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# Morphology and Ultrastructure of the Hindgut of the Oriental Fruit Fly Bactrocera dorsalis (Diptera: Tephritidae)【Research report】

## 東方果實蠅Bactrocera dorsalis後腸形態及超薄結構之研究【研究報告】

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## Abstract

The hindgut of the Oriental fruit fly, Bactrocera dorsalis (Hendel), was studied with light and transmission electron microscopy. The hindgut of this fly consists of the pylorus, ileum, rectal valve, and rectum. The pylorus is a bulbously shaped structure located between the midgut and ileum of the hindgut. The structure of the pylorus is composed of two layers: the epithelium of the outer layer which connects to the epithelium of ileum and the inner layer which extends from the epithelium of the midgut and appears as two lines. The lumen of the pylorus is the pathway from the midgut to the hindgut. The ileum is shaped like a cylindrical winding tube, and its epithelium is covered only by an epicuticle. The apical and basal plasma membranes of the epithelial cell are infolded into the cell to form the canaliculi, which are closely associated with the mitochondria. The mitochondria are well developed with numerous cristae. The musculature coat is well developed with circular and longitudinal muscles. The rectal valve is a very short small tube located between the ileum and rectum. Its epithelium has a very thick cuticle, particularly the endocuticle. The epithelial cells are undeveloped and only surrounded by a thick circular muscle, but not by the longitudinal muscle. The rectum is an enlarged sac with sexual dimorphism. The female rectum appears elongate and a round bottom and two pairs of conical rectal papillae on the anterior region. The male rectum is S-shaped, with the enlarged posterior region forming the reservoir and secretory sac. During mating activity, the entire rectum enlarges like a balloon. The ultrastructure of the rectal wall in both the female and male is the same in the anterior regions, but differs in the posterior region. The posterior rectal wall of the female is the same as the anterior region, while that of the male has a much thicker epithelium and a more-complicated cytoplasm compartment. The musculature coat of the rectum is well developed in both the male and female.

## 摘要

本研究報告係利用光學顯微鏡和穿透性電子顯微鏡方法，觀察研究東方果實蠅Bactrocera dorsalis (Hendel) 後腸 (hindgut) 之形態和超薄顯微的構造。它的後腸可分為四部份：幽門部 (pylorus)、迴腸 (ileum)、直腸瓣 (rectal valve) 和直腸 (rectum)。幽門部位於中腸與後腸的迴腸間，為一小梨形構造，其結構分內外兩層，內層再分為兩層，內層的上皮細胞層係連接中腸上皮細胞層，基部向上彎而形成兩層。外層則連續迴腸細胞。其腸腔為中腸到後腸的通道。迴腸為一彎曲的長管道，其表皮 (cuticle)，只有上表皮，細胞的上質膜和基質膜皆向細胞內突，形成許多小管 (canaliculi)，這些小管多與粒線體靠近。迴腸被環肌和縱走肌包圍著。直腸瓣係一短小而狹窄的小管體，位於迴腸末端，連接直腸，直腸瓣的表皮很厚，形成瓣狀，上皮細胞退化，環走肌發達，縱走肌闕如。直腸為一囊狀體，東方果實蠅的直腸為雌雄不同形，雌蠅直腸呈橢圓形，前端具四個直腸突起的突出構造，雄蠅直腸呈S形，前端有四個直腸突起的突出，後端膨大為儲藏部 (reservoir) 和分泌囊 (secretory sac)。性成熟交尾時，雄蠅直腸膨脹呈球狀，雌蠅直腸不會變化。直腸壁的微細結構，表皮可分為上表皮和內表皮，上皮細胞結構簡單，具有粒線體，內質網，游離的核醣體和空泡等。外圍有發達的環走肌和縱走肌。雄蠅直腸前端的腸壁與雌蠅直腸者之結構相似，但後端腸壁的上皮細胞特別加厚，細胞質複雜，外被有發達的肌肉層包圍著。

**Key words:** ileum, pylorus, rectal valve, rectum

**關鍵詞:** 幽門部，迴腸，直腸瓣，直腸。

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# Morphology and Ultrastructure of the Hindgut of the Oriental Fruit Fly *Bactrocera dorsalis* (Diptera: Tephritidae)

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## ABSTRACT

The hindgut of the Oriental fruit fly, *Bactrocera dorsalis* (Hendel), was studied with light and transmission electron microscopy. The hindgut of this fly consists of the pylorus, ileum, rectal valve, and rectum. The pylorus is a bulbously shaped structure located between the midgut and ileum of the hindgut. The structure of the pylorus is composed of two layers: the epithelium of the outer layer which connects to the epithelium of ileum and the inner layer which extends from the epithelium of the midgut and appears as two lines. The lumen of the pylorus is the pathway from the midgut to the hindgut. The ileum is shaped like a cylindrical winding tube, and its epithelium is covered only by an epicuticle. The apical and basal plasma membranes of the epithelial cell are infolded into the cell to form the canaliculi, which are closely associated with the mitochondria. The mitochondria are well developed with numerous cristae. The musculature coat is well developed with circular and longitudinal muscles. The rectal valve is a very short small tube located between the ileum and rectum. Its epithelium has a very thick cuticle, particularly the endocuticle. The epithelial cells are undeveloped and only surrounded by a thick circular muscle, but not by the longitudinal muscle. The rectum is an enlarged sac with sexual dimorphism. The female rectum appears elongate and a round bottom and two pairs of conical rectal papillae on the anterior region. The male rectum is S-shaped, with the enlarged posterior region forming the reservoir and secretory sac. During mating activity, the entire rectum enlarges like a balloon. The ultrastructure of the rectal wall in both the female and male is the same in the anterior regions, but differs in the posterior region. The posterior rectal wall of the female is the same as the anterior region, while that of the male has a much thicker epithelium and a more-complicated cytoplasm compartment. The musculature coat of the rectum is well developed in both the male and female.

**Key words:** ileum, pylorus, rectal valve, rectum

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## Introduction

The hindgut of insects is located in the posterior region of the alimentary canal. It connects to the midgut anteriorly and ends with the anus posteriorly. There is a paucity of information on the functional morphology and ultrastructure of the hindgut of dipterous insects using light and electron microscopy. However, a number of papers had contributed significantly to certain aspects of the rectal papillae, such as Greham-Smith (1934), Gupta and Berridge (1966a,1966b), and Berridge and Gupta (1967, 1968) on *Calliphora,* and Lee *et al*. (1990, 1992) on *Bactrocera (=Dacus)*. Few papers, however, are available which studied the rectum via electron microscopy (Lee and Chang, 1986), the pheromone-producing gland located in the rectum of the male fly (Lee *et al*., 1989) and the rectal papillae of the male fly (Lee *et al*., 1990, 1992). This study is a continuation of previous studies on the foregut and midgut of the alimentary canal of the Oriental fruit fly, *Bactrocera dorsalis* (Lee *et al*. 1998, Hung *et al*. 2000). It is a further attempt to understand the functional morphology and ultrastructure of its hindgut.

## Materials and Methods

Mature Oriental fruit flies, both males and females, were used for the study. Flies were reared in the laboratory as described by Lee *et al*. (1998). More than 100 individual insects were dissected in Tyrode's solution (Lillie, 1965). The hindgut was dissected out and photographed under a Wild M8 microscope. Each fresh hindgut was separated from the other parts of the alimentary canal in 0.1 M cacodylate buffer. The fixative used was a mixture of 2.5% glutaraldehyde in 0.1 M cacodylate buffer as a prefixative and 2% osmium tetroxide in the same buffer as a postfixative for the light and electron microscopic studies. After dissection, the hindguts was transferred to the prefixative for 2 h at 4-6℃, then washed with the 0.1 M cacodylate buffer twice for 15 min each, and postfixed in ice-chilled postfixative for 2 h at 4-6℃. Specimens were then stained with saturated uranyl acetate in 50% absolute alcohol and dehydrated in an alcohol series and embedded in Spurr's resin (Spurr, 1969). Sections were made with a Reichart Jung Ultracut-E microtome. For light microscopic studies, sections were cut at a thickness of 0.9-1.5 $\mu$m with glass knives and stained with 1% toluidine blue. Preparations were investigated and photographed with a Nikon Optiphot Research microscope. For ultrastructural studies, sections were cut at a thickness of 600-1000 Å (golden/gray in color) with a diamond knife, and co-stained with uranyl acetate, if necessary, and lead citrate (Reynold 1963). They were then examined with a Hitachi H-7000 TEM operated at 75 kV , and photographs were taken.

## Results

The wide variation in insect hindgut structures has led to some inconsistencies in nomenclature. The terminology used in this paper follows that of Miller (1965) and Noble-Nesbitt (1998).

The hindgut of the Oriental fruit fly, *B. dorsalis,* consists of four general regions: the pylorus, ileum, rectal valve, and rectum. The morphology and ultrastructure of these regions are considered separately as follows.

***Pylorus***

The pylorus is a bulbous portion of the hindgut, which lies immediately posterior to the midgut and follows the ileum of the hindgut (Fig. 1). This organ is hidden from the coiled portion of the midgut lying in the fourth abdominal segment and receives a pair of Malpighian tubules. The size of the pylorus is about 0.2-0.4 mm in diameter and 0.2-0.6 mm in length.

In longitudinal section under light microscopic observation, the epithelium of the pylorus is composed of three layers: one outer and two inner layers (Fig. 2). The outer layer of the epithelium is connected to the ileum by cuboidal epithelial cells and is surrounded by a layer of longitudinal muscle and bundles of circular muscles. The epithelium of the inner layer is an extension of the midgut epithelium. Figure 3 shows that the epithelium of the inner part of each side extends downwards to the posterior portion of the pylorus, then reverses toward outside, and reaches the insertion of the Malpighian tubule which exits in the antero-pleural region of the pylorus. These epithelial cells appear columnar in shape with a clear nucleus. Figure 3 also shows that the lumen of the pylorus located in the middle of the organ is a pathway from the midgut to the hindgut. Small globules and membranous materials can be faintly observed from the micrograph and appear to be undigested materials, excretory granules, and/or the broken peritrophic membrane.

Figure 4 is a micrograph of the epithelium outer layer. A simple tubular epithelium lines a single layer of cuticle, and overlies a well-developed longitudinal muscle. The epithelial cells are simple, containing only free ribosome, a few randomly orientated microtubules, and the nuclei. The profile of the lateral membranes of the epithelium shows that they are wound with the cellular junctions. The inner layer of the epithelium extends to the midgut epithelium. The epithelial cells are column-shaped with a disordered arrangement of degenarative microvilli on top of the apical surface (Fig. 5). The cells have abundant free ribosome, vacuoles, and ellipsoid nuclei.

***Ileum***

The ileum is a cylindrical tubular organ connecting with the pylorus anteriorly and the rectal valve posteriorly (Fig. 1). It forms a counter-clockwise loop in the hemocoel of the fourth abdominal segment. The ileum measures about 3.0-4.8 mm in length and 0.1-0.4 mm in width. In the longitudinal section of light microscopy, the epithelium of the ileum consists of a single layer of cuboidal epithelial cells with rounded nuclei, and it is surrounded by longitudinal and circular muscle (Fig. 8). The electron micrograph in Fig. 6 shows that the cuticle of the ileum has only one layer which is referred to as the epicuticle, and which attaches with different-sized electron denses. The apical plasma membrane of the epithelium is invaginated, with infoldings extending into the cytoplasm of the apical region of the cell. These infoldings are arranged in different directions to form canaliculi distributed in the cytoplasm, and some are closely associated with mitochondria. The mitochondria mostly appear in an ellipsoidal shape, and are well developed with numerous cristae. Abundant groups of free ribosome and individual microtubules are scattered throughout the cytoplasm.

The basal region, i.e.,the basal plasma membrane of the epithelial cell, is highly infolded into the cell, and produces curly meandering canaliculi, which are associated with mitochondria (Fig. 7). Free ribosomes and microtubules distribute throughout the cytoplasm. The electron denses appear at the point of the basal plasma membrane infoldings adjacent to the basement membrane (basal laminae, basal membrane). The basement membrane is composed of fibrillar structures, and the musculature is well developed.

***Rectal valve***

The rectal valve is a very constricted short tube which is joined to the ileum anteriorly and rectum posteriorly (Fig. 1). This organ is about 0.05-0.1 mm in width and 0.1-0.12 mm in length. In transverse section with light microscopy, the cuticle of this organ is very thick and shows several projections protruding into the lumen (Fig. 9). The muscle coat of the rectal valve consists of a single layer of developed and closely set circular fibers. The longitudinal fibers cannot be seen. In longitudinal section, the epithelium of the rectal valve appears much reduced as a plate-like feature, while the cuticle is thick and strong (Fig. 10). The plate is covered with a thick intima with a wriggler structure at the outside edge. Figure 11 is an ultrastructure micrograph of the rectal valve. Its epithelium covers with a comparatively thick cuticle (1-2.3 $\mu$m) which is distinguished by the epicuticle and a large endocuticle. The epithelial cells are modified with a few membranous structures or vacuoles. The basement membrane lies under the epithelium. The muscles of the rectal valve are well developed with thick myofilaments and many mitochondria located in an I-band and between the myofibrils.

***Rectum***

The rectum is usually an enlarged sac-like structure which connects with the anal tube posteriorly (Fig. 1). It lies along the mediodorsal line from abdominal segment 5 to the anal segment. According to Lee *et al*. (1986), the rectum of the Oriental fruit fly is sexually dimorphic. The female fly has an elongated ball-shaped rectum, with a round posterior end, small anal tube, and two pairs of conical rectal papillae protruding onto the anterior region (Fig. 12). The rectum of the male appears as an S-shape with two structures, the reservoir and the secretory sac in the posterior region, and two pairs of conical rectal papillae in the anterior region (Fig. 13). During sexual activity, the rectum of the male enlarges to a ball shape, but the rectum of the female remains the same.

The rectum of the female *B. dorsalis* consists of a thin-walled epithelium with cuboidal epithelial cells (Fig. 14). The cuticle of the epithelium contains an epicuticle and an endocuticle. Both apical and basal plasma membranes of the epithelial cell are rarely invaginated. The cytoplasm of the epithelial cell contains well-developed mitochondria, smooth endoplasmic reticulum, occasional small vacuoles, and abundant free ribosomes. The basement membrane is located at the basal surface of the epithelium. The muscular coat of the rectum appears very strong and well developed with circular and longitudinal muscles.

The rectal papillae of *B. dorsalis* are isolated from each other and project into the lumen of the rectum. Their morphology and ultrastructure were reported by Lee *et al*. (1986, 1992).

The epithelium of the rectal wall in the male fly differs from that of the female. It can be distinguished from the anterior region and the posterior region of epithelium by virtue of its ultrastructure. The epithelium of the anterior region of the male rectum and female is the same (Fig. 14). However, in the posterior region or the reservoir, the epithelium is more enlarged and modified in the male. The posterior region of the epithelium consists of thicker columnar epithelial cells of between 16 to18 $\mu$m in thickness, while the anterior region of the epithelium is about 4-5 $\mu$m in thickness (Fig. 15). Although the cuticle also contains the epicuticle and endocuticle, both apical and basal plasma membranes are frequently invaginated and produce many disconnected canaliculi scattered in the cytoplasm, especially in the basal part of the cell. The large well-developed mitochondria are located

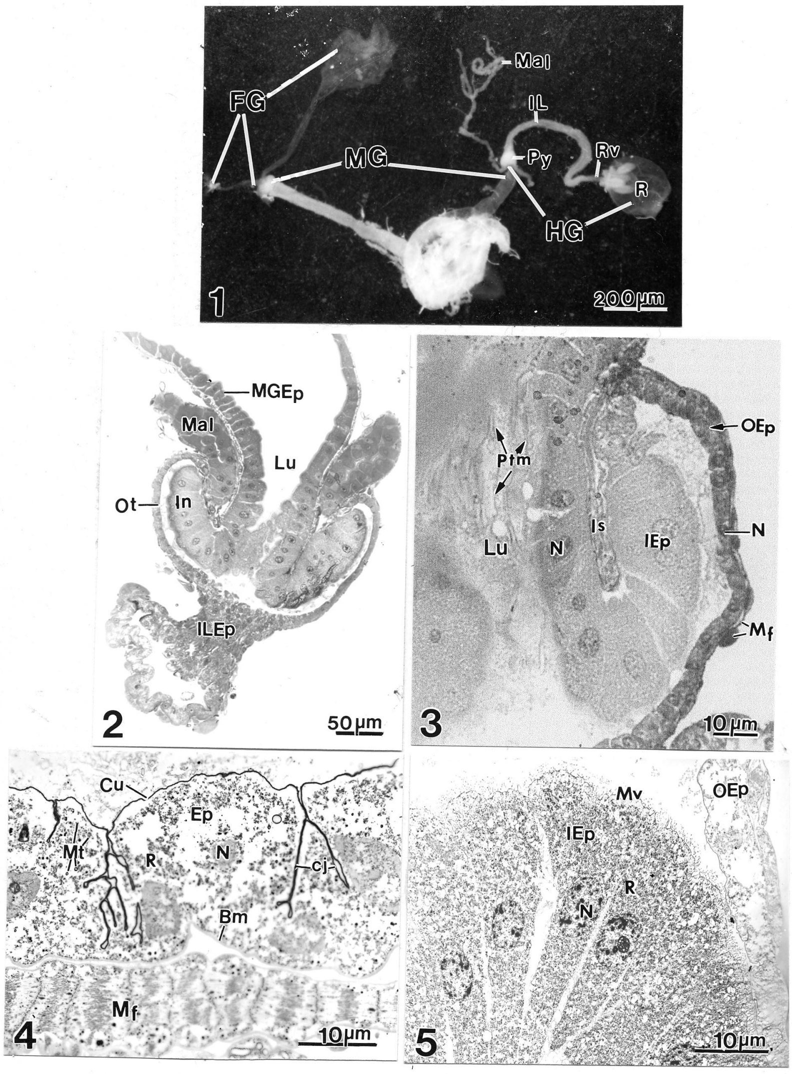


Fig. 1-5. 1. General view of the alimentary canal of *Bactrocera dorsalis.* FG, foregut; HG, hindgut; L, ileum; Mal, Malpighian tubules; MG, midgut; Py, pylorus; R, rectum; Rv, rectal valve. 2. Light microscopic longitudinal section showing the pylorus distinguished into the outer (Ot) and inner layers (In). The outer layer of the epithelium is connected with the epithelium of the ileum (ILEp), while the inner layer extends from the midgut epithelium (MGEp). Lu, lumen; Mal, Malpighian tubule. 3. Light microscopic longitudinal section showing the lumen of the pylorus (Lu) with the broken peritrophic membrane (Ptm). The outer layer of the epithelium (Oep) is surrounded by the circular and longitudinal muscles (Mf). Iep, inner epithelium; Mal, Insertion of the Malpighian tubule; N, nucleus. 4. Ultrastructural micrograph of the pyloric epithelium showing the cuboldal shape of the epithelial cells and the abundant free ribosomes (R), several microtubules (Mt), and a nucleus (N) in each cell. Bm, basement membrane; Cj, cellular junction; Cu, cuticle. 5. Longitudinal section of the pyloric inner layer of the epithelium showing the elongated columnar shape of the epithelial cells, the greater numbers of free ribosomes (R), and the disordered arrangement of the degenerative microvilli (Mv) on the top of the cell. The nucleus (N) of each cell has an elliptical shape. Oep, outer epithelium.

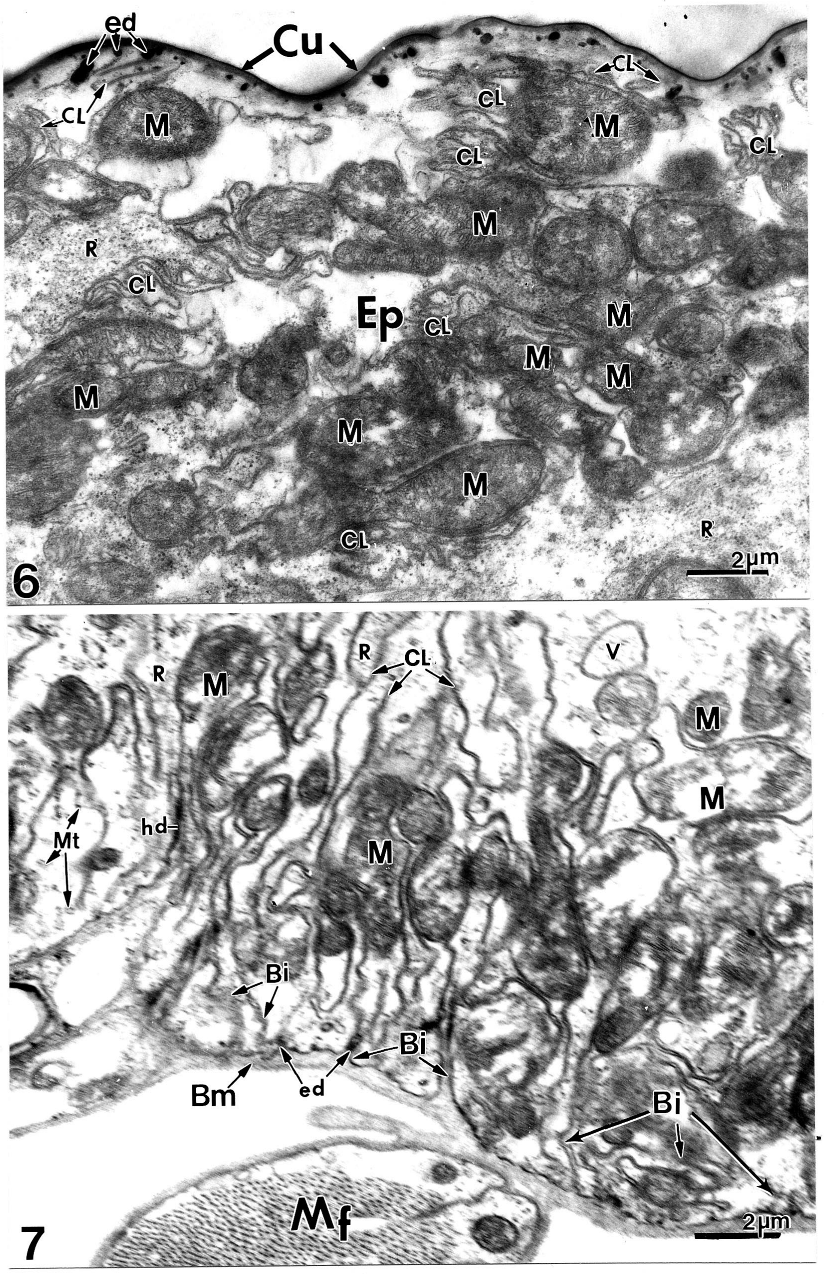


Fig. 6-7. 6. Ultrastructure of the apical portion of the ileal epithelial cell (Ep). The apical plasma membrane infolds and extends into the cell from different directions, forming the canaliculi (CL) throughout the cytoplasm; most of them are associated with mitochondria (M). The epithelium is covered by a single layer of cuticle, the epicuticle (Cu). ed, electron dense; Mt, microtubules; R. ribosomes. 7. Ultrastructure of the basal portion of the ileal epithelial cell (Ep). The basal plasma membrane invaginates and extends into the cell which is termed the canaliculi (CL) which are associated with the mitochondria (M). Bi, infoldings; Bm, basement membrane; ed, electric dense; Mt, microtubules; R, ribosomes.

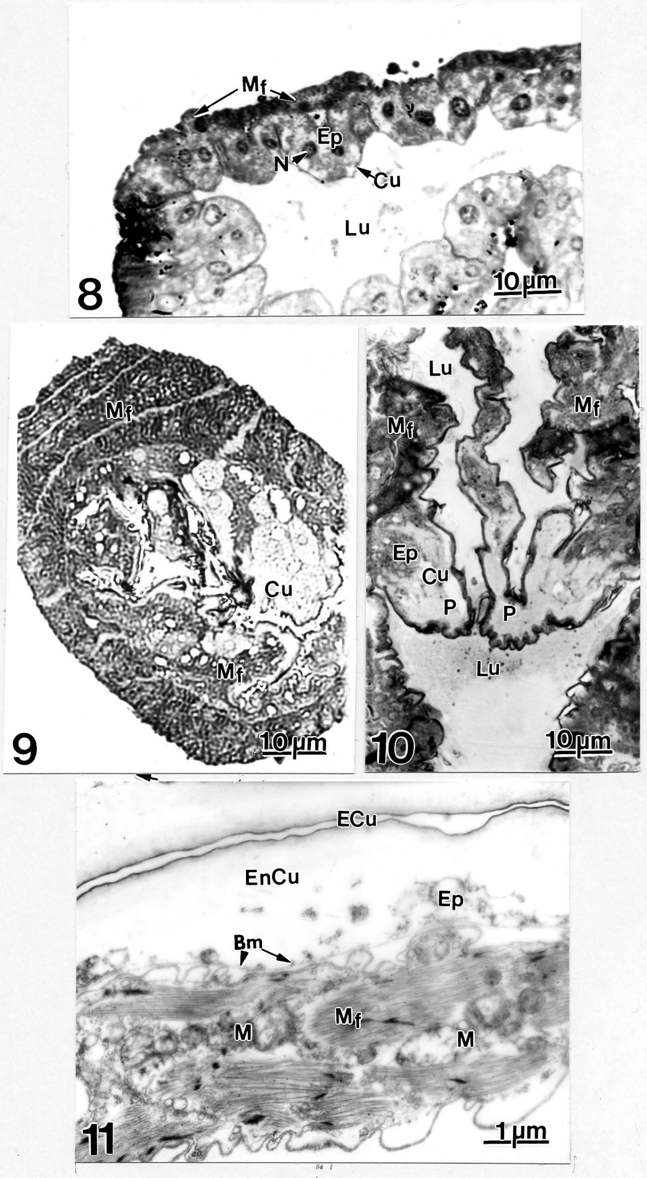


Fig. 8-11. 8. Transverse section, by light microscopy, of the ileum showing the cuboidal epithelial cells (Ep) surrounded by the muscles (Mf) in the hemocoel side and covered by a layer of cuticle (Cu) on the luminal side (Lu). 9. Transverse section, by light microscopy, of the rectal valve showing the large area of the cuticle (Cu), which almost completely occupies the lumen of the rectal valve, and is surrounded the very well-developed circular muscle (Mf). The longitudinal muscle is absent from this organ. The epithelium is very difficult to distinguish. 10. Longitudinal section of a light micrograph of the rectal valve. The cuticle (Cu) is well developed to form a plate (P). The epithelium (Ep) is barely visible. Lu, lumen; Mf, muscle. 11. Electron micrograph of the rectal valve showing that the cuticle consists of the epicuticle (ECu) and endocuticle (EnCu). The endocuticle is well developed and thick, while the epithelium is much reduced. The micrograph faintly shows that the basement membrane (Bm) is situated between the epithelium and musculature (Mf). M, mitochondria.

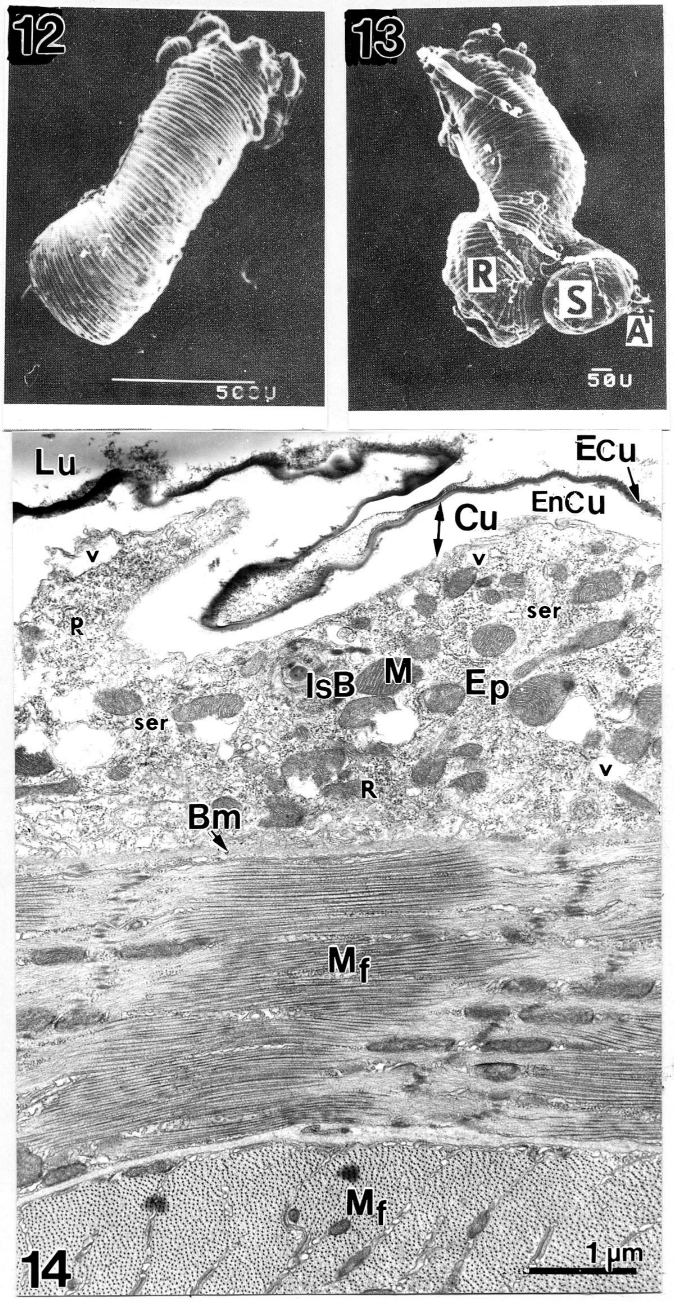


Fig. 12-14. 12. Scanning electron micrograph showing the female rectum as an elongated ball. A, anal tube; C, rectal valve; Rp, rectal papillae ( After Lee *et al.* 1986). 13. Scanning electron micrograph showing the male rectum as a S- shape. A, anal tube; S, secretory sac; R, reservoir. ( After Lee *et al.* 1986 ). 14. Ultrastructure of the female rectum showing the structure of the epithelium (Ep) covered by a cuticle, which consists of the epicuticle (ECu) and endocuticle (EnCu). An epithelial cell is composed of abundent free ribosomes (R), smooth endoplasmic reticulum (ser), well- developed mitochondria (M), a isolation body (IsB), and a few vesicles (v). The basement membrane (Bm) clearly lies underneath the epithelium. The musculature (Mf) is strong and well developed.

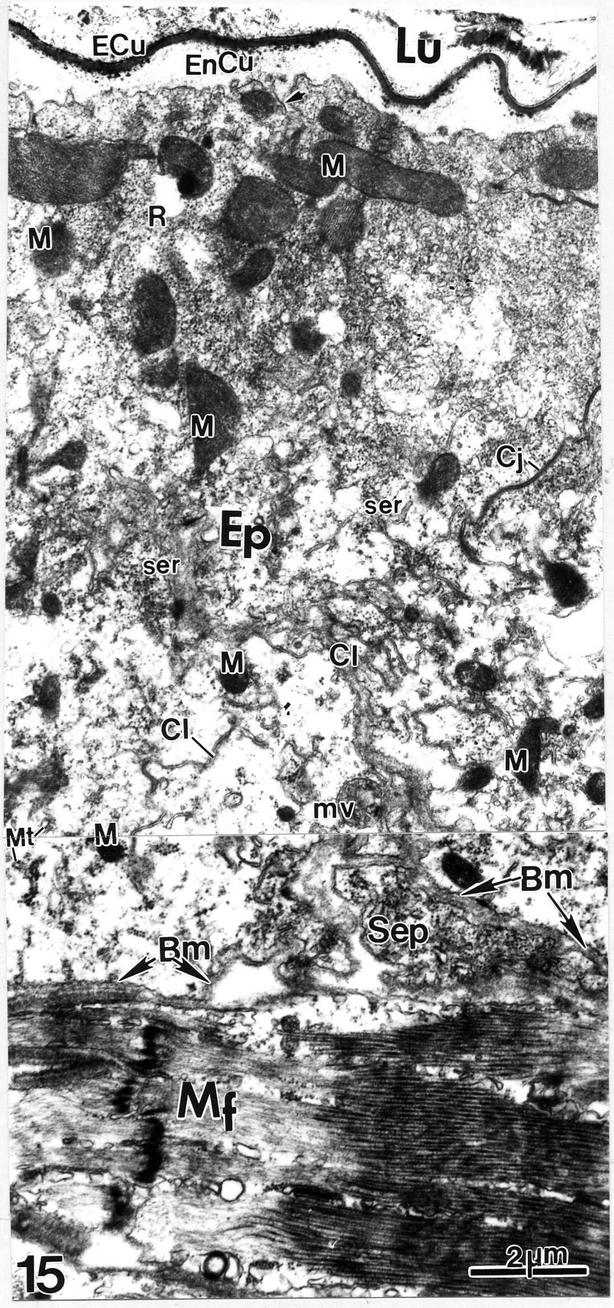


Fig. 15. The posterior region of the male rectum showing a thick epithelium. The epithelial cell (Ep) contains large mitochondria (M) in the apical part of the cell, and small ones scattered in the lower part. The cuticle consists of the epicuticle (ECu) and endocuticle (EnCu). The cytoplasmic compartment of the epithelium appears very complicated with canaliculi (CL), additional free ribosomes (R) and smooth endoplasm reticulum (ser) in the apical part of the cell, and a multivesicle (mv) and several microtubules (Mt) in the basal part. The subepithelium (Sep) can be found under the epithelium between the basement membrane (Bm) and the strong musculature coat (Mf).

in the apical part of the cell, while the small undeveloped mitochondria are located at the basal part of the cell. The apical part of the cytoplasm contains abundant ribosomes and smooth endoplasmic reticulum. More canaliculi, microtubules, and a multivesicular body are distributed in the basal part of the cytoplasm. The lateral plasma membrane of the cell is in juxtaposition with another cell and thus forms a cellular junction between the two cells. The basement membrane lies at the bottom of the epithelium. A subepithelial sinus is found below the basement membrane, which contains microtubules and ribosomes. The musculature, as that of the anterior region of the rectal sac, is strong with well-developed muscle fibers. The secretory sac is located between the reservoir and anal tube. Its morphology and ultrastructure were previously reported by Lee and Chang (1989), and Lee *et al*. (1989).

## Discussion

The alimentary canal of insects consists of three primary regions: the foregut (stomadeum), midgut (mesenteron), and hindgut (proctodeum). The epithelium of the foregut and hindgut is embryonically ectodermal, while that of the midgut is endodermal. Foregut and hindgut cells secrete a substance to form a cuticle, which continuously covers the epithelium. The midgut cells do not secrete a cuticle, but the cell membrane on the lumen side forms microvilli in most cells. In the majority of insects, the hindgut is involved in the later stages of digestion, of absorption of nutrients, and of the excretory process, and is included important stages in osmoregulation (Noble-Nesbitt, 1998).

The hindgut in most insects is typically differentiated into the ileum and colon of the anterior region and the rectum of the posterior region (Snodgrass, 1935; Wigglesworth, 1965; Noble-Nesbitt, 1998). Chapman (1998) defined the hindgut of insects as distinctly divided into the pylorus, ileum, and rectum. The hindgut of Lepidoptera larvae is divided into four regions: the pylorus, ileum, colon, and rectum (Judy and Gilbert, 1970; Byers and Bond, 1971). Miller (1965) distinguished the hindgut of *Drosophila melanogaster* as the anterior instestine, which includes the ileum and rectal valve, and posterior intestine or rectum. The pylorus is the posterior portion of the ventriculus (midgut) where it terminates in an abruptly narrowed region. The present study divides the hindgut of *B. dorsalis* into four regions: the pylorus, ileum, rectal valve, and rectum.

The pylorus is located between the midgut and ileum of the hindgut. Chapmen (1998) stated that it is a region of the hindgut, sometimes with the pylorus forming a valve between the midgut and hindgut. Judy and Gilbert (1970), in describing the pylorus of the larvae of *Hyalophora cecropia* (Lepidoptera), stated that the anterior region of the pylorus has small spines arranged in clusters over the epithelial cells. In the middle region of the pylorus, certain cells within the pyloric valve bear some small cuticular teeth over the entire luminal surface. Reinecke *et al*. (1973) investigated the hindgut of *Manduca sexta* (Lepidoptera, Sphingidae) larvae and reported that the pylorus was divided into three regions: the posterior interstitial ring, the pyloric cone, and the pyloric valve. The intima of the pyloric interstitial ring and pyloric cone contained numerous posteriorly directed spines, and the pylorus was surrounded by longitudinal and circular muscles. The activity of these muscles was basically myogenic in nature and appeared to be inhibitory. Dapples and Lea (1974) found that the pyloric ampulla of the mosquito, *Aedes aegypti,* was covered with posteriorly projecting spines on its luminal surface. This structure of spines and thick muscles might indicate a function of inhibiting digested residue from moving backward from the hindgut to the midgut. There is scant information on the morphology and ultrastructure of the pylorus in dipteran insects. The function of inhibiting undigested materials flowing from the hindgut backward to the midgut in these insects is still unknown. The present study of the hindgut in *B. dorsalis* indicates that the pylorus does not provide the function of inhibiting any undigested residues from moving backwards from the hindgut to the midgut. This is due to the absence of any strong muscle surrounding the outer epithelium and lining the inner epithelium, and also due to the lack of strong supporting spines on the luminal surface of the inner epithelium.

The ileum is the first part of the anterior intestine according to the terminology of Snodgrass (1935). In most insects, the ileum is an undifferentiated tube running to the rectum from the pylorus. But in some termites, the ileum forms a pouch, and the flagellates vital to cellulose digestion residue in the pouch. The ileum of Scarabaeoidea larvae is comparable to a fermentation chamber, and the cuticle is produced into elongate spines. These spines probably serve as attachments for microorganisms (Chapmen, 1984). Similar structures are present on the ileum of cockroaches and crickers with a bacterial flora (Chapmen, 1998). In the blowfly larvae, certain cells of the ileum excrete ammonia (Waterhouse, 1957). The hormone proctodone is secreted by cells of the ileum in *Ostrinia* (Beck *et al.*, 1965).

Chapman (1998) stated that only a single cell type is present in the ileum of many insects. The apical plasma membrane of cells has extensive infoldings and is closely associated with the abundant mitochondria. The basal plasma membrane may also be folded, but the folds are less extensive than those of the apical ones. In the present study of the ileum of *B. dorsalis,* the ultrastructure showed that the apical and basal plasma membranes folded into the cell forming the infoldings. However, the infoldings of the apical plasma membrane protruded into different directions and formed many canaliculi throughout the cell associated with the mitochondria. In Protura, the anterior region of the hindgut has numerous narrow plasma membrane infoldings (microvilli) beneath the cuticle, and mitochondria are present in the basal part of the cell (Dallai, 1977). Epithelial cells of the ileum in *Locusta migratoria* are characterized by extensive infoldings of the apical and basal cell membranes to produce a maze of interconnecting channels and spaces. Mitochondria are closely associated with both of these infoldings (Peacock, 1986). A striking feature of ileal cells was found in the diapausing European corn borer, *Ostrinia nubilalis,* in which some microvilli appeared on the apical and lateral surfaces, and some were extensively deep in the cytoplasmic region of the cell. Sometimes a whorled structure appeared at the base of microvilli. Mitochondria mostly occupied spaces at the sides or near the base of microvilli (Hassemer and Beck, 1969). The ileum of *Ephydrella* sp. (Diptera) consists of two sizes of epithelial cells: small cells have long apical leaflets containing elongate mitochondria and short basal channels, while large cells of the apical membrane forms short microvilli and long basal channels. It was suggested that the large cells function in reabsorbing water while the small cells function in reabsorbing secretions (Marshall and Wright, 1974).

On the luminal side, the cuticle-lined epithelium is more or less permeable to water and ions, but not the large molecules (Noble-Nesbitt, 1998). The structure of the cuticle differs in different species of insects. *Acerentomon* and *Eosentomon* of the Protura have a very thin, homogeneous cuticle (Dallai, 1977). The cuticle of the ileum in *L. migratoria* consists of a thin outer epicuticle and an inner laminal endocuticle containing a variety of membrane-bound vesicles; also a subcuticle of varying size is present between the epithelium and endocuticle (Peacock, 1986). In *Ephydrella* larvae (Marshall and Wright, 1974) and *B. dorsalis* flies, the ileum consists of a thin cuticle, the epicuticle, and epithelium without the endocuticle.

The flat sheet of the ileal epithelium is thrown into the complex folds by the action of the circular musculature coat (Noble-Nesbitt, 1998). In the ileum of *L. migratoria,* the circular muscle surrounds the epithelium on the hemocoel side. The longitudinal muscles are present in six regions where they lie as discrete bundles (Peacock, 1986). In *H. cecropia,* the longitudinal and circular muscles covering the ileum insert into the apodeme-like bulges of the epithelial cells (Judy and Gilbert, 1970). Marshall and Wright (1973) found that the ileum of *Ephydrella* larvae was surrounded by a thin layer of muscle. In the present investigation, the ileum of *B. dorsalis* was surrounded by a longitudinal muscle underneath the basement membrane and a circular muscle was lied on the hemocoel side.

The rectal valve in *B. dorsalis* is located between the ileum and rectum, similar to that of the colon in the cockroach and larval lepidopterans (Judy and Gilbert, 1970; Byers and Bond, 1971; Reinecke *et al*., 1973). The ultrastructure shows that the rectal valve of *B. dorsalis* greatly differs from the colon. The colon of cockroach and locusta consists of a complete epithelium with the extensive folds from the apical and basal plasma membranes, mitochondria, and other organelles in the cytoplasm, while the cuticle contains the epicuticle and endocuticle (Bignell, 1980; Peacoak, 1985). The rectal valve in *B. dorsalis* is a short visible intestine, followed by a constriction joining it to the rectum. Its epithelium is much reduced and modified to form a very simple structure of membrane-bound vacuoles. A strong circular muscle surrounds the epithelium, but the longitudinal muscle is absent. The structure of the rectal valve in *B. dorsalis* is similar to that in *D. melanogaster* (Miller, 1965). There are, however, minute spines borne on the inner edges of the plates in *D. melanogaster,* but these spines were not found in *B. dorsalis*. Miller (1965) stated that these plates and spines are probably instrumental in drawing the peritrophic membrane backward into the rectal valve. The circular muscle fibers in this region are much thicker than elsewhere, thus forming a strong sphincter to open or shut the rectal valve.

The role of the rectum is generally the absorption of water and ions from the excretion, also as a conduit for the elimination of food residues and excretion products (Berridge, 1972). In some species of insects, the rectum is also the site of water uptake from the atmosphere (Noble-Nosbitt, 1998). In caterpillars, the rectum contributes to the osmoregulatory ability of the hindgut (Byers and Bond, 1974). Chapmen (1998) stated that the rectum is usually an enlarged sac with a thin epithelium, except for certain regions, such as the rectal pads in cockroaches, and the rectal papillae in the Diptera. Both the rectal pad and rectal papillae contain a special structure of the epithelium with thick epithelial cells. These thick cells show that the apical and basal plasma membrane which are infolded and extend into the cell have an association with the mitochondria. The cuticle is thin and unsclerotized (Gupta and Berridge, 1966; Oschman and Wall, 1969; Noirot and Noirot-Timothee, 1976). Water and ions can be absorbed from the rectal lumen through the cell to the hemocoel (Berridge, 1970). There is sufficient evidence that rectal absorption takes place in the rectal papillae of dipterous insects (Baccetti, 1962; Gupta and Berridge, 1966; Hopkins, 1966; Berridge and Gupta, 1967; and Lee *et al*., 1992). There have been very few investigations into the morphology and ultrastructure of the rectal wall. Results of the present studies suggest that the rectum does not have a role in absorption. However, it may function in the elimination of food residues and excretion from the anus via constriction. The epithelial cells of the reservoir in the male rectum appear much thicker than that of the anterior region. This suggests that this area of epithelium may be that which is stretched and appears as a balloon during sexual activities.

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# 東方果實蠅 *Bactrocera dorsalis* 後腸形態及超薄結構之研究

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## 摘　要

本研究報告係利用光學顯微鏡和穿透性電子顯微鏡方法，觀察研究東方果實蠅 *Bactrocera dorsalis* (Hendel) 後腸 (hindgut) 之形態和超薄顯微的構造。它的後腸可分爲四部份：幽門部 (pylorus)、迴腸 (ileum)、直腸瓣 (rectal valve) 和直腸 (rectum)。幽門部位於中腸與後腸的迴腸間，爲一小梨形構造，其結構分內外兩層，內層再分爲兩層，內層的上皮細胞層係連接中腸上皮細胞層，基部向上彎而形成兩層。外層則連續迴腸細胞。其腸腔爲中腸到後腸的通道。迴腸爲一彎曲的長管道，其表皮 (cuticle)，只有上表皮，細胞的上質膜和基質膜皆向細胞內突，形成許多小管 (canaliculi)，這些小管多與粒線體靠近。迴腸被環肌和縱走肌包圍著。直腸瓣係一短小而狹窄的小管體，位於迴腸末端，連接直腸，直腸瓣的表皮很厚，形成瓣狀，上皮細胞退化，環走肌發達，縱走肌闕如。直腸爲一囊狀體，東方果實蠅的直腸爲雌雄不同形，雌蠅直腸呈橢圓形，前端具四個直腸突起的突出構造，雄蠅直腸呈 S 形，前端有四個直腸突起的突出，後端膨大爲儲藏部 (reservoir) 和分泌囊 (secretory sac)。性成熟交尾時，雄蠅直腸膨脹呈球狀，雌蠅直腸不會變化。直腸壁的微細結構，表皮可分爲上表皮和內表皮，上皮細胞結構簡單，具有粒線體，內質網，游離的核醣體和空泡等。外圍有發達的環走肌和縱走肌。雄蠅直腸前端的腸壁與雌蠅直腸者之結構相似，但後端腸壁的上皮細胞特別加厚，細胞質複雜，外被有發達的肌肉層包圍著。

**關鍵詞**：幽門部，迴腸，直腸瓣，直腸