THE ALIMENTARY TRACT OF *PHANAEUS VINDEX* MACL. (SCARABAEIDÆ).*

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INTRODUCTION.

While on a collecting trip to Crane Hollow which is ten miles west of Logan, Ohio, the author noticed the green dung-beetle Phanaeus vindex MacL., was quite abundant in an upland sheep pasture near the Hollow. Upon the suggestion of Dr. C. H. Kennedy the writer spent the day collecting these beetles. The Scarabs were brought back to Columbus alive. They were killed with potassium cyanide, immediately placed in Kahle's Fixative solution and left for two days. The insects were then transferred to 70% alcohol in which they remained from May until fall.

ACKNOWLEDGMENTS.

The author wishes to acknowledge his appreciation to Dr. C. H. Kennedy at whose suggestion and under whose direction the work was carried on. His Lecture Notes and an unpublished thesis, "On the Alimentary Canal of *Megilla fuscilabris*," by Mr. B. J. Landis, have been available for consultation.

GROSS STRUCTURE OF THE ALIMENTARY TRACT.

The alimentary tract of *Phanaeus vindex* MacL. or *P. carnifex* L. (Scarabaeidæ) is a much coiled though relatively simple structure. In common with most dung-feeding insects the tube is of great length, averaging a little less than eight times that of the body. There are three distinct divisions of the tract; the oesophagus or fore-intestine, the stomach or mid-intestine (mesenteron), the hind-intestine (proctodeum).

The head is flattened so that the front and clypeus extend forward, forming a semicircle as illustrated in Fig. 1. The mouth, which is ventral, is approximately one-third the head length posterior to the front margin.

The buccal cavity is continuous with the pharnyx. The latter converges into the oesophagus, which is a straight, narrow, thin-walled

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tube lying along the mid-line of the body. The posterior limit of the oesophagus is just within the thorax and is marked by the oesophagal valve which separates it from the mid-intestine. No crop or gizzard is present.

The mid-intestine is somewhat larger than the oesophagus and is covered with numerous crypts or papillæ. It continues along the mid-body line until the abdominal cavity is reached. Here the tube begins to coil, making in all nine complete rings of varying circumferences. In Fig. 1 the intestine consists of eight equal coils placed outside the body cavity. To show the length and structure of the intestine it was necessary to be diagramatic in this one instance. The mid-intestine is by far the largest part of the tract, for it averages six and three-fourths times the body length. Just posterior to the oesophageal valve the intestine is often slightly distended but is otherwise of uniform circumference throughout its length.

The four Malpighian tubules arise at the posterior end of fore-intestine. These form a mat of twisted tubes around and in loops of hind-intestine. Following these is a band-like constriction, the pyloric valve. The canal then widens and forms several bends under the dorsal wall of the abdomen. The rectum precedes the anus and appears as a decided enlargement of the hind-intestine. (Fig. 1).

Both fore and hind-intestines are directly attached to the body wall, due to their origin as ectodermal invaginations. The anterior portion of the oesophagus is also supported by fine strands of muscle or connective tissue attached in the head. The mid-intestine lies between the large wing muscles and apparently has no actual supporting tissue. The canal rests free in the abdomen but may be partially held in place by the sac-like tracheæ surrounding it.

The following discussion will deal with the histological structure of the canal, beginning at the anterior end.

The Histology of the Alimentary Canal.

THE PHARYNX.

The pharynx has a heavy chitinous lining which bears short, backward-projecting spines scattered over the surface. The structure is otherwise similar to the oesophagus.

THE OESOPHAGUS.

The intima of the oesophagus is continuous with the cuticula of the body wall and extends the entire length of the fore-intestine, ending in the oesophageal valve. In the anterior portion of the tube it breaks into a series of longitudinal folds which separate preceding the valve. There are no spines in the oesophagus. The primary cuticula is very thin and stains dark with Delafield's Haematoxylin, while the secondary cuticula is thick and almost transparent. The epithelium is composed of a thin layer of cells whose walls are very indistinct, probably due to the fixative (Fig. 2 and 4). There was no apparent basement membrane.

A layer of thin longitudinal muscle strands cover the epithelium. These extend from the anterior end to the region of the valve, where some emerge and continue along the mid-intestine. Due to the strands' interweaving, no long pieces appear in the longitudinal sections (Fig. 2 and 4). Around the longitudinal muscles is a layer of circular muscles which varies in thickness. Toward the oesophageal valve the muscles become more numerous.

Fragments of a peritoneal membrane are found along the oesophagus, indicating that this part of the tube is probably surrounded by it. The membrane is very thin with large, flat nuclei in it. The cell walls are not distinguishable.

OESOPHAGEAL VALVE.

The oesophageal valve divides the oesophagus from the mid-intestine. At this point the mid-intestine and oesophagus seem to have telescoped—the mid-intestine pushing out over the oesophagus, forcing the oesophagus inward, thus partially closing the canal. The narrow epithelium of the oesophagus, in a longitudinal section is bent back to form an S. At the S the layer is somewhat thicker than in other sections and the nuclei are larger. Both divisions of the cuticula continue into the second loop. Outside the epithelium is a dense layer of circular muscle strands. Longitudinal muscles appear as isolated bundles beyond these strands. (Fig. 4).

TRANSITION FROM OESOPHAGUS TO MID-INTESTINE.

The transition of the epithelium of the oesophagus to the columnar type epithelium of endodermal origin is gradual in respect to the change in shape and size. The intima stops abruptly in the interior of the S which denotes a sudden change in the tissue. The first noticeable change in the cells themselves is the appearance of definite cell walls as it continues posteriorly. The cells appear cuboidal and the nuclei round. Gradually the cells lengthen and narrow to the shape typical for the anterior portion of the mid-intestine. The striated border appears and quickly thickens to its average width. In this region the longitudinal muscles come from under the circular and continue along the intestine above the circular muscles.

HISTOLOGY OF THE MID-INTESTINE.

A peritropic membrane is formed in the intestine. This membrane completely encloses the food and continues to surround it throughout the remainder of the canal. Just how or where this membrane is secreted the author was unable to determine.

No intima is present in the mid-intestine.

The epithelium has a striated border lining the lumen. The striæ are very close together and appear to emerge in tufts from each cell. the internal limits of these striæ are not clear. The epithelium is of the columnar type. In the anterior portion they are long, narrow, irregular cells with oblong nuclei. Further along, the cells shorten and thicken with the nuclei becoming oval and granular. Scattered along the basement membrane at the distal portion of the epithelium

are a few small replacement cells or nidi. The writer thinks these cells are non-functional for there is no evidence to show that they develop into full-sized cells.

At intervals, breaking through the muscle layers are large evaginations of the epithelium. These are known as crypts or papillæ, and in many insects they aid in the increase of absorptive surface or produce secretions. In the latter case they are usually connected by tubes to the lumen of the intestine.

A longitudinal section of a crypt shows it to have a group of nuclei forming a cell nest at its distal extremity. No cell walls are visible in this region. Passing inward, elongate cells form leaving an open space along the mid-line of the crypt. Where the crypt passes through the muscle layers this space appears to be choked with irregular shaped cells. The same cells are loosely scattered between the basement membrane and the muscle layers. No opening into the intestine was demonstrated. In the region of the oesophageal valve a ring of large crypts appear. (Figs. 4 and 10.)

The basement membrane is a structureless partition between the epithelium and the muscles. It is thin but shows heavier than the cell walls.

The position of the muscle layers are reversed in the fore and mid-intestine. In the mid-intestine the circular muscles form a single layer next to the basement membrane. The strands of this layer are thin but numerous. The longitudinal muscles consist of narrow, isolated strands continuous with the strands of the fore-intestine. No trace of a peritoneal membrane could be found.

Attached to the striæ and projecting into the lumen of the intestine are small droplets of secretion which stain in Haematoxylin. From this and the fact that none of the epithelial cells show nuclei moving toward or near the striated border; and that there is no indication of the replacement cells acting, the writer concludes that the secretion is probably merocrene.

PYLORIC VALVE.

A thick-walled structure, the pyloric valve, divides the mid-intestine from the hind-intestine. The valve is lined with a thin intima, which begins on the anterior face of the first fold in the valve. The primary and secondary cuticula stain as in the oesophagus. (Fig. 8).

The epithelium consists of a thin layer of tissue similar in appearance to that found in the oesophagus. The nuclei are small, staining dark in Haematoxylin. The cell walls were not discernible. A basement membrane was not found.

Outside the epithelium is a dense layer of circular muscle strands. This layer becomes thicker toward the posterior end of the valve. Isolated strands of longitudinal muscle are found beyond the circular layer.

TRANSITION FROM MID TO HIND-INTESTINE.

In the posterior portion of the mid-intestine the epithelial cells become very elongate as in the anterior portion and from folds. (Fig. 8).

The cells shorten at the Malpighian tubules beyond which is another fold. In this fold many nuclei are present but the cell walls disappear. Posteriorly the fold diminishes into a thin layer in which no cell walls appear. As the hind-intestine is reached the layer gradually widens, cell walls appear and the cells become the elongate type found in the hind-gut.

The muscle layers are continuous with those of the mid-intestine but the longitudinal muscles apparently end at the posterior end of the valve.

HISTOLOGY OF THE HIND-INTESTINE.

The hind-intestine immediately follows the pyloric valve. It is composed of two regions—the ileum and the rectum.

ILEUM.

The ileum includes most of the hind-intestine. It is a tube of more or less equal diameter until the transition area of the rectum is reached. (Fig. 3). The thin intima of the ileum is continuous and identical with that of the pyloric valve.

Columnar cells of ectodermal origin constitute the epithelial layer. These cells have no striated border. The nuclei are large, oval, and stain granular, while the cytoplasm stains uniformly clear. There are longitudinal grooves in the epithelium, thus all the cells are not of equal height or length. The basement membrane surrounding the epithelium is very pronounced. In places not covered by the muscles it appears as a heavy homogeneous layer.

The circular muscles consist of large, round, isolated, bundles which twist around the tube in a loose spiral. Longitudinal muscles were not found in the region of the ileum nor was there a peritoneal membrane present.

TRANSITION FROM ILEUM TO RECTUM.

The intima gradually thickens due to the widening of the secondary cuticula. The transition of the epithelium is slow from the usual columnar type of the ileum to the flat cells of the rectum. The epithelium produces longitudinal strips or folds which extend along the rectum and project into the lumen of the canal. The basement membrane is continuous from ileum to rectum. Isolated strands of longitudinal muscle appear outside the basement membrane. These strands increase in number toward the rectum. Circular muscles also become more numerous, crossing the longitudinal at right angles.

RECTUM.

The rectum immediately precedes the anus and has the greatest diameter of any part of the canal. (Fig. 7). The intima is heavy due to the thickening of the secondary cuticula. The epithelium is a very thin layer of tissue. Longitudinal folds of this extend far into the lumen of the canal. The nuclei are very small, granular, and oval. The cell walls are not apparent in this layer. The basement membrane is not visible.

Longitudinal muscles are very numerous and closely packed. Where these muscles attach at the anterior end the writer was unable to determine. Several layers of circular muscles are present beyond the longitudinal muscles, the strands of which interlace.

Surrounding the rectum is a thin peritoneal membrane.

In the female beetle attached to the ventral wall of the rectum is the vagina, a portion of which is shown in Fig. 7.

MALPIGHIAN TUBULES.

The four Malpighian tubules are evaginations of the hind-intestine at its anterior limit. Various cross-sections of the tubes show them to be irregular in diameter. The courses of the tubes could not be followed but the author found no evidence to show they were attached except at their origin. (Figs. 5, 6 and 9).

No intima was visible in the tubules. The epithelium is composed of large, irregular cells with large round nuclei. Outside the epithelium is the basement membrane which is continuous with that of the hind-intestine. A layer of connective tissue or muscle surrounds the tubules.

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EXPLANATION OF PLATES.

PLATE I.

Fig. 1. A dorsal view of the alimentary canal showing all structures in place except the mid-intestine. The ileum includes all of the hind-intestine save the enlarged posterior part which is the rectum.

Fig. 2. A cross-section of the oesophagus.

Fig. 3. A cross-section of the ileum.

Fig. 4. A longitudinal section of the oesophageal valve. One side only is shown.

Figs. 5 and 6. Cross-section of Malpighian tubules showing variation in size.

PLATE II.

Fig. 7. A cross-section of the rectum with a portion of the vagina attached to the ventral surface.

Fig. 8. A longitudinal section of the pyloric valve.

Fig. 9. A longitudinal section of the junction of the mid-intestine and the pyloric valve, showing the entrance of a Malpighian tubule. The tubule is cut at an angle and thus appears closed. C—Portion of crypt.

Fig. 10. A cross-section of the mid-intestine taken midway from its limits.

KEY TO FIGURES.

B. M.—Basement membrane.
C.—Crypt.
C. M.—Circular muscle.
EPI.—Epithelium.
F. T.—Fat tissue.
H. I.—Hind-intestine.
INT.—Intima.
L. M.—Longitudinal muscles.
MALP (MAL) TUB.—Malpighian tubules.
M. I.—Mid-intestine.
NI.—Nidi.
OE.—Oesophagus.
OE. V.—Oesophageal valve.
P. E.—Peritropic membrane.
P. V.—Pyloric valve.
S. B.—Striated border.
T.—Trachea.
VAG.—Vagina.

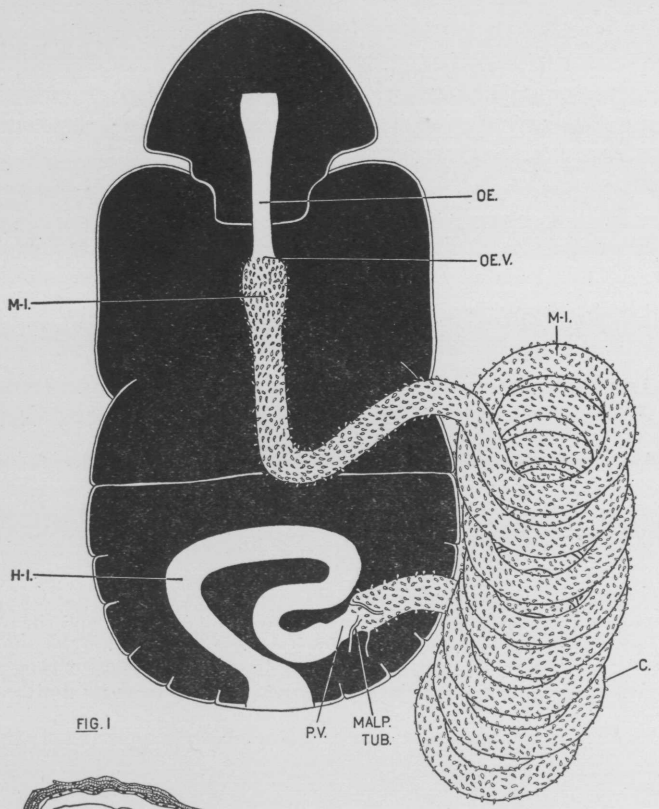

FIG. 1

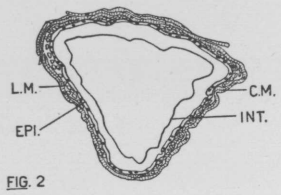

FIG. 2

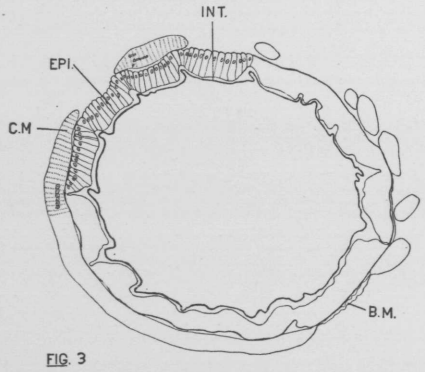

FIG. 3

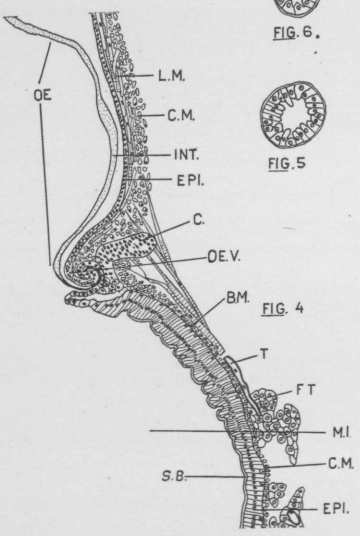

FIG. 4

FIG. 6.

FIG. 5

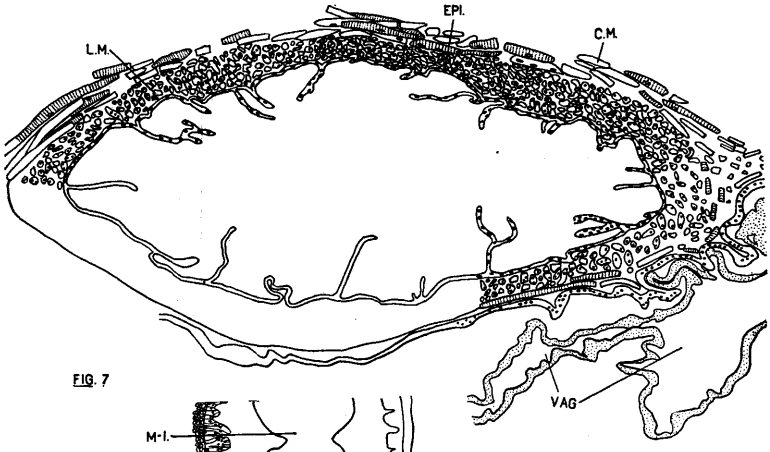

FIG. 7

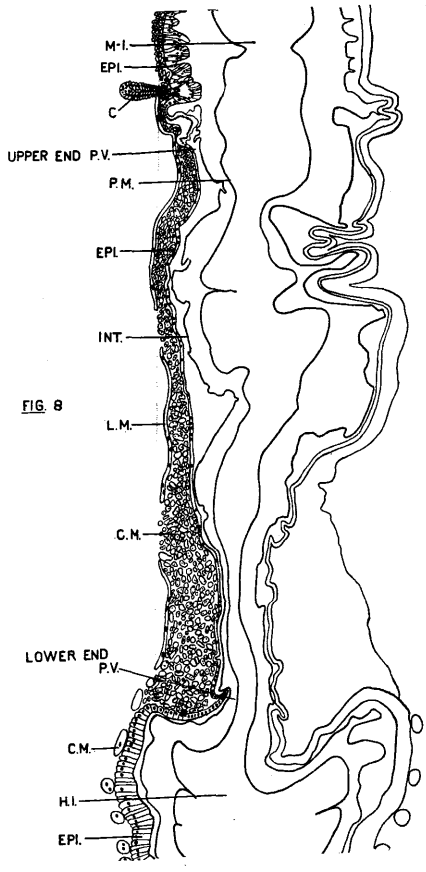

FIG. 8

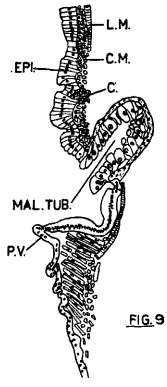

FIG. 9

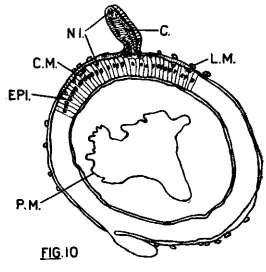

FIG. 10