

**The Alimentary Canal and Pro-epithelial Re-
generation in *Coccinella septempunctata* with
a comparison of Carnivorous and Herbivorous
Coccinellids.**

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1. INTRODUCTION.

THE work on the alimentary canal of Coccinellid beetles was taken up with a view to studying the structural differences that

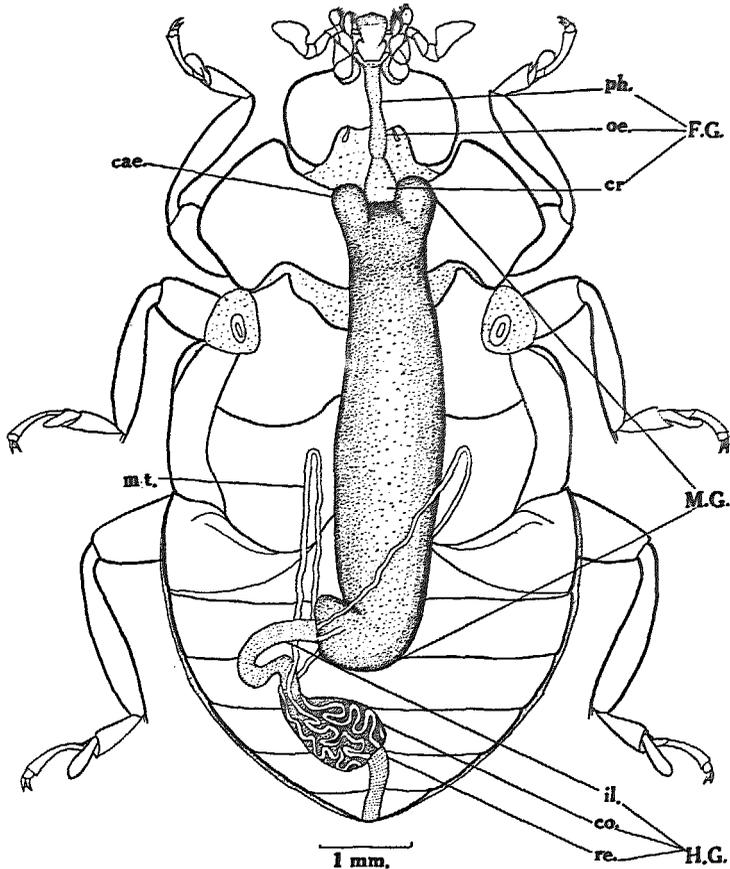
might have accompanied the difference in dietetic habits of carnivorous and herbivorous Coccinellids. A detailed study of the alimentary canal of *Epilachna indica* as a type of herbivorous Coccinellids has already been published (Pradhan, 1936). The present account deals with the anatomical and histological study of the alimentary canal of a mainly carnivorous type, namely, *Coccinella septempunctata*, Linn.

Besides examining the two species mentioned above, I have studied the digestive tract of five other species of Coccinellids. Of these five species four are mainly carnivorous, and their alimentary canals essentially resemble that of *Coccinella septempunctata*, while the fifth is a herbivorous species and resembles *Epilachna indica* in the character of its alimentary canal. These five species are:

- | | |
|--|--------------------------|
| 1. <i>Chilomenes sexmaculata</i> , Fabr. | } Mainly
carnivorous. |
| 2. <i>Synia melanaria</i> , Muls. | |
| 3. <i>Brumus suturalis</i> , Fabr. | |
| 4. <i>Chilocorus nigritus</i> , Fabr. | |
| 5. <i>Epilachna vigintioctopunctata</i> , Fabr. Herbivorous. | |

In *Coccinella septempunctata*, as in *Epilachna indica*, the results obtained have proved interesting and important not only from the point of view of the differences observed, but also in adding a few new facts to our knowledge of insect histology. It has been found that the mid-gut epithelium presents certain peculiarities, and that these are associated with a special type of epithelial regeneration which has not been recorded so far.

Coccinella septempunctata has been reported as 'one of the most economically valuable insects in India', but in spite of its economic interest it has not attracted sufficient attention at the hands of the entomologists. Examination of its gut-contents as well as field observations on its habits show that it consumes a large quantity of pollen, besides feeding on harmful insects. Lefroy's statement that 'this species is found only in the cold weather' does not hold good for this place (Lucknow), as it is generally available except in some of the coldest and the hottest weeks, when it is not in evidence.



TEXT-FIG. 1.

The alimentary canal of *Coccinella septempunctata* in situ: the coils of the ileum have been slightly opened. *cae.*, glandular diverticula; *ph.*, pharynx; *oe.*, oesophagus; *cr.*, crop; *M.G.*, mid-gut; *m.t.*, malpighian tubules; *il.*, ileum; *co.*, colon; *re.*, rectum; *F.G.*, fore-gut; *H.G.*, hind-gut.

2. ANATOMY OF THE ALIMENTARY CANAL.

Except for a slight convolution in the posterior region, the alimentary canal of *Coccinella septempunctata* (Text-fig. 1) is an almost straight tube of varying diameter, consisting

as usual of the fore-gut (*F.G.*), the mid-gut (*M.G.*), and the hind-gut (*H.G.*). It is about one-fourth longer than the length of the insect-body, the actual measurements in one case being: insect-body, 7.6 mm.; fore-gut, 1.4 mm.; hind-gut, 3.2 mm.; length of the whole gut, 9.4 mm.

The dimensions of the fore-gut vary in the same way as in *Epilachna indica* (Pradhan, 1936).

The Fore-gut.—The fore-gut resembles more or less that of *Epilachna indica* in size and shape, and is divisible into buccal cavity, pharynx, oesophagus, crop, and the oesophageal valve, there being a distinct constriction between the oesophagus and the crop.

I propose to describe in some detail (*a*) the 'extrinsic musculature', and (*b*) the nervous supply of the cephalic stomodaeum as they have not been well described in *Epilachna indica*.

(*a*) Extrinsic Musculature of Cephalic Stomodaeum.

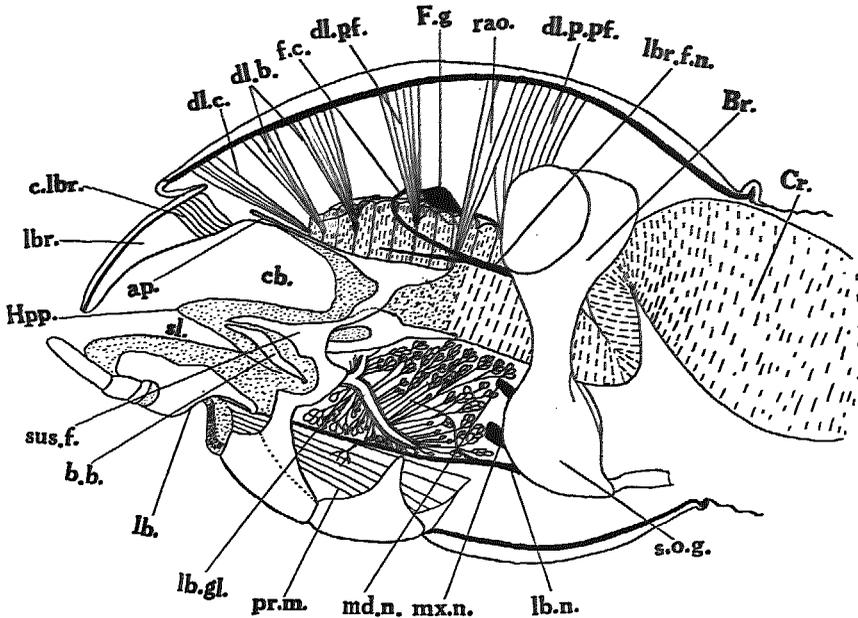
The 'extrinsic musculature' of the cephalic stomodaeum includes a number of paired dilator muscles inserted on the roof of the cibarium, buccal cavity, and the pharynx (Text-fig. 2). Each pair of these dilator muscles is separated from the others by thick stout bands of circular muscles. It is noteworthy that no muscles are inserted on the ventral wall of the cephalic stomodaeum in *Coccinella septempunctata*, and in this respect it differs from *Epilachna indica* in which there is a pair of ventral dilator muscles in the pharynx. Adopting Snodgrass's nomenclature, the following pairs of muscles can be distinguished in *Coccinella septempunctata*.

1. *Compressores Labri*.—The fibres of these muscles (*c.lbr.*) run between the anterior and posterior walls of the labrum, and their contraction raises the epipharyngeal wall of the labrum.

2. *Dilatores Cibarii*.—These are a pair of muscles (*dl.c.*) arising from the dorsal wall of the cranium and inserted dorsally on the epipharyngeal wall of the cibarium, just anterior to the oral opening, i.e. just in front of the first band of circular muscles. Besides this pair of muscles, there is an almost uniform

distribution of muscle-fibres (which are much shorter and weaker) on the epipharyngeal wall of the cibarium, behind the compressores labri.

3. Dilatores Buccales.—Taking the position of the



TEXT-FIG. 2.

Sectional view of the head of *Coccinella septempunctata* (reconstructed from dissections and sections). *ap.*, apophysis; *Hpp.*, hypopharynx; *sl.*, salivarium; *cb.*, cibarium; *lbr.*, labrum; *c.lbr.*, compressores labri; *dl.c.*, dilatores cibarii; *dl.b.*, dilatores buccalis; *f.c.*, frontal connectives; *F.g.*, frontal ganglion; *dl.p.f.*, dilatores pharyngis frontales; *dl.p.pf.*, dilatores pharyngis post-frontales; *lbr.f.n.*, labro-frontal nerve; *Br.*, brain; *Cr.*, crop; *s.o.g.*, sub-oesophageal ganglion; *lb.n.*, labial nerve; *mx.n.*, maxillary nerve; *md.n.*, mandibular nerve; *pr.m.*, premental muscle; *lb.gl.*, labial gland; *lb.*, labium; *b.b.*, basal bar; *sus.f.*, suspensorial fork; *rao.*, Retractores Angulorum Oris.

frontal ganglion as marking the posterior limit of the buccal cavity, we find that there are two pairs of dilator muscles (*dl.b.*) inserted on the roof of the buccal cavity. Both these pairs take their origin from the dorsal wall of the cranium.

4. *Dilatores Pharyngis Frontales*.—These muscles (*dl.p.f.*) are inserted on the dorsal wall of the pharynx just posterior to the frontal nerve-connectives; they take their origin from the dorsal wall of the cranium at a little distance behind the origin of the *dilatores buccales*.

5. *Dilatores Pharyngis Post-frontales*.¹—The origin of these muscles (*dl.p.pf.*) is as much behind that of muscle no. 4 as the origin of the latter is behind that of muscle no. 3. The insertion of these muscles on the roof of the pharynx lies beneath the supra-oesophageal ganglion.

6. *Retractores Angulorum Oris*.—These muscles (*rao.*) are inserted on the oral branches of the suspensorium of the hypopharynx; their origin is from the same place as that of *dilatores pharyngis post-frontales*.

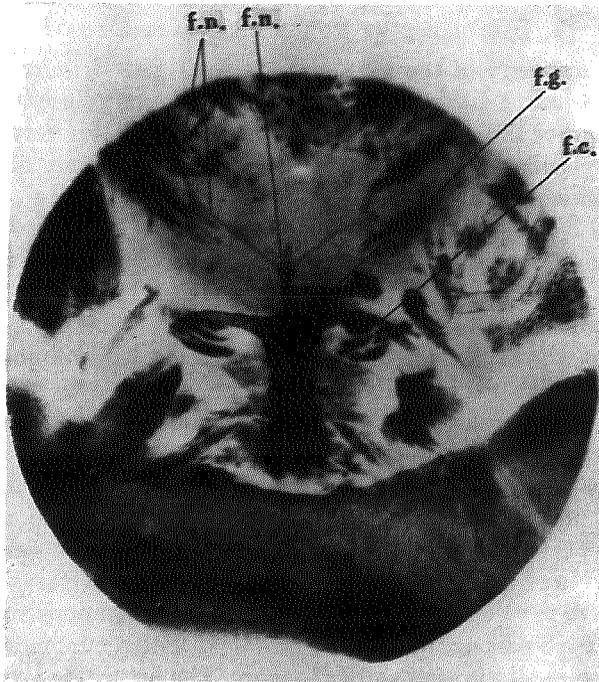
(b) Nervous Supply of Cephalic Stomodaeum.

As in other insects, the nerve supply of the cephalic stomodaeum of Coccinellids consists of a comparatively large frontal ganglion, and the various nerves given off from it. A pair of stout nerve-connectives arise from the tritocerebrum, one on either side, in common with the labral nerves and, after running a short distance forwards, turn round the *dilatores pharyngis frontales* and join the frontal ganglion, which lies on the fore-gut. The frontal ganglion gives off two main nerves, an anterior and a posterior, besides giving off several minute nerves to the circular muscles of the stomodaeum just beneath itself. The anterior nerve immediately forms a slight thickening and gives off a branch, on either side, before its termination (Text-fig. 3). These lateral branches divide and subdivide to innervate the dilator muscles in front of the frontal ganglion. The branching of these nerves is markedly symmetrical and almost dichotomous. The posterior recurrent nerve continues beneath the supra-oesophageal ganglion, and gives off branches both to the circular and dilator muscles behind the frontal

¹ Although the areas of the dorsal wall of the head-capsule (frontal, post-frontal, &c.) are not distinguishable separately, the terms *frontales* and *post-frontales* have been retained in the same order as given by Snodgrass 1935), as he asserts that the homology of these muscles is constant.

ganglion. The recurrent nerve ends on the oesophagus without forming any ganglion.

The Mid-gut.—The mid-gut forms a straight tube extending along the median line from the prothorax to about the middle of the third segment of the abdomen. When examined



TEXT-FIG. 3.

Photo-micrograph of the frontal ganglion and its nerves of *Coccinella septempunctata* taken from a free-hand section. *Br.*, brain; *f.c.*, frontal connective; *f.n.*, frontal nerves; *f.g.*, frontal ganglion.

under a binocular microscope in a fixed specimen, its outer surface presents a uniformly dotted appearance due to the prominence of the nidi. At its anterior extremity it gives off a pair of small glandular diverticula (*cae.*).

The Hind-gut.—The hind-gut is divisible into the ileum, colon, and rectum. The ileum is a short convoluted tube about 1.5 mm. in length; the colon is pear-shaped, although sometimes it looks like a thickened tube, while the rectum, which is only about 0.7 mm. in length, is much more muscular than the other two regions of the hind-gut.

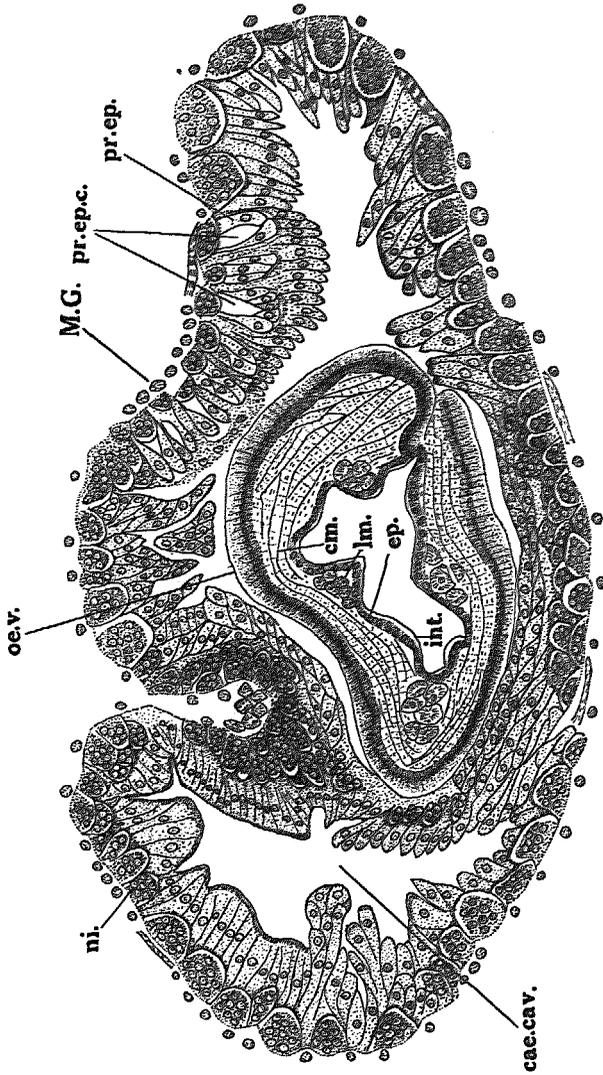
3. HISTOLOGY OF THE ALIMENTARY CANAL.

The histology of the fore- and the hind-guts is more or less typical, and I have therefore described it very briefly. The histology of the mid-gut, on the other hand, shows very interesting peculiarities, and I have therefore recorded my observations on it in some detail.

The Fore-gut.—The wall of the fore-gut (Text-fig. 4), from the lumen outwards, consists of: (1) the chitinous intima (*int.*), (2) the epithelium (*ep.*), (3) the basement membrane (not clearly distinguishable), and (4) the musculature. The wall of the fore-gut shows longitudinal epithelial folds, the number and size of which vary in different regions and also in the same region in different specimens. The thickness of the chitinous intima also varies rather irregularly. Both the chitinous intima and the longitudinal folds become much less pronounced in the region of the oesophagus in front of the crop. The musculature of the oesophagus is specially elaborate as described in *Epilachna indica*. The wall of the crop is thrown into four well-developed major folds, with a small minor fold between each pair of adjacent major folds. These minor folds are not seen in all the sections of the crop. The bristles are confined only to the top of these major folds. There are no teeth in the fore-gut.

The Oesophageal Valve.—The so-called oesophageal valve (Text-fig. 4) is well developed and looks funnel-shaped¹ in a longitudinal section. Unlike the case in *Epilachna indica*, the chitinous intima in this species does not end at the posterior free end of the valve, but extends a little beyond

¹ I have not sketched the longitudinal section through this region showing this difference from *Epilachna indica* as the rest of the structure is essentially similar to that in *Epilachna indica*.



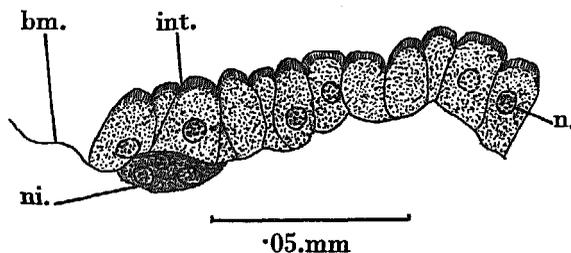
0.1mm.

TEXT-FIG. 4.

Transverse section through the oesophageal valve of *Coccinella septempunctata*. *M.G.*, mid-gut; *pr.ep.c.*, cavities in the pro-epithelial layer; *pr.ep.*, pro-epithelial cell; *oe.v.*, oesophageal valve; *ni.*, *nidi*; *cae.cav.*, cavity of glandular diverticulum; *ep.*, epithelium; *int.*, intima; *cm.*, circular muscles; *lm.*, longitudinal muscles.

this point. The base of the oesophageal valve is surrounded by a cellular girdle which, according to Wigglesworth, secretes the peritrophic membrane.

The Mid-gut.—The peculiarities of the mid-gut are confined only to the epithelial lining (Text-figs. 4–13), the other layers, i.e. the musculature and the basement membrane being more or less typical. On examining several series of sections



TEXT-FIG. 5.

First type of epithelium from the mid-gut of *Coccinella septempunctata*. *ni.*, nidi; *int.*, striated border; *n.*, nucleus.

through the mid-gut, I have come across variations which can be grouped into four categories as follows:

A. Epithelial cells contiguously arranged both above and in between the nidi.

First type. Epithelial cells short.

Second type. Epithelial cells long and columnar.

B. Epithelial cells separately grouped over the nidi.

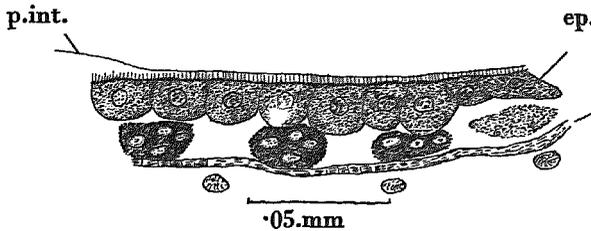
Third type. Simple groups of epithelial cells confined to the tops of the nidi.

Fourth type. Two layers of cells over the nidi; the one adjacent to the nidi formed of separate groups of large cells enclosing a big cavity.

First Type.—This type (Text-fig. 5) is found at places where new epithelium has been formed after the old epithelium has been sloughed off. The epithelial cells are evenly arranged both over and in between the nidi.¹ The cells are more or less

¹ The nidus is a small multinucleate mass of cytoplasm over which the columnar epithelium forms an arch. The cell-walls are sometimes distinct

cubical in form with a slight convexity on their inner border. The nidi are quite regularly arranged although their number per unit area is subject to much variation at different places. The striated border is generally well developed. This type of epithelium should be carefully distinguished from that (Text-fig. 6) having the same general appearance, and seen at places where the wall of the mid-gut is distended on account of the accumulation of the food material or of gas bubbles. In case of distension



TEXT-FIG. 6.

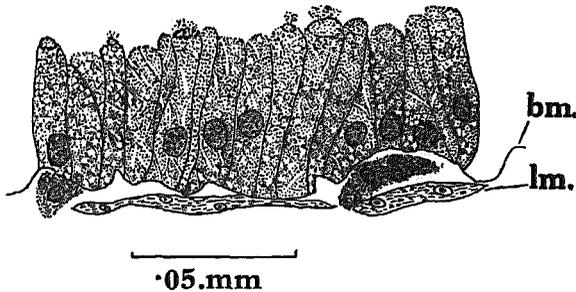
Stretched epithelium from the mid-gut. *ep.*, epithelium; *cm.*, circular muscle; *p.int.*, peeled off portion of striated border.

the height of the epithelial cells goes on decreasing with the distension of the wall, till the cells come to assume the isodiametric form of the newly formed cells. In extreme cases of distension, however, the cells are flattened, and their inner borders, instead of being convex as in the new epithelial cells, are flat or even slightly concave. The nature of the striated border also affords a clue by which one can distinguish the distended epithelium, since the border looks quite stretched, and the striations, instead of being close-set, lie far apart from one another.

In the distended epithelium we often observe that the inner lining of the striated border is peeled off (*p.int.*), the peeled off portion contributing to the formation of the peritrophic membrane. The portion of the border left behind gives at places the appearance of cilia arranged in a 'brush-border' fashion, and at others that of 'pore-canals' arranged in a line.

and sometimes indistinct. A detailed description of the nidi has been given in my paper on the alimentary canal of *Epilachna* (1936).

It may be noted that all these terms, namely, 'striated intima', 'striated border', 'pore-canal', 'cilia', &c., have been used by various workers in describing the inner border of the gut-epithelium. Hodge (1936) has given a good resumé of the various views on the nature of this inner border. Newell and Baxter (1936) and Zilch (1936) have published their own critical



TEXT-FIG. 7.

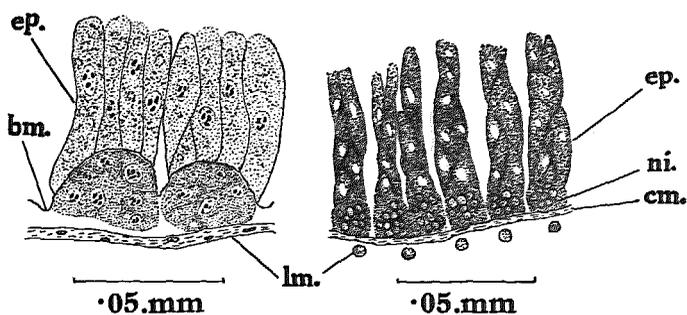
Second type of epithelium from the mid-gut of *Coccinella septempunctata*. *l.m.*, longitudinal muscle; *bm.*, basement membrane.

and decisive studies in this field. All the same the problem appears to be still far from a final solution.

Second Type.—This type (Text-fig. 7) is quite normal and resembles the typical epithelium described in various insects. The cells are generally much longer than broad and form a columnar epithelium. Sometimes the cells of a particular area are of equal height, while at other times this very area forms, as it were, crests and troughs of a wave. At some places the nuclei are arranged regularly, while at others irregularly; in the former case they generally follow the contour of the epithelium, while in the latter they are found at various levels in different cells, thus showing the different stages in their migration towards the lumen of the gut. The irregularity results from the physiological activity of the cells. The striated border is more clearly defined in the resting epithelium than in the active one. The distribution of the nuclei varies from a state of absolute contiguity (Text-fig. 4) to a widely separate condition

(Text-fig. 7). Their form and size range from small globular masses to high dome-shaped structures.

Third Type.—This type (Text-figs. 8 and 9) of epithelium resembles that sketched by Landis (1936) in the Coccinellid *Ceratomegilla fuscilabris*. The epithelial cells are confined to the tops of the nidi and form separate nidal groups. The cells are elongate, being many times taller than broad; the nuclei are found at different levels in different cells; the striated



TEXT-FIGS. 8 and 9.

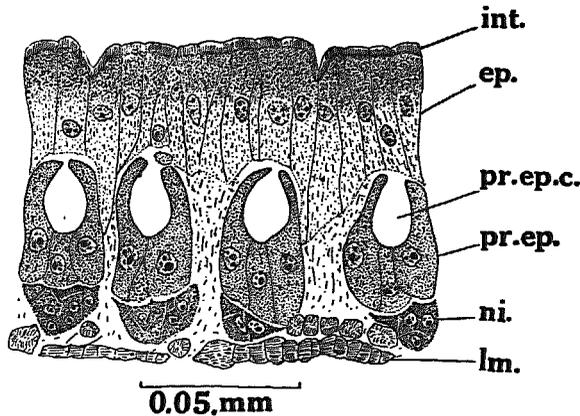
Fig. 8. Third type of epithelium.

Fig. 9. Third type of epithelium from a different series of sections.

border is rarely visible, and the nidi are quite regular but not contiguous.

Fourth Type.—This type puzzled me for a very long time. Both transverse and longitudinal sections of the mid-gut show an arrangement of cells, as shown in Text-figs. 10 and 11; on an examination of sections under lower magnifications, the epithelium at first sight appears to consist of two layers of cells besides the nidi. Closer examination under higher magnifications, however, reveals a peculiar and interesting arrangement. On the top of each nidus are seen two large, compactly built and darkly staining cells enclosing a big cavity between their apical (inner) portions. These cavities are sometimes empty and sometimes filled with a liquid which appears finely granular in sections. The basal portions of these cells are broad, while their apical portions are narrow and hook-shaped, the cavity being present between the hook-shaped portions. On the top

of these large cells there is another layer of narrow elongate cells which lie contiguous to one another. As seen in the figures, these cells differ from the large cells both in size and form, as well as in their behaviour towards staining reagents. The inner borders of these cells are sometimes well defined and striated, but at other times (Text-fig. 12) they are indefinite and broken



TEXT-FIG. 10.

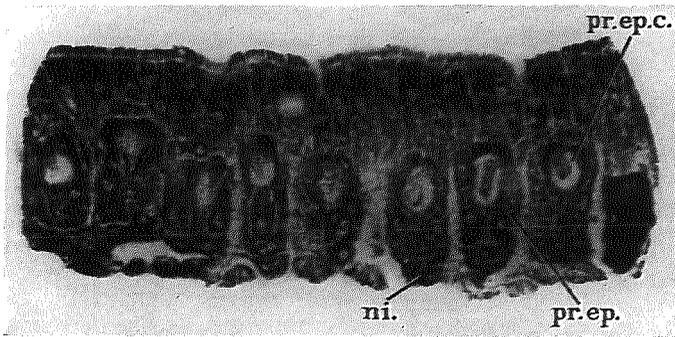
Fourth type of epithelium. *int.*, striated border; *ep.*, epithelium; *pr.ep.*, pro-epithelial cells; *pr.ep.c.*, pro-epithelial cavity; *ni.*, nidi; *lm.*, longitudinal muscle.

on account of active secretion. At still other times, this layer of narrow cells is seen to be sloughed off into the lumen of the gut (Text-fig. 13). In suitable preparations, specially those made at the time when the layer of narrow cells is being sloughed off, we can observe a well-defined structureless membrane furnishing a basement membrane to the narrow cells.

An examination of tangential sections (Text-fig. 14) of the wall of the mid-gut renders the structure of this type of epithelium clearer. Such sections passing through the cavities referred to above show that these cavities are surrounded by eight to ten large cells. It is obvious, therefore, that on the top of each nidus there is a group of eight to ten cells enclosing a big cavity within their distal portions. Thus the arrangement of

the various components of the wall of the mid-gut having this fourth type of epithelium is as follows: (1) longitudinal muscles, (2) circular muscles, (3) nidi, (4) groups of large pro-epithelial cells (the reason for this name is discussed later), (5) basement membrane,¹ and (6) layer of narrow elongate cells.

As far as is known to me, this arrangement of cells has not been recorded before. Pavlovsky and Zarin (1922) have described some vacuoles above the nidi in the ventriculus of

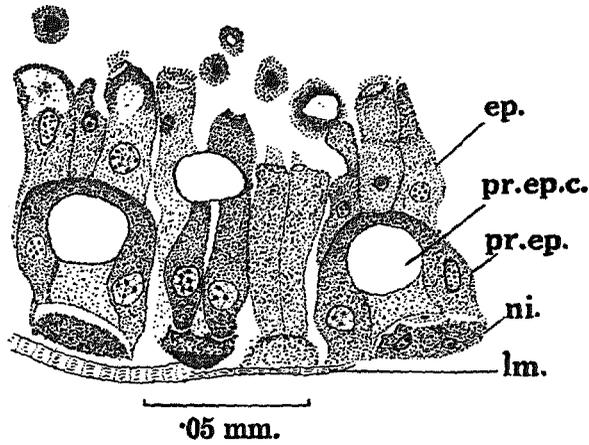


TEXT-FIG. 11.

Photo-micrograph of the fourth type of epithelium (touched up).
pr.ep., pro-epithelial cells; *pr.ep.c.*, pro-epithelial cavity; *ni.*, nidi.

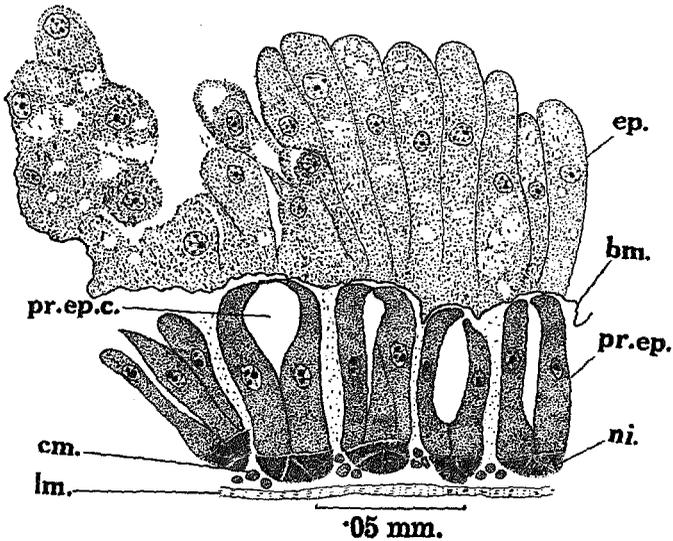
the honey-bee. These vacuoles, at first sight, seem to bear the same relation to the nidi as the cavities observed in this species, but in the bee the vacuoles open directly into the gut, there being no layer of cells on the top of these vacuoles. Also the vacuoles in the case of the honey-bee are not surrounded by specially large cells as they are in *Coccinella septempunctata*.

¹ This statement naturally raises the question: Are the nidi outside the basement membrane? Green (1931) has severely criticized Potts (1927) for describing the nidi as lying outside the basement membrane. Some suitable sections stained with iron haematoxylin showed beyond doubt that the basement membrane extends between the layer of narrow cells and that of pro-epithelial cells. Subsequent examination of other sections of the mid-gut confirmed the fact that the basement membrane extends above the nidi, and that it is formed anew between the nidi and the new epithelium when the old epithelium has been shed.



TEXT-FIG. 12.

Fourth type of epithelium showing active secretion. *ep.*, epithelium; *pr.ep.*, pro-epithelial cells; *pr.ep.c.*, pro-epithelial cavity; *ni.*, nidi; *lm.*, longitudinal muscle.

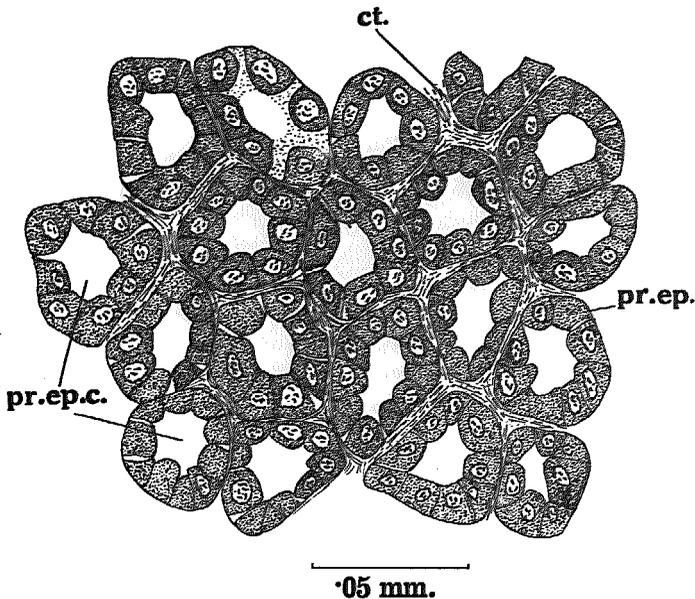


TEXT-FIG. 13.

Fourth type of epithelium showing the sloughing off of the epithelium. *ep.*, epithelium; *bm.*, basement membrane; *pr.ep.*, pro-epithelial cells; *pr.ep.c.*, pro-epithelial cavity; *ni.*, nidi; *cm.*, circular muscle; *lm.*, longitudinal muscle.

Relation between the various Types of Epithelium.

Except the first type, which is found only in small patches, the other three types generally do not coexist in the same specimen. It is, therefore, very difficult to appreciate the relations between these various types until a large number of series of sections has been examined and the rather rare cases of



TEXT-FIG. 14.

Tangential section through the pro-epithelial layer of the fourth type of epithelium. *ct.*, connective tissue; *pr.ep.*, pro-epithelial cells; *pr.ep.c.*, pro-epithelial cavity.

coexistence of two types observed. When I examined the first series of sections through the mid-gut, I found that the entire lining was made up of what I have described as the fourth type of epithelium, and I took it as an inexplicable modification of the typical epithelium of an insect mid-gut. The problem became still more puzzling when subsequent series of sections through this very region showed, in the same species, absolutely

different types of cellular arrangement as described above. Fortunately, however, a closer study of a large number of series made it possible to observe the intermediate stages between these types, and now I am clear in my mind that these various types are, to use Hirsch's term, due to the 'monophasic' nature of the epithelial cells, and that they are really correlated with different phases of their physiological activity. There seems to be no doubt that the rarity of their coexistence is due to the fact that, using Hirsch's term again, these epithelial cells are generally 'synchronous' in their activity.

As to the relation between the first and the second types, it is easy to appreciate that the difference is due merely to age. Besides, the gradations among them are fairly easy to find. A glance at Text-figs. 8 and 9 makes it easy to imagine that the second type can possibly be derived from the third simply by a spreading out of the groups of epithelial cells, which will thus form a continuous layer instead of remaining confined in small groups on the tops of the nidi. The manner in which the third and the fourth types of epithelium come to be formed becomes clear after studying the following peculiar process of regeneration, which has probably not been recorded so far.

Pro-epithelial Regeneration.

In the epithelium of the second type, some of the topmost cells of the nidi begin to grow inwards, pushing the basement membrane and the whole of the existing epithelium in front of them. Simultaneously with the growth of these nidal cells there appears a cavity within each group of them. These cavities contain varying amounts of secretion which appears to be either digestive or only macerative in shedding off the epithelium in front, or both. Thus the ordinary second type of epithelium is transformed into the fourth type. It may be noted that presumably it is on account of the continuity of the basement membrane that the epithelial cells between the nidi are also dragged inwards.

As the narrow top-cells of the fourth type either drop off gradually or are sloughed off in a body, the large nidal cells enclosing the cavities, better termed the pro-epithelial

cells, come to form the new epithelium (hence the name Pro-epithelial regeneration); and as the contents of these cavities are also emptied into the lumen, the large cells round the cavities become more regular and columnar in shape, and form separate groups over the nidi as seen in the third type of epithelium (Text-figs. 8 and 9). Thus during the complete process of regeneration we get the third type of epithelium derived from the second type, with the fourth type as an intermediate phase. The third type can presumably change into the second type, as already suggested, and thus the cycle may be completed.

The formation of the first type of epithelium takes place either when the sloughing off of the epithelium occurs without the formation of the pro-epithelial cells, or when the sloughing off is so vigorous that even the pro-epithelial cells are thrown off into the lumen. In either case the new epithelium is formed by the activity of the nidi, at least some of which remain sticking to the gut-wall.

The Pyloric Valve.—The position of the pyloric valve is indicated externally by the origin of six malpighian tubules at equal distances round the gut. At this place the mid-gut is slightly telescoped into the hind-gut forming the so-called pyloric valve. The closure, as has already been described in the case of *Epilachna indica*, is not effected by the valve but by the sphincter behind it. The change in the nature of the epithelial cells and the musculature is almost similar to that described in *Epilachna indica*.

The Hind-gut.—The histological structure of the hind-gut hardly needs an elaborate description. The variation along the hind-gut chiefly concerns the epithelial folds and the development of musculature. The epithelium consists almost uniformly of iso-diametric cells covered on their inner surfaces by a chitinous intima. The posterior portion of the ileum and the colon show the adherence of the malpighian tubules. The rectum is hardly more than an elongated sphincter.

The Malpighian Tubules.—The malpighian tubules are six in number, arising at the junction of the mid- and hind-guts. They are proportionately smaller in length in this species than in *Epilachna indica*, and show an intimate

re-association with the hinder portion of the ileum and colon. The phenomenon of re-association has been described and discussed in a separate paper.

The Salivary Glands.—There are several pairs of glands in connexion with the mouth-parts, but there are grave doubts about their salivary nature. A note on the glands in association with the labium of *Coccinella septempunctata* has already been published (Pradhan, 1936), while a full account of the various gnathal glands has been incorporated in a separate paper (Pradhan, 1939).

4. COMPARISON OF THE ALIMENTARY CANALS OF CARNIVOROUS AND HERBIVOROUS COCCINELLIDS.

A comparison of the alimentary canal of *Coccinella septempunctata*, a type of the carnivorous Coccinellids with that of *Epilachna indica* (Pradhan, 1936), a type of the herbivorous Coccinellids, reveals the following important differences:

1. The length of the gut is about three times the length of the body in *Epilachna*, while it is only one and one-half times in the case of *Coccinella*.

2. The cells of the mid-gut epithelium are generally polyphasic¹ in *Epilachna* and generally monophasic¹ in *Coccinella*.

3. The cells of the mid-gut epithelium are generally asynchronous¹ in their activity in *Epilachna* and synchronous¹ in *Coccinella*.

4. The pro-epithelial process of regeneration takes place in *Coccinella* but not in *Epilachna*.

5. The proximal extension of the hypopharyngeal skeleton in the floor and sides of the buccal cavity is weaker in *Epilachna* than in *Coccinella*.

6. The ventral dilator muscle of the hypopharynx is present in *Epilachna* but absent in *Coccinella*.

7. The malpighian tubules are proportionately smaller in *Coccinella* than in *Epilachna*.

¹ I have taken these terms of G. C. Hirsch (1931). These terms are explained at length in the next section.

5. PROBABLE EXPLANATION OF DIFFERENCES.

In order to explain these differences with any degree of certainty, a much greater knowledge of physiology is required than we possess at present; I am, however, offering the following tentative explanation. There is no doubt that the various differences recorded here are chiefly due to difference in diet of the two insects. The chief differences in the animal and vegetable foods are:

(a) that the latter is generally more abundant than the former;

(b) that the former is in a more concentrated form than the latter.

The effect of the first difference may be that whereas a herbivore can go on feeding continuously, a predator may have to wait till a prey is available, and on finding the prey it may have not only to pounce upon the prey, but that the whole process of feeding and digestion may have to start all of a sudden. The physiological process in a herbivore probably goes on evenly, rather at ease without any particular consideration of time, but in the case of a predator there is greater likelihood that the physiological activity of the digestive cells may show clear-cut and rather sudden breaks, the cells becoming suddenly active when the prey is available, and then remaining quiescent till the prey is seized upon.

The effect of the second difference, on the other hand, should be that the animal food, though smaller in quantity, requires abundant secretion of enzymes, &c., on account of the food being in a concentrated form; the vegetable food, on the other hand, being larger in quantity and less concentrated in nourishment, must be retained in the gut for a longer period before the nourishment is extracted from it.

These speculations find some support from my comparative study of the two types of alimentary canals.

1. Length of the Gut.—It is a general rule that the length of the digestive tract in herbivorous animals is longer than that in the carnivorous forms. This rule holds good here, the gut of the herbivorous insect being proportionately double the length

of that of its immediate carnivorous ally. It may also be noted that this difference concerns mainly the secretory and absorptive portion, i.e. the mid-gut, the lengths of the fore- and hind-guts being almost the same in the two cases.

2. Phases of Activity.—The difference in the phases of activity of the epithelial cells conforms to our expectations. In the herbivorous *Epilachna* in which the food is held in a convoluted mid-gut for a long period where secretion as well as absorption goes on rather slowly, the digestive cells are polyphasic, i.e. the cells repeat the secretory process several times before getting finally exhausted. But, in the carnivorous *Coccinella*, the digestive cells are monophasic, i.e. the secretory activity is generally more violent and the whole cell, or in fact the whole epithelium, is generally completely used up during one period of secretion and a new epithelium has to be formed for the next time.

3. Synchrony of Activity.—The difference in the synchrony of secretion is also as would be expected. As *Epilachna* is generally feeding continuously and the various stages of digestion go on in the long convoluted mid-gut, the digestive cells are found at any time to be in various phases of secretion, i.e. they are asynchronous in their activity, some cells being in one phase of secretion while others in another phase at the same time. In the carnivore *Coccinella*, on the other hand, the whole of the epithelium of the mid-gut is generally found in one and the same phase of digestive activity, so much so as to make it difficult, as already pointed out, to observe the intermediate stages. This is what is meant by saying that the digestive cells are synchronous in their activity. The reason is that as the animal food is concentrated in form it requires only a short length of the gut, i.e. the region of digestive activity is narrowed down; and consequently the chances of variation in the phase of the digestive cells are lessened.

4. Pro-epithelial Regeneration.—The presence of this peculiar process of regeneration in the carnivorous *Coccinellids* and its absence in the herbivorous species form the most striking difference between the carnivorous and herbivorous mid-guts. The formation of the pro-epithelial cells

between the existing epithelium and the nidi has already been explained to be a preparation for the sloughing off of the existing epithelium, and casting it into the lumen of the gut as soon as the need arises. One might, therefore, argue that the reason for this difference is that while the predator is waiting for a chance to catch the prey, the epithelium is getting ready for the occasion when the whole of it will be almost suddenly thrown into the lumen to be used up for the purpose of digestion. Such a preparation is obviously not needed in a herbivorous form. A serious criticism against this argument, however, is that the aphids on which these predators feed occur mostly as apterous forms and in very large numbers, and are therefore easily preyed upon, there being no necessity for the predator to wait.

5. Sclerotization of the Hypopharyngeal Skeleton.—This difference is of a minor character. As all the mouthparts are strongly sclerotized in a predator, the hypopharyngeal skeleton is also better sclerotized.

6. Dilatores pharyngis Ventralis.—The presence of this muscle in a herbivore and its absence in a carnivore seem to be related to the consistency of the food-morsel. The predator Coccinellid, as I have observed in *Coccinella*, catches hold of the aphid between its mandibles and sucks up its body-fluid for a time and then swallows the soft aphid. The food-morsel of the herbivore, I feel, may be comparatively more solid and thus to force it into the pharynx may be more difficult. This difficulty might be facilitated by extending the cavity of the pharynx somewhat by means of the ventral dilator muscle. It might be contended that the pharyngeal dilators are generally more needed in the case of liquid feeders, but it may be noted that that is the case where the ingestion takes place by suction and not by swallowing as in Coccinellids.

7. Malpighian Tubules.—Why the malpighian tubules should be proportionately smaller in carnivorous than in herbivorous forms is difficult to explain.

6. MATERIAL AND TECHNIQUE.

The insects used during these studies were either brought

fresh from the fields or reared in the laboratory, the species which were kept in the laboratory for fairly long periods being *Epilachna indica*, *Epilachna vigintioctopunctata*, *Coccinella septempunctata*, and *Chilomenes sexmaculata*. The former two of these species were fed on the solanaceous and curubitaceous leaves, while the latter two flourished well on every available species of aphids.

The general technique employed has been almost the same as has been published in the paper on the alimentary canal of *Epilachna indica* (Pradhan, 1936).

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8. SUMMARY.

The paper incorporates:

1. The anatomy of the alimentary canal of *Coccinella septempunctata* as a type of carnivorous Coccinellid.
2. A detailed account of the extrinsic musculature and the nerve-supply of the cephalic stomodaeum, which have been studied in very few insects and never in Coccinellids.
3. The histology of the alimentary canal, specially the mid-gut, distinguishing four definite types of epithelium, one of which is surprisingly peculiar and has not been described before. This type of epithelium shows apparently two layers of cells,

one superimposed over the other, the outer having large, regularly arranged, intercellular vacuoles as have not been described before, at least in the gut of insects.

4. A discussion on the relations of the four types of epithelium to one another, recognizing that this peculiar type of epithelium is just a phase in a unique process of Pro-epithelial Regeneration in the mid-gut epithelium.

5. A comparison of the chief characteristics of the alimentary canal of carnivorous and herbivorous Coccinellids based on the study of seven species of lady-bird beetles.

6. Probable explanations of the differences between the alimentary canals of the carnivorous and herbivorous Coccinellids.

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