STUDIES ON THE DIGESTIVE SYSTEM OF *IPHITA LIMBATA* STAL. (PYRRHOCORIDAE : HETEROPTERA)

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By :

RANJINI. K.R. M.Phil

Under the guidance of
Dr. U.V.K. MOHAMED
PROFESSOR & HEAD

DEPARTMENT OF ZOOLOGY, UNIVERSITY OF CALICUT
KERALA, INDIA

1999

cup 234-b-97

DEPARTMENT OF ZOOLOGY

UNIVERSITY OF CALICUT

DR. U. V. K. MOHAMED
PROF. & HEAD OF THE DEPARTMENT

Grams UNICAL
Fax 0493 80[illegible]269
Phone : Office : [illegible] 800 271
Res [illegible] 800 303
CALICUT UNIVERSITY P.O.
673 635 KERALA

No.

Date

CERTIFICATE

This is to certify that this thesis is an authentic record of work carried out by **Ranjini. K.R.**, from August 1995 to April 1999 under my supervision and guidance in partial fulfilment of the requirements for the degree of **DOCTOR OF PHILOSOPHY** under the faculty of Science of the University of Calicut. No part of this thesis has been presented before for any other degree. I also certify that Smt. Ranjini. K.R. has passed the M.Phil degree of Calicut University in September 1988.

Dr. U.V.K. MOHAMED

DECLARATION

I hereby declare that this thesis has not previously formed the basis for the award of any degree/diploma.

Ranjini

(Ranjini. K.R.)

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CONTENTS

GENERAL INTRODUCTION

In insects, the alimentary canal is generally in the form of a tube, extending from the anterior to the posterior end and consisting of three major divisions viz. foregut (Stomodaeum), midgut (Mesenteron) and hindgut (Proctodaeum). The lumen of the alimentary canal receives and holds food in close proximity to digestive and absorptive surfaces. Since the pattern and nature of digestion is mostly determined by the functional organisation and structure of the digestive system, a thorough study of the alimentary canal is required to understand the mode of digestion and absorption of food materials. A study of the anatomical features of the alimentary canal will help to understand its functional organisation.

Considerable work has been done on the cytology, anatomy and histomorphology of the various orders of insects to show the importance of this organ in digestion and absorption (Snodgrass, 1935; Kurup, 1961 a, b, 1962, 1964, 1966; Goodchild, 1966; Judy and Gilbert, 1969, 1970; Mathur, 1973; Muraleedharan, 1983; Baker *et al.*, 1984; Caetano, 1984; Dimitriadis and Kastritsis, 1984; Goncalves, 1985 a, b, 1990; Kabir and Ameen, 1986; Singh and Sharma, 1987 a, b, c; Ahmad *et al.*, 1988; Al-Sandouk, 1989; Pakrutty and Mohamed, 1989a; Pathak *et al.*, 1990; Baldwin and Hakim, 1991; Del Bene *et al.*, 1991; Dimitriadis, 1991; Limongi, 1991; Rahman and Ameen, 1991; Werner *et al.*, 1991; Barbehenn and Martin, 1992; Hallberg, 1993; Hochuli *et al.*, 1994; Singh *et al.*, 1996; Srivastava, 1997). The digestive tracts of insect species show a wide variety of morphological structures, corresponding to widely different digestive functions.

Of the different groups of insects investigated so far, on these aspects, the Hemiptera are of special interest, for the insects of this group are the most successful one in thriving in almost every type of ecological niche. Though many authors have studied the digestive system of Hemiptera (Breakey, 1936; Hood, 1937; Harris, 1938; Kurup, 1961 a, b, 1962, 1964, 1966; Goodchild, 1963 a, b, 1966; Khanna, 1964; Mall, 1979; Haridas and Ananthakrishnan, 1981; Goverdhan

et al., 1981; Singh and Sharma, 1987 a, b, c; Pakrutty and Mohamed, 1989a), investigation in pyrrhocorid has been carried out only in *Pyrrhocoris apterus* (Mayer, 1874), *Dysdercus koenigii* (Khanna, 1964; Kurup, 1964) and in *D. cingulatus* (Muraleedharan, 1983).

For a better understanding of the physiology of digestion, a detailed knowledge on the morphology and histology of the digestive system is essential. Compared to such information available on other families our knowledge about the digestive system of pyrrhocorids remains fragmentary. Hence in the present work an attempt is made to conduct a detailed study of the anatomy and histology of the alimentary canal of the pyrrhocorid cotton bug *Iphita limbata* and also on the changes in the midgut epithelium of this insect during the process of digestion of food materials.

HISTORICAL REVIEW

Anatomy of the Alimentary Canal of Insects

The alimentary canal of insects is a tube of epithelium enveloped by muscle layers, either straight or coiled if it is longer than the body. As a rule, the great length of alimentary canal occurs in insects which feed on juices rather than on the more solid tissues of animals and plants. Morphologically the alimentary canal is divisible into three primary regions, the foregut (Stomodaeum), the midgut (Mesenteron) and the hindgut (Proctodaeum), according to their method of embryonic origin. The foregut and hindgut arise as an anterior and posterior ectodermal invaginations of the body wall respectively and midgut which connects the two develops as an endodermal sac (Wigglesworth, 1972; Richards and Davies, 1977; Chapman, 1982). These differences in embryonic origin result in marked histological differences in the structure of the midgut as compared with the other regions. Both the foregut and hindgut being invaginations of the body-wall resemble the latter in their essential histology and are lined with cuticle.

The Foregut

The foregut commences at the buccal cavity into which open the salivary glands. This is followed by pharynx, oesophagus, crop and the proventriculus. The preoral food cavity is the space lying between the mouth-parts and the labrum and is not really a part of the gut. In insects with mandibulate mouth-parts this space is divided by the hypopharynx into an anterior cibarium and a posterior salivarium. The cibarium, whose walls are connected to the post-clypeus by the cibarial dilator muscles may form only a small pouch for the temporary storage of food or is modified into a sucking-pump as in Thysanoptera and Hemiptera. The salivarium is modified to form the salivary syringe of the Hemiptera and the silk-regulator of lepidopterous larvae.

In many orthopterans, such as *Gryllodes sigillatus* (Narula, 1971) *Gryllotalpa fossor* (Prasad, 1975) *Aulacobothrus luteipes* (Pakrutty, 1987) *Gryllotalpa gryllotalpa* (Srivastava, 1988) *Schizodactylus monstrosus* (Srivastava, 1990) and *Gryllus*

domesticus (Srivastava, 1997), the foregut is composed of pharynx, oesophagus, crop and proventriculus. In many Hemiptera the foregut consists of cibarium, pharynx and oesophagus (Sutton, 1951; Marks, 1958; Srivastava and Singh, 1966; Mall, 1979 and Singh and Sharma, 1987a), in some it is formed of pharynx and oesophagus (Kurup, 1961a; Bhaskaran *et al.*, 1969; Pakrutty and Mohamed, 1989a) whereas in others the foregut proper consists of only oesophagus (Goodchild, 1952; Kurup, 1961b, 1962, 1966). In adult Lepidoptera (Chauthani and Callahan, 1967; Beals and Berberet, 1976) the foregut consists of a narrow oesophagus. But in the larva (Judy and Gilbert, 1969; Chi *et al.*, 1975; Beals and Berberet, 1976), it is simple and consists of a short oesophagus and a broad crop. In mature larva of *Prodenia litura* (Mathur, 1973) and in adult *Spodoptera mauritia* (Ani Chacko, 1990), the foregut comprises pharynx, oesophagus and crop.

In higher Diptera (Kumar and Nutsugah, 1976) and in Nematocera (Wigglesworth, 1972), the foregut consists of a narrow oesophagus and a lateral dilation, the crop. In adult Hymenoptera (Green, 1931), the foregut consists of distinct regions of pharynx, oesophagus, crop and proventriculus, while in the larva of Hymenoptera Apocrita, and in larvae of Myrmeleon and other Neuroptera (Wigglesworth, 1972), the foregut is very simple consisting of a narrow oesophagus only. In Coleoptera (Ekis and Gupta, 1971), the foregut is usually simple. In *Anthonomus grandis* (Sundman and King, 1964; Mac Gown and Sikorowski, 1981) the foregut is formed of pharynx, oesophagus and proventriculus.

***Pharynx*:** The pharynx is the region between the mouth and the oesophagus. It is normally provided with dilator muscles which run from its dorsal surface to the frontal region of the head-capsule and are separated from the cibarial dilator muscles by the frontal ganglion of the stomatogastric nervous system. These muscles are best developed where the pharynx participates in the

formation of a well-developed sucking pump (Lepidoptera, Hymenoptera, Neuroptera and Dytiscidae).

Oesophagus: The oesophagus is a simple tube passing from the hinder region of the head into the fore part of the thorax. It is variable in length and inner walls are longitudinally folded. It is usually a narrow tube leading to the midgut as in Collembola (Boelitz, 1933; Toth, 1942).

Crop: The crop is present as a dilation of the posterior portion of the oesophagus in *Gryllus mitratus* (Hsu, 1931), *Gryllodes sigillatus* (Narula, 1971), *Schizodactylus monstrosus* (Narain, 1972; Srivastava, 1990) and *G. domesticus* (Srivastava, 1997). It is extremely variable in form and functions mainly as a food reservoir, though digestion occurs when its contents are mixed with salivary enzymes and some lipids may be absorbed there (Eisner, 1955). In most Orthoptera and Dictyoptera it is very capacious and constitues the major portion of the foregut. In a few insects it is developed as a lateral dilation of one side of the oesophagus as in *Gryllotalpa australis* (Sayce, 1898). *G. fossor* (Prasad, 1975) *G. gryllotalpa* (Srivastava, 1988); certain Isoptera, the larvae of *Myrmeleon* and Curculionidae. The crop is a symmetrical dilation in the cockroach, caterpillars, predaceous adult Coleoptera and in the bee. In *Periplaneta* its movements are under nervous control and emptying depends on the osmotic pressure of its contents (Davey and Treherne, 1963). In *Sitophilus granarius* the crop region contains numerous uniformly scattered spines (Baker *et al.*, 1984). In *Altica cyanea* crop was well differentiated from oesophagus by means of a constriction (Singh *et al.*, 1996).

***Proventriculus*:** The crop is followed by the proventriculus or gizzard. It is the terminal region of the stomodaeum and is structurally the most highly specialised part of the alimentary canal. In structure, it varies from a simple sphincter like valve to a powerful muscular organ armed with spines and teeth. It

is best developed in Orthoptera and Coleoptera (Thiel, 1936, Balfour-Brown, 1944; Judd, 1948). It is also found in Mecoptera, Odonata, Isoptera and various Hymenoptera. It is reduced to a valve in the honey bee and in most Diptera. In its simpler form it is merely the narrowed posterior region of the stomodaeum which is invaginated into the anterior end of the midgut to form the cardiac valve. In adult insects that feed on solid food the proventricular region becomes differentiated as a definite part of the alimentary canal between the crop and midgut. Its inner walls are armed with strong cuticular plates or teeth. Eidmann (1924) suggests that the proventricular armature is a primitive equipment of the insect alimentary canal which has been lost in most of the sucking orders.

The structure of the proventriculus in *Grylloblatta* (Sayce, 1898), *Gryllus* (DuPorte, 1918), cockroach (Sanford, 1918; Eidmann, 1925) and *Stenopelmatus* (Davis, 1927) was described in detail. In *Gryllotalpa gryllotalpa* (Srivastava, 1988) the proventriculus is differentiated into a long narrow tube, anterior proventriculus and a small ball-like posterior proventriculus. The proventriculus of *Gryllodes sigillatus* (Narula, 1971), *G. fossor* (Prasad, 1975), *Schizodactylus monstrosus* (Srivastava, 1990) and *Gryllus domesticus* (Srivastava, 1997) consists of a small peduncle like anterior proventriculus and a ball-like posterior proventiculus. Proventriculus of males of *Scaptotrigona postica* are smaller than those of workers and queens (Serrao and Cruz-Landim, 1995a).

The proventriculus consists of longitudinal folds projecting into the lumen. The number of folds varies from four, six, or eight. A simple condition is found in the Acrididae where the walls of the proventriculus are produced into six longitudinal elevations; each deeply grooved anteriorly and tapering posteriorly to the margin of the short proventricular valve. In the grasshopper the surface of the lobes are sclerotized. They are armed only with a few marginal teeth. In *Plebiogryllus guttiventris* (Dakshayani and Mathad, 1972), the proventriculus is globular and highly sclerotized. In Blattidae the six folds of the proventricular

valve are densely sclerotized anteriorly forming an armature of six plates. Each plate is produced centrally into a strong sharp process with the point turned somewhat posteriorly. In the more tapering posterior half of the proventriculus behind the plates the folds are again thickened, forming a circle of six soft cushion like lobes covered with hairs or spines directed backward. Beyond the cushions is the region of the stomodaeal valve. Crop and proventricular spines with multiple prongs are found in *Paulinia acuminata* and *Marellia remipes* (Pereira and Lorier, 1992) and in *Locusta migratoria* (Hochuli *et al.*, 1994). Singh *et al.* (1996) have reported the absence of a proventriculus in *Altica cyanea*

***Stomodaeal or Cardiac Valve*:** At the junction between the foregut and midgut usually there is a valve-like fold called stomodaeal or cardiac valve. The cardiac valve is essentially a circular fold of the stomodaeal wall projecting into the ventriculus from the posterior end of the stomodaeum. The function of cardiac valve is to prevent the return movement of the food from the stomach but the fold does not entirely occlude the stomach entrance since in some insects digestive juices flow forward from the latter in to the crop. In most insects this occlusion mechanism is effected by the proventriculus (Sinety, 1901; Whitcomb and Wilson, 1929; Armbruster, 1931). However, digestive juices and regurgitated materials can pass anteriorly through the cardiac valve in various Orthoptera (Abbott, 1926; Eisner, 1955), Odonata (Ballentine, 1940), Coleoptera (Dennel, 1942), and Mallophaga (Waterhouse, 1953).

The Midgut

Midgut or mesenteron is the middle part of the alimentary canal and is also termed stomach or ventriculus. Morphologically the ventriculus commences at the base of the outer fold of the stomodaeal valve, the line being marked by the termination of the stomodaeal intima. The walls of ventriculus are distinguished from those of the stomodaeum by the larger size and more spongy appearance of

the epithelial cells, by the absence of a permanent or uniform intima and by a reversal in the arrangement of the muscle fibres. The midgut ends posteriorly a short distance before the bases of the Malpighian tubules.

In most insects the midgut is an elongated tube of approximately uniform diameter. Occasionally it shows differentiation into different regions. In the horse fly *Tabanus* the ventriculus is differentiated into a slender anterior tubular region, the cardia and a posterior dilated region the stomach, the two differing both histologically and functionally (Cragg, 1920). In mosquito the cardia is less differentiated (Wigglesworth, 1930). In some Diptera, the midgut is differentiated into an anterior cardiac chamber and a long ventriculus (Snodgrass, 1935). In the adult boll weevil *Anthonomus grandis grandis* (Mac Gown and Sikorowski, 1981) the midgut consists of an enlarged anterior midgut and an elongated posterior midgut diverticulum. In *Gryllodes sigillatus* (Narula, 1971), *Gryllotalpa gryllotalpa* (Srivastava, 1988) and *Gryllus domesticus* (Srivastava, 1997) the midgut or mesenteron consists of a short tubular anterior mesenteron and a broad posterior mesenteron. The midgut is limited to two large caeca in *Scapteriscus vicinus*, *S. cletus*, *S. abbreviatus* and *Neocurtilla hezadactyla* (Nation, 1983).

The regional differentiation of the midgut attains the highest degree in Hemiptera. In gymnocerate Hemiptera, the midgut is generally differentiated into 4 distinct regions (Glasgow, 1914; Woolley, 1949; Yanai, 1952; Khanna, 1964; Kurup, 1964; Srivastava and Singh, 1966; Bhaskaran *et al.* 1966; Mall, 1979; Muraleedharan, 1983 and Singh and Sharma, 1987b). The first midgut is a dilated chamber and in a well-fed insect it distends to form a bulbous sac. The second midgut is a long coiled tube with a uniform diameter and it measures more than half the total length of the entire alimentary canal. The third midgut is very short and appears as a swollen chamber. The fourth midgut is short slender tube and it bears four rows of gastric caeca in some insects. But 3 regions are reported by Weber (1930) and Breaky (1936). Only the first, second and third ventriculi are

reported in cryptocerates, *Laccotrephes maculatus* (Kurup, 1961a), *Ranatra elongata, Sphaerodema rusticum* (Kurup, 1961b), *Anisops fieveri, Agraptocorixa hyalinipenis* (Kurup, 1962) and *Abedus ovatus* (Goverdhan *et al.*, 1981). In *L. robustus* (Pakrutty and Mohamed, 1989a) the midgut is divided into 3 regions, promesenteron, mesomesenteron and metamesenteron.

In *Chrysocoris patricius, Clavigralla gibbosa* and *Dysdercus koenigii* (Kurup, 1964), *Bagrada cruciferarum* Kirkaldy (Mall, 1979), *D. cingulatus* (Muraleedharan, 1983), the mesenteron is differentiated into four divisions each of which differs from the other in length and contour. No valves are found at their junctions. In some Bryocorinae (Miridae) according to Goodchild (1952) each region of the midgut is divided from the other by constrictions which function as valves.

In some Heteroptera, the first part of the midgut is a sac lying within the filter chamber, the second is a crop like enlargement and the third is a long tube, often called the "ascending intestine." Since it turns forward to re-enter the filter chamber in Homoptera, certain authors (Kershaw, 1913; Hickernell, 1920; Dobroscky, 1931) refer to the anterior expansion of the midgut as the "crop". In some Hemiptera the 4th ventriculus immediately below the third is dilated (Glasgow, 1914).

The alimentary canal of aphids show more marked dilation of the anterior midgut into a "stomach". In Amphibicorisae, in addition to the anterior dilation, the midgut tends to form a bulbous enlargement at the posterior end and its tubular middle portion may form more than one loop. The posterior swelling of the midgut is variable in size in different species and usually smaller than the anterior one. In some species, the posterior swelling is only temporarily formed, as food residues accumulates but in other it seems to be permanent. The Hydrometridae (Sprague, 1956; Miyamoto, 1961) has narrow tubular midgut.

In *Agraptocorixa* (Kurup, 1962) the ventriculus is an elongated reservoir which is held in place by the radial muscles and the tracheal ramification. Its wall is distensible. In *L. maculatus* and *Ranatra elongata* (Kurup, 1961a, b) the first ventriculus is the longest portion of the midgut. The second ventriculus is narrow and tubular followed by a bulbous third ventriculus. Hamilton (1931) named it as "pyloric collar" in *Nepa cinerea* while Bordas (1905) called it as sphincter. The midgut is expanded anteriorly in Cryptocerata, but the posterior bulb is only slightly developed. There is no distinct pylorus. The Malpighian tubules open to the posterior end of the midgut. In Fulgoroidea the midgut is a narrow tube throughout its length and is coiled into a knot-like cluster of loops. Between the oesophageal valve and the junction on the Malpighian tubules the cluster of the midgut loops is enclosed in a membranous sheath.

Licent (1912) observed in *Cixius* and *Issus* species a free loop of the midgut emerged from the central knot, and suggested that the midgut is equivalent of the midgut loop of Cicadoidea, with filtration of excess water taking place within the knot. Families of Fulgoromorpha (Flatidae, Issidae and Delphacidae) possess a diverticulum that forms of the midgut wall and extends anteriorly to the tip of the snout. The midgut is tubular in form and may become tightly coiled within the abdomen. In Cicadoidea the midgut has a clearly defined anterior sac, a narrow tubular intestine which passes towards the rear end of the abdominal cavity and then returns to a point near the oesophageal valve. Filter chamber is found in this group. The whole filter complex forms a smooth rounded capsule on the right side of midgut (Anterior sac). In the sub-family Typhlocybinae of the Jassidae, a true filter chamber is not formed (Licent, 1912; Willis, 1949; Saxena, 1955). The posterior end of the midgut just posterior to the junction with the Malpighian tubules is closely applied to the slightly anterior end of the midgut and bound hitherto by delicate strands of muscle. The filter chamber is also present in

Dalbulus maidis and *Graminella nigrifrons* (Tsai and Perrier, 1996) and in *Hyalopterus* (Ponsen, 1990).

In *Pyrilla perpusilla* (Mishra, 1980) the midgut is divisible into an anterior sac-like diverticulum and a posterior long tubular structure. The epithelial cells of the midgut are thinner at the point of attachment and coiled portions are surrounded by a cellular sheath. Alimentary canals of Coccidae have been described by Berlese (1893), Hough (1925), Misra (1931), Negi (1934) and Pesson (1933, 1935, 1936, 1942). The region of contact of the extremities of the midgut is sunk into an invagination in the anterior end of the sac-like, thin walled rectum which appears to be lined entirely with non-glandular cells. The midgut of Diapsididae is reduced to blind sac, there is no filter apparatus (Pesson, 1942).

In the most advanced sap sucking groups, the Pentatomidae and Coreidae the position of the opening of the Malpighian tubules into the gut lumen has changed so as to bring it closer to the ileo-rectal (pyloric) valve, the ileum becoming a diverticulum receiving only the fluid from the Malpighian tubules. It has been observed (Miyamoto, 1961) that in these species in which the intestine is discontinuous between the third and fourth midgut regions, the anterior end of the latter (caeca-bearing) region is enlarged into an additional bulb, which is in communication with the caecal region.

In Plataspidae, Dinidorinae, and a few Coreidae and Lygaeinae the midgut is discontinuous posterior to the caecal region, which then becomes an isolated mycetome-like organ, still retaining its additional bulb. In Plataspidae and Dinidorinae the caeca are shallow and tend to merge with the central tube, which is no longer thick walled. The opening of the midgut into the ileum, near its junction with the rectum is wide in *Gonopsis affinis* and *Dalsira distinctus* (Miyamoto, 1961) but is a very narrow capillary in *D. bohnroff* (Goodchild, 1963a).

In certain larvae of insects, the midgut is closed posteriorly and these larvae feed only liquid food. This condition is prevalent in Apocrita Hymenoptera, Neuroptera, *Planipennia, Glossina* and other viviparous Diptera.

***Gastric Caeca*:** In many insects midgut diverticula or gastric caeca are present. They are usually situated at the anterior end surrounding the stomodaeal valve. They serve to increase the secretory and absorptive area. The fine structure of the cells of the gastric caeca of *Aedes* larva supports the view that they are concerned mainly with absorption (Jones and Zeve, 1968). Their number usually varies from 2 to 6. In certain dipterous larvae, in Gryllidae and in Tettigoniidae (Yu, 1980) only two large caeca are present. In the gryllids *Plebiogryllus guttiventris* (Dakshayani and Mathad, 1972) and *Nemobius sylvestris* (Richards and Davies, 1977) there are only 2 large caeca. In Dictyoptera and larval Culicidae there are eight, while in the larvae of Scarabicidae there are numerous caeca arranged in 3 annular series. Among various predacious Coleoptera there are numerous villiform caeca. Gastric caeca are absent in Collembola and Lepidoptera. In some larval Lepidoptera (Chi *et al.*, 1975) numerous small caeca are present. In structure the caeca are simple, blunt tapering processes. In Acrididae each caecum is divided at its base into an anterior and a posterior branch. In the larva of *Ptychoptera contaminata* there is a circle of 8 small caeca near the anterior end of the ventriculus (Van Gehuchten, 1890). In *Hydrophilus piceus* the ventriculus is covered with small papilliform diverticula but these structures are the crypts of epithelial regenerative cells (Rengel, 1898).

Glasgow (1914) conducted extensive studies of the gastric caeca of the Hemiptera. In many families the fourth ventriculus is provided with caecal diverticula. In *Peliopelta abbreviata* the caeca are short and uniform, while in *Blissus leucopterus* they are fewer in number and vary in length and are symmetrically grouped. Four rows of gastric caeca are present in *Chrysocoris patricius* and 2 rows in *Clavigralla gibbosa* (Kurup, 1964). In the families of

Pentatomorpha on the section of midgut anterior to the ileum are several tubular or pouch-like gastric caeca (Whitfield, 1929; Breakey, 1936; Harris, 1938; Yanai, 1952; Bocharrova-Messener, 1960; Bentz and Kallenborn, 1995).

The midgut has a large anterior expansion followed by a tubular intestine, the length of which is variable forming several loops on the ventral side of the anterior sac in Scutellerinae and Phyllocephalinae (Pentatomidae) and in Acanthostomatidae and Largidae, but being greatly abbreviated in Urostylidae, Plataspidae, Tessaratominae and Dinidorinae. The gastric caeca are borne on tubular region following the posterior bulb, the length of which varies from a small fraction to as much as 3/4 of the total midgut. No gastric caeca are found in *Leptocoris trivittatus* (Woolley, 1949) and in *Gerris spinoli* (Kurup, 1966).

The eumastacid *Gomphomastax clavata* (Podgornaja, 1971) presents a peculiar arrangement of gastric caeca. In addition to the 12 midgut caeca, there are 6 caeca on the hindgut. In *Blatella germanica* (Yu, 1980), the caeca do not have posterior lobes. In the Madagascar hissing cockroach *Gromphadorhina portentosa* (Dailey and Graves, 1976) there are 8 caeca, two of which are very small, like short stubs.

According to Glasgow (1914) the gastric caeca of Heteroptera are invariably filled with bacteria. The presence of bacteria is hereditory, the organism appearing early in the alimentary canal of the developing embryo. He suggests that the function of caeca is merely to provide a safe place for the multiplication of the bacteria of the gut. In *Dysdercus intermedius* pouch-like gastric caeca are situated at the posteriosr end of the midgut and are free of both extra and intra cellular micro-organisms, whereas bacteria are regularly housed in the lumen of the midgut tube (Bentz and Kallenborn, 1995).

The Hindgut

The hindgut is the posterior ectodermal part of the alimentary canal and is normally marked by a pyloric valve and the insertion of Malpighian tubules. The hindgut plays an important role in the elimination of metabolic wastes and in the maintenance of salt and water balance. Thus it maintains a constant or stable internal environment in insects. Though the hindgut is divisible into two regions, the anterior intestine and the posterior rectum, it shows great anatomical diversity and has been divided into different regions by various authors. The hindgut in *Anthonomus grandis* (Sundman and King, 1964), *Dysdercus koenigii* (Khanna, 1964), Calyptrate Diptera (Singh and Judd, 1966), Calyptrate Muscids (Hori, 1967), *Elasmopalpus lignosellus* (Beals and Berberet, 1976) and in *Stegobium paniceum* (Serjdukova, 1984) consists of an intestine and rectum. Often the intestine is sub-divided into an anterior ileum and a posterior colon. Such an arrangement has been observed in *Hyalophora cecropia* (Judy and Gilbert, 1969), larvae and adults of *Phyllophaga anxia* (Berberet and Helms, 1972), *Aedes aegypti* (Odland and Jones, 1975), *Dactylosternum hydrophilioides* (Shukla and Upadhyay, 1976) and in *Gromphadorhina portentosa* (Dailey and Graves, 1976).

In *Gryllotalpa gryllotalpa* (Srivastava, 1988) and in *Gryllus domesticus* (Srivastava, 1997) the hindgut consists of proximal short narrow tube ileum, middle colon and distal broad pear shaped rectum. In cryptocerates and gymnocerates (Goodchild, 1952, 1966; Kurup, 1961a,b, 1962, 1966; De Carlo *et al.*, 1973; Goverdhan *et al.*, 1981; Muraleedharan, 1983; Singh and Sharma, 1987c; Pakrutty and Mohamed, 1989a), the hind gut is composed of ileum and rectum. In Cryptocerata the rectum has a rectal caecum. In the larvae of Lepidoptera such as *Heliothis zea, Spodoptera frugiperda* (Chi *et al.*, 1975) and *Manduca sexta* (Reinecke *et al.*, 1973) the hindgut is divisible into four distinct regions, viz., the pylorus, ileum, colon and rectum.

The hindgut is formed of only ileum and rectum in Hydrometridae (Sprague, 1956; Miyamoto, 1961), *Ephydrella* species (Marshall and Wright, 1974), *Sphaerodema rusticum* (Ameen and Imam, 1976), *Bagrada cruciferarum* (Mall, 1979), *Abedus ovatus* (Goverdhan *et al.*, 1981) and in *Ips typographus* (Hallberg, 1993). While it is differentiated into colon and rectum in *Uropelta carovei* (Green, 1979) and in *Dolamia americana* (Soldan, 1979). The hindgut is divided into 6 regions in *Marasmia trapezalis* (Mall, 1980) whereas it is divided into an anterior (hindgut I) and posterior (hindgut II) portion and a terminal anal membrane in *A. grandis* (Mac Gown and Sikorowski, 1981).

In most insects the ileum is an undifferentiated tube running to the rectum. In some termites it forms a pouch in which flagellates concerned with cellulose digestion live. In Scarabaeidae there is a fermentation chamber in which the intima is produced into spines. In Heteroptera the ileum is concerned with the removal of water from haemolymph (Goodchild, 1963a).

The hindgut presents a single convolution in *Lepisma saccharinum* (Barnhart, 1961). But it is a narrow tube in Aleyrodoidea and Psylloidea (Goodchild, 1966). The hindgut in Diproceridae (Heteroptera) is primitively sac-like. In Trichoptera the hindgut is extremely short and is divided into two successive more or less globular chambers (Richards and Davies,1977). It is extremely thin, expanded membranous and transparent in *Schizaphis graminum* (Saxena and Chada, 1971). In *Phausis splendidula* and in *Lampyris sanguineus* the hindgut is looped and fairly long, but it is shorter and narrower than the midgut in Buprestoidea (Kasap and Crowson, 1975). In *Diopsis thoracica* the hindgut forms a loop before entering the slightly enlarged rectum (Kumar and Nutsugah, 1976). The hindgut is an expanded flexible tube in Fulgoromorpha (Fick, 1983). In some mole crickets (Nation, 1983) all the gut posterior to the caeca had a cuticular lining and was considered to be the hindgut. Thus more than one half of the

hindgut is anterior to the origin of Malpighian tubules. The long hindgut contains clearly delineated anterior, middle and posterior regions.

Pylorus: In many insects, the anterior part of the hindgut is often differentiated as a well-defined pylorus (Snodgrass, 1935). Deegener (1909) and Rungius (1911) used the term pylorus which means "the gate keeper", since the pyloric valve is usually situated in this region. Srivastava and Bahadur (1961) opined that in *D. koenigii* the pylorus is formed by the fusion of vesicles developed at the bases of Malpighian tubules. In *Anasa tristis* (Breakey, 1936) and in *Dacus cucurbitae* (Zaka-ur-Rab, 1971) the anterior region of the hindgut is termed pylorus.

Pylorus is present in many representatives of Hemiptera (Cragg, 1914; Glasgow, 1914; Hood, 1937; Yanai, 1952; Miyamoto, 1961; Kurup, 1964; Goodchild, 1966; Haridas and Ananthakrishnan, 1981; Muraleedharan, 1983) and in the larvae of Lepidoptera (Judy and Gilbert, 1969; Reinecke *et al.*, 1973; Chi *et al.*, 1975; Beals and Berberet, 1976). In the larva of *Manduca sexta* (Reinecke *et al.*, 1973), *Heliothis* and *Spodoptera* (Chi *et al.*, 1975) the pylorus is divided into 3 distinct regions, anterior, middle and posterior. In Cryptocerata no distinct pylorus has been reported (Kurup, 1961a,b; 1962; Goodchild, 1966). Dallai and Burroni (1982) have given a comparative analysis of the pyloric region in two Diplura genera *Japyx* and *Campodea*.

Pyloric and Rectal valves: The presence of both pyloric and rectal valves have been reported in several Hemiptera (Cragg, 1914; Painter, 1930; Goodchild, 1963b; Khanna, 1964; Mall, 1979; Haridas and Ananthakrishnan, 1981). In Cimicomorpha (Cragg, 1914; Painter, 1930; Goodchild, 1963b) and in Reduviids (Haridas and Ananthakrishnan, 1981) the valves occur anteriorly and posteriorly in the pylorus whereas in *D. koenigii* (Khanna, 1964) valves occur at the anterior and posterior end of intestine. In *Bagrada cruciferarum* (Mall, 1979) the

ileum is anteriorly marked by the pyloric valve and posteriorly by the ileo-rectal valve.

In *D. koenigii* (Khanna, 1964) the pyloric valve is a fold-like projection from the wall of the mesenteron. Kurup (1966) described a pyloric valve formed by the infoldings of ventricular wall. But Beals and Berberet (1976) showed that in adult *E. lignosellus* the pyloric valve was formed by an infolding from the anterior end of the intestine. Pyloric valve has been reported in adult *Phyllophaga gracilis* (Fletcher, 1930), *Prociphilus tesselata* (Pelton, 1938); larvae of *H. cecropia* (Judy and Gilbert, 1969); *D. cucurbitae* (Zaka-ur-Rab, 1971); *P. anxia* (Berberet and Helms, 1972); larvae of *E. lignosellus* (Beals and Berbret, 1976); *Aspidomorpha* spp. (Kumar and Attah, 1977); *A. grandis* (Mac Gown and Sikorowski, 1981) in Fulgoromorpha (Fick, 1983) and in *Altica cyanea* (Singh *et al.*, 1996). Pyloric valve is represented by a muscular sphincter in *Acerentomon maius* and *Eocentomon transitorium* (Dallai, 1976). However pyloric valve is said to be absent in *Longistigma caryae* (Knowlton, 1925); *Oncopeltus faciatus* (Hood, 1937), *Macrosiphum solanifolii* (Smith, 1969), *Myzus persicae* (Forbes, 1964) and in *S. graminum* (Saxena and Chada, 1971). In bees, the pyloric valve is formed by folds of the hindgut epithelium (Serrao and Cruz-Landim, 1996a).

The opening from the intestine into the rectum is often guarded by a circular fold or group of lobes, termed the rectal valve. In some cases a fold is formed by the invagination of the posterior end of the intestine into the rectum while in others the wall of the rectum at the mouth of the opening are produced into opposing lobes forming an occlusion mechanism (Snodgrass, 1935). Rectal valve has been reported in *Dalsira bohndroffi*, *Phalix titan* (Goodchild, 1963a), Calyptrate Diptera (Singh and Judd, 1966) and Calyptrate Muscid (Hori, 1967). In adult *Calliphora* there is a muscular rectal valve bearing spines (Graham-Smith, 1934). Though the epithelium is thickened at the junction of anterior intestine and

rectum there is no functional rectal valve in the adult *E. lignosellus* (Beals and Berberet, 1976).

Intestine: Intestine is very short in *D. koenigii* (Khanna, 1964). In *D. cucurbitae* (Zaka-ur-Rab, 1971), the intestine is narrow and gets looped over itself before joining the rectum. In the larvae of *Stegobium paniceum* (Serjdukova, 1984) the thin intestine has three divisions. A tube runs along the third division of the intestine and rectum. A substance appears to be secreted via this tube which is used by the larvae for the construction of cocoons. In *Heliothis zea* (Chauthani and Callahan, 1967) there is an anterior and posterior intestine. The latter comprises rectum, rectal sac and anus.

Ileum: In *Leptocorisa varicornis* (Akbar, 1958), Plataspidae, Dinidorinae and a few Coreidae and Lygaeidae the ileum is well developed (Goodchild, 1966). Ileum is a straight tube in the larvae of *H. cecropia* (Judy and Gilbert, 1969) but it is long and slightly coiled in adult. In *A. aegypti* (Odland and Jones, 1975) the ileum is narrow and coiled. Tubular ileum is present in Hydrometridae (Sprague, 1956; Miyamoto, 1961), Cryptocerata (Goodchild, 1966) and in *S. rusticum* (Ameen and Imam, 1976). The ileum is broad, tubular, thick walled and slightly coiled in *A. ovatus* (Goverdhan *et al.*, 1981). In *D. bohndorffi* (Goodchild, 1963a) the ileum is enormously inflated and together with the proximal parts of the anal tubules is enclosed in a chamber formed by the edges of the sac-like anterior rectum. The ileum leaves the rectum in the form of a thin walled tube and becomes bifurcated just before it enters the filter chamber. The branches of ileum are flask shaped and contract slightly in diameter at their ends where they merge into inflated Malpighian tubules, two tubules arising from each branch.

The ileum is a very short region in *G. portentosa* and located at the centre of the ventricular coil (Dailey and Graves, 1976). In *B. cruciferarum* ileum is a short rounded structure (Mall, 1979). The ileum is the longest subdivision of the

digestive tract in the larvae of *Prionus laticollis* and loops to the left of the alimentary tract whereas in adult the ileum is the only section of the alimentary tract that loops back and forth itself (Benham, 1970).

Colon: Colon is a straight tube in *H. cecropia* (Judy and Gilbert, 1969); but it is divided into sac-like anterior colon and tubular posterior colon in the larvae and adults of *P. anxia* (Berberet and Helms, 1972). A large bulbous colon is reported in *A. aegypti* (Odland and Jones, 1975). In *G. portentosa* (Dailey and Graves, 1976) the anterior portion of the colon lies towards the ventricular coil. In *Dolamia americana* (Soldan, 1979) the colon is sub-cylindrical and its proximal portion is rounded and extended without any rectal projections.

Rectum: The posterior intestine or the rectum is generally dilated into a rectal sac and narrowed posteriorly in a straight tubular part or rectum proper that goes direct to the anus (Snodgrass, 1935). A sac-like rectal chamber and a tubular rectum proper has been reported in many insects (Khanna, 1964; Judy and Gilbert, 1969; Zaka-ur-Rab, 1971; Beals and Berberet, 1976; Mall, 1979). Sac-like rectum is observed in Hydrometridae (Sprague, 1956; Miyamoto, 1961), *Chrysocoris patricius, Clavigralla gibbosa, Graptostethus servus, D. koenigii* (Kurup, 1964), Pentatomidae, many Fulgoroidea (Goodchild, 1966) and in *A. ovatus* (Goverdhan *et al.*, 1981). In *U. carovei* the rectum is divided into an anterior branchial chamber and a short posterior vestibule (Green, 1979).

In *H. cecropia* adult (Judy and Gilbert, 1969) the entire rectal pouch is pearshaped. In *P. laticollis* (Benham, 1970), the rectum is flattened dorsally and ventrally. In *G. portentosa* the rectum is oval and ends at the anus which is bordered externally by the paraprocts (Dailey and Graves, 1976). Muraleedharan (1983) recorded that the rectum in *Dysdercus cingulatus* is a pear shaped membranous sac. In adult *Callosobruchus analis* and *C. chinensis* rectum is

differentiated into anterior rectal pad and posterior rectal papillae regions (Rahman and Ameen, 1991).

Rectum often gives out a blind pouch called the rectal caecum. A rectal caecum is present in *Nepa cinerea* (Hamilton, 1931), *Anasa tristis* (Breakey, 1936), cryptocerate Hemiptera (Kurup, 1961a,b 1962; Pakrutty and Mohamed, 1989a), *H. cecropia* (Judy and Gilbert, 1969), in *S. rusticum* (Ameen and Imam, 1976) and in *A. ovatus* (Goverdhan *et al.*, 1981) whereas a rectal diverticulum packed with protozoa in its inner lining is found in *Leptocoris trivittatus* (Woolley, 1949).

In Dytiscidae the hind intestine gives off a conspicuous rectal pouch an organ which is characteristic of that family. Although it is a relatively small sac in *Ilybius*, it attains enormous dimensions in *Dytiscus* and bears an apical tubular appendix. A posterior caecum is found in *Silpha* and *Necrophorus* (Richards and Davies, 1977). However, a rectal caecum is said to be absent in *C. patricius, C. gibbosa, Graptostethus servus* and in *D. koenigii* (Kurup, 1964). In some insects the distal ends of the Malpighian tubules are closely applied to the rectum and invested by a layer of epithelial cells, pronephric epithelium. A space known as pronephric chamber is found between the rectal epithelium and pronephric epithelium (Mohamed and Murad, 1977a). This type of arrangement is known as cryptonephridium (Saini, 1964; Rahman *et al.*, 1991; Hallberg, 1993) or nephro-rectal complex (Mohamed, 1974).

Opening of the Malpighian tubules: Opening of the Malpighian tubules to the alimentary canal is observed to be at different locations in different insects. In some it opens to the midgut, in some to the junction of midgut and hindgut and in still others to the hindgut.

Malpighian tubules opening to the posterior most region of midgut is observed in *Pleretes* (Bordas, 1911), *Stenopelmatus* (Davis, 1927), *Hapialus* (Henson, 1932), and in Cryptocerata (Goodchild, 1966). In most Hemiptera the

Malpighian tubules open to intestine at the midgut and that the epithelium of midgut and tubule junction are similar (Goodchild, 1966).

In *Opatroides punctulatus* (Verma, 1970), *P. anxia* (Berberet and Helms, 1972), *Periplaneta americana* (Crowder and Shankland, 1972; Schmidt, 1979). *D. thoracica* (Kumar and Nutsugah, 1976), *Calpodes ethlius* (Ryerse, 1979), *Arachnocampa luminosa* (Green, 1980) and in *A. ovatus* (Goverdhan *et al.*, 1981), the Malpighian tubules open to the midgut-hindgut junction.

Malpighian tubules opening into the anterior most region of pylorus has been reported in gymnocerate Hemiptera (Kurup, 1964), *A. grandis* (Sundman and King, 1964), *Catholsius molosus* (Shukla and Upadhyay, 1980) and in *Laccotrephes maculatus* (Mohamed, 1984). Srivastava *et al.* (1983) have noticed that the opening of Malpighian tubules in *Papilio demoleus* is in the pylorus in the larva whereas it is shifted to the midgut-hindgut junction in the pupa during development.

In Reduviids (Haridas and Ananthakrishnan, 1981) and in *Dysdercus cingulatus* (Muraleedharan, 1983), the ampullae of 4 Malpighian tubules open into the pylorus. A common Malpighian duct inserts through the musculature on the pylorus of *Heliothis* and *Spodoptera* (Chi *et al.*, 1975).

Malpighian tubules opening into the hindgut is reported in *Serrodes inara* (Grice, 1968), *Prodenia litura* (Mathur, 1972), *Callograma festiva* (Mohamed and Murad, 1977a), *Conocephalus indicus* (Mohamed and Murad, 1977b), *Dacus cucurbitae* (Mohamed and Murad, 1978), *Coccinella septumpunctata* (Mohamed, 1983) and in *Spodoptera mauritia* (Chandrika, 1985). In *Solenopsis invicta* the Malpighian tubules open to the intestine (Petralia and Vinson, 1980). Malpighian tubules opening to the ileum has been reported in Pentatomorpha (Goodchild, 1966) and in *Bagrada cruciferarum* (Mall, 1979). In *Necrophorus* and *Gnaptor* (Gorka, 1914) and in Fulgoromorpha (Fick, 1983) the Malpighian tubules open

into the midgut just anterior to the pyloric valve. In *Mylabris pustulata* (Mohamed, 1980) and *Vespa bicolor* (Mohamed, 1982) the tubules open into the gut above the proctodaeal valve. In *D. koenigii* they open to the intestine immediately behind the pyloric valve (Khanna, 1964). In *H. cecropia* the common Malpighian duct inserts beneath the pyloric sphincter to empty into the hindgut (Judy and Gilbert, 1969). In *P. anxia* the Malpighian tubules enter the gut posterior to the pyloric valve (Berberet and Helms, 1972).

Histology of the Alimentary Canal of Insects

The alimentary canal consists of a single layer of epithelium invested by muscles. Absence of multiple layers and absence of striated epithelia are two important characteristics of insect gut. Snodgrass (1935) has given details of arrangement of tissues of various regions and modifications. The histology of the alimentary canal of insects belonging to various orders has been studied by Hodge (1940, 1943), Sutton (1951). Goodchild (1952), Kurup (1961a, b, 1962, 1964), Judy and Gilbert (1970), Muraleedharan (1983), Chapman (1985), Cruz-Landim (1985, 1994), Singh and Sharma (1987a, b, c), Ahmed *et al.* (1988), Srivastrava (1988), Pakrutty and Mohamed (1989a), Goncalves (1990), Lopez and Moron (1990), Pathak *et al.* (1990), Rahman *et al.* (1990, 1991), Weaver and Scott (1990), Limongi (1991), Moron Rios and Moron (1991), Moron Rios and Rojas (1991), Rahman and Ameen (1991), Vijayakumar and Mohamed (1991), Hallberg (1993), Hochuli *et al.* (1994), Singh *et al.* (1996) Desai *et al.* (1997), Marana *et al.* (1997) and Srivastava (1997). The epithelium of the fore and hindgut exhibits very little changes during the process of digestion. But the histology of the midgut is of special interest because of the rapid regeneration and replacement of its cells.

The Foregut

The wall of the foregut has a simple structure. Passing from outside towards the lumen the following layers are recognisable, the circular muscle fibres, the longitudinal muscle fibres, the basement membrane, the epithelium and the intima. The circular muscle fibres run continuously around the foregut without attachment to it. The oesophagus is strongly muscularised by circular muscles in *Icerya purchasi* (Johnston, 1912). Five groups of circular muscles in the foregut of *Phormia regina* (Thomson, 1975) act as crop valves. The longitudinal muscle layer is more developed in the posterior proventriculus than in pharynx, oesophagus and crop of *Gryllus domesticus* (Srivastava, 1997). In *Spilostethus macilentus* (Singh and Sharma, 1987a) in the anterior half of oesophagus circular muscles and in the posterior half longitudinal muscles are better developed. Livingstone (1967)

reports nine bundles of longitudinal fibres in *Tingis*. A reverse arrangement of muscle layers is also reported in various groups of insects (Kurup 1961a, b, 1962, Singh and Sharma, 1987a, and Pakrutty and Mohamed, 1989a).

The epithelium of the foregut consists of flat or cuboidal cells (Rahman and Ameen, 1991, and Rahman *et al.*, 1991) which are not clearly defined. In *S. macilentus* it presents an appearance of syncytium (Singh and Sharma, 1987a). The epithelium is produced into longitudinal folds (Livingstone, 1967; Singh and Sharma, 1987a). These folds enable the lumen to expand as the foregut becomes filled with food. The oesophagus of *Laccifer lacca* is lined with cylindrical epithelium (Misra, 1931). Epithelium is made of rectangular cells with small nuclei and indistinct boundaries in *Schizodactylus monstrosus* (Srivastava, 1990) and *G. domesticus* (Srivastava, 1997). In *Gryllotalpa gryllotalpa* (Srivastava, 1988), these cells are rectangular with oval nuclei and granular cytoplasm. Larson (1973) has reported the constant occurrence of a type of bacterium aggregated at the luminar border of intima in association with the stomodaeal epithelium of *Lepisma*.

The epithelial cells secrete the intima which is thicker in oesophagus than in pharynx. It is non-cellular, chitinous and armoured with bristles or spines. Foregut intima of insects bear microspines (Hodge, 1939; Singh, 1965; Narula, 1971; Muralirangan and Ananthakrishnan, 1974; Bondreaux, 1980; Singh and Sharma, 1987a; Srivastava, 1990 and Singh *et al.*, 1996). The intima is without bristles in *Gryllotalpa fossor* (Prasad, 1975); and *G. gryllotalpa* (Srivastava, 1988). Observations of the foregut intima of *Locusta migratoria* (Hodge, 1939; Albrecht, 1953; Hochuli *et al.*, 1992) have shown numerous spines of differing morphologies directed posteriorly. Their major role is related to the antiperistalsis of enzymes from the midgut forward to the foregut and they retard and hold the food in the foregut which functions as a storage chamber.

In *Callosobruchus analis* and *Callosobruchus chinensis* (Rahman and Ameen, 1991) the intima of the foregut is modified into pharyngeal spines, oesophageal spines and proventricular needles in the pharynx, oesophagus and proventriculus respectively. The proventricular needles are numerous in number and they almost block the lumen of the anterior part of proventriculus. The intima is thickened and complexly developed in the proventriculus of *Anthonomus grandis* (Sundman and King, 1964). In *Plebeiogryllus guttiventris*, the intima is highly sclerotized and have minute spiny structures on the tooth like structures which project into the lumen of the proventriculus (Dakshayani and Mathad, 1972). The intima of pharynx is provided with denticle like projection in *Alphitobius diaperinus* larvae (Rahman *et al.*, 1990). Crop and proventricular spines are with multiple prongs in *L. migratoria* (Hochuli *et al.*, 1994) and they are used to regulate the passage of food through the foregut. Cuticular ridges and spines in crop and proventriculus are also observed in *Paulinia acuminata* and *Marellia remipes* (Pereira and Lorier, 1992). In fleas there are altogether 12 types of proventricular spines and there is a series of lateral teeth on the spines (Jin-P, 1994). There are numerous scattered spines in the crop region and rows of interlocking spines found on the sieve plates in proventriculus of *Sitophilus granarius* (Baker *et al.*, 1984). Internal armature of pharynx with dorsal and lateral plates was used to identify females of 5 species of *Sergentomyia sensu stricto* (Benabdenubi *et al.*, 1996). Oesophageal bristles are present in *Dendroctonus adjunctus* (Zuniga-Bermudez *et al.*, 1994). In the proventriculus of cockroach and cricket the intima is dense and produced into lobes and teeth forming a special armature. In the oesophagus the intima is very thick and appears to be divided into two layers (Pesson, 1944).

The crop epithelium of *Drosophila auraria* (Dimitriadis and Papamanoli, 1992) displays continuous folds and consists of a single layer of thin epithelial cells whose apex is covered with cuticle. The epithelial cells contain small amounts of rough endoplasmic reticulum, golgi complex and secretory granules.

In Cockroach (Eidmann, 1924), the anterior part of proventriculus is a crushing apparatus while the posterior part serves as a sphincter. In the flea (Faasch, 1935) the proventriculus is lined by long backwardly directed spines.

At the junction of foregut and midgut there is often a cardiac or oesophageal valve formed by the wall of the foregut being prolonged into the cavity of the midgut and then reflected upon itself and passing forwards to unite with the midgut wall. It probably prevents or reduces regurgitation of food from the midgut. The cardiac valve of *L. migratoria* (Hochuli *et al.*, 1992) is heavily sclerotized. In *S. macilentus* (Singh and Sharma, 1987a) the posterior end of oesophagus hangsdown freely into the lumen of the midgut forming oesophageal valve. The free hanging valve consists of two layers of oesophageal epithelium which are closely apposed to each other and consists of tall columnar cells. Cuticular intima lines the oesophageal valve on its outer as well as inner surface.

The Midgut

The midgut is composed of a layer of longitudinal and a layer of circular muscle fibres, basement membrane, a layer of epithelium and peritrophic membrane. The midgut musculature is usually described as being composed of two layers, with the longitudinal muscles in a discrete layer outside the circular muscles. The circular muscles are composed of a single layer of fibres and constitute the principal layer. The longitudinal muscles comprise bundles of longitudinally arranged fibres originating anteriorly (Snodgrass, 1935). Fibres of circular and longitudinal muscles were located in *Sitophilus granarius* (Baker *et al.*, 1984). The arrangement of circular and longitudinal muscle layers in the midgut is different from that of fore and hindgut in *G. gryllotalpa* (Srivastava, 1988). The outer longitudinal muscle layer is more developed in posterior mesenteron than in the anterior mesenteron. The circular muscle layer is thick in both the parts of mesenteron and it is inner to the longitudinal muscle layer. A series of

longitudinal and circular muscle fibres surrounds the midgut epithelium in *Sinentomon erythanum* (Dallai *et al.*, 1989). The site of the former fibres is clearly indicated by introflexions of the outer cell profile. The circular muscle fibres constitute a sphincter which contracts to reduce the gut lumen. Pathak *et al.* (1990) reported that the muscular layer of midgut of *Aulacophora foveicollis* was thicker than that of *Coccinella septempunctata*. The muscle fibres of the midgut are attached to the basement membrane and to each other by sheet of fascia and also by sheets of connective tissue which overlies the whole gut (Green, 1931).

The basement membrane on which the epithelial cells rest appears to be a product of the cell bases. Electron microscopic studies on basement membrane revealed that there is no internal differentiation or it contains collagen micro-fibrils or shows an elaborate and regular internal differentiation (Richards and Richards, 1968; Reinhardt and Hecker, 1973). The basement membrane is always closely associated with the plasma membrane at the base of epithelial layer. At occasional spots it may extend a short distance into an infolding of the basal labyrinth or form a small out pocketing (Richards and Richards, 1968). In *Tenebrio molitor* (Gouranton, 1970), the basal lamina of the midgut epithelium has an unusual structure. In a transverse section, the upper part of the basal lamina shows a dense and discontinuous sheet formed from a sheet of hexagonal plates connected by filaments. Collagen is the main constituent of these plates. The basal lamina of *S. granarius* (Baker *et al.*, 1984) consists of an amorphous substrate into which are embedded fibrils or lead-like lamellae. In *Musca domestica* (Terra *et al.*, 1988) the basement membrane is highly infolded with few apertures in the underlying space. The basement membrane projects into the lumen in the form of 6 small unequal, blunt folds covered by epithelial layer in *A. foveicollis* (Pathak *et al.*, 1990). The basement membrane in *Drosphila auraria* (Dimitriadis, 1991) is folded in many sites forming a complex net work of wide extracellular compartments.

According to Smith *et al.* (1969) the three types of cells which have been identified in insect midgut epithelium are columnar cells, goblet cells and small basally located nidi. The midgut epithelium of all lepidopterous larvae (Wigglesworth, 1972) is composed of columnar and goblet cells. Chi *et al.* (1975) are of opinion that the goblet cells and columnar cells may be maturation phases of the same cell type. They describe that both goblet and columnar cells are involved in secretion of digestive enzymes. Regenerative cells or nidi are interspersed adjacent to the basement membrane of the midgut.

Most of the midgut cells are columnar with irregular inner ends projecting into the lumen of the stomach. In *Lucilia* larva (Waterhouse and Wright, 1960) the columnar cells comprise ultra-structurally distinct lipophilic and cuprophilic cells, the former with large inclusions of storage fat and lamellate border. In *Blatella* (Threadgold and Gresson, 1962) there are histological differences between the secretory and absorptive columnar cells. Columnar cells are numerous in both anterior and posterior regions of midgut in *S. granarius* (Baker *et al.*, 1984). In *G. gryllotalpa* (Srivastava, 1988) the epithelium is differentiated into functional epithelium which is towards the lumen and regenerative epithelium which is dome shaped mass of irregular cells lying outer to the functional epithelium under the circular muscle layer. The epithelial cells are elongated columnar cells. Columnar cells have different morphology along the midgut and even in the same region in the dipteran fly *M. domestica* (Terra *et al.*, 1988).

Midgut epithelium in *Manduca sexta* (Baldwin and Hakim, 1991) consists predominantly of columnar and goblet cells. These are arranged in a characteristic pattern with each goblet cell surrounded by a single layer of 4-6 columnar cells. Goblet cells are most conspicuous in lepidopteran larvae, becoming more numerous towards the posterior end of the gut (Shinoda, 1927). These cells have reduced cytoplasm and striated cell surface, which is invaginated to form a deep cavity as in *Vanessa* (Henson, 1929, 1931). In *Tineola* three zones can be

distingusihed in the midgut. A fore and hind part in which there are typical goblet cells between columnar cells with high striated borders and containing inorganic granules and a middle part in which goblet cells are flask-shaped and the columnar cells have lower striated borders and contain no inorganic granules (Lotmar, 1942; Waterhouse, 1952). According to Day (1949) the contents of the goblet cells are not mucoid. In *Tineola* larvae the goblet cells are able to accumulate sulphides formed from metal ingested with their food (Waterhouse, 1952).

The cytoplasm of the columnar cells appears granular or spongy. Abundant invaginated plasma membranes in the basal zone has been reported in Orthoptera, Coleoptera and Diptera (Baccetti, 1960). In *Calliphora* (Priester, 1971) and in the larvae of *Hyalophora* (Anderson and Harvey, 1966) and *Ephestia* (Smith, 1969) the cytoplasm of the cells is divided basally into compartments by deep infoldings of the plasma membrane forming the brush border.

In some Coleoptera, Mecoptera (Grell, 1938) and in hymenopteran *Microbracon* (Soliman, 1941) the regenerative cells occur at the bottom of the crypts. In *Dytiscus* the new cells are supported from these regenerative cells for the intercryptal epithelium as old cells degenerate (Rungius, 1911; Duspiva, 1939). In *Passalus* the regenerative cells are located at the sides of the crypts, the remainder of the crypt apparently assuming the function of a digestive gland (Patterson, 1937). In *Sitophilus oryzae* some of the crypt cells harbour bacteria (Mansour, 1934).

Awati and Dike (1939), Barendrecht (1941), Kurup (1964) and Goodchild (1966) reported absence of regenerative cells from midgut epithelium in Thrips, *Contarinia, Chrysocoris patricius* and *Chrysocoris purpureus* respectively. In *A. foveicollis* (Pathak *et al.*, 1990) the epithelial layer is with small villi and a few regenerative cells. Midgut epithelium is formed of tall columnar cells with regenerative nidi in *Callosobruchus analis* (Rahman and Ameen, 1991). It is found

that the epithelium which is damaged or exhausted during secretory activity is regenerated from portions of the parent cells that are left behind (Kurup, 1964; Bhaskaran *et al.*, 1969). The regenerative type of cells are found in Thysanura, Collembola, Odonata, Orthoptera and many other groups. The frequency and arrangement of the regenerative cell determine the form of the midgut.

Usually lumen surface of the midgut epithelial cells is striated. Its nature is unknown, but the elements of which it is composed lack basal granules and do not show motile characteristics of cilia (Zilch, 1936; Newell and Baxter, 1936). According to Newell and Baxter (1936) there are two types of striated border, one made up of rod-like elements which are held together to form a rigid structure called the "Honey-comb border" and the other composed of independent hair-like filaments which can be passively moved about, called "Brush border." The straited appearance at the base of the cells results from the numerous deep perpendicular invaginations of the plasma membrane (Beams and Anderson, 1957).

In *Altica cyanea* (Singh *et al.*,1996) there is a brush border on the luminar surface. The midgut epithelium of the adult honey bee (Raes *et al.*, 1994) consists of columnar and endocrine cells, both originating from regenerative crypt cells. The regenerative crypt is formed of stem cells and differentiating cells. The stem cells generate two forms of endocrine cells along with differentiating enterocytes of two distinct stages. At first they can be seen as light crypt cells which are not actively secretory, they then develop into more electron dense, active secretory crypt cells.

In the midgut epithelial cells of *Schistocerca gregaria* (Bowen, 1968) and *Periplaneta americana* (Couch and Mills, 1968) contain numerous autophagic vacuoles or cytolysosomes derived from mitochondria, the size and number of which increase during starvation. Andries and Tramu (1985) conducted ultra-

structural and immunohistochemical studies of endocrine cells in the midgut of the cockroach *Balberus cranifer* and identified ten types of such endocrine cells.

The columnar cell nuclei are centrally located in *S. granarius* (Baker *et al.*, 1984). An extensive network of rough endoplasmic reticulum and numerous mitochondria are located in both supranuclear and infranuclear regions. In some cells vesicular golgi complexes are present in the supranuclear region. In addition to columnar cells, cells containing numerous small to very large vacuole like structures are found in anterior midgut of *S. granarius*. In *G. gryllotalpa* (Srivastava, 1988) the nuclei of columnar cells are large and round. The cytoplasm of columnar cells of *M. domestica* (Terra *et al.*, 1988) contains abundant rough endoplasmic reticulum, golgi elements and secretory vesicles.

In *S. erythanum* (Dallai *et al.*, 1989) the cytoplasm of the apical region is rich in mitochondria and there is abundance of golgi complexes and rough endoplasmic reticulum. The midgut cell cytoplasm of the posterior region is almost completely filled with microtubules, small dense droplets intermingled with these microtubules are visible. The anterior and the posterior midgut of *D. auraria* (Dimitriadis, 1991) have similar quantities of rough endoplasmic reticulum and of golgi complexes. The posterior midgut is the important site for secretory granule accumulation and secretion. The cup-shaped cells of the middle midgut may be primarily involved in generating and managing the acid pH in the middle midgut lumen. According to Richards (1975) and Waterhouse and Wright (1960) in insects gogli complexes are poorly developed or are absent.

The brush border of the midgut epithelium of cockroaches and termites are well studied by Noirot and Noirot-Timothee (1972) and they found that the regular microvilli are longer. Inside each microvillus runs a core of axial filaments which extends as an intra-cytoplasmic rootlet. The posterior cells of the midgut epithelium of Proturans *Eocentomon* and *Acerentomon* (Dallai, 1976) carry short

microvilli. A brush border consisting of numerous microvilli extends apically into the midgut lumen of *S. granarius* (Baker *et al.*, 1984). In some cells microvilli are more uniform than in others. The epithelial cells towards the lumen have inner brush border made of long fine filaments in *G. gryllotalpa* (Srivastava, 1988). In *M. domestica* (Terra *et al.*, 1988) the apical membrane is undulated and shows conspicuous and well developed microvilli close to which there are series of small vesicles. The midgut cells of posterior region have microvilli in *S. erythanum* (Dallai *et al.*, 1989). These microvilli progressively decrease in number and length. In *A. foveicollis* small villi are observed in the epithelial cells facing the lumen (Pathak *et al.*, 1990). The apices of epithelial cells display long microvilli in *D. auraria* (Dimitriadis, 1991). According to Del Bene *et al.* (1991) the microvilli have two different types of glycocalyx in *Frankliniella occidentalis*. In the anterior part of the midgut they are surrounded by a myelin-like membrane and in the posterior region, the microvilli have numerous rod like projections arranged to form a continuous layer of microfilaments which according to them cross each microvillus.

The microvilli of digestive cells in adult stingless bees are very long with a large base narrowing to the tip, where supporting microfilaments are lacking. The apical cytoplasm presents a web of microfilaments with supporting filaments of microvilli, numerous elongated mitochondria and lipid inclusions-an adaptation for absorption of nutrients (Serrao and Cruz-Landim, 1995a). In the anterior midgut of female *Rhodnius prolixus* the basal plasma membrane is highly folded and within two hours of feeding these folds separate so that a large surface area of membrane is exposed for rapid transport of water across the epithelium. On the apical surface, extra cellular membrane layers are produced but their extensive proliferation is not seen (Billingsley and Downe, 1989a).

The midgut of *Bemisia tabaci* and *Trialeurodes abutilonea* are looped so that the anterior and posterior extremities are in contact with each other. The basal

lamina at this point is breached and the basal epithelial membrane of either extremity are contiguous. On the anal side of the contact is a filter-organ which acts as an osmoregulatory device; fluid food directed into the looped midgut gets concentrated by passive transport of water through the filter organ (Cicero *et al.*, 1995).

Four types of cells can be distinguished in the epithelium of the caeca of three species of mosquito larvae *Aedes, Anopheles and Culex* (Volkman and Peters, 1989). The gastric caecal epithelium of *Dysdercus intermedius* (Bentz and Kallenborn, 1995) consists of secretory cells which are characterized by the apical border of microvilli, mitochondria crowded into the apical and basal cytoplasm, large amounts of rough endoplasmic reticulum profiles and secretory granules.

Peritrophic membrane: The midgut epithelium lack a cuticular intima. However, the epithelial cells do not come into direct contact with the food because the food is enclosed within a thin-walled tube, the peritrophic membrane. This membrane extends from the anterior end of the midgut to the hindgut. The membrane consists of mucoprotein in which chitin fibrils are arranged irregularly or in hexagonal or orthagonal arrays (Peters, 1968, 1969; Platzer-Schultz and Welsch, 1969). In *Heliothis* (Pyerse *et al.*, 1992) and *Phlebotomus perniciosus* (Walters *et al.*, 1993), the peritrophic membrane is mainly composed of protein and chitin. The peritrophic membrane protects the midgut from abrassion by food particles. It is absent from insects feeding on liquid diet such as Hemiptera, except Corixidae (Sutton, 1951), many adult Lepidoptera and blood sucking insects. However they occur in *Cicadella* (Gouranton and Maillet, 1965), mosquitoes and *Glossina* (Moloo *et al.*, 1970; Freeman, 1973).

Two types of peritrophic membranes are recognized according to their mode of formation (Wigglesworth, 1930; Waterhouse, 1953). In some Lepidoptera, Diptera and Dermaptera, it is secreted by cells near the junction of fore and midgut extruded in tubular form by a muscular press in this region (Young-Tai, 1929;

Aubertot, 1932; Von Dehn, 1933). This type of peritrophic membrane is made up of concentric lamellae, independent or loosely attached to one another. It is produced by the separation of thin sheets from the surface of the cells throughout the length of the midgut. Each new sheet appears as a limiting membrane at the surface of the striated border as in the bee (Trappman, 1923) and in *Galleria* larva (Young-Tai, 1929). This type is always of uniform circumference throughout its length. In other insects it arises by delamination from part or all of the general surface of the midgut and a series of concentric membranes formed by successive delaminations is often present.

Black–burn *et al.* (1988) studied the ultrastructure of the peritrophic membrane of the female sand fly *Phlebotomus papatasi*. The formation of peritrophic membrane has been described by many workers (Wigglesworth, 1930; Von Dehn, 1933; Waterhouse, 1953; Peters, 1969; Becker, 1973; Richards and Richards, 1977; Pabst *et al.*, 1988; Ryerse *et al.*, 1994 and Singh *et al.*, 1996). A characteristic feature of peritrophic membranes of Diptera is their longitudinal subdivision into anisotrophic sections which are probably different in chemical composition (Becker, 1973). The formation rate of peritrophic membrane *in vitro* is influenced by pH, temperature and external osmolarity (Becker *et al.*, 1975). In *Glossina* the formation of peritrophic membrane is stimulated by a blood meal (Wigglesworth, 1929). The peritrophic membrane of the adult *Drosophila auraria* consists of two layers, the thicker one of which is positioned towards the endoperitrophic space. The two components of the peritrophic membrane are loosely connected to each other (Dimitriadis, 1991).

The Hindgut

The commencement of the hindgut is normally marked by a pyloric valve and the insertion of the Malpighian tubules (Snodgrass, 1935). In most insects the hindgut is divisible into three regions, the ileum, colon and rectum.

The hindgut is composed of the same layers as the foregut. The muscle layer of the hindgut is less regular than that of the other regions of the alimentary canal and is frequently absent on some of the intestinal regions (Snodgrass, 1935). The musculature consists of an external longitudinal fibres and an internal circular fibres, resembling the muscle sheath of the midgut rather than that of the foregut. The relative development of the layers of fibres varies greatly in different parts of the hindgut and there may be additional muscles either outside or inside the usual layers. Generally the longitudinal fibres are arranged in a single layer while the circular fibres are arranged in several layers. Towards the posterior region of the hindgut the longitudinal fibres disappear and the circular fibres are reduced to a single layer (Green, 1931). This condition extends throughout the rest of the small intestine.

Pylorus: The epithelium of the pylorus of *Dacus cucurbitae* (Zaka-ur-Rab, 1971) is very flat and syncytial. In the pyloric region of *Acerentomon marius* and *Eocentomon transitorium* (Dallai, 1976) the epithelial cells are lined with very long microvilli. In collembolan species (Dallai and Callaini, 1979) the pyloric region is made up of three zones, posterior midgut cells, connecting cells and pyloric ring-cells. In *Dysdercus cingulatus* (Muraleedharan, 1983) the epithelial cells of the pyloric region are club-shaped with irregular borders.

The pyloric valve of Coleoptera (Snodgrass, 1935) consists of one or two transverse folds of epithelial cells which are cut by longitudinal folds of the pyloric wall into a series of opposing lobes. In *Hyalophora cecropia* (Judy and Gilbert, 1970) the anterior pylorus is thrown into six shallow longitudinal folds which form the pyloric valve. In the pyloric valve of *Phyllophaga anxia* (Berberet and Helms, 1972) a ring of very elongate cells extends into the lumen. In *Elasmopalpus lignosellus* (Beals and Berberet, 1976) the pyloric valve consists of constricted folds. In *Bagrada cruciferarum* (Mall, 1979) the pyloric valve is provided with elongated cells with deeply staining cytoplasm and rounded nuclei. Intima is absent in the

pyloric valve. In Ectrichodinae (Haridas and Ananthakrishnan, 1981) the pyloric intestinal valve is composed of flattened uninucleated cells. In all other reduviids the valve is composed of binucleate cells.

The pyloric chamber in *Sinentomon erythanum* (Dallai *et al.*, 1989) is formed by cells with microvilli pointing anteriorly, the secretion from six Malpighian papillae flows into this cavity. The cuticle of pyloric valve in bees has spine-like structures at the proximal end of the valve, while in the distal end they are lacking (Serrao and Cruz-Landim, 1996a), The transition between mid and hindguts is marked by flat cells where the cuticle begins to appear. The cells of the pyloric valve are cubical and have a cytoplasm with clear regions. At their apex there are short microvilli. The Malpighian tubules occur in front of the pyloric valve. In bee larvae, Malpighian tubule insertions are in the hindgut (Serrao and Cruz-Landim, 1996a).

Ileum: The wall of the ileum of *Ostrinia fasciatus* (Hood, 1937), Cacao capsid bugs (Goodchild, 1952), several phytophagous bugs (Rastogi, 1962) and in *Bagrada cruciferarum* (Mall, 1979) consists of thin-walled epithelium with small nuclei but without cell boundaries. The ileum is made up of two different types of epithelium in several insects (Hamilton, 1931; Presswalla and George, 1936; Rastogi, 1961; Kurup, 1961 a, b, 1962; Ameen and Imam, 1976; Goverdhan *et al.*, 1981; Gross *et al.*, 1981; Pakrutty and Mohamed, 1989a). The ileum is histologically divided into two portions; one part is made up of thick layer of cells, and the other of a thin layer in which the cell boundaries are ill-defined, but the nuclei are prominent. The thin-walled portion is a specialised condition and it is found to be secretory. The ileal wall of *Hyalophora cecropia* (Judy and Gilbert, 1970) is thin and divided by deep infolds into six longitudinal bulges. In the larva of *Spodoptera* and *Heliothis* (Chi *et al.*, 1975) the ileum is composed of squamous

epithelial cells with branching nuclei. In *Melipona quadrifasciata* ileum consists of 4 types of epithelial cells in addition to the valve cells (Cruz-Landim, 1994).

Colon: In *Popilia japonica* Swingle (1930) observed spines projecting from the epithelial cells of colon to hold the fibrous materials in position. In *Ostrinia nubilalis* (Hassemer and Beck, 1969) the epithelial cells of the colon are more rounded and smaller than those of the ileum. In *Hyalophora cecropia* (Judy and Gilbert, 1970) the wall of the colon is thrown into six folds. In *Phyllophaga anxia* (Berberet and Helms, 1972) the epithelium of the anterior colon is surrounded by longitudinal muscles and is arranged into alternating papillae and small inward folds that form rings around the gut. In the larvae of *Manduca sexta* (Reinecke *et al.*, 1973; Reinecke and Adams, 1977) the ileum and colon have super contractor circular muscles and 6 pairs of major longitudinal muscles in addition to normal circular and longitudinal fibres.

Ultra structural studies of the epithelium of colon of *Periplaneta americana* (Bignell, 1980) show that the cells are provided with extensive foldings of apical plasma membrane associated with mitochondria and an internal coating of ultra size particles. Peacock (1985) studied the ultra structure of the colon of *Locusta migratoria* and found that the epithelial cells are characterised by the invaginations. The bulk of the mitochondria are located in the apical region of the cell. Vitellaro *et al.* (1985) have described the fine structure and physiological features of the colon of *Leucophaea maderae*.

Rectum: In the majority of insects the epithelium of the rectum is modified to form rectal pads or rectal glands. When it is not modified to form pads the epithelium is cuboidal (Wigglesworth, 1932). The epithelium of the rectal pads are composed of a single layer of columnar cells with large and oval nucleus located in the middle or basal region of the cells (Maddrell, 1971). Simple stratified rectal epithelium has been observed in Apterygota (Fain-Maurel and

Cassier, 1972). In several anisopteran nymphs (Schmitz and Kominick, 1976; Leader and Green, 1978; Kukulies, 1982) the rectal epithelium is modified as rectal chloride cells. In Thysanura, Odonata, Orthoptera and Phasmida the rectal glands are composed of single layer of tall epithelial cells, while in Neuroptera, Hymenoptera, Lepidoptera and Diptera they are composed of two layers. In the bee there is a cavity between the two layers (Evenius, 1933; Lotmar, 1945). In the rectal pad epithelium of *Locusta migratoria* Peacock (1979) has reported two types of cells, type A cells and type B cells. Type A cells have large ovate nucleus. Type B cells occur singly in the distal region of the rectal pad epithelium. Their nuclei are small and located in the distal region of the epithelium. Type B cells contain numerous lysosome-like bodies (Locke and Collins, 1965).

The number of rectal pads varies in different insects. Typically there are six pads. In *Pyrilla perpusilla* (Mishra, 1980) and in reduviids (Haridas and Ananthakrishnan, 1981) only a single rectal gland is present. In the noctuid *Serrodes inara* (Grice, 1968) there are numerous rectal pads, while in *Hyalophora cecropia* (Judy and Gilbert, 1970) there are as many as 300 pads on the rectal wall. In *Elasmopalpus lignosellus* (Beals and Berberet, 1976) there are numerous oval pads, each of which is composed of three cells with large nuclei. Engel (1924) reported that the usual number of rectal papillae in Diptera is 4 to 6. In *Mydas clavatus* (Jahn, 1930) there are 33 rectal papillae that are roughly arranged in three longitudinal rows. There are four rectal papillae in *Diopsis thoracica* (Kumar and Nutsugah, 1976) and *Dacus cucurbitae* (Zaka-ur-Rab, 1971). Marzo *et al.* (1978) studied the anatomical, histological and ultrastructural and physiological study of the rectum of *Dacus oleae* and correlated them with the sex pheromone production in the males. Associated with the rectum a sex pheromone gland has been detected in many dipteran males and females (Jacobson, 1972). The same has been observed in the males of *Dacus tryani* (Fletcher, 1968, 1969), *D. oleae*, *Dacus dorsalis* and *Dacus cucurbitae* (Schultz and Bousch, 1971). In the dipteran

Gonia cinerascens (Campadelli and Gardenghi, 1985) generally have 4 rectal papilla, in some both sexes have 6 while in some males have 4 and females 6. Caetano (1984) compared the rectal pads of seven species of ants and found that in all species there are only three rectal pads.

The general organisation of the rectum is constant in all termites. The rectal pads are composed of two layers, principal and basal cells and are surrounded by a very narrow junctional cells (Noirot and Noirot-Timothee, 1977). In most insects the rectal glands are highly tracheated.

The ultrastructure of the rectal pads and papillae has been thoroughly investigated by Gupta and Berridge (1966 a, b); Hopkins (1966); Berridge and Gupta (1967, 1968); Oschman and Wall (1969); Noirot and Noirot-Timothee (1971, 1976, 1977); Wall and Oschman (1973); Peacock and Anstee (1977); Peacock (1979); Mishra (1980); Petralia and Vinson (1980) Caetano and Lage-Filho (1982); Nation (1983); Peacock (1985, 1986); Elliot and King (1985) and Jairal (1992).

In adult *Agrotis ypsilon* (Chen-changkun *et al.*, 1996) rectal papilla is discal and consists of five layers of cuticle intima, papillary cells, basal lamella, muscle and peritoneal membrane. Papillary cells are divided into four types, cap cell, tracheolar cell, netty cell and discal base cell. In *Callosobruchus analis* and *Callosobruchus chinensis* (Rahman and Ameen, 1991) the rectum is clearly distinguishable into anterior rectal pad and posterior rectal papillae regions. The top of each rectal papilla bears rectal spines.

Usually in the lepidopteran larvae, the rectal wall and the distal ends of the Malpighian tubules form a cryptonephridial complex (Chi *et al.*, 1975; Beals and Berberet, 1976). The cryptonephridial complex has been reported in *Vanessa utricae* (Henson, 1931), *Prodenia eridania* (Woke, 1941), *Anthonomus grandis* (Sundman and King, 1964) *Callograma festiva* (Mohamed and Murad, 1979),

Papilio demoleus (Kumar and Srivastava, 1981), *C. analis* and *C. chinensis* (Rahman and Ameen, 1991), *Alphitobius diaperinus* larvae (Rahman *et al.*, 1991) and in *Ips typographus* (Hallberg, 1993).

40A

Functional significance of various regions of the Alimentary Canal of Insects

10

The Foregut

The crop may serve as a temporary reservoir of food which pass on to the midgut as it is evacuated. Digestion occurs when its contents are mixed with salivary enzymes, and some lipids may be absorbed there (Eisner, 1955). In *Glossina* large quantity of blood is stored in the crop and transferred to the midgut as required (Lester and Lloyd, 1928). This is also found in *Musca, Calliphora* and other insects feeding on exposed fluids (Graham-Smith, 1934). In *Haematopota* the blood goes first into the stomach, when the stomach is full it is diverted to the crop (Cameron, 1934). In *Periplaneta* the movements of the food are under nervous control and emptying depends on the osmotic pressure of its contents (Davey and Treherne, 1963). In the bee (Sarin, 1923) the nectar is converted into honey in the crop. In some of the Lepidoptera which take no food in the adult stage the crop functions as a receptacle for the air that is swallowed and distends the body at ecdysis (Stober, 1927).

According to Petrunkevitch (1900) and Sanford (1918) in the cockroach, the crop is the seat of absorption. Schluter (1912) opined that absorption did not take place in the crop. Eidmann (1922) found that it is impermeable to water. According to Abbott (1926) sugar will not pass through the crop. Olive oil will pass through it and fat may be absorbed in it.

The oesophageal diverticula may have some accessory functions. In the larva of the sawfly *Lophyrus* (Saint Hilaire, 1931) a pair of small pouches serve as receptacles for the unwanted resin from the surface of the pine needles on which the larva feeds. In mosquitoes (Mac Gregor, 1930) the diverticula take up any air swallowed with the food.

The structure of the proventriculus of various termites is modified according to the type of food (Lebrun, 1985). In its simpler form it acts merely as a sphincter between the crop and the midgut to regulate the passage of food materials into the

latter. In many beetles (Thiel, 1936) it transmits the contents of the crop in small quantities at a time acting as a sieve. In *Calandra* (Dennel, 1942) it serves to retain minute particles in the crop while allowing the digestive fluid from the midgut to pass forwards. In ants (Eisner, 1957) the proventriculus is mainly concerned with the regulation of the passage of fluid to the midgut. In the flea (Faasch, 1935), during digestion of blood the proventriculus contracts rhythmically driving the spines backward into the midgut and breaking up the corpuscles in the ingested blood. In *Galleria* larva (Bittner, 1954) the proventriculus is covered with small teeth which serve to grind the wax particles in the food.

In the queen bee and in *Drosophila* the oesophageal invagination is the site of large deposits of glycogen (Wigglesworth, 1949; Fyg, 1961). The small spines in the cardiac valves of *Locusta migratoria* (Hochuli *et al.*, 1992) function in regulation of food through the digestive tract. These valves control the passage of solid food past the foregut without interrupting antiperistalsis. Small gaps between the valves allow the digestive enzymes from the midgut into the foregut.

The foregut is the major site of digestion (Williams, 1954) although no enzymes are secreted from its walls and no nutrients are absorbed through them. In its dual role as a storage and digestive chamber food is held in the foregut and then digested by enzymes secreted by the salivary glands and the midgut (Uvarov, 1966). Enzymes are pumped forward from the midgut to the foregut by antiperistalsis (Baines, 1979).

The Midgut

Secretion, digestion and absorption are the main functions of the midgut in insects. Digestion is effected by the secretion of digestive enzymes by the midgut epithelial cells. Haseman (1910) distinguished two types of secretion, merocrine and holocrine secretion. In the merocrine type of secretion the discharge is

gradual and continuous and the cell remains active for a long period. In the holocrine type the whole cell contents are discharged at once, and new cells arise.

Merocrine type of secretion is characteristic of insects that feed continuously thus requiring a continuous supply of digestive enzymes. Holocrine is observed in predaceous insects. Here the secretory cells gradually increase in size until they are capable of secretion. When the stimulus of the presence of food is introduced, these cells burst releasing their contents to be mixed with the food. These burst cells are replaced by the regenerative cells of the nidi characteristic of insects with holocrine secretion. The ultrastructural studies (Bertram and Bird, 1961; Threadgold and Gresson, 1962; Staubli *et al.*, 1966; Gander, 1968) have confirmed the observations of Duspiva (1939) and Schonfeld (1958) on the changes of the midgut epithelium during the process of secretion. But Day and Powning (1949), Khan and Ford (1962), Smith *et al.* (1969) and Priester (1971) reported that secretory activities do not show any visible signs. According to them these changes are degenerative or they represent absorptive processes.

Pradhan (1940) made a comparative study between carnivorous and herbivorous coccinellids. In carnivorous forms secretion is monophasic and synchronous while in herbivorous forms it is polyphasic and asynchronous. In *Glossina* the midgut epithelial cells elongate and give off cytoplasmic globules in the first hour of feeding. After a large meal this is followed by a phase in which the epithelium is flattened and shows no signs of the productions of cytoplasmic globules. It has not recovered its resting condition 48 hours after feeding (Wigglesworth, 1929).

In *Blatella* digestive enzymes increase after feeding at which time the epithelium is cytologically uniform. Quantitative estimations of enzymatic activity are clearly necessary to prove that cytological changes in the epithelium is indeed the result of the secretion of enzymes (Day and Powning, 1949). According to

Semichon (1933) many cases of cytological secretions are artifacts. In *Tabanus* (Cragg, 1920) vacuoles alone may be discharged or the inner border of the cell may give way and a mass of granular cytoplasm carrying the nucleus be set free into the lumen. In *Dytiscus* the cells go through a definite secretory cycle before degeneration and replacement occur (Duspiva, 1939). In the flea (Faasch, 1935) some cells show little change while others break away entirely and disintegrate in the cavity of the gut. In beetles (Newcomer, 1914) the entire lining of the midgut is shed off and replaced every forty eight hours. Cyclic changes of the epithelial cells have been reported in Coleoptera (Duspiva, 1939) and Diptera (Buchmann, 1929). In *Dytiscus* the resting cells decrease from about 95% to 5% within 45 minutes after feeding while the secretory cells increase from 0 to about 60%. It is clear that the histological changes are correlated with the output of the digestive enzymes (Duspiva, 1939).

In *Spilostethus macilentus* (Singh and Sharma, 1987b) there are 3 types of midgut secretion. First type of secretion is apocrine. The epithelial cells are elongate and the secretory granules are collected at the free ends. The cells have an abundance of secretion along the peripheral border causing swelling of the cell in that region forming a vesicle. In certain other cases from the inner striated border or brush border of the epithelial cells are given off some protrusions which later take a blister like appearance. These swellings in the form of blisters are constricted off as non nucleated globules and their places are taken up by similar swellings and a large number of globules are thrown into lumen. In the second type of secretion, certain cells show sign of rupturing their peripheral border. The contents of the cells including the nucleus are thrown into the lumen. These cells are pushed to the periphery by regenerative cells. This mode of secretion is called "modified merocrine." In the third type, often portion or strings of complete cell layer with nuclei are sloughed off from the epithelial cells into the lumen. When these cells are completely sloughed off their places are taken up by growing

regenerative cells. This type of secretion is called "holocrine" where complete cells along with the nuclei are detached.

The epithelium of ventriculus of *Pachycondyla striata* (Caetano *et al.*, 1994) consists of cells with a central nucleus and an elongated and dilated apex. Goblet cells are present. At the base of these cells there are generative cells which form elongated club-shaped processes in the apical region which eventually detach and are released into the lumen of the ventriculus in the form of small spheres which produce apocrine type secretions. Upon release into the lumen, the spheres migrate to the peritrophic membrane, pass still intact into the space limited by this membrane and proceed towards the central region where they can be detected in various stages of lysis.

In *Apis mellifera, Scaptotrigona postica* and *Melipona quadrifasciata* (Cruz-Landim *et al.*, 1996) several types of protrusions are evident in the apical surface of the midgut cells. Large apical protrusions are formed by the whole apical surface of the cells, whose content has a homogeneous cytoplasmic matrix devoid of organelles and with a different electron density from the subjacent cytoplasm. These protrusions can be cast out to the midgut lumen. Second type of large apical protrusion is produced between the cell microvilli presenting many ribosomes and polyribosomes. Two other kinds of small ones - one type crowned the cell apex forming small spheres with irregular contours near the cells and increasing in size further way. Other type is characterized by the microvilli swelling with an electron lucent content.

The midgut epithelium of larval *Aeshna cyanea* (Kominick and Kukulies, 1987) consists of four types of differentiated cells, which display secretory activity. Pure secretory cells are the mucocytes and two morphologically distinguishable types of endocrine cells while the enterocytes exert the dual function of secretion and absorption. The heaviest accumulation of secretion granules was observed

after a few days of starvation following a long period of regular feeding. Then the enterocytes resembled typical protein secreting exocrine gland cells. Two types of endocrine cells occur in the midgut of adult worker honey bee *Apis mellifera* (Raes and Verbeke, 1994). These cells, one of a basal granular type and other of a vesicular type, are evenly distributed throughout the posterior three quarter of the midgut. The granular cells release their secretory granules at the cell base in a typical endocrine way. In young vesicular cells the secretory vesicles are released at the cell base and in the inter cellular spaces. Old cells are still filled with vesicles when they are shed in the midgut lumen. These cells have both an endocrine and an exocrine function, the latter apparently by holocrine release.

Damage to the midgut epithelium caused by food in the absence of peritrophic membrane is studied in *Bombyx mori* by Sudha and Muthu (1988). Insects seen to absorb the products of digestion entirely through the cells of the midgut (Treherne, 1962, 1967; Berridge, 1970). Water, inorganic ions and dissolved nutrients pass in mainly through the walls of its anterior region, including the gastric caeca. The uptake of water, concentrates the aminoacids in the lumen and thus creates more pronounced gradients for their diffusion. Similar gradients for monosaccharides arise through their conversion to trehalose immediately after entering the haemocoel. In both these processes an important part is probably played by the well-developed extracellular space that is formed through extensive basal infolding of the midgut cells. In the posterior region of the midgut fluid is secreted into the lumen from the haemolymph, so that a forwardly directed cycle of fluid movement occurs. At the same time food particles are moving posteriorly within the peritrophic membrane, which means that digestion can proceed along the whole midgut with the soluble digestive products being swept forwards to the absorptive sites while the residues accumulate posteriorly.

In *Abedus ovatus* (Goverdhan *et al.*, 1981) the midgut epithelium contain rich quantities of proteins and midgut and hindgut epithelium show abundant

quantities of lipids. In the midgut and hepatic caeca of *Periplanata americana* proteins are detected by Rastogi and Lohiya (1972). Hassemer *et al.* (1968) report the presence of lipids in the epithelial cells of the midgut of *Ostrinia nubilalis*.

In *A. ovatus* (Goverdhan *et al.*, 1981) absorption of the glycogen occurs mainly in the first midgut. Digestion and absorption of proteins and fats are reported to take place in the posterior region of midgut and anterior part of hindgut. Absorption of glucose in *P. americana* occur mainly in the midgut (Rastogi and Lohiya, 1972).

In stingless bees the anterior end of the midgut has no role in nutrient absorption because its lumen is reduced by a thick cuticle that lines the outer epithelium of the cardiac valve (Serrao and Cruz-Landim, 1996b). According to Dobson and Peng (1997) in *Chelostoma florisomne* most of the digestion of lipids and proteins occur in the anterior and median midgut where as digestion of carbohydrates take place more slowly and mainly in the median and posterior midgut. In *Rhodnius prolixus* (Billingsley and Downe, 1984) the luminal apical membrane proliferates during the digestion period to form loosely organised extracellular membrane layers which may function as a peritrophic membrane.

In *Abracris flavolineata* (Marana *et al.*, 1997) the anterior caeca are the main sites of digestive enzyme secretion, digestion and nutrient absorption. Chapman (1988) suggested that posterior caeca have a major role in detoxification. The epithelial pockets present in the posterior caeca may have a role in the removal of phenolics from the gut (Bernays, 1981; Chapman, 1988).

In many insects such as *Galleria* (Young-Tai, 1929), Termites, *Blatella* (Weyer, 1936) and *Tineola* (Lotmar, 1942) the midgut epithelium is destroyed by phagocytosis. According to Henson (1946) the changes in the epithelium at metamorphosis is a continuation of embryonic development. In Orthoptera and Isoptera feeding ceases shortly before the moult and most of the gut contents are

emptied. The midgut epithelium becomes uniformly vacuolated and the entire epithelium is cast off into the lumen. A layer of squamous epithelial cells surrounds the old epithelium. The new epithelium is rapidly formed below the old one. This squamous epithelium and its contents later form an amorphous mass known as the yellow body (Weyer, 1936) as is formed in *Vanessa* (Henson, 1929) and *Popillia* (Ludwig and Abercrombie, 1936). In Lepidoptera (Gray, 1931), in Diptera (Perez, 1910) and in Coleoptera (Mansour, 1927) the larval midgut becomes the yellow body and there is well-formed pupal epithelium also. In the six day old pupa of *Tineola*, Lotmar (1942) observed three types of epithelium; the remains of larval epithelium, the degenerating pupal epithelium and the beginning of adult epithelium. In *Aedes* larvae multiple chromosome complexes develop in the nuclei of the columnar epithelium thereby permitting rapid cell division (Berger, 1938). According to Duspiva (1950) free amino acids are produced during dissolution of the silk. In the silk worm the pupal gut produces a proteinase which causes the dissolution of the cocoon (Honda, 1926). In cockroach the midgut secrete hormones (Nitshutsutsuji and Endo, 1981).

In three species of mosquito larvae *Aedes*, *Anopheles* and *Culex*, the main type of caecal cell seems to be responsible for final degradation, resorption and storage of nutrients and for the secretion of enzymes (Volkman and Peters, 1989). The caecal membrane acts as a permeability barrier. Particulate material and substances which cannot be graded or resorbed accumulate in the caeca and they are involved in osmoregulation. In *Dysdercus intermedius* (Bentz and Kallenborn, 1995) the secretion in the caecal lumen is involved in the transmission of the symbionts from one generation to the next.

The insect midgut is a dynamic organ where transport of ions, water, nutrients and wastes to haemolymph, faeces and intra epithelial storage sites occurs (Seidman *et al.*, 1986). The anterior midgut of *Chironomus thummi* (Seidman *et al.*, 1986) play an important role in the storage of crystalline material

and of lipids and glycogen, where as the posterior midgut is a region of active protein synthesis and of final digestion and cadmium and nutrient absorption. In *Protaetia accuminata* (Cheung and Low, 1975) the posterior midgut is capable of fluid secretion as in mosquito larvae and cicadas (Wigglesworth, 1932; Ramsay, 1950; Cheung and Marshall, 1973) and may play a role in ionic regulation and facilitate the digestive residues to be swept towards the anterior midgut for absorption (Berridge, 1970). In *Bemisia tabaci* and *Trialeurodes abutilonea* (Cicero *et al.*, 1995) the Malpighian tubules are absent and the midgut serve the excretory needs of the flight muscles.

In *Campodea* and *Collembola* (Szklarzewicz and Tylek, 1987) there are no Malpighian tubules and the midgut takes over the excretory function (Nijhout, 1975). Metabolic products, mainly water and urates in crystalline form are accumulated in the cytoplasm of gut cells in the form of urospherites (Krzysztofowicz *et al.*, 1973; Klag *et al.*, 1981). In *Rhodnius prolixus* spherites have been regarded as a holding site for minerals which can be mobilized as required (Billingsley and Downe, 1989a). Lipid storage vesicles are evenly distributed throughout the midgut in larval stages (Bauer, 1981) but are concentrated in the stomach cells of adults (Billingsley and Downe, 1989a). In adults lipids are digested and absorbed in the intestine then transported to the stomach cells for storage (Billingsley, 1988; Billingsley and Downe, 1989a).

The Hindgut

The most obvious function of the hindgut in many insects is the absorption of water from the lumen content. Two main systems are involved in the process of hindgut absorption, the rectal papillae and the cryptonephric system (Ramsay, 1964, 1971; Saini, 1964; Grimstone *et al.*, 1968). In both cases the rectum can conserve water by absorbing it actively from the faeces into the haemolymph or the lumen of the Malpighian tubules (Phillips, 1964a, Stobbart, 1968). The rectal

glands probably play an important part in the absorption of water (Wigglesworth, 1932). Ions of potassium, sodium, and chloride are also absorbed by the hindgut. Highly tracheated structure of rectal glands is concerned with important process of salt and water absorption that occurs in the hindgut and their ultrastructure reflects their functions (Baccetti, 1962; Gupta and Berridge, 1966a; Berridge and Gupta, 1967; Berridge, 1970; Noirot and Noirot-Timothee, 1971; Wall and Oschman, 1973). In *Locusta* a curious distribution of alkaline phosphate around the intercellular tracheae has been observed by Day (1949).

The rectal pads of the desert locust and the rectal papillae of the adult blowfly have been shown to be involved in the uptake of ions and water (Philips, 1961, 1964a, b, c, 1965, 1969). The rectal pads are thought to absorb water from the faecal matter (Wall and Oschman, 1973). Rectal pads of insects play a key role in osmotic and ionic regulation as they selectively reabsorb water, ions and other solutes that are secreted by the Malpighian tubules (Phillips, 1970; Maddrell, 1971; Ramsay, 1971). Absorption is regulated according to the demands placed upon the insect by its environment. The solutes absorbed by the epithelium are used again and again to maintain the local concentration gradients that bring about osmotic water uptake (Wall and Oschman, 1973). In the rectal pads of *Periplanata americana* (Wall and Oschman, 1970; Wall, 1977) water absorption occurs against a high osmotic gradient even in the absence of transportable solutes which are probably recycled within the epithelium. In *Schistocerca* (Phillips, 1964b) the intima of the rectum acts as a sieve restricting the penetration of large molecule. Phillips and Dockrill (1968) postulated that the pores traversing the intima are responsible for permeability. This has been confirmed by Wall and Oschman (1970), Maddrell and Gardiner (1980). In *Stegobium paniceum* (Serjdukova, 1984) the rectal intima serves as a press for the formation of faeces.

In the wood-eating termites and lamellicorn beetles the hindgut is very large and one segment is greatly dilated. This dilated segment is the chief site of

digestion and absorption. In blood-sucking insects such as mosquitoes, *Glossina* and *Cimex* absorption is complete in the midgut and nothing but a little haematin enters the hindgut. In the hindgut of *Lucilia* larvae there is a functional differentiation among the epithelial cells. Some of the cells take up ammonia from the haemolymph and transfer to the hindgut as bicarbonate (Waterhouse, 1952). In *Dytiscus* larvae the rectal ampulla serves to hold large quantities of water which are swallowed at the time of moulting. The contents of this ampulla vary so as to compensate for the varying state of nutrition of the insect (Rungius, 1911).

Some other important functions are also exercised by the hindgut of certain insects. The rectal pouch of many Isoptera contains symbiotic protozoa while in anisopteran nymphs, there are rectal gills. Females of the scolytid beetle *Trypodendron lineatum* produce an attractant pheromone from sensory cells near the junction of ileum and rectum (Schneider and Rudinsky, 1969). In the larvae of the moth *Ostrinia nubilalis* the cells of the ileum secrete a diapause controlling hormone, proctodone (Alexander and Fahrenbach, 1969; Hassemer and Beck, 1969).

In *Aspidomorpha* species (Kumar and Attah, 1977) the pyloric valve serves as an occlusor mechanism as well as an active secretory organ. In Orthoptera (Baccetti, 1960) and Thysanura (Noirot and Noirot-Timothee, 1971) the ileum serves as a water absorbing organ while in *Blatella* (Ballan-Dufrancois, 1972) it is a site of mineral accumulation. In Heteroptera (Goodchild, 1963b) the ileum is concerned with the removal of water from the haemolymph. In *Ephydrella* species (Marshall and Wright, 1974) the smaller cells of the ileum are concerned with ion absorption, while the larger ones with water absorption. In the larva of *Phyllophaga anxia* (Berberet and Helms, 1972) the anterior colon is absorptive in function whereas in *Gromphadorhina portentosa* (Dailey and Graves, 1976) the anterior colon stores waste products. The colon of *Periplaneta americana* (Bignell,

1980) absorbs organic solutes in the gut. In *Leucophaea maderae* (Vitellaro *et al.*, 1985) net water transfer take place in the colon from haemolymph to lumen.

In *S. erythanum* (Dallai *et al.*, 1989) the anterior part of the hindgut has a series of specialized cells which are engaged in active water reabsorption. In *Melipona quadrifasciata* the anterior end of the ileum seems to be less active in reabsorption while the posterior region contains cells which are active in absorption and ion-pump (Cruz-Landim, 1994). The hindgut of most bark beetle species have been shown to be involved in the production or emission of aggregation pheromones, which play an important role in host and mate finding mechanisms in this group of insects (Wood, 1982). Wigglesworth (1931 a,b) has shown that the distal part of the Malpighian tubules is secretory in function while the proximal part is involved in reabsorption. It has been shown that the secretory fluid liberated from the Malpighian tubules is further modified in the rectum.

EXPERIMENTAL STUDIES

ANATOMY AND HISTOLOGY OF ALIMENTARY CANAL OF *IPHITA LIMBATA*

Introduction

Though the anatomy of the alimentary canal in insects has been the subject of several workers (Day and Waterhouse, 1953; Goodchild, 1966; Wigglesworth, 1972) histomorphological details of alimentary canal have been investigated only in a few species of Heteroptera. Earlier studies include the species belonged to the families Pyrrhocoridae (Mayer, 1874; Khanna, 1964; Kurup, 1964; Muraleedharan, 1983), Nepidae (Locy, 1884; Hamilton, 1931; Kurup, 1961a), Cimicidae (Cragg, 1914), Notonectidae (Bogiawlensky, 1925; Kurup, 1962), Coreidae (Breakey, 1936; Woolley, 1949; Akbar, 1958; Singh and Sharma, 1987 a, b,c) Lygaeidae (Hood, 1937; Rastogi, 1960), Pentatomidae (Malouf, 1933; Hamner, 1936; Harris, 1938; Kurup, 1964), Corixidae (Sutton, 1951); Capsidae (Goodchild, 1952) and Tingidae (Livingstone, 1967). Parsons (1959) gives an account of midgut of the aquatic Heteroptera with emphasis on histological aspects and Miyamoto (1961) has examined gross anatomy of the digestive system of most families of Heteroptera. From the work of all these investigators certain generalisations regarding morphology of the gut in Heteroptera can be arrived at, like the elongated midgut and its differentiation into three or four distinct regions, remarkable development of caecal appendages from the ventriculus, the extremely short hindgut etc.

The anatomical and histological features of the various parts of the alimentary canal particularly concerned with digestive and absorptive functions have been described by many workers (Snodgrass, 1935; Day and Waterhouse, 1953; Goodchild, 1952, 1966; Kurup, 1961, 1962, 1964, 1966; Judy and Gilbert, 1969, 1970; Muraleedharan, 1983; Pakrutty and Mohamed, 1989 a,b). Although there exists some fundamental similarities in the histomorphological pattern of the alimentary canal of hemipteran insects, remarkable variations can be observed in different species in the anatomy and histology of the alimentary canal related to

their particular feeding habits and taxonomic position. Therefore, a detailed study on the anatomy and histomorphology of the alimentary canal of adult *Iphita limbata* has been carried out in the present study.

Materials and Methods

Adult *Iphita limbata* of both sexes are collected from field. In the laboratory they are kept in cages and are fed with banana. Adults are removed from the stock culture kept in separate containers and are fed with banana for 20-30 minutes when they attain well-fed condition. These well-fed insects are starved for 3 days. These insects are considered as 'normal' insects. The normal insects are used for the histomorphological investigation in the present work.

Insects are etherised and dissected in Insect Ringer solution under a binocular dissection microscope. The alimentary canal is dissected out and fixed in alcoholic Bouin's fluid for about 24 hours. For the preparation of whole mounts staining was done with borax carmine. For serial sections, the alimentary canal is cut into different gut regions before they are fixed. After 24 hours of fixation the tissues are washed with 70% alcohol to remove the fixative and dehydrated through the usual grades of alcohol, cleared in methyl benzoate with celloidin for 10 minutes and then treated with benzene for 5 minutes. The tissues are infiltered with paraffin for about 30 minutes and finally embedded in pure paraffin. 5-7μ thick sections are cut by a rotary microtome. Sections are stained with Delafield's Haematoxylin and counter stained with eosin. A research microscope was used for observation and for microphotography.

Results

a) Anatomy of the Alimentary Canal

The alimentary canal of *Iphita limbata* (Fig.1) is very long and highly convoluted and extends from head to last abdominal segment to open to outside by anus. In well-fed insects it is partially covered by fat body. In starved ones the fat body is comparatively lesser. The alimentary canal is slightly longer in females than in males. It measures about 5-5.5 cm in length in adult male and about 6-6.5 cm long in adult female. It is composed of three regions namely the foregut (Fg), the midgut (Mg) and the hindgut (Hg). No marked difference was noticed in the alimentary canal of two sexes.

The Foregut

The foregut (Fig. 1. Fg.) of *I. limbata* is very simple and it extends from cibarium to the posterior end of oesophageal valve. The foregut is comprised of three regions namely cibarium, pharynx and oesophagus. The cibarium and pharynx form the sucking pump. The oesophagus (Fig. 1. Oe) is a short tubular structure about 3 mm long and 0.5 mm broad. It starts from the region very near to the middle of brain and extends upto the posterior end of the prothorax. It is transparent and resembles the tracheal tube in appearance. In starved insects, the foregut appears to be transparent and lies in a collapsed state, but in fed insects the foregut is milky in appearance. The anterior portion of the oesophagus is slightly narrower than the posterior portion. The diameter of the former measures about 0.5 mm while that of the latter is about 0.6 mm. The posterior extremity of the oesophagus is telescoped into .the anterior part of the first midgut region. Transverse sections of the first midgut contain enclosed portions of the oesophagus in the centre. This is the region of the cardiac or oesophageal valve. Oesophagus

lies above the thoracic ganglionic mass. Posteriorly its lumen opens into the midgut through a distinct oesophageal valve, without external demarcation.

The Midgut (Ventriculus)

The midgut (Fig. 1. Mg) forms the longest part of the alimentary canal. It measures about 4.5 to 5 cm and about 5-6 cm in length in male and female respectively. Anteriorly the oesophageal valve demarcates it from the foregut and at the posterior end the pylorus separates it from the hindgut. Commencing at the oesophageal valve it extends back from the mesothorax upto the 6th abdominal segment to open into the hindgut. Based on the morphological differences observed in the entire length of midgut of *I. limbata*, it is divided into five distinct regions (Fig. 1). These five regions are referred to as first (V_1), second (V_2), third (V_3), fourth (V_4) and fifth ventriculi (V_5). The junction between adjacent regions are marked by constrictions. Neither male nor female possesses gastric caeca.

First Ventriculus: The first ventriculus (Fig. 1. V_1) is the widest part of the gut having a length of about 1.2 cm and forms the anterior 1/4 portion of the gut. Shape depends upon the food present inside. It commences at the oesophageal valve and is a spacious sac. Its anterior part forms a bulbous structure called cardia (Cd) in which oesophageal valve hangs. Posterior to cardia the wall of first ventriculus is convoluted due to many transverse folds while posteriorly it gradually widens to form a pear shaped sac having smooth external surface. The wall of the first ventriculus is thin and transparent. The anterior part measures about 2 mm in diameter. The middle part is the widest portion and measures about 3-3.5 mm in diameter. The size of the posterior part is more or less the same as that of the anterior part. The anterior and posterior parts measure about 0.3 mm and 0.4 mm respectively in length whereas the middle part measures about 0.5 mm in length. The first ventriculus extends upto the fifth abdominal segment to open into the second ventriculus and the posterior limit is marked by a

constriction. Air bubbles are invariably present in the lumen of this region. In starved individuals this part of the ventriculus becomes greatly distended due to the presence of large number of air bubbles.

Second Ventriculus: Second ventriculus (Fig. 1. V_2) is the longest tubular division of the midgut, measuring about 2-2.5 cm in males and 2.8-3 cm in females. It has a diameter of about 1-2 mm. The junction of the second ventriculus with the first is marked by a constriction which acts as a valve (Fig. 1. Jn. 1). After its origin it runs forward along the ventro-lateral margin of the first ventriculus till it reaches the second abdominal segment. It then crosses to the right and passes beneath the first ventriculus and runs backward reaching upto fourth abdominal segment. The posterior end of the second ventriculus is constricted where it joins the third ventriculus (Fig. 1. Jn.2).

Third Ventriculus: Third ventriculus (Fig. 1. V_3) is a short, dilated oval sac located between the 5th and 6th abdominal segment. It measures about 0.5-0.7 cm in length and about 3 mm in diameter. It is a thin walled "retention chamber" lying ventral to the first ventriculus and encircled by the coiled second ventriculus. The lumen of third ventriculus is always filled with reddish brown or black viscous substance irrespective of whether the insect is well-fed or starved. It is constricted posteriorly and joins the fourth ventriculus (Fig. 1. Jn. 3).

Fourth Ventriculus: Fourth ventriculus (Fig. 1. V_4) is a short narrow tubular region, much narrower than the second ventriculus. It measures about 0.5 cm in length and lies in the sixth abdominal segment. It joins posteriorly to the fifth ventriculus.

Fifth Ventriculus: Fifth ventriculus (Fig. 1. V_5) is a small part of the alimentary canal. It measures about 0.5 mm in length and present in between the fourth ventriculus and hindgut. It forms a bulbous portion on either side where from a pair of Malpighian tubules (Mal) comes out. In this bulbous portion there is

a pair of slightly swollen dorso-lateral outgrowths, the ampulla (Am) each one of which receives each pair of Malpighian tubules. Each pair empties into ampulla independently. Tubules are cream white in colour. Each tubule lies freely in the body cavity. They are comparatively short and slightly coiled. They are attached to the alimentary canal and fat body by tracheal branches.

The Hindgut

The hindgut (Fig. 1. Hg) is marked by the bases of the fifth ventriculus. It is short and measures about 0.5 cm - 0.7 cm in length. The width of the hindgut varies at different regions. It is narrower at both ends. The anterior end and the posterior end measure in width about 1.5 mm and about 0.5 mm respectively, while the middle region is enlarged into a sac-like structure and has a diameter of about 2 mm. The hindgut is divisible into two regions, the anterior pylorus (Py) and a large posterior rectum (Rec).

Pylorus: Pylorus (Fig. 1. Py) is a narrow region about 0.2 mm diameter and forms the junction between the midgut and the rectum. It is characterised by the presence of pyloric valve.

Rectum: Rectum (Fig. 1. Rec) is about 5-6 mm long. Pyloric valve forms the anterior extremity of the rectum and controls the flow of contents in the lumen from the midgut to rectum. It is a thin sac and tapers posteriorly to open out through the anus (An). In fed insects, it is an enlarged sac and contains a fluid material. Anteriorly and posteriorly it is narrower than the middle region. It measures about 1 mm in width and about 1.0 mm in length at the anterior region and is about 2 mm in width and about 3.5 mm in length at the middle and is about 0.5 mm in width and is about 1.5 mm in length at the posterior region.

b) Histology of the Alimentary Canal

The Foregut

Oesophagus (Fig. 1. Oe) forms the main part of foregut in *I. limbata*. It is a thin walled tube. . The wall of this region is composed of thick musculature consisting of longitudinal muscles (Figs. 2 & 3. Lm) and circular muscles (Cm), basement membrane (Bmb), epithelium (Epth) and intima (Int). The musculature of the foregut is well developed. It is composed of an outer layer of longitudinal muscles (Lm) and an inner layer of circular muscles (Cm). The longitudinal muscle consists of large number of closely arranged parallel fibres. Each muscle strand is composed of a single fibre. This fibre has a diameter of about 18 μ. The circular muscle consists of two or three layers. It is about 20 μ thick in the anterior region and about 32 μ thick in the posterior region. The epithelial layer rests upon a basement membrane. The cell limits are indistinct and so the epithelial layer gives an appearance of a syncytium. A large number of nuclei are surrounded by a thin layer of cytoplasm. The epithelium is produced into folds. In the anterior part of the oesophagus, the outlines of the cells of the epithelium are not distinct. But the nuclei (N) can be clearly observed. Towards the posterior part, the epithelium thickens. The cells and their nuclei become more prominent. The cells are small and cuboidal measuring about 15 to 20 μ in size. In the posterior part, the cells become spindle shaped with many nuclei and project into the lumen (Lu). The nuclei are spherical and have a diameter of about 4 to 4.5μ. The cytoplasm of the cells is slightly granular. The diameter of the oesophageal lumen is about 232 μ. The chitinous intima (Int) secreted by the epithelial cells is thicker and is thrown into the lumen as freely hanging longitudinal plates. These plates remain folded in a complicated manner and appears to fill almost the entire lumen of the oesophagus and extend upto the first ventriculus. The length of the intima at each fold is about 45 μ. At the junction of foregut and midgut the posterior end of

oesophagus hangs down freely into the lumen of the first ventriculus forming an oesophageal valve or cardiac valve (Fig. 4. Ov).

The Oesophageal Valve: The part of the oesophagus which hangs into the lumen of the first ventriculus (Fig.4 V_1l) measures about 0.44 mm to 0.66 mm in length. It consists of two layers of oesophageal epithelium which are closely apposed to each other, an outer layer (Figs. 5 & 6. Ol) facing the first ventriculus and an inner layer (Il) facing the lumen of the valve. These two layers are continuous and have a small intravalvular space (IVS) in between the two. The epithelium of the valve consists of small columnar cells (Cc). The cells of the outer layer are larger than those of the inner layer. The cells of the outer and inner layers measure about 73.5μ and 46 μ respectively in length and their cell boundaries are not distinct. The nuclei are small and spherical and situated centrally. The diameter of the nucleus is about 2.5 μ. The nucleus has about 6 to 8 deeply staining chromatin granules. The cytoplasm of the cells is clear and devoid of any granules. The lumen of the valve region has a diameter of 0.12 mm. The muscle layer is also well developed and consists of circular muscle layer of 7.5 μ thick and longitudinal muscle layer of 5.5 μ thick. The cuticular intima lines the oesophageal valve on its inner surface and this highly folded intima hangs well behind the posterior limit of the oesophageal valve to about 22 μ in length. This has been termed "entonnoir" (Ent). A perivalvular space (Pvs) is formed in the first ventriculus as the intimal lining hangs freely. This space is much narrowed around the invagination of the oesophageal epithelium. The entonnoir of both sides appose each other closely and internally the entonnoir shows longitudinal folds.

The Midgut

The wall of the midgut (Figs. 7-37) is composed of longitudinal muscles (Lm), circular muscles (Cm), basement membrane (Bmb) and epithelium (Epth). The longitudinal muscles form the outer layer and are in the form of longitudinal

fibres arranged in groups. The number of fibres in a group varies in different regions of the midgut. In the anterior region (Figs. 7-25) longitudinal muscles are poorly developed and in the posterior region (Figs. 28-36) they are well developed. The circular muscle layer is found below the longitudinal muscle layer. The epithelium consists of single layer of cells resting on a basement membrane which is well developed. Chitinous intima or peritrophic membrane is not observed on the inner surface of the epithelium. The epithelial cells are generally columnar (Cc) with moderately large, round, spherical or oval nuclei. Uninucleate, binucleate and multi-nucleate cells are found. Cuboidal cells (Cbc) are also found among columnar cells at certain regions. Nidi of reserve cells (Rgc) which are regenerative in function are present. The nidi usually contain one or two cells.

The midgut shows differences in histological structure at various regions of it. Based on the histological details exhibited by different regions of the midgut it can be divided into five regions namely first ventriculus (V_1), second ventriculus (V_2), third ventriculus (V_3), fourth ventriculus (V_4) and fifth ventriculus (V_5).

First Ventriculus: The epithelium of first ventriculus (Figs. 7 & 8. Epth) is produced into circular internal folds or crypts which extend into the lumen. The number of folds varies from 20-25. In the anterior part, the epithelium is produced into many large folds (Fig. 8. f). These folds decrease in size and number in posterior region (Fig. 12). At the oesophageal valve region, the oesophageal cells forming the valve are compactly arranged with no distinct cell boundaries (Fig. 6a. Oc). The ventricular cells (Vc) are columnar, formed into folds, club shaped with bulbous ends. They are of two types - short columnar cells (Scc) and tall columnar cells (Tcc). The cells in the centre of the crypts are taller whereas the cells seen towards the margin are shorter in size. The cells are provided with more than one nucleus. The cells vary in size. The height of the fold is about 126μ and the diameter of the fold varies from 43-54μ. The short columnar cells are seen mainly towards the inner sides of the valve and the tall columnar cells are seen towards

the outerside. The cells are with uniformly distributed granular cytoplasm. The cells are usually uninucleated. Both bi and multinucleated cells are also observed in this region. There are dilator muscle layer (Fig. 6a. Dm) of about 18μ thick in between the epithelial layer. Circular and longitudinal muscles are also well developed. The circular muscle layer and longitudinal muscle layer measure about 7.5 μ and about 13 μ in diameter respectively. The nuclei are seen more towards the cell tip or towards the lumen side. Immediately after the valve region, the height as well as the width of the folds decrease. It measures about 105 μ in height and about 39 μ in width. The nucleus (N) of this region is about 7.5 μ in diameter. The lumen of the first ventriculus is oval in appearance and its diameter is about 0.58 mm x 0.62 mm. The diameter of the lumen increases steadily and in the middle region it is about 2.95 mm x 1.8 mm and towards posterior region the diameter of the lumen decreases to about 87 μ x 36 μ.

In the middle region of the first ventriculus, the cells of one side is broader with tall columnar cells (Figs. 9, 10 & 11. Tcc) and of the other side it is narrower with short columnar (Fig. 12, Scc) and cuboidal cells (Figs. 13 & 14, Cbc). The tall columnar cells measure about 73.5 μ in height and about 12.5 μ in width. The cell tips of these cells are bulbous and vacuolated. The short columnar cells measure about 49.5 μ in height and is about 10 μ in width. Cuboidal cells have a height of about 23.5 μ and width about 21 μ. The tips of these cells are flat and granular cytoplasm accumulates towards the tip. These cells are uni or binucleated. All the three types of cells consist of spherical nuclei of same size and each nucleus measures about 7.5 μ in diameter. The regenerative cells (Rgc) are present singly at the base of the columnar cells. During their elaboration or differentiation, regenerative cells are gradually enlarged to become large columnar vacuolated secretory cells. The diameter of circular muscle (Cm) of middle region of the first ventriculus is about 10 μ and of longitudinal muscle (Lm) is about 7.5 μ. The

basement membrane (Bmb) is seen to be penetrated into cell layer in the form of a short finger shaped process (Figs. 9-14. fp).

Towards the posterior region (Figs. 15 & 16) the cells become much shorter and the epithelial height decreases. In the broader region the cells are short columnar (Scc) type and have a height of about 40 μ and width of about 21 μ and narrow region consists mainly of cuboidal cells (Cbc) of height about 18.5 μ and width of about 20 μ. The nuclei (N) are either round or oval measuring about 7.5 μ and 10 x 12 μ respectively. The muscle layers are weaker. The circular muscle (Cm) layer is about 5 μ thick and longitudinal muscle (Lm) layer is about 8 μ thick. Some of the cells have become vacuolated (V) and each cell is provided with large single nucleus (LN) measuring about 14.5 μ diameter. The vacuolated cells break at the tip and the large nuclei are liberated into the lumen (Fig. 16). In the posterior most region the lumen size decreases considerably and the cells become folded (Fig. 17).

The junction between the first and second ventriculus is very narrow and it forms a sphincter or valve (Fig. 18). The size of the lumen of this region is about 181 μ x 16.5 μ. The height of the epithelial fold is about 58 μ and its width is about 52 μ. The cells measure about 42.6 μ in height and is about 8 μ in width. The small nucleus is about 7.5 μ in diameter and the large oval shaped nucleus measures about 10x12 μ in size. The circular muscle layer has a diameter of about 9.5 μ and longitudinal muscle layer has a diameter of about 10.5 μ. Vacuolated cells with large nucleus also is present in this region, but are fewer in number. Basement membrane appears to penetrate into the cell layer.

Second Ventriculus: This is the longest part of the midgut. The epithelium of the second ventriculus (Fig. 19) is also thrown into a few long (LF) and short folds (SF). In the anterior region of the second ventriculus, long folds measure about 89 μ in height and about 95 μ in width and short folds measure

about 56 μ in height and about 69.5 μ in width. The epithelium consists of tall columnar cells and short columnar cells. The size of the lumen is about 102.5 μ x 32.19 μ in size. The tall columnar cells measure about 66.5 μ in height and 10 μ in width and the short columnar cells measure about 40 μ in height and 9.5 μ in width. The nuclei are of two types. Some of them are small (N) and round. Each nucleus of this type measures about 7.5 μ in diameter and others are large (LN) in size. Each nucleus of this type measures about 15-16.5 μ in diameter. Each nucleus contains about 20-25 chromatin granules. The regenerative cells are found at the base of columnar cells. The muscle layer is moderately developed and consists of inner circular muscles of about 7.5 μ diameter and outer longitudinal muscles of 16.5 μ thickness. The cell tip is bulbous and cytoplasm contains granules (Gr). These granules are seen more towards the cell tip (Figs. 20 & 21, Gr). Some cells contain large darkly stained nucleus (LN) and vacuoles (V) are seen around such nucleus. These nuclei appear to move towards cell tip and cell tips break off liberating the cell contents into the lumen. The basement membrane is distinct and penetrates into cell layer. The lumen contains full of material consisting of cell fragments as well as food.

The epithelium of the middle part of the second ventriculus (Fig. 22) is produced into occasional infolding while the rest of the surface is produced into many bulging groups of secretory cells. Both holocrine and merocrine mode of secretions are seen in this region (Figs. 23 & 24). The holocrine secretory cells (HC) filled with secretory material detach out their distal secretory part enmass into the lumen. The basal regenerative cells (Rgc) further emerge out in the process of elaboration. The merocrine cells (MC) have apices filled with vacuoles and granular secretory materials are regularly pinched out into the lumen in the form of vacuoles. The lumen of the second ventriculus is slightly oval in shape and measures about 190.72 μ x 250.86 μ in size. The cells are arranged to form a few folds. Large nuclei are seen in this region and are more in number than in the

anterior region of the second ventriculus. The tall columnar cells (Tcc) have a height of about 79.5 μ and the width is about 16 μ. Some of the cells are with small round nuclei whereas large oval nuclei (LN) are also observed in many cells. Each round nucleus measures about 7.5 μ in diameter and each large nucleus measures about 22.5 x 12.5 μ. Short columnar cells (Scc) have a height of about 45 μ and width of about 13.5 μ. Small nuclei and large nuclei which are comparable in size to those found in tall columnar cells are also seen in this region. Regenerative cells (Rgc) are present more in number than in the anterior region and placed in groups of 2-3 cells with small nuclei. Each nucleus is filled with 13-20 chromatin granules. The muscle layer thickness does not vary from that of anterior region. Lumen is full of contents (Figs. 22 & 23) similar to secretory material.

The posterior part of the second ventriculus (Figs. 25 & 26) contains tall columnar cells. Each cell is filled with small round nucleus which is located at the centre of the cell. Cells are not arranged into folds. All the cells are of the same size and is about 66 μ x 13.5 μ. The size of the nucleus is 7.5 μ in diameter. Large nucleus observed in the anterior region is not detectable in the posterior region. Lumen has a length of about 264.18 μ and a width of about 175.38 μ. The circular muscle layer has a diameter of about 10 μ and longitudinal muscle layer is about 19 μ thick. The cell tip forms a uniform darkly stained layer. The cytoplasm at this region is filled with dark granules and cells contain small vacuoles (V). The basement membrane penetrates into the cell layer. Regenerative cells are present but fewer in number than in the middle part of the second ventriculus. The lumen does not contain any material. The distal end of the cells is provided with granular material.

The junction between the second and third ventriculus is a narrow region (Fig. 27) which forms a sort of sphincter or valve. The lumen of this region has a length of about 54 μ and width of about 10.5 μ. The epithelial cells are tall

columnar and are arranged compactly. The cell boundary is not very distinct. These cells measure about 68 μ in height and about 7.5 μ in width. The nuclei are large and round and are compactly arranged at the centre of the cell. Each nucleus has a diameter of about 10 μ. Regenerative cells (Rgc) are seen, but fewer in number. The muscle layer does not vary much from the previous region. The circular muscle layer (Cm) has a diameter of about 10 μ and longitudinal muscle layer (Lm) has a diameter of about 12.5 μ.

Third Ventriculus: The epithelium of third ventriculus (Figs. 28-36. Epth) consists of tall columnar (Tcc) and short columnar (Scc) cells. The epithelium is folded at certain regions. Very few cuboidal cells (Cbc) are also seen in between the columnar cells. At the anterior region (Figs. 28, 29 & 30) the lumen is oval in shape and measures about 228.6 x 350.76 μ in size. The tall columnar cells (Tcc) have a height of about 122.5 μ and width of about 12.5 μ. Short columnar cells (Scc) measure about 46.5 μ in height and about 12.5 μ in width. Two types of nuclei are observed in this region. Some of them are small and round and measure about 7.5 μ in diameter. The second type of nuclei are large (LN) giving the appearance of binucleated condition and measure about 10 μ in diameter. Nuclei are present either at central or basal part of the cell. Only a few nuclei are seen near the tip of the cell. Regenerative cells (Rgc) are present at the base of columnar cells and they are more frequently observed. Some cells are vacuolated. Others contain uniformly distributed cytoplasm. The cytoplasm is seen more towards cell tip in some cells and the tip forms a bulbous structure. The muscle layer consists of inner circular muscle (Cm) of about 10 μ diameter and outer longitudinal muscle (Lm) of about 12.5 μ thick. At certain regions the basement membrane (Bmb) penetrates into the cell layer. The lumen contains full of food materials and secretory materials.

Towards the middle region of the third ventriculus (Figs. 31, 32 & 33) the lumen further widens and measures about 745 x 874.68 μ in diameter. Tall

columnar cells have a height of about 64.5 μ and width of about 16 μ. The spherical nucleus measures about 7.5 μ in diameter. The muscle layer of this region consists of circular muscles of about 12 μ thickness and longitudinal muscles of about 8.5 μ thickness. The lumen contains food material but less than that found in the anterior region. The regenerative cells are also present. The columnar cells exhibit bulbous tips filled with cytoplasm and at certain regions, these tips break off into the lumen. The cell tips at certain regions are darkly stained similar to the contents in the lumen. Most of lthe cells are mononucleate but some cells show the presence of two nuclei. These cells are secretory in nature. Small vesicles or blisters (Bl) are present on the cell tip which are found detached from the cells at certain regions. Regenerative cells are present at the base of columnar cells.

In the posterior region (Figs. 34, 35 & 36) the lumen measures about 996.78 μ x 739.26 μ in diameter. The size of the muscle layer is same as that of the middle region. Tall columnar cells have a height of about 101 μ and width of about 12.5 μ whereas the short columnar cells are about 58 μ in height and about 11.5 μ in width. The round nuclei measure about 7.5-8.5 μ. The secretory activity shown by the columnar cells is similar to that in the middle region. Towards the posterior most region the size of the third ventriculus decreases. The lumen measures about 526.14 x 257.52 μ in size. The height of the tall columnar cells of this region decreases from 101 μ in the posterior region of the third ventriculus to 65 μ. But their width is more or less similar. Short columnar cells have a height of about 35 μ and width of abut 12.5 μ. The nuclei have a diameter of about 7.5 μ. The lumen contains fewer contents than in previous regions. The secretory activity is also less in this region.

The junction between third and fourth ventriculus is narrow and is histologically similar to that between second and third ventriculus.

Fourth Ventriculus: The epithelium of the fourth ventriculus (Fig. 37) consists of narrow tall columnar cells (Tcc). They are club shaped with long lobe-like tip projecting into the lumen. The lumen is very narrow and measures about 158 x 48 μ in size. The height of the cells are about 80 μ and their width is about 8.5 μ. The nuclei have a diameter of about 7.5 μ and they are seen in a row at the centre of the cell. Cytoplasm is uniformly distributed without granules and in some cells smaller vacuoles are seen at the cell tip. The nucleus contains chromatin granules, about 15-20 granules per nucleus. In some cells, the vacuolated cell tip with secretory material is pinched off from the free border of the cells into the lumen. The muscle layer consists of circular muscle (Cm) and longitudinal muscle (Lm). The circular and longitudinal muscles measures about 7.5 μ and about 14.5 μ in diameter respectively. Basement membrane (Bmb) is seen to penetrate into the cell layer.

Fifth Ventriculus: There is no separate junction between the fourth ventriculus and the fifth ventriculus as seen in between the other ventriculi. Fifth ventriculus (Fig. 38) is the region of the midgut where opens the ampulla of the Malpighian tubules. The muscle layer is moderately developed and consists of circular muscle fibres (Fig. 38. Cm) and longitudinal muscle (Lm) fibres. The circular muscle layer is about 5 μ thick and longitudinal muscle fibre is about 11.5μ thick. A well developed basement membrane (Bmb) supports the epithelium which is folded. These folds are tall at some part of the fifth ventriculus. It consists of tall columnar cells (Tcc) and small cuboidal cells (Cbc). These cuboidal cells are present in between the folds. Cells have uniform cytoplasm. The cells are uni-nucleate or bi nucleate. Height of the fold is about 76 μ and its width is about 39 μ. The cells have a height of about 26 μ and the width is about 14 μ. Nuclei (N) measure about 12.5 μ in diameter. Nucleus is located towards the tip of the folds. The lumen measures about 51.5 μ x 18.5 μ in diameter. Regenerative cells (Rgc) are present. They are very small and few in number. On either side of

this region opens the ampulla (Fig. 39. Am) of the Malpighian tubules (Fig. 40. Mal). There are dilator muscle (Fig. 39. Dm) in between the ampulla and fifth ventriculus. Cells of the ampulla are similar to cells of the fifth ventriculus. The lumen of ampulla measures about 78.5 μ x 14 μ in size. The height of the cells of ampulla is about 46 μ and their width is about 13.5 μ. The nucleus has a diameter of about 12.5 μ. The nucleus shows darkly stained chromatin granules. Each nucleus contains about 20-25 granules. The opening of the ampulla to the fifth ventriculus is regulated by tall folds in the ventricular epithelium which controls the flow of urine into the lumen of fifth ventriculus.

The Hindgut

Histologically, the hind gut is differentiated into anterior pylorus (Py) and posterior rectum (Rec). The pylorus is characterised by the pyloric valve. The rectum is characterised by regional differentiation of the epithelial cells of the dorsal wall and of ventral wall.

***Pylorus*:** The epithelium of the pyloric region is thrown into a series of opposing lobes by the folds of the pyloric valve (Fig. 41. Pv). This valve controls the flow of undigested food and urine from the fifth ventriculus to the rectum. The epithelium is modified into 6-7 valvular folds (vf) which project into the lumen (Lu). These folds consist of closely packed elongated epithelial cells with indistinct cell boundaries, small round nucleus (N) and clear cytoplasm. The height of each fold is about 57 μ and its width is about 37.5 μ. Round nucleus measures about 5 μ in diameter. The lumen in this region measures about 184 μ x 102.5 μ in size. The muscle layer consists of longitudinal muscle (Lm) of about 13.5 μ thickness and circular muscle (Cm) of about 10.5 μ thickness. A thin layer of chitinous intima (Int) is present on the inner surface of the folds.

***Rectum*:** The anterior region of the rectum (Fig. 42) consists of narrow cells. Most of the anterior part of the rectum is tube-like and cells do not have distinct cell boundaries. At some region long folds of rectal gland cells (RglC) project into lumen. Intima (Int) and spines (Sp) are present on the inner surface of the rectal gland cells. The lumen measures about 293.04 μ x 20 μ in size. The height of the fold is about 80.5 μ and width is about 27 μ. Nuclei are of various shapes and sizes and the size ranges from 7.5 μ x 12.5 μ to 9 μ x 12.5 μ. The nuclei contain fewer chromatin granules. There are about 15-20 granules per nucleus. The muscle layer consists of outer longitudinal muscle of 5 μ thickness and inner circular muscle of about 7.5 μ thickness.

The middle region of the rectum (Figs. 43, 44 & 45) shows regional differentiation of epithelial cells. The length of the dorsal wall is about 1.96 mm. The cells in the dorsal wall (Fig. 44. DW) is modified into rectal glands (RglC). These cells are larger. Some of these cells are dome shaped and others are irregularly shaped cells. The cytoplasm is finely granular and vacuolated (V) with large coarsely granular nucleus (N). The nuclei vary in shape. They are oval, spherical or bilobed. The border of the rectal gland cells are lined with small foldings of intima (Int) and provided with spiny (Sp) projections. Trachea (Tr) and fine tracheal branches are observed in this region. Fine tracheal branches diffuse into the cytoplasm of rectal gland. The lumen (Lu) is very large measuring about 1.003 mm x 0.67 mm in size. The muscle layer of dorsal wall consists of circular muscle of about 10 μ thickness and longitudinal muscle of about 15 μ thickness. Rectal gland cells have a height of about 79 μ and width of about 33 μ. The size of the nuclei of rectal gland cells is about 9 x 15 μ. The length of the ventral wall is about 0.67 mm. The epithelium of the ventral wall is (Fig. 45. VW) formed of irregularly shaped small cells. The boundaries of these cells are indistinct. So the nuclei are scattered in the form of a syncytium (Syn). The thickness of epithelium of ventral wall is about 51.5 μ and nuclei are small and

measure about 5 μ in diameter. The inner surface is coated with chitinous intima (Int).

The posterior region of the rectum (Figs. 46 & 47) consists of three types of cells namely the rectal gland cells (RglC), syncytial cells (Syn) and very narrow epithelial cells. The regional differentiation into dorsal and ventral wall is indistinct. The rectal gland cells and syncytial cells are very few in number. The height of the cells of rectal gland in this region is about 41.5 μ and its width is about 16.5 μ. The nuclei measure about 10 μ in diameter. The cytoplasm is granular and slightly vacuolated. The size of the lumen measures about 0.95 mm x 0.52 mm in size. The thickness of the epithelium formed of syncytial cells is about 12 μ. The nuclei are small and measure about 5 μ in diameter. The cell boundaries of narrow epithelial cells are indistinct. The inner surface of the epithelial layer is coated with chitinous intima. The muscle layer of dorsal wall consists of circular muscle of about 7 μ thickness and longitudinal muscle of about 12 μ thickness. The muscle layer of ventral wall consists of circular muscle of about 8 μ thickness and longitudinal muscle of about 5 μ thickness.

The terminal part of the posterior region of the rectum is tubular in nature. It is provided with uniform syncytial epithelium. The cells are similar to those of the ventral wall of the rectum.

Fig. 1. The diagrammatic representation of the external anatomy of the alimentary canal of *Iphita limbata.*

Am - Ampulla of the Malpighian tubules; An - Anus; Cd - Cardia;
Fg - Foregut; Hg - Hindgut; Jn.1 - Junction 1 between the first and second ventriculi; Jn.2 - Junction 2 between the second and third ventriculi;
Jn. 3 - Junction 3 between the third and fourth ventriculi; Mal - Malpighian tubules; Mg - Midgut; Oe - Oesophagus; Py - Pylorus; Rec - Rectum;
V_1 - First Ventriculus; V_2 - Second Ventriculus; V_3 - Third Ventriculus;
V_4 - Fourth Ventriculus; V_5 - Fifth Ventriculus.

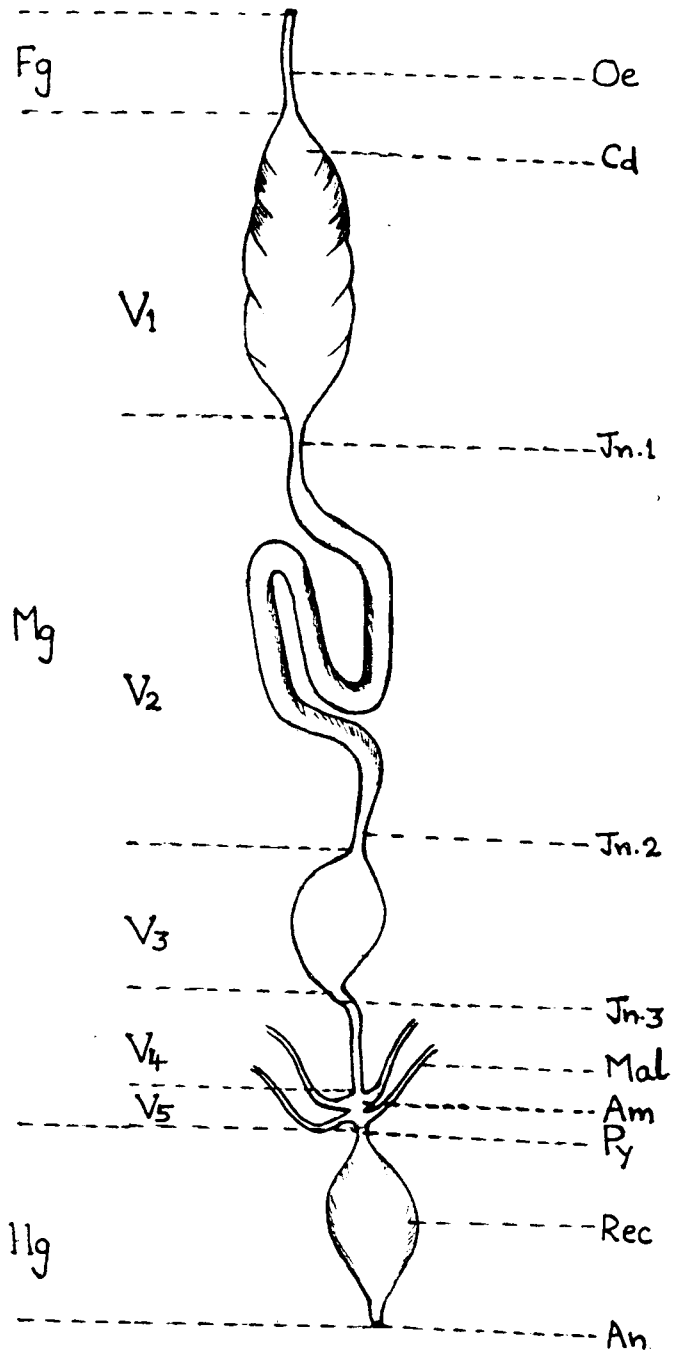

Fig. 1.

PLATE - I

Fig. 2. T.S. of oesophagus of *Iphita limbata* (x 250).

Fig. 3. T.S. of oesophagus, a portion enlarged (x 750).

Fig. 4. L.S. of foregut-midgut junction showing oesophageal valve (x 250).

Fig. 5. L.S. of foregut-midgut junction - a portion enlarged (x 400).

Fig. 6. T.S. of oesophageal valve region (x 200).

Fig. 6a. A portion of the oesophageal valve region enlarged to show the dilator muscle between cell layers (x 800).

Fig. 7. T.S. of anterior region of the first ventriculus (x 100).

Fig. 8. T.S. of anterior region of the first ventriculus, a portion enlarged (x 250).

Fig. 9. A portion of the T.S. of the middle region of first ventriculus showing tall columnar cells (x 250).

Fig. 10. An enlarged portion of the middle region of the first ventriculus showing tall columnar cells (x 750).

Bmb - Basement membrane; Cc - Columnar cells; Cm - Circular muscles; Dm - Dilator muscles; Ent - Entonnoir; Epth - Epithelium; f - folds; fp - finger-like processes of the basement membrane; Il - Inner layer, Int - Intima; IVS - Intravalvular space; Lm - Longitudinal muscles; Lu - Lumen; N - Nucleus; Oc - Oesophageal cells; Oe - Oesophagus; Ol - Outer layer; Ov - Oesophageal valve; PVS - Perivalvular space; Rgc - Regenerative Cells; Tcc - Tall Columnar Cells; V_1C - First ventricular Cells; V_1l - Lumen of the first ventriculus

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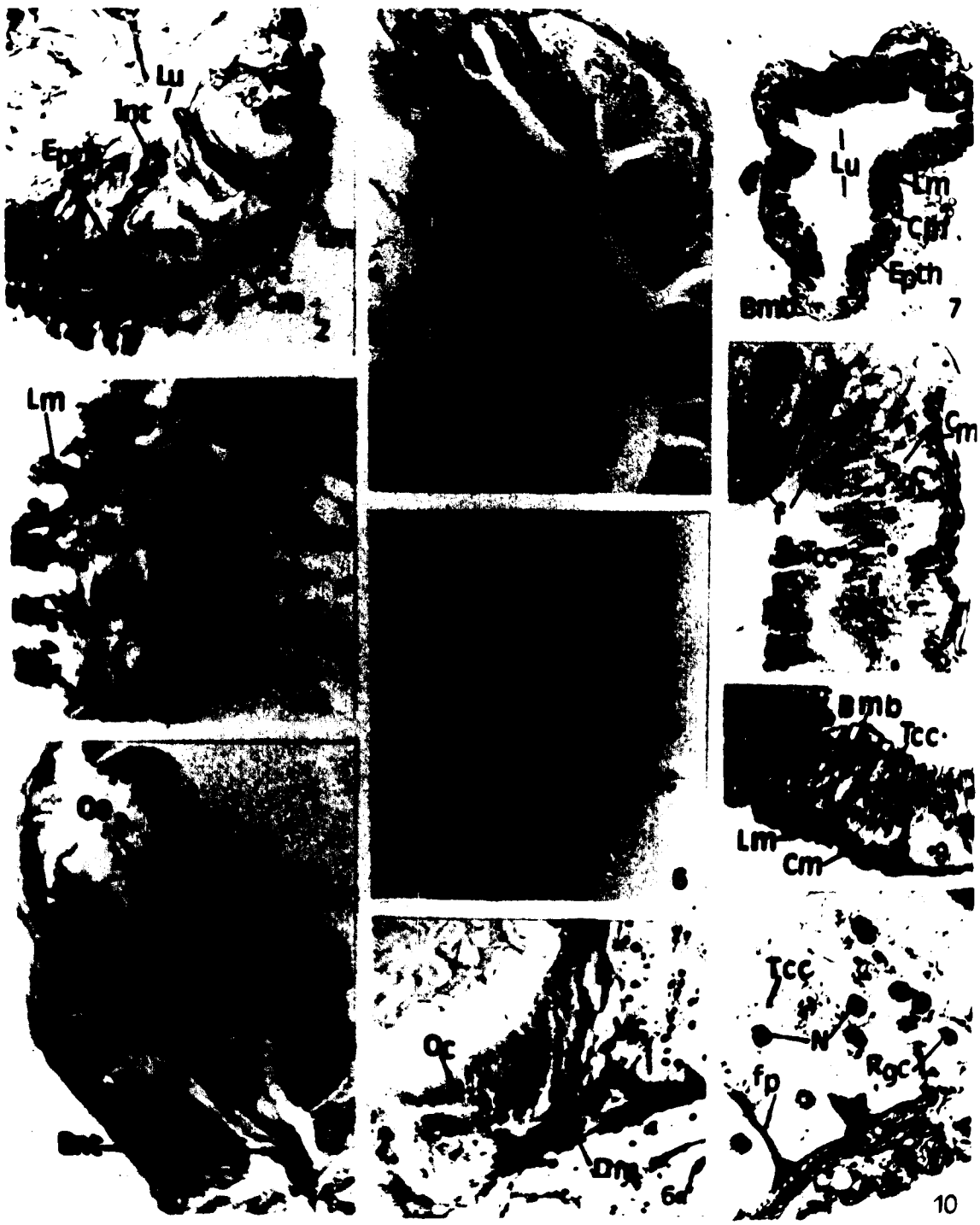
Lu
Int
Epth
2
Lm
Oc
Bmb
Lu
Lm
Cm
Epth
7
Cm
Oc
Bmb
Tcc
Lm
Cm
8
Oc
Dm
6
Tcc
N
Rgc
fp
10

PLATE - 2

Fig. 11. An enlarged portion of the T.S. of the middle region of the first ventriculus showing tall columnar cells (x 750).

Fig. 12. A portion of the T.S. of the middle region of the first ventriculus showing short columnar cells (x 300).

Fig. 13. A portion of the T.S. of the middle region of the first ventriculus showing cuboidal cells (x 300).

Fig. 14. An enlarged portion of the T.S. of the middle region of the first ventriculus showing cuboidal cells (x 800).

Fig. 15. A portion of the T.S. of the posterior region of the first ventriculus showing broad and narrow regions (x 250).

Fig. 16. A portion of the T.S. of the posterior region of the first ventriculus showing large nucleus (x 100).

Fig. 17. A portion of the T.S. of the posterior region of the first ventriculus showing folded epithelium and narrow lumen (x 250).

Fig. 18. T.S. of the junction between the first and second ventriculi (x 250).

Fig. 19. T.S. of the anterior region of the second ventriculus (x 250).

Fig. 20. A portion of the T.S. of the anterior region of the second ventriculus (x 250).

Bmb - Basement membrane; Cbc - Cuboidal Cells; Cm - Circular muscle;

f - folds; fp - finger like processes of the basement membrane; Gr - Granules ;

Lf - Long folds; Lm - Longitudinal muscle; LN - Large Nucleus; Lu - Lumen;

N - Nucleus; Rgc - Regenerative Cells; Scc - Short Columnar Cells;

Sf - Short folds; Tcc - Tall Columnar Cells; VC - Vacuolated Cells.

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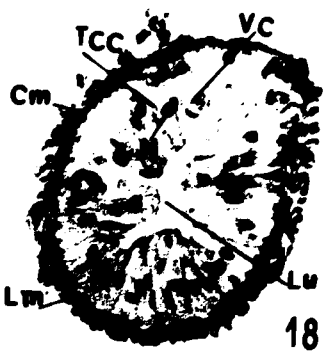

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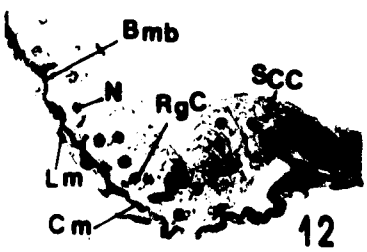

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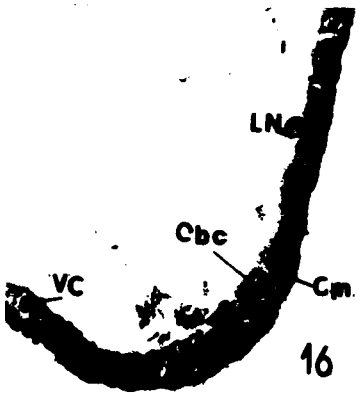

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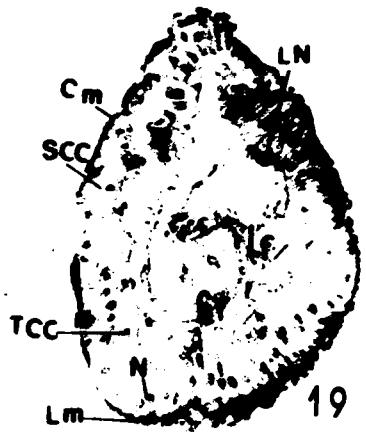

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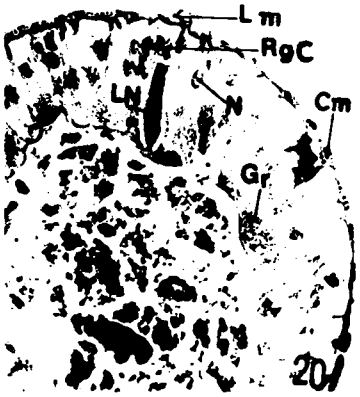

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PLATE - 3

Fig. 21. An enlarged portion of the T.S. of the anterior region of the second ventriculus (x 800).

Fig. 22. T.S. of the middle region of the second ventriculus (x 200).

Fig. 23. A portion of the T.S. of the middle region of the second ventriculus (x 250).

Fig. 24. An enlarged portion of the T.S. of the middle region of the second ventriculus (x 400).

Fig. 25. T.S. of the posterior region of the second ventriculus (x 200).

Fig. 26. An enlarged portion of the T.S. of the posterior region of the second ventriculus (x 350).

Fig. 27. T.S. of the junction between the second and third ventriculi (x 250).

Fig. 28. T.S. of the anterior region of the third ventriculus (x 100).

Fig. 29. A portion of the T.S. of the anterior region of the third ventriculus (x 250).

Bmb - Basement membrane; Cbc - Cuboidal Cells; Cm - Circular muscle;

Epth - Epithelium; fp - finger like processes of the basement membrane;

Gr - Granules ; HC - Holocrine Cells; Lm - Longitudinal muscle;

LN - Large nucleus; Lu - Lumen; MC - Merocrine Cells; N - Nucleus;

Rgc - Regenerative Cells; SCC - Short Columnar Cells; Sm - Secretory material

Tcc - Tall Columnar Cells; V - Vacuole.


Cm
N
Tcc
27
Tcc
Epth
Rgc
Cm
28
Scc
RgC
N
LN
Cm
Sm
Tcc
Lm
N
Tcc
26
Sm
Tcc
29

PLATE - 4

Fig. 30. A portion of the T.S. of the anterior region of the third ventriculus (x 300).

Fig. 31. A portion of the T.S. of the middle region of the third ventriculus (x 350).

Fig. 32. A portion of the T.S. of the middle region of the third ventriculus (x 300).

Fig. 33. A portion of the T.S. of the middle region of the third ventriculus (x 400).

Fig. 34. A portion of the T.S. of the posterior region of the third ventriculus (x 200).

Fig. 35. A portion of the T.S. of the posterior region of the third ventriculus (x 300).

Fig. 36. A portion of the T.S. of the posterior region of the third ventriculus (x 350).

Fig. 37. A portion of the T.S. of the fourth ventriculus (x 300).

Fig. 38. A portion of the T.S. of the fifth ventriculus (x 400).

Bl - Blisters; Bmb - Basement membrane; Cbc - Cuboidal Cells;

Cm - Circular muscle; fp - finger like processes of the basement membrane;

Lm - Longitudinal muscle; LN - Large Nucleus; Lu - Lumen;

N - Nucleus; Rgc - Regenerative Cells; Scc - Short Columnar Cells;

Sm - Secretory material; Tcc - Tall Columnar Cells; V - Vacuole.

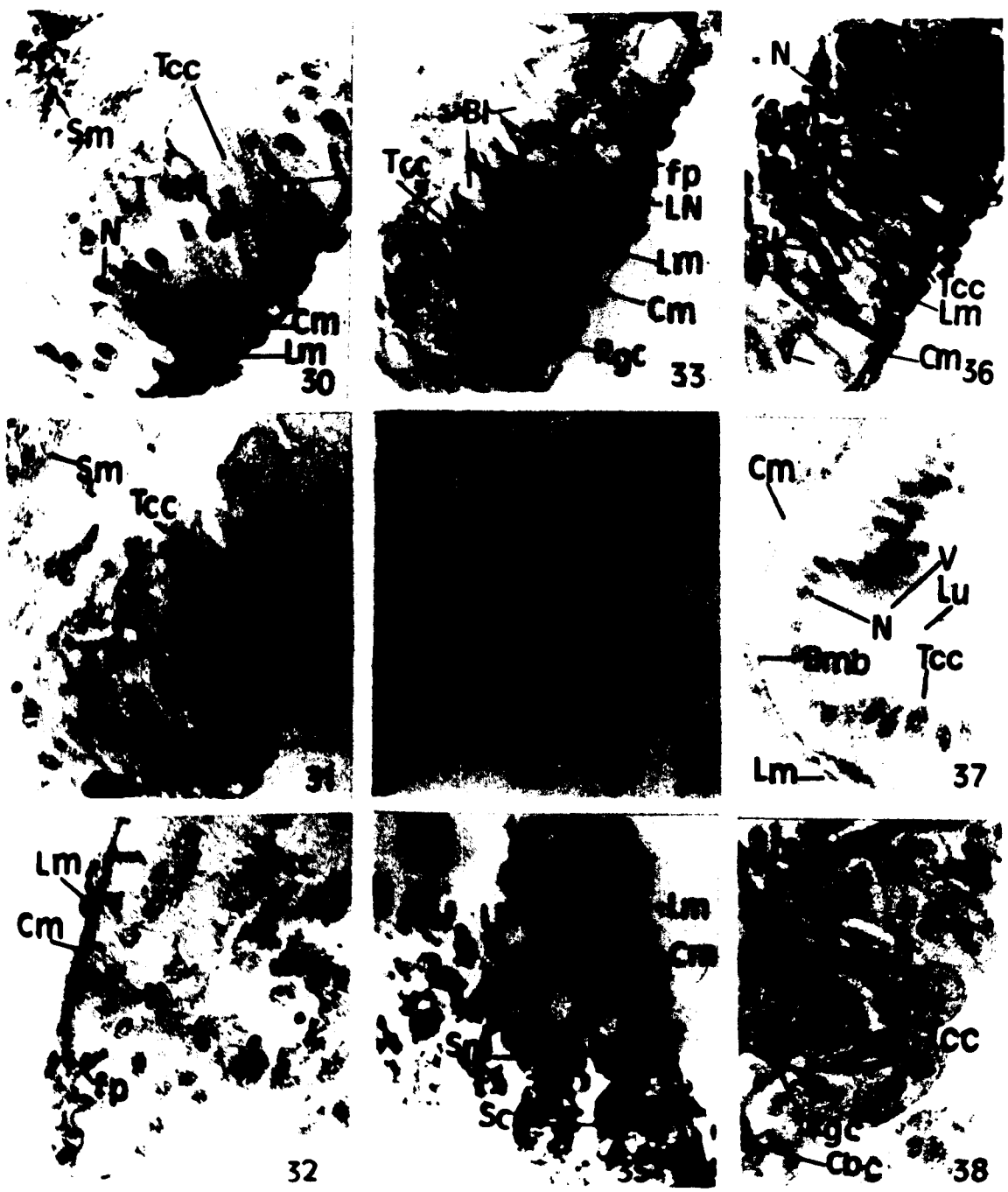

Tcc
Sm
N
Cm
Lm
30
Bl
Tcc
fp
LN
Lm
Cm
Bgc
33
N
Tcc
Lm
Cm
36
Sm
Tcc
31
Cm
V
Lu
N
Bmb
Tcc
Lm
37
Lm
Cm
fp
32
Lm
Cm
Sc
35
CC
Cbc
38

PLATE - 5

Fig. 39. T.S. of the fifth ventriculus and the ampullae of the Malpighian tubules (x 100).

Fig. 40. A portion of the T.S. of the ampullae showing the opening of the Malpighian tubules (x 400).

Fig. 41. T.S. of the pylorus (x 350).

Fig. 42. T.S. of the anterior region of the rectum (x 200).

Fig. 43. A pòtion of the T.S. of the middle region of the rectum (x 100).

Fig. 44. A portion of the T.S. of the middle region of the rectum showing the dorsal wall (x 400).

Fig. 45. A portion of the T.S. of the middle region of the rectum showing the ventral wall (x 400).

Fig. 46. A portion of the T.S. of the posterior region of the rectum showing the dorsal wall (x 750).

Fig. 47. A portion of the T.S. of the posterior region of the rectum showing the ventral wall (x 750).

Am - Ampulla of the Malpighian tubules; Cm - Circular muscle;

Dm - Dilator muscle; DW - Dorsal Wall; Int - Intima;

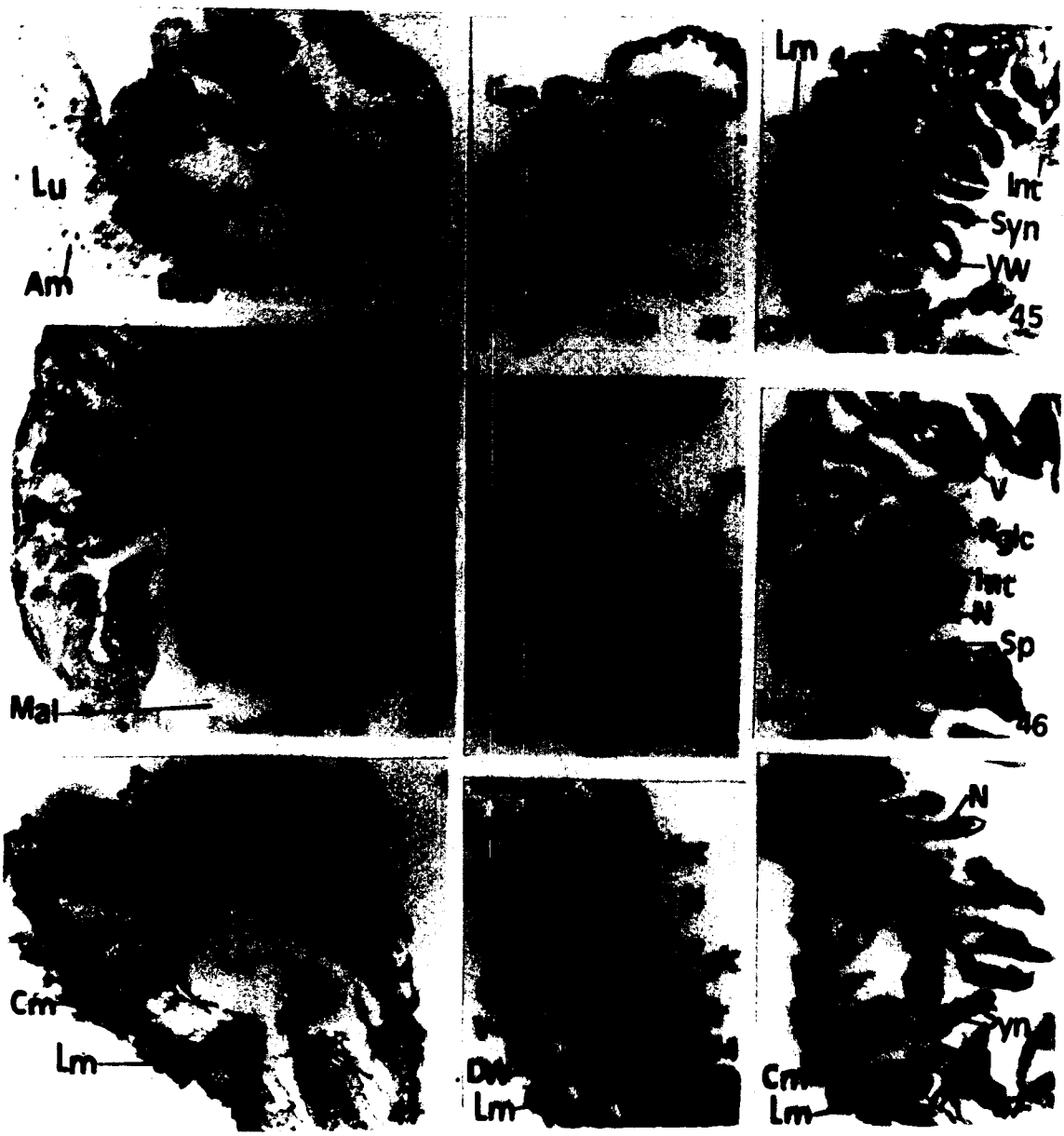
Lm - Longitudinal muscle; Lu - Lumen; Mal - Malpighian tubule;

N -Nucleus; OMal - Opening of the the Malpighian tubule

Pv - Pyloric valve; Rgc - Regenerative Cells; RglC - Rectral gland Cells;

Sp - Spiny projections; Syn - Syncytium; Tcc - Tall Columnar Cells; Tr - Trachea;

V - Vacuole; Vf - Vavular folds; VW - Ventral Wall; V_5 - Fifth ventriculus


Lu
Am
Lm
Int
Syn
VW
45
Mal
V
glc
Int
N
Sp
46
Cm
Lm
Dv
Lm
N
Syn
Cm
Lm

Discussion

a) Anatomy of the Alimentary Canal

The digestive tract of *Iphita limbata* is a typical hemipteran type characterised by an extraordinary lengthening of the midgut and a great shortening of the hindgut. In insects the size of the alimentary canal is inversely proportional to the amount of food taken by the insects (Snodgrass, 1935). Thus the alimentary canal of *I. limbata* which is a fluid feeder is longer. The alimentary canal of *I. limbata* is very long about 5-6.5 cm and highly convoluted in the midgut region. Alimentary canal about two times longer than the body length has been found in *Dysdercus koenigii* (Khanna, 1964), *Gryllotalpa fossor* (Prasad, 1975), *Gryllotalpa gryllotalpa* (Srivastava, 1988), *Schizodactylus monstrosus* (Srivastava, 1990) and *Gryllus domesticus* (Srivastava, 1997). In *Rhizopertha dominica* (Singh, 1987) alimentary canal is 1.3 times longer than the body length which is anteriorly simple and straight whereas posteriorly it is coiled. The tubular alimentary canal of *Chalcophora verginica* (Desai *et al.*, 1997) is four times longer than the body length and differentiated into foregut, longest midgut and hind-gut. The gross anatomy of the alimentary canal of *I. limbata* is similar to that of other gymnocerates such as *D. koenigii* (Khanna, 1964), *Dysdercus cingulatus* (Muraleedharan, 1983) and *Spilostethus macilentus* (Singh and Sharma, 1987 a, b, c). Alimentary canal of *I. limbata* exhibits three well distinct regions — foregut, midgut and hindgut as seen generally in the members of group, Insecta.

The Foregut

In sucking insects the foregut is simple. In *I. limbata* the division of foregut into cibarium, pharynx and oesophagus is similar to that observed in *S. macilentus* (Singh and Sharma, 1987a). It is the shortest and thinnest part of alimentary canal. As in *S. macilentus* the cibarium and pharynx help in the formation of

sucking food pump. In the case of insects belonged to the order Hemiptera, the cibarium is transformed into the sucking pump of the feeding mechanism (Snodgrass, 1935). In certain insects the foregut has been reported to include a single tubular region, the oesophagus as in *Murgantia histrionica* (Harris, 1938), *Dysdercus intermedius* (Mac Gill, 1947) and Capsidae (Goodchild, 1952). In these insects the entire region of the gut in front of the level of the brain which serves as the sucking pump has been termed the cibarium. In certain other insects, viz., *Anasa tristis* (Breaky, 1936), *Leptocorisa varicornis* (Akbar, 1958) and *D. koenigii* (Khanna, 1964) the sucking pump is regarded to consists of two regions, the cibarium and pharynx.

The region of the alimentary canal just behind the food pump in *Notonecta undulata, Ranatra fusca, Belostoma flumineum* and *Hesperocorixa escheri* (Marks, 1958) is swollen slightly to form the accessory pump and is provided with weak dilator muscles. In *B. flumineum* (Marks, 1958) there is second accessory pump which emerges from the head. Kurup (1961 a,b, 1964) who has studied the anatomy and histology of a number of cryptocerate and gymnocerate Hemiptera in detail, does not report an accessory pump or pharynx and describes the oesophagus only under the foregut. According to Goodchild (1952) the foregut of Corixidae is composed of the buccopharyngeal region and oesophagus. However, the foregut is formed of cibarium, pharynx and oesophagus in *Leptocoris trivittatus* (Woolley, 1949), *Lygaeus pandurus* (Rastogi, 1960), *D. koenigii* (Khanna, 1964), *Chrysocoris stollii* (Srivastava and Singh, 1966), *Bagrada cruciferarum* (Mall, 1979) and *Dysdercus cingulatus* (Muraleedharan, 1983). Goverdhan *et al.* (1981) has recorded the presence of pharynx and oesophagus in the foregut of the belostomatid *Abedus ovatus*.

In *I. limbata* the oesophagus is short tubular structure extending from the region where middle of the brain is located to the posterior end of the prothorax. In a fluid feeder a narrow oesophagus may be advantageous to drain the fluid from

the pharynx into the crop by capillary rise. In Hemiptera a crop is usually absent in the alimentary canal. In *I. limbata* the oesophagus directly opens into the first ventriculus which is the largest portion of the alimentary canal. But Kurup (1962) has reported that in *Anisops fieveri* the oesophagus just before its entry into the ventriculus is slightly widened out and this widened portion corresponds to the crop of other insects which temporarily stores the ingesta. No such stomodaeal chitin-lined crop is found in *I. limbata*. However, in *Nezara viridula* (Malouf, 1933) and *Leptocorisa varicornis* (Akbar, 1958) the dilated first ventriculus is regarded as a part of the foregut and is termed as 'crop'. Since in *N. viridula* no chitin-lined intima is observed in this region and it is lined with glandular epithelium, this view is considered to be erroneous (Hamner, 1936). But in *I. limbata* a swollen part similar to cardia in *S. macilentus* is seen which is regarded as the anterior most part of first ventriculus since it is structurally and histologically similar to that of midgut.

In *I. limbata* a proventriculus is absent as in the case of fluid sucking insects. However, a proventriculus is reported in fluid feeding insects such as *Corixa punctata* and *Sigara falleni* (Sutton, 1951). Based on the structural details the function attributed to proventriculus is the trituration of the food particles into small pieces. Such a mechanism is not required for fluid feeding insects. Proventriculus is absent in the larvae of *Spodoptera mauritia* (Pakrutty, 1987) and larvae of *Orthaga exvinacea* (Joseph, 1997) which feed on solid food materials. Hence it is not possible to accept the generalisation that this structure is absent in fluid feeding insects and present in insects which feed on solid food materials.

The Midgut

The midgut of insects shows considerable morphological variations within the same group. The midgut of *I. limbata* is the largest part of the alimentary canal, about 3 to 4 times the length of the foregut. The midgut or ventriculus of

almost all the heteropteran insects is differentiated into 3 or 4 distinct regions (Woolley, 1949; Sutton, 1951; Goodchild, 1963b; Srivastava and Singh, 1966; Mall, 1979; Muraleedharan, 1983 and Singh and Sharma, 1987b, Pakrutty and Mohamed, 1989a). But the midgut of *I. limbata* consists of five different regions. In various heteropterans such as *Cimex* (Cragg, 1914), *Rhodnius* (Wigglesworth, 1936) the midgut exhibits only two regions whereas in *Anasa tristis* (Breakey,1936), *Murgantia* (Harris, 1938) and *Laccotrephes* (Kurup, 1961a; Pakrutty and Mohamed, 1989a) three regions are recognized.

Miyamoto (1961) reports only two divisions in the midguts of eight species of aquatic Hemiptera representing three different families: *Notonecta triguttata* (Notonectidae), *Laccotrephes japonensis, Ranatra chinensis* (Nepidae) and *Belostoma flumineum, Lethocerus americana, Diplonychus japonicus, Kirkaldyia deyrollei* and *Benacus griseus* (Belostomatidae). But in the belostomatid *Sphaerodema rusticum* (Kurup, 1961b), *Lethocerus mazzai* (De Carlo *et al.*, 1973) and *Oxycarenus hyalinipennis* (Al-Sandouk, 1986) the midgut is composed of 3 divisions. Parsons (1959) reports the presence of longest midgut in Belostomatidae among the five families of aquatic Hemiptera.

In *Blissus* and *Peliopelta* (Glasgow, 1914), *Leptocoris trivittatus* (Woolley,1949), *Chrysocoris patricius, Clavigralla gibbosa* (Kurup, 1964), *D. koenigii* (Khanna, 1964; Kurup, 1964), *B. cruciferarum* (Mall, 1979), *D. cingulatus* (Muraleedharan, 1983) and *S. macilentus* (Singh and Sharma, 1987b), the midgut has differentiated into first, second, third and fourth ventriculi. *Iphita limbata* differs from these insects in the differentiation of the midgut into five regions. The midgut in *I. limbata* is shorter in male than that of female and it shows constrictions between the adjacent regions as in *D. cingulatus* (Muraleedharan, 1983) and in *S. macilentus* (Singh and Sharma, 1987b).

In *Periplaneta americana* (Bordas, 1898) the midgut is long and coiled, but is of uniform diameter. In the cricket *Nemobius sylvestris* (Chopard, 1949) the midgut is composed of two portions, an anterior 1/3 is smooth and tubular while the posterior 2/3 is wider and has sacculated surface. The midgut of the cricket *Plebeiogryllus guttiventris* (Dakshayani and Mathad, 1972) is irregularly coiled. In *Blatta germanica* and *Paratenodera sinensis* (Yu, 1980) the posterior part of the midgut is a simple coil. In *Acridida cinerea* and *Conocephalus glegiatus* (Yu, 1980) the midgut is short and straight. In the Madagascar hissing cockroach *Gromphadorhina portentosa* (Dailey and Graves, 1976) the midgut is coiled like a spring. The proximal portion of the coil trails under the colon and then spirals anteriorly over the dorsal surface of the colon where it is continuous as winding path until it terminates at the Malpighian tubules. The midguts of *Bemisia tabaci* and *Trialeurodes abutilonea* are looped so that the anterior and posterior extremities are in contact with each other (Cicero *et al.*, 1995).

Various terminologies have been used for the sub divisions of the midgut of insects belonging to the order Hemiptera by different authors. Hamilton (1931) uses the terms first chamber, second chamber and third chamber for the three regions of the midgut in *Nepa cinerea*. Goodchild (1952) while describing the alimentary canal of West African Cacao capsid bugs uses the terms first midgut, second midgut and third midgut, while Parsons (1959) uses the terms Midgut Region I, Midgut Region II and Midgut Region III. Kurup (1961a,b, 1962, 1964, 1966) who has studied the anatomy and histology of a number of cryptocerates and gymnocerates uses the term ventriculus for the midgut and designates its subdivisions as first ventriculus, second ventriculus, third ventriculus and fourth ventriculus, while De Carlo *et al.* (1973) use mesenteron I, mesenteron II and mesenteron III in *Lethocerus mazzai*. In the present study the subdivisions of the midgut of *I. limbata* are termed first ventriculus, second ventriculus, third ventriculus, fourth ventriculus and fifth ventriculus.

The first ventriculus of *I. limbata* forms the anterior one third portion of the midgut and is a wide elongated sac with much folded wall as in gymnocerates (Kurup, 1964), *D. koenigii* (Khanna, 1964), *B. cruciferarum* (Mall, 1979), *D. cingulatus* (Muraleedharan, 1983), *S. macilentus* (Singh and Sharma, 1987b) and *Laccotrephes robustus* (Pakrutty and Mohamed, 1989a). The width of the first ventriculus varies according to the physiological state of insects. In starved individuals, it becomes greatly distended due to the presence of a large number of air bubbles while in freshly fed individuals the first ventriculus is less wide due to the absence of air bubbles. The first midgut of all cryptocerates and gymnocerates is a dilated sac-like structure. But the anterior part of midgut in many heteropterans shows variation in its morphology. It is expanded anteriorly in Cryptocerata and Amphibicorisae. It is a narrow tube in Hydrometridae while in the families of Pentatomorpha the midgut has a large anterior expansion followed by a tubular intestine (Goodchild, 1966). As in *S. macilentus* (Singh and Sharma, 1987b), the anterior part of first ventriculus of *I. limbata* forms a bulbous structure called cardia in which hangs the oesophageal valve. Posterior to cardia the first ventriculus is convoluted due to many transverse circular folds while posteriorly it gradually widens to form a pear shaped sac having smooth external surface. The first ventriculus in starved individuals of *I. limbata* becomes distended due to the presence of air bubbles. This has also been reported in *D. koenigii* (Khanna, 1964) and *S. macilentus* (Singh and Sharma, 1987b). In *Ranatra elongata* Kurup (1961b) observes a circular opening in the wall of the first midgut. But he has not assigned any function to the opening. No such opening has been observed in the midgut of *I. limbata*.

The second ventriculus of *I. limbata* is tubular and coiled as in many hemipterans. It forms a spiral coil around the third ventriculus. It may be as long as the first ventriculus in male while in female it is two or three times longer than the first ventriculus. This is in agreement with the observations in *D. koenigii*

(Khanna, 1964), *Bagrada cruciferarum* (Mall, 1979), *D. cingulatus* (Muraleedharan, 1983) and *Laccotrephes robustus* (Pakrutty and Mohamed, 1989a). It has narrow constrictions at two ends. Some authors (Hamilton, 1931; Sutton, 1951) have used the term intestine for the second midgut region. It has been reported by Goodchild (1966) that the second midgut region in Amphibicorisae is of variable lengths and usually forms loops on the ventral side of the first midgut region whereas the second midgut region is greatly reduced in Urostylidae, Plataspidae, Tessaratonidae and Dinidorinidae. He has also suggested that the size of the second midgut region in gymnocerates is generally smaller than that of the cryptocerates.

In *I. limbata* the third ventriculus is distinct as a short dilated sac probably serving as a storage compartment. Its lumen is always filled with reddish brown or black viscous substance. This condition is prevalent in *C. patricius, C. gibbosa, Graptostethus servus* (Kurup, 1964), *D. koenigii* (Khanna, 1964; Kurup, 1964) and *B. cruciferarum* (Mall, 1979). Similar morphology has been reported in other gymnocerates by Hamner (1936) and Srivastava and Singh (1966). In Amphibicorisae there is a posterior swelling of the midgut which is variable in size in different species and usually smaller than the anterior one. In some species this swelling is only temporarily formed as food residues accumulate. In Cryptocerata the posterior part of tubular midgut is occluded by a pasty mass of 'coagulum'. The retention of food in third ventriculus probably result from the action of the proctodaeal valve at the junction of midgut and hindgut (Singh and Sharma, 1987b). Hamilton (1931) names it as "pyloric collar" in *Nepa cinerea* while Bordas (1905) calls it "sphincter". The morphology of the third midgut in gymnocerates and cryptocerates is more or less similar.

Breakey (1936) in *A. tristis* and Harris (1938) in *M. histrionica* are not able to differentiate the third midgut because of its tubular nature and considers it as part of the second midgut region. Goodchild (1952) has observed a tubular but

short third midgut in four species of Cacao Capsid bugs namely *Sahlbergella singularis, Distantiella theobroma, Brycoropsis latticottis* and *Heliopelta bergrithi.*

In *I. limbata* the fourth ventriculus following the third is a short much narrower tubular portion. In this respect the midgut of *I. limbata* resembles that of *D. koenigii* (Khanna, 1964), the gymnocerates (Kurup, 1964) and *D. cingulatus* (Muraleedharan, 1983). In some Hemiptera, Glasgow (1914) observes a dilation of the fourth ventriculus immediately below the third but no such dilation has been noticed in *I. limbata.* The fourth ventriculus is marked off from the third by a constriction. A similar constriction is also found by Goodchild (1963b) in certain pentatomids, Srivastava and Singh (1966) in *C. stollii* and Mall (1979) in *B. cruciferarum.*

In many of the hemipterans caecal diverticula are borne in this region of the midgut. No such caecal diverticula are seen in *I. limbata.* Caecal diverticula are absent in cryptocerate Hemiptera (Kurup, 1961 a, b, 1962). It has not been observed in *Oncopeltus fasciatus* (Hood, 1937), *L. trivittatus* (Woolley,1949), *Gerris spinoli* (Kurup, 1964), *B. cruciferarum* (Mall, 1979) and *S. macilentus* (Singh and Sharma, 1987b). Glasgow (1914) has found gastric caeca only in the females of *D. suturellus.* They occur in plant feeding gymnocerates (Glasgow, 1914; Breakey, 1936; Harris, 1938; Kurup, 1964). Kurup (1964) describes four rows of gastric caeca in *C. patricius* and two rows in *C. gibbosa.* Similarly Khanna (1964) and Muraleedharan (1983) have reported their occurrence being restricted to females of *D. koenigii* and *D. cingulatus* respectively. In the families of Pentatomorpha the midgut anterior to the ileum bears numerous tubular or pouch like gastric caeca.

The number and arrangement of caeca vary greatly in different insects. In gryllids such as *N. sylvestris* (Chopard, 1949) and *P. guttiventris* (Dakshayani and Mathad, 1972) there are two large caeca. Two types of gastric caeca have been described in Heteroptera. The first type of gastric caeca are short and of uniform

size and arranged in two or four rows as in *Peliopelta abbreviata* (Glasgow, 1914), *C. patricius, C. gibbosa* (Kurup, 1964), *D. koenigii* (Khanna,1964; Kurup, 1964) and *Chrysocoris purpureus* (Bhaskaran *et al.*, 1969). The second type of gastric caeca are fewer in number varying in length and are often asymmetrically grouped as in *Blissus leucopterus* (Glasgow, 1914). In *G. portentosa* (Dailey and Graves, 1976) there are 8 caeca, but two of them are very short and appear as small stubs. The remaining six caeca are elongated and irregular in shape.

According to Goodchild (1966) the caeca are secondarily vestigeal in Pyrrhocoridae, Rhopalidae, Lygaeinae and some other Lygaeidae and Asopinae. The fourth ventriculus and the gastric caeca are absent in *G. servus* (Kurup, 1964). The third ventriculus in this insect passes directly into the hindgut.

In *I. limbata* fifth ventriculus is a small and slightly wider part of the alimentary canal lying posterior to the fourth ventriculus. In this bulbous portion there is a pair of slightly swollen dorso-lateral outgrowths, the ampulla each one of which receives a pair of Malpighian tubules. Each pair of Malpighian tubules empties into ampulla independently by separate pores. In Homoptera the region of the midgut that receives the openings of the Malpighian tubules is not differentited from the rest of the midgut, while in Heteroptera this region is distinct from the rest of the intestine and is marked by a valve-like constriction (Goodchild, 1966). In Cryptocerata the pyloric region is not distinct and the tubular anterior part of the hindgut is termed the ileum by Goodchild (1966). The swollen region where the Malpighian tubules open into the midgut has been variously termed. In *D. koenigii* (Khanna, 1964) it has been called intestine, in *C. purpureus* (Bhaskaran *et al.*, 1969), *Bagrada cruciferarum* (Mall, 1979) and in *S. macilentus* (Singh and Sharma, 1987c), this region has been named ileum and in *D. koenigii* (Kurup, 1964) and in *D. cingulatus* (Muraleedharan, 1983) it has been termed pylorus. In all these cases it has been regarded as part of hindgut even though this region does not possess a chitinous intima. Snodgrass (1935) has pointed out that the ileum in

gymnocerates should be regarded as a segment of the mid-intestine and not to be homologized with the ileum of other insects which is considered part of the hind-intestine.

In *I. limbata* two pairs of Malpighian tubules join the midgut through the ampullae just anterior to the pyloric sphincter as in *Necrophorus* and *Gnaptor* (Gorka, 1914) and in Fulgoromorpha (Fick, 1983). In *I. limbata* a pair of Malpighian tubules empty into each of the ampullae independently. This is in accordance with the findings of Khanna (1964) in *D. koenigii* and Muraleedharan (1983) in *D. cingulatus*. Haridas and Ananthakrishnan (1981) have reported flask shaped ampullae of 4 Malpighian tubules surrounding the pylorus in Reduviidae. However, in *Rhodnius prolixus* (Wigglesworth, 1931b) each tubule opens with separate ampullae into the extreme posterior end of midgut. In most Heteroptera and Fulgoridae (Goodchild, 1966) the Malpighian tubules open with separate ampulla. In Homoptera the region of the midgut that receives the openings of the Malpighian tubules is not differentiated from the rest of the midgut, while in Heteroptera this region is distinct from the rest of the intestine and is marked by a valve-like constriction (Goodchild, 1966).

In gymnocerate Hemiptera (Kurup, 1964), *Catholsius macculatus* (Shukla and Upadhyay, 1980) and in *Laccotrephes macculatus* (Mohamed, 1984) the Malpighian tubules open into the anterior most region of the pylorus. In *D. koenigii* (Khanna, 1964) the tubules open to the intestine immediately behind the pyloric valve. In coccids, Weber (1930) is of the opinion that the Malpighian tubules open very close to the commencement of hindgut. The Malpighian tubules in *Conocephalus indicus* (Mohamed and Murad, 1977b), *Dacus cucurbitae* (Mohamed and Murad, 1978), *Vespa bicolor* (Mohamed and Murad, 1982) and in *Coccinella septumpunctata* (Mohamed, 1983) open into the hindgut. The

Malpighian tubules of *Rhodnius prolixus* (Wigglesworth, 1931b) open into a large rectal pouch.

The number of Malpighian tubules are variable in the different groups of insects. In Orthoptera the number is large and over hundred. But they are usually arranged in groups (Snodgrass, 1935). In *Spathosternum praciniferum* (Mohamed and Murad, 1980) there are 12 Malpighian ampullae and 12 Malpighian tubules are given off from each ampullae. In Gryllidae (Dakshayani and Mathad, 1972) only a single primary short tubule is present, but this one divides into a bunch of 100 or more long secondary tubules.

The Hindgut

The hindgut of *I. limbata* is short and consists of an anterior pylorus and a posterior rectum. The hindgut is long and nearly half the length of entire alimentary canal in *Rizopertha dominica* (Singh, 1987). In *I. limbata* pylorus forms the junction between the midgut and the rectum and is characterised by the presence of pyloric valve. The pyloric valve is observed just behind the opening of the Malpighian tubules. But there is much controversy regarding the identity of the anterior region of hindgut whether it can be termed pylorus or ileum. Kurup (1961a,b, 1962) has not reported the presence of pylorus in the cryptocerate species he studied. The use of the term ileum in Heteroptera has been considered by Rastogi (1962) and Bahadur (1963a).

The hindgut shows great anatomical diversity and has been divided into different regions by various authors. The hindgut consists of an intestine and rectum in *Anthonomus grandis* (Sundman and King, 1964), *Dysdercus koenigii* (Khanna, 1964), Calyptrate Diptera (Singh and Judd, 1966), Calyptrate Muscids (Hori, 1967), *Elasmopalpus lignosellus* (Beals and Berberet, 1976) and in *Stegobium paniceum* (Serjdukova, 1984). In *Gryllotalpa gryllotalpa* (Srivastava, 1988) and in *Gryllus domesticus* (Srivatava, 1997) the hindgut consists of proximal short narrow

tube, ileum, middle colon, and distal broad pear shaped rectum. In cryptocerates and gymnocerates (Goodchild, 1952, 1966; Kurup, 1961a,b, 1962, 1966; De Carlo *et al.*, 1973; Goverdhan *et al.*, 1981; Muraleedharan, 1983; Singh and Sharma, 1987c; Pakrutty and Mohamed, 1989a) the hindgut is composed of ileum and rectum. In Cryptocerata the rectum has a rectal caecum.

The hindgut is divisible into pylorus, ileum, colon and rectum in *Heliothis zea, Spodoptera frugiperda* (Chi *et al.*, 1975), *Mandcua sexta* (Reinecke *et al.*, 1973) and *Marasmia trapezalis* (Mall, 1980). The hindgut is divided into an anterior (hindgut I) and posterior (hindgut II) portion and a terminal anal membrane in *A. grandis* (Mac Gown and Sikorowski, 1981). The hindgut is the largest portion of alimentary canal in *Rhizopertha dominica* (Singh, 1987). It is simple tubular structure without caeca. Anteriorly it becomes convoluted and distinguished into four regions, pyloric region, ileum, colon and rectum proper. The hindgut is an expanded flexible tube in Fulgoromorpha (Fick, 1983). Hindgut is divisible into ileum, colon (fermentation sac) and rectum in *Heteronychus arator* (Sheehan *et al.*, 1982).

In the Cryptocerata where a pyloric region is not distinct, the tubular anterior part of the hindgut is termed ileum. Harris (1938) claimed to have detected a chitinous intima in the ileum of *Murgantia histrionica* and concluded that pylorus is a modified ileum. However, it has been accepted by Srivastava and Bahadur (1961) that the pentatomorph ileum belongs to midgut and the hindgut commences at the ileo-rectal or pyloric valve. Miyamoto (1961) has observed the presence of a distinct pylorus in most primitive Heteroptera. Hood (1937) has observed no chitinous intima in the pylorus of *Oncopeltus fasciatus* and therefore considered it as continuation of mesenteron. In *Melipona quadrifasciata* (Cruz-Landim, 1994) the pylorus consists of a small bulb-like dilation in the transition

between the midgut and the ileum and the Malpighian tubules empty in this portion.

As in *Bagrada cruciferarum* (Mall, 1979), *D. cingulatus* (Muraleedharan, 1983) and *S. macilentus* (Singh and Sharma, 1987c) the rectum of *I. limbata* is membranous sac which narrows down posteriorly and finally opens outside through anus. In *D. cingulatus* (Muraleedharan, 1983) the wall of the rectum is thrown into numerous folds. No such folds are seen in the rectal wall of *I. limbata*. A rectal caecum is invariably present in cryptocerate Hemiptera (Kurup, 1961 a, b 1962) but none occurs in the gymnocerates. The rectal portion of the hindgut in dictyopteran, dermapteran and carabidean insects generally have six longitudinal cushion shaped thickenings known as rectal pads (Wall and Oschman, 1973). Such rectal pads are absent in *I. limbata*. In some insects the distal ends of the Malpighian tubules are closely applied to the rectum and form the cryptonephridium (Ramsay, 1964; Rahman *et al.*, 1991; Hallberg, 1993; Desai *et al.*, 1997) or nephro-rectal complex (Mohamed, 1983). Cryptonephry has been described with the colon in many beetles (Hafeeze & Gardiner, 1964; Benham, 1970; Morgan *et al.*, 1970; Mukharji and Singh, 1971; Singh, 1987).

b) Histology of the Alimentary Canal

The Foregut

The foregut of *Iphita limbata* is a thin walled tube consisting of a narrow short oesophagus. The wall of the oesophagus is composed of an outer longitudinal muscle layer, an inner circular muscle layer, basement membrane, a layer of epithelium and intima as reported in the foregut of other gymnocerates (Khanna, 1964; Kurup, 1964; Bhaskaran *et al.*, 1969; Mall, 1979; Muraleedharan, 1983; Singh and Sharma, 1987a). The musculature of the foregut is well developed in *I. limbata*. The general arrangement of musculature in the foregut of insect orders other than Heteroptera is the presence of an outer layer of circular muscles and an inner layer of longitudinal muscles. But this pattern in the foregut of Heteroptera shows difference in different groups. The pattern recorded in *Clavigralla gibbosa, Chrysocoris patricius, Graptostethus servus* and *Dysdercus koenigii* (Kurup, 1964), *Gerris spinoli* (Kurup, 1966), *Bagrada cruciferarum* (Mall, 1979), *D. cingulatus* (Muraleedharan, 1983) and *Spilostethus macilentus* (Singh and Sharma, 1987a) agrees with the general pattern. The foregut musculature in *I. limbata* is formed of an outer layer of longitudinal muscles and an inner layer of circular muscles as seen in cryptocerates (Kurup, 1961a,b, 1962; Ameen and Imam, 1976; Pakrutty and Mohamed, 1989a). It has been reported that there is only a longitudinal layer of muscles in the foregut of aquatic Hemiptera, *Notonecta undulata, Ranatra fusca, Belostoma flumineum* and *Hesperocorixa escheri* (Marks, 1958) and *Abedus ovatus* (Goverdhan *et al.*, 1981). In West African Cacao capsids (Goodchild, 1952) there is a thin sheath of longitudinal muscles outside the oesophageal epithelium and outer to it there are strands of circular muscles.

The oesophagus is strongly muscularised by circular muscles in the foregut of *Icerya purchasi* (Johnston, 1912). In *S. macilentus* (Singh and Sharma, 1989a), the circular muscles are well developed in the anterior half of oesophagus whereas

the longitudinal muscles are well developed in the posterior half of the oesophagus. In *Anasa tristis* (Breakey, 1936) longitudinal muscles occur only in the posterior part of the oesophagus. In *Prodenia litura* (Mathur, 1973), *Elasmopalpus lignosellus* (Beals and Berberet, 1976) and *Marasmia trapezalis* (Mall, 1980), dilator muscles are present between the circular muscles and the epithelium. The histology of the gut wall of *Heliothis zea* and *Spodoptera frugiperda* (Chi *et al.*, 1975) is peculiar because there is no longitudinal muscle layer. In *Phormia regina* (Thomson and Holling, 1975) the foregut has five groups of circular muscles which act as valves during crop-emptying process. In *Plebiogryllus guttiventris* (Dakshayani and Mathad, 1972) the proventriculus is provided with numerous circular and longitudinal muscles. In *Aulacophora foveicollis* (Pathak *et al.*, 1990) some longitudinal muscles are found in the layer of circular muscles.

The musculature of the foregut mainly helps in the feeding and conduction of food into the midgut. The dilator muscles in the pharynx are best developed in the case of insects where pharynx participates in the formation of well-developed sucking pump as seen in the adults of Lepidoptera, Hymenoptera, Neuroptera and Dyticidae (Richards and Davies, 1977).

In *I. limbata* the epithelial cells rest upon a basement membrane. The basement membrane is very prominent in *Prodenia litura* (Mathur, 1973), *D. cingulatus* (Muraleedharan, 1983) and in *S. macilentus* (Singh and Sharma, 1987a). In *P. litura* (Mathur, 1973), the basement membrane of oesophageal epithelium is deeply pressed by muscle bundles forming a valvular structure.

The cell limits of epithelial cells of the foregut of *I. limbata* are indistinct. The epithelium of the foregut of adult *Callosobruchus analis* and *Callosobruchus chinensis* (Rahman and Ameen, 1991) and adult *Alphitobius diaperinus* (Rahman *et al.*, 1991) is not clearly defined. But it has been reported that these epithelium is

formed of flat or cuboidal cells. In *D. cingulatus* (Muraleedharan, 1983) it is made up of uninucleate columnar or cuboidal cells. Since the cell limits of the epithelium in *I. limbata* are indistinct, the epithelial layer gives an appearance of a syncytium with prominent nuclei. Similar observations are reported in *Laccotrephes maculatus, Anisops fieveri* (Kurup, 1961a, 1962), *P. litura* (Mathur, 1973), *Abedus ovatus* (Goverdhan *et al.*, 1981), *S. macilentus* (Singh and Sharma, 1987a) and *L. robustus* (Pakrutty and Mohamed, 1989a). In *I. limbata* in the posterior part, the cells become spindle shaped with many nuclei and project into the lumen. In *M. trapezalis* (Mall, 1980) oesophagus has syncytial epithelium with six longitudinal folds, of which two are large. In corixids (Sutton, 1951) the oesophageal epithelium is formed of single layer of columnar or horizontally flattened cells. Columnar epithelium in oesophagus is also reported in *C. patricius, C. gibbosa,G. servus* and *D. koenigii* (Kurup, 1964). In West African Cacao capsid bugs (Goodchild, 1952) the oesophagus has a cuboid epithelium of small uninucleate cells.

In *Plebiogryllus guttiventris* (Dakshayani, and Mathad, 1972) the oesophageal epithelium consists of columnar cells with distinct nuclei, whereas in *Gryllotalpa gryllotalpa* (Srivastava, 1988) it is formed of distinct rectangular cells with clear oval nuclei and granular cytoplasm. Cuboidal epithelium with relatively large nuclei is reported in *E. lignosellus* (Beals and Berberet, 1976) and *H. zea* and *S. frugiperda* and *S. ornithogalli* (Chi *et al.*, 1975). Epithelium is made of rectangular cells with nuclei and indistinct boundaries in *Schizodactylus monstrosus* (Srivastava, 1990) and *Gryllus domesticus* (Srivastava, 1997).

The epithelium of the foregut in insects is produced generally into folds. The oesophageal epithelium of *I. limbata* is produced into longitudinal folds as observed in the posterior region of the oesophagus of *Laccotrephes maculatus, Ranatra elongata* and *Sphaerodema rusticum* (Kurup, 1961a,b), *Tingis buddleiae* (Livingstone, 1967), *S. macilentus* (Singh and Sharma, 1987a) and *L. robustus*

(Pakrutty and Mohamed, 1989a). These folds enable the lumen to expand as the foregut becomes filled with food. It appears that these folds press the food from all the sides so that food moves from the oesophagus to the next region. In *A. fieveri* and *Agraptocorixa hyalinipenis* (Kurup, 1962) no foldings are observed in the wall of oesophagus.

The innermost layer of the foregut wall is formed of non-cellular chitinous intima which is variously modified in correlation with the function performed by that region. In *I. limbata* the chitinous intima secreted by the epithelial cells is thicker and is thrown into the lumen as freely hanging longitudinal plates. These plates remain folded in a complicated manner and appears to fill almost the entire lumen of the oesophagus and extend upto the first ventriculus as reported in *S. macilentus* (Singh and Sharma, 1987a). The intima is without spines or bristles in *I. limbata*. Generally the intima of foregut of fluid feeding insects is thin and not modified in the form of spines or bristles. The intima is thrown into small wavy folds in *Bagrada cruciferarum* (Mall, 1979). The intima of the oesophagus and crop is thick and is devoid of spines in *Orthaga exvinacea* (Joseph, 1997) and it is also without bristles in *Gryllodes sigillatus* (Narula, 1971), *Trilophidia annulata*, *Gryllotalpa fossor* (Prasad, 1975) and *G. gryllotalpa* (Srivastava, 1988). An appraisal of the literature shows that the intima of foregut of some insects bear microspines (Hodge, 1939; Singh, 1965; Narula, 1971; Muralirangan and Ananthakrishnan, 1974; Bondreaux, 1980; Srivastava, 1990 and Singh *et al.*, 1996). Observations of the foregut intima of *Locusta migratoria* (Hodge, 1939; Albrecht, 1953; Hochuli *et al.*, 1992) have shown numerous spines of differing morphologies directed posteriorly. In *C. analis* and *C. chinensis* (Rahman and Ameen, 1991) the intima of the foregut is modified into pharyngeal spines, oesophageal spines and proventricular needles in the pharynx, oesophagus and proventriculus respectively. In *P. litura* (Mathur, 1973) oesophageal intima bears sharp chitinous spines whereas intima of crop is thin and devoid of spines. In *M.*

trapezalis (Mall, 1980) the oesophageal intima is two layered and have short spines. Oesophageal bristles are present in *Dendroctonus adunctus* (Zungia Bermudez *et al.*, 1994). The intima of pharynx is provided with denticle like projection in *Alphitobius diaperinus* larvae (Rahman *et al.*, 1990). The foregut intima bears a series of spines in *Aulacophora foveicollis* (Pathak *et al.*, 1990) whereas intima has rough margin without spines in *Coccinella septumpunctata* (Pathak *et al.*, 1990). Crop and proventricular spines are with multiple prongs in *L. migratoria* (Hochuli *et al.*, 1994). These structures formed by the modification of the intima help in mastication of food and also regulate the passage of food through the foregut.

The Oesophageal Valve: In *I. limbata* at the junction of foregut and midgut, the posterior end of oesophagus hangs down freely into the lumen of first ventriculus forming the oesophageal valve. The structure of the valve varies in different insects and it has also been termed variously — as stomodaeal valve by Woke (1941), Mathur (1973), Srivastava (1988, 1990, 1997) and Joseph (1997); as oesophageal valve by Kurup (1961a,b, 1962, 1964, 1966), Goverdhan *et al.* (1981), Singh and Sharma (1987a), Pakrutty and Mohamed (1989a); as Cardiac valve or Cardiac sphincter by Livingstone (1967), Sutton (1951) and Hochuli *et al.* (1992). In *I. limbata* the oesophageal valve consists of two layers of oesophageal epithelium which are closely apposed to each other, an outer layer facing the first ventriculus and an inner layer facing the lumen of the valve. These two layers are continuous and have a small intravalvular space in between the two. The epithelium of the valve consists of small columnar cells. The muscle layer is also well developed. The cuticular intima lines the oesophageal valve at its inner surface and this highly folded intima hangs well behind the posterior limit of the oesophageal valve forming the entonnoir. Similar observations are reported in *Pelocoris femoratus* (Parsons, 1957), *G. servus, D. koenigii* (Kurup, 1964) and in *S. macilentus* (Singh and Sharma, 1987a). But an intravalvular space is not present

in *S. macilentus*. In *Pelocoris femoratus* (Parsons, 1957) the cells of the outer layer of the oesophageal valve are somewhat taller than those of the inner one. The intra valvular spaces found between the two layers of epithelium contain fine connective tissue fibrils. In this insect the cells of the outer cell layer becomes taller at the anterior limit of the invagination, where they gradually merge with the annular cells which are a group of compactly placed cells present at the posterior termination of the intima (Parsons, 1957; Singh and Sharma, 1987a). These annular cells are not prominent in *I. limbata*. Degenerating cells which are not observed in *I. limbata* are reported to be present within the oesophagus or oesophageal valve region of corixids (Parsons, 1957).

In some of the insects intima lining the oesophageal valve, becomes highly folded with plates or spines and hangs well behind the posterior limit of the cardia. This structure has been termed as "entonnoir" by Aubertot (1932), Sutton (1951) and Parsons(1957). The presence of entonnoir is characteristic of Cryptocerata (Sutton, 1951; Parsons, 1957; Marks, 1958; Kurup, 1962). Harris (1938) recorded a more or less similar structure in *Murgantia histrionica*. No entonnoir has been observed in the terrestrial bug, *Tingis buddleiae* (Livingstone, 1967). It is well developed in *Iphita limbata*. Sutton (1951) considers a complex valve of this type as a primitive condition. The entonnoir helps to direct the flow of fluid in the gut (Singh and Sharma, 1987a).

The cells at the posterior tip of the invagination of the valve usually contain at their apical ends large vacuoles (Parsons, 1957)which are not observed in *I. limbata*. Such vacuoles occur less frequently in the more anteriorly located cells of the inner and outer cell layers or in the annular cells. Their presence appears to be associated with the secretion of intima and with the pulling away of the cuticle to form the entonnoir. But these vacuoles are rarely found in *Belostoma, Notonecta* and *Ranatra* (Parsons,1957). Vacuolated cells have been described in the

oesophageal valves of *Ptychoptera contaminata* (Van Gehuchton, 1890) and in two species of aphids (Weber, 1928; Miller, 1932).

The presence of circular muscle strands within the intravalvular space of the invagination of the oesophageal valve seen in *I. limbata* has been reported in corixids (Sutton, 1951; Marks, 1958). According to Parsons (1957), there are no muscle strands but only connective tissue fibres which along with small tracheoles penetrate the intravalvular space of the oesophageal invagination. Sutton (1951) claims the presence of blood sinuses in the intra-valvular space, the action of which brings about the distention and elongation of the valve, which thus actively takes part in moving the food posteriorly into the midgut. Valvular action in *Notonecta* and *Ranatra* (Parsons, 1957) is derived from the circular muscle sphincter at the junction of the oesophagus which when it contracts draws together the tall columnar cells. In *Gerris spinoli* (Kurup, 1966) the valve is formed of four villi by the infolding of the epithelium at or near the point of its entry. The intima is not drawn over the villi to form entonnoir. A ring of cells immediately behind the oesophageal valve has been observed in *Chrysocoris stollii* (Srivastava and Singh, 1966) and these cells are considered to be homologous to those cells secreting peritrophic membrane. These structures which are associated with the formation of peritrophic membrane are not observed in *I. limbata*. In *L. maculatus, R. elongata* and *S. rusticum* (Kurup, 1961a,b) there is no specialised cardiac sphincter. There are only four villi which perform the functions of the sphincter. The cells of the villi are multinucleate.

The oesophageal extension into the ventriculus prevents the reflex of regurgitation in most insects. The function of the oesophageal valve is supposed to prevent the return movement of food from the midgut to the foregut. Since the valve does not occlude or close the lumen completely in *I. limbata*, it is presumed that some food and digestive juices may flow into the foregut as reported in various insect orders such as Coleoptera (Dennel, 1942; Sinha, 1958), Orthoptera

(Abbot, 1926; Eisner, 1955); Odonata (Ballentine, 1940), Mallophaga (Waterhouse, 1953). In *Blatella germanica* (Yu, 1980) the stomodaeal valve is long and extends upto about 1/4th the distance into the midgut and the valve regulates the passage of food from the crop into the midgut so that food from the foregut is moved into the midgut as digestion is being completed in the latter.

The Midgut

The midgut, the most important region of the alimentary canal in insects, is the major portion in most Hemiptera. Histologically, the midgut of *Iphita limbata* conforms to the basic hemipteran ground plan. The midgut wall consists of a layer of epithelium, surrounded externally by an inner circular and an outer longitudinal layers of muscles. The bases of epithelial cells rests upon the basement membrane. It contains columnar and cuboidal cells which are uninucleated, binucleated or multinucleated. Yanai (1952) and Yanai and Iga (1956) have found that the frequency of uninucleate cells correlates with the abundance of nidi of regenerative cells. In the highly carnivorous Cryptocerata nearly all the cells are uninucleate and nidi are very abundant. In phytophagous Pentatomidae there are few of this uninucleate cells (Goodchild,1963b).

The midgut musculature of *I. limbata* is similar to that of other gymnocerates and cryptocerates (Goodchild, 1952; Kurup, 1961a, 1962, 1964, 1966; Khanna, 1964; Bhaskaran *et al.*, 1969; De Carlo *et al.*, 1973; Mall, 1979; Muraleedharan, 1983; Singh and Sharma, 1987b; Pakrutty and Mohamed, 1989a). The longitudinal muscles form the outer layer and are poorly developed in the anterior region. These muscles are well developed in the posterior region. Longitudinal muscles have been reported to be absent from the posterior region of the midgut of *Cimex* (Cragg, 1914), *Chrysocoris stollii* (Srivastava and Singh, 1966) and *Bagrada cruciferarum* (Mall, 1979). In *Sitophilus granarius* (Baker *et al.*, 1984) midgut wall has fibres of circular and longitudinal muscles. The arrangement of

circular and longitudinal muscle layers in the midgut is different from that of fore and hindgut in *Grylltotalpa gryllotalpa* (Srivastava, 1988). A series of longitudinal and circular muscle fibres surrounds the midgut epithelium in *Sinentomon erythanum* (Dallai *et al.*, 1989). The midgut musculature of the desert locust *Schistocerca gregaria* (Anderson and Cochrane, 1978) is divided into three distinct layers, (a) the external longitudinal muscle, (b) circular muscle and (c) the internal longitudinal muscle between the circular muscle and epithelium.

In *I. limbata* the basement membrane which supports the epithelium is well developed and prominent. At certain regions, the basement membrane penetrates into cell layer in the form of short finger shaped process. Basement membrane is a non-cellular membranous lining. Electron microscopic studies revealed that it contains collagen microfibrils or shows an elaborate and regular internal differentiation (Richards and Richards, 1968; Reinhardt and Hekcer, 1973). The basement membrane is closely associated with the plasma membrane at the base of epithelial layer. At occasional spots it extends a short distance into an infolding of the basal labyrinth or form a small out pocketing (Richards and Richards, 1968). The basal lamina of *Sitophilus granarius* (Baker *et al.*, 1984) consists of an amorphous substrate into which are embedded fibrils or lead like lamellae. In *Musca domestica* (Terra *et al.*, 1988) the basement membrane is highly folded with few apertures in the underlying space. The basement membrane projects into the lumen in the form of six small unequal blunt folds covered by epithelial layer in *Aulacophora foveicollis* (Pathak *et al.*, 1990). The basement membrane in *Drosophila auraria* (Dimitriadis, 1991) is folded in many sites forming a complex network of wide extra cellular compartments.

The midgut epithelium of *I. limbata* consists of a single layer of cells which are generally columnar with moderately large round or oval nuclei. The epithelium is produced into few internal folds which project into the lumen. Uninucleate, binucleate and multinucleate cells are found in the epithelium. Yanai

and Iga (1956) found that the presence of binucleate cells in the midgut epithelium is characteristic of gymnocerates whereas the cryptocerate midgut cells are always uninucleate. Goodchild (1966) assumed that the uninucleate midgut cells are abundant in highly carnivorous Cryptocerata and binucleate midgut cells are usually found in the phytophagous Hemiptera. Cuboidal cells are also found in the midgut epithelium of *I. limbata*. Regenerative cells are few in number and are seen in small groups or separately at the base of the columnar cells. So it is evident that the midgut epithelium of *I. limbata* is typically gymnocerate type (Goodchild, 1952; Kurup, 1964; Mall, 1979; Muraleedharan, 1983; Singh and Sharma, 1987b). Yanai (1952) points out 2 main histological differences between Cryptocerata and Gymnocerata — (i) the epithelial cells of the cryptocerate midgut are always mononucleate whereas in gymnocerates they are binucleate and (ii) the regenerative cells in Cryptocerata are grouped into nests while in Gymnocerata the regenerative cells occur separately.

Parsons (1959) studied the midguts of five aquatic Hemiptera, *Hesperocorixa interrupta, Notonecta undulata, Belostoma flumineum, Pelocoris femoratus* and *Ranatra fusca*. According to her the midgut epithelium of Cryptocerata presents two different histological patterns — Type I and Type II. In Type I epithelium, the basement membrane is thrown into folds which she calls "villiform ridges" and the epithelial cells in the crypts are closely packed together so that their tips interdigitate whereas in Type II epithelium, the villiform ridges are not always present and in the crypt only the basal columnar cells interdigitate. The digestive cells of the midgut epithelium of most of the insects show uniform cell structure throughout the midgut except for their differences in size in different parts of the midgut. The midgut epithelium of *I. limbata* differs from these two types for the reason the crypts are not so prominent and have no villiform ridges.

According to Smith *et al.* (1969) the three types of cells which have been identified in insect midgut epithelium are columnar cells, goblet cells and small

basally located nidi. In *I. limbata* the midgut epithelium is composed of mainly of columnar cells, a few regenerative cells and cuboidal cells. Goblet cells are absent. The midgut epithelium of all lepidopterous larvae (Wigglesworth, 1972) is composed of columnar and goblet cells. Chi *et al.* (1975) are at the view point that the goblet cells and columnar cells may be maturation phases of the same cell type. They describe that both goblet and columnar cells are involved in secretion of digestive enzymes. But in larval Lepidoptera and Trichoptera and in some other insects, the midgut epithelium contains goblet cells with less rough endoplasmic reticulum, less regular microvilli and a highly folded plasma membrane that encloses the invaginated or vacuole like goblet chamber and are involved in active transport of potassium ions across the gut wall (Joseph, 1997). In *Altica cyanea* (Singh *et al.*, 1996) the midgut epithelium has columnar and rectangular cells.

Columnar cells are numerous in both anterior and posterior regions of the midgut in *Sitophilus granarius* (Baker *et al.*, 1984). In *Gryllotalpa gryllotalpa* (Srivasava, 1988) the epithelium is differentiated into functional epithelium which is towards the lumen and regenerative epithelium which is dome shaped mass of irregular regenerative cells lying outer to the functional epithelium under the circular muscle layer. Columnar cells show different morphology along the midgut and even in the same region in the dipteran fly *M. domestica* (Terra *et al.*, 1988). In *Lucilia* larva (Waterhouse and Wright, 1960) the columnar cells comprise ultrastructurally distinct lipophilic and cuprophilic cells, the former with large inclusions of storage fat and lamellate border. In *Periplaneta* (Threadgold and Gresson, 1962) there are histological differences between the secretory and absorptive columnar cells.

Goblet cells which are absent in *I. limbata* are most conspicuous in lepidopterous larvae, becoming more numerous towards the posterior end of the gut (Shinoda, 1927). These cells have reduced cytoplasm and striated cell surface, which is invaginated to form a deep cavity as in *Vanessa* (Henson, 1929, 1931).

Midgut epithelium of *Manduca sexta* (Baldwin and Hakim, 1991) consists prominently of columnar and goblet cells. Anderson and Harvey (1966) suggest that the goblet cells may be involved in the transport of K^+ ions across the gut wall. Fain-Maurel *et al.* (1973) have observed peculiar goblet cells in the midgut of *Petrobius maritimus* which are scattered among columnar cells.

The presence of nidi of reserve cells which are regenerative in function have been reported in various insect species (Snodgrass, 1935; Wigglesworth, 1972; Kurup, 1961, a,b, 1962; Khanna, 1964; Mathur, 1973; Cheung and Low, 1975; Mall, 1979, 1980; Goverdhan *et al.*, 1981; Muraleedharan, 1983; Singh and Sharma, 1987b; Pakrutty and Mohamed, 1989a; Marana *et al.*, 1997). They are observed at the bases of crypts in *Laccotrephes maculatus, Ranatra elongata* and *Sphaerodema rusticum* (Kurup, 1961a,b). In *I. limbata* the regenertive cells are scattered near the bases of epithelial cells as in *B. cruciferarum* (Mall, 1979). In the phytophagous Pentatomidae there are few regenerative cells while in the highly carnivorous cryptocerate nidi are very abundant (Goodchild, 1966). No nidi cells have been found in the midgut of *Anisops fieveri* (Kurup, 1962), *Clavigralla gibbosa, Graptostethus servus* and *Chrysocoris patricius* (Kurup, 1964). The regenerative cells or nidi are absent from the midgut epithelium of phytophagous insect *Chrysocoris purpureus* (Bhaskaran *et al.*, 1969) throughout its life. However it is found that the epithelium damaged or exhausted during secretory activity is regenerated from portions of the parent cells that are left behind (Kurup, 1964; Bhaskaran *et al.*, 1969). In *Dytiscus* new cells develop from these regenerative cells as old cells degenerate (Rungius, 1911; Duspiva, 1939). In *Passalus* the regenerative cells are located at the sides of the crypt apparently assuming the function of a digestive gland (Patterson, 1937).

The midgut of larval *Aeshna cynea* is lined by a single layer of epithelium composed of several types of epithelial cells — enterocytes, mucocytes and regenerative cells (Kominick and Kukulies, 1987). The midgut epithelial cells of

Schistocerca gregaria (Bowen, 1968) and *Periplaneta americana* (Couch and Mills, 1968) contain numerous autophagic vacuoles or cytolysosomes derived from mitochondria the size and number of which increase during starvation. The midgut epithelium of the adult honey bee consists of columnar cells, originating from regenerative crypts (Raes *et al.*, 1994). In *Gryllus domesticus* (Srivastava, 1997) the epithelium of the anterior mesenteron is differentiated into functional and regenerative epithelium. The former is made of elongated columnar cells with torn boundaries, brush border and secretory in nature. The latter is made of dome shapely arranged regenerative cells which replace the torn functional epithelial cells. No such differentiation is found in the posterior mesenteron and its cells are without brush border.

Usually lumen surface of the midgut epithelial cells is striated. Its nature is unknown, but the elements of which, it is composed lack basal granules and do not show motile characteristic of cilia (Zilch, 1936; Newell and Baxter, 1936). In *I. limbata* the striated border is not distinct in the midgut epithelial cells. In *Gerris najas* (Werner *et al.*, 1991) the luminal surface of the midgut epithelium is always covered by a coat which is produced by differentiating columnar cells. Such membranous surface coats are considered to be a peculiar form of peritrophic membrane (Burgos and Guitierrez, 1976; Lane and Harrison, 1979).

Neither chitinous intima nor peritrophic membrane which separates the epithelium from food stuff is present on any part of the ventriculus in *I. limbata*. The peritrophic membrane is not a permanent structure, it is secreted as and when food reaches the midgut to protect the latter from abrasion by food particles. Peritrophic membrane has not been reported in gymnocerates (Kurup, 1964), *D. koenigii* (Khanna, 1964), *B. cruciferarum* (Mall, 1979), *D.cingulatus* (Muraleedharan, 1983) and *Laccotrephes robustus* (Pakrutty and Mohamed, 1989a). Although it has been generally held that a peritrophic membrane is absent from Hemiptera, some authors (Kershaw, 1913; Woolley, 1949; Sutton, 1951)

claim to have detected a fragmentary membrane in some insect species. The presence of peritrophic membrane has been reported in *Corixa punctata* (Sutton, 1951) and *Ranatra fusca* (Parsons, 1957), larval lepidopterans (Richards and Davies, 1977), blood sucking insects such as *Cicadella* (Gouranton and Maillet, 1965), mosquitoes and *Glossina* (Moloo *et al.*, 1970; Freeman, 1973). The peritrophic membrane in larvae of *Diabrotica undecimpunctata* (Ryerse *et al.*, 1994) forms along the full length of the midgut epithelium.

The midgut shows difference in histological structure at various regions of it. Based on histological details exhibited by different regions of the midgut, it can be divided into five regions namely first ventriculus, second ventriculus, third ventriculus, fourth ventriculus and fifth ventriculus.

The epithelium of first ventriculus of *I. limbata* is produced into internal folds. Histologically, the epithelium in the anterior region is different from that in the posterior region. In the anterior region, the folds are large consisting of tall columnar cells and short columnar cells. In the posterior region, the epithelium has short columnar cells and cuboidal cells. Similar observations have been reported by Cragg (1914) in *Cimex*, Srivastava and Singh (1966) in *Chrysocoris stollii* and Mall (1979) in *B. cruciferarum*. In *B. cruciferarum* (Mall, 1979) the first ventriculus is differentiated into an anterior and posterior region. Anterior region is provided with much taller epithelial cells with granular and vacuolated cytoplasm. In phytophagous *Lygaeus pandurus* (Goodchild, 1966) the majority of the cells in the first midgut are uninucleate, but some are tri or quadri nucleate and Goodchild (1952) in Cacao capsid bugs observed some quadrinucleate cells among the usually binucleate cells of the midgut epithelium. The short cells are newly formed cells from the regenerative cells. In the posterior part the epithelium has short columnar cells of more or less uniform height with granular cytoplasm.

In *I. limbata*, the anterior region of the first ventriculus just beyond the oesophageal valve, contains tall columnar cells with richly granular cytoplasm. The cytoplasm as well as nuclei are seen more towards the distal end of the cells facing the lumen and the basal region is more vacuolated. In the middle region of the first ventriculus, both tall columnar and short columnar cells are seen, the former seen in the broader region and the latter in the narrower region which contains also cuboidal cells. The tall columnar cells have less granular cytoplasm and are more vacuolated towards the tip of the cells. The short columnar and cuboidal cells have more granular cytoplasm and are less vacuolated and their free ends are flat. In *Spilostethus macilentus* (Singh and Sharma, 1987b) the midgut first has bi and multi nucleate cells of variable size. The cells are large, tall columnar, medium columnar, low columnar and the cuboidal cells. Groups of regenerative cells are distributed at the base of secretory cells and they gradually enlarged to become large columnar vacuolated secretory cells. They also act as absorptive cells.

In *I. limbata* both merocrine and holocrine type of secretion are observed. In the secretory cells the free surface bulges out into lumen to form a vesicular appearance. The blister may fill the entire tip of the cell or part of it. The nuclei are found at a short distance below the vesicle. The enzyme containing vesicle break at their tip and liberate the contents to the lumen. In *B. cruciferarum* (Mall, 1979) and *D. cingulatus* (Muraleedharan, 1983) the principal mode of secretion in the first ventriculus is merocrine.

Midgut epithelium of *I. limbata* also shows mass breakdown where the entire cell containing secretion along with nucleus detaches from the basement membrane and drops into the lumen. Similar nature of secretory activities are reported in *Sigara falleni* (Sutton, 1951), *L. maculatus* (Kurup, 1961a), *R. elongata*, *S. rusticum* (Kurup, 1961b), *Anisops fieveri* (Kurup, 1962), *C. patricius*, *C. gibbosa*, *G. servus* and *D. koenigii* (Kurup, 1964) and *S. macilentus* (Singh and Sharma,

1987b). At certain cells the nuclei fuse to form large nuclei which move to the cell tip and are eventually liberated into the lumen. Similar extrusion of hypertrophied nuclei has been reported in *Laccotrephes robustus* (Pakrutty and Mohamed, 1989b) during digestion i.e., about 2 hours after feeding. But they have observed no secretory activity during starvation.

Sutton (1951) suggests that in the midgut cells of corixids both merocrine and holocrine secretion occur. He thought that the "nucleated vesicles" are degenerate cells. Day and Powning (1949) in *Blatta* and Khan and Ford (1962) in *Dysdercus fasciatus* observed that the extrusion droplets by the midgut epithelium are maximum when the insects are starved and the epithelium appears to be "resting" when the insect is fed. In the digestive tract of *Laccotrephes* and *Ranatra* (Kurup, 1961a, b) which are starved, excessive proliferation and dehiscence of the epithelial cells of the midgut together with fluid secretion of the usual type are noted. The secretory activity is at its maximum when the alimentary tract is empty of food. The secretion from the midgut is a mixture of fluid and cellular debris.

The posterior region of the first ventriculus of *I. limbata* exhibits short columnar cells and cuboidal cells. The cytoplasm of these cells are granular and vacuolated. Nuclei of some cells fuse to form large nucleus surrounded by vacuole and these nuclei move towards the tip of the cell and are liberated into the lumen by breaking the cell tip. The nuclei of midgut cells have a great secretive ability (Bielenin and Weglarska, 1967). According to Wigglesworth (1972) the nuclei of the midgut cells may secrete minute granules (chromidia) migrating to the gut lumen and changing into vacuoles.

The second ventriculus of *I. limbata* is lined with tall columnar cells with richly granular and vacuolated cytoplasm. In the anterior part, the epithelium is produced into occasional infoldings while in the posterior part the epithelium is not produced into folds. It has moderately developed inner circular muscles and

scattered longitudinal muscles. The basement membrane is distinct and supports the epithelium. Both uninucleated and binucleated cells occur in this region and the nuclei are arranged at different regions in the cytoplasm of the cell. At certain cells the nuclei fuse to form large nuclei which move to the cell tip and are eventually liberated into the lumen. It has been reported in *Leptocoris trivittatus* (Woolley, 1949) that the second midgut musculature consists of outer circular muscle and inner longitudinal muscle.

Functionally the second ventriculus of *I. limbata* resembles the first ventriculus and is primarily secretory. The exhausted cells are replaced by the regnerative cells. Similar functional features have been recorded in the second ventriculus of *Anasa tristis* (Breakey, 1936), certain pentatomids and coreids (Goodchild, 1963b; Kurup, 1964), *D. koenigii* (Khanna, 1964), *C. stollii* (Srivastava and Singh, 1966), *B. cruciferarum* (Mall, 1979), *D. cingulatus* (Muraleedharan, 1983) and in *S. macilentus* (Singh and Sharma, 1987b). Some of the cells in this region are filled with secretory material and are multinucleated having basal regenerative part, consisting of many large round spherical nuclei. Such groups detach out their distal secretory part enmass into the lumen. Some other cells in this region are mostly uninucleate having round or oval nuclei in the centre of the cell and are seen more towards the anterior and middle part. The apices of these cells are filled with vacuolated and granular secretory material which is regularly pinched out into the lumen with degenerating nuclei in the form of fine vacuoles. So it is presumed that both holocrine and merocrine mode of secretions occur in this region. The lumen of these regions contain full of secretory material. In the posterior part tall columnar cells have central, oval or round nuclei. Since the epithelial cells of this region do not show any symptom of secretory activity and the lumen is devoid of any material, it has been suggested that the cell debris are absorbed and accumulated as granules at the distal end of the cell. Regenerative cells are present more in number in the middle part than in the anterior and

posterior part, which suggests that the secretory activity is more in the middle part of the second ventriculus. Intense secretory activity has been reported in the second midgut of *Chrysocoris purpureus* (Bhaskaran *et al.*, 1969).

The third ventriculus of *I. limbata* is similar to that of hemipterans studied by Hamner (1936), Khanna (1964), Kurup (1964), Mall (1979), Muraleedharan (1983) and Singh and Sharma (1987b). Histologically it has poorly developed layer of circular and longitudinal muscle fibres. Basement membrane is thick. The single layered epithelium is smooth except for a few occasional low folds all along its length. The cells are mainly tall columnar and short columnar and a few cuboidal cells are seen in between the columnar cells. Most of the cells are uninucleated; some are binucleated and secretory in nature. Two types of nuclei are present. Some of them are small and round while others are large. Nuclei are present either at central or basal part of the cell. The nuclei take very little stain. Failure of the nuclei to take stain may be due to degeneration. Hood (1937) observed maximum secretory activity in the third ventriculus in *Oncopeltus fasciatus*. Some cells are vacuolated. Others contain uniformly distributed cytoplasm. In *B. cruciferarum* (Mall, 1979) the epithelial cells of third ventriculus have faint cytoplasm and only circular muscle layer is present. Lumen of the third ventriculus of *I. limbata* always contains food material. Breaky (1936) in *Anasa tristis* and Harris (1938) in *Murgantia histrionica* have observed a yellowish green substance in the third midgut and considered this region as a storage compartment.

The epithelium of this region in *I. limbata* is thrown out into the lumen with its cytoplasm and ruptured small nuclei presenting a modified type of holocrine secretion. The secretion is also deposited in the apex of some of the secretory cells in the form of vesicles, which later are thrown out into the lumen.

Histologically, the fourth ventriculus of *I. limbata* has moderately developed outer longitudinal and inner circular muscle layers. Basement membrane is thick. The epithelial cells are tall columnar. They are club shaped with long lobe-like tip projecting into the lumen. The lumen is very narrow and shows no deposit of any secretory material. The nuclei are large round and are seen at the centre of the cell. Cytoplasm is uniformly distributed without granules and in some cells small vacuoles are seen at the tip. The above mentioned features together with the reduction in the regenerative cells indicate that they are scarcely secretory. Its function is probably mainly absorption. Goodchild (1966) opined that cells of an absorptive nature, may have a border extended into the lumen as a long lobe as found in the midgut of many phytophagous Hemiptera. The present findings are in agreement with those of Khanna (1964) in *D. koenigii*, Mall (1979) in *B. cruciferarum*, Muraleedharan (1983) in *D.cingulatus* and Singh and Sharma (1987b) in *S. macilentus*.

In *I. limbata* a few regenerative cells are seen singly at the bases of columnar cells. Khanna (1964) also observed regenerative cells which occur singly in the fourth ventriculus of *D. koenigii*. Malouf (1933) reported a reverse arrangement of the muscle in the fourth ventriculus of *Nezara viridula*, the circular muscles being external to the longitudinal ones. Mall (1979) in *B. cruciferarum* observed only circular muscles. In *C. purpureus* (Bhaskaran *et al.*, 1969) the epithelium of fourth ventriculus is not thrown into villi like folds and secretory activity is practically absent in this region. In some Hemiptera Glasgow (1914) observed a dilatation of the fourth ventriculus immediately below the third, but no such dilation was found in *I. limbata*. Food in transit does not appear to remain long in the fourth ventriculus as its lumen is usually empty.

Gastric caeca are found with fourth ventriculus of some gymnocerates. But no gastric caecum is observed in the wall of fourth ventriculus of *I. limbata*. In *C. patricius* (Kurup, 1964) there are four rows of gastric caeca and in *C.gibbosa*

(Kurup, 1964) there are two rows of gastric caeca closely appressed to one another and occuring on the posterior 2/3 of the fourth ventriculus. In *D. suturellus* (Glasgow, 1914), *D. koenigii* (Khanna, 1964; Kurup, 1964), *D. cingulatus* (Muraleedharan, 1983) gastric caeca occur only in females. Both the fourth ventriculus and gastric caeca are wanting in the lygaeid *G. servus* (Kurup, 1964) and *Gerris spinoli* (Kurup, 1966). Glasgow (1914) found both the fourth ventriculus and gastric caeca in some Lygaeidae but a fourth ventriculus without gastric caeca is recorded in lygaeid *Oncopeltus fasciatus* (Hood, 1937). The wall of gastric caeca is made up of a layer of epithelial cells which differ from those of the fourth ventriculus in being short and cuboidal in shape. These cells are uninucleate and are filled with uniformly finely granular cytoplasm (Khanna, 1964).

The fifth ventriculus of *I. limbata* is a very short swollen or globular region in between the fourth ventriculus and the pylorus. There is no separate junctional demarcation externally between the fourth ventriculus and fifth ventriculus as seen in between the other ventriculi. It is the region of the midgut where the ampullae of the Malpighian tubules open. This region in *I. limbata* is regarded as a part of the midgut since it is not lined with chitinous intima, the columnar epithelial cells are like columnar midgut cells and very few regenerative cells are also present. This region has been variously named and considered as a part of the hindgut by many authors even though chitinous intima is not present in this region. It has been termed intestine (Khanna, 1964), ileum (Bhaskaran *et al.*, 1969; Mall, 1979 and Singh and Sharma, 1987c) or pylorus (Kurup, 1964; Muraleedharan, 1983). Snodgrass (1935) has pointed out that the ileum in gymnocerates should be regarded as a segment of the mid-intestine and not to be homologized with the ileum of other insects which is considered as a part of the hind-intestine. Hood (1937) has observed that the ileum of *Oncopeltus fasciatus* does not possess a chitinous intima and based on this feature the author considers the ileum as part of

the midgut. In *B. cruciferarum* (Mall, 1979) the ileum where the tubules open and the anterior part of rectum are all without intima. Rastogi (1962.) is of opinion that the ileum of phytophagus bugs is truely an endodermal part or at least midgut continuation and the ileum of predaceous bugs is truly a proctodaeal region since there is a chitinous lining in it. This condition has been reported in several species (Hood, 1937; Goodchild, 1952; Rastogi, 1962.) which differ from those of several gymnocerates and predaceous bugs in which a chitinous intima is present in the ileum. Some authors (Kurup, 1964; Haridas and Ananthakrishnan, 1981; Muraleedharan, 1983) consider the region where the Malpighian tubules open as pylorus. In bees (Serrao and Cruz-Landim, 1996a) the midgut cells at the transitional region between mid and hindgut are different from the rest and they do not seem to have any role in digestion and absorption, since they have rough endoplasmic reticulum, basal plasmic infoldings and weakly developed mitochondria. In *I. limbata* also the fifth ventriculus which is a transitional region do not seem to have any role in digestion and absorption.

The muscle layer of the fifth ventriculus of *I. limbata* is moderately developed and consists of inner circular and outer longitudinal layer. The epithelium is folded and consists of tall columnar cells. Cells have uniform cytoplasm and are uninucleate or binucleate. Nucleus is located towards tip of the folds. Regenerative cells are very small and few in number. The cells of the ampulla where the Malpighian tubules open are similar to cells of the fifth ventriculus.

The transitional regions between first and second, second and third, third and fourth ventriculi are constricted. The epithelial cells are more compactly arranged here. These regions regulate the flow of food from one ventriculus to the other.

Hindgut

The hindgut of *I. limbata* comprises of a short anterior pylorus and posterior sac-like rectum. The epithelium of the pyloric region is thrown into a series of opposing lobes by the folds of the pyloric valve which project into the lumen. These folds consist of closely packed elongated epithelial cells with indistinct cell boundaries, small round nucleus and clear cytoplasm. A thin layer of chitinous intima is present on the inner surface of the folds. Similar observations has been reported by Khanna (1964), Kurup (1964, 1966) and Mall (1979). The pyloric valve of *I. limbata* is similar to the ileo-rectal valve of *Chrysocoris purpureus* (Bhaskaran *et al.*, 1969) and *Spilostethus macilentus* (Singh and Sharma, 1987c). The pylorus is a transitional region between mid and hindgut that is marked by the pyloric valve which is a fold of the midgut epithelium (Caetano and Lage-Filho, 1982; Caetano, 1984; Lopez-Guerrero and Moron, 1990; Cruz-Landim, 1994). The pyloric valve is formed by a fold of the hindgut epithelium, since it is lined by a cuticle (Caetano and Letizio-Machado, 1982; Serrao & Cruz-Landim, 1996a).

In *Bagrada cruciferarum* (Mall, 1979) the pyloric valve is formed by the dorsal part of the fourth ventriculus and the ventral part of the ileum. The valve is provided with tall cells having deeply staining cytoplasm and rounded nuclei without intima. In *Abedus ovatus* (Goverdhan *et al.*, 1981) there is proctodaeal valve formed by the epithelium of the ileum. Circular muscles of this region probably functions as a sphincter. The wall of the valve is composed of tall columnar epithelial cells resembling those of the fourth midgut. There is no intima but the free cell borders are provided with radial striations. The pyloric valves of *Conocephalus gladiatus* and *Paratenodera sinensis* (Yu, 1980) are composed of the midgut epithelial cells in pyloric portion. But in *Blatella germanica* (Yu, 1980) the pyloric valve is formed by the epithelial cells of anterior hindgut.

In *Phyllophaga tesselata* (Pelton, 1938) the pyloric valve is formed of a slight constriction and differentiation of cells at the region where the large irregular cells of the hindgut arise. The pylorus in gymnocerate Hemiptera (Kurup, 1964) has an epithelial layer of cells with irregular borders and conspicuous nuclei. In *Phalix titan* (Goodchild, 1966) the edges of the pyloric valve is composed of small cuboidal cells with dark-staining nuclei and chitinous intima. In *Phyllophaga anxia* (Berberet and Helms, 1972) a ring of very tall cells extends into the lumen of the pyloric valve. In *D. cingulatus* (Muraleedharan, 1983) the epithelial cells of the pyloric region are club-shaped with irregular borders. Nuclei are also very large and club-shaped. The epithelium of the pylorus of *Dacus cucurbitae* (Zaka-ur-Rab, 1971) is very flat and syncytial. In *Anthonomus grandis* (Mac Gown and Sikorowski, 1981) the intima of the pyloric valve is essentially a large area composed of closely spaced overlapping scale-like plates, each with several caudally projecting teeth.

In *Hyalophora cecropia* (Judy and Gilbert, 1970) the anterior pylorus is thrown into six shallow longitudinal folds which form the pyloric valve. In *Elasmopalpus lignosellus* (Beals and Berberet, 1976) the pyloric valve consists of constricted folds. In Cimicomorpha well defined valves occur anteriorly and posteriorly (Cragg, 1914; Painter, 1930; Goodchild, 1963b). However, pyloric valve is said to be absent among Aphidoidea (Knowlton, 1925; Forbes, 1964; Smith, 1969; Saxena and Chada, 1971). The pyloric valve is also absent in *Acrida cinerea* (Yu, 1980).

In bees the pyloric valve is formed by fold of the hindgut epithelium. The cells of the pyloric valve are cubical and the cuticle of pyloric valve has spine-like structures at the proximal end of the valve, while in the distal end they are lacking (Serrao and Cruz-Landim, 1996a). In the Cryptocerata where a pyloric region is not distinct the tubular anterior part of the hindgut is termed ileum by Goodchild (1966).

The pylorus of *Prodenia litura* (Mathur, 1973), *Manduca sexta* (Reinecke *et al.*, 1973), *Marasmia trapezalis* (Mall, 1980) and *Orthaga exvinacea* (Joseph, 1997) is divisible into 3 regions — anterior, middle and posterior pylorus. There is a pyloric valve which regulates the passage of undigested food from the ileum to the colon.

As in *Gerris spinoli* (Kurup, 1966), in *I. limbata* also the pylorus appears to be a chamber primarily to accommodate and operate the pyloric valve. In *G. spinoli* (Kurup, 1966) the valve is prominent and is a fold of the ventricular epithelium jutting into the lumen of the pylorus. But in *I. limbata* the valve is formed of hindgut epithelium since it is covered by an intima. The valve might be controlling the passage of food from the ventriculus into the rectum and also prevents the back flow of food material (Dallai *et al.*, 1989).

The rectum of *I. limbata* shows regional differentiation of epithelial cells. The dorsal wall is made up of larger dome-shaped cells and the ventral wall is with syncytial epithelium. The rectal epithelium is folded and have a well developed intima that is produced into spines, which is well pronounced on the dorsal wall gland cells. These cells are similar to those identified in *C. patricius, Clavigralla gibbosa, Graptostethus servus* (Kurup, 1964), *P. titan* (Goodchild, 1966) and in *B. cruciferarum* (Mall, 1979). According to Goodchild (1966) there are two main cell types in the epithelium of the hindgut of Hemiptera. One type is a thin syncytium with scattered nuclei and the other is cuboidal cells with large nucleus and eosinophilic cytoplasm. In *B. cruciferarum* (Mall, 1979) the epithelium of the posterior part of the rectum is composed of a uniform syncytium without distinct cell boundaries as in *I. limbata*. But in *Dysdercus koenigii* (Khanna, 1964) and *D. cingulatus* (Muraleedharan, 1983) the whole rectum is composed of syncytial epithelium. The rectum and rectal caecum have a syncytial epithelium in *Sphaerodema rusticum* (Ameen and Imam, 1976). Mall (1979) has also reported the presence of rectal pads in the dorsal wall of rectum in *B. cruciferarum*. The

dorsal half of the epithelium in certain heteropteran insects (Breakey, 1936; Harris,1938; Goodchild, 1952, 1963b, 1966; Kurup, 1964; Bhaskaran *et al.*, 1969) is composed of well defined cuboidal cells with large nucleus and eosinophilic cytoplasm while the ventral half is composed of small cells with highly staining cytoplasm. The first type of cells are supposed to be gland cells. Such glandular cells are reported to be absent from the rectum of *Oncopeltus fasciatus* (Hood, 1937), *Leptocoris trivittatus* (Woolley, 1949) and *Lygaeus pandurus* (Rastogi, 1960). But Bhaskaran *et al.* (1969) is of opinion that these authors might have overlooked the presence of gland cells in the rectum of the insects. In *C. purpureus* (Bhaskaran *et al.*, 1969) the gland cells of the rectal epithelium exhibit difference in the size of their nuclei and in the degree of vacuolisation of their cytoplasm.

There exists some differences of opinion regarding the presence of rectal glands in Heteroptera. Hood (1937), Woolley (1949) and Rastogi (1960) have reported the absence of rectal glands in Hemiptera. According to Goodchild (1952) the Miridae, Brycorinae are the only Hemiptera definitely known to lack rectal gland cells. Miyamoto (1961) did not recognize the rectal gland in Pentatomorph and denied their presence in Cryptocerata. In Reduviids the rectal gland always occupies the anterior end of the rectum (Wigglesworth, 1931a; Bahadur, 1963b; Miyamoto, 1961; Goodchild, 1963b; Haridas and Anathakrishnan, 1981). In Pyrrhocorid *Dysdercus koenigii* (Khanna, 1964) and *D. cingulatus* (Muraleedharan, 1983) rectal pad is absent. But according to Bahadur (1963b) and Goodchild (1966) the rectal glands take the form of pads in Hemiptera. In *Cenocorixa bifida* (Jairal and Scudder, 1970) the rectum show a simple squamous epithelium with a thick cuticle. But no distinct rectal pads or papillae are evident.

According to Palm (1949) in a majority of insects the epithelium of the rectum is modified as a series of pads termed as rectal pads. In others the epithelium is composed of cuboidal gland cells (Wigglesworth, 1932). Based on

cytological features Goodchild (1966) has reported that the gland cells can absorb either water or solute. The gland cells are mainly concerned with the absorption of water from the rectal fluid in *C. purpureus* (Bhaskaran *et al.*, 1969).

The tracheae are present in the rectal gland epithelium of *I. limbata.* The presence of tracheae in the rectal pad epithelium has been observed by many workers. Highly tracheated structure of rectal glands is concenred with important process of salt and water absorption that occurs in the hindgut and their ultra-structure reflects their functions (Baccetti, 1962; Gupta and Berridge, 1966a,b; Berridge and Gupta, 1967; Berridge, 1970; Noirot and Noirot-Timothee,1971; Wall and Oschman, 1973). According to Marshall (1945) the abundance of tracheae in the rectal pad epithelium would propose some extra activity. According to Berlese (1909) resorption of remaining nutrients from the rectal contents takes place in the rectum. Borri (1925) tried to demonstrate the resorption of fat and sugar in the rectal papillae of *Calliphora* but did not succeed. The excreta is dried and concentrated in the rectal sac. The resorption of water plays an important role in the water conservation in insects (Wigglesworth, 1932). The rectal pads of the desert locust and rectal papillae of adult blowfly have been shown to be involved in the uptake of ions and water (Phillips, 1961, 1964a,b,c, 1965, 1969). The presence of heavily granulated cytoplasm, variously shaped multilobate nuclei, and numerous cytoplasmic vacuoles are interpreted as indications of synthetic activity (Beck *et al.*, 1965). Since these characters are found in the rectal gland cells of *I. limbata*, it has been suggested that some synthetic activity may take place in these cells.

The rectal part of the hindgut in *I. limbata* is not provided with any accessory structures whereas a rectal caecum has been observed in cryptocerate Hemiptera (Kurup, 1961a). A rectal caecum is present in *Anasa tristis* (Breakey, 1936), *S. rusticum* (Ameen and Imam, 1976) and in *A. ovatus* (Goverdhan *et al.*, 1981). Woolley (1949) in *L. trivittatus* reported the presence of rectal

diverticulum packed with protozoa in its inner lining but did not give the cellular details. Though rectal caecum is not present in gymnocerates Kurup (1964) is of view that half of their rectal wall with compact cells is histologically akin to the rectal caecum of the cryptocerates where again the epithelial cells are folded and cellular outline is indistinct. Similar histological structures are present in the rectal wall of *I. limbata*. So it may be concluded that these cells perform the same function done by caecum. In a fluid feeder like *I. limbata* it is not essential to conserve water, it is therefore regarded that the rectal gland cells may play a role in the resorption of ions as reported in the secondary cell of the cockroach recta (Wall and Oschman, 1970, 1975). The musculature of the rectal wall of *I. limbata* is poorly developed. Since the musculature of the hindgut is mainly concerned with the formation of excreta and movement of faecal pellets, in a fluid feeder like *I. limbata* the musculature of the rectum is not essential to be well developed.

HISTOLOGICAL CHANGES IN THE MIDGUT OF *IPHITA LIMBATA* DURING DIGESTION

Introduction

In insects, the midgut is known to be the site of digestion, absorption and secretion of digestive enzymes. Drastic histological changes occur in the midgut during feeding and digestion. Very little is known about the histological changes of the midgut epithelium of insects during digestion of a meal and during starvation period apart from the works of Sutton (1951); Parsons (1959); Kurup (1961 a, b, 1962, 1964, 1966); Bhaskaran *et al.* (1969); Tadkowsky and Jones (1978); Muraleedharan (1983); Dimitriadis (1985); Singh and Sharma (1987 b); Pakrutty and Mohamed (1989b) Cruz-Landim and Costa Leonards (1990) and Cruz-Landim *et al.* (1996).

Differences between gut epithelial cells are often recorded and changes are known to occur in relation to development and the stage in a secretory or absorptive cycle. But these descriptions are almost invariably of a qualitative nature. The works of Hecker and Brun (1975) and Rudin and Hecker (1976) on the midgut of mosquitoes and of Pakrutty and Mohamed (1989 b) are notable exceptions. Based on the methodology of Weibel (1969), Hecker and Brun (1975) and Rudin and Hecker (1976) give data on the absolute volumes and surface areas of cells and organelles. Priester (1972) has applied similar methods to changes in the abundance of lysosomes in the midgut of *Calliphora erythrocephala* and Bignell (1980) used this approach in a study of the hindgut cells of *Periplaneta americana* subjecting the results to some statistical treatment.

Morphometric analysis in Hemiptera is limited to the works of Marks (1959), Sabesan and Ramalingam (1978) and Pakrutty and Mohamed (1989 b). It is therefore planned to study the digestive changes that occur in the histology of the midgut epithelium of *Iphita limbata* during digestion.

Materials and Methods

Adult *Iphita limbata* are removed from their rearing containers and kept in separate empty containers. They are allowed to starve for three days. These starved *I. limbata* are grouped into two and are kept separately in two containers. Starved *I. limbata* of one group are fed with banana and those in the second group are fed with soaked green gram. These insects are removed from the containers after the commencement of feeding at various intervals as given below:

At 30 minutes after feeding

At 1 h after feeding

At 2 h after feeding

At 4 h after feeding

At 8 h after feeding

At 16 h after fedding

At 24 h after feeding

At 48 h after feeding

The insects removed from the containers at various intervals after the commencement of different diets are anaesthetised and dissected in Insect Ringer solution under a binocular to remove the entire part of the midgut. The first, second, third and fourth and fifth ventriculi are cut and fixed separately. The tissues are processed, sectioned and stained as described elsewhere. A research microscope was used for observation and for microphotometry. The height of the tall and short columnar cells, height of the cuboidal cells, size of their nuclei etc. are estimated. For the estimation of the size of the cells and their nuclei, five cells and their nuclei in different regions of the sections are measured. The average height of the cells and their nuclei and the standard error are calculated.

Results

Iphita limbata is a phytophagous continuous fluid-feeding insect. The epithelium of the midgut undergoes considerable morphometric and cytological changes at different intervals after feeding. The histological variations could be correlated with the amount of time which had elapsed since feeding. When observations have been made it has been found that considerable changes occur in the midgut epithelium of well-fed adult *Iphita limbata* during the period from 2 to 8 h after feeding. After this period the changes are less significant. No significant changes are found during the period from 24-48 h after feeding. After 48 h the midgut epithelium shows the characteristics of midgut epithelium of starved insects.

a) Presence of food

Table I indicates the approximate time that food is retained in each part of the alimentary canal of *I. limbata* after it has been well-fed. Since most of the insects were found dead at about 72 h after feeding, observations were carried out only upto 48 h after feeding. The food is retained in the foregut for a considerably shorter period of time than in mid and hind guts (Table 1). No significant changes have been observed in the foregut epithelium after consumption of food, whereas changes begin to appear in the midgut epithelium at about 30 minutes after feeding. The food is retained in the foregut for a period of 2 h after feeding and after this period the foregut gradually empties its lumen and becomes completely free of food at about 4 h after feeding. In the midgut, the food is retained in the first ventriculus upto 16 h after feeding and in the second ventriculus upto 48 h after feeding. The food is always present in the third ventriculus and in the fourth ventriculus food is observed for a period upto 24 h after feeding. This is followed by the emptying of food from the midgut and then from the hindgut. The undigested food materials appears in the hindgut at about 2 h after feeding and the

hindgut shows no undigested material at about 24 h after feeding. After 48 h the entire gut is without food material. From this period onwards the insect is considered to be under starvation.

b) Morphometric Analysis

1. *Changes in the midgut epithelium of adult I. limbata fed on banana*

The results of morphometric analysis of the epithelial cells of the different regions of the midgut and their nuclei are given in Tables 2 to 6. In general, the height of the columnar cells and the diameter of their nuclei varied inversely with the time which was elapsed since the insect was well-fed. The insect is considered to be under starvation from 48 h after feeding. In normal insects tall columnar cells with round nucleus situated towards the lumen side has been observed. The size of the columnar cells and that of their nuclei are slightly reduced during starvation.

(i) Changes in the epithelium of the first ventriculus

In the first ventriculus, the size of the cells and their nuclei increase gradually from 30 min. after feeding to 2 h after feeding (Tables 2 & 3). At 1 h after feeding there is a sudden decrease in cell size which increases at 2 h after feeding and after that there is a gradual decrease in the size of the cells and their nuclei upto 24 h. At 48 h after feeding there is a sudden increase in the size of the cells.

Immediately after the fully fed condition, i.e. about 30 min. after feeding, the height of the columnar cells is considerably increased. The increase in height of tall columnar cells is from 73.5 to 123.5μ and that of short columnar cells is from 49.5 to 70.5μ and that of short columnar cells is from 49.5 to 70.5μ in the anterior region of the first ventriculus (Table 2). In the posterior region of the first

ventriculus, the increase in height of tall columnar cells is from 60.5 to 156μ, that of short columnar cells is from 29.5 to 43.5μ and that of cuboidal cells is from 12.5 to 20.5μ (Table 3). The size of the nucleus also increases slightly in the anterior region of the first ventriculus whereas the size of the nucleus does not vary much in the posterior part except in cuboidal cells, where there is an increase in size from 7.5 to 10μ. At this period, the cells (Figs. 48 & 49) are mainly tall columnar, formed into crypts in some parts, whereas they are flat with bulbous tips (Bt) which are vacuolated (v) in other parts. Cells have granular cytoplasm. Nuclei are large and are usually seen towards the basal region. Few are present at cell tip. Cells are either binucleate or multi-nucleate. Regenerative cells (Rgc) are present. Cell tips (Ct) of some cells pinch off (Fig. 50). In the posterior region nuclei move more towars the cell tip and cell tip with cytoplasm and nuclei pinch off into lumen. Two types of cells are mainly seen - tall columnar and short columnar. Cuboidal cells are very few in number. The secretory activity of cells is less in the posterior region compared to anterior part and there are more epithelial folds. Vacuolated cells with large nuclei as seen in starved condition are also absent.

At 1 h after feeding the size of the cells of first ventriculus decreases considerably (Table 2). In the anterior region the height of tall columnar cells decreases from 123.5 to 75μ and that of short columnar cells from 70.5 to 43μ. Similar reduction in size of tall columnar and short columnar cells occurs in the posterior region of the first ventriculus; but there is no change in the size of cuboidal cells (Table 3). The size of the nucleus of these cells increases during this period. Cells (Figs. 51 & 52) are vacuolated at their bases and cytoplasm is seen towards cell tips which appear granular and bulbous (Bt). In some cells, a complete layer of cytoplasm along with nuclei is pinched off into the lumen (Fig.53). Regenerative cells (Rgc) are present. In the posterior region, secretory activity is less. Cells are vacuolated near the cell tip. Regional differentiation into broad and narrow regions are observed. Cuboidal cells are seen in narrow regions.

At 2 h after feeding there is sudden increase in the size of the cells of the first ventriculus. In the anterior part, the height of tall columnar cells increases from 75 to 130μ and that of short columnar cells from 43 to 56μ (Table 2). Similar increase in size of the tall columnar, short columnar and cuboidal cells occurs in the posterior region of the first ventriculus (Table 3). The size of the nucleus does not vary during this period. Cells are more or less similar to those seen at 1 h after feeding. The secretory activity is also of similar nature. Cell tip with cytoplasm and nuclei pinches off (Figs. 54, 55 & 56.Ct). Compared to starved condition, the cells are with more granular cytoplasm. The basement membrane penetrates into the cell layer, which is also observed during starved condition.

The size of the cells of first ventriculus decreases gradually from the period 4 h after feeding to 24 h after feeding. The height of tall columnar cells decreases from 125.5 to 76.5μ during this and that of short columnar cells from 79 to 40μ, in the anterior region of the first ventriculus (Table 2). A similar reduction in size of the tall columnar, short columnar and cuboidal cells was observed in the posterior region of the first ventriculus (Table 3). The height of tall columnar cells decreases from 99 to 35.5μ; that of short columnar cells from 51.5 to 21μ and of cuboidal cells from 19.5 to 12.5μ. The size of the nuclei also decreases during 8 h after feeding to 24 h after feeding from 10 to 7.5μ. The cells have granular cytoplasm and large nuclei. Most of the cells at 16 h after feeding have cytoplasm concentrated towards cell tip along with nuclei. Cell tip is bulbous and flat. These cells have basal region vacuolated with less cytoplasm. Nuclei are also present at the basal region. In certain regions cell tips (Figs. 57 & 58) with little bit of cytoplasm and/nucleus pinch off from the cell at 4 h and 16 h after feeding. In certain other regions a layer of cells with cytoplasm along with nuclei is pinched off from cell tip at 4h, 8 h and 16 h after feeding (Figs. 59 & 60). Cell tips of some cells are vacuolated (Fig. 61). Secretory activity of the cells decreases with the time. In the posterior part, the broad and narrow regions are observed. In the

narrow region, cuboidal and short columnar cells are compactly arranged, their cell tips are flat and continuous, not formed into folds (Fig. 62). Nuclei are round and dense. Cells are with granular cytoplasm. Vacuoles are very few. In broad region, cells are tall and columnar. They are arranged in folds. Cell tip is either flat or bulbous. The bulbous ends of these cells are formed into small vesicles at 16 h after feeding (Fig. 63, vs). Basal region of the cells is with less cytoplasm. From the cell tip, the cytoplasm along with nuclei pinches off into lumen (Fig. 64a). Secretory activity is less than in the anterior region. In the posterior most region, cells are mainly short columnar and cuboidal. These cells are with dense granular cytoplasm and have very few vacuoles (Fig 64b). Nuclei are round and have chromatin granules. Dense granular material is seen at some cell tip.

At 48 h after feeding there is slight increase in the size of the cells of first ventriculus (Table 2). The height of tall columnar cells increases from 76.5 to 112μ and that of short columnar cells from 40 to 45μ in the anterior region of the first ventriculus. A similar increase in size of the tall columnar and short columnar cells was observed in the posterior region of the first ventriculus (Table 3). The height of tall columnar cells increases from 35.5 to 65.5μ and that of short columnar cells from 21 to 29.5μ. The size of the cuboidal cells and the size of the nuclei do not change much. Crypts of the epithelial cells are not prominent. Cells are with granular cytoplasm which is seen more towards the cell tip. Basal region of the cells is with less cytoplasm and with small vacuoles. Nuclei are mainly small and round. They are seen both at basal and cell tip regions. The nuclei of some cells fuse to form a large dark single nucleus which moves towards the tip of the cell and pinches off into lumen (Fig. 65, NB). Cell tip is bulbous and darkly stained. Cell tips of some cells are vacuolated. In the posterior part, the epithelium shows broad and narrow regions. Broad region has tall columnar cells and narrow region has short columnar cells and cuboidal cells. Cells are with granular cytoplasm and round nuclei. In some cells, vacuoles with large nucleus

are seen (Fig. 66). Cells are not formed into crypts and their tips are flat. Nuclei are scattered in the central or at the basal region. Very little secretory activity is found in this region.

(ii) Changes in the epithelium of second ventriculus

In the second ventriculus the cells are mainly of two types - tall columnar and short columnar cells. The height of both types of cells at 30 min. after feeding increases considerably (Table 4). The height of tall columnar cells increases from 79.5 to 99μ and that of short columnar cells from 45 to 63μ. The cells are formed into crypts. Cells have granular cytoplasm and round nuclei. Nuclei are seen in the central part of the cell and some are seen at the tip. Some nuclei fuse to form large nucleus. Cell tip of some cells are bulbous. Cytoplasm accumulates towards cell tip and along with nuclei, it pinches off into the lumen (Fig. 67). Regenerative cells are fewer in number than in the epithelium of first ventriculus.

From 1 h after feeding to 2 h after feeding there is a slight decrease in the size of the cells of second ventriculus (Table 4). The height of tall columnar cells decreases from 99 to 75.5μ and that of short columnar cells from 63 to 42μ. Cells are seen in crypts. Cells are with granular cytoplasm and their tips are bulbous and flat. Nuclei are seen more towards basal region and some cell tip along with cytoplasm and nuclei pinch off into lumen (Figs. 68 & 69). At 2 h period cells become vacuolated at the basal region and towards cell tip cytoplasm is granular (Figs. 70 a & 70 b). Nucleus is slightly larger in size. Regenerative cells are seen; but fewer in number. Basement membrane penetrates into the cell layer.

At 4 h after feeding there is a sudden increase in the height of cells of second ventriculus (Table 4). The height of tall columnar cells increases from 75.5 to 112.5μ and that of short columnar cells increases from 42 to 76.5μ. Cells are very tall formed into crypts and contains granular cytoplasm which is accumulated more towards cell tip. Basal region of these cells are with less cytoplasm and

mostly vacuolated. Nuclei are round and seen more towards the cell tip. Nuclei (Figs. 71 & 72) fuse to form dark dense material, the nucleated bodies (NB) which move to cell tip and pinch off into lumen. Food materials are present in large amount in the lumen. Not only the nucleated bodies, but also the cytoplasm along with nuclei pinch off from the cell tips.

From 8 h (Figs. 73 & 74) to 16 h (Figs. 75 & 76) after feeding, the size of the cells of second ventriculus further decreases (Table 4). The height of tall columnar cells decreases from 81 to 61μ and that of short columnar cells from 36 to 34μ. Cells are with granular cytoplasm and are not formed into crypts. The cytoplasm is seen more towards the cell tip. Some cell tips are bulbous and vacuolated. Basal region is mostly with less cytoplasm and with vacuoles. But the vacuoles are lesser in number. Nuclei are round and are located either at basal region or at cell centre. In some cells, the cell tip breaks off into lumen.

From 24 h after feeding to 48 h after feeding the size of the cells again increases (Table 4). The height of tall columnar cells increases from 89.5 to 104.5μ and that of short columnar cells from 46.5 to 62.5μ. Cells are tall and narrow and their tips are bulbous and darkly stained. Cytoplasm is granular and with small vacuoles. Nuclei are small, round and mostly seen at the centre of the cell. Some are present at cell tip. Tips of some cells are vacuolated and break off into lumen (Figs. 77 & 78). Lumen contains food material.

(iii) Changes in the epithelium of third ventriculus

Third ventriculus can be regarded as the retention chamber as food is always present in this region. There is a slight increase at about 30 min. after feeding in the size of the cells of third ventriculus (Table 5). The height of the tall columnar cells increases from 101 to 106.25μ and that of short columnar cells from 58 to 63.5μ. The size of the nucleus of these cells also increases slightly from 7.5 to 10μ and 8.5 to 9μ. Cells are seen in folds and most of the cells are

vacuolated. Cytoplasm is seen towards the cell tip. Cell tip break off and cytoplasm and nuclei are liberated into the lumen (Figs. 79 a & 79 b). Nuclei are large, round fewer in number.

During the period from 1 h after feeding to 2 h after feeding, the size of the cells decreases (Table 5). The height of tall columnar cells decreases from 76 to 71.5μ and that of short columnar cells from 49 to 38μ. The size of the nuclei does not vary much. Nuclei are large and round and is seen towards basal region. Basal region of some cells are vacuolated. Regenerative cells are present. Basement membrane penetrates into the cell layer. At 1 h after feeding the cells are with granular cytoplasm and their tips are bulbous (Fig. 80). At 2 h after feeding the cell tips of some cells break off liberating granular material (Fig. 81).

The size of the cells again increases at 4 h after feeding (Table 5). The height of tall columnar cells increases from 71.5 to 81μand that of short columnar cells increases from 38 to 52.5μ. Most of the cells are vacuolated with less cytoplasm. Nuclei are round large with less chromatin granules and cell tip breaks off liberating material into the lumen (Fig. 82).

At 8 h after feeding there is a sudden decrease in the size of the cell (Table 5). The height of the tall columnar cells decreases from 81 to 45.5μ and that of short columnar cells decreases from 52.5 to 31μ. The size of the nuclei does not change. Cells are with granular cytoplasm which is accumulated towards cell tip. Cell tip is bulbous. Both basal regions and apical regions of some cells are vacuolated. Cell tips with cytoplasm break off into lumen (Fig. 83 & 84). In some cells cytoplasm is thick and granular. The granules in the digested food material present in the lumen are similar in colour and nature of the granules found in the cytoplasm of the cells. Nuclei are seen towards cell tip or at basal region.

From 16 h after feeding to 48 h after feeding, the size of the columnar cells increases steadily (Table 5). The height of tall columnar cells increases from 83.5

to 129.5μ and that of short columnar cells from 39.5 to 80μ. Cells are with granular cytoplasm which is seen more towards the cell tip. At 16 h (Fig. 85) after feeding at certain regions the cell tips elongate and break off into lumen. During the period between 16 h (Fig. 86) and 24 h (Fig. 87) at certain regions cells show granular cytoplasm with accumulated digested food material at the periphery of the cells with clear cell limits towards the lumen. Basal regions of some cells at 48 h after feeding are with less cytoplasm and with vacuoles (Fig. 88) and in some cells, cell tips become elongated and vacuolated and their tips break off (Fig. 89). Nuclei are small, round and mostly located towards basal region or at centre. Basement membrane penetrates into cell layer. Lumen is with less digested food material.

(iv) Changes in the epithelium of fourth ventriculus

The epithelium of fourth ventriculus consists of tall columnar cells only and these cells show less secretory activity. But their size varies slightly during different periods of time after feeding (Table 6). At about 30 min. after feeding there is slight increase in the height of the cells from 80 to 92μ. The size of the nuclei also inceases from 7.5 to 10μ. The tall columnar cells (Fig. 90) are arranged compactly and large nuclei are seen arranged in a row at the centre of the cell. Cell tips of some cells bulge and break off. The lumen is free of any material.

At 1 hour after feeding there is a sudden decrease in the cell size (Table 6). The height of the cell decreases from 92 to 61.5μ and the size of the nucleus also decreases from 10 to 7.5μ. The structure of the cells does not change much from that of cells at 30 min. after feeding. In most of the cells, (Fig. 91) cytoplasm is seen more towards the cell tips. Vacuoles are very few. Regenerative cells (Rgc) are present. Basal region is with less cytoplasm.

At 2 h after feeding there is a slight increase in the size of the cells. The height increases from 61.5 to 78.5μ. The size of the nuclei also increases from 7.5

to 10μ. Cells are with granular cytoplasm and vacuolated towards cell tip. Some cells (Fig. 92) have dark granular bodies (NB) which are seen towards the cell tip. Nuclei are seen at basal region.

From 4 h after feeding to 16 h after feeding the height of the cells decreases from 73 to 48μ (Table 6). The size of the nucleus also decreases slightly. Cells are tall columnar, compactly arranged with granular cytoplasm. Vacuoles are very few. Cell tip is bulbous and tips of some cells pinch off into lumen (Figs. 93 & 94). Nuclei are round and seen mostly towards the centre of the cell. Some nuclei are seen towards the cell tip. Regenerative cells are seen.

From 24 h after feeding to 48 h after feeding the height of cells increases slightly from 56.5 to 72μ (Table 6). The size of the nucleus does not vary much. The structure of the cells is similar. Tall narrow columnar cells are compactly arranged with uniform granular cytoplasm. Cell tip is elongated and pointed. Cell tips of some cells are vacuolated. They pinch off into the lumen (Fig. 95). Nuclei are large and centrally arranged in a row. Lumen is narrow without any food material. Regenerative cells are present but very few in number. Secretory activity is very much less.

There is no change in the structure as well as secretory activity of the cells of fifth ventriculus.

2. *Changes in the gut epithelium of adult I. limabta fed on green gram*

The results of morphometric analysis of the epithelial cells of different regions of the midgut and their nuclei are given in Tables 7-11. There is no general pattern in the changes of the sizes of cells and their nuclei during different periods of time. But after feeding, there is slight increase in the cell size when compared to the starved condition.

(i) Changes in the epithelium of first ventriculus

At about 30 min. after feeding the size of the cells as well as their nuclei slightly increases (Tables 7 & 8). In the anterior region of first ventriculus, the height of tall columnar cells increases from 73.5 to 114.5μ and that of short columnar cells from 49.5 to 54.5μ (Table 7). In the posterior region of the first ventriculus, the increase in height of tall columnar cells is from 60.5 to 64.5μ (Table 8). Short columnar cells have no change in size whereas the height of cuboidal cells increases from 12.5 to 17μ. In most of the cells, the cytoplasm as well as nuclei are seen towards the lumen side and the basal region is vacuolated. Cell tip along with cytoplasm and nuclei break off (Figs. 96 & 97). The lumen contains cell fragments. Regenerative cells are present. Nuclei are round and small. Compared to anterior region the secretory activity is less in the posterior region (Fig. 98). Cells are mostly with flat tips.

From 1 h after feeding to 2 h after feeding the size of the cells decreases. The height of tall columnar cells decreases from 94.5 to 82.5μ and that of short columnar cells from 44 to 39μ in the anterior region of the first ventriculus (Table 7). At the same time, there is an increase in size of tall columnar cells in the posterior region (Table 8). It increases from 79.5 to 97μ. A slight decrease in size occurs in short columnar cells and cuboidal cells. It decreases from 46.5 to 43.5μ and from 24.5 to 20μ respectively. The size of the nucleus does not vary much. The cells are seen in low folds or crypts. The cytoplasm of the cells is granular. The cytoplasm as well as nucleus are seen more towards cell tip and it is darkly stained. Cell tip is bulbous and tips of some cells are vacuolated (Figs. 99 & 100) and break off into lumen. Basal regions of some cells are vacuolated. Lumen contains food material towards posterior region.

From 4 h after feeding to 8 h after feeding there is an increase in cell size. The tall columnar cells increase in height from 92 to 103μ and short columnar cells

increase in height from 92 to 103μ and short columnar cells increase in height from 42.5 to 52.5μ in the anterior region of first ventriculus (Table 7). The size of the nucleus does not change much. In the posterior region, the height decreases from 64.5 to 53.5μ, from 41 to 31.5μ and from 22.5 to 21.5μ of tall columnar, short columnar and cuboidal cells respectively (Table 8). There is no change in the size of the nucleus. Columnar cells are seen in folds. Cell tip is bulbous and cytoplasm and nuclei are seen at the tip (Fig. 101). Small vacuoles are present in the cell at the basal region. In the posterior part, cells are not formed into crypts. Cell tip is bulbous with granular cytoplasm and are darkly stained (Fig. 102). Nuclei are small and round. These nuclei are seen in the central region of the cell or towards the basal region of the cell. Cell tips of some cells are vacuolated and break off into lumen. Lumen contains food material. Regenerative cells are present.

From 16 h after feeding to 48 h after feeding the size of the cells increases slightly. In the anterior region the height of tall columnar cells increases from 86 to 107μ and that of short columnar cells from 51.5 to 58μ (Table 7). In the posterior region the height of tall columnar cells and short columnar cells increases from 57 to 86μ and 38.5 to 49μ respectively (Table 8). At the same time the height of the cuboidal cells slightly decreases from 22 to 18.5μ and then increases to 19.5μ at 48 h after feeding. The size of the nuclei does not change. Cells are formed into low folds. Cytoplasm and nuclei are concentrated towards the cell tip. Tip is bulbous and flat. Some cell tips are vacuolated. Nuclei are also seen at basal region. Basal region is slightly vacuolated (Figs. 103, 104 & 105). Lumen contains material.

ii) Changes in the epithelium of second ventriculus

At about 30 min. after feeding there occurs slight decrease in the size of the cells of second ventriculus (Table 9). The height of tall columnar cells decreases

from 79.5 to 78.5μ and that of short columnar cells from 45 to 38.5μ. The size of the nuclei does not vary much. At this period cells are with granular cytoplasm. A very few vacuoles are found in the cytoplasm. Cell tip is bulbous and some cells have vacuoles at their tip. Nuclei are seen mostly towards the centre of cell and lumen contains food material (Fig. 106).

From 1 h after feeding to 4 h after feeding there is an increase in the size of the cells (Table 9). The height of tall columnar cells and short columnar cells increases from 78.5 to 93.5μ and from 42.5 to 56.5μ respectively. The size of the nuclei does not change much. Cells are mostly of tall columnar type. Only a few cells are of short type and both these types of cells are involved in the formation of crypts. Cytoplasm and nuclei are seen more towards cell tip and it is bulbous. The basal region of the cells are vacuolated. Cell tip of some cells break off (Fig. 107). Nuclei are small and round. Lumen contains food material.

From 8 h after feeding to 24 h after feeding, the size of the cells decreases (Table 9). The height of tall columnar cells decreases from 83.5 to 77.5μ and that of short columnar cells from 52.5 to 42.5μ. The size of the nuclei does not change. The cells have fine cytoplasm and nuclei are accumulated towards cell tip. The basal region of the cells are vacuolated. Some cells have vacuolated tips. Cell tips of some cells break off. Nucleus is small and round. Some nuclei are seen at cell tip and some others are found in the central region (Fig. 108). Lumen contains food material.

At 48 h after feeding there is slight increase in the cell size (Table 9). The height of tall columnar cells and short columnar cells increase from 77.5 to 102.5μ and from 42.5 to 49μ respectively. The size of the nucleus does not change. Cells are mostly tall columnar and narrow. They are compactly arranged. Lumen is also narrow and contains material. Cell tip is bulbous, darkly stained and contains

granular cytoplasm. Nuclei are seen in a row at central region of the cell. Some cells are vacuolated (Fig. 109).

(iii) Changes in the epithelium of third ventriculus

The size of the cells of third ventriculus steadily decreases from about 30 min. to 2 h after feeding (Table 10). The height of tall columnar cells decreases from 95.5 to 80μ and that of short columnar cells from 45.5 to 40.5μ. The size of the nucleus does not vary much. At 1 h period cytoplasm is seen more towards the cell tip. The cell tip of some cells breaks off (Fig. 110). The nuclei are seen at basal or central region of cells. Lumen contains less material. At 2 h period cells are mostly vacuolated (Fig. 111).

At 4 h after feeding there is an increase in the size of the cells and after that upto 16 h after feeding, the size of the cells decreases (Table 10). The height of tall columnar cells decreases from 120.5 to 96μ and that of short columnar cells decreases from 71.5 to 56.5μ. There is no conspicuous change in the size of the nucleus. Some cells are vacuolated whereas others have granular cytoplasm. The tips of some cells are elongated, bulbous (Fig. 112). Some cell tips are vacuolated. The nuclei are small round and are present at basal or central region. Cell tips of some cells break off (Fig. 113).

From 24 h after feeding to 48 h after feeding the height of the tall columnar cells increases from 107 to 111μ whereas that of short columnar cells decreases at 24 h after feeding from 56.5 to 41μ and then increases at 48 h after feeding to 67μ. The nucleus shows no conspicuous change. Some cells are mostly vacuolated at their tips. Cell tip contains granular cytoplasm in some cells and it is bulbous and darkly stained. Nuclei are small, round and are seen at central or basal region. Cell tips of some cells break off. Lumen contains material (Fig. 114).

(iv) Changes in the epithelium of fourth ventriculus

At about 30 min. after feeding, the size of the columnar cells of fourth ventriculus decreases from 80 to 65.5μ (Table 11). But the size of the nucleus does not change. Cells are tall, narrow, columnar, compactly arranged and their tips are either bulbous or pointed. The cytoplasm in some cells are with few vacuoles. Nuclei are seen towards basal region. Cell tips of some cells break off (Fig. 115).

At 1 h after feeding there is slight increase in cell height from 65.5 to 78μ and thereafter upto 4 h after feeding the height of the cell decreases slightly from 78 to 74μ. The size of the nucleus increases slightly. The cells are with granular cytoplasm and their tips are bulbous. Nucleus is seen at central or basal region. Some cells have vacuolated tips. Lumen contains material (Fig. 116).

At 8 h after feeding the height of cells increases from 74 to 78μ and then decreases to 68.5μ at 16 h after feeding. Thereafter there is slight increase in cell height. The height of the cell is 70μ at 24h after feeding and 71.5μ at 48 h after feeding. The nucleus shows no change in their size. Cells are tall, columnar, narrow with bulbous or pointed tips. Some cells are vacuolated. Others contain cytoplasm. Cell tips of some cells break off (Fig. 117). Nuclei are round and are seen at basal or central region. Lumen contains no material.

There is no change in the structure as well as secretory activity of the cells of fifth ventriculus.

TABLE 1

Approximate maximum time food is retained in various subdivisions of alimentary canal of adult *Iphita limbata*

Condition of Insect	Foregut	Midgut				Hindgut
		First Ventriculus	Second Ventriculus	Third Ventriculus	Fourth Ventriculus	
Normal	-	-	-	+	-	-
1/2 h.a.f.	+	+	+	+	-	-
1 h.a.f.	+	+	+	+	-	-
2 h.a.f.	+	+	+	+	±	±
4 h.a.f.	-	+	+	+	±	±
8 h.a.f.	-	+	+	+	±	±
16 h.a.f.	-	±	+	+	±	±
24 h.a.f.	-	-	±	+	±	-
48 h.a.f.	-	-	±	+	-	-

h.a.f = hour after feeding
\+ = presence of food
\- = absence of food
± = only very little food is present.

TABLE 2

Morphometric data of epithelium in the anterior region of first ventriculus of adult *I. limbata* fed on banana

Condition of insect	Tall Columnar Cells			Short Columnar Cells		
	Height	Width	Nucleus size	Height	Width	Nucleus size
Normal	73.5 ± 0.54	12.5 ± 0.27	7.5 ± 0.00	49.5 ± 0.59	10.0 ± 0.00	7.5 ± 0.00
1/2 h.a.f.	123.5 ± 1.75	13.5 ± 0.22	9.0 ± 0.22	70.5 ± 0.52	10.5 ± 0.18	9.0 ± 0.00
1 h.a.f.	75.0 ± 0.98	11.0 ± 0.22	10.0 ± 0.00	43.0 ± 0.22	13.5 ± 0.22	10.0 ± 0.00
2 h.a.f.	130.0 ± 0.80	11.0 ± 0.22	10.0 ± 0.00	56.0 ± 0.67	11.0 ± 0.22	10.0 ± 0.00
4 h.a.f.	125.5 ± 1.21	11.0 ± 0.22	9.0 ± 0.22	79.0 ± 1.28	11.0 ± 0.22	10.0 ± 0.00
8 h.a.f.	110.5 ± 0.33	10.5 ± 0.18	10.0 ± 0.00	50.5 ± 0.59	10.5 ± 0.18	10.0 ± 0.00
16 h.a.f.	94.5 ± 0.33	10.0 ± 0.00	7.5 ± 0.00	45.5 ± 0.33	10.5 ± 0.18	7.5 ± 0.00
24 h.a.f.	76.5 ± 0.54	8.5 ± 0.22	7.5 ± 0.00	40.0 ± 0.28	8.5 ± 0.22	7.5 ± 0.00
48 h.a.f.	112.0 ± 0.33	10.0 ± 0.00	7.5 ± 0.00	45.0 ± 0.28	14.5 ± 0.18	7.5 ± 0.00

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

TABLE 3

Morphometric data of epithelium in the posterior region of first ventriculus of adult *I. limbata* fed on banana

Condition of Insect	Tall Columnar Cells			Short Columnar Cells			Cuboidal Cells		
	Height	Width	Nucleus size	Height	Width	Nucleus size	Height	Width	Nucleus size
Normal	60.5 ± 0.33	10.0 ± 0.00	7.5 ± 0.00	29.5 ± 0.77	10.0 ± 0.00	7.5 ± 0.00	12.5 ± 0.00	10.0 ± 0.00	7.5 ± 0.00
1/2 h.a.f.	156.0 ± 1.84	12.5 ± 0.28	7.5 ± 0.00	43.5 ± 0.46	11.0 ± 0.22	7.5 ± 0.00	20.5 ± 0.33	18.5 ± 0.22	10.0 ± 0.00
1 h.a.f.	92.0 ± 0.52	13.5 ± 0.22	10.0 ± 0.00	35.0 ± 0.33	10.5 ± 0.18	10.0 ± 0.00	20.5 ± 0.33	18.5 ± 0.22	10.0 ± 0.00
2 h.a.f.	130.5 ± 0.91	10.5 ± 0.18	10.0 ± 0.00	53.0 ± 0.52	9.5 ± 0.18	10.0 ± 0.00	30.0 ± 0.49	18.5 ± 0.22	10.0 ± 0.00
4 h.a.f.	99.0 ± 1.78	8.5 ± 0.22	10.0 ± 0.00	51.5 ± 0.67	10.5 ± 0.18	10.0 ± 0.00	19.5 ± 0.52	20.0 ± 0.40	10.0 ± 0.00
8 h.a.f.	64.5 ± 0.91	11.0 ± 0.22	10.0 ± 0.00	34.0 ± 0.46	11.0 ± 0.22	10.0 ± 0.00	18.5 ± 0.28	14.0 ± 0.22	10.0 ± 0.00
16 h.a.f.	52.0 ± 0.33	10.0 ± 0.00	7.5 ± 0.00	28.5 ± 0.46	10.5 ± 0.18	7.5 ± 0.00	18.0 ± 0.22	13.0 ± 0.18	10.0 ± 0.00
24 h.a.f.	35.5 ± 0.33	10.5 ± 0.18	7.5 ± 0.00	21.0 ± 0.22	7.5 ± 0.00	7.5 ± 0.00	12.5 ± 0.00	10.0 ± 0.00	7.5 ± 0.00
48 h.a.f.	65.5 ± 0.33	10.0 ± 0.00	7.5 ± 0.00	29.5 ± 0.77	10.0 ± 0.00	7.5 ± 0.00	12.5 ± 0.00	10.0 ± 0.00	8.5 ± 0.22

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

TABLE 4

Morphometric data of epithelium of second ventriculus of adult *I. limbata* fed on banana

Condition of insect	Tall Columnar Cells			Short Columnar Cells		
	Height	Width	Nucleus size	Height	Width	Nucleus size
Normal	79.5 ± 0.82	16.0 ± 0.22	7.5 ± 0.00	45.0 ± 0.85	13.5 ± 0.22	7.5 ± 0.00
1/2 h.a.f.	99.0 ± 0.67	9.5 ± 0.18	7.5 ± 0.00	63.0 ± 0.33	9.0 ± 0.22	7.5 ± 0.00
1 h.a.f.	90.0 ± 0.49	11.5 ± 0.22	7.5 ± 0.00	52.5 ± 0.40	10.0 ± 0.00	7.5 ± 0.00
2 h.a.f.	75.5 ± 1.07	11.0 ± 0.22	10.0 ± 0.00	42.0 ± 0.33	11.0 ± 0.22	10.0 ± 0.00
4 h.a.f.	112.5 ± 1.23	9.0 ± 0.22	10.0 ± 0.00	76.5 ± 1.18	9.5 ± 0.18	10.0 ± 0.00
8 h.a.f.	81.0 ± 1.48	10.0 ± 0.00	8.0 ± 0.18	36.0 ± 0.36	11.0 ± 0.22	8.0 ± 0.18
16 h.a.f.	61.0 ± 0.61	11.0 ± 0.22	10.0 ± 0.00	34.0 ± 0.46	10.0 ± 0.00	7.5 ± 0.00
24 h.a.f.	89.5 ± 0.33	7.5 ± 0.00	5.0 ± 0.00	46.5 ± 0.46	7.5 ± 0.00	5.0 ± 0.00
48 h.a.f.	104.5 ± 0.82	11.0 ± 0.22	7.5 ± 0.00	62.5 ± 0.49	10.5 ± 0.18	7.5 ± 0.00

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

TABLE 5

Morphometric data of epithelium of third ventriculus of adult *I. limbata* fed on banana

Condition of Insect	Tall Columnar Cells			Short Columnar Cells		
	Height	Width	Nucleus size	Height	Width	Nucleus size
Normal	101.0 ± 1.08	12.5 ± 0.00	7.5 ± 0.00	58.0 ± 1.11	11.5 ± 0.22	8.5 ± 0.22
1/2 h.a.f.	106.25 ± 0.67	11.0 ± 0.22	10.0 ± 0.00	63.5 ± 1.18	12.5 ± 0.00	9.0 ± 0.22
1 h.a.f.	76.0 ± 0.67	12.5 ± 0.00	10.0 ± 0.00	49.0 ± 0.46	12.0 ± 0.18	10.0 ± 0.00
2 h.a.f.	71.5 ± 0.86	10.0 ± 0.28	10.0 ± 0.00	38.0 ± 0.87	10.5 ± 0.18	10.0 ± 0.00
4 h.a.f.	81.0 ± 1.0	10.5 ± 0.18	10.0 ± 0.00	52.5 ± 0.40	10.5 ± 0.18	10.0 ± 0.00
8 h.a.f.	45.5 ± 0.18	11.5 ± 0.22	10.0 ± 0.00	31.0 ± 0.22	11.0 ± 0.22	10.0 ± 0.00
16 h.a.f.	83.5 ± 1.51	10.5 ± 0.18	7.5 ± 0.00	39.5 ± 0.33	11.5 ± 0.22	7.5 ± 0.00
24 h.a.f.	101.5 ± 0.78	11.0 ± 0.22	7.5 ± 0.00	49.5 ± 1.33	10.0 ± 0.00	7.5 ± 0.00
48 h.a.f.	129.5 ± 0.71	11.0 ± 0.22	7.5 ± 0.00	80.0 ± 0.85	10.5 ± 0.18	7.5 ± 0.00

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

TABLE 6

Morphometric data of the epithelium of fourth ventriculus of adult *I. limbata* fed on banana

Condition of Insect	Tall Columnar Cells		
	Height	Width	Nucleus size
Normal	80.0 ± 0.49	8.5 ± 0.22	7.5 ± 0.00
1/2 h.a.f.	92.0 ± 0.66	8.5 ± 0.22	10.0 ± 0.00
1 h.a.f.	61.5 ± 0.46	7.5 ± 0.00	7.5 ± 0.00
2 h.a.f.	78.5 ± 0.61	10.0 ± 0.00	10.0 ± 0.00
4 h.a.f.	73.0 ± 0.44	10.5 ± 0.18	9.0 ± 0.22
8 h.a.f.	66.5 ± 0.61	12.0 ± 0.18	9.0 ± 0.22
16 h.a.f.	48.0 ± 0.44	7.5 ± 0.00	7.5 ± 0.00
24 h.a.f.	56.5 ± 0.78	7.5 ± 0.00	7.5 ± 0.00
48 h.a.f.	72.0 ± 0.71	7.5 ± 0.00	7.5 ± 0.00

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

TABLE 7

Morphometric data of epithelium in the anterior region of first ventriculus of adult *I. limbata* fed on green gram

Condition of insect	Tall Columnar Cells			Short Columnar Cells		
	Height	Width	Nucleus size	Height	Width	Nucleus size
Normal	73.5 ± 0.54	12.5 ± 0.27	7.5 ± 0.00	49.5 ± 0.59	10.0 ± 0.00	7.5 ± 0.00
1/2 h.a.f.	114.5 ± 0.96	10.5 ± 0.18	8.5 ± 0.22	54.5 ± 0.71	14.0 ± 0.22	7.5 ± 0.00
1 h.a.f.	94.5 ± 1.9	11.0 ± 0.22	7.5 ± 0.00	44.0 ± 0.22	11.5 ± 0.22	7.5 ± 0.00
2 h.a.f.	82.5 ± 0.85	12.0 ± 0.18	7.5 ± 0.00	39.0 ± 0.61	10.5 ± 0.18	7.5 ± 0.00
4 h.a.f.	92.0 ± 0.87	12.0 ± 0.18	7.5 ± 0.00	42.5 ± 0.40	9.5 ± 0.18	7.5 ± 0.00
8 h.a.f.	103.0 ± 0.96	11.0 ± 0.22	7.5 ± 0.00	52.5 ± 0.94	9.5 ± 0.18	8.0 ± 0.18
16 h.a.f.	86.0 ± 1.04	9.5 ± 0.18	7.5 ± 0.00	51.5 ± 0.78	11.5 ± 0.22	7.5 ± 0.00
24 h.a.f.	86.5 ± 0.46	11.0 ± 0.22	7.5 ± 0.00	55.0 ± 0.49	12.0 ± 0.18	7.5 ± 0.00
48 h.a.f.	107.0 ± 0.77	10.5 ± 0.18	7.5 ± 0.00	58.0 ± 0.52	11.0 ± 0.22	7.5 ± 0.00

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

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TABLE 8

Morphometric data of epithelium in the posterior region of first ventriculus of adult *I. limbata* fed on green gram

Condition of Insect	Tall Columnar Cells			Short Columnar Cells			Cuboidal Cells		
	Height	Width	Nucleus size	Height	Width	Nucleus size	Height	Width	Nucleus size
Normal	60.5 ± 0.33	10.0 ± 0.00	7.5 ± 0.00	29.5 ± 0.77	10.0 ± 0.00	7.5 ± 0.00	12.5 ± 0.00	10.0 ± 0.00	7.5 ± 0.00
1/2 h.a.f.	64.5 ± 0.59	12.5 ± 0.18	8.5 ± 0.22	29.5 ± 0.52	11.0 ± 0.22	9.0 ± 0.22	17.0 ± 0.33	13.0 ± 0.18	8.0 ± 0.18
1 h.a.f.	79.5 ± 0.71	10.5 ± 0.18	7.5 ± 0.00	46.5 ± 0.46	11.0 ± 0.22	7.5 ± 0.00	24.5 ± 0.33	19.5 ± 0.33	7.5 ± 0.00
2 h.a.f.	97.0 ± 1.42	12.0 ± 0.18	7.5 ± 0.00	43.5 ± 0.46	10.5 ± 0.18	7.5 ± 0.00	20.0 ± 0.28	16.5 ± 0.22	7.5 ± 0.00
4 h.a.f.	64.5 ± 0.52	11.0 ± 0.22	7.5 ± 0.00	41.0 ± 0.22	10.5 ± 0.18	7.5 ± 0.00	22.5 ± 0.4	20.0 ± 0.28	7.5 ± 0.00
8 h.a.f.	53.5 ± 0.67	12.0 ± 0.18	7.5 ± 0.00	31.5 ± 0.61	12.5 ± 0.00	7.5 ± 0.00	21.5 ± 0.22	19.5 ± 0.33	7.5 ± 0.00
16 h.a.f.	57.0 ± 0.91	12.0 ± 0.18	7.5 ± 0.00	38.5 ± 0.22	12.0 ± 0.18	7.5 ± 0.00	22.0 ± 0.33	19.0 ± 0.22	7.5 ± 0.00
24 h.a.f.	82.5 ± 0.85	9.5 ± 0.18	7.5 ± 0.00	45.5 ± 0.71	12.0 ± 0.18	7.5 ± 0.00	18.5 ± 0.22	20.5 ± 0.33	7.5 ± 0.00
48 h.a.f.	86.0 ± 0.85	9.5 ± 0.18	7.5 ± 0.00	49.0 ± 0.46	9.0 ± 0.46	7.5 ± 0.00	19.5 ± 0.18	20.5 ± 0.33	7.5 ± 0.00

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

1971

TABLE 9

Morphometric data of epithelium of second ventriculus of adult *I. limbata* fed on green gram

Condition of insect	Tall Columnar Cells			Short Columnar Cells		
	Height	Width	Nucleus size	Height	Width	Nucleus size
Normal	79.5 ± 0.82	16.0 ± 0.22	7.5 ± 0.00	45.0 ± 0.85	13.5 ± 0.22	7.5 ± 0.00
1/2 h.a.f.	78.5 ± 0.54	8.5 ± 0.22	7.5 ± 0.00	38.5 ± 0.46	8.5 ± 0.22	8.0 ± 0.18
1 h.a.f.	78.5 ± 0.54	11.0 ± 0.22	8.0 ± 0.18	42.5 ± 0.40	9.0 ± 0.22	7.5 ± 0.00
2 h.a.f.	91.0 ± 0.61	11.5 ± 0.22	7.5 ± 0.00	49.0 ± 0.22	11.0 ± 0.22	7.5 ± 0.00
4 h.a.f.	93.5 ± 0.78	13.0 ± 0.18	7.5 ± 0.00	56.5 ± 0.78	11.0 ± 0.22	7.5 ± 0.00
8 h.a.f.	83.5 ± 0.46	11.5 ± 0.22	7.5 ± 0.00	52.5 ± 0.40	9.0 ± 0.22	7.5 ± 0.00
16 h.a.f.	80.0 ± 0.49	10.5 ± 0.18	7.5 ± 0.00	51.0 ± 0.83	11.5 ± 0.22	7.5 ± 0.00
24 h.a.f.	77.5 ± 0.40	10.5 ± 0.18	7.5 ± 0.00	42.5 ± 0.40	9.5 ± 0.18	7.5 ± 0.00
48 h.a.f.	102.5 ± 0.40	7.0 ± 0.18	7.5 ± 0.00	49.0 ± 0.46	9.5 ± 0.18	7.5 ± 0.00

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

TABLE 10

Morphometric data of epithelium of third ventriculus of adult *I. limbata* fed on green gram

Condition of insect	Tall Columnar Cells			Short Columnar Cells		
	Height	Width	Nucleus size	Height	Width	Nucleus size
Normal	101.0 ± 1.08	12.5 ± 0.00	7.5 ± 0.00	58.0 ± 1.11	11.5 ± 0.22	8.5 ± 0.22
1/2 h.a.f.	95.5 ± 0.71	11.5 ± 0.22	7.5 ± 0.00	45.5 ± 0.33	11.5 ± 0.22	7.5 ± 0.00
1 h.a.f.	82.0 ± 0.66	11.5 ± 0.22	7.5 ± 0.00	40.5 ± 0.33	11.0 ± 0.22	8.0 ± 0.18
2 h.a.f.	80.0 ± 0.75	12.0 ± 0.18	8.0 ± 0.18	40.5 ± 0.22	15.5 ± 0.33	7.5 ± 0.00
4 h.a.f.	120.5 ± 0.86	11.5 ± 0.22	7.5 ± 0.00	71.5 ± 0.54	12.5 ± 0.00	8.0 ± 0.18
8 h.a.f.	100.0 ± 1.41	13.0 ± 0.18	7.5 ± 0.00	61.0 ± 1.08	12.0 ± 0.18	7.5 ± 0.00
16 h.a.f.	96.0 ± 0.83	10.5 ± 0.18	7.5 ± 0.00	56.5 ± 1.12	12.0 ± 0.18	7.5 ± 0.00
24 h.a.f.	107.0 ± 1.25	11.0 ± 0.22	7.5 ± 0.00	41.0 ± 0.46	10.5 ± 0.18	7.5 ± 0.00
48 h.a.f.	111.0 ± 1.51	11.0 ± 0.22	7.5 ± 0.00	67.0 ± 0.87	10.0 ± 0.28	7.5 ± 0.00

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

TABLE 11

Morphometric data of the epithelium of fourth ventriculus of adult *I. limbata* fed on green gram

Condition of Insect	Tall Columnar Cells		
	Height	Width	Nucleus size
Normal	80.0 ± 0.49	8.5 ± 0.22	7.5 ± 0.00
1/2 h.a.f.	65.5 ± 0.33	9.0 ± 0.22	7.5 ± 0.00
1 h.a.f.	78.0 ± 0.52	11.0 ± 0.22	8.5 ± 0.22
2 h.a.f.	76.5 ± 0.33	10.5 ± 0.18	8.0 ± 0.22
4 h.a.f.	74.0 ± 0.67	8.0 ± 0.18	8.0 ± 0.18
8 h.a.f.	78.0 ± 1.25	8.0 ± 0.18	7.5 ± 0.00
16 h.a.f.	68.5 ± 0.46	8.0 ± 0.18	7.5 ± 0.00
24 h.a.f.	70.0 ± 0.33	8.5 ± 0.22	7.5 ± 0.00
48 h.a.f.	71.5 ± 0.67	7.0 ± 0.18	7.5 ± 0.00

h.a.f. = hour after feeding
All measurements are in microns
Data are means of five determinations ± SE.

PLATE - 6

Fig. 48. A portion of the T.S. of the anterior region of the first ventriculus at 30 minutes after feeding showing cells with flat and bulbous tips (x 400).

Fig. 49. A portion of the T.S. of the anterior region of the first ventriculus at 30 minutes after feeding showing cells with vacuolated tips (x 400).

Fig. 50. A portion of the T.S. of the anterior region of the first ventriculus at 30 minutes after feeding (x 400).

Fig. 51. A portion of the T.S. of the first ventriculus at 1 h after feeding (x 400).

Fig. 52. A portion of the T.S. of the first ventriculus at 1 h after feeding (x 400).

Fig. 53. A portion of the T.S. of the first ventriculus at 1 h after feeding showing liberation of complete layer of cytoplasm (x 300).

Fig. 54. A portion of the T.S. of the first ventriculus at 2 h after feeding (x 400).

Fig. 55. A portion of the T.S. of the first ventriculus at 2 h after feeding (x 400).

Fig. 56. A portion of the T.S. of the first ventriculus at 2 h after feeding (x 400).

Bt - Bulbous tip; Ct - Broken Cell tip; Cytl - layer of cytoplasm; N - Nucleus;

Rg - Regenerative Cell; V t - Vacuolated tip; V - Vacuole.

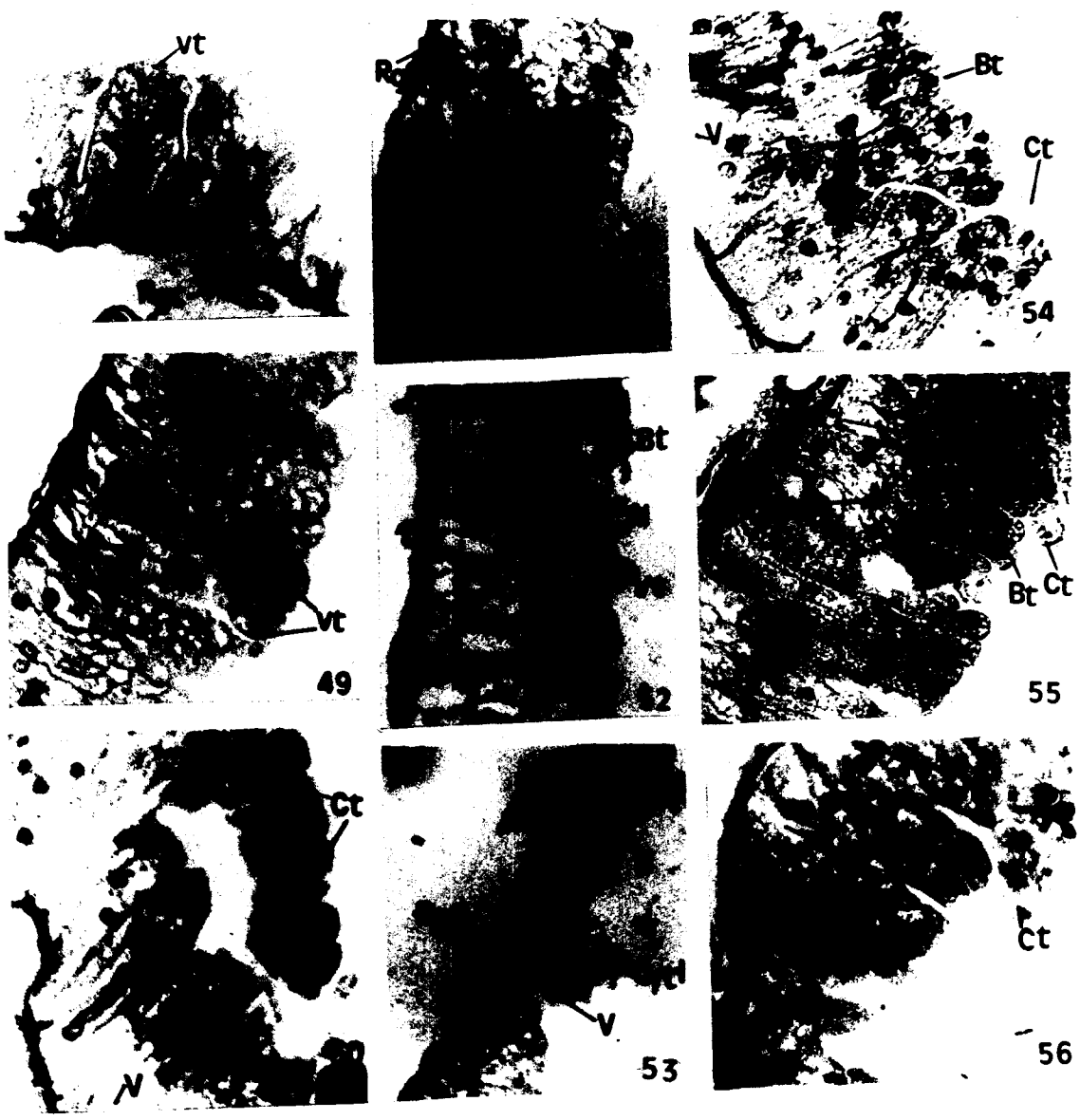

Vt
Bt
V
Ct
54
Vt
49
Bt
Ct
55
Ct
V
53
Ct
56

PLATE - 7

Fig. 57. A portion of the T.S. of the first ventriculus at 4 h after feeding (x 400).

Fig. 58. A portion of the T.S. of the first ventriculus at 16 h after feeding (x 450).

Fig. 59. A portion of the T.S. of the first ventriculus at 4 h after feeding (x 400).

Fig. 60. A portion of the T.S. of the first ventriculus at 8 h after feeding (x 300).

Fig. 61. A portion of the T.S. of the first ventriculus at 4 h after feeding showing vacuolated cell tips (x 300).

Fig. 62. A portion of the T.S. of the first ventriculus at 8 h after feeding showing flat cells tips (x 400).

Fig. 63. A portion of the T.S. of the first ventriculus at 16 h after feeding showing the vesicles at cell tip (x 400).

Fig. 64a. A portion of the T.S. of the first ventriculus at 4 h after feeding showing the cell tip with cytoplasm and nuclei pinched off (x 400).

Fig. 64b. A portion of the T.S. of the first ventriculus at 8 h after feeding showing the cell tip with dense granular cytoplasm (x 300).

Bt - Bulbous tip; Ct - Broken Cell tip; Cytl - layer of cytoplasm; Ft - Flat tip;

N -Nucleus; Rgc - Regenerative Cell; Scc - Short Columnar Cell;

V - Vacuole; Vs - Vesicle; V t - Vacuolated tip.


Ct
Bt
57
vt
60
VS
N
V
63
V
Ct
Bt
N
N
vt
61
N
Ct
Bt
64a
N
Cl
59
N
Ft
62
Rgc
N
SCC
Ft
64b

PLATE - 8

Fig. 65. A portion of the T.S. of the first ventriculus at 48 h after feeding showing the nucleated bodies at cell tip (x 400).

Fig. 66. A portion of the T.S. of the first ventriculus at 48 h after feeding showing vacuolated cells with large nucleus (x 350).

Fig. 67. A portion of the T.S. of the second ventriculus at 30 minutes after feeding (x 600).

Fig. 68. A portion of the T.S. of the second ventriculus at 1 h after feeding (x 400).

Fig. 69. A portion of the T.S. of the second ventriculus at 1 h after feeding (x 400).

Fig. 70a. A portion of the T.S. of the second ventriculus at 2 h after feeding (x 350).

Fig. 70b. A portion of the T.S. of the second ventriculus at 2 h after feeding (x 350).

Fig. 71. A portion of the T.S. of the second ventriculus at 4 h after feeding (x 450).

Fig. 72. A portion of the T.S. of the second ventriculus at 4 h after feeding (x 400).

Bt - Bulbous tip; Ct - Broken Cell tip; fp - finger like processes of basement membrane; Ft - Flat tip; GC - Granular Cytoplasm; LN - Large Nucleus; N - Nucleus; NB - Nucleated Body; Rgc - Regenerative Cell; Sm - Secretory material; V - Vacuole; V t - Vacuolated tip.

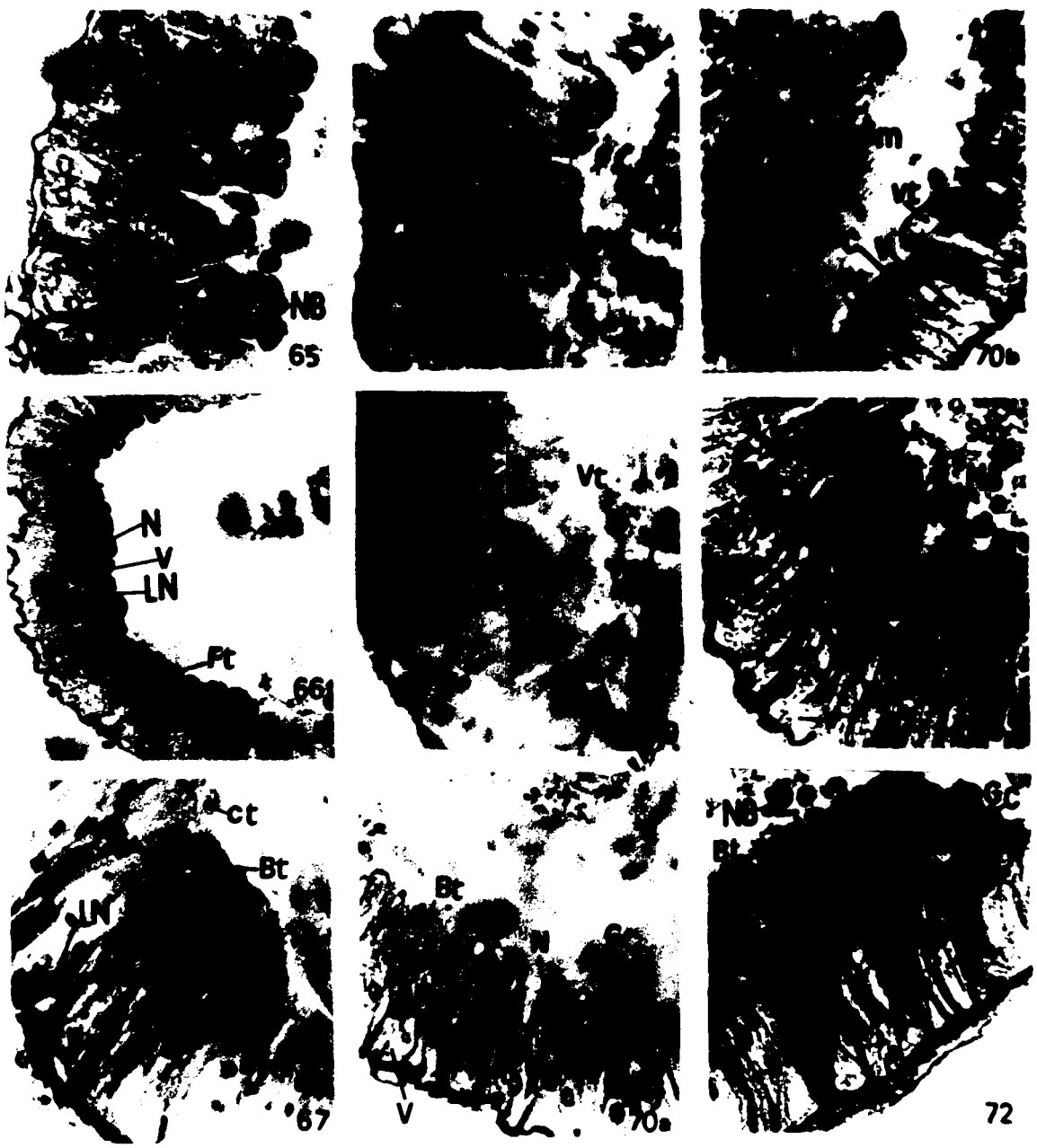

NB
65
m
Vt
70b
N
V
LN
Pt
66
Vt
ct
Bt
LN
67
Bt
V
70
NB
Bt
GC
72

PLATE - 9

Fig. 73. A portion of the T.S. of the second ventriculus at 8 h after feeding (x 350).

Fig. 74. A portion of the T.S. of the second ventriculus at 8 h after feeding (x 400).

Fig. 75. A portion of the T.S. of the second ventriculus at 16 h after feeding (x 350).

Fig. 76. A portion of the T.S. of the second ventriculus at 16 h after feeding (x 350).

Fig. 77. A portion of the T.S. of the second ventriculus at 24 h after feeding (x 400).

Fig. 78. A portion of the T.S. of the second ventriculus at 48 h after feeding (x 400).

Fig. 79a. A portion of the T.S. of the third ventriculus at 30 minutes after feeding (x 450).

Fig. 79b. A portion of the T.S. of the third ventriculus at 30 minutes after feeding (x 300).

Fig. 80. A portion of the T.S. of the third ventriculus at 1 h after feeding (x 400).

Bt - Bulbous tip; Ct - Broken Cell tip; GC - Granular Cytoplasm; N - Nucleus; Rgc - Regenerative Cell; Sm - Secretory material; V - Vacuole; V t - Vacuolated tip.

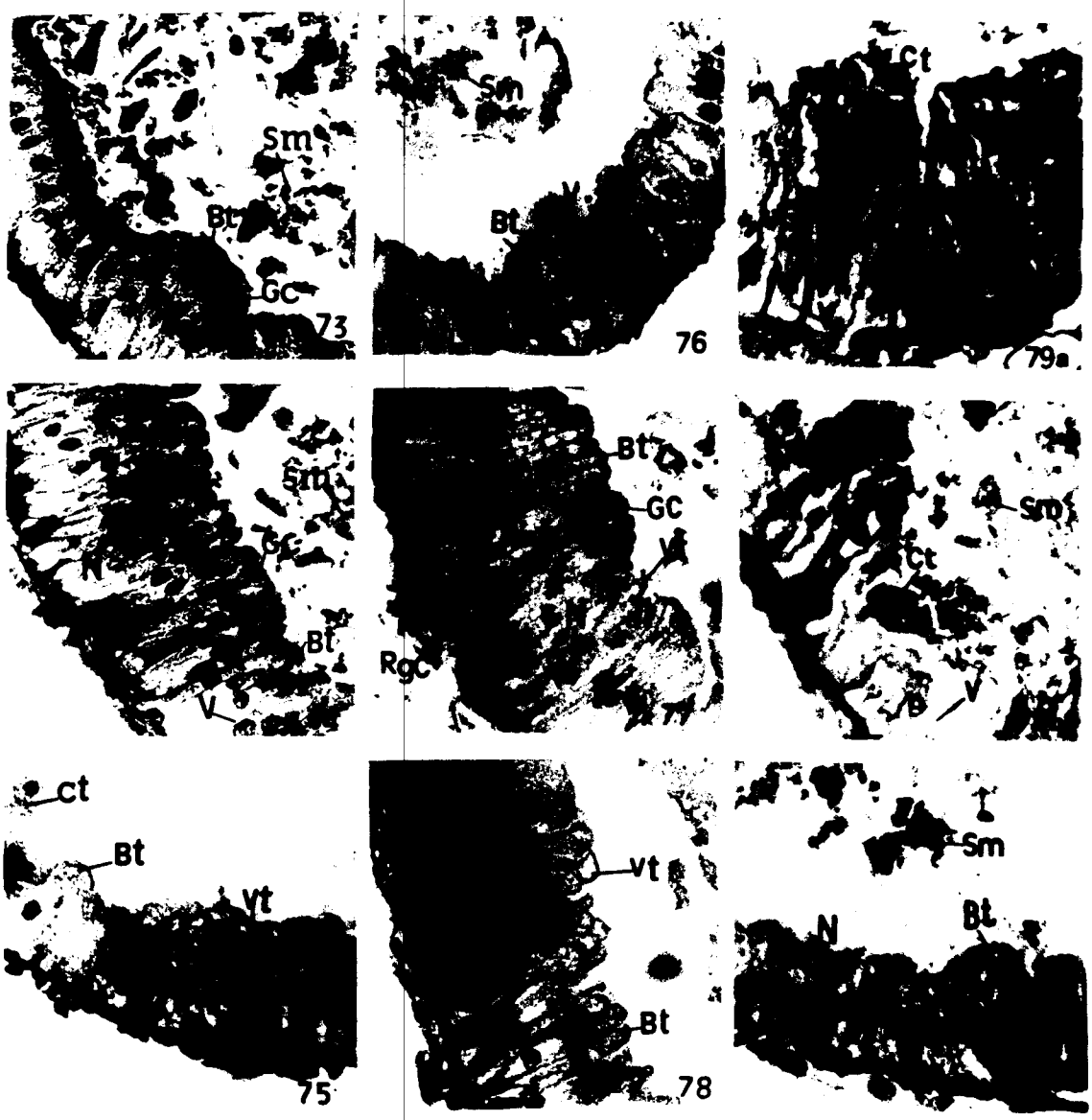

Sm
Bt
GC
73
Sm
Bt
76
Ct
79a
Sm
GC
N
Bt
V
Bt
GC
Rgc
V
Sm
Ct
V
ct
Bt
Vt
75
Vt
Bt
78
Sm
N
Bt

PLATE - 10

Fig. 81. A portion of the T.S. of the third ventriculus at 2 h after feeding (x 400).

Fig. 82. A portion of the T.S. of the third ventriculus at 4 h after feeding (x 400).

Fig. 83. A portion of the T.S. of the third ventriculus at 8 h after feeding (x 450).

Fig. 84. A portion of the T.S. of the third ventriculus at 8 h after feeding (x 400).

Fig. 85. A portion of the T.S. of the third ventriculus at 16 h after feeding (x 300).

Fig. 86. A portion of the T.S. of the third ventriculus at 16 h after feeding (x 350).

Fig. 87. A portion of the T.S. of the third ventriculus at 24 h after feeding (x 400).

Fig. 88. A portion of the T.S. of the third ventriculus at 48 h after feeding (x 400).

Fig. 89. A portion of the T.S. of the third ventriculus at 48 h after feeding (x 400).

Bt - Bulbous tip; Ct - Broken Cell tip; Ft - Flat- tip; GC - Granular Cytoplasm; N -Nucleus; Sm - Secretory material; V - Vacuole; V t - Vacuolated tip.

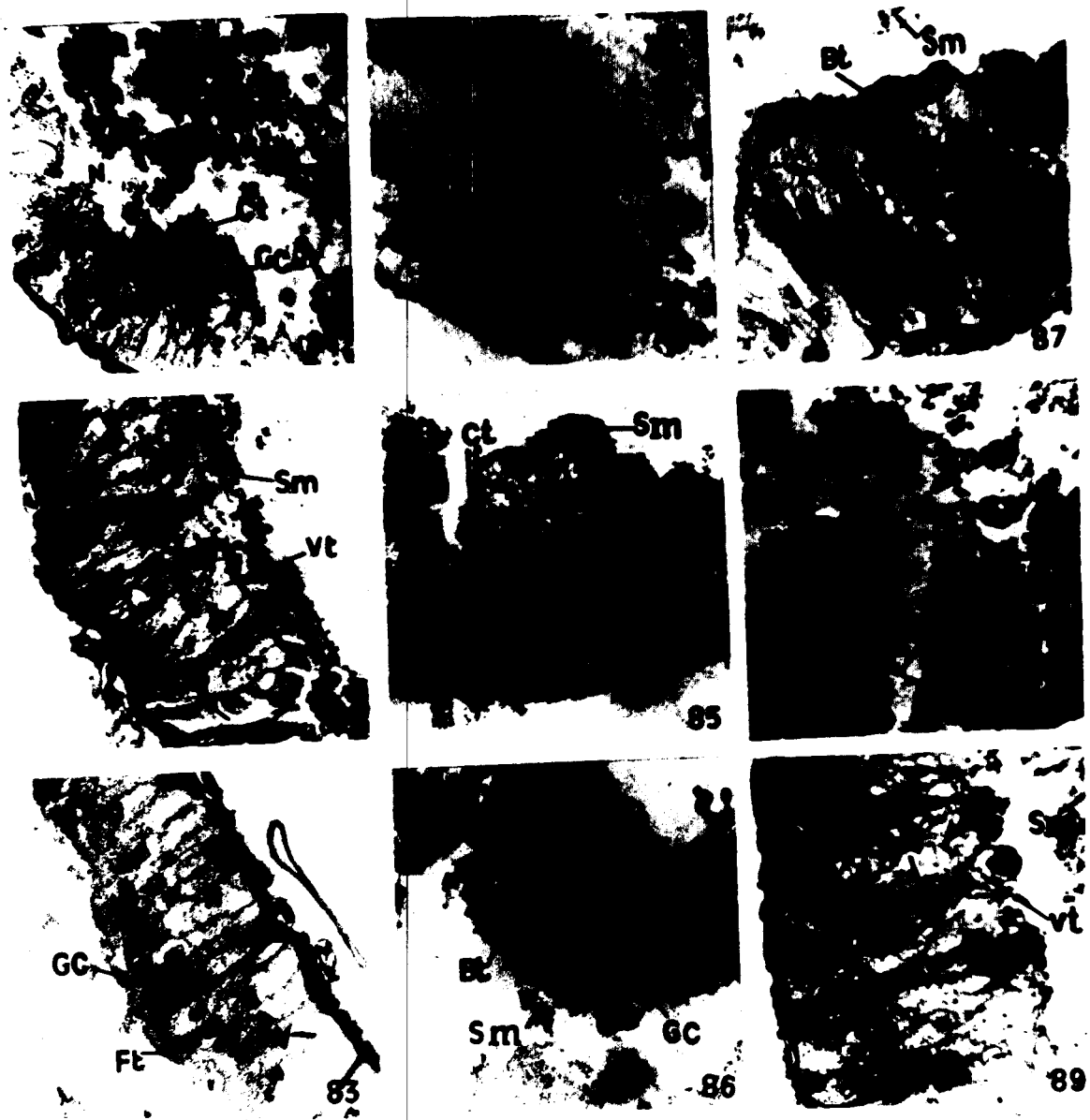

Sm
Bt
87
Sm
Vt
Ct
Sm
85
GC
Ft
83
Bt
Sm
GC
86
Vt
89

PLATE - 11

Fig. 90. A portion of the T.S. of the fourth ventriculus at 30 minutes after feeding (x 400).

Fig. 91. A portion of the T.S. of the fourth ventriculus at 1 h after feeding (x 400).

Fig. 92. A portion of the T.S. of the fourth ventriculus at 2 h after feeding (x 400).

Fig. 93. A portion of the T.S. of the fourth ventriculus at 4 h after feeding (x 400).

Fig. 94. A portion of the T.S. of the fourth ventriculus at 16 h after feeding (x 400).

Fig. 95. A portion of the T.S. of the fourth ventriculus at 48 h after feeding (x 400).

Fig. 96. A portion of the T.S. of the first ventriculus at 30 minutes after feeding (x 350).

Fig. 97. A portion of the T.S. of the first ventriculus at 30 minutes after feeding (x 400).

Fig. 98. A portion of the T.S. of the first ventriculus at 30 minutes after feeding (x 350).

Bt - Bulbous tip; Ct - Broken Cell tip; GC - Granular Cytoplasm; Lu - Lumen; N - Nucleus; NB - Nucleated Body; Sm - Secretory material; V - Vacuole; V t - Vacuolated tip.

Vt
Lu
Bl
Vt
Bl
GC
98

PLATE - 12

Fig. 99. A portion of the T.S. of the first ventriculus at 1 h after feeding (x 400).

Fig. 100. A portion of the T.S. of the first ventriculus at 2 h after feeding (x 400).

Fig. 101. A portion of the T.S. of the first ventriculus at 4 h after feeding (x 400).

Fig. 102. A portion of the T.S. of the first ventriculus at 8 h after feeding (x 300).

Fig. 103. A portion of the T.S. of the first ventriculus at 16 h after feeding (x 250).

Fig. 104. A portion of the T.S. of the first ventriculus at 24 h after feeding (x 400).

Fig. 105. A portion of the T.S. of the first ventriculus at 48 h after feeding (x 400).

Fig. 106. A portion of the T.S. of the second ventriculus at 30 minutes after feeding (x 350).

Fig. 107. A portion of the T.S. of the second ventriculus at 2 h after feeding (x 400).

Bt - Bulbous tip; f - fold; Ft - Flat- tip; GC - Granular Cytoplasm; Lu - Lumen; N -Nucleus; Sm - Secretory material; V - Vacuole; V t - Vacuolated tip.


Bl
Gc
Lu
V
Vl
Gc
V
104
107

PLATE - 13

Fig. 108. A portion of the T.S. of the second ventriculus at 8 h after feeding (x 350).

Fig. 109. A portion of the T.S. of the second ventriculus at 48 h after feeding (x 400).

Fig. 110. A portion of the T.S. of the third ventriculus at 1 h after feeding (x 400).

Fig. 111. A portion of the T.S. of the third ventriculus at 2 h after feeding (x 300).

Fig. 112. A portion of the T.S. of the third ventriculus at 8 h after feeding (x 400).

Fig. 113. A portion of the T.S. of the third ventriculus at 16 h after feeding (x 400).

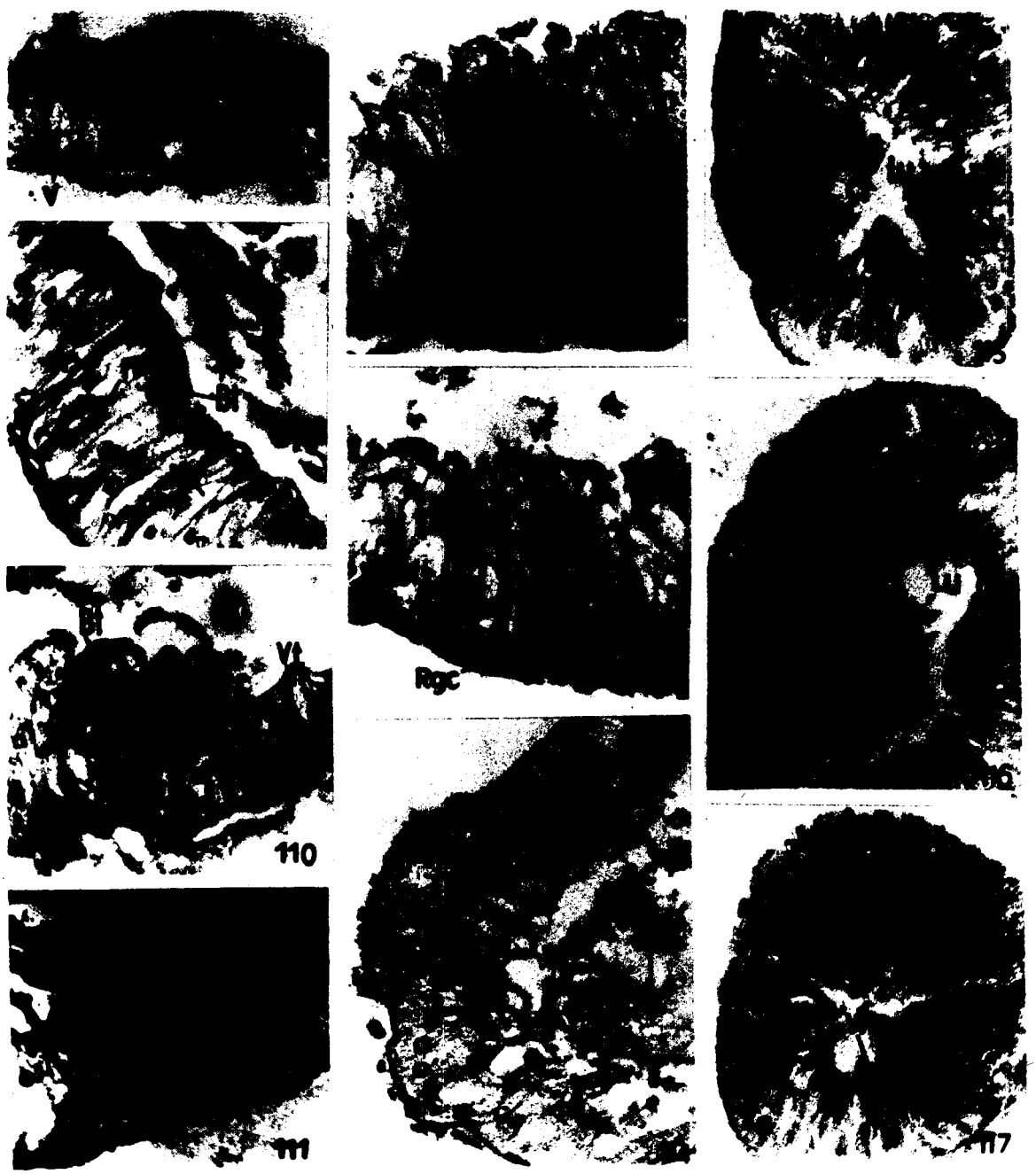
Fig. 114. A portion of the T.S. of the third ventriculus at 48 h after feeding (x 400).

Fig. 115. A portion of the T.S. of the fourth ventriculus at 30 minutes after feeding (x 400).

Fig. 116. A portion of the T.S. of the fourth ventriculus at 4 h after feeding (x 350).

Fig. 117. A portion of the T.S. of the fourth ventriculus at 24 h after feeding (x 350).

Bt - Bulbous tip; Ct - Cell tip; GC - Granular Cytoplasm; Lu - Lumen; N - Nucleus; Rgc - Regenerative Cell; Sm - Secretory material; V - Vacuole; VC - Vacuolated Cell; V t - Vacuolated tip.


Rgc
110
111
117

Discussion

The nature of food and mode of feeding vary widely among different groups of insects. The duration of the food intake depends on both the nature of food and feeding habits. Based on the nature of feeding, insects are of two classes, continuous feeders and intermittent feeders.

Newcomer (1914) and Pradhan (1940) have described several characters which may distinguish intermittent feeders from continuous feeders. Intermittent feeders are carnivorous and possess a definite cycle of activity in the midgut which may be correlated with feeding. The presence of well developed nidi or regenerative cells observed in intermittent feeders is correlated with the periodic holocrine secretion. Breakdown of epithelium of the midgut wall into the lumen is followed by a growth and development of regenerative cells. These two processes occur in the form of a cycle in intermittent feeders. Phytophagous continuous feeders on the other hand lack such a definite cycle. Secretion is constant and is either merocrine or apocrine type. Cell breakdown is not frequent and nidi are not well developed.

In the case of *Iphita limbata* which is a phytophagous continuous feeder, well-fed condition is attained about 20-25 minutes after the commencement of feeding. The time taken to attain well-fed condition since the commencement of feeding is different in different groups of insects. Parsons (1959) who carried out feeding experiments with aquatic Hemiptera observed that both corixids and carnivorous bugs reached the well-fed condition 2 hours after the commencement of feeding. In the case of carnivorous bugs they were considered to be feeding as long as their stylets are inserted into their prey.

The period of food retention in the different regions of the alimentary canal is also different for continuous and intermittent feeders. The time taken by the

food to reach the entire gut region is also different. In *I. limbata* it takes about 2 hours for the food to reach the entire gut region after the commencement of intake of food. The rate of movement of food after a full meal is variable in insects. The rate of movement of food through alimentary canal increases with the factors such as hunger and muscular activity whereas it decreases with certain poisons and chemicals (Pakrutty, 1987). In fluid feeders the excrement is also in the fluid state and it may be retained for long periods in the rectum.

The midgut in insects is the seat of secretion of digestive enzymes, digestion of food and absorption of nutrients. Both the production and secretion of digestive enzymes and absorption of the products of digestion may be carried out by the same midgut cells. The midgut cells have a limited life and the midgut epithelium is continuously replaced from small replacement cells at the base of the epithelium (Chapman, 1985).

In *I. limbata*, the height of the columnar cells in different regions of the gut varies according to the secretory activity at different time intervals after feeding. The increase and decrease in the height of the columnar cells may be correlated to the formation of secretory material and the rupture of the cell tip for the release of the material respectively. Thus there is cyclic secretory activity in the digestive epithelium of *I. limbata*.

The cell size as well as the variation in their height during different time intervals also differ in *I. limbata* which are fed on different food. But no significant difference has been observed in the secretory activity when they are fed with different food. The columnar cells in the first ventriculus and fourth ventriculus attain the maximum height at about 30 minutes after feeding, in the second ventriculus at about 4 h after feeding, and in the third ventriculus at about 48 h after feeding in *I. limbata* fed on banana whereas the columnar cells attains the maximum height at about 30 minutes and 2 h after feeding in the anterior and the

posterior region respectively of the first ventriculus, at about 4 h after feeding in the second and third ventriculus, at about 1 and 8 h after feeding in the fourth ventriculus in insects fed on green gram.

A relationship between the epithelial height and the time after feeding was observed in the first midgut of *Ranatra, Belostoma, Notonecta* and other corixids (Parsons, 1959). In these insects, the height of the epithelium is very low during the first 12 to 24 h after feeding and is high after this period. The variation in the height of the epithelium during the first 8 to 24 h due to the presence of food is reported in *Laccotrephes robustus* by Pakrutty (1987). Marks (1959) has observed a similar decrease in the epithelial height during the first 4 h after feeding and an increase from 36 h after feeding onwards in water bugs. After the secretory activity and absorption of nutrients the digestive epithelium gradually returns to normal condition. By 48 h after feeding the alimentary canal of *I. limbata* is completely free of food. The insects are considered to be under starvation after this period. In *I. limbata* the cell size increases slightly as the starvation period increases where as in *Aulacobothrus luteipes* the cell size and nuclear diameter decreases gradually as the starvation period increases and reaches a minimum at about 48 h after feeding which is considered to be the maximum starvation period in *A. luteipes* (Pakrutty, 1987).

The midgut cells of *I. limbata* formed by division and differentiation from regenerative cells, undergo a cycle of changes associated with enzyme production and absorption. In adult *Tenebrio molitor* all the cells in the midgut are replaced by every 4 days (Thomas and Gouranton, 1973). Such cycles of development do not occur in the midgut of larval Cyclorrhapha where the increasing size of the gut results from cell enlargement, not from an increase in cell numbers (Nopanitaya and Misch, 1974).

When the normal insects are fed the response of the midgut epithelium to the food reflects on the structure of the cells. Starvation and feeding affect not only the epithelium of the midgut but also the cytoplasm and inclusions of the epithelial cells (Woodruff, 1933; Gresson, 1934; Day and Powning, 1949). The secretory cells of the midgut epithelium of *I. limbata* become active and they pour their secretion into the lumen of the midgut. The secretions are first collected in the vacuolated tips of the epithelial cells and are released into the lumen by a rupture on the vacuolated tips. Billingsley and Downe (1989a) stated that induction and control of the digestive events occurred at the cellular level and may be controlled by the midgut content. This action of the food on the digestive cells has been reported in predaceous and hematophagous insects which have defined feeding cycles (Pradhan, 1940; Rudin and Hecker, 1979; Billingsley and Downe, 1984). Bees have no feeding cycles, but nourishment initially serves as a trigger for the secretory process in the digestive cells (Serrao and Cruz-Landim, 1996b).

There are different modes of release of the secretory products into the lumen of the gut. Haseman (1910) distinguished two types of cell secretion in insects-merocrine and holocrine. In the merocrine secretion the discharge is gradual and continuous and the cells remain functional for a long period. Merocrine secretion is of different methods-by vacuolisation of the cells, exudation of secretory products or by budding. In the holocrine secretion the whole content of the cell is discharged, thus resulting in the death of the cells and the development of new epithelium from the regenerative cells. It is usually believed that the aquatic Cryptocerata secrete by total breakdown of the cells (holocrine) and in the terrestrial Hemiptera, self destruction does not take place (Goodchild, 1966). Pradhan (1940) found that holocrine secretion is characteristic of the intermittent feeding carnivorous and merocrine secretion of the continuously feeding phytophagous coccinellids. In addition to the two types described above, Singh and Sharma (1987b) have reported another type of secretion in *Spilostethus*

macilentus i.e. apocrine, in which the epithelial cells elongate, secretory granules collect at the free ends, causing swelling and formation of a vesicle. In certain other cases from the inner border of the epithelial cells are given off some protrusions which later take a blister like apearance. These blisters are constricted off as non-nucleated globules and are liberated into lumen. Apocrine secretion seems to be the only way of extrusion of bulky inclusions and the extrusion is different from the elimination of degenerate cells (King and Akai, 1984).

In *I. limbata* apocrine, merocrine and holocrine modes of secretion take place in the midgut. The main mode of secretion is merocrine. In the first ventriculus, which is mainly secretory in function, holocrine and merocrine modes of secretion are observed. A layer of cytoplasm along with nuclei are seen to be pinched off into the lumen from certain portions of the epithelium of anterior region of first ventriculus at 4 h. after feeding, 8 h after feeding and at 24 h after feeding. It is therefore suggested that holocrine secretion occurs in this region of the midgut. Many cell tips at other parts of the first ventriculus enlarge and form into vacuoles at 30 minutes and 1 h after feeding. So it appears that merocrine secretion in the first ventriculus is mainly by vacuolisation. In the first ventriculus the presence of granular cytoplasm with nuclei at the tip of the cells which later pinch off into the lumen indicates another mode of merocine secretion in this region of midgut of *I. limbata*. This type of seretion occurs at 2 h, 4 h, 8 h & 16 h after feeding. At 16 h after feeding small vesicles are seen at the tip of the cells which can be in the process of liberating into the lumen. At 48 h after feeding it has been observed that in some cells nuclei fuse to form large nucleated bodies which move to the tip of the cells and are liberated into the lumen. These observations show that various processes of merocrine and apocrine secretions are present in the first ventriculus of *I. limbata*. In gymnocerates, Kurup (1964) has described 3 types of secretion (a) by rupture of the cell walls and discharge of the contents as secretory granules leaving empty vacuoles within the cells, (b) by

budding of certain cells of the epithelium and (c) by wholescale separation of major parts of the epithelium.

Both merocrine and holocrine secretions have been reported in the midgut of corixids (Sutton, 1951), cryptocerates (Kurup, 1961b, 1962), gymnocerates (Kurup, 1964, 1966) and in the first and third midguts of *Sphaerodema rusticum* (Ameen and Imam, 1976) and in the larva of *Orthaga exvinacea* (Joseph, 1997). In the case of *O. exvinacea* high secretory activity is noticed in the first four regions of the midgut, where it has been observed that in the folded region, the nuclei of some of the epithelial cells migrate to the base and the enlarged anucleated tips are nipped off at the free striated border of the cells as secretory vesicles. However, Kurup (1961b) and Rastogi (1961) have reported only holocrine secretion in *S. rusticum*. The secretion is holocrine in *Anasa tristis* (Breakey, 1936).

In *Laccotrephes robustus* (Pakrutty and Mohamed, 1989b), the secretion is exclusively holocrine in the first midgut during the period from 2 to 8 h after feeding. Though Parsons (1959) reports the absence of holocrine secretion in belostomatids, corixids and nepids it has been reported to be present in *L. maculatus* (Kurup, 1961 a), *R. elongata S. rusticum* (Kurup, 1961 b), *Anisops fieveri, Agraptocorixa hyalinipenis* (Kurup, 1962) and *Gerris spinoli* (Kurup, 1966). In *S. rusticum* (Kurup, 1961 b) the first ventriculus shows a complete obliteration of crypts during increased secretory activity. Many of these groups of cells drop into the lumen enbloc and become disintegrated and dissolved and the lumen is cleared up again. In *Anisops fieveri* (Kurup, 1962) two methods of secretion occur in the epithelial cells of the first ventriculus. In the first type, the epithelial cells at first hypertrophy and a portion from the tip buds off and finally drops into the lumen. The nuclei also hyptertrophy in this process. The portions of the cell with or without the nucleus and other cytoplasmic inclusions are discharged into the lumen of the first ventriculus. In the second method large number of epithelial cells become unloosened and rupture or discharge off from the basement

membrane and drop into the lumen. Sometimes the wave of activity affects many a group of cells simultaneously. Clusters of cells with their nuclei are discarded which disintegrate within the lumen. Periodic mass break down of the midgut epithelium is usually considered to be holocrine secretion and is common among intermittent feeders Rengel, 1898; Cragg, 1920; Pradhan, 1940). Such mass breakdown of epithelial cells has not been observed in the midgut of *I. limbata*. Hodge (1936) has considered that the extrusion of cells is due to holocrine secretion but at the same time he does not totally reject the possibility that it may be due to the elimination of wornout cells after a period of merocrine secretion. He along with Shinoda (1927) shares the opinion that secretion may be merocrine or holocrine depending on the physiological state.

In *Agraptocorixa hyalinipenis* (Kurup, 1962) during secretion epithelial cells enlarge in size, acquire a narrow stalk and constrict off from the parent cells. Cells after cells are thus budded off and cast into the lumen. Sometimes separation of entire crypts takes place resulting in complete discharge of clusters of cells into the lumen. By budding and constriction, the cytoplasmic constituents are all poured into the lumen and the epithelium is completely depleted leaving only the reserve pockets to regenerate and reform it.

In *Gerris spinoli* (Kurup, 1966) the merocrine secretion by exudation and budding as seen in *I. limbata*, takes place in the first ventriculus. The epithelium of the first ventriculus is active immediately after feeding. The secretory products collect together at the apices of the cells which appears to be fluid-filled bulbs and the secretion is exuded into the lumen. The secretory matter can be seen adhering to the borders of epithelial cells suggesting the exudative nature of the discharge. The nuclei remain intact, eventhough the cells undergo shrinkage by sustained secretory activity. In budding, the cells which elongate their tips become enlarged and globular in shape. Nuclei hypertrophy migrate to the base of the cells and finally the anucleated vesicular tips become nipped off and cast into lumen to be

broken down later. Sometimes there is mitotic division in the nucleus and the daughter nuclei are equally shared by the discarded bud and the remaining cell fragment. Holocrine activity has not been observed in the first ventriculus of *G. spinoli.*

In *Graptostethus servus* and *Dysdercus koenigii* (Kurup, 1964) first ventriculus has vacuoles in its epithelial cells. Following this vacuolisation, the cytoplasmic inclusions are seen to collect in the apices of the cells, the nuclei migrating to the basal portion. Intracellular tension leads to the rupture of the cell membrane and release of secretory granules. Probably golgi bodies are associated with the formation and maturation of the secretory granules. As in *I. limbata*, the merocrine mode of secretion in the first ventriculus is mainly by vacuolisation, in the midgut epithelium of the grasshoppers *Melanoplus differentialis* and *M. femur-rubrum* (Woodruff, 1933). The vacuoles according to Woodruff (1933) and early investigators are either due to aging or due to poor fixation. Hodge (1936) does not agree with Woodruff and has ascertained that there are two types of secretory products in the secretory cells. There are a clear vacuole and a dense granule. When *Blattella* (Day and Powning, 1949) with resting midgut epithelium are fed with water, gelatine or fat, there was a conspicuous appearance of vacuoles in the cytoplasm of the epithelium. They considered the presence of these vacuoles as a part of the secretory activity.

In well fed *Dysdercus koenigii* (Khanna, 1964) in the epithelial cells of the first ventriculus, a large number of coarse granules appear in the cytoplasm. Such granules gradually accumulate towards the striated border of the cells and finally the granular material is extruded into the lumen. In *I. limbata* also similar granular cytoplasm at the tip of the cells of first ventriculus is observed and they pinch off into the lumen. The accumulation of secretory granules rarely occurs in insect midgut cells and seems more extensive in the predaceous and hematophagous insects which have a defined feeding cycles (Pradhan, 1940;

Lehane, 1976; Becker, 1977; Rudin and Hecker, 1979; Berner *et al.*, 1983; Billingsley and Downe, 1984).

In a variety of secretory cells (Palade, 1975) secretion granules are formed in the Golgi apparatus, then stored in the apical region and finally discharge their content in the lumen by exocytosis, the membrane of the granules fusing with the apical membrane of the cell. In *Chironomus thummi* (Seidman *et al.*, 1986) secretory granules are seen in anterior midgut I, anterior midgut II and anterior midgut III and budding of the apical cytoplasm appears to occur in the anterior midgut I and part of anterior midgut II. In the anterior midgut of *Culiseta melanura* the secretion is by budding of apical cytoplasmic droplets into the lumen (Weaver and Scott, 1990).

In *I. limbata*, at 16 h after feeding small vesicles are formed at the tip of epithelial cells of first ventriculus. The formation of vesicles can be regarded as a mode of apocrine secretion. The anterior intestinal cells of hemipteran midgut contain electron dense secretory vesicles. The cells also possess synthetic and secretory cellular components in greater amounts. The nuclei of the cells undergo changes in their DNA content after feeding (Billingsley, 1989). The post feeding modifications to the nuclei, rough endoplasmic reticulum, lysosomes and golgi bodies all occur in preparation for enzyme synthesis and are initiated by stretching of the midgut and stimulated by blood factors (Billingsley and Downe, 1989b). In *Rhodnius prolixus* intracellular membranous vesicles have been noted in intestinal cells 2 h after the blood meal and endocytic release of similar vesicles has been observed in non hematophagous hemipteran *Nepa cinerea* (Andries and Torpier, 1982), According to Wigglesworth (1972) no digestion occurs in the first midgut of *Rhodnius*, but in capsids the epithelial cells pass through cycles of secretion and regeneration though most digestion occurs in the more posterior segments of the midgut (Chapman, 1985).

In *I. limbata*, compared to changes in the first ventriculus, the secretory activity is more in the second ventriculus. The secretion is exclusively merocrine in the second ventriculus i.e. by vacuolisation and extrusion of material through the cell tips. Intense secretory activity has been reported in the second midgut of *Chrysocoris purpureus* (Bhaskaran *et al.*, 1969). In *Notonecta glauca* (Bogiawlensky, 1925) and corixids (Sutton, 1951) the second midgut is both secretory and absorptive. Vacuolated cytoplasm has been observed in the epithelial cells of second ventriculus of *D. koenigii* (Khanna, 1964) and these vacuoles remain as such in cytoplasm and not liberated into the lumen in fed insects whereas in starved individuals, vacuoles are gradually nipped off in the form of vesicles which are liberated into the lumen. In *G. spinoli* (Kurup, 1966) in fed insects the secretory activity in the second midgut is also by vacuolisation. Numerous empty spaces appear within the cells of the epithelium which gradually grow bigger and bigger and the cells unable to withstand the tension offered by the presence of the vacuoles, burst and pour their contents into the lumen. Merocrine activity by budding also takes place in the second ventriculus of *G. spinoli*. The tips of the epithelial cells enlarge to form buds which become constricted off and drop into lumen. Holocrine activity has not been observed in the second ventriculus.

In *Naucoris cimicoides* and *Notonecta glauca* (Sutton, 1951) the secretion is by formation of anucleate vesicles. During secretory activity the cells enlarge, the nuclei hypertrophy and migrate to the bottom of the cells. Then the anucleated vesicles bud off and drop into the lumen. Small vesicles released from digestive cells are reported in many insects (Priester, 1971; Barker and Lehener, 1972; Baker *et al.*, 1984; Santos *et al.*, 1984; Cruz-Landim, 1985; Peng *et al.*, 1986; Jimenez and Gilliam, 1990). In some insects these vesicles do not have digestive enzymes and their participation in peritrophic membrane formation has been suggested (Bignell *et al.*, 1982; Berner *et al.*, 1983; Santos *et al.*, 1984). On the other hand, Jimenez and Gilliam (1990) have observed similar vesicles in the posterior midgut

of *Apis mellifera* which are related with the increase of trypsin activity and suggest that they are involved in the digestive enzyme secretion. In a recent immunocytochemical investigation, Jordao *et al.*, (1996) demonstrate that some trypsin is released by apocrine secretion in *Stomoxys calcitrans*. The presence of acid phosphatase in the bubble cast out into the midgut lumen shows that these enzymes are released during apocrine discharge, but their extracellular capacity is of doubt (Glaumann *et al.*, 1981).

In *I. limbata* it has been observed in some cells of the first ventriculus at 4 h after feeding, the nuclei fuse to form nucleated bodies, which move to the tip of the cells and are liberated into the lumen. Extrusion of nucleated spherical bodies are seen in the second and third midguts of *Laccotrephes robustus* (Pakrutty, 1987). Pakrutty (1987) is of opinion that these vesicles cannot be compared with the exhausted cells described by Sutton (1951) in corixids because these cells are released into the gut lumen containing food. So this process of release of nucleated vesicles is connected with secretion of digestive enzymes. Pesson (1944) speculates that the chromatin of the nuclei and the cytoplasmic granules mix together to form a digestive enzyme which is discharged into the lumen during secretory activity in coccides.

In *I. limbata* during the period from 8 h to 16 h after feeding, cytoplasm of cells of second ventriculus is highly granular, cell tips are bulbous and darkly stained and in some cells, the cell tips break into the lumen which is not free of food. So it is suggested that digestion takes place during this period. Since there is a reduction in the amount of materials observed in the lumen, it is opined that absorption also occurs during this period in this region. In *Aedes aegypti* (Rudin and Hecker, 1976) the anterior part of the midgut is more involved in absorption and cellular transport than the posterior part.

In *I. limbata* the third ventriculus is both secretory and absorptive. Secretion is mainly by merocrine i.e. by vacuolisation and by extrusion of secretory material through the cell tip mainly at 4 and 8 h after feeding. Absorption mainly takes place at 16 h after feeding since the lumen contains less material. Hood (1937) and Kurup (1961 b) have reported secretory activity in the third midgut of cryptocerate insects. Secretory activity in the third ventriculus is not as intense as in the first ventriculus in *G. servus* and *D. koenigii* (Kurup, 1964). In *Bagrada cruciferarum* (Mall, 1979) no secretory activity is observed in the third ventriculus and it acts as an absorptive region. Hood (1937) has observed maximum secretory activity in the third ventriculus in *Oncopeltus fasciatus*. In the third ventriculus of *G. spinoli* (Kurup, 1966) the secretion is by holocrine mode. Groups of cell become separated from the epithelium and cast off into the lumen along with their nuclei. At certain regions there is complete cellular break down. The exhausted and damaged wall is renovated by the remnants of the cells that are still left behind after secretion. In *D. koenigii* (Khanna, 1964) in the third ventriculus also the epithelial cells have finely granular cytoplasm with full of certain globules which accumulate towards the cell borders and are finally discharged into the lumen as viscuous fluid. In the third midgut of *S. rusticum* (Ameen and Imam, 1976) epithelial cells remain more or less intact with short brush border without any degenerative changes.

In *I. limbata*, secretory activity in the fourth ventriculus is very less. Since the epithelial cells of this region are taller than those in other regions and have uniformly distributed granular cytoplasm and without much epithelial folds it is considered as mainly absorptive in function. In Cacao capsid bugs (Goodchild, 1952) the first two regions of the midgut are concerned with secretion and digestion while the third midgut with absorption. In most insects, secretion of enzymes and absorption of digested food are carried out by the same cells. But in the larva of *Galleria mellonella* (Young-Tai, 1929) there is convincing evidence that

the goblet cells are exclusively secretory while columnar cells may be either secretory or absorptive. In *Periplaneta orientalis* (Gresson, 1934) secretion and absorption do not take place side by side in the same cell as claimed by Sanford (1918). Steudel (1913) states that cells in which secretory globules are forming do not absorb, but that the secretory phase alternates with absorptive phase. Gresson (1934) has also reported that the posterior region of the midgut is mainly absorptive in function. Prolonged periods of absorption are followed by degeneration of all the actively secreting cells and are rapidly replaced by regenerative cells. The young cells at first absorb the food material, but later become secretory in function. The posterior intestinal cells of hemipteran midgut are actively involved in blood digestion and it is the major site of nutrient absorption. Posterior intestinal cells possess a greater luminal surface area and show increase in mitochondrial density. These cells continue to accumulate sugars until at least 20 days after blood meal (Billingsley, 1988; 1990). Studies also have shown that both secretion and absorption occur in different regions of the midgut (Billingsley, 1990; Silva and Terra, 1994; Joseph, 1997). The midgut of *Orthaga exvinacea* (Joseph, 1997) larva is both secretory and absorptive in function. Secretory activity is observed in the first four regions of the midgut. In the fifth region which is mainly absorptive, the epithelial cells are taller than those in other regions, cytoplasm contains uniformly distributed cytoplasmic granules. The number of goblet cells are more in this region and no epithelial folds are observed.

Merocrine, apocrine and holocrine secretions have formerly been proposed as the extrusion mechanism of digestive enzymes and the peritrophic membrane material into the midgut lumen Platzer-Schultz and Welsch, 1969; Heinrich and Zebe, 1973; Seifert, 1975). Although Brunings and De Priester (1971) have shown that apical protrusions suggestive of merocrine and apocrine secretions by the midgut enterocytes of *Calliphora* are only fixation artifacts, Heinrich and Zebe (1973) have tended to exclude this for the midgut of

Locusta. They still considered apical cell budding, rupture of apical cell membrane and vesiculation of microvilli as indicative of apocrine secretion because they could not observe zymogen granules in the cells. Khan and Ford (1962) have found that the activity of digestive enzymes of *Dysdercus* is not related to the production of cytoplasmic protrusions which increase with time of starvation and cell degeneration. They ascribe the apical protrusions and extrusions of whole cells which are more frequently observed during starvation and shortly after feeding to the hastening of cell degeneration in response to starvation and to an increased extrusion of degenerating cells in response to mechanical stress put on the epithelium by food ingestion. The degeneraing cells, when extrude into the lumen contribute to the digestive juice with their lysosomal enzymes and contents of secretion granules. Other investigators (Fain Maurel *et al.*, 1973; Humbert, 1979; Bignell *et al.*, 1982; Youson and Horbert, 1982) propose that these structures are correlated with a physiological state of the cells i.e. the discharge of the degenerating cells. Thorpe (1984) suggests it is likely that such enzymes are stored free in the apical cytosol before discharge. In *Drosophila auraria* these extrusions have been observed throughout development of the larvae (Dimitriadis and Kastritsis, 1984). The number of these extrusions increased at the beginning of the pupation and this fact possibly indicates their relation to degenerative processes (Dimitriadis, 1985). Terra *et al.* (1988) has pointed out that apical cell extrusions are due to natural cell 'Squamation" whose significance has not yet been determined. Squamation being more intense in the anterior region. It is as a means of discarding material from the cell or part of the cell.

Cruz-Landim *et al.* (1996) believe that extrusion are not classic fixation artifacts because they are observed with various fixatives as well as different embedding media and insect species (Caetano *et al.*, 1994; Serrao and Cruz-Landim, 1995 a,b). In the first type of bubble observed, where no organelles are present, fluids containing ions or salts or other small molecules unnecessary for the

cell are eliminated in a kind of osmotic regulation. The second type of macroprotrusion may not be eliminated since it contains many ribosomes; it may function in renewing the cell synthetic apparatus by elimination of some of their components. This may be necessary to a change in cell function. Pakrutty (1987) is also of the opinion that different fixatives do not make much change in the nature of the extrusions and the extrusions can be correlated with a specific physiological activity since they appear at a definite period of cell cycle. Exocytosis has been observed in some species (Fain-Maurel *et al.*, 1973; Lehane, 1976). The normal release mechanism of digestive enzymes and peritrophic membrane material confined in membrane-bound vesicles is apparently exocytosis(Becker and Peters, 1985a,b).

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SUMMARY

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The alimentary canal of *Iphita limbata* can be differentiated into the foregut, midgut and hindgut. The foregut is a simple thin tube and consists of cibarium, pharynx and oesophagus. Oesophagus is a short tubular transparent structure. The posterior extremity of the oesophagus is telescoped into the anterior part of the first ventriculus region, forming the oesophageal valve. The midgut forms the longest part of the alimentary canal and is differentiated into five regions - first, second, third, fourth and fifth ventriculi and the junction between the various regions is marked by constrictions. First ventriculus is broad, pear shaped and is the widest part of the gut. The wall of the first ventriculus is thin and transparent. Anteriorly the wall of the first ventriculus is convoluted due to transverse folds while posteriorly it has smooth surface. The second ventriculus is the longest tubular division of the midgut and is coiled around first and third ventriculi. Third ventriculus is short dilated oval sac having thin wall and its lumen is always filled with reddish brown viscuous substance. Fourth ventriculus is a short narrow tube. The fifth ventriculus is the smallest part of the midgut and it forms a bulbous portion and on eitherside is slightly swollen lateral outgrowths, the ampulla into which empties a pair of Malpighian tubules. The hindgut is differentiated into short anterior pylorus and a large posterior rectum. Pylorus forms the junction between midgut and the rectum and is characterised by the presence of pyloric valve. Rectum is a thin sac and tapers posteriorly to open out through the anus.

The histological layers distinguished in the foregut region are longitudinal and circular layers of muscles, basement membrane, a single layer of epithelial cells and a layer of chitinous intima. The epithelium is produced into folds and the outlines of the cells are not distinct; hence it gives an appearance of a syncytium. The chitinous intima is thrown into the lumen in a folded manner. At the junction of the foregut and midgut the posterior end of the oesophagus hangs down freely into the lumen of the first ventriculus forming the oesophageal valve.

The midgut wall consists of a layer of epithelium with a basement membrane surrounded by an inner circular and outer longitudinal layers of muscles. The midgut epithelium is composed mainly of uni, bi or multinucleate columnar cells, both tall and short cells and a few cuboidal cells. Regenerative cells are fewer in number and are not found in groups. The midgut shows differences in histological structure at various regions of it. Peritrophic membrane is lacking. The basement membrane is observed to penetrate the cell layer. The columnar cells are secretory in nature. Both holocrine and merocrine secretion are observed in the gut epithelium.

The wall of the hindgut consist of musculature, epithelium and the intima. The epithelium of the pyloric region is thrown into a series of opposing lobes by the folds of the pyloric valve. The folds consists of closely packed elongated epithelial cells with indistinct cell boundaries and small round nuclei. A thin layer of chitinous intima is present on the inner surface of the folds. The rectum shows regional differentiation of epithelial cells. The cells in the dorsal wall is modified into rectal gland cells which are larger, irregularly shaped with large coarsely granular nucleus. The intima lining the rectal gland cells are provided with spiny projections. The epithelium of the ventral wall is formed of irregularly shaped small cells. The boundaries of these cells are indistinct and the epithelium appears to be syncytial.

In *I. limbata* well-fed condition is attained about 20-25 minutes after the commencement of feeding and it takes about 2 h after feeding for the food to reach the entire gut region. The height of the columnar cells and cuboidal cells in different regions of the midgut epithelium varies according to the secretory activity at different time intervals after feeding. The increase and decrease in the height of the columnar cells may be correlated to the formation of secretory material and the rupture of the cell tip for the release of the material respectively. By 48 h after

feeding the alimentary canal of *I. limbata* is completely free of food. The insects are considered to be under starvation after this period.

In *I. limbata* holocrine, merocrine and apocrine modes of secretion take place in the midgut. The main mode of secretion is merocine. In the first ventriculus the holocrine mode of secretion is observed at 4h, 8h and 24 h after feeding at certain parts of the anterior region of first ventriculus. Merocrine and apocrine secretion occurs in the different portion of the first ventriculus by vacuolisation, extrusion of secretory materials and by formation of vesicles and nucleated bodies and their release into the lumen. In the second ventriculus, the secretion is exclusively merocrine by vacuolisation, extrusion of material through cell tips and by formation of nucleated bodies. At some regions of the second ventriculus, absorption also take place. In the third ventriculus also both secretion and absorption occurs. Secretion is mainly merocrine, by vacuolisation and by extrusion of secretory material. Secretory activity in the fourth ventriculus is very less and it is considered as mainly absorptive in function. There is no change in the structure as well as secretory activity of the cells of the fifth ventriculus. Eventhough there are variations in cell size and height during different intervals after feeding in insects fed on different food, no diiference has been observed in the mode of secretion in different regions of the midgut epithelium.

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