emerging from the pancreatic lobes. The duct of the ink sac opens on the inner side of the rectum. Sphinctor muscles are present on the rectal bulb on either side of this opening.

The inner wall of the intestine is lined with a ciliated mucus epithelium, which is thrown into a series of longitudinal folds. Two prominent ridges run along the dorsal wall as the continuation of the main mucus ridge. In *S. aculeata* and in *S. inermis* these ridges reach up to the rectal bulb but in *L. duvauceli* they run only a short distance (Plate VI a,b,c).

5. HISTOLOGY OF THE ALIMENTARY CANAL

The gut wall in cephalopods is generally composed of four layers, the serosa, the muscularis, the sub-mucosa and the mucosa. The full complement of these layers does not exist in all the regions of the gut, and one or two layers may be absent. The serosa is a uniform thin layer forming the outer wall. It encloses few blood vessels. The muscularis is differentiated into a longitudinal and a circular muscle layer. In all the regions except in the caecal wall the layer of the circular muscle is external and the longitudinal muscle is internal. The circular muscle generally forms a continuous layer while the longitudinal muscle forms bundles enclosed in sheaths of connective tissue. The muscularis is better developed in the stomach wall than in any other region.
of the alimentary canal. The submucosa is an extensive, vascular and well defined layer of connective tissue. Its outer portion is loose while the portion adjacent to the mucosa is dense. The mucosa is the inner most layer and shows much variation in structure in different parts of the alimentary canal.

The midgut glands consist of two unequal parts, the larger anterior portion is called the liver and the smaller posterior portion is called the pancreas. Their histology has been interpreted in several ways as stages of secretion have been mistaken for distinct cell types. In *L. duvauceli* it was possible to detect only one type of cell while in *S. aculeata* and in *S. inermis* two types of cells were distinguished.

5.1 *Loligo duvauceli*

5.1.1 Oesophagus

In the oesophageal wall the serosa, the circular muscle, longitudinal muscle fascicles, the submucosa and the mucosa are present. The serosa forms a very thin layer and is composed of cuboidal cells with large nucleus placed in the middle. The circular muscle layer is well developed. The longitudinal muscle fascicles are distributed discontinuously and appears as part of the submucosal layer. The submucosa is somewhat extensive, and extends into an intensely folded
The cells of the mucosal epithelium probably give rise to the cuticle lining. This lining varies in thickness (5-7 μm) depending on the stage of shrinkage of the oesophageal wall. The shape of the epithelial cells ranges from cubicle to columnar according to the degree of contraction of the organ. The cytoplasm is fibrillar in nature. The nuclei of these cells are small, darkly stained and are placed towards the basal region. The formative layer is not observed between the cuticle and the mucosal epithelium (Plate VII a).

5.1.2 Stomach

In the stomach wall muscle layers are thick especially the circular layer, and glands are absent. The histology of this region is almost same as that of the oesophagus. The mucosa has numerous folds, some folds are larger while others are smaller. The formative layer present in between the cuticle and the epithelium is somewhat thicker. This formative layer as pointed out by Bidder (1950) is present everywhere on the wall of the stomach between the epithelium and the cuticle. The mucosa is composed of a single row of columnar cells with large centrally placed oval nuclei, showing large chromatin granules. The contents of these cells provide a fibrillar pattern. Like the oesophagus the thickness of the cuticle varies according to the state of contraction of the stomach wall. In a fully distended wall the cuticle has a thickness of 9-11 μm. The maximum thickness is observed in the middle.
PLATE VII

*L. duvauceli* (histology; transverse sections)

a. Oesophagus

b. Stomach

c. Caecal leaflet

d. Intestine

e. Rectal cell

f. Liver

g. Pancreas

1. Cuticle lining

2. Mucosa

3. Submucosa

4. Longitudinal Muscle

5. Circular muscle

6. Serosa

7. Formative layer

8. Mucous cells

9. Ciliated cells

10. Calcareous cells

11. Fat droplets
region of the stomach where the folds are comparatively prominent and higher (Plate VII b).

5.1.3 Caecum

The serosa is very thin. The muscle layers are in the reverse order, with the longitudinal outer and the circular inner. A layer of delicate connective tissue rich in blood capillaries separates the two layers of muscles. This connective tissue is not seen in other parts of the alimentary canal. The mucosal epithelium consists of a layer of ciliated cells. The shape of the cells varies from cubical to columnar. The nucleus is oval and placed basally. The cilia rise from basal granules and have long parallel rootlets. The cytoplasm is finely granular.

The cells of the ciliated leaflets are typically columnar with the cilia provided with well developed basal granules and parallel rootlets. The cytoplasm is granular and the nucleus is large and oval in shape and occupies the basal half of the cell. Two types of mucous cells are observed in the ciliated leaflets. One is vesicular and crowded on the free edges of the leaflets and the contents are discharged through a common pore. The second type of cells are pyriform mainly found on the secondary leaflet grooves and opening separately (Plate VII c).
5.1.4 Intestine and Rectum

The serosa is very thin. The outer circular layer of muscle is very prominent, but the inner longitudinal layer is thinner and continuous. The submucosa is somewhat narrower. The mucosal epithelium consists of tall columnar ciliated cells interspersed with mucus glands. The columnar cells are more regular than those of the oesophagus and the stomach walls. The mucosal epithelium is thrown into a number of longitudinal ridges, which are subtended by the connective tissue containing longitudinal muscle fibres, and vary in thickness. The ciliated cells have cilia, 4.5-7 μm long with basal granules and parallel rootlets. The cells have a well marked bush border. The oval shaped nucleus is nearly central. The basal portions of these cells are stack-like and their fibrils are closely intertwined with the basement membrane, as in the cells of the oesophageal wall. Scattered among these cells are the mucus producing goblet-shaped cells, opening independently into the intestine. These cells have large darkly staining basal nuclei. The contents of these cells provide a reticulate pattern (Plate VII d).

Histologically the rectum resembles the intestine, but the ciliated cells are replaced by cells with a hyaline border. These cells are interspersed with saclular mucus cells. The mucosal epithelium of the terminal part is characterised by special type of cell, which can discharge long retractile
processes. The cells are cuboidal and the processes arise in bunches, and the length of this ranges from 35-45 μm. Each process is supported by a median long dark filament. Bidder (1950) named it as axial filament (Plate VII e).

5.1.5 Midgut Glands

5.1.5.1 Liver

The liver consists of bundles of tubules interspersed with soft transparent connective tissue fibres packed in a delicate layer of muscular sheath. The tubules communicate with a central lumen on each side. Fine blood capillaries run around the tubules. Though in paraffin sections these have a lacunar structure the luminae of the smaller tubules are nearly obliterated by the swollen ends of liver cells. The cells are tall and columnar with bulging granular free ends. Alternating with the columnar cells are small pyramidal cells, which form a basal formative layer (Bidder 1950). Only one type of cell was observed in L. duvaucelii which has two phases of activity: in the secretory phase the cytoplasms generally filled with granules or clusters of granules enclosed in vacuoles, and often contains fat droplets towards the base of the cells. In the excretory phase of the cell the cytoplasm is filled with a single large granular mass. The nuclei are in the basal portion of the cell (Plate VII f).
5.1.5.2 Pancreas

The pancreatic tissue lies within the kidney sac and is covered by the renal epithelium. The tubules are wide with a thin epithelial lining. The spongy walls of the tubules are in intimate communication with the cavity of the hepatic ducts. The epithelial lining has a well marked cell-border, which is basophilic in nature. The individual cells are difficult to differentiate in paraffin sections. The nuclei are oval and distal in position. The nature of cytoplasm is fibrillar. The secretory vacuoles usually contain solid spheres and scattered granules which stain darkly with haematoxylin. The blood capillaries are distinguished by the clearly staining blood cells (Plate VII g).

The paired hepatopancreatic ducts are non-glandular in structure. A sphincter can be distinguished, where they leave the liver, is made up of a layer of muscle fibres.

5.2 Sepiella inermis

The histology of the alimentary canal of S. inermis is broadly similar to that of L. duvauceli.

5.2.1 Oesophagus

The serosa, the circular muscle layer and the longitudinal muscle layer are typical. The submucosa is rather extensive
and the mucosa is much folded. The mucosa has a single row of columnar cells with small darkly staining nuclei occupying their basal region. The cytoplasm is fibrillar in nature. These cells secrete a layer of cuticle. The thickness of the mucosal folds and the cuticle varies according to the stages of contraction of the oesophageal wall. The formative layer is not observed between the cuticle and the mucosal epithelium (Plate VIII a).

5.2.2 Stomach

The serosa, the circular muscle layer and the longitudinal muscle fascicle constitute the outer region of the stomach wall, as in the oesophagus. The circular layer of muscle is thick. The mucosa is thrown into a number of folds. The epithelial cells of the mucosa are columnar, with a large nucleus near the middle region of the cells. The cytoplasm is fibrillar in nature. These cells secrete a layer of cuticle. The mucosal folds are comparatively prominent in the middle region of the stomach. The thickness of the cuticle also varies from 10-13 μm depending upon the nature of contraction of the stomach wall. The formative layer is present in between the cuticle and the epithelial layer (Plate VIII b).

5.2.3 Caecum

The thin serosa, the reverse order of arrangement of the muscle layers, and the connective tissue with rich blood
PLATE VIII

*S. inermis* (histology; transverse sections)

a. Oesophagus
b. Stomach
c. Caecal leaflets
d. Intestine (along typhlosole)
e. Rectal cell
f. Liver
g. Pancreas

1. Cuticle lining
2. Mucosa
3. Submucosa
4. Longitudinal Muscle
5. Circular muscle
6. Serosa
7. Formative layer
8. Mucus cells
9. Ciliated cells
10. Calcareous cells
11. Fat droplets
The capillaries are similar to that of *L. duvauceli*. The mucosal epithelium is formed of a layer of cuboidal to columnar shaped ciliated cells. The cytoplasm is granular in nature, the nucleus is oval in shape and occupies the basal portion of the cells.

The cells of the ciliated leaflets are columnar, with a basally situated large oval shaped nucleus. The cilia are with basal granules and parallel rootlets. The cytoplasm is granular in nature. The mucus cells are sacculair in shape, only one type of mucus cell occurs in this species. They occur in groups and the contents are discharged through a common pore (Plate VIII c).

### 5.2.4 Intestine and Rectum

The serosa is thin, but the circular layer of muscle is somewhat thick, and the thin inner longitudinal muscle is continuous. The sub-mucosa is somewhat thinner. The mucosal epithelium consists of a single layer of tall columnar ciliated cells interspersed with mucus cells. The mucosal epithelium is thrown into a number of longitudinal ridges supported by connective tissue containing muscle fibres. The ciliated cells have long cilia with basal granules and parallel rootlets. The cytoplasm is fibrillar in appearance. The nucleus is oval in shape and occupies more or less the middle region of the cell. Scattered among these ciliated cells are mucus producing goblet cells. These cells have a reticular cytoplasm with basally situated large nucleus (Plate VIII d).
The rectum resembles the intestine in histology but the ciliated mucosal cells are replaced by non-ciliated cells with a hyaline border. The inner wall is frequently longitudinally ridged. The ridges are supported by the underlying bands of longitudinal muscle layer. The contractile rectal cells are present (Plate VIII e).

5.2.5 Midgut Glands

5.2.5.1 Liver

In S. inermis the liver is a bilobed structure composed of innumerable tubules placed in a thin layer of muscular sheath. The tubules of each lobe open into a central lumen. Each tubule is surrounded by a system of fine blood capillaries. Two types of cells are met within this organ. One type is a secretory - excretory - absorptive type which has usually a granular cytoplasm and basal nucleus. The cytoplasm contains larger granules, single or aggregates, enclosed in vacuoles, and often contains fat droplets basally. In the secretory phase the cells contain densely filled granules, while in the excretory phase granular masses or spherules appear. In the absorptive phase the cells have a highly vacuolated inner area, finely granular cytoplasm at the blunt end ending in brush border. The cell probably passes through a sequential phase and the activity of the gland on the whole is rhythmically
controlled. The second type of cells are calcareous cells, which are involved in the formation of the cuttle bone. These cells are low, broadly based with a pyramid like contour, and containing granules and spherules, and usually occurring between the bases of other cells (Plate VIII f).

5.2.5.2 Pancreas

The pancreatic follicles are covered by the renal epithelium in *S. inermis*. Each follicle has its own narrow duct opening into the hepatopancreatic duct. The histological characters are same as in the case of *L. duvauceli*. Each follicle has a wide lumen with a narrow lining of epithelial cells. They have a well marked basophil cell border. The individual cell boundaries are not distinct. The nucleus is oval in shape and usually terminal in position. The cytoplasm is fibrillar in nature. Blood capillaries are evident in sections with the blood cells staining deeply (Plate VIII g).

5.3 *Sepia aculeata*

The histology of the alimentary canal of *S. aculeata* is almost identical with that of *S. inermis*.

5.3.1 Oesophagus

The serosa form a very thin layer. The circular layer of muscle is well developed, while longitudinal muscle
fascicles are discontinuous. The submucosa is somewhat extensive and the mucosa has a large number of folds. The mucosal epithelium is a single layer of columnar cells. The cytoplasm is fibrillar with a small basally situated darkly staining nucleus. The thickness of the cuticle varies according to the contraction of the oesophageal wall. The formative layer is not distinguishable (Plate IX a).

5.3.2 Stomach

The stomach is a thick muscular sac, with longitudinal ridges internally covered by a chitinous layer which is supported by the columnar epithelium as in S. inermis. The thickness of the chitinous layer in a fully extended region varies from 9-13 μm. The cells of the mucosal epithelial layer are columnar with fibrillar cytoplasm and large oval nuclei (Plate IX b).

5.3.3 Caecum

The serosa, the order of arrangement of muscle layers are all resemble with that of S. inermis. The mucosal epithelium is formed of a layer of ciliated cuboidal cells. The cytoplasm is granular with an oval nucleus occupying the basal portion of the cell.

The cells of the ciliated leaflets are columnar and the cilia are with well developed basal granules and parallel
PLATE IX

*S. aculeata* (histology; transverse sections)

a. Oesophagus

b. Stomach

c. Caecal leaflet

d. Intestine (along typhlosole)

e. Rectal cell

f. Liver

g. Pancreas

1. Cuticle lining

2. Mucosa

3. Submucosa

4. Longitudinal muscle

5. Circular muscle

6. Serosa

7. Formative layer

8. Mucus cells

9. Ciliated cells

10. Calcareous cells

11. Fat droplets
rootlets. The cytoplasm is granular with large oval nucleus. The mucous cells are saccular, occur in groups and open through a common pore (Plate IX c).

5.3.4 Intestine and Rectum

The lining epithelium consists of tall columnar ciliated cells interspersed with goblet cells. The layer is underlain by submucosal connective tissue followed by longitudinal and circular muscle layers (Plate IX d).

The rectal epithelium is non-ciliated and the cells are with hyaline border. The retractile rectal cells are present (Plate IX e).

5.3.5 Midgut Glands

5.3.5.1 Liver

The histology of the liver of _S. aculeata_ has much similarity with that of _S. inermis_. The gland is a bilobed structure composed of a large number of tubules thickly packed in a delicate sheath of muscle and connective tissue. The tubules are open into a wide central lumen. Two types of cells are met within this gland. The first type of cells are tall, cylindrical in form with cytoplasm filled with granules, vacuoles and often fat droplets at the base. This type of
cells carry out excretory, secretory and absorptive functions. In the excretory phase the cells are filled with vacuoles containing spherules. In the secretory phase the cells are densely filled with fine granules and with swollen ends. At times this swollen ends obliterate the luminal spaces. In the absorptive phase the cells contain vacuoles and the free ends are filled with clusters of granules and usually with a brush border. The second type of cells are pyramidal in shape with darkly staining cytoplasm containing granules and spherules. These cells are mainly associated in the formation of cuttle bone (Plate IX f).

5.3.5.2 Pancreas

As in the case of S. inermis the pancreatic follicles are covered by the renal epithelium. Each follicle is communicating with the hepatopancreatic duct through a short narrow duct. The boundaries of the individual cells were not able to make out in the paraffin sections. The luminal space is lined with a low epithelium having a well marked basophil cell border. The cytoplasm is fibrillar in appearance. The oval nucleus usually occupies the terminal portion (Plate IX g).

6. GLANDS RELATED TO THE ALIMENTARY CANAL

The glands of the digestive system can be classified mainly as (a) Fore gut glands and (b) Mid gut glands. The