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The Alimentary Canal of *Anisolabis littorea* (White) (Dermaptera: Labiduridae), with Special Reference to the Peritrophic Membrane

By E. T. GILES

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Abstract

THE alimentary canal of *Anisolabis littorea* (White, 1846) (Dermaptera: Labiduridae) is described macroscopically and histologically. The organ, which is generalised in structure and typical of Orthopteroid insects, is almost straight; the only coil lies in the anterior intestine. There are no enteric caeca; an undivided fold of the midgut probably represents them. The anterior intestine is not divided to ileum and colon. Considerable attention is paid to the peritrophic membrane, including electron micrography of several regions. The long thread-like malpighian tubules are arranged in four groups. They are shown to open into the extreme anterior end of the hindgut. Comparisons are made with the alimentary canal of the European earwig, *Forficula auricularia* L.

INTRODUCTION

THIS paper on the alimentary canal of *Anisolabis littorea* (White, 1846), the endemic coastal earwig of New Zealand, is the last of the present series, earlier papers having dealt with the biology, head capsule and antennal growth, and the male and female reproductive systems (Giles, 1952, 1953, 1961, 1961a). The general morphology of the gut, including its histology, is described, but cellular activity in relation to feeding is not dealt with. This would be a profitable study.

Most work on the Dermapteran alimentary canal has been done on the European earwig *Forficula auricularia* L. Cuénot (1895) briefly mentions some aspects of the physiology of the alimentary canal of *F. auricularia* but deals more fully with the peritrophic membrane. Bordas (1897) figures and gives a fairly detailed description of the structure and histology of the gut of this species. He notes that in both *Anechura bipunctata* (Fabricius, 1781) and *Labidura riparia* (Pallas, 1773) the organ is essentially similar to that of *F. auricularia.* Lhoste (1941) describes the alimentary canal of *F. auricularia*—the external morphology briefly and the histology in more detail.

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It might be mentioned that on the basis of certain points of similarity between the alimentary canals of *F. auricularia* and some Phasmids, Bordas (1897) grouped the Dermaptera and the Phasmida (ranked by him as the families Forficulidae and Phasmidae, respectively) into the same suborder, the Acolotasia, within the Orthoptera *s. lat.* These points of resemblance include the division of the alimentary canal into six distinct parts, the complete absence of enteric caeca, the fairly well developed salivary glands, the relatively numerous malpighian tubules and the small gizzard. However, these features are insignificant beside the tremendous weight of evidence provided by the exoskeleton which places the Dermaptera and the Phasmida in separate orders of the Orthopteroidea, and fairly widely separated as well (Giles, 1963).

Technique

The gut was examined in 1% saline and dissections carried out on material hardened in 70% alcohol. For histology, Eltringham's Fixative B (Eltringham, 1930) gave good results, followed by impregnation using the technique of Awati (1914) for whole insects. Erlich's haematoxylin counterstained with van Gieson proved satisfactory.

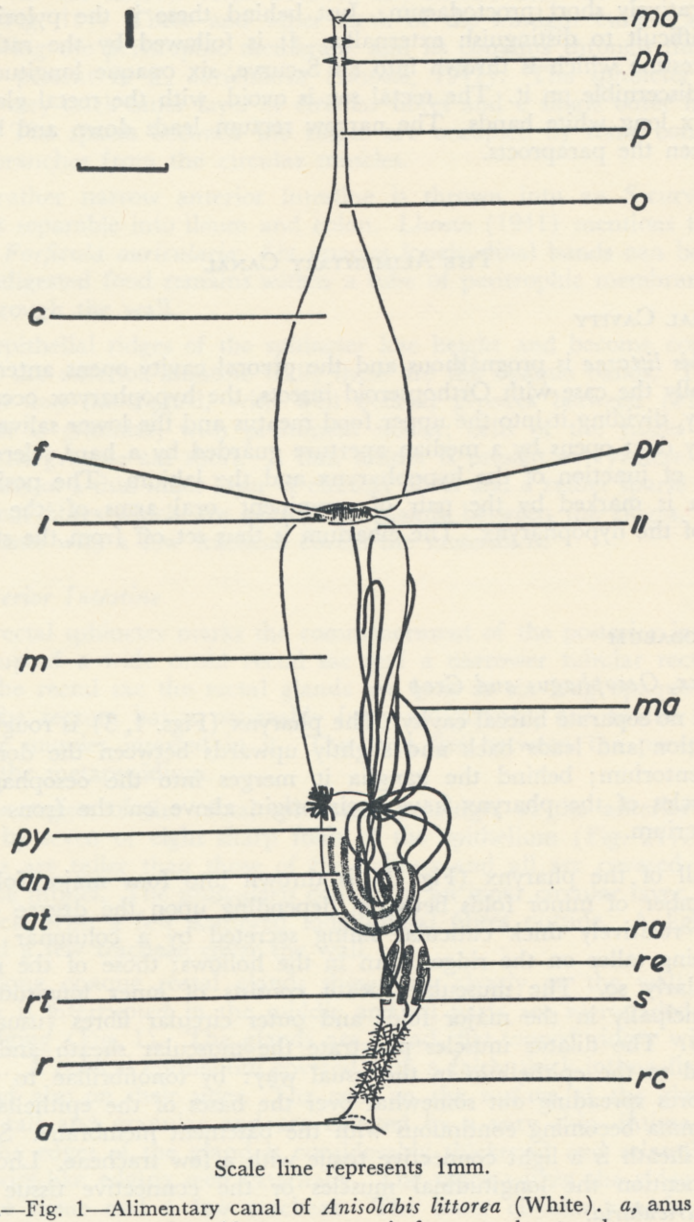
For electron microscopy the peritrophic membrane was dissected out of the alimentary canal in pieces and as much debris as possible cleaned away. A suspension of the membrane in water was subjected to 10 to 15 seconds' ultrasonic cleaning and disintegration in an M.S.E. head with a Mullard amplifier. Droplets of the suspension were then transferred to a grid, dried and shadowed with gold-palladium. Examination was by means of Siemens Elmiskop I and II microscopes.

Acknowledgments

The assistance received from Dr T. E. Woodward, Department of Entomology, University of Queensland, is gratefully acknowledged. Dr D. G. Drummond, Electron Microscopist at the University of Sydney, kindly agreed to the electron micrographs of the peritrophic membrane being taken in his Unit; his help and interest is very greatly appreciated. Special thanks are due to Mr C. D. Shorey, who prepared the difficult material and made the electron micrographs.

Outline of the Structure of the Alimentary Canal

The gut, which is almost straight, except for a slight flexure in the oesophagus and a single coil in the anterior intestine, is generally similar to that of an Orthopteroid insect (Fig. 1). The slit-like preoral cavity is marked off from the stomodaeum by the paired oral arms of the suspensory apparatus of the hypopharynx. The pharynx passes upward and backward from the mouth to the middle of the head. The oesophagus is only slightly wider than the pharynx and passes back through the neck into the prothorax where it dilates into the large pyriform crop which extends back to the first or second abdominal segment. The proventriculus is seen as little more than a very narrow ring, the remainder of the organ being almost obscured by the crop and the midgut.



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TEXT-FIG. 1.—Fig. 1—Alimentary canal of *Anisolabis littorea* (White). *a,* anus; *an,* anterior intestine; *at,* anterior intestine ridge; *c,* crop; *f,* free muscle strands; *m,* midgut; *ma,* malpighian tubules (cut short on left); *mo,* mouth; *o,* oesophagus; *p,* pharynx; *ph,* pharyngeal dilator muscles; *pr,* proventriculus; *py,* pylorus; *r,* rectum; *ra,* rectal valve; *rc,* rectal dilator muscles; *re,* rectal glands; *rt,* rectal sac; *s,* sclerotised margin; *I,* first midgut fold; *II,* second midgut fold.

The midgut continues back to the hindgut as a straight thick-walled tube, fairly wide in front, but slightly narrower behind.

The ring of four bundles of malpighian tubules lies at the commencement of the comparatively short proctodaeum. Just behind these is the pyloric sphincter which is difficult to distinguish externally. It is followed by the rather narrow anterior intestine which is thrown into an S-curve, six opaque longitudinal bands being just discernible on it. The rectal sac is ovoid, with the rectal glands clearly visible as six long white bands. The narrow rectum leads down and back to the anus, between the paraprocts.

THE ALIMENTARY CANAL

THE PREORAL CAVITY

Anisolabis littorea is prognathous and the preoral cavity opens antero-ventrally. As is typically the case with Orthopteroid insects, the hypopharynx occupies much of the cavity, dividing it into the upper food meatus and the lower salivary channel. The salivary duct opens by a median aperture guarded by a hard sclerotised ridge on the line of junction of the hypopharynx and the labium. The position of the true mouth is marked by the pair of prominent oral arms of the suspensory apparatus of the hypopharynx. The cibarium is thus set off from the stomodaeum proper.

THE STOMODAEUM

The Pharynx, Oesophagus and Crop

There is no separate buccal cavity. The pharynx (Figs. 1, 3) is roughly circular in cross-section and leads back and slightly upwards between the dorsal ganglia and the tentorium; behind the ganglia it merges into the oesophagus. The dilator muscles of the pharynx have their origin above on the frons and below on the tentorium.

The wall of the pharynx (Fig. 3) is thrown into four major folds, with a varying number of minor folds between, depending upon the degree of dilation. There is a relatively thick cuticular lining secreted by a columnar epithelium, the cells being taller on the ridges than in the hollows; those of the major folds are particularly so. The muscular sheath consists of inner longitudinal fibres, located principally in the major folds and outer circular fibres (usually two or three deep). The dilator muscles penetrate the muscular sheath and the fibres are attached to the epithelium in the usual way: by tonofibrillae to the intima, with the fibres spreading out somewhat over the bases of the epithelial cells and the sarcolemma becoming continuous with the basement membrane. Surrounding the muscle sheath is a light connective tissue with a few tracheae. Lhoste (1941) does not mention the longitudinal muscles or the connective tissue sheath in *Forficula auricularia*.

Behind the dorsal ganglia the pharynx merges almost imperceptably into the slightly wider oesophagus, which may be regarded as passing from the back of the head to the anterior part of the prothorax. A number of differences from the pharynx are apparent: there are no dilator muscles, the internal ridges are more numerous and are not arranged in major and minor series and the muscle sheath is much thicker. Although the cuticular lining of the oesophagus is similar to that of the pharynx, the epithelial cells are somewhat taller in the oesophagus. The two muscle layers are similar to those of the pharynx but, associated with the more uniform height of the folds in the wall of the oesophagus, the longitudinal muscle fibres are fairly evenly spaced. A thin connective tissue with associated tracheae is also present. According to Lhoste (1941) the oesophagus of *Forficula auricularia* is not differentiated from the pharynx.

The crop dilates from the oesophagus, becoming widest in the first or second abdominal segment where it is abruptly rounded off to meet the gizzard. The crop can be greatly distended and when full of food occupies virtually the whole of the haemocoele in this region. The food contents are clearly visible through the thin wall. In material immersed in Bouin, the longitudinal and circular muscles are very conspicuous and form a regular network.

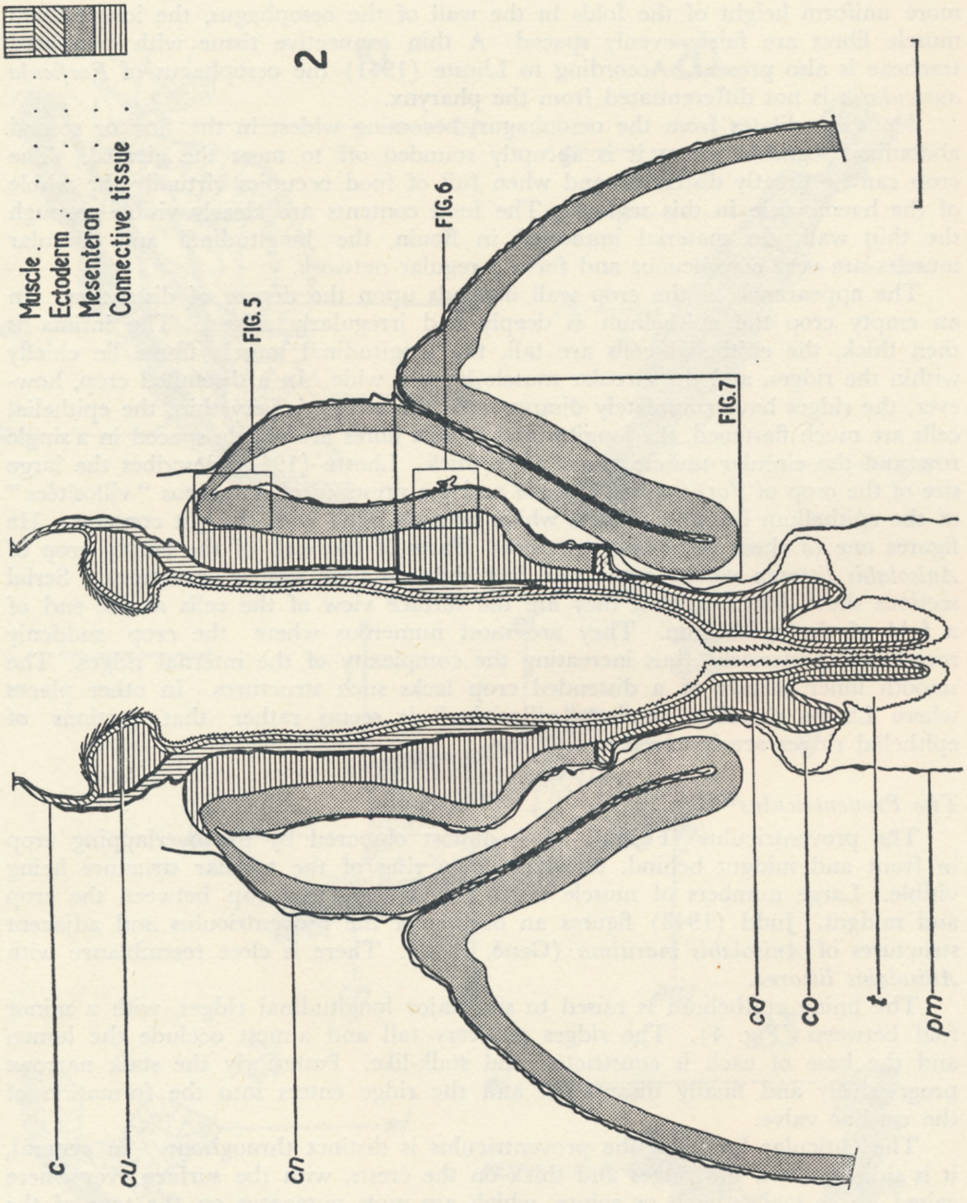
The appearance of the crop wall depends upon the degree of distention. In an empty crop the epithelium is deeply and irregularly ridged. The intima is then thick, the epithelial cells are tall, the longitudinal muscle fibres lie chiefly within the ridges, and the circular muscle layer is wide. In a distended crop, however, the ridges have completely disappeared, the intima is very thin, the epithelial cells are much flattened, the longitudinal muscle fibres are widely spaced in a single row and the circular muscle is one fibre thick. Lhoste (1941) describes the large size of the crop of *Forficula auricularia* and the presence of numerous " villositées " of the epithelium forming pockets which become filled with the gut contents. He figures one of these villus-like structures. Parts of the wall of the empty crop of *Anisolabis littorea* would appear at first sight to bear similar structures. Serial sections show, however, that they are the surface view of the cells at the end of a fold of the epithelium. They are most numerous where the crop suddenly rounds off posteriorly, thus increasing the complexity of the internal ridges. The smooth inner surface of a distended crop lacks such structures. In other places where Lhoste describes similar " villositées " it seems rather that sections of epithelial ridges are involved.

The Proventriculus

The proventriculus (Figs. 1, 2) is almost obscured by the overlapping crop in front and midgut behind, only a narrow ring of the tubular structure being visible. Large numbers of muscle fibres bridge the slight gap between the crop and midgut. Judd (1948) figures an outline of the proventriculus and adjacent structures of *Anisolabis maritima* (Gené, 1832). There is close resemblance with *Anisolabis littorea.*

The lining epithelium is raised to six major longitudinal ridges, with a minor fold between (Fig. 4). The ridges are very tall and almost occlude the lumen and the base of each is constricted and stalk-like. Posteriorly the stalk narrows progressively and finally disappears, and the ridge enters into the formation of the cardiac valve.

The cuticular lining of the proventriculus is distinct throughout. In general, it is thin between the ridges and thick on the crests, with the surface everywhere raised up as scales, teeth or spines, which are most numerous on the tops of the major ridges. Anterior to each major ridge is a small rectangular " cushion " of backwardly directed spines (Judd's " cushion of bristles "). In *Anisolabis maritima* this cushion is triangular with the base foremost (Judd, 1948). Cuticular teeth at the opening of the proventriculus of *Forficula auricularia* are described by Lhoste (1941). In the major ridges the epithelial cells are shorter on the crest than on the sides, whereas in the minor ridges they become taller towards the crest. The major ridges are occupied internally by connective tissue, but the minor ridges are formed solely by lengthened epithelial cells. The longitudinal muscle fibres also lie mainly within the major ridges, the circular fibres forming a thick outer layer.



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Text-fig. 2.—Fig. 2—Diagrammatic longitudinal section of the proventriculus and adjacent structures of the alimentary canal of *Anisolabis littorea* (White). *c,* crop; *ca,* cardiac valve; *cn,* connective tissue sheath; *co,* collar; *cu,* cushion of bristles; *pm,* peritrophic membrane; *t,* thickened cuticle.

The cuticle on the inner surface of each cardiac valve process bears large teeth; that on the outer surface is considerably thickened in two discrete areas and a pronounced collar is formed (Fig. 2). The epithelium is cubical and each process is filled with connective tissue.

The junction between the stomodaeal and mesenteric epithelium is reflected forward around the outer surface of the cardiac valve to a point roughly level with its base, where short ectodermal cells with cuticular intima are suddenly replaced by tall mesodermal cells with brush borders.

THE MESENTERON

The midgut (Fig. 1) is a straight tube slightly wider in front than behind. Externally it is clearly marked off from the proventriculus, which is partly overlapped by the midgut, and from the proctodaeum, which commences at the level of the malpighian tubules. There are no hepatic caeca.

The wall is thick, pale cream in colour in life and in front is thrown into two concentric folds. The inner wall of the first fold is in close contact with the proventriculus and the outer wall runs back to the level of the cardiac valve. Here the midgut wall turns forward to form the second fold and runs to a point near the middle of the first fold, where it turns back to form the main tube of the mesenteron. The hepatic caeca of most Orthopteroid insects are found in the same position as the second fold. It seems not unlikely that the second fold, in the course of evolution, could be broken up and reduced to detached caeca. However, the digestive function of this second fold is unknown. Further study would be worthwhile.

The mesenteric epithelium (Figs. 5–9) consists of very tall cells with a striated border, resting on a basement membrane. The cells are noticeably granular, but the position of the granules and depth of staining varies with the location of the cells. The nuclei are large and usually in the centre of the cells, forming a distinct line parallel to the free surface of the epithelium; the nucleoli are large and deeply-staining. The striated border is the typical brush border of mesenteric epithelium, consisting apparently of short hyaline rods. The striations are everywhere prominent, except towards the anterior of the inner wall of the first fold. As will be seen below, this region is concerned with the production of the peritrophic membrane. The free surface of the epithelium is clothed with granulate, spherical, brightly-shining globules secreted by the cells; where there are large numbers, mutual pressure causes deformation. These are the typical secretory globules of the insect midgut.

The free surface of the midgut wall is fairly closely pitted. The shorter cells of the pits have a noticeably less granular cytoplasm than the taller cells. Scattered about on the basement membrane between the bases of the tall epithelial cells are groups of two or three spherical regenerative cells. The midgut epithelial cells rapidly become shorter just before their junction with the proctodaeal epithelium (Fig. 9).

The muscle sheath of the mesenteron is very thin, both the inner circular and outer longitudinal layers being only one or two fibres thick. Enveloping the whole is a delicate connective tissue sheath incorporating a few tracheae.

Lhoste (1941) briefly describes the appearance and the histology of the midgut of *Forficula auricularia*; it is very similar to that of *Anisolabis littorea.*

The Peritrophic Membrane

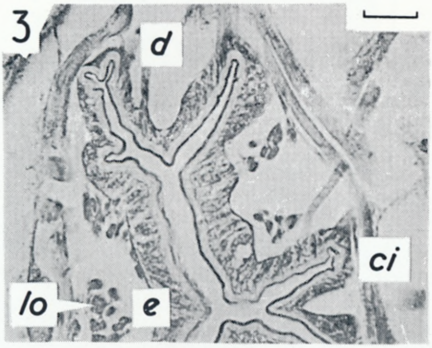
The peritrophic membrane (PM) of *Anisolabis littorea* is seen in the mesenteron and proctodaeum as a discrete, apparently uniform tube. It may be dissected out right up into the angle of the first fold of the midgut (Fig. 2). However, there is often a tendency to breakage at the level of the cardiac valve and the membrane seems to be rather thicker behind the valve. The PM lies close to the inner wall of the first fold of the midgut, but occasionally bulges away (Fig. 2). In the narrow ring between the fold of the midgut and the cardiac valve the membrane is more buckled, but over the cuticular collar of the valve it is restored to approximately its original diameter (Fig. 2). Thence the PM passes through the midgut, isolating the food contents from the gut wall. In the hindgut it is, as usual, drawn backwards by the peristaltic action of the wall and the backwardly directed teeth on the cuticular lining.

The PM is associated very closely with a ring of cells, about 15 wide, on the inner wall of the first fold of the midgut lying immediately behind the anterior angle of the fold (Figs. 2, 5). These cells are rather darker than nearby ones. The differential staining is more pronounced on the slides than in the photomicrographs. Lhoste (1941) says that chitin or a related substance from vacuoles of cells (apparently from the anterior region of the midgut) contributes to the formation of the PM of *Forficula auricularia.* However, this explanation is so different from that given by other authors that it seems that Lhoste must have been mistaken. Rizki (1956) shows the presence of a fairly wide, darkly staining ring of cells just behind the anterior extremity of the midgut of *Drosophila melanogaster.* He makes a series of histochemical tests—principally the periodic acid-Schiff reaction, which shows the presence of polysaccharides in the ring cells and the PM, and the positive chitosan test on the PM. He concludes that the secretions of the ring cells " are immediate precursors of chitin-polysaccharides " and further that this ring is the formative zone of the cuticular PM.

The general staining methods used with *Anisolabis littorea* can only demonstrate that more active secretion is taking place in the dark ring of cells than in other nearby areas. However, upon comparing the condition in *A. littorea* with Rizki's descriptions and figures, the writer is convinced that the PM in *A. littorea* is secreted as a distinct membrane by this ring of darkly staining mesenteric cells (Figs. 2, 5–7). It is fully formed and multi-lamellate before it reaches the cardiac valve (Figs. 6, 7) and is apparently the only PM present. However, a few sections of the midgut and contents have shown a number of irregular pieces of membrane which could result either from the folding of a single membrane or from the presence of more than one membrane. No further suitable material is now available to the writer for re-examination of this point by serial sections.

Cuénot (1895) says that in *Forficula auricularia* the PM is secreted at the vertex of the annular fold surmounting the midgut. He figures a condition very similar to that in *Anisolabis littorea,* except for a multi-layered condition within the midgut tube. There is no evidence of Wigglesworth's press (see below). Cuénot also says that the PM of both *Ectobia* and *Periplaneta* (Blattaria) is a secretory product of a ring of cells occupying the extreme anterior region of the midgut and that it is thick and made up of concentric layers. His figure of the formation of the membrane in *Ectobia* (which he says is the same as in *Periplaneta*) is quite clearly identical with that in *Anisolabis littorea* (type I, below).

Wigglesworth (1930) says that in *Blattella germanica* (Blattaria) the arrangement is similar to that figured by Cuénot in *Ectobia.* The oesophageal valve is long and thin walled and in freshly killed insects dissected in normal saline is often found to be distended with fluid, so forming an efficient press for the chitinous peritrophic membrane.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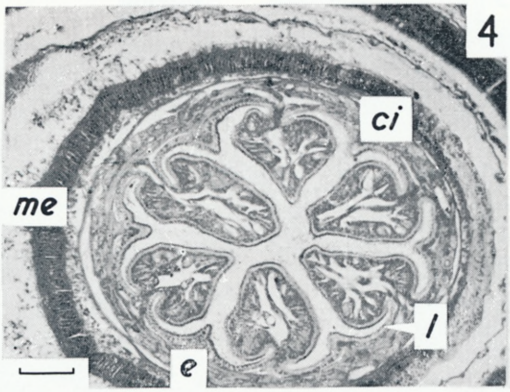
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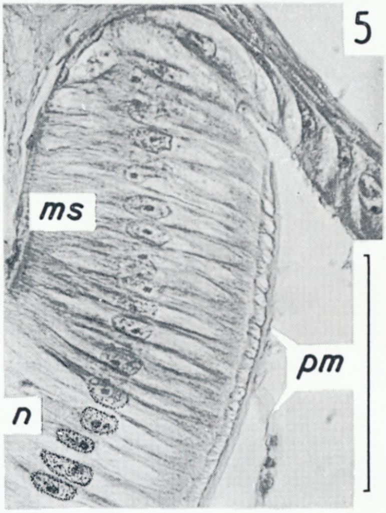
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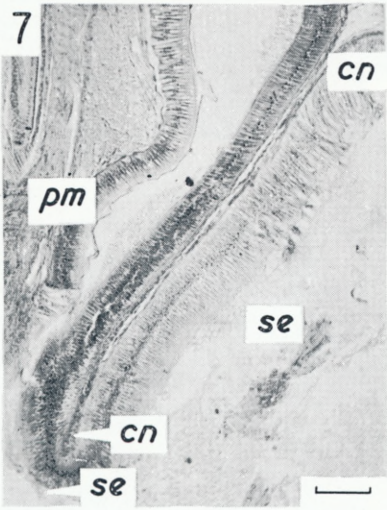
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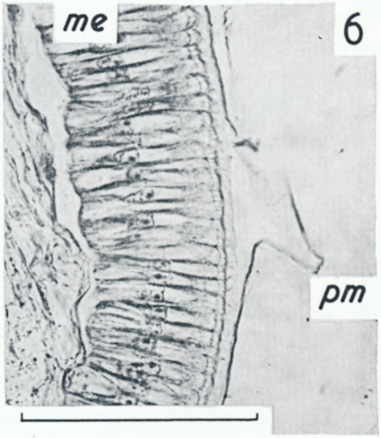
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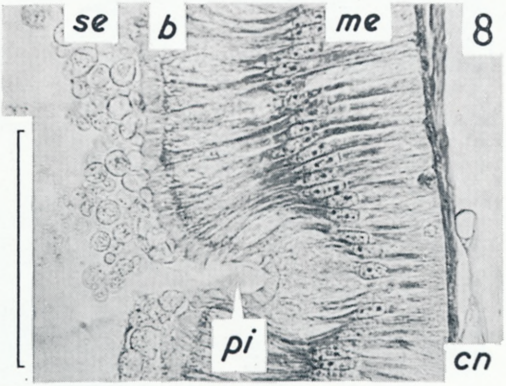
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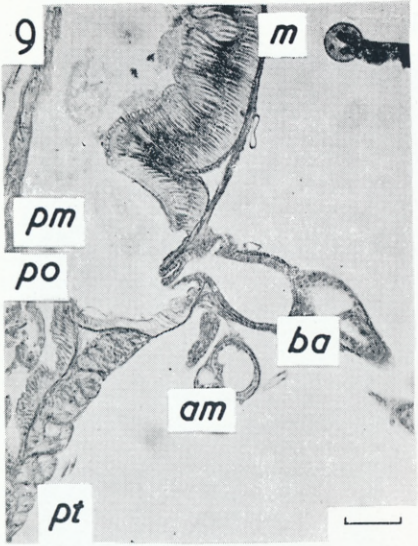
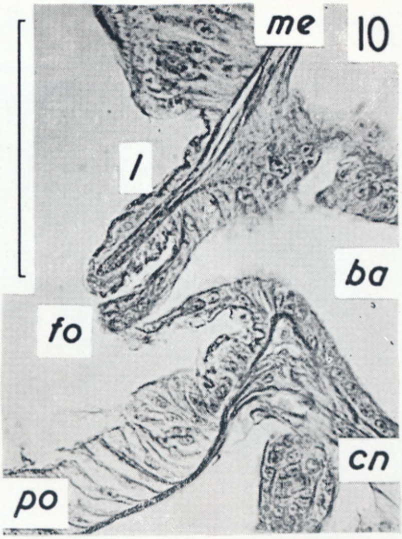
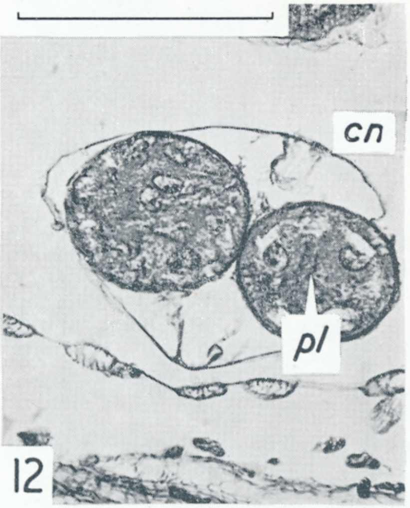
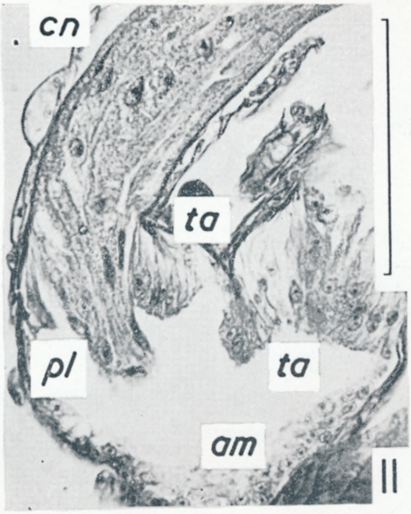
FIG. 3.—T.S. of pharynx in region of dilator muscles. Fig. 4.—T.S. of proventriculus. Fig. 5.—L.S. of extreme anterior of inner wall of first fold of mesenteron. Fig. 6.—L.S. near middle of inner wall of first fold of mesenteron. Fig. 7.—L.S. of posterior section of first fold of mesenteron. Fig. 8.—L.S. of wall of mesenteron, posterior region. *b,* brush border; *ci,* circular muscle; *cn,* connective tissue sheath; *d,* dilator muscles; *e,* epithelium; *l,* cuticular lining; *lo,* longitudinal muscle; *me,* mesenteric epithelium; *ms,* mesenteric cells secreting peritrophic membrane; *n,* mesenteric cells not secreting peritrophic membrane; *pi,* pit; *pm,* peritrophic membrane; *se,* secretory globules.









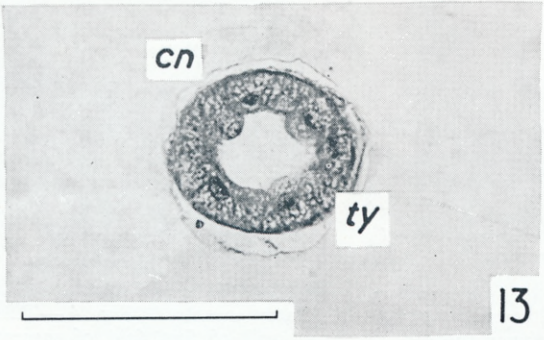


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FIG. 9.—L.S. of junction of midgut and hindgut, with basal vesicle of one cluster of malpighian tubules. Fig. 10.—L.S. of aperture of basal vesicle. Fig. 11.—L.S. of ampulla and proximal portion of malpighian tubule. Fig. 12—T.S. of malpighian tubules, proximal regions. Fig. 13.—T.S. of malpighian tubule, distal region. *am,* ampulla; *ba,* basal vesicle of cluster of malpighian tubules; *cn,* connective tissue sheath; *fo,* folds; *l,* cuticular lining; *m,* midgut; *me,* mesenteric epithelium; *pl,* plug of cellular material; *pt,* pyloric sphincter; *pm,* peritrophic membrane; *po,* proctodaeal epithelium; *ta,* tall epithelial cells; *ty,* typical malpighian tubule cells.

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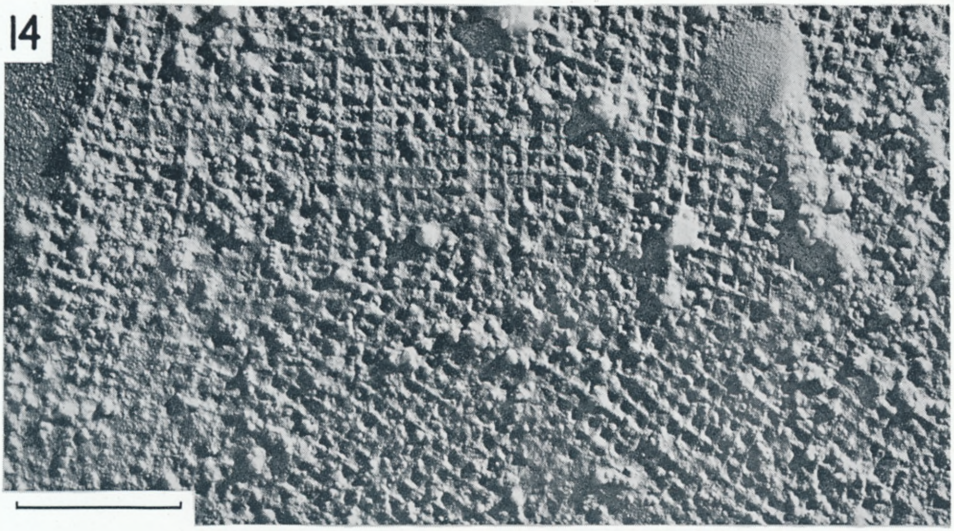

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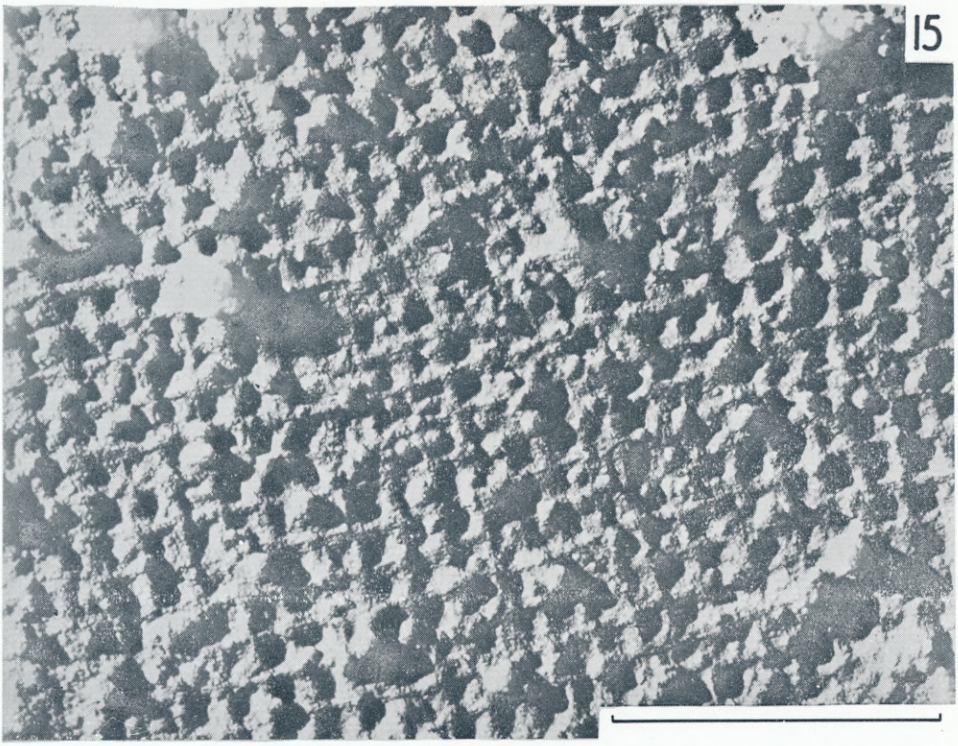

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Electron micrographs of peritrophic membrane (some debris adhering). Fig. 14.—Within the first fold of the midgut, between Insets 5 and 6 (Text-fig. 2). Fig. 15.—Higher magnification of portion of membrane from Fig. 14.

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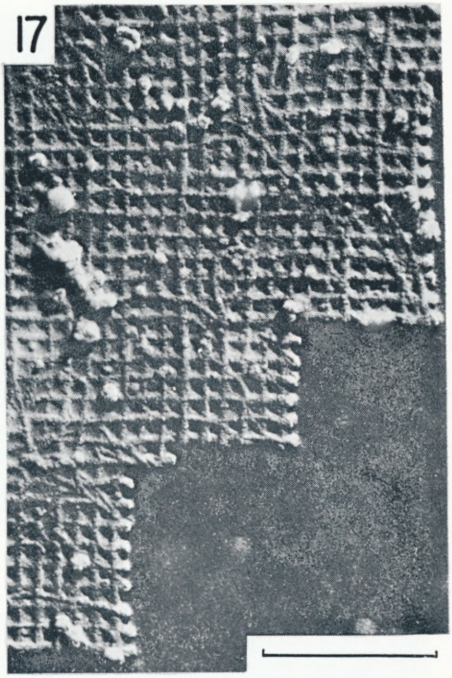

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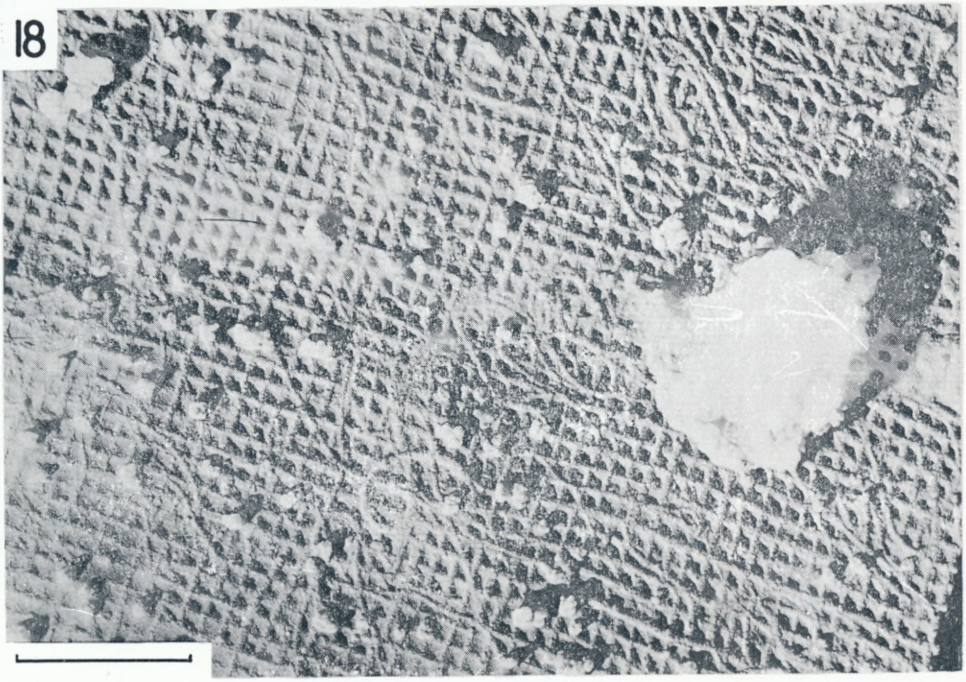

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Electron micrographs of peritrophic membrane (some debris adhering). Fig. 16.—Just behind the cardiac valve. Figs. 17, 18.—Well behind the cardiac valve (in the midgut).

Wigglesworth (1953) quotes Aubertot (1934) as authority for saying that the PM of *Forficula* is added to by delamination from the midgut wall. Waterhouse (1954) also followed Aubertot in recognising this condition in the Dermaptera. However, he now feels that the evidence does not definitely point to the membrane being of double origin (personal communication).

Wigglesworth (1930, 1939) shows a fundamentally different method of formation of the tubular PM of *Forficula auricularia* from that in *Anisolabis littorea.* It is secreted, he says, by an anterior ring of cells as a viscous material. This is moulded into a homogeneous tube as it passes through an annular press having for its inner jaw the collar of the cardiac valve and for its outer the angle of the midgut wall where it turns forward to form the second fold. The outer jaw is held against the inner by the contraction of a circular muscle in the angle of the wall. This is the typical type II PM of Wigglesworth (1939 and later editions) and type I of Waterhouse (1953, 1953a, 1954) and Day and Waterhouse (1953). The nomenclature of the latter authors will be followed here, although the method of PM formation in *A. littorea* is not strictly the same as in *F. auricularia.* There is no functional press of this type in *A. littorea,* for the constrictor muscle is absent and the midgut wall is clothed with secretory granules which would be swept off during the operation of a press (Figs. 2, 7). It would also seem that peristalsis of the gut would not allow the jaws of the press to be closed for lengthy periods.

Electron micrographs (Figs. 14–18) of three regions of the PM of *Anisolibas littorea* were made: from within the first fold of the midgut, from just behind and also from well behind the cardiac valve. There is some contamination from adherent debris, but not enough to mask the basic structure. It should be pointed out that this material was taken from specimens which had been preserved in spirit for 15 years.

In each of these positions the PM shows the same structure—namely, a fibrillar network with a regular squared arrangement. There appears to be a " less well-organized material overlying the net and filling the interstices " (Waterhouse, 1953a). However, in some places " holes " appear in the interstices (Fig. 18). The rectangular lines of breakage should be noted (Fig. 17), as should the difference between the trends of the meshes in the upper and lower parts of Fig. 14. It looks almost as though two pieces of somewhat differently oriented membrane may be joined. However, no completely convincing explanation comes to mind. While the general appearance shows great similarity to the P.M. of *Periplaneata americana* (Mercer and Day, 1952) there are some important differences. The characteristic hexagonal symmetry of *P. americana* is entirely lacking; there is no " honeycomb network ", except in the shadow of large pieces of debris (Fig. 18); the " irregular meshwork " of *P. americana* is not present; the network meshes in *Anisolabis littorea* are smaller, but the fibrils are much stouter.

Mercer and Day (1952) advance an interesting hypothesis to relate the network structure of the PM of *Periplaneta* to the rodlets of the brush border of the midgut epithelium, for they say that the PM is formed by a process of " exfoliation " and " delamination from a surface " (type II). In the light of Mercer and Day's argument that the PM of *Periplaneta* is a product of exfoliation, and its essentially similar ultrastructure to that of *Anisolabis littorea,* then the PM of *A. littorea* should be delaminated from the surface of the cells secreting it. How, then, is a continuous PM tube produced by the activity of such a narrow ring of cells? Is the tube formed like the ribbon on a microtome—namely, a length of membrane equal to the width of the secretory cell ring is formed, passed backwards and joined to the next, and so on? This may account for the sudden change in the trend of the network meshes seen in Fig. 14. Or do the lamellae and ultrastructure result from forces set up during the hardening of the cellular secretions which form the PM? Possibly the most important question to be settled is whether there are in fact two general methods of formation of the PM.

The ultrastructure of the PM of other insect species has been described and figured. Huber (1950) deals with the membrane of several species: *Carausius morosus* (Mantodea) has a multi-layered PM comprised of a fibrillar network with more or less hexagonal irregularly arranged meshes; the PM of *Blatta orientalis* (Blattaria) is also a multi-layered fibrillar network, but with regular, nearly square meshes; the fibrillar, multi-layered PM of the larva of *Tenebrio molitor* (Coleoptera) also has regular square meshes and the larva of *Bombyx mori* (Lepidoptera) has a very thick multi-layered PM with no visible structure. Lagermalm, Philip and Gralén (1950) show the PM of the larval clothes moth (*Tineola bisselliella*) to be of three different types: a regular fibrillar network with trapezium-shaped meshes, a rather irregular network with the meshes filled with some background substance and an arbitrary arrangement of fibres without apparent pattern. Martignoni (1952) examined single layers of the thick multi-layered PM of the larva of *Peridroma margaritosa* (Lepidoptera) and found a disordered framework with distinct micelles. Wildbolz (1954) shows differences in the ultrastructure of the PM of *Melolontha melolontha* (Coleoptera) following various treatments. After 12 hours with 3% pepsin the membrane appears as a fibrillar network with regular nearly-square meshes which are covered with a thin structureless film. After 48 hours with 3% " Sericym " (a proprietary protease) the PM appears as a rather irregular fibrillar network with the individual fibrils visible, and distinct " holes " occupying the positions of the meshes, now elliptical and somewhat variable in size.

Unfortunately there is little information on the mode of formation of the PM in these insects.

There can be no doubt that a thorough investigation of the formation and ultrastructure of the PM in a wide range of insects with differing feeding habits would be profitable.

THE PROCTODAEUM

The commencement of the hindgut is marked by the four clusters of malpighian tubules opening into the alimentary canal.

The midgut epithelium slopes down to meet the hindgut epithelium (Figs. 9, 10), the first portion of which consists of a narrow ring of cubical cells with a thick cuticular lining. This is followed by a longer region of vacuolated columnar cells. The cuticular lining is thin and discontinuous, but is clearly seen under phase contrast; it is discernible in Figs. 9, 10. Posteriorly is a columnar epithelium with a continuous, distinct cuticular lining. The pyloric sphincter commences well forward in the section of columnar epithelium (Fig. 9).

The Malpighian Tubules

Thirteen to sixteen malpighian tubules enter each vesicle. The tubules are long and fairly slender, and in life olive green for most of their length, but cream apically. They lie principally in the posterior part of the haemocoele and are usually entangled in the reproductive organs and fat body, but are not in close association with the alimentary canal. With a specimen in saline, the tubules are constantly writhing, but this appears to be more in sympathy with the gut peristalsis than from power of independent movement. The base of each tubule is dilated as a small spherical ampulla (Fig. 9). Usually several ampullae are associated and have a common aperture into the basal vesicle (Fig. 9); the groups of ampullae are irregularly arranged on the vesicle. Numerous tracheae ramify over the vesicle and among the bases of the tubules. The linear arrangement of malpighian tubules in *Forficula auricularia* (Henson, 1946) is undoubtedly correlated with the smaller number of tubules in that species (five to each basal vesicle). In *F. auricularia*, Bordas (1897) describes 8 to 10 or 12 tubules in two groups and Lhoste (1941) says there are 8 to 10. Henson points out that Bordas is incorrect. It is also difficult to reconcile Lhoste's describtion with his figure showing a single group of 4 tubules, but he may have been dealing with a nymph.

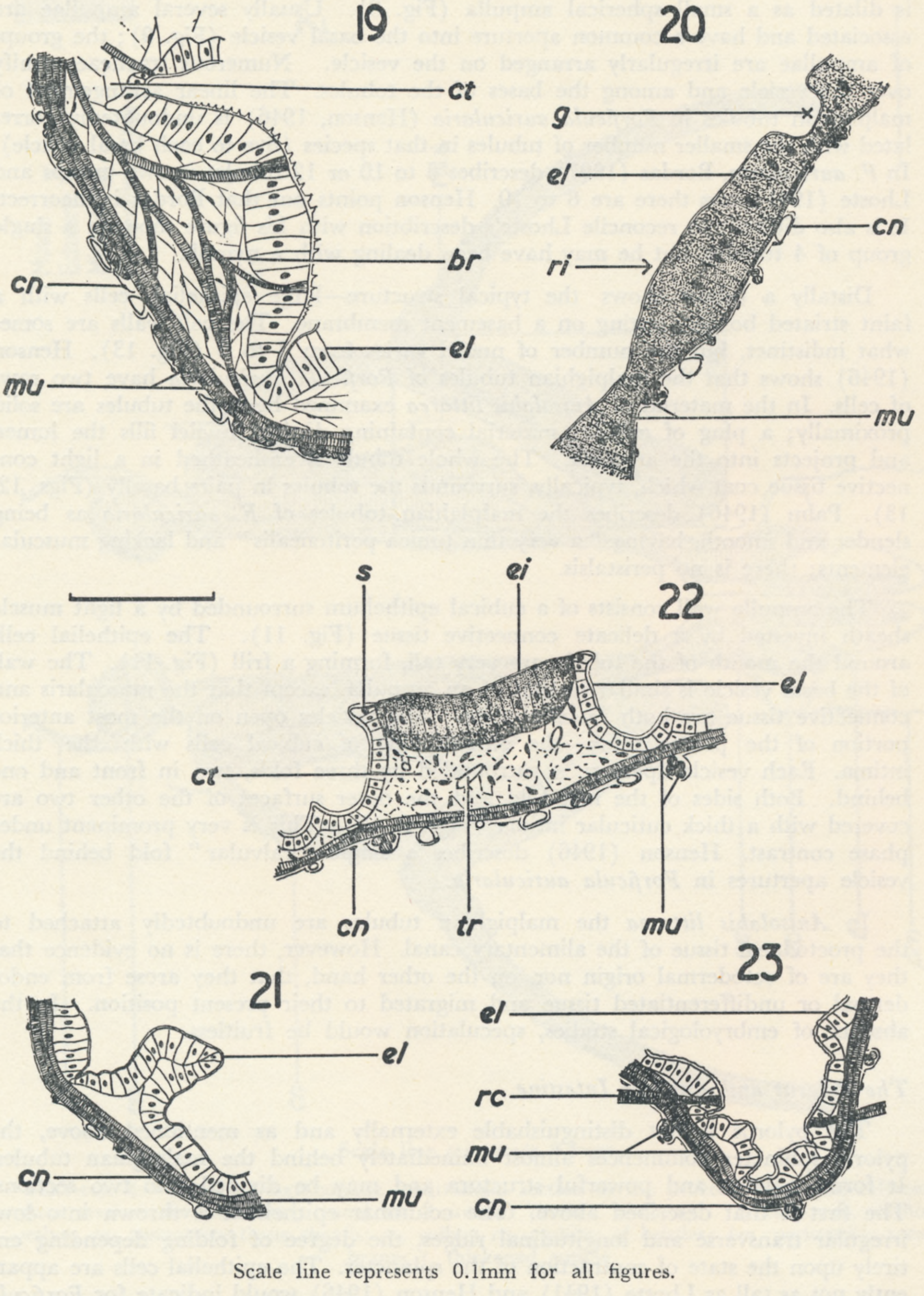
Distally a tubule shows the typical structure—large epithelial cells with a faint striated border, resting on a basement membrane. The cell walls are somewhat indistinct, but the number of nuclei varies from 3 to 5 (Fig. 13). Henson (1946) shows that the malpighian tubules of *Forficula auricularia* have two rows of cells. In the material of *Anisolabis littorea* examined here, the tubules are solid proximally; a plug of cellular material containing distinct nuclei fills the lumen and projects into the ampulla. The whole tubule is ensheathed in a light connective tissue coat which, typically, surrounds the tubules in pairs basally (Figs. 12, 13). Palm (1946) describes the malpighian tubules of *F. auricularia* as being slender and smooth, having " a very thin tunica peritonealis " and lacking muscular elements; there is no peristalsis.

The ampulla wall consists of a cubical epithelium surrounded by a light muscle sheath invested by a delicate connective tissue (Fig. 11). The epithelial cells around the mouth of the tubule are very tall, forming a frill (Fig. 11). The wall of the basal vesicle is similar to that of an ampulla, except that the muscularis and connective tissue are both much thicker. The vesicles open on the most anterior portion of the proctodaeum—the narrow ring of cubical cells with the thick intima. Each vesicle aperture is surrounded by three folds, two in front and one behind. Both sides of the first fold and the outer surfaces of the other two are covered with a thick cuticular intima (Figs. 9, 10). This is very prominent under phase contrast. Henson (1946) describes a single " valvular " fold behind the vesicle apertures in *Forficula auricularia.*

In *Anisolabis littorea* the malpighian tubules are undoubtedly attached to the proctodaeal tissue of the alimentary canal. However, there is no evidence that they are of ectodermal origin nor, on the other hand, that they arose from endodermal or undifferentiated tissue and migrated to their present position. In the absence of embryological studies, speculation would be fruitless.

The Pylorus and Anterior Intestine

The pylorus is not distinguishable externally and as mentioned above, the pyloric sphincter commences almost immediately behind the malpighian tubules. It forms a large and powerful structure and may be divided into two sections. The first is that described above. The columnar epithelium is thrown into low, irregular transverse and longitudinal ridges, the degree of folding depending entirely upon the state of contraction of the sphincter. The epithelial cells are apparently not as tall as Lhoste (1941) and Henson (1946) would indicate for *Forficula auricularia.* In the second section the epithelium is raised to six distinct longitudinal flat-topped ridges, which arise as a result of the concentration of the disordered ridges of the first section. The epithelial cells on the tops of the ridges are tall and invested with a thick intima covered with backwardly directed teeth,



Scale line represents 0.1mm for all figures.

TEXT-FIG. 3.—Fig. 19—T.S. of ridge of pyloric sphincter. Fig. 20— T.S. of ridge of anterior intestine. Fig. 21—T.S. of rectal valve. Fig. 22—T.S. of a rectal gland. Fig. 23—T.S. of rectum. *br,* branching muscles; *cn,* connective tissue sheath; *ct,* connective tissue; *ei,* epithelium with very thin intima; *el,* epithelium with cuticular lining; *g,* groove; *mu,* muscularis; *rc,* rectal dilator muscles; *ri,* ridge; *s,* sclerotised margin; *tr,* trachea.

but those in the narrow folds between are shorter and the intima is thin and smooth (Fig. 19). These and other teeth of the hindgut cuticle are concerned with drawing the peritrophic membrane and its contents through the gut. Similar teeth are present in *F. auricularia* (Lhoste, 1941). The sphincter muscle consists of a very thick inner layer of circular fibres and a single outer layer of longitudinals. The spaces between the ridges are occupied by some connective tissue and by branches from the circular muscles.

The rather narrow anterior intestine is thrown into an S-curve posteriorly, but is not separable into ileum and colon. Lhoste (1941) mentions the same condition in *Forficula auricularia*. Six opaque longitudinal bands can be seen on the wall. Undigested food remains within a tube of peritrophic membrane are usually visible through the wall.

The epithelial ridges of the sphincter lose height and become continuous with ridges on the anterior intestine wall; these are the opaque bands. The ridges are low, wide and flat-topped, with well defined grooves between (Fig. 20). The epithelium is granular, with prominent nuclei; cells of the ridges are tall, but those of the grooves are short. A thin intima is present everywhere. The muscularis consists of a thin inner layer of circular fibres and a rather sparse outer layer of longitudinal fibres which are aggregated mainly between the ridges. A light connective tissue with a few tracheae covers the muscularis.

The Posterior Intestine

The rectal sphincter marks the commencement of the posterior intestine, which is made up of a wide ovoid rectal sac and a narrower tubular rectum. On the wall of the rectal sac the rectal glands are seen as six long opaque bands. The wall of the rectum has a noticeably furry appearance, due to the large number of dilator muscles inserted in it. The anus lies between the paraprocts just in front of the metapygidium.

In the region of the rectal sphincter the ridges of the anterior intestine are replaced by seven or eight sharp folds of the epithelium (Fig. 21). The cells of the ridges are taller than those of the hollows and all are covered by a smooth, fairly thick intima. The muscularis consists of an inner circular layer, three or four fibres thick, with a few scattered longitudinal fibres outside. A light connective tissue and a few tracheae cover the wall.

The long opaque rectal glands show very clearly on the wall of the rectal sac; each is interrupted in the middle and all parts are surrounded by a narrow brown edging (Fig. 1). The glands are broad, flat-topped ridges with steep sides (Fig. 22). A cubical epithelium covered with a fairly thick intima lies between the ridges and also on their sides. The cells on the surface of the glands, however, are very tall and granular and are covered by a very thin intima. The lining around the edges of the gland is considerably thickened and sclerotised, the continuous wire-like edging seen externally. The space within the ridge is filled with connective tissue and a few tracheae. The inner circular muscle is two fibres thick and the outer longitudinals are aggregated into small groups. Covering the whole is a light connective tissue incorporating tracheae which are most numerous outside the glands. *Forficula auricularia* has six elliptical rectal glands arranged in two alternating rows (Lhoste, 1941). Each is composed of a few very large cells with indistinct boundaries and small spherical deeply-staining nuclei. Lhoste says there are about a dozen cells on the long axis and half a dozen on the short. Snodgrass (1935) figures a section of the rectal gland of *Eremobia* (Saltatoria: Acrididae). This shows a striking resemblance to the condition in *Anisolabis littorea.*

In the rectum the lumen is almost occluded by the ridges on the wall. The epithelial cells are tall, the intima is thick and rough, and the muscularis consists of an inner circular layer of three to five fibres, with the outer longitudinal fibres grouped into small bundles (Fig. 23). There is a delicate connective tissue sheath with many tracheae. The fibres of the rectal dilator muscles pass between the circular muscles and are inserted on the cuticular lining. There is a powerful anal sphincter. The wall of the rectum of *Forficula auricularia* is generally similar (Lhoste, 1941).

Throughout the length of the proctodaeum the gut contents are contained in a tube of the peritrophic membrane. The faeces are made up of rather solid dark brown matter and a more fluid buff coloured portion. They would appear to be more liquid than in *Forficula auricularia*, as indicated by Wigglesworth (1932).

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DR E. T. GILES,
Department of Zoology,
University of New England,
Armidale, N.S.W.,
Australia.