ALIMENTARY CANAL AND MALPIGHIAN TUBULES OF CERATOMEGILLA FUSCILABRIS (MULS.)

(Coccinellidae, Coleoptera)

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The spotted lady beetle, *Ceratomegilla fuscilabris* (Muls.) (erroneously *Megilla maculata* Deg., a subtropical species), is abundant throughout temperate United States. The adults are gregarious at the time of hibernation and may be found during the winter in clusters under bark of trees or beneath fallen leaves on well-drained slopes.

The larvae feed on insect eggs, aphids and other soft-bodied insects. The adults feed also on pollen and fungi. Examination of the stomach contents of adults revealed, in a few cases, much of the food taken to be conidiospores of *Alternaria* sp., one of the Ascomycetes.

METHODS

Adult beetles collected from foliage or taken from hibernation were killed, fixed in Kahle's fixative, and preserved in 70 percent alcohol. The methods followed in gross dissection and microscopical technique were similar to those used by Jahn $(1)^1$ except that for some structures a double stain consisting of Fast Green and eosin was preferable to Delafield's haematoxylin and eosin.

GROSS ANATOMY OF THE ALIMENTARY CANAL

Except for a short loop occurring in the ileum, the digestive tract is a straight tube extending dorsally along the long axis of the beetle (Fig. 1). The pharynx and rectum are supported by suspensory muscles, and the remaining organs float in the body fluids although supported somewhat by tracheae and fatty tissue.

The fore-intestine: The labrum, the mandibles, and the hypopharynx are enclosed by an extra-oral mouth cavity. The flat, triangular pharynx narrows posteriorly and joins the oesophagus posterodorsally. The narrow oesophagus lies entirely within the head capsule. Within this transparent organ several longitudinal folds can be seen in gross dissection. In some individuals a pair of pouches appears at the junction of the oesophagus and proventriculus. The proventriculus is a pear-shaped bulb, twice the diameter of the oesophagus, lying in the anterior part of the prothorax. It is attached to the stomach,

¹Numbers in parenthesis refer to Literature Cited, pp. 19-20.

or mid-intestine, posteroventrally and is partly obscured laterally by the paired caeca of the mid-intestine (Figs. 1, 2, and 3). There are no salivary glands.

The mid-intestine: The stomach is a straight tube extending from the middle of the prothorax to the fifth abdominal segment, where it narrows to half its former width (Fig. 1). Anteriorly, where the greatest width of the digestive system occurs, a pair of gastric caeca appears. These caeca are covered with minute papillae containing the nidi, or cell nests, of the enteric epithelium.

The hind-intestine: The ileum, which is much narrower than the stomach, turns to one side of the midline of the body cavity and forms a complete loop. Like the oesophagus, the ileum is semitransparent, and several internal longitudinal folds are visible from without. The colon is slightly wider than the ileum and increases to its greatest width posteriorly at the junction with the rectum. The rectum is narrower than the colon and is twice as long as wide.

HISTOLOGY OF THE ALIMENTARY CANAL

FORE-INTESTINE

The stomodaeal pharynx and oesophagus (Figs. 2 and 4): The primary intima is heavy throughout the fore-intestine. In the pharynx the intima is smooth but becomes undulated and deeply pitted in the oesophagus. Each pit contains a thick, short spine (Fig. 4, SP) which projects posteriorly into the lumen. Farther posteriorly the pits and spines are replaced by posteriorly directed overlapping scales, each of which contains five or six minute striae. The secondary intima (S INT) has no definite shape and varies throughout the fore-intestine both in thickness and in amount of granular material. The cells of the epithelium (EP) are indistinct but appear to be elongate.

Two to three sets of longitudinal muscles (LON MUS) are found outside the pharyngeal epithelium. Occasionally epithelial cells are pushed aside by suspensory muscles having their insertion on the intima (INT). One or two sets of circular muscles (CIR MUS) persist throughout the length of the fore-intestine.

The proventriculus (Figs. 2 and 3): The intima supports 12 or more rows of spines, each having 15 to 25 posteriorly directed spines (SP) which project into the lumen.

The epithelium is prominent in the fore part of the proventriculus but diminishes gradually posteriorly, where flattened nuclei alone are distinguishable.

The longitudinal muscles of the proventriculus are heavy, especially in the posterior part, where many of them are inserted on the intima (Fig. 2). The circular muscles are heaviest at each end of the organ. Just posterior to the oesophageal valve and throughout the length of the mid-intestine, the external layer of longitudinal muscles is found outside of the circular muscles.

The oesophageal value (Fig. 2, OES VALVE): The posterior end of the proventriculus projects into the mid-intestine, where it becomes constricted to form the oesophageal value.

The primary cuticula within the valve is smooth but becomes slightly undulated as it turns into the mid-intestine.

The epithelium is similar to that of the proventriculus, but on the outer side of the valve facing the lumen of the mid-intestine the cells become three times as long as wide for a distance of 30 cells.

The heavy circular muscles of the posterior part of the proventriculus regulate the opening and closing of the valve.

MID-INTESTINE

The peritrophic membrane (PER M) of the mid-intestine or stomach (Figs. 3, 5, and 6), a non-cellular grayish membrane, may be secreted by the well-defined press. Food passing the oesophageal valve into the stomach is enclosed by the peritrophic membrane, which may serve as protection to the enteric epithelium. Between the peritrophic membrane and the enteric epithelium (E EP) are bits of cells sloughed from the epithelium.

The enteric epithelium functions in a holocrine manner. After food passes into the stomach, the cells rupture and the remaining cell fragments slough as new cells push out from the cell nests. Individuals not having fed for some time have long epithelial cells. During hibernation these cells grow until they nearly close the lumen, but as dormancy is broken the old cells are voided. Enteric epithelial cells are formed first in nidi (Figs. 3, 5, and 6, *NID*). The nidi are embedded in a screen-like matrix of circular and longitudinal muscles (Fig. 5). Seventeen embryonic cells were counted in one nest. In beetles that have not fed for some time the ends of the epithelial cells bordering the lumen bear a striated border, generally known as the "rhabdorium."

The basement membrane $(\vec{B} \ MEM)$ is more clearly defined in the mid-intestine than elsewhere in the digestive tract. It appears as a thin layer of indistinct cells bordering the epithelium and is perforated at intervals by cell nests.

One to three sets of circular muscles are found separating the cell nests. The longitudinal muscles are few and inconspicuous and show best in cross section.

HIND-INTESTINE

The pyloric value (Fig. 11): The pyloric value is not so distinct in C. fuscilabris as in the phytophagous coccinellids. The value occurs at the juncture of the ileum and the mid-intestine and slightly below the origin of the Malpighian tubules (MAL T). It is supported by three sets of circular muscles which pinch the epithelial folds of the ileum. These folds are continuous with the insertions of the Malpighian tubules.

The epithelial cells are long and narrow, in contrast with the flat cells of the ileum.

The ileum (Fig. 13): The intima is thin and convoluted and possesses overlapping scales bearing posteriorly directed striae.

The longitudinal muscles of the mid-intestine divide, on reaching the ileum, part continuing posteriorly outside the circular muscles and the remainder passing between the circular muscles and the epithelium. Circular muscles cover the ileum throughout its length. The colon (Fig. 12): The intima is slightly heavier in the colon than in the ileum and faces the six folds of large epithelial cells.

The musculature is similar to that found in the ileum.

The rectum (Fig. 7): The intima is thinner than that of the colon and possesses long spines near the anal opening.

The epithelial cells are small and appear in eight to ten longitudinal folds.

Suspensory muscles are attached to the intima at several points on the rectum.

THE MALPIGHIAN TUBULES

The Malpighian tubules of insects arise as evaginations of the ileum near the junction of the mid- and hind-intestines. Their evagination, loci, number, length, and course throughout the body cavity often differ between taxonomically related species having dissimilar food habits and waste products.

In C. fuscilabris the Malpighian tubules are six in number and arise in the same plane equidistant from each other and at the anterior end of the ileum. For convenience in discussion the tubule may be divided into two parts: (a) a free, beaded undulated portion extending from the evagination on the alimentary canal forward through the body cavity to the anterior limits of the stomach, then back into the posterior part of the abdomen, and finally returning to the proximity of the alimentary canal near the junction of the ileum and the colon; and (b) and enclosed, or reassociated portion, lying between the layers of the peritoneum encasing the colon.

The fact that the tubules return to the hind-intestine suggests that there may be a second or posterior termination through which wastes are voided. Woods (2), quoting Ramdohr, lists 22 genera of Coleoptera, representing 10 families, in which the Malpighian tubules become reassociated with the alimentary canal at their distal ends. Ishimori (3) has figured the terminalia of the tubules in a great many lepidopterous larvae in which the same condition exists.

The writer believes that there is an indirect passage in C. fuscilabris and other Coleoptera possessing the reassociated condition of the Malpighian tubules, by means of which liquid wastes are passed into the hind-intestine.

In C. fuscilabris the reassociated portions of the tubules are gathered from the body cavity by an inverted funnel-shaped matrix or envelope of peritoneal tissues (Figs. 12, 13, 14, 15, and 16, *PERI*). The enclosed tubules follow the contour of the colon posteriorly and spread in a definite and apparently specific pattern around the colon (Fig. 16). The envelope holds the tubules loosely at the anterior end of the colon but narrows posteriorly, forcing the tubules between the intestinal musculature until the junction of the colon and the rectum is reached, where the peritoneum cuts through the layers of intestinal tissues obliquely and is inserted on a narrow ring of non-staining primary intima peculiar to this region. The peritoneal envelope consists of an outer heavy layer bathed by fluids of the body cavity and one to eight or more inner layers (varying with the species) (Figs. 13,

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14, and 15), which follow loosely the general contour of the outer heavy layer and the reassociated parts of the Malpighian tubules. In gross dissection this envelope may be removed intact from around the alimentary canal (Fig. 16).

The Malpighian tubules are attached at many places to the heavy outer layer of peritoneum, causing the tubules to appear ovoid in cross section. At these points of attachment ducts (Fig. 15, DUCT) open up in the wall of the tubule through which a part of the contents of the collapsed cells of the tubule stream out into the matrix of the peritoneal tissues. However, the cell nuclei lodge in the mouths of the ducts and are retained within the tubules.

After entering the peritoneal matrix, the liquid wastes appear to be transported posteriorly to the insertion of the peritoneum on the intima of the intestine. The large, flat epithelial cells characteristic of the hind-intestine do not appear between the insertions of each peritoneal layer on the intima, but are replaced by spindle-shaped cells having prominent nuclei.

As previously stated, the insertions of the peritoneal envelope at the junction of the colon and the rectum occur on a narrow ring of non-staining sclerotic intima (Figs. 13, 14, and 15). Sections of this brittle sclerotic material examined under oil immersion reveal a maximum of six rows of minute openings leading from the peritoneal matrix through the region of the intima and opening in the lumen of the intestine.

Tracing liquid wastes from the reassociated portion of the Malpighian tubule to the hind-intestine (Fig. 15), we find that certain cells of the tubule secrete their contents into the lumen of the tubule and pass through ducts in the walls of the tubule into the matrix of the peritoneal envelope, where they are transported posteriorly to the insertion of the layers of the peritoneum and pass through minute openings in the non-staining ring of intima into the lumen of the hind-intestine.

Sections made through the colon and the rectum of adults of Chelymorpha cassidea Fab., Diabrotica vittata Fab., Epilachna corrupta Muls., Epilachna mexicana Guer., Penthe pimelia Fab., Bolitotherus cornutus Panz., and Tribolium confusum Jacq.-Duv., reveal essentially the same relationship between the Malpighian tubules and secondary terminalia as in Ceratomegilla fuscilabris. These conditions will be presented in another paper.

The work of Poll (1934), on certain Buprestids, presents an interesting variation of the conditions reported by the present writer. Poll was unable to trace a luminal connection between the reassociated ends of the Malpighian tubules and the hind intestine. Instead, he found at the junction of the colon and rectum a series of small supplemental tubules having sclerotized luminal connections with the intestine. These he describes as true intestinal caecae.

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EXPLANATION OF PLATES

PLATE I

- Gross dissection of adult of Ceratomegilla fuscilabris (Muls.), showing Fig. 1. organs of the alimentary canal and the Malpighian tubules. Camera lucida drawing of longitudinal section through the oesophagus,
- Fig. 2. proventriculus, and oesophageal valve.

PLATE II

- Fig. 3. Camera lucida drawing of cross section through proventriculus and paired caeca of mid-intestine.
- Longitudinal section through the fore-intestine, showing undulating Fig. 4. intima and spines.
- Camera lucida drawing of longitudinal section through the enteric epithelium of the mid-intestine (from hibernating adult). Fig. 5.
- Fig. 6. Camera lucida drawing of cross section through the mid-intestine.

PLATE III

- Fig. 7. Camera lucida drawing of cross section through rectum.
- Fig. 8. Cross section of Malpighian tubule in wall of colon.
- Fig. 9. Longitudinal section through wall of rectum.
- Fig. 10. Cross section of Malpighian tubule.
- Fig. 11. Camera lucida drawing of cross section through the pyloric valve near insertion of the Malpighian tubules.
- Camera lucida drawing of cross section of colon, showing peritoneal Fig. 12. matrix and enclosed Malpighian tubules.

PLATE IV

- Fig. 13. Camera lucida drawing of longitudinal section through the junction of colon and rectum, showing insertion of peritoneal matrix on intima (Epilachna mexicana Guer.).
- Fig. 14. Camera lucida drawing of longitudinal section through junction of colon and rectum, showing insertion of peritoneal matrix on intima (Ceratomegilla fuscilabris Muls.).
- Fig. 15. Diagrammatic drawing showing how liquid wastes (illustrated by stippling) leave the Malpighian tubule and enter the hind-intestine.
- Fig. 16. Specific ramification of the reassociated portion of the Malpighian tubule in the peritoneal matrix.

ABBREVIATIONS USED ON PLATES

<i>B MEM</i> —basement membrane.	OES-oesophagus.
CIR MUS-circular muscles.	OES VALVE-oesophageal valve.
<i>E EP</i> —enteric epithelium.	PERI-peritoneum.
EP—epithelium.	PER M—peritrophic membrane.
INT—intima.	SB-striated border.
LON MUS—longitudinal muscles.	S INT—secondary intima.
LUM—lumen.	SP—spine.
MAL T-Malpighian tubule.	TRA-trachea.
NID-nidus.	

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FIG. 1.



FIG. 2.



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____ FIG. 10.

FIG. 12.



FIG. 13.

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