Bull. Inst. Zool., Academia Sinica **24**(1): 11-26 (1985)

FUNCTIONAL MICROSCOPIC ANATOMY OF THE ALIMENTARY CANAL OF *SARCOPHAGA RUFICORNIS* (FABR.) (DIPTERA: SARCOPHAGIDAE)

KAVITA ROHATGI

Zoology Department University of Allahabad,
Allahabad-211002 (INDIA)

(Received July 12, 1984)

Kavita Rohatgi (1985) Functional microscopic anatomy of the alimentary canal of *Sarcophaga ruficornis* (FABR.) (Diptera: sarcophagidae). *Bull. Inst. Zool., Academia Siuica* **24**(1): 11-26. The histological differences in the different regions of the alimentary canal of *Sarcophaga ruficornis* (Fabr.) have been interpreted from their functional point of view. The variations in size, shape and internal organization of the epithelial cells of the first three regions of the midgut present two types of merocrine secretion; vacuolar budding of the cytoplasm and granular secretion; suggestive of their digestive role. Whereas, the remaining two regions of the midgut do not exhibit such structures and possess well developed striated border indicating their absorptive nature.

The well developed proventriculus histology amply justifies its role as a sphincter, a valve, and in the formation of peritrophic membrane. A pyloric valve, not reported in Diptera except by Singh and Judd (1966), is present in *Sarcophaga* which prevents the backward flow of food into the mesenteron.

The complexity of the rectal valve suggests that it is more than merely a device for assisting the passage of the peritrophic membrane. The functional significance of the rectal epithelium having large cells and well developed rectal papillae, has been discussed. The presence of heavily loaded crystalline material in the cells of the wall of the rectal pouch is suggestive of its excretory role.

Key-words: ***Functional-histology-gut-Diptera.***

Dipterans exhibit great diversity in their food and feeding mechanism. Consequently they possess a variety of organs of alimentation to meet their physiological needs. Wigglesworth (1929) studied the alimentary canal of tsetse fly, while Graham-Smith (1934) that of the *Calliphora erythrocephala.* Dixon (1952) and Megahed (1956) contributed to the histomorphology of the gut of *Hylemya brassicae* and *Culicoides nebeculosus* respectively. Owsley (1946) has given a comparative account of the gut of four species of the family Asilidae, while Hori (1962) has dealt with the gut of several other species. Singh and Judd (1966) have worked on the comparative morphology and histology of several families of the Calyptrate Diptera with a view to elucidate some of the taxonomic differences of the group. In spite of all this, the available information on the subject is still scanty. The gross morphology of the alimentary canal of *Sarcophaga ruficornis*, a fly of veterinary importance, has already been described by Chaudhry (1972). In the present investigation, therefore, its microscopic anatomy has been dealt with and functional correlations of the histological elements have been discussed.

MATERIALS AND METHODS

Sarcophaga ruficornis (Fabr) were obtained from the culture maintained in the laboratory. The different regions of the gut were fixed in Bouin's fluid as well as in Zenker's fixative. The microtome paraffin sections at 6–8μ were cut and stained with Delafield's haematoxylin-eosine and Mallory's triple stain.

OBSERVATIONS

Foregut

Histologically the foregut of *Sarcophaga ruficornis* is distinguishable, as it is morphologically, into a pharynx, oesophagus (OES), crop duct (CD) and proventricular oesophagus (POES) that connects to proventriculus.

Oesophagus: The wall of the oesophagus (Fig. 1) from within outwards is made up of chitinous intima (IN), epithelium (EP), basement membrane (BM) and muscle layer. The epithelium consists of small more or less cuboidal cells (CB) with centrally placed small nuclei (NU). The inner margin of these cells is lined with a thick chitinous intimal layer provided with minute denticle-like spicules, while their outer ends rest on a fine basement membrane. The epithelium along with basement membrane and intima is thrown into a few low longitudinal folds. The muscle layer consists of a outer band of circular muscle fibres (CM). The inner longitudinal muscles (LM) tend to become grouped in bands within the longitudinal folds of the epithelial layer. The histological nature of the pharynx is similar to that of the oesophagus except for the thickness of muscle layers.

Crop Duct: The epithelium of the crop duct (Fig. 2) which is thrown into several longitudinal folds is formed of irregular cells with distinct intercellular walls and large spherical nuclei. Externally it is covered by a basement membrane and internally by a distinct cuticular intima. The muscular sheath consists of outer thick layer of circular muscle fibres and inner sparsely distributed longitudinal muscle fibres.

Corp: The epithelial cells of the crop are large flattened with centrally placed nuclei. Their height depends on the degree of distension of the crop and their inner free surface is lined by a intima. The musculature consists of an outer thin layer of circular muscle fibres and inner feebly developed and scattered bundles of longitudinal fibres. In an empty and collapsed crop (Fig. 3) the epithelial layer is thrown into numerous irregular longitudinal as well as transverse folds projecting into its lumen (LU). In this condition the epithelial cells appear greatly elongated showing numerous inward projecting finger-like prolongations with their nuclei towards the basal ends. The cell boundaries became indistinct and the circular muscle layer gets thicker due to contraction.

Proventriculus

A prominent bulb-like proventriculus, is present between the foregut and the midgut (Fig. 4). It consists of two distinct parts: (1) an external wall formed by the distended spherical funnel-like continuation of the anterior end of the ventriculus (V) and accommodated within it, (2) a plug-like structure derived by pushing in of the posterior end of the oesophagus. The plug, which forms the central core of the proventriculus, is an inverted mushroom-shaped structure with an umbrella-like flange and a hollow stalk the proventricular oesophagus. Near the base of the stalk around the anterior distended part of the proventricular wall (PW) are two glandular ring-like swellings, the annular

---

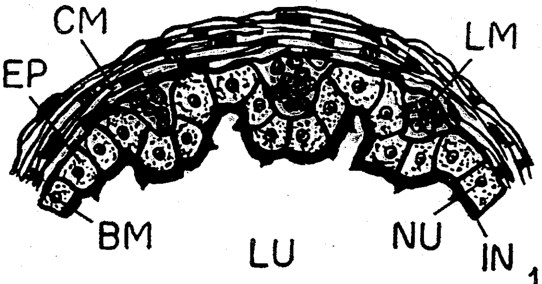
Explanation of Figures

Fig. 1. Diagram of the T. S. of oesophagus showing well developed denticulated intima.

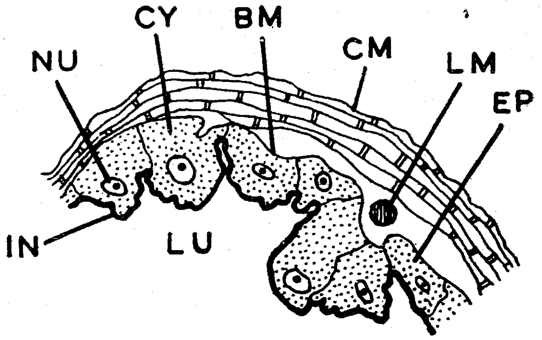
Fig. 2. Diagram of the T. S. of crop duct.

Fig. 3. Diagram of the T. S. of the collapsed crop showing highly irregular epithelial cells.

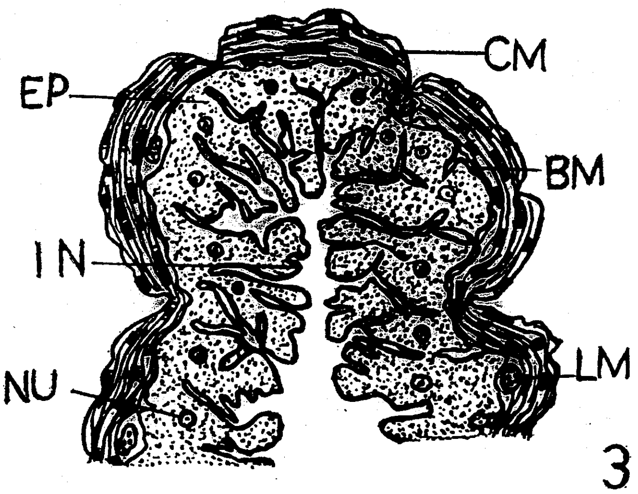
Fig. 4. Diagram of the L. S. of proventriculus.


CM
LM
EP
BM
LU
NU
IN

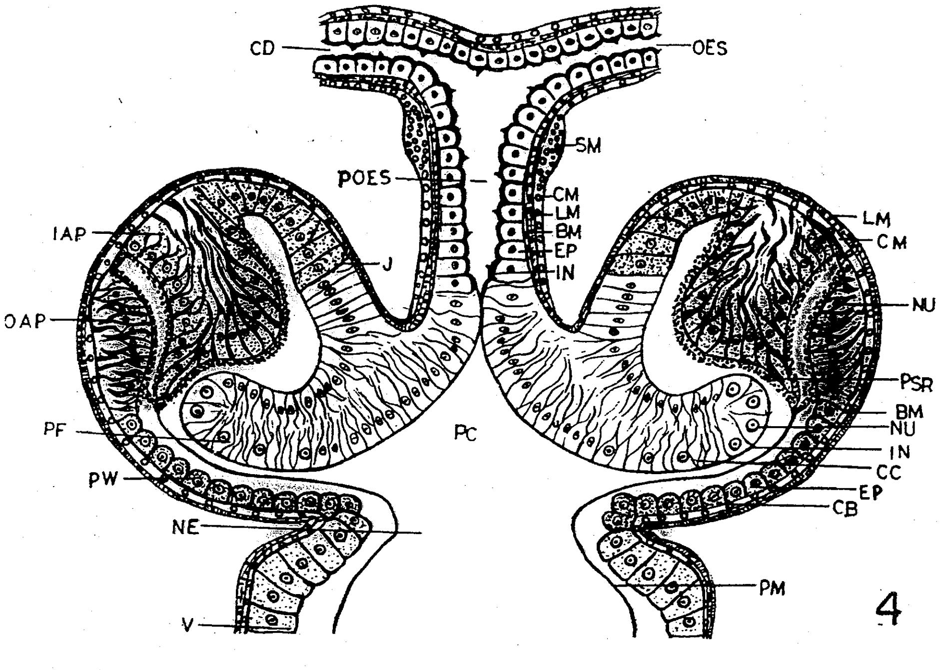
1


CY
BM
NU
CM
LM
EP
IN
LU

2


CM
EP
BM
IN
NU
LM

3


CD
OES
SM
POES
CM
LM
BM
EP
IN
IAP
J
OAP
LM
CM
NU
PSR
BM
NU
IN
CC
EP
CB
PF
Pc
PW
NE
PM
V

4

pads. The narrow proventricular cavity (PC), which lies between the plug and the external wall of the proventriculus, is in communication behind with the ventriculus through a constricted neck (NE)-like opening.

The proventricular-oesophagus (Fig. 5) is a continuation of the oesophagus showing the same histological structure. At its beginning, just behind the emergence of the crop duct, is seen a sphincter muscle (SM).

The edge of the proventricular flange (PF) projects as a double layered fold into the proventricular cavity and is reflected forwards towards the annular pads (Figs. 4 and 6). The intima of the flange is thin and its epithelium consists of pale-staining long columnar cells (CC) with small oval nuclei. The middle portion of the flange between the epithelial layers does not show any distinct basement membrane or muscular tissue. Its epithelium is continuous with the epithelium of the annular pads, and the line of demarcation (J) between the two is clearly visible in haematoxylin-eosin stained sections.

The two pads (Figs. 4 and 6), differ in their size and form. The inner annular pad (IAP) is large and anterior while the outer annular pad (OAP) is small and lies laterally. The inner pad, the outer pad, and the flange remain separated from one another by means of clefts which are continuations of the proventricular cavity. The annular pads consist of narrow elongated epithelial cells with deeply staining cytoplasm (CY) and large spherical nuclei situated mesially. These cells are secretory and their free borders are seen engaged in secreting the peritrophic secretion (PSR). They rest on a fine basement membrane just internal to the thin muscular layer of the proventricular wall. An intima is not visible on the pads.

The wall of the rest of proventriculus is thin made up of a single layer of cuboidal cells possessing large spherical mesially situated nuclei. Its musculature consists of an inner circular and an outer longitudinal muscle layer. An intima is absent.

The lumen of the proventricular oesophagus opens posteriorly into the proventricular cavity (Fig. 5). This opening is guarded by proventricular flanges which normally remains closed due to their adnate nature. The entire complex, therefore, functions as a valve. It prevents the back flow of food, but allows its passage from the oesophagus into the proventricular cavity.

Midgut

Morphologically the midgut of *S. ruficornis* is divided into five regions (Chaudhry-Rohatgi, 1972): the thoracic ventriculus, abdominal ventriculus, proximal loop, helicoid region and the post-helicoid region. Histologically, the wall of each of these regions is composed of the epithelium, basement membrane, and the muscularis. An intimal lining is absent. Instead internally a characteristic striated-border (SB) particularly in the hinder regions is present. The epithelial cells of midgut are large granular having spongy or vacuolar cytoplasm, showing great variations in the different regions depending upon the state of their digestive activity.

Thoracic Ventriculus: The epithelium of the thoracic ventricular region (Fig. 7) comprises a number of tall attenuated columnar

---

Explanation of Figures

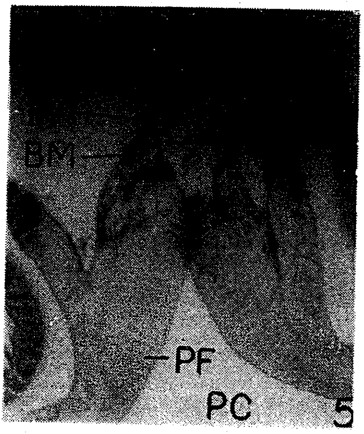
Fig. 5. Photomicrograph of L. S. of the proventriculus showing proventricular oesophagus and valve.

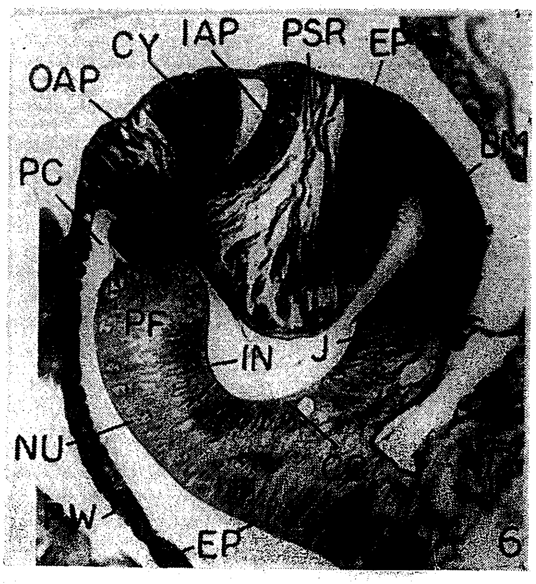
Fig. 6. Photomicrograph of L. S. of the proventriculus showing proventricular wall, flange and annular pads.

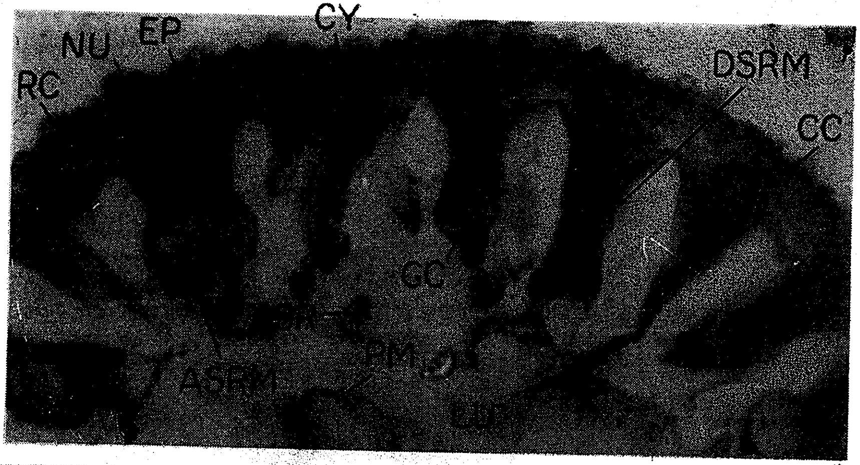
Fig. 7. Photomicrograph of T. S. of thoracic ventriculus showing goblet cells and secretion.

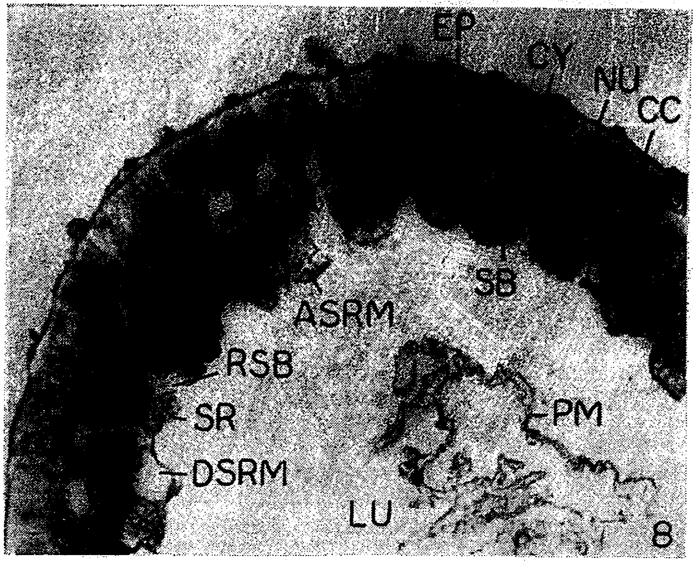
Fig. 8. Photomicrograph of T. S. of abdominal ventriculus showing columner cells in active secretory phase.

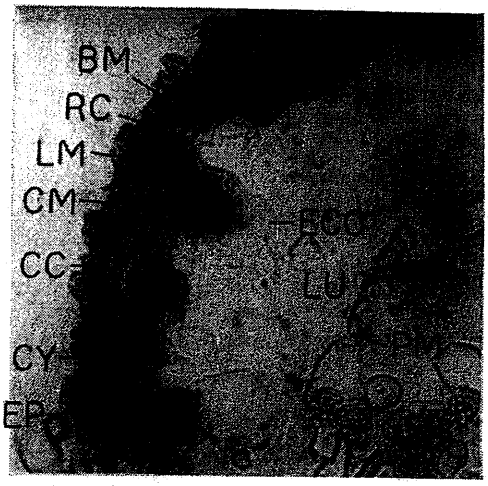
Fig. 9. Photomicrograph of T. S. of proximal loop showing exhausted epithelial cells and regenerative cells.


BM
PF
PC
5


CY
IAP
PSR
EP
OAP
BM
PC
PF
IN
J
NU
W
EP
6


NU
EP
CY
RC
DSRM
CC
GC
ASRM
PM
LU


EP
CY
NU
CC
SB
ASRM
RSB
SR
PM
DSRM
LU
8


BM
RC
LM
CM
ECC
CC
LU
CY
EP

cells with pointed apices and broader base, ranging in height from 20 to 27μ. Most of these cells are goblet (GC) or calyciform type with secretory material accumulated (ASRM) in a large vesicle close to their apices. The vesicle is sometimes seen leading into a narrow canal opening on the apex of the cell discharging the secretory material (DSRM). In between the goblet cells slightly smaller inactive columnar cells devoid of secretory accumulations and with basal nuclei are visible.

Abdominal Ventriculus: The epithelial cells of the abdominal ventriculus (Fig. 8) are also columnar but are much taller and broader ($44 \times 21\mu$) than those of the thoracic ventriculus, possessing mesially situated nuclei. They are the tallest cells in the midgut region and are almost of uniform size A striated inner border is visible in a few cells. Towards the basal side these cells possess granular cytoplasm. Whereas, towards their free ends they show accumulation of secretory granules and secretory vacuoles which are often visible being extruded out from the inner surface of the epithelial cells through the ruptures of the striated border (RSB). These ruptures get repaired as soon as the secretion (SR) of the cells pass out into the lumen.

Proximal Loop: The epithelial cells of the proximal loop region (Fig. 9) are slightly smaller ($35 \times 17\mu$) than those of the abdominal ventriculus. Their nuclei are prominent and mesial. The characteristic feature about these cells is that their inner half portion appear quite empty (ECC) due to the discharge of their secretory material into the lumen. They thus represent the exhausted state of the cells.

Helicoid Region: The epithelial cells of the helicoid region (Fig. 10) are also columnar but much smaller than those of the proximal loop, measuring about $24 \times 13\mu$. They are more protoplasmic and possess a few graules and centrally situated nucleus. They hardly show any vacuolization or secretory material but possess very distinct striated border.

Post-helicoid Region: In the last portion of the midgut, the post-helicoid region, the epithelial cells are much smaller and cuboidal. They do not show any secretory substance or granules but are provided with a striated border.

Scattered throughout the midgut length occur a few regenerative cells (RC), more frequently present in the anterior than in the posterior regions. They (Fig. 11) lie in between the bases of the digestive cells. They are very small, spherical with large rounded nuclei and little cytoplasm.

Immediately external to the basement membrane in all these regions is a circular muscle layer which is comparatively thicker in the posterior three than in the anterior two regions. The longitudinal muscles are found scattered in the form of 40–45 narrow longitudinal bands just around the circular layer of muscles. In the anterior and posterior two regions of midgut the longitudinal muscles are thin and less, whereas in the middle region, the proximal loop they are thicker and numerous.

Throughout the midgut length a distinct thin transparent Peritrophic membrane(PM) is visible. Wherever food bolus is present

Explanation of Figures

Fig. 10. Photomicrograph of T. S. of helicoid region showing striated border of the epithelial cells.

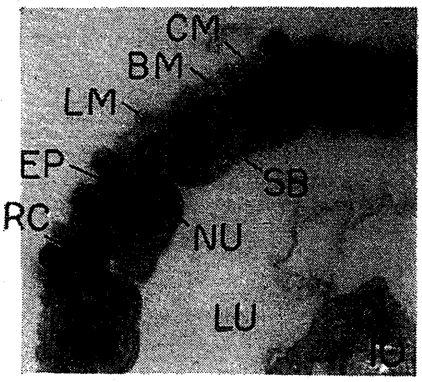
Fig. 11. Photomicrograph of T. S. of midgut showing regenerative cells.

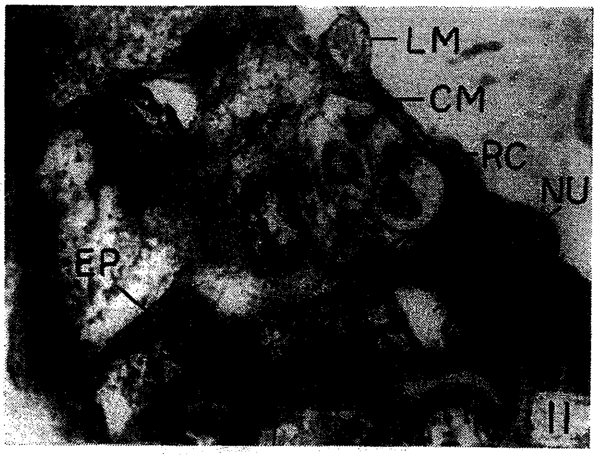
Fig. 12. Photomicrograph of L. S. passing through the junction of midgut and hindgut showing pyloric valve.

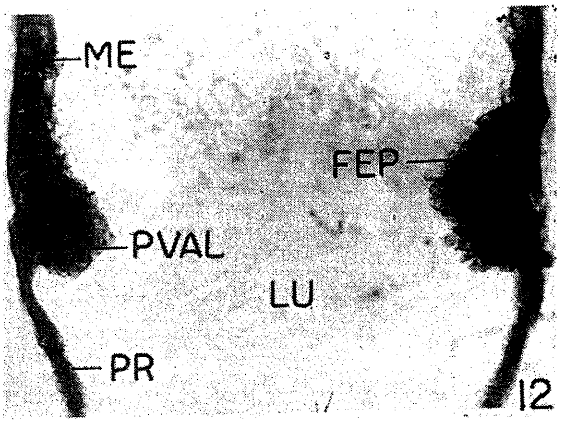
Fig. 13. Photomicrograph of T. S. of the pyloric valve region showing the opening of the Malpighian tubules into the gut.

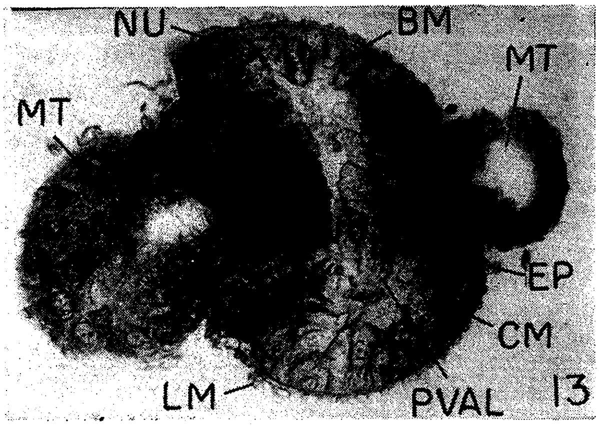
Fig. 14. Photomicrograph of T. S. of the anterior intestine showing intima lining.

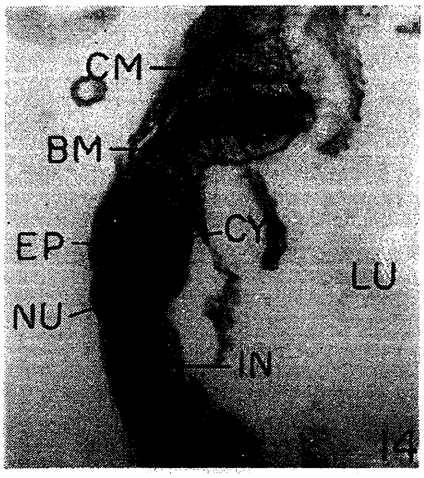
Fig. 15. Photomicrograph of T. S. of the middle portion of anterior intestine showing deep epithelial folds with long spines and broken pieces of peritrophic membrane in the lumen.

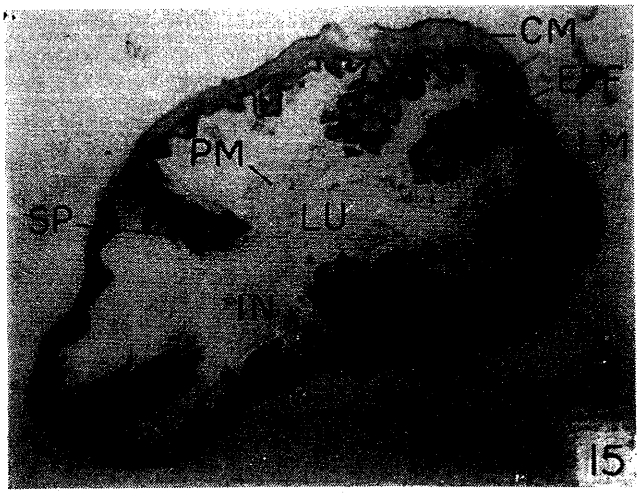

CM
BM
LM
EP
SB
RC
NU
LU
10


LM
CM
RC
NU
EP
11


ME
FEP
PVAL
LU
PR
12


NU
BM
MT
MT
EP
CM
LM
PVAL
13


CM
BM
CY
EP
LU
NU
IN
14


CM
EP
IN
PM
LM
SP
LU
IN
15

this membrane is seen to encircle it. But in an empty gut it appears shrunken lying loose in the lumen like a tube.

Hindgut

The hindgut of *S. ruficornis* is marked anteriorly by a pyloric valve (PVAL) (Fig. 12). Histologically, this valve appears as a small circular internal fold of epithelial cells (FEP) of the posterior mesenteron (ME), extending slightly backwards into the proctodaeum (PR). The cells of this region possess distinct large spherical nuclei but are devoid of an intima. The musculature is differentiated into a thin inner circular muscle layer and an outer layer of scattered longitudinal muscle bands. The two common ducts of the Malpighian tubules (MT) open laterally into the gut in this region (Fig. 13).

Histologically, the hindgut is differentiated into an anterior (AIN) and a posterior intestine (PIN) separated by the presence of the rectal valve (RVAL). The posterior intestine is further distinguished into three parts (Chaudhry-Rohatgi, 1972): the first part of rectum, rectal pouch bearing four cone-shaped rectal papillae and the anal rectum. The hindgut is formed of the usual layers of tissues as found in the foregut. But the epithelium usually comprises larger cells which towards the hind end tend to increase in number thus forming longitudinal folds.

Anterior Intestine: The anterior intestine histologically shows marked variations anteroposteriorly. The single layered epithelium (Fig. 14) rests on a fine basement membrane. The epithelial cells are more or less cuboidal varying in length from 18-20μ, and possessing conspicuous and rounded nuclei 5-6μ in diameter which lie towards their bases. Near the middle of this region the epithelium gets folded into 5-7 longitudinal folds (EPF) projecting into the lumen. At the commencement, these folds are thin and quite apart from each other (Fig. 15). But with their approach towards the rectal valve posteriorly they become thicker and their basal portions approximate each other reducing the lumen into a star-shaped cavity. Like the stomodaeal region a cuticular intima is present which is thin and slightly denticulated in the anterior portion and becomes considerably thicker with increasingly larger backwardly pointed broad spines (SP) posteriorly particulary on the epithelial folds. The musculature which primarily consists of a 2-3μ thick layer of circular muscles anteriorly, also gets considerably thickened (26-30μ) posteriorly. The longitudinal muscles are very poorly developed throughout. In the fold-free anterior part of the lumen the peritrophic membrane still persists in a tubular form, but in the region of the folds it is seen broken into pieces (Fig. 15).

Rectal Valve: At the junction of the anterior and posterior intestine there is a marked constriction of the gut, surrounded by connective tissue and thick circular muscle layer, forming a rectal valve. The muscle-controlled epithelial annulus (EPA) in the valve region, as seen in longitudinal section (Fig. 16), appears projecting backwards from the wall into the lumen. The epithelial cells forming the annulus are cuboidal with small rounded

---

Explanation of Figures

Fig. 16. Photomicrograph of L. S. passing through the junction of anterior and posterior intestine showing rectal valve.

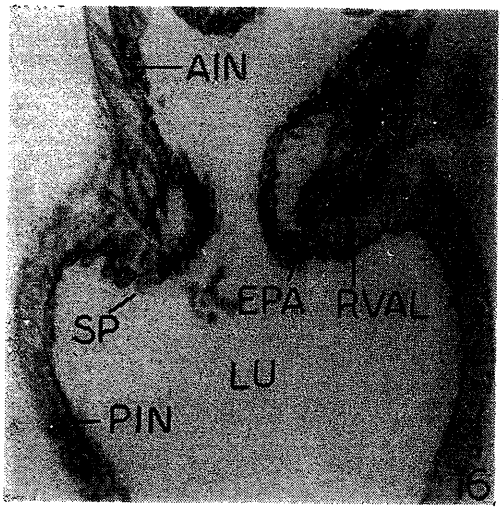
Fig. 17. Photomicrograph of T. S. through rectal valve region showing thick circular muscle band, and long bristle-like spines in the lumen.

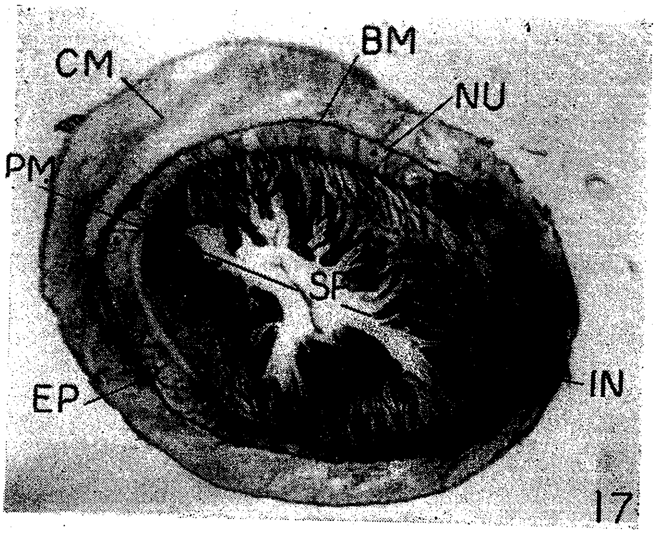
Fig. 18. Photomicrograph of T. S. of the first part of the rectum showing denticulated intima.

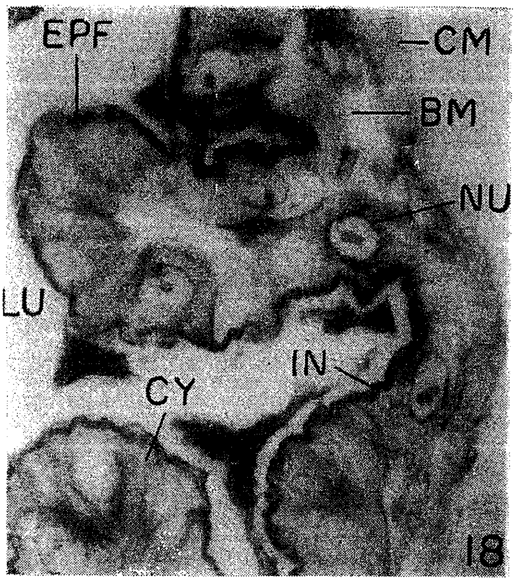
Fig. 19. Photomicrograph of T. S. of rectal pouch wall showing epithelial cells loaded with crystalline bodies, regenerative cells and well developed circular muscles.

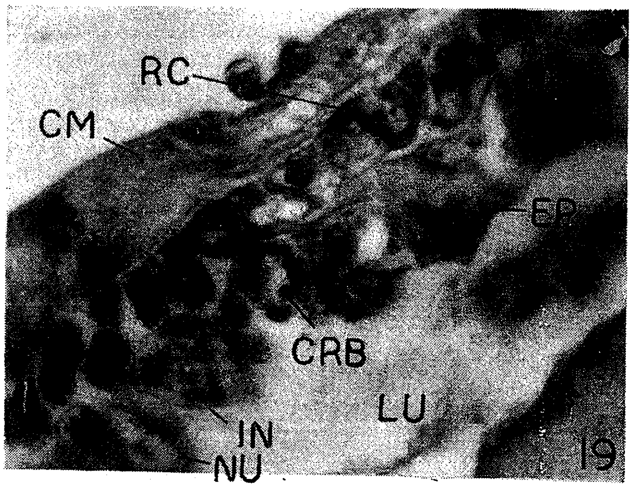
Fig. 20. Diagram of the T. S. of rectal pouch wall.

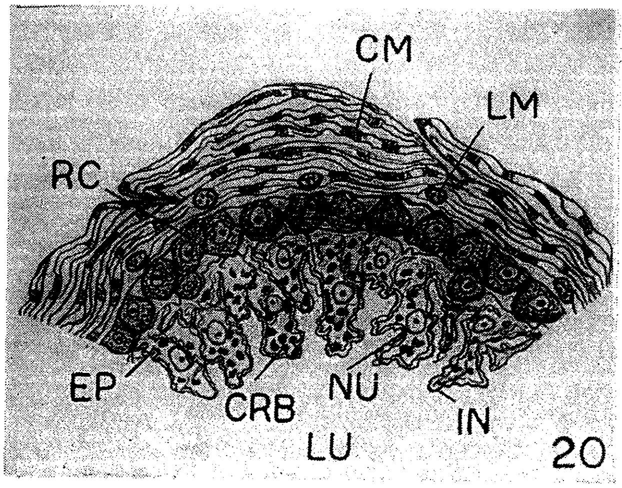
Fig. 21. Photomicrograph of a section of rectal papilla showing the cortical and medullary regions.

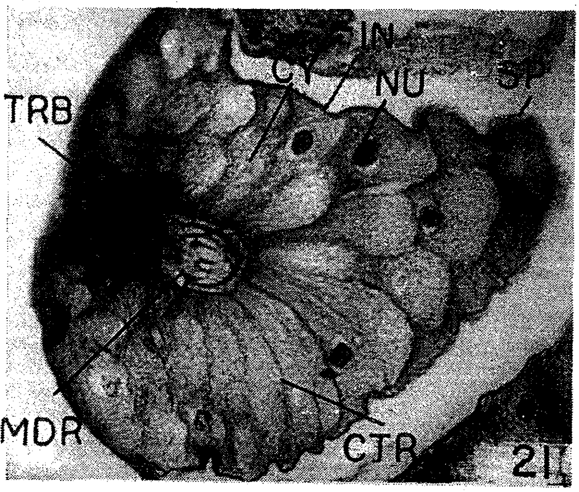

AIN
SP
EPA
RVAL
LU
PIN
16


CM
BM
NU
PM
SP
EP
IN
17


EPF
CM
BM
NU
LU
IN
CY
18


RC
CM
EP
CRB
LU
IN
NU
19


CM
LM
RC
EP
CRB
NU
IN
LU
20


IN
CY
NU
SP
TRB
MDR
CTR
21

nuclei. The intima lining them is thick and provided with long bristle-like spines which practically obliterate the passage between the anterior and posterior intestine (Fig. 17).

First Part of Rectum (Fig. 18): The epithelium of this region is thrown into five to seven deep longitudinal folds. Basically the histology of this first part is similar to that of the anterior intestine with minor differences. The epithelial cells here are cuboidal ($17 \times 17\mu$) with large spherical nuclei measuring 6–7μ in diameter. Internally these cells are lined by a thick denticulated chitinous intima. The musculature consists of a 4–5μ thick layer of circular band which do not conform to the infolding epithelium. Longitudinal muscles are poorly developed.

Rectal Pouch: The wall of the rectal pouch is thin. The epithelium (Figs. 19 and 20) consists of highly irregular cells with small spherical nuclei. The intima lining them is spineless and thin. The epithelial cells are heavily loaded with irregular crystalline bodies (CRB), possibly of some waste matter. The nature and the structure of these epithelial cells indicate as if they are undergoing degeneration and are in the process of being shed off. The presence of a very clear distinct row of regenerative cells which lie beneath the epithelium possibly ready for replacement lends support to this idea. The longitudinal muscle bands lie inner to the circular muscle layer which is folded, the folds showing an imbricate arrangent.

Rectal Papillae: Each of the four rectal papillae (Fig. 21) whose base is embeded in the wall of rectal pouch is composed of a central medullary region (MDR) and an outer cortical region (CTR). The medulla consists chiefly of tracheal branches (TRB) which run along the axis of the medullary region. The cortical cells are tall, columnar with somewhat granular cytoplasm which is denser towards the medullary region. The nuclei are large 10–13μ in diameter and are situated more towards the periphery. Externally each papilla is covered by an intima which is thicker towards the base and apically provided with a row of fine parallel tubular spines.

Anal Rectum: The histological structure of the anal rectum is similar to that of the anterior intestine, except that the musculature is slightly thicker near the anus probably performing the function of an anal sphincter.

DISCUSSION

The foregut intima in this fly *Sarcophaga ruficornis* is always single layered and slightly denticulated in contrast to the double layered spiny intima of other insects feeding on solid food such as *Epilachna* (Potts, 1927) and *Sesamia* (Durr, 1966). No trace of any tracheal tissue covering the internal intimal lining as recorded by Owsley (1946) in the family Asilidae, has ever been found in *S. ruficornis*.

The structure of proventriculus varies considerably in different species of Diptera and there have been controversies regarding its nature and functions. Lowne (1895) regarded it as a gizzard which is ectodermal in origin. The histological details of the proventriculus of *Sarcophaga* show great similarity of its plug-like portion, having chitinous intima, with the oesophagus; while that of the cup-like portion, except for the striated border, with the anterior ventriculus. Thus, it is partly ectodermal and partly endodermal and therefore cannot be homologised with the gizzard or real proventriculus of other forms. Still for the sake of convenience the term proventriculus is applied to it. Miller (1950) in *Drosophila* has embryologically come to a similar conclusion.

According to Patton and Cragg (1913) the proventriculus functions like a valve. Heweitt (1914) has assigned a dual function to it, that of a valve and a pump. Wigglesworth (1929) and Graham-Smith (1934) proposed that since the circular musculature of the plug is thick, it acts as a sphincter rather than a valve. Singh and Judd (1966) opine that at least it plays two important roles, that of a sphincter and the production of peritrophic membrane. In *Sarcophapa*, the presence of the sphincter muscle in the proentricular-oesophagus, and the occurrence of the secretory material of annular pads in continuation with the peritrophic membranous tube fully corroborate the conclusions of Singh and Judd (1966). Furthermore, the opening of the proventricular-oesophageal lumen, into the proventricular cavity in *Sarcophaga* usually remains closed due to the adnate thick proventricular flange. This suggests that it controls the passage of food through it. Thus the possibility of the proventriculus acting as a valve also cannot ruled out.

Histologically, the epithelial cells of the midgut are columnar in the anterior and cuboidal in the posterior regions being tallest in abdominal ventriculus>thoracic ventriculus>proximal loop>helicoid region>post-helicoid region. Somewhat similar condition has also been reported by Dixon (1952) in *Hylemya*.

Singh and Judd (1966) who worked on *Sarcophaga haemorrhoidalis* and other flies could histologically divide the midgut into an anterior and a posterior ventriculus only, except in *Cuterebra*, *Hypoderma*, and *Cephenemyia* where even this differentiation was absent. Wigglesworth (1929) in *Glossina palpalis* has distinguished a third region in the posterior ventriculus portion characterized by the presence of giant cells.

The epithelial cells of the thoracic ventriculus, abdominal ventriculus and proximal loop of *S. ruficornis* are predominantly secretory is evident from their highly glandular nature. Majority of these cells are goblet type showing accumulation of secretory granules and secretory products towards their free ends. While many other cells show characteristic secretory changes, such as the breakdown and repair of their inner walls after the release of the stored secretory products into the lumen, they exhibit merocrine mode of secretion. At the same time in the thoracic ventriculus streaming cytoplasmic secretion of granules have been observed extending out into the gut lumen from the epithelial cells. This has also been reported by Wigglesworth (1929) in *Glossina* and by Graham-Smith (1934) in *Calliphora*. These histological evidences are further corroborated on physiological grounds by Rohatgi (unpublished) in her studies on *Sarcophaga* which show that there is far greater enzymatic activity in the anterior part of the midgut as compared to its hinder portion thus, indicating greater digestive activity of the former.

The epithelial cells of the helicoid and posthelicoid regions of the midgut of *S. ruficornis* show poor secretory activity and are usually seen to possess a distinct striated border. These cells are devoid of granules and, as suggested by Wigglesworth (1965), should be rearded on histological grounds as absorbing cells. Sanford (1918) suggests that the striated border forms some sort of protective covering for the enteric epithelial cells. Snodgrass (1935) has defined it as a delicate limiting membrane. The presence of a striated border in the midgut of feeding, and its general absence in the non-feeding forms like *Hypoderma*, *Cephenemyia*, and *Cuterebra* makes it possible to conclude that the ciliated border is in some way associated with the absorptive function (Singh and Judd, 1966). Further, electron microscopic studies of striated border have shown that the striations represent microvilli arising from the inner margin of the epithelial cells, which increase the surface area extensively. Thus, it would be logical to reaffirm that the helicoid and post-helicoid regions of midgut are mainly concerned with the absorption of food.

Scattered throughout the length of the midgut epithelium occur a few regenerative cells. These cells usually occur singly and never form groups or nidi as reported by Megahed (1956) in *Culiciods*. Functionally the regenerative cells are said to replace the older secretory cells (Day and Waterhouse, 1953). Singh and Judd (1966) have even recorded the mitotic division in these regenerative cells.

The peritrophic membrae of *S. ruficornis* is well developed as a thin transparent tube extending internally throughout the length of the mesenteron and part of the proctodaeum. Waterhouse (1953) reported the general occurrence of the peritrophic membrane in Cyclorrhapha, and Zhuzhikov (1963) in Orthorrhapha. However, Singh and Judd (1966) noted the absence of this membrane in *Hypoderma*, *Cuterebra* and *Cephenemyia* and Owsley(1946) in the asilids.

There are different views regarding the origin of the peritrophic membrane in insects. Van Gehuchten (1890) traced its origin in *Ptychoptera* by the secretion of the anterior midgut cells. Durr (1966) in *Sesamia* found that it arises by the process of delamination of the entire midgut epithelium. Folsom and Welles (1906) reported that the peritrophic membrane is formed by the direct transformation of the striated border of the midgut epithelium. In mosquitoes and certain other blood sucking Diptera the peritrophic membrane is produced by the general midgut epithelium (Waterhouse, 1953). But in majority of Diptera, however, the peritrophic membrane appears to be produced by a band of specialized cells in the anterior end of the proventriculus, as reported by Wigglesworth (1930), Snodgrass (1935), Zhuzhikov (1963) and Singh and Judd (1966). This is also true for *S. ruficornis*.

Most workers believe that the peritrophic membrane is broken up in the hindgut. In *Calliphora*, Graham-Smith (1934) suggested that it is broken by the rectal valves and the churning movement of the rectal papillae which are covered by spines. The hindgut wall which may carry backwardly directed spines may also act mechanically to tear the membrane and push it backwards (Hoare, 1931). In *S. ruficornis* the peritrophic membrane remains intact as a tube in the midgut and the beginning of the hindgut. Beyond it, the membrane is seen in the form of broken pieces lying in the lumen of the spinous region of the anterior intestine and the rectal valve region. Similar observations were also made by Singh and Judd (1966) in all the feeding forms of flies studied by them.

As regards the function of the peritrophic membrane, usually a protective role is assigned to it implying the safeguarding of the midgut epithelium against injuries by solid particles of food (Wigglesworth, 1929, 1965; Waterhouse, 1953, 1957). In flies which imbibe liquid food, as pointed by Zhuzhikov (1964), this protective role is performed in a different manner. According to him, the protein food on entering the midgut very forcefully attracts water, due to which the contents of the midgut get swollen and stretch the peritrophic membrane. In the absence of this membrane the entire pressure would be on the intestinal wall which could injure and even rupture it. Besides the protective function, the peritrophic membrane also plays an appreciable role physiologically and physiochemically. Zhuzhikov (1964) in *Musca domestica* and *Calliphora erythrocephala* recorded that the peritrophic membrane in these species is a complex system with selective permeability to various substances. It conducts the enzymes of the midgut to the food, and lets through for absorption by the epithelium only the end products of digestion.

The existence of a pyloric valve in flies has not been reported by the earlier workers. However, Singh and Judd (1966) recorded its presence at the junction of the midgut and hindgut in all the flies studied by them. The presence of a similar structure has also been reported by Owsley (1946) in Asilidae. In *S. ruficornis*, a well developed pyloric valve is present whose probable function is to prevent the backward flow of food into the mesenteron.

The histological observations made on the anterior intestine of *S. ruficornis* are in agreement with the dipterans studied by Graham-Smith (1934) and Dixon (1952). However, these workers failed to comment on the gradual increase in the thickness of the enteric folds and in the size of the spines present thereon, as well as the thickness of the circular muscle surrounding them towards the rectal valve, as observed in *Sarcophaga* in the present work. Singh and Judd (1966) also recorded similar structures in the flies studied by them.

Though a rectal valve in flies was first recorded by Lowne (1895) but some of the subsequent workers like Hewitt (1914) and Wigglesworth (1929) somehow failed to observe it in the insects they studied. However, Patton and Cragg (1913), Graham-Smith (1934), Dixon (1952), Hori (1962) and Singh and Judd (1966) have all recorded its presence in the flies studied by them. A distinct rectal valve, histologically similar to that described by Dixon (1952), is present in *Sarcophaga.* These structures, as suggested by Singh and Judd (1966), possibly play an important role in breaking up the peritrophic membrane and pushing back the broken pieces. The valve, further prevents the back flow of these pieces.

The rectal sac of *S. ruficornis* show almost the same histological structure as described by Owsley (1946), Dixon, (1952) and Singh and Judd (1966), except in the arrangement of the circular muscles. Dixon (1952) has recorded closely packed circular muscle bands, whereas Singh and Judd found them to be arranged in a peculiar horseshoe-shaped manner. They however, did not elaborate on this peculiar arrangement. In *Sarcophaga* it has been found that the circular muscles are thrown into a few longitudinal internal folds, permitting great expansion of the rectal sac. The muscle bands in between the folds overlap each other in an imbricate manner, which in transverse section appear as crescentic or horseshoe-shaped muscular bodies.

The epithelial cells of the rectal pouch possess small irregular masses of crystalline bodies, the nature of which has not been established. Cells of the enteric epithlium of certain insects are reported to accumulate some nitrogenous substances though their excretory role is still uncertain. However, Folsom and Welles (1906) have recorded that in Collembola the epithelium of the midgut is periodically cast off and this has been regarded as an excretory process. Gersch (1942) asserts that some special subsances are certainly eliminated by the gut in *Periplaneta.* He has further recorded that in Aphids when fluorescein dye is injected it is excreted by the walls of the gut into the rectal pouch. Waterhouse (1955) reported that in the hindgut of *Lucilia* larvae some of the cells appear to take up ammonia from the haemolymph to eliminate it into the hindgut as bicarbonate. It is, therefore, not unlikely that the crystalline masses found in the rectal cells of *Sarcophaga* may be excretory in nature. The irregular and highly disorganized pattern of these epithelial cells bearing these bodies indicate their degenerated nature. They are possibly in the process of being cast off thereby eliminating the waste crystalline matter contained in them. The presence of a well defined row of regenerative cells at the base of this degenerating epithelial lining, ready for replacement, further lend support to the above contention.

The number of rectal papillae inside the rectal pouch varies among Diptera from two to six, while they are absent in *Clunio* (Okada, 1954). Hori (1962) observed sexual dimorphism in the arrangement of the rectal papillae of flies in the genera *Ophyra*, *Lyperosia*, *Pyrellia* and *Stomoxys.* In *Sarcophaga*, though four cone-shaped rectal papillae are present, no sexual dimorphism has been observed. Histologically the rectal papillae of *S. ruficornis* agree with the descriptions of Dixon (1952), Graham-Smith (1934) and Singh and Judd (1966). It is only in *Hypoderma* that Singh and Judd (1966) have reported the lack of an intimal covering on the papillae, instead the surface of the papillae is crooked and the margin of the cortical cells produces cytoplasmic projections into the lumen.

The function of the rectal papillae is not well understood. Some authors like Graham-Smith (1934) have suggested that these papillae serve for breaking up the peritrophic membrane. This, however, cannot hold good in *Sarcophaga* as here the peritrophic membrane is broken up much earlier by the spines of the anterior intestine. According to Wigglesworth (1932) the rectal papillae reabsorb water from the fecal matter and thus play an important role in water conservation. Wherers, according to Srivastava and Rahman (1969) these papillae reabsorb essential substances from the gut contents of the insect, which otherwise may be lost by defecation. In *S. ruficornis*, since the covering of intima is more dense on the surface of the papillae than elsewhere, it possibly plays little nutritive role, The main function that can reasonably be assigned to the papillae is water conservation.

Acknowledgements: The author is very grateful to Prof. H. S. Chaudhry and Dr. S. S. Krishna for their kind supervision, and to Prof. A. N. Chattoraq Head of the Zoology Department, Allahabad University, for his guidance and help in the preparation of this paper. Thanks are also due to the University Grants Commission, New Delhi, for the award of a Research Associateship to the author.

REFERENCES

CHAUDHRY (ROHATGI), K. (1972) Morphology of the alimentary canal of *Sarcophaga ruficornis* (Fabr.) (Diptera: Sarcophagidae). *Zool. Beitrage*, **18**(3): 361-369.

CHAUDHRY (ROHATGI), K. (1984) Hydrogen-ion concentration in the gut of *Sarcophaga ruficornis* (Fabr.) (Diptera: Sarcophagidae). *Bull. Inst. Zool., Academia Sinica*, **23**(I): 75-79.

DAY, M. F. and D. F. WATERHOUSE (1953) Structure of alimentary system. In: *Insect Physiology*. (K. D. Roeder ed.). J. Wiley and Sons, New York.

DIXON, S. E. (1952) The anatomy and histology of the digestive tract of *Hylemya brassicae* (Bouche) (Diptera: Anthomyiidae). *Annu. Rep. Entomol. Soc. Ontario*, **82**: 47-60.

DURR, H. J. R. (1966) Histology of the foregut and mesenteron of the larva of the sugarcane borer, *Sesamia calamistis* (Lepidoptera: Noctuidae). *S. African J. Agric Sci.*, **9**: 639-650.

FOLSON, W. and M. U. WELLES. (1906) Epithelial degeneration, regeneration and secretion in the mi-intestine of Collumbola. *Univ. of Illinois Studies*, **2**(2): 31.

GERSCH, M. (1942) Excretion of flourescent substance by insects. *Z. vergl. Physiol.*, **29**: 506-51.

GRAHAM-SMITH, G. S. (1934) The alimentary canal of *Calliphora erythrocephala* L. with special reference to its musculature and to the proventriculus, rectal valve and rectal papillae. *Parasitology* **26**: 176-248.

HEWITT, C. G. (1914) The housefly *Musca domestica* Linn. Cambridge Univ. Press England.

HOARE, C. A. (1931) The peritrophic membrane of *Clossina* and its bearing upon the life cycle of *Trypanosoma grayi*. *Trans. Roy. Soc. Trop. Med. Hyg.*, **25**: 57-64.

HORI, K. (1962) Comparative anatomy of the internal organs of the calyptrate muscoid flies. III. The alimentary canal of adult flies. *Sci. Rep. Kanazawa Univ.*, **8**: 69-88.

LOWNE, B. T. (1895) The anatomy, physiology and development of the blow-fly (*Calliphora erythrocephala*). 2 Vos. R. H. Porter. London.

MECAHED, M. M. (1956) Anatomy and histology of the alimentary tract of the female of the biting midge *Culicoides nubeculosus* Meigen (Diptera: Heleidae-Ceratoponidae). *Parasitology*, **46**: 22-47.

MILLER, A. (1950) The internal anatomy and histology of the imago of *Drosophila melanogaster*. In *Biology of Drosophila*. (M. Demerec, ed.) J. Wiley and Sons, New York.

OKADA, T. (1954) Comparative morphology of the drosophilid flies. VI. Rectal papillae, their number, arrangement and shape. *Zool. Mag. Tokyo*, **63**: 262-265.

OWSLEY, W. B. (1946) The Comparative morphology of internal structure of the Asilidae (Diptera). *Ann. Entomol. Soc. Am.*, **39**: 33-68.

PATTON, W. S. and F. W. CRAGG (1913) A textbook of medical entomology. Christian Literature Society for India, London.

POTTS, S. F. (1927) The alimentary canal of the Mexican bean beetle. *Ohio J. Sci.*, **27**(3): 127-137.

SANFORD, E. W. (1918) Experiments on the physiology of digestion in Blattidae. *J. Exp. Zool.*, **25**: 355-411.

SINGH, S. B. and W. W. JUDD (1966) A comparative study of the alimentary canal of adult Calyptrate Diptera. *Proc. Entomol. Soc. Ont.*, **96**: 29-80.

Snodgrass, R. E. (1935) Principles of insect morphology. McGraw-Hill, New York.

Srivastava, U. S. and M. P. Rehman (1969) On the function of rectal pads in insects. *Proc. Nat. Acad. Sci. India Sec. B*, **37**(1): 57-64.

Van Gehuchten, A. (1890) Recherches histologiques sur l' appareil digestif de la larva de la *Ptychoptera contaminata*. I. Etude du revetement epitheliale et recherches sur la secretion. *La Cellule*, **6**: 185-289.

Waterhouse, D. F. (1953) The occurrence and significance of the peritrophic membrane, with special reference to adult Lepidoptera and Diptera. *Aust. J. Zool.*, **1**: 299-318.

Waterhouse, D. F. (1955) Functional differentiation of the hindgut in *Lucilla* larva. *Aust. J. Biol. Sci.*, **8**: 514-529.

Waterhouse, D. F. (1957) Digestion in insects. *Ann. Rev. Ent.*, **2**: 1-15.

Wigglesworth, V. B. (1929) Digestion in tsetse fly: A study of structure and function. *Parasitology*, **21**: 288-321.

Wigglesworth, V. B. (1930) The formation of peritrophic membrane in insects with special reference to the larva of mosquito. *Quart. J. micr. Sci.*, **73**: 593-616.

Wigglesworth, V. B. (1932) On the function of the so-called "rectal glands" of insects. *Quart. J. micr. Sci.*, **75**: 131-150.

Wigglesworth, V. B. (1965) The Principles of Insect Physiology. Methuen and Co. London.

Zhuzhikov, D. P. (1963) The structure of peritrophic membrane in Diptera. *Vest. Moskov. Univ. Sec.* **18**(1): 24-35.

Zhuzhikov, D. P. (1964) Function of the peritrophic membrane in *Musca domestica* L. and *Calliphora erythrocephala* Meig. *J. Ins. Physiol.*, **10**: 273-278.

肉蠅 (*Sarcophaga ruficornis*) (Fabr.) 消化道顯微解剖及功能之研究

Kavita Rohatgi

肉蠅（*Sarcophaga ruficornis*）消化道各部份的組織變化隨其功能而不同。中腸（Mid-gut）前三段之上皮細胞（Epithelial cells）之大小和細胞內構造（Internal organization）各異，但具有兩種分泌型式：局部分泌（Merocrine secretion）和細胞質芽生空泡及顆粒分泌，均認爲具有消化功能，中腸後兩段，却沒有此等構造，但具有發達的絨毛層(Striated border)，此被認爲具吸收功能。

前胃（Proventriculus）的組織，具有發達的肌肉層，瓣和生成圍食膜（Peritrophic membrane）的細胞組織。肉蠅具有許多雙翅目（Diptera）昆蟲所沒有的幽門瓣（Pyloric valve）可預防食物由中腸倒流。

直腸瓣（Rectal valve）的組織結構爲能使圍食膜通過，其上皮層（Epithelium）具有大型細胞和發育之直腸突起（Rectal papillae），其功能討論於原文。直腸囊 (Rectal Pouch) 細胞內具有許多結晶體，因此被認爲具排泄作用。