The Formation of the Peritrophic Membrane in Insects, with Special Reference to the Larvae of Mosquitoes.

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With 10 Text-figures.

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1. INTRODUCTION.

In the larvae and adults of those Diptera in which a peritrophic membrane is present, it is a remarkably uniform and
discrete structure, and any theory of its formation must take this fact into account. Now it has recently been found (Wigglesworth, 1929) that in the tsetse-fly the peritrophic membrane is produced in the proventriculus as a fluid secretion, which is drawn through an annular cleft and so pressed and moulded to form a membranous tube. A similar origin was suggested by van Gehuchten (1890) for the membrane in the larva of Ptychoptera (Tipulidae); and Vignon (1901) showed that the proventriculus of Chironomus contains a beautiful delicate press in which the peritrophic membrane is milled. It is rather surprising that, although the anatomy of the intestine of various Diptera has been described, and the origin of the peritrophic membrane in them discussed, no attempt should have been made to discover cognate mechanisms by which the pressing of the membrane might be effected.

The present paper arose from an attempt to find such a mechanism in the larva of Anopheles. When this attempt proved successful the investigation was extended to the larvae of other Nematocera, and to the Diptera generally. Finally, it was found that analogous structures occur in most of the chief orders of insects. But before discussing briefly the varied forms which this mechanism may assume in other insects, a more detailed account will be given of the conditions present in the larvae of certain mosquitoes.

2. FORMATION OF THE PERITROPHIC MEMBRANE IN MOSQUITO LARVAE.

The majority of writers on the larvae of mosquitoes are agreed that the peritrophic membrane takes origin at the upper end of the mid-gut. At this point the fore-gut, the oesophagus, is invaginated into the mid-gut to form the structure usually referred to as the ‘oesophageal valve’, an unfortunate term that attributes to this part of the intestine a property which it does not possess; for the invagination acts not as a valve but as a sphincter. In the present paper the oesophageal valve together with the surrounding mid-gut will be referred to as the
proventriculus \(^1\). The mid-gut of this region is conveniently called the ‘cardia’.

The proventriculus of Culex and Anopheles larvae is accurately described by Thompson (1905). ‘In the anterior part of the thorax the oesophagus dips into the cardia as the oesophageal valve... a deep curtain, thicker at the base than at the free border. At the free border the space between the inner or direct face and the outer or reflected face is occupied by a blood sinus. Above, the space is filled by the circular fibres of the annular muscle... The oesophageal valve of Anopheles larva is very like that of Culex, but has a band of longitudinal muscles within the valve between the annular muscles and the epithelial cells of the upper part of the reflected face.’ The description given by Imms (1907) agrees with this. In addition, he describes the peritrophic membrane as coming from the large, deeply staining cells of the cardia; but neither he nor Samtleben (1929) mention any mechanism by which this uniform membrane may be produced.

Such a mechanism has been sought in Anopheles plumbeus, Culex pipiens, and Aedes (Stegomyia) argenteus. A large number of larvae were rapidly killed by immersion in Carnoy’s fixative; the proventriculus was dissected out, cleared, and mounted whole, either unstained or stained lightly with acid fuchsin. In this way the natural relations of the parts have been determined. The histological details have been elaborated from longitudinal sections. A striking thing about the proventriculus, when it is dissected out from all these species, is its rigidity. It maintains its cylindrical form when the other parts of the intestine readily collapse.

(a) Anopheles plumbeus.

In addition to the structures described by Thompson and by Imms, it has been found that in Anopheles plumbeus the longitudinal muscle of the oesophageal valve is inserted into the chitinous covering of the reflected face, and that at the point

\(^1\) This terminology may be used throughout the Diptera; but the ‘proventriculus’ in many insects (e.g. Hymenoptera) is a muscular organ belonging entirely to the fore-gut.
of insertion the chitin is greatly thickened to form a rigid ring; a ring which is covered with delicate curved spines directed backwards and closely applied to the surface. In the normal position of relaxation (Text-fig. 1 A) this chitinous ring lies pressed against the lower end of the sheet of deeply staining cardiac cells which are regarded as the secreting cells of the peritrophic membrane. This sheet of cells has a somewhat conical form, tapering in front. It is clear, therefore, that when the longitudinal muscle contracts, the chitinous ring will be drawn forwards, firmly pressed against the secreting cells; and in so doing the secretion which these discharge will be rolled out. When the muscle relaxes and the chitinous ring moves backwards again, the spines upon its surface will carry with them the newly formed sheet of peritrophic membrane. The rather delicate circular muscles outside the mid-gut will assist in keeping the parts in intimate contact. The circular muscle within the oesophageal valve will serve as a sphincter to close the upper part of the orifice; and when the sinuses in the free margin are distended they will serve to close the lower part.

Text-figs. 1 B and c show in action the various mechanisms deduced in the last paragraph from considerations of structure. In Text-fig. 1 B the circular muscles of the valve are firmly contracted and the blood sinuses tensely distended so as to occlude the lumen of the oesophagus. The longitudinal muscle is relaxed, and the chitinous ring lies at the hind end of the proventriculus. In Text-fig. 1 c the longitudinal muscle is contracted and the ring of chitin is drawn far forwards. The circular muscles also are contracted, but the sinuses are only partially distended.

The peritrophic membrane in mosquito larvae is not produced with such rapidity as that in the tsetse-fly (Wigglesworth, 1929), so that the secretory activity of the cells which produce it is proportionally less. But occasionally, in sections (Text-fig. 1 d), globules of secretion may be seen in process of extrusion from the cells. As in the case of the tsetse-fly again, since the membrane arises by the condensation of this fluid secretion into a solid sheet, it must necessarily fit the mould in which it is produced. This explains the well-known fact that the gut contents
Proventriculus of *Anopheles plumbeus*. A, in normal position of relaxation; B, with sphincter muscle contracted and sinuses distended; C, with longitudinal muscle contracted; D, detail of cells secreting peritrophic membrane. 1, sphincter muscle; 2, longitudinal muscle; 3, blood sinuses; 4, chitinous thickening bearing spines; 5, cells of cardia secreting peritrophic membrane; 6, peritrophic membrane; 7, gut contents; 8, secretory vacuoles; 9, globules of secretion passing through striated border.

of the mosquito larva are always in the form of a cylindrical mass, equal in diameter with the oesophageal invagination and uniform throughout; whereas the wall of the intestine may show
considerable irregularities, including the large 'gastric caeca'. As in the tsetse-fly, the peritrophic membrane is composed of chitin. It resists solution in hot caustic alkalies, but after such treatment it gives the colour reactions for chitosan (Wester, 1910).

(b) Culex pipiens and Aedes (Stegomyia) argenteus.

In Culex pipiens the general mechanism is similar to that in Anopheles; but in place of a narrow ring near the free margin of the oesophageal valve, there is a general thickening of the chitin on the reflected surface. This surface has a double curve (Text-fig. 2 a), and at the free margin is provided with an everted rim. In short, the whole structure is more rigid than in Anopheles. The longitudinal muscle is absent, and no evidence could be obtained that the invagination moves up and down appreciably. No spines could be seen upon the chitinous thickening. On the other hand, the blood sinuses are well developed, and often, during closure of the orifice, they are fully distended (Text-fig. 2 b) and serve to occlude the lower end of the oesophagus, driving onwards the contents of the gut.

In Aedes argenteus (Text-fig. 2 c) the structure is almost identical with that in Culex pipiens. The chitinous covering of the free margin of the valve is, however, even more greatly thickened. It is worth noting that the characteristic form of this chitinous thickening is figured by Raschke (1887) in the larva of 'Culex nemorosus' (= Aedes (Ochlerotatus) nemorosus), but it is not so clearly shown in the figures of subsequent authors.

3. Formation of the Peritrophic Membrane in other Diptera.

It is evident that the formation of the peritrophic membrane in the larvae of Culicidae is brought about in the same general way as that in the larvae of Ptychoptera and Chironomus. Indeed it seems probable, from an examination of the
literature, that the same is true for the larvae of all the Nematocera.

Thus in Simulium (Strickland, 1913) the 'oesophageal valve' contains a longitudinal muscle, as in Anopheles, and

**Text-fig. 2.**

A, proventriculus of *Culex pipiens* in position of relaxation; B, the same with sphincter muscle contracted and sinuses distended; C, proventriculus of *Aedes argenteus*. 1, sphincter muscle; 2, blood sinuses; 3, chitinous thickening; 4, cells secreting peritrophic membrane; 5, peritrophic membrane; 6, gut contents; 7, wall of gastric caeca.

its free margin is covered with a thickened layer of chitin which bears rows of spines upon its surface. Strickland suggests that these spines serve to draw the peritrophic membrane backwards as it is formed, but he does not consider the possibility that the structure may act as a press. In Forcipomyia (Ceratopogonidae) Saunders (1924) figures the oesophageal valve and shows
a very thick layer of chitin on the outer surface, with a projecting flange near the free border. This doubtless has the same function. Wagner (1864) and Mecznikow (1866) figure the peritrophic membrane in Miastor (Cecidomyidae) as a tube,

**Text-fig. 3.**

![Diagram of Proventriculus](image)

Proventriculus of *Sciara* (A), *Rhyphus* (B), and *Telmatoscopus* (C). 1, sphincter muscle; 2, blood sinus; 3, chitinous thickening; 4, cells secreting peritrophic membrane; 5, peritrophic membrane; 6, wall of mid-gut; 7, circular muscle of 'press'; 8, gastric diverticula; 9, large vacuolated cells which fill the upper part of the 'oesophageal valve'.

I have myself examined the larvae of *Corethra* (Culicidae), *Rhyphus* (Rhyphidae), *Sciara* (Mycetophilidae), and *Telmatoscopus* (Psychodidae). In each of these there is a typical 'press' (Text-fig. 3 A, B, C) which it is unnecessary to describe in detail. The structure in *Telmatoscopus* is of particular
interest, for this is the only Nematocerous larva I have examined in which the arrangement resembles that described by Vignon (1901) in Chironomus, where the 'press' is entirely separated from the secretory cells.

Among the higher Diptera the same principle is encountered again. In the larva of Calliphora (figured by Perez, 1910) the 'oesophageal valve' is a solid cellular structure forming a plug which completely fills the proventriculus. There is no need for any thickening of the chitinous intima, the cells of the cardia which secrete the peritrophic membrane press directly upon this solid plug. The arrangement in the adult of Drosophila (figured by Chatton, 1920) is precisely the same and represents a condition intermediate between that present in the larvae of the Nematocera and in the adults of the Muscidae. In these the oesophageal invagination is everted funnel-wise and reflected over the enlarged epithelial cells which produce the membrane (Wigglesworth, 1929). One result of this change is that the diameter of the press is enlarged so that the diameter of the peritrophic membrane also is greatly increased.

4. Formation of the Peritrophic Membrane in Other Orders of Insects.

Where the peritrophic membrane is a strictly uniform tube, as it is in the Diptera, it is difficult to conceive any mechanism by which it could be formed unless this be in the nature of an annular mould or press. It was to be expected, therefore, that similar structures would be found in insects of other orders, and as will be shown in the account which follows, these have been observed in most of the main orders that have been examined.

(a) Hymenoptera.

In the larva of the wasp and bee, Anglas (1901) believed the peritrophic membrane to be secreted by large mid-gut cells which overlie the oesophageal valve, but no flattening mechanism was described. I have not examined these insects, but in a small saw-fly larva (Tenthredinidae) the peritrophic membrane arises from a ring of special cells in the cardia. Below this ring the oesophageal valve is pressed against the wall of the gut.
either by the distension of the contained sinuses with fluid (Text-fig. 4 A), or by pressure of the gut contents as they pass through the valve. The membrane is composed of chitin.

Text-fig. 4.

![Diagram of oesophageal valve](image)

'Oesophageal valve' of saw-fly larva (A) and *Bombus* adult (B).
1, sphincter muscle; 2, longitudinal muscle; 3, cells secreting peritrophic membrane; 4, sinuses; 5, peritrophic membrane; 6, circular muscle of mid-gut.

In the adult of the bumble-bee (*Bombus*) Swingle (1927) states that the membrane is secreted by a collar of cells around the base of the oesophageal valve. The valve itself he figures in a collapsed state with folds of thin chitin trailing down the mid-gut; and this indeed is the usual appearance of the valve in mounted specimens; but if the gut of a freshly killed bumble-bee is dissected in normal saline, the valve will often be found tensely distended with fluid so that it is pressed against the wall of the mid-gut (Text-fig. 4 B) and the sleeve-like peritrophic membrane may be traced forwards over its surface to the ring.
of cells by which it is produced. The precise mechanism by which the sinuses of the oesophageal valve, in this insect and others, are distended with fluid, is not clear; but the valve in the bee contains well-developed longitudinal and circular muscles at its base and these may play a part. In Text-fig. 4B the membrane is shown as arising from the basal fold alone. It is uncertain whether the succeeding rings contribute to its formation; but if they do, this would account for the fact that in longitudinal sections the thickness of the membrane is seen to increase gradually up to the end of the oesophageal valve and then to remain constant. Furthermore, when the membrane is carefully dissected out in the fresh state it may sometimes be seen to be composed of several concentric layers. This membrane is chitinous.

In the honey-bee (Apis) Pavlovsky and Zarin (1922) and Snodgrass (1925) describe the peritrophic membrane as being produced by repeated delamination of the surface membrane of the mid-gut, brought about by the secretion pressure of the cells below. Certainly the membrane consists of a number of concentric layers, and between these layers are fragments of cytoplasm, often containing nuclei, which have clearly been shed off from the epithelium. It would be surprising, however, to find two such different modes of origin for the membrane in related forms with their anatomy so similar as the bumble-bee and the honey-bee. Moreover, the membrane gives the reactions of chitin, a fact which does not support the idea that it is shed off from the entire mid-gut.

A number of longitudinal sections of the mid-gut of the honey-bee have been examined. In these the appearance of the mid-gut cells varies considerably with the state of digestion; but in some sections they are precisely as figured by Pavlovsky and Zarin; overlaid by a number of delicate concentric membranes with cellular debris between, and it is impossible to doubt that these membranes are derived from the cells immediately beneath them. On the other hand, the main mass of the membrane always arises clearly from the anterior end of the mid-gut. Text-fig. 5 is typical of sections in this region. It will
be seen that the greater part of the membrane is streaming off the first fold of the mid-gut at the base of the oesophageal valve. Succeeding folds contribute to the membrane, but in diminishing degree, as the folds succeed each other down the gut.

**Text-fig. 5.**

[Diagram showing longitudinal section of anterior end of mid-gut in *Apis.* 1, sphincter muscle; 2, cells of 'oesophageal valve'; 3, blood sinus in collapsed state; 4, basal fold of mid-gut, from which the greater part of the peritrophic membrane is arising; 5, smaller contributions to the membrane by succeeding folds; 6, peritrophic membrane.]

It must, therefore, be concluded that the peritrophic membrane of the honey-bee is of two-fold origin; a chitinous basis, itself composed probably of several concentric tubes, secreted at the anterior end of the mid-gut; and a series of indefinite membranes which condense upon the outside of this as it proceeds down the gut. The pressing of the basic membrane is probably brought about in the same way as in *Bombus*; but the efficiency of this press, at least in the honey-bee, is not so great as of those described in the Diptera, and the membrane is not such a clean-cut and uniform tube.

1 I have not actually demonstrated that the inner layers are chitinous and the outer layers not chitinous. F. L. Campbell (1929), *Ann. Ent. Soc. Amer.*, xxii., has also shown the presence of chitin in the peritrophic membrane of the bee.
(b) **Coleoptera.**

A peritrophic membrane is present in many Coleoptera, though it is said to be absent in certain of the carnivorous groups (Carabidae, Dytiscidae). For the purpose of this paper it has been studied in the larva of *Tenebrio molitor* and the adult of *Coccinella septempunctata*. In both of these

**Text-fig. 6.**

'**Oesophageal valve**' of young larva of *Tenebrio molitor* (A) and *Coccinella* adult (B). 1, sphincter muscle; 2, longitudinal muscle; 3, rigid ring of chitin-covered cells forming the inner surface of the 'press'; 4, cells secreting peritrophic membrane; 5, peritrophic membrane; 6, wall of mid-gut.

a press is present (Text-fig. 6 A, B) and in both of them the membrane is chitinous.

(c) **Lepidoptera.**

Vignon (1901) examined the oesophageal valve of the silkworm. He could not detect any mechanism for flattening the peritrophic membrane and concluded that this was formed by the condensation of secretion from the general epithelium of the mid-gut upon the surface of the gut contents; and associated with this mode of origin he noted that the thickness of the membrane varied greatly in different parts. Bordas (1911) studied the intestine in a great many lepidopterous larvae and found in every case that the peritrophic membrane was secreted by a ring of deeply staining granular cells around the base of
the oesophageal valve. No mechanism for pressing the membrane was described.

The question has been re-investigated in the larva of *Cheimabacche fagella* (Oecophoridae), *Ephesia kuhniella* (Pyralidae), and *Sitotroga cerealella* (Gelechiidae). In

TEXF-FIG. 7.

A, 'oesophageal valve' of lepidopterous larva (*Cheimabacche fagella*). 1, sphincter muscle; 2, invaginated portion of fore-gut; 3, cells secreting peritrophic membrane; 4, peritrophic membrane; 5, mid-gut; 6, gut contents. B, surface view of one of the three delicate leaflets which compose the invaginated portion of the fore-gut (2).

all these the oesophageal valve hangs down into the mid-gut as a most delicate curtain made up of several overlapping leaflets which, in *Cheimabacche fagella*, are three in number and are regularly fringed at the lower border (Text-fig. 7 b). In the normal state of the larva the gut is always firmly distended, and this chitinous curtain is pressed against the epithelium of the mid-gut and not drawn inwards as it would be were it acting as a valve (Bordas, 1911).\(^1\) So long, therefore, as the gut is

\(^1\) The incompetence of this structure to serve as a valve may be demonstrated by removing the head of a freshly killed larva. The contents of the mid-gut are instantly driven forwards into the fore-gut, often carrying with them the peritrophic membrane and causing retroversion of the 'oesophageal valve'.

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distended, the ‘oesophageal valve’ will constitute a more or less efficient press for the peritrophic membrane, which extends forwards beneath it to the anterior limit of the mid-gut (Text-fig. 7 A). In those larvae in which the valve contains blood sinuses (as described by Bordas in Isoirene) these may perhaps become distended and press upon the membrane as observed in

Text-fig. 8.

The ‘oesophageal valve’ of flea larva (Ceratophyllus wickhami) (A) and of termite (B). 1, sphincter muscle; 2, longitudinal muscle; 3, chitinous ring forming inner surface of ‘press’; 4, cells secreting peritrophic membrane; 5, peritrophic membrane; 6, mid-gut; 7, blood sinus.

the tenthredinid larva (Text-fig. 4 A). As in the other insects, the membrane in the lepidopterous larva is chitinous.

(d) Aphaniptera.

In the larva of Ceratophyllus wickhami (Text-fig. 8 A), the oesophageal invagination does not bear even a superficial resemblance to a valve. The margins of the invagination are composed of thickened chitin and are reflected over and
closely applied to the cells which secrete the peritrophic membrane.

(e) Isoptera.

The general appearance of the crop, the proventriculus and the upper end of the mid-gut in the termite is strikingly similar to that in the bumble-bee, and the similarity extends to the mode of origin of the chitinous peritrophic membrane (Text-fig. 8 b). It should be noted that the base of the oesophageal valve is surrounded by an annular fold which secretes the membrane, but that the succeeding projections from the wall of the gut are villi and not complete circular folds as they are in Bombus. The oesophageal valve is a hollow vascular structure as in the bee, and again the pressure is probably effected by its distension with fluid.

(f) Neuroptera.

The alimentary tract in the larva and adult of Chrysopa was studied by McDunnough (1909). He considered that in the larva the peritrophic membrane was secreted by the general epithelium of the mid-gut. In the adult he observed that the membrane was attached at the anterior end of the mid-gut to a ring of deeply staining columnar cells around the base of the oesophageal valve. He did not, however, regard these cells as the source of the membrane, but believed that it arose by separation of the surface-layer of the epithelial cells of the mid-gut, and that this separation failed to occur in the neighbourhood of the oesophageal valve.

A few larvae of Hemerobius have been examined. The peritrophic membrane was found to be composed of chitin, but its mode of origin was not determined. As shown by McDunnough in Chrysopa, the oesophageal valve in these larvae is very much reduced. In a single adult of Hemerobius the structure of the oesophageal invagination was precisely similar to that figured by McDunnough in Chrysopa. In the living state the sinuses in the invagination were firmly distended and in contact with the wall of the gut below the ring of
cells to which the peritrophic membrane was attached. There seems no reason to doubt that the manner of production of the membrane is the same here as in the other insects described.

(g) Odonata.

The formation of the peritrophic membrane in the larva of Aeschna was carefully studied by Voinov (1898); and since his conclusions are at variance with those recorded in this paper it is necessary to consider the question in some detail. Voinov observed a ring of deeply staining columnar cells at the point of junction of the fore-gut and mid-gut in the larva of Aeschna, and he noted that the peritrophic membrane was attached to this ring of cells. He did not believe, however, that they were responsible for its formation. He considered the membrane to be the striated border of the cells of the mid-gut separated by the globules of secretion beneath; and stated that, in sections, the peritrophic membrane may be seen in places to become continuous with the striated border. Not having the conception of an annular press, he points out with perfect justice that the production of a membrane by a simple ring of cells is 'incomprehensible'.

Larvae of Aeschna have been studied by dissection, by clearing and mounting the gut entire, and by microscopic sections. The usual appearance of the gut in longitudinal section is seen in Text-fig. 9 A, which shows the extensive invagination of the fore-gut and the attachment of the peritrophic membrane near the free border of this invagination. No pressing mechanism can be seen. This, however, is the appearance in the fasting larva; whereas the production of the peritrophic membrane will be most active after a meal. A number of larvae were therefore given a copious feed of Lucilia maggots and examined at varying intervals thereafter. Many of the larvae in this series showed the appearance indicated in Text-fig. 9 B. The invagination of the fore-gut was not so extreme, and the ring of deeply staining cells now lay nearer the front end of the mid-gut. The circular sinuses in the free
margin of the invagination were more or less distended, coming in contact with the wall of the mid-gut beyond the ring of cells, and forming a press for the secretion of these cells, which issued from the cleft as the peritrophic membrane.

There seems little doubt that the mode of formation described in the other insects in this paper obtains also in the larva of *Aeschna*; and here again the membrane is composed of

**Text-fig. 9.**

'**Oesophageal valve**' of the larva of *Aeschna*. A, in position of relaxation; B, drawn forwards, with sinuses distended. 1, sphincter muscle; 2, longitudinal muscle; 3, blood sinuses; 4, chief cells secreting peritrophic membrane; 5, cells which contribute to the membrane; 6, wall of mid-gut; 7, peritrophic membrane composed of several layers.

chitin. On the other hand, the histological changes in the mid-gut as figured by Voinov undoubtedly occur, and, at certain stages of digestion, indefinite membranes formed from the mid-gut secretion separate from the cells and condense upon the contents of the gut. But these membranes are merely added to the outside of the chitinous tube which is the peritrophic membrane proper.¹ A further complication arises from the fact that the cells of the mid-gut adjacent to the initial ring also contribute to the membrane (see Text-fig. 9 B). The result is

¹ See foot-note, p. 604.
that the peritrophic membrane in this insect, as ordinarily observed, is a somewhat indefinite structure derived from a number of sources.

(h) Orthoptera.

Cuénot (1895) described the peritrophic membrane in Peri-

TEXT-FIG. 10.

'Oesophageal valve' of Blatella germanica (A) and For-
ficula (B). 1, sphincter muscle; 2, blood sinus; 3, rigid ring of chitin; 4, cells secreting peritrophic membrane; 5, peritrophic membrane; 6, circular muscle actuating the 'press'; 7, epithelium of mid-gut.

planeta and Ectobia as being secreted by a ring of special cells at the base of the oesophageal valve.

In Blatella germanica (Text-fig. 10 A) the arrangement is similar to that figured by Cuénot in Ectobia. The oeso-

phageal 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.
(i) Dermaptera.

Cuénot (1895) figured the peritrophic membrane in the earwig (Forficula) as derived from special cells as in the Orthoptera, but he did not describe any flattening mechanism. On re-examining this insect, however, it was apparent at once that the secretory cells in question are large and extensive, and that their secretion passes through a very rigid and efficient press (Text-fig. 10 b). It is not surprising, therefore, that the peritrophic membrane in the earwig should be a very well-defined and tough chitinous tube.

5. Discussion.

It is the current opinion of most writers upon the peritrophic membrane of insects that this is a different morphological structure in different orders; an opinion supported mainly by the observations on the honey-bee (Apis) and on the larva of the dragon-fly (Aeschna), which have already been discussed. The observations recorded in the present paper do not entirely refute this view; but they serve to show, on the one hand, that wherever a peritrophic membrane is present it is composed of chitin, and, on the other, that an annular press is very frequently responsible for its formation. The work is not sufficiently extensive to warrant any generalization, but it does suggest that the so-called 'oesophageal valve' of insects, which, under the non-committal term of 'Rüssel', Schneider (1889) showed to be of such widespread occurrence, never functions as a valve at all, but always as a sphincter between the fore-gut and the mid-gut, and frequently as a press for the peritrophic membrane.

The mechanical efficiency of this press varies greatly from one order to another; and the mechanism attains its most specialized forms in the Diptera. It is not surprising that the perfection of the peritrophic membrane should run parallel with the refinement of the press in which it is milled. Where the press is best developed the cells which produce the membrane are most clearly differentiated. Where the press is less efficient (as is well seen inApis and in the larva of Aeschna) the
specialization of certain cells for the production of the membrane is incomplete; and although the greater part of the substance is derived from the anterior end of the mid-gut, the cells further back contribute to it to some extent. This suggests the possibility that in yet other insects (or other Arthropods) the production of the membrane may be more generalized still, and distributed throughout the length of the mid-gut.\(^1\)

With regard to the composition of the peritrophic membrane, it is interesting to recall certain observations by Wester (1910). On examining the mid-gut of various arthropods he noted that this was completely lined with chitin in *Periplaneta* and *Melolontha*, though not in *Dytiscus*. In *Scolopendra* there was chitin in one specimen but not in another. Wester does not appear to have been familiar with the peritrophic membrane, but his results may be readily understood in the light of what is known of the distribution of that structure.

As to the function of the peritrophic membrane, no direct evidence can be adduced. It is present in the majority of insects, and its distribution is generally said to follow fairly closely the nature of their food. It is present, for example, in the more primitive orders, but has been lost in the Hemiptera and in adult Lepidoptera, insects which feed only upon fluids, and in the Carabidae and Dytiscidae among Coleoptera, in which digestion is extra-intestinal. It is, therefore, said to be 'protective' to the epithelium. No such structure, however, is present in the alimentary canal of vertebrates; but there the entire tract is furnished with mucous glands, which provide the epithelium with a protective coating of mucin, lubricating the solid masses in the gut. Mucous glands are entirely wanting in the alimentary tract of insects,\(^2\) and it is possible that their

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\(^1\) Balbiani (1890) states that in *Cryptops* (Myriapoda), in which oesophageal invagination is wanting, the peritrophic membrane is a product of the general epithelium of the mid-gut.

\(^2\) The 'goblet cells' recently described by Henson (1929) in the larva of *Vanessa urticae* (Lepidoptera), and which contain material 'optically indistinguishable from striated border', appear to be of a different nature from the mucous glands of the vertebrate gut.
function is served by the peritrophic membrane. It has been shown in the case of the tsetse-fly to be freely permeable to the digestive enzymes and to the products of digestion (Wigglesworth, 1929).

6. SUMMARY.

In the larvae of mosquitoes (Anopheles, Culex, and Aedes) the secretion from the cells of the cardia, in the proventriculus, is drawn through an annular press and thereby moulded to form the peritrophic membrane. The mechanism of this press has been described in detail.

It seems probable that, throughout the Diptera, the peritrophic membrane is formed by similar mechanisms. Figures are given of those in the larvae of Sciara (Cecedyidae), Rhyphus (Rhyphidae), and Telmatoscoopus (Psychodidae).

Analogous structures (a zone of secreting cells in connexion with an annular press) have been found in most of the main orders of insects, as follows: Hymenoptera [adult of Bombus and Apis and the larva of a saw-fly (Tenthredinidae)]; Coleoptera [larva of the mealworm (Tenebrio molitor) and the adult of Coccinella]; Lepidoptera [larvae of Cheimabacche fagella (Oecophoridae), Sitotroga cerealella (Gelechiidae) and Ephemedia kuhniella (Pyralidae)]; Aphaniptera (larva of Ceratophyllus wickhami); Isoptera; Neuroptera (adult of Hemerobius); Odonata (larva of Aeschna); Orthoptera (Blatella germanica); and Dermaptera.

In every case, in addition to its function as a press, the so-called 'oesophageal valve' was found to act not as a valve but as a sphincter.

In the honey-bee (Apis), the larva of the dragon-fly (Aeschna), and possibly in other insects, indefinite membranes are shed off by the cells farther back in the mid-gut, and added to those produced in the annular press.

In all the insects examined, chitin formed the basis of the peritrophic membrane.
The observations recorded give a coherent significance to much of the previous work on the subject, which, before, appeared contradictory.

7. References.

Cuénot, L. (1895).—“Études physiologiques sur les Orthoptères”, ‘Arch. de Biol.’, xiv.