flat cells of the oesophagus to the columnar type of the mid-intestine, and (2) to the infoldings of this epithelial tissue. Circular muscles are well developed throughout the length of the mid-gut, but longitudinal muscles are very few.

It is probable that the ring of epithelial cells surrounding the oesophageal valve does not secrete the peritrophic membrane, since it has an inner cuticular covering which is continuous with that of the oesophagus. Whether the epithelial lining of the mid-intestine secretes the peritrophic membrane has not been determined.

The type of secretion is probably holocrine, i. e., it is due to the destruction of cells of the inner epithelium (Plate IV, Fig. 7). On the inner surface of the epithelium there is no striated border, but there are numerous globules of secreted fluid "budding" off from the ends of the cells. In some cases it appears that the whole end of the cell is breaking away. Ends of some cells also seem to have transparent vacuoles.

New cells are formed in round outward extensions of the epithelium. Some of these extensions break through the basement membrane and constrict at the outer surface to form round cellular aggregations. Some of these epithelial masses lie in the muscles, detached from the inner epithelial layer. At intervals the inner epithelial layer itself extends through to the outer surface, forming papillae there. The separate masses may be regenerative cells, as also may be the papillae-like extensions. Their function could not be demonstrated.

The Hind-Intestine

The mid-gut tapers off somewhat abruptly to form the ileum. The six Malpighian tubules enter in this region. A longitudinal histological examination of this region of union between the mesenteron and hind-intestine shows that the pyloric valve is relatively simple—if it can be called a valve (Plate IV, Fig. 7). This examination also shows that the Malpighian tubules enter the alimentary tract just at the posterior extremity of the mesenteric epithelium, and anterior to the tongue-like projection of the cuticular covered epithelium of the ileum. Everly found in his study of the Margined Blister Beetle, that the Malpighian tubules entered just posterior to this intima-covered invagination of the epithelium. The intima of this epithelium is relatively thick. The wall of the ileum just posterior to the entry of the Malpighian tubules contains an abundance of circular muscles from three to five layers deep.

Posteriorly the ileum has a thin wall (Plate V, Fig. 12). The intima, as in the region of the oesophageal valve, does not have spines or tooth-like projections which were found in the Margined Blister Beetle by Everly. In *E. pennsylvanica* the intima of the ileum is relatively smooth. The epithelium consists of a single layer of short cuboidal cells. There is a single layer of circular muscle cells, but longitudinal muscle cells are few.

At the bend over the mesenteron where the hind-intestine turns laterally and posteriorly, the ileum and colon meet. In this bend there is an increase in the number of layers of circular muscles. Longitudinal muscles are present in this region definitely grouped around the circumference of the outer layer of circular muscles.

The colon extends from the above described bend of the hind-intestine to the rectum. The wall of the anterior colon is thick (Plate V, Fig. 10). It has large infoldings of intima which are filled with epithelium. Surrounding the epithelium are the circular muscles, four and five layers deep. These muscles are arranged in six symmetrical groups or bundles, and have the appearance of being "tied in" at six equidistant points by groups of several longitudinal muscles.

The colon enlarges gradually toward the rectum, the wall becoming thinner. At the posterior end the colon is about one and one-third times the diameter of the rectum, and about one-half the diameter of the mid-gut (Plate V, Fig. 13). The colon is constricted abruptly in the seventh abdominal segment to form the rectum.

The anterior rectum has from 10 to 12 cuticular invaginations filled with epithelium (Plate V, Fig. 11), which nearly fill the lumen of the rectum. The wall is quite thick, made up almost entirely of circular muscles, only a few scattered longitudinal muscles being present. The rectum enlarges slightly toward the anal opening. In general, the rectum is wrinkled in appearance, although this is somewhat obscured in gross dissection by the connective membrane which covers the colon and rectum.

The Malpighian Tubules

The Malpighian tubules, six in number, enter the gut at the anterior end of the hind-intestine. At the point of entry they are covered with a broad ring of circular muscles (Plate IV, Fig. 8). There is also a definite covering of connective membrane evident in longitudinal and cross sections of the Malpighian tubules.

There are two semi-circular folds in the wall of the hind-intestine between the openings of each of the tubules (Plate IV, Fig. 9). There is no external indication of this; however, there is a clearing and smoothing of the region between the points of entry of the tubules, due to the absence of papillae. The opening of the Malpighian tubules into the lumen is surrounded by a ring of columnar epithelial cells (Plate IV, Fig. 8).

After many bendings throughout the body cavity the tubules enter under the connective tissue which covers the colon. They occur all along the colon under this membrane and end abruptly at the point where the colon constricts to the size of the rectum (Plate V, Fig. 13).

SUMMARY

In general, the morphology of *E. pennsylvanica* is like that of the Margined Blister Beetle as determined by R. T. Everly. There is little or no differentiation of the fore-intestine, except for a well-developed oesophageal valve. This valve has six finger-like pieces of chitin on its inner surface as it extends into the mesenteron. In this it differs from the Margined Blister Beetle which, according to Everly, has just four such chitinous "fingers."

Secretion is holocrine. There are evaginations of the mesenteric epithelium through the circular muscles to the surface of the mesenteron, forming papillae which are visible externally.

The Malpighian tubules, six in number, empty into the hind-intestine just at the point of union with the mid-gut, and not posterior to the poorly developed pyloric valve as was found in the Margined Blister Beetle by Everly. These tubules, after convolutions through the body cavity, enter under the connective membrane of the colon, where, with many short bendings, they extend to the rectal constriction of the colon. No connection with the lumen of the intestine in the region of the posterior colon could be demonstrated.

The ileum is somewhat muscular anteriorly, but the greater part is a thin wall of intima, epithelium, circular muscles, and a few longitudinal muscles.

The anterior colon has a well-developed muscular system. The circular muscles are "tied in" at six equidistant points by bundles of longitudinal muscles.

The rectum is quite muscular. The rectal lumen is well filled with invaginations of intima.

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ABBREVIATIONS USED ON PLATES

B M	Basement Membrane.	LU	Lumen.
C Mus	Circular Muscles	M INT	Mid-Intestine.
CH	Chitin.	MALP	Malpighian Tubules.
COL	Colon.	NI	Nidus.
CT	Connective Tissue.	OES	Oesophagus.
EPI	Epithelial Tissue.	OV	Oesophageal Valve.
FT	Fat Tissue.	PROV	Proventriculus.
IL	Ileum.	PV	Pyloric Valve.
IN	Intima.	RECT	Rectum.
L MUS	Longitudinal Muscles.	SEC	Secreting Cells.

EXPLANATION OF PLATES

Plate I

Fig. 1. A dorsal view of the alimentary tract in gross dissection.

Plate II

Figs. 2, 3, and 4. Three cross-sections of the oesophagus drawn to the same scale, showing the gradual enlargement of the oesophagus toward the mid-intestine.

Plate III

Fig. 5. Longitudinal section through the oesophageal valve, showing the sleeve-like extension of the oesophagus into the mesenteron.

Fig. 6. Cross-section of the extension of the oesophagus into the mesenteron showing the six chitinous fingers on the inner surface.

Plate IV

Fig. 7. Longitudinal section through the pyloric valve.

Fig. 8. Detail of cross-section of union of mid-intestine and hind-intestine showing the entry of Malpighian tubules.

Fig. 9. Diagrammatic drawing showing the distribution of the Malpighian tubules in a transverse plane at their point of entry into the hind-intestine.

Plate V

Fig. 10. Cross-section through the anterior colon.

Fig. 11. Cross-section through the rectum.

Fig. 12. Cross-section through the ileum.

Fig. 13. Longitudinal section through the colon and rectum, showing the constriction of the colon at the rectum, and the Malpighian tubules under the connective membrane of the colon.

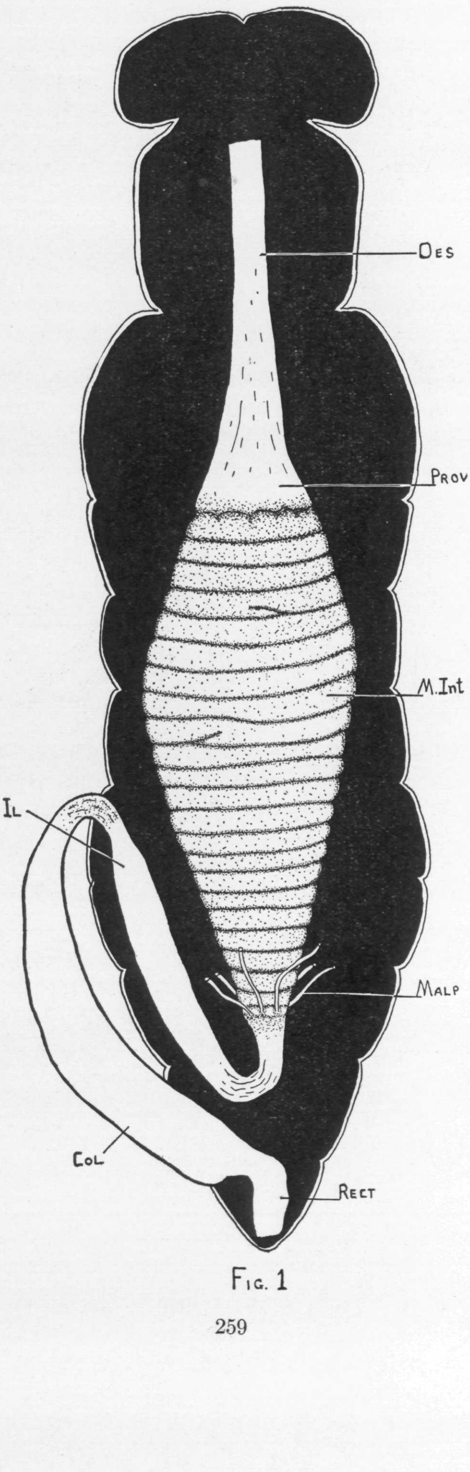
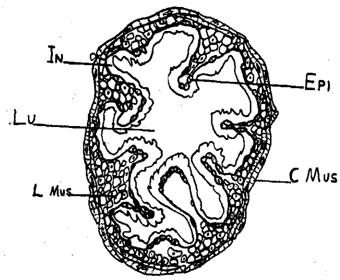


FIG. 1



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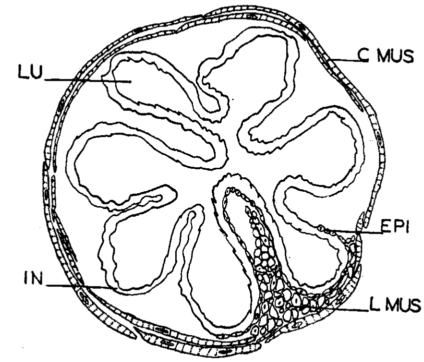

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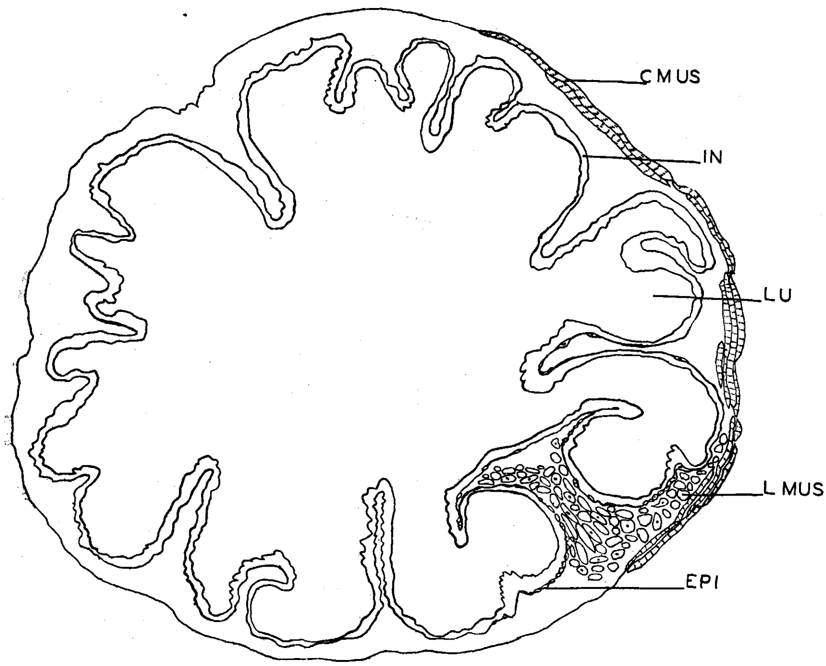

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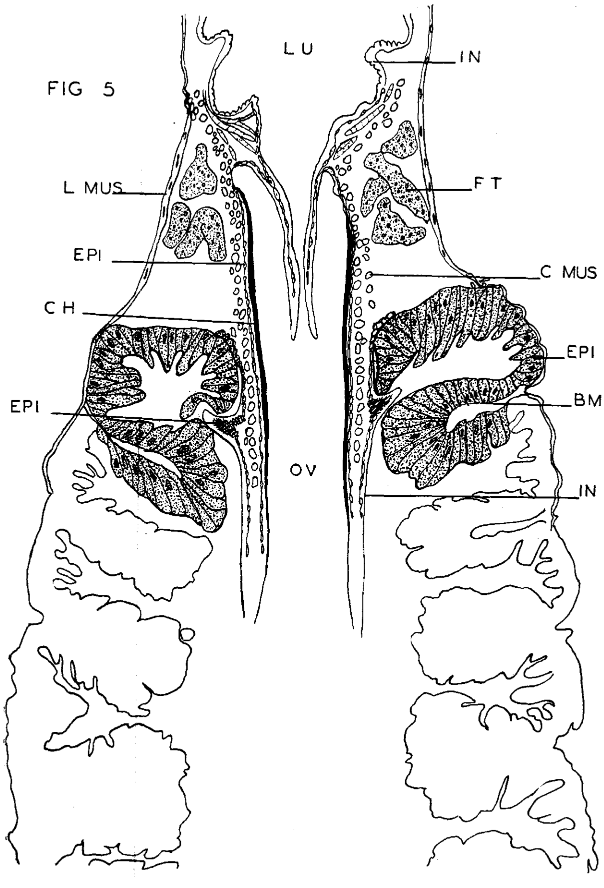

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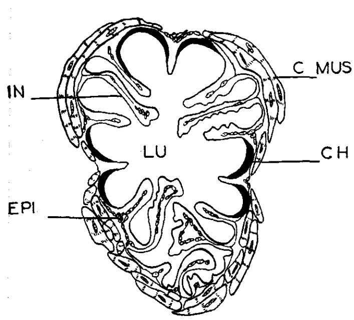

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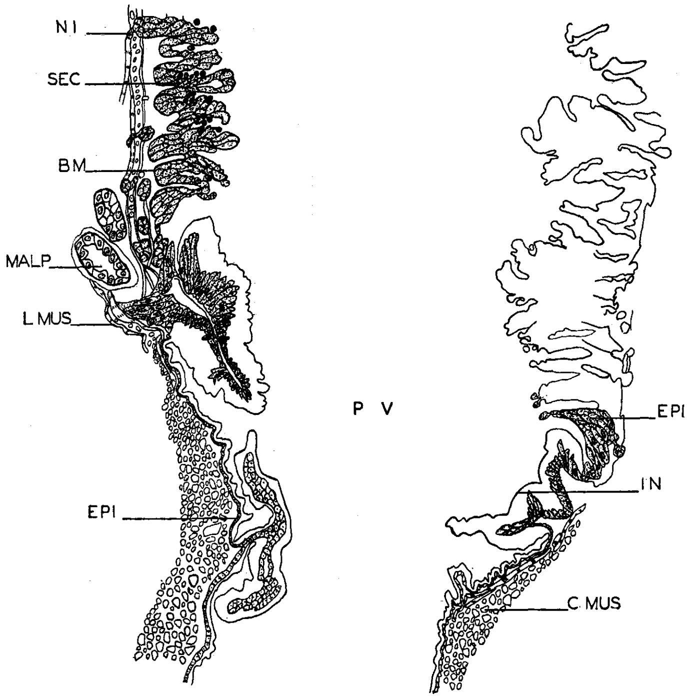

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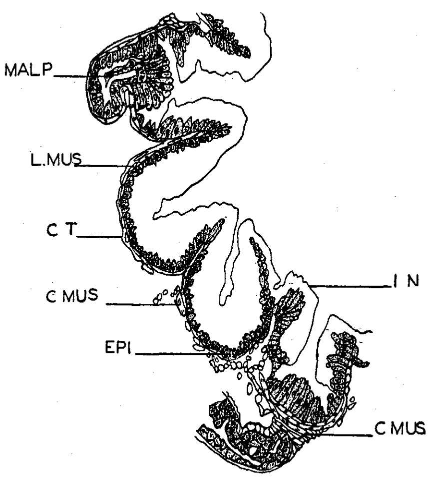

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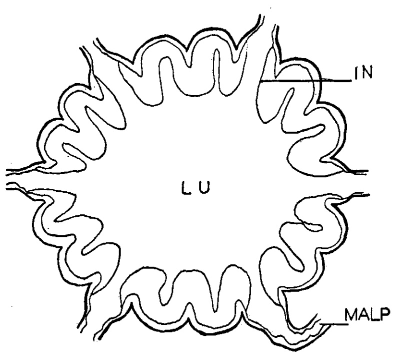

FIG. 9

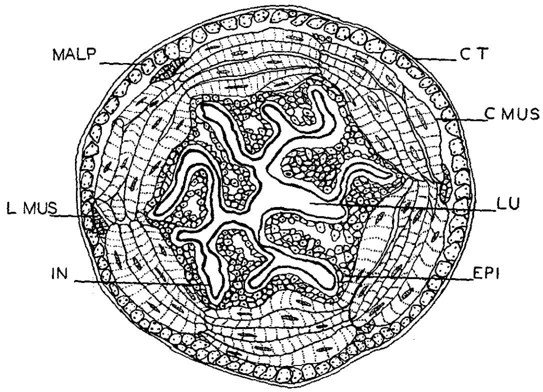

FIG 10

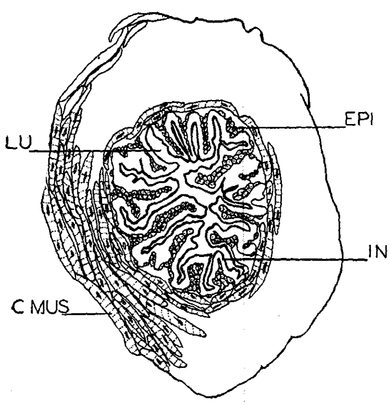

FIG. 11

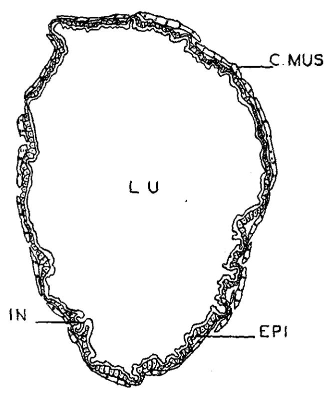

FIG. 12

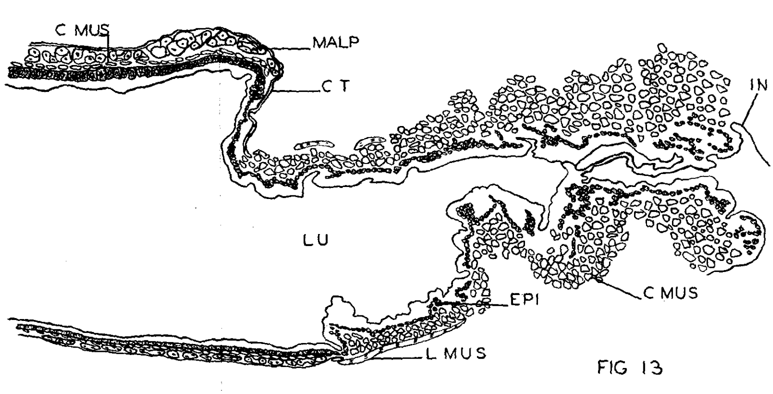

FIG 13