THE ESOPHAGEAL VALVE OF SOME AQUATIC HEMIPTERA

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Only two previous comparative studies have been made on the esophageal valves of the aquatic Hemiptera. Sutton (1951) described this region in *Sigara falleni* Fieb. and *Corixa punctata* Ullig, and compared it briefly with the valves of naucorids and notonectids. More recently, Marks (1958) compared the esophageal valves of four species of aquatic Hemiptera, representing four different families; *Notonecta undulata* Say (Notonectidae), *Ranatra fusca* P.B. (Nepidae), *Belostoma flumineum* Say (Belostomatidae), and *Hesperocorixa escheri* (Heer) (Corixidae).

In the present investigation, the valves of the first three species of Marks were studied. The Corixidae used were *Sigara ornata* (Abbt.) and *Hesperocorixa interrupta* (Say) ; *Pelocoris femoratus* P.B., representing the family Naucoridae, was also examined. Both transverse and longitudinal serial sections through the valve were employed, the digestive tracts being fixed in aqueous Bouin's, alcoholic Bouin's, Held's, and Zenker's fluids and sectioned by the paraffin method. The stains most commonly used were Mallory's triple connective tissue stain, Mallory's phosphotungstic acid hematoxylin, and Delafield's hematoxylin and eosin.

The purposes of the present paper are (1) to compare the esophageal valve of *Pelocoris* with that of the other aquatic Cryptocerata, and (2) to offer a few comments on the works of Sutton (1951) and Marks (1958).

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### THE ESOPHAGEAL VALVE OF PELOCORIS FEMATORUS P.B.

Figure A and Text-figure 2 show the general structure of the *Pelocoris* esophageal valve. The invagination consists of two layers of foregut epithelium, an inner and an outer one, which are continous with each other. The cells of the outer layer are somewhat taller than those of the inner one. In most of the specimens examined, the two layers are contiguous, but a few individuals show a small intra-valvular space between them. Such intravalvular spaces contain fine connective tissue fibrils, but never muscle.

The cells of the outer cell layer become taller at the an-terior limit of the invagination, where they gradually merge with the annular cells, a ring of tall cells encircling the foregut-midgut junction. This corresponds to the "terminal pad" of cells described by Marks in other water bugs, and will be discussed later. The annular cells, like those of the invagination, have basally located nuclei, and are covered by a cuticular intima which is continuous with that of the esophagus. The intima adheres closely to the annular cells, but is pulled away from the epithelium of the invagination to form a definite "entonnoir" (Aubertot, 1934), similar to, although not as pronounced as, that of the Corixidae. The entonnoir and the cells of the invagination are usually connected by fine strands of cuticula which run from the entonnoir to the spaces between the cells.
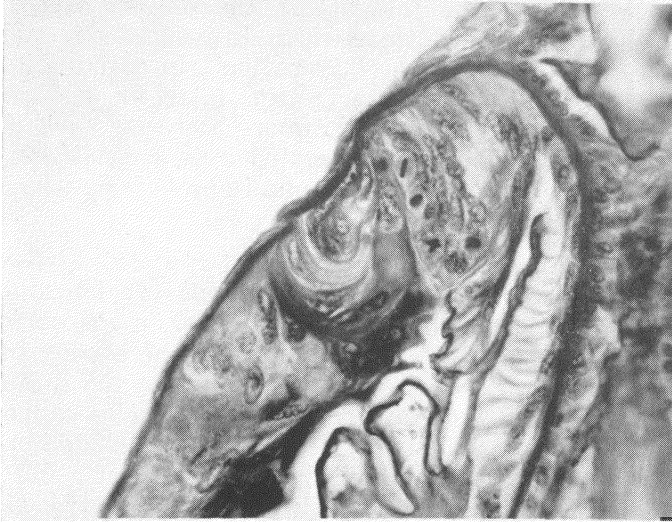
The cells at the posterior tip of the invagination usually contain, at their apical ends, large vacuoles. Such vacuoles occur less frequently in the more anteriorly located cells of the inner and outer cell layers or in the annular cells. Their presence appears to be connected with the secretion of the intima, since in many cases they seem to be passing from the cells into the space between the epithelium and the entonnoir.

EXPLANATION OF PLATE 12

Figure A. Photomicrograph of the esophageal invagination of *Pelocor-is femoratus*. See Text - figure 2 for explantion. Held's, Delafield's hema-toxylin and Eosin Y. 225 X. Figure B. Photomicrograph of the annular cell region of *Sigara ornata*. See Text - figure 3 for orientation. Aqueous Bouin's, Delafield's hematoxylin and Eosin Y. 600 X.
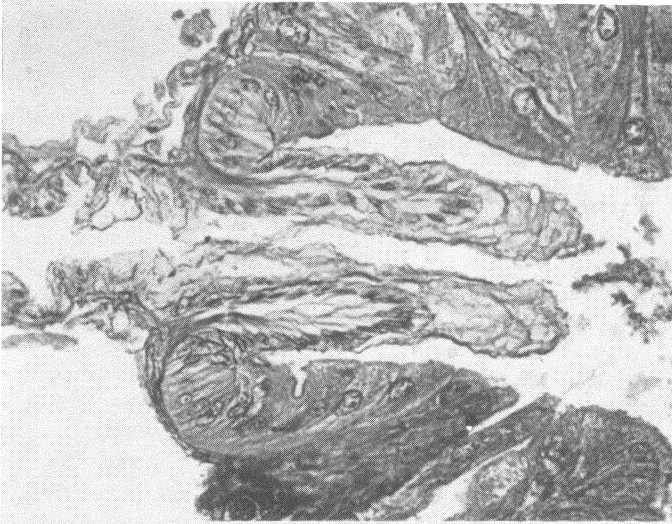
A

B

PARSONS — ESOPHAGEAL VALVE OF HEMIPTERA

Vacuoles similar to these may be seen in the cells at the tip of the invagination in *Hesperocorixa* and *Sigara,* but they are rarely found in *Belostoma, Notonecta,* or *Ranatra.* This suggests that they may be associated with the pulling away of the cuticula to form the entonnoir, a phenomenon found in corixids and in *Pelocoris* but not in the other three bugs. Vacuolated cells have been described in the esophageal valves of *Ptychoptera contaminata* (van Gehuchten, 1890), and in two species of aphids (Weber, 1928, and Miller, 1932), all of these having a cuticula which is somewhat separated from the cells of the invagination.

Sutton, after examining *Naucoris cimicoides,* concluded that there are two "varieties" of that species. The first of these, she stated, has a "long oesophageal valve" (Sutton, 1951, p. 489; she did not say how long), with a shorter entonnoir than that found in corixids, and possesses a definite corixid-like "proventriculus". The latter term is misleading, since it has been used by some authors to designate the "gizzard" of the foregut; in the present study, the "proventriculus" of Sutton, which is part of the midgut, will be called the "perivalvular region". In corixids it surrounds the esophageal invagination (Text-fig. 3), and is narrower in diameter than the more posterior part of the midgut, from which it is separated by a constriction. No such perivalvular region was found in any of the naucorids examined in this study.

Sutton found a second "variety" of *Naucoris cimicoides* in which there is no distinct perivalvular region and the esophageal valve is reduced to a vestige. In *Pelocoris,* all the esophageal invaginations appeared to be equally prominent. Whether *Pelocoris* is more similar to the first "variety" or the second "variety" of *N. cimicoides* cannot be definitely determined, since Sutton did not include illustrations of the valves of both of these; the lack of a differentiated perivalvular region in *Pelocoris,* however, suggests that it more closely resembles the second "variety". This theory is supported by the conclusion of Marks (in press) that the food pump of *Pelocoris* bears more similarity to the second "variety" of *N. cimicoides* than to the first.

NOTES ON THE ESOPHAGEAL VALVE OF

OTHER AQUATIC HEMIPTERA

A. ESOPHAGUS

Since Marks' description of the histology of the crypto-cerate esophagus was brief, a few additional observations may be mentioned here. The epithelium consists, as that author has stated, of a single layer of cuboidal cells, with an inner cuticular intima. It is surrounded by an inner circular and an outer longitudinal layer of muscle.

The present investigation has shown that the histology of the corixid esophagus differs somewhat from that of *Belostoma, Ranatra,* and *Notonecta.* The intima in the latter three adheres fairly closely to the esophageal cells; it generally has a scalloped appearance in section, the scallops more or less corresponding to the individual cells which secrete it. In these three bugs, the esophageal epithelium is usually quite folded, the folds projecting into the lumen. In *Sigara* and *Hesperocorixa,* on the other hand, the epithelium is less folded and the intima is pulled away from the cells, lying free and much folded in the lumen of the esophagus. In many preparations, the cells appear to be secreting additional layers of intima beneath the ones which fill much of the lumen.

It has been shown by other authors (Hungerford, 1917; Griffith, 1945; Sutton, 1951) that the corixids ingest particulate matter. In this respect they differ from the other Hemiptera, which, as far as has been demonstrated, take in only fluids. It may be that the pulling away of the esophageal cuticula and the secretion of additional layers beneath it is a protective phenomenon, shielding the epithelium from abrasion by particles.

The histology of the esophagus of *Pelocoris* resembles that of the fluid-feeding water bugs rather than that of the corixids. Although Sutton found that *Naucoris cimicoides* was able to ingest solid food, no particulate matter was observed in any of the *Pelocoris* guts in the present study.
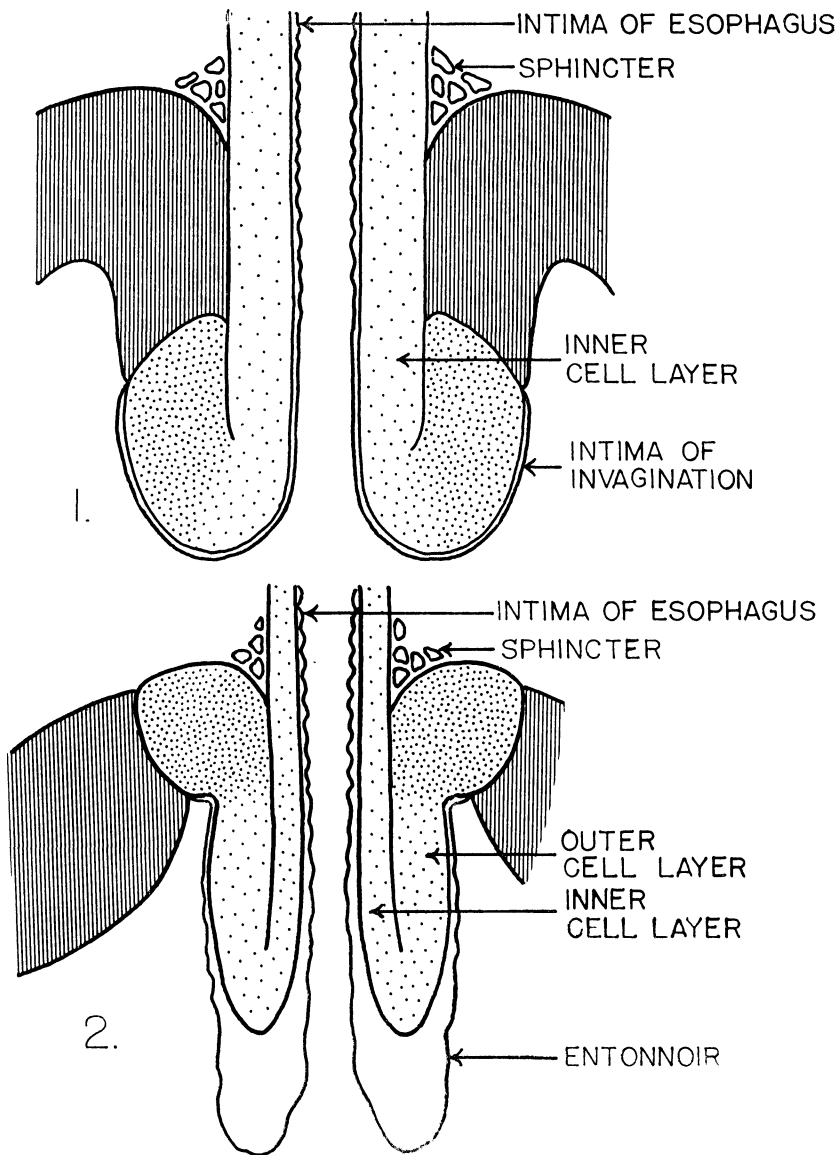
INTIMA OF ESOPHAGUS

SPHINCTER

INNER
CELL LAYER

INTIMA OF
INVAGINATION

1.

INTIMA OF ESOPHAGUS

SPHINCTER

OUTER
CELL LAYER
INNER
CELL LAYER

2.

ENTONNOIR

Fig. 1. Diagram of the esophageal invagination of *Belostoma flumin-eum*. Heavy stippling indicates annular cell region; light stippling indicates rest of foregut epithelium; shading indicates midgut epithelium. Muscle is omitted except for that of the sphincter. 300X.

Fig. 2. Diagram of the esophageal invagination of *Pelocoris femoratus*. Legend same as for Text - figure 1. 375X.

B. Esophageal Valve

1. *Location of the Muscle*

In their studies of the esophageal valve of corixids, both Sutton and Marks described circular muscle strands within the intravalvular space of the invagination. In the present study, muscle was absent in this area in all 36 corixids examined. The muscle is limited to a strongly developed sphincter at the point where the esophagus enters the midgut (Text-fig. 3) and a less well developed longitudinal layer overlying this sphincter.

It is the author's belief that the "muscle strands" of Sutton and Marks were only fine connective tissue fibers; these are very common in the subepithelial tissue of the gut, and appear to run between the basement membrane of the epithelium and the sarcolemma of the muscle. Such fibers have been described in the connective tissue surrounding the gut of other insects (Rengel, 1896; Nazari, 1899; Leger and Duboscq, 1902). In the corixids, these connective tissue fibers, along with small tracheoles, penetrate the intravalvular space of the esophageal invagination, and may quite easily be mistaken for muscle strands (Mr. Marks has examined my material, and agrees with this conclusion).

2. *The Annular Cells*

In all five bugs, the junction of the foregut and midgut is encircled by a ring of tall foregut cells. These correspond to the "terminal pad" of Marks, who showed them in his figures of *Hesperocorixa, Belostoma, Ranatra,* and *Notonecta.* Sutton apparently mistook them for midgut cells, as Marks has pointed out.

Text-figure 3 shows the location of the annular cells in *Sigara* and *Hesperocorixa.* The annular cell region in corixids is more extensive than Marks' figures (1958, his plate VII, figures 1, 3, and 4) would indicate; the author has examined Marks' slides, and found that this region showed some distortion in his material, which probably accounts for this difference.

The most outstanding feature of the annular cells, which was overlooked by both Sutton and Marks, is their high

mitotic rate. This is particularly evident in the corixids; one
specimen of *Sigara ornata* showed 181 mitoses in the an-
nular cell region. Figure B shows a detail of the annular
cells in this specimen. Mitoses are not nearly as frequent in
the annular cells of representatives of the other four fami-
lies, although Table 1 (below) shows that some amount
of cell division is always present.

TABLE 1

	A	B	C
Notonecta undulata	28	5	3
Ranatra fusca	17	3	8
Pelocoris femoratus	21	4	6
Belostoma flumineum	24	11	14
Hesperocorixa interrupta and *Sigara ornata*	36	28	181

Frequency of mitotic figures observed in the annular cell region. Column
A, number of valves examined; Column B, number of valves showing
mitoses in annular cell region; Column C, maximum number of mitoses
seen in any one valve.

It is difficult to account for this high mitotic rate in
corixids. Verson (1897) reported that in the silkworm,
cell division in this region adds to the cells of the esopha-
geal valve. However, degenerating cells are rarely observed
within the esophagus or the esophageal invagination of cor-
ixids, and there appears to be no real need for such frequent
cell addition. The location of the annular cells corresponds
to that of the imaginal disc which regenerates the foregut
of nymphs after a moult; it may be that the annular cells
are remnants of this highly active nymphal region, which
retain their high mitotic rates.

3. *Comparative Aspects*
In his study of the esophageal valves of four species of
water bugs, Marks described a sequence of increasing com-
plexity in the following order: *Notonecta, Ranatra, Belosto-
ma,* and *Hesperocorixa.* In general, the present study sup-
ports this conclusion.

The valvular action in *Notonecta* and *Ranatra* is derived
from the circular muscle sphincter which, when it contracts,
draws together the tall annular cells. There is no real

invagination in either of these bugs. The valves of *Noton-ecta* and *Ranatra* appear, to the author, to be equally simple, although Marks considered the latter to be somewhat more developed than the former.

The form of the valve in *Belostoma* is more complex (see Text-fig. 1). Here a shallow invagination is present, which may offer resistance to the passage of material from the midgut into the foregut. Although an inner cell layer is present, there is nothing corresponding to the outer cell layer of *Hesperocorixa* or *Pelocoris;* instead, the annular cells occupy the posterior and outer surfaces of the invagination.

The *Pelocoris* valve is more complicated than that of *Belostoma,* but less so than that of *Hesperocorixa* and *Sigara.* In its degree of complexity, therefore, it appears to be an intermediate between these two groups. The invagination is deeper than that of *Belostoma* but shallower than the invagination of corixids. The presence of an entonnoir indicates another advancement in complexity. In *Pelocoris* an outer cell layer is present, but the annular cell region appears to extend part way into the invaginated area, gradually merging with the tall cells of the outer cell layer (Text-fig. 2).

The increased length of the invagination, the prominence of the entonnoir, and the placement of the annular cells in the corixid valve make it the most complex of the five. Sutton's assertion that the entonnoir may extend as much as two-thirds of the length of the midgut was not borne out in the present study. The cuticula does extend farther into the midgut than in the other four bugs, but it was never observed to penetrate more than one-tenth the length of the mesenteron in the material used in the present study. In corixids, the annular cell region never extends into the invagination, as it does in *Belostoma* and *Pelocoris.* It is, instead, sharply set off from the outer cell layer, forming a distinct region which encircles the area between the termination of the invagination and the beginning of the midgut (see Text-fig. 3).

The conclusion of Sutton that the corixid esophageal invagination is long when the midgut contains small

amounts of food, and either extended or retracted with large quantities, was not supported in the present study. In the four corixids with the shortest invaginations, the midgut was empty. Sutton's claim that the intravalvular space contains a blood sinus may be true, but there is no evidence from the present study to support her theory that the valve takes an active part in moving the food posteriorly into the midgut.
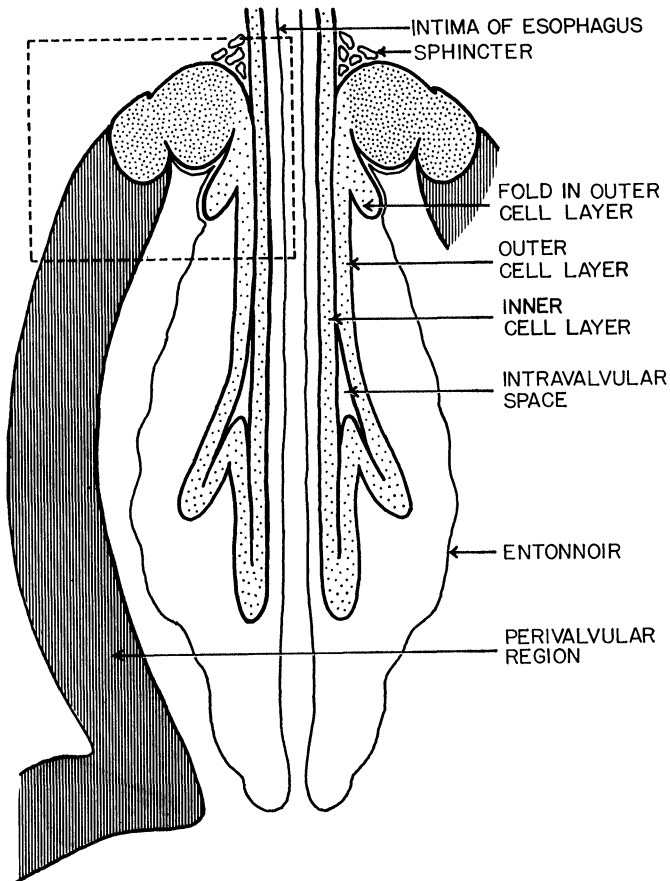

Fig. 3. Diagram of the esophageal invagination of *Sigara ornata* or *Hesperocorixa interrupta*. Legend same as for Text - figure 1. Dotted lines indicate region from which Figure B (Plate 12) was taken. 330X.

Although the increasing complexity of the valve, from *Notonecta* and *Ranatra* to the corixids, represents a morphological sequence, I, like Marks, will not here attempt to draw any phylogenetic conclusions. In terrestrial Heteroptera, both simple and complex esophageal valves are represented; in *Oncopeltus fasciatus,* the valve resembles that of *Notonecta* (Hood, 1937), while the esophageal invagination of the cacao capsid bug (Goodchild, 1952) is similar to that of corixids.

4. *Sutton's Interpretation of the Significance of the Corixid Esophageal Valve*

Sutton proposed that the complex valve of corixids is a primitive feature. This theory was based primarily on her belief that the primitive corixids secreted two kinds of peritrophic membranes, one from the cells of the posterior midgut (the Type I of Wigglesworth, 1950) and a second from the anteriormost midgut cells of the perivalvular region (Wigglesworth's Type II). Sutton's hypothesis was that modern corixids have lost the second type of membrane, but have retained the first type. The latter theory is to be the subject of another paper (Parsons, in press); the proposal that corixids once secreted a Type II membrane will be discussed here, however, since part of Sutton's evidence for this hypothesis is based upon an apparently incorrect interpretation of the nature of the annular cells.

When the ancestral corixid secreted a Type II peritrophic membrane, according to Sutton, a long esophageal invagination was present; this helped to mould the membrane and to move it posteriorly by alternate extension and retraction. The membrane was secreted by the anterior cells of the perivalvular region. In the course of evolution, the latter region has lost its ability to secrete chitin, but it has not yet acquired a digestive function. If any food were to get into this non-functional region, it would only decompose; to prevent this, Sutton claimed, the long esophageal invagination has been retained in modern corixids.

Sutton cited the work of Aubertot (1934), who, in his study of the peritrophic membrane in many orders of insects, distinguished a groove or "sillon" which marks the

boundary between foregut and midgut. It is from the midgut cells directly posterior to this groove that the Type II peritrophic membrane is secreted, and the sillon marks its anteriormost point of insertion. This secretory group of midgut cells, the "massif des cellules-mères de la péritrophique" of Aubertot, is histologically distinct from the rest of the midgut in some insects.
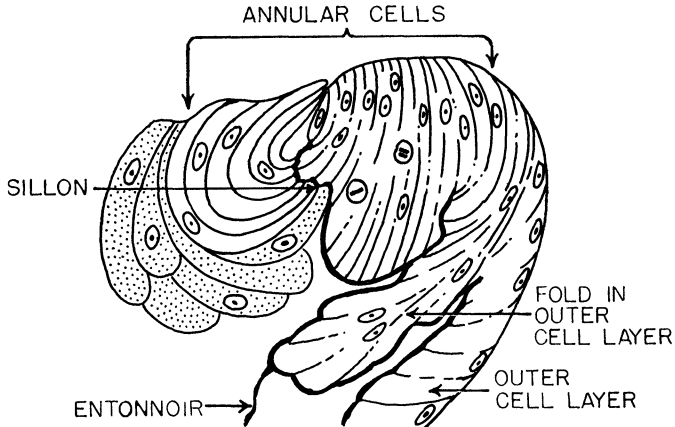

Fig. 4. Detail of the annular cell region in *Sigara ornata*. Heavy line indicates the cuticular intima of the foregut, with which the entonnoir is continuous. Orientation same as that of Figure B (Plate 12); the esophagus and inner cell layer are not shown. The midgut epithelium is stippled. 850 X.

It appears, however, that Sutton has mistaken the annular cells, which are definitely of foregut origin, for midgut epithelium, perhaps believing them to represent a "massif". In so doing, she has taken the groove between the annular cells and the esophageal invagination to be the sillon; this appears to be the case in her figure 10. In the present study, however, the intima was seen to cover the annular cells and to end at a point more posteriorly located than the sillon of Sutton's diagram. This area is quite complicated in corixids, since the annular cells which are closest to the migut bend inwards, towards the lumen, forming a whorl. The true sillon lies at the apices of these curved annular cells, and the terminal part of the intima therefore extends up into the whorl (see Text-fig. 4). There is rarely

a distinct groove here, and the sillon is obscured by the close approximation of the whorl of annular cells with the anteriormost midgut cells.

The evidence cited by Sutton to support her theory of a Type II peritrophic membrane in the corixid ancestor appears to be two-fold: the presence of a distinct sillon in about half of her specimens, and the existence of a non-secretory perivalvular region in all of them. The present study casts considerable doubt upon her first piece of evidence, since the true sillon of corixids is not a distinct groove. Her observation of a non-secretory perivalvular region in corixids was correct, however, and will be discussed in a later paper. Whether or not this is sufficient evidence to support the idea that the corixids once secreted a Type II peritrophic membrane is difficult to say; it may be that the lack of a secretory function in this area is due to other causes. Certainly her theory that the long esophageal invagination is a device for keeping food out of this region is open to question; long valves are present in *Anasa tristis* (Breakey, 1936) and the cacao capsid bug (Goodchild, 1952), neither of which has a non-secretory perivalvular region.

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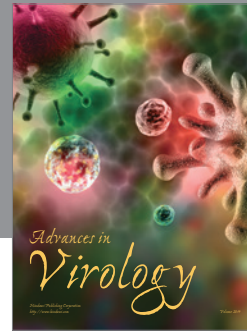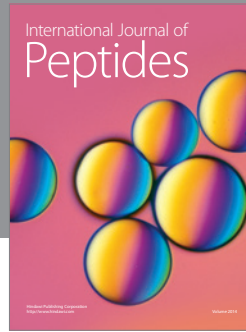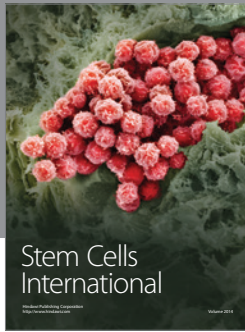Verson, E.
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