Functional morphology of pylorus and rectal glands in Reduviidae (Insecta—Heteroptera)

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MS received 23 September 1980

Abstract. Anatomical and histological studies of the alimentary organs of sixteen reduviids, with diverse food habits indicate structural variations. The terminal part of the tubular second midgut of these predaceous insects has a permanent sac-like region with distinct histology, concerned with absorption of digested food. In addition, the digestive system is characterised by a reduced pylorus with pyloric-intestinal and pyloric-rectal valves, surrounded by flask-shaped ampullae of the four malpighian tubules. The ampullary cells with their filamentous apices and with fibrillar cytoplasmic processes are concerned with water absorption. Commonly in all these terrestrial insects, the anterior end of the rectum also bears a well-developed, inverted cup-like rectal gland, the cells of which also absorb water from the excreta stored in the impermeable, intima lined rectum. Members of Ectrichodiinae show simple ampullary cells and a unique rectum, reported for the first time among reduviids with scattered dome-shaped glandular cells as found in Homoptera and in some phytophagous Heteroptera. The simple nature of the alimentary organs indicates its primitive organization within the reduviid subfamilies.

Keywords. Reduviids; third midgut; pylorus; ampulla; rectal gland; water absorption.

1. Introduction

Reduviids are among the largest groups of terrestrial Heteroptera highly specialised for a predatory life, feeding on a variety of arthropods and on vertebrate blood (Miller 1971). Their unique alimentary system is characterised by a narrow oesophagous, saccular and tubular midguts, reduced pylorus at the junction of the ampullae of the four malpighian tubules, and rectum (Miyamoto 1961; Goodchild 1963, 1966). Although the elimination of excess water from the ingesta, as in plant sap feeding bugs, does not occur in these predatory insects, their terrestrial, fluid-feeding habits impose on them problems regarding water balance. Extensive studies carried out on the digestive system of Heteroptera, including some Reduviidae, by Miyamoto (1961), Bahadur (1963a, b), Goodchild (1963, 1966) and on the process of excretion in *Rhodnius prolixus* Stal by Wigglesworth (1932) have

indicated the presence of specialised regions like ampullae of the malpighian tubules, pylorus (=ileum), and rectal gland (=rectal pad) in terrestrial bugs that play an important role in water regulation and conservation. A study of the structural diversity of ampullae and rectal glands among Reduviidae is herein attempted, based on an analysis of sixteen species belonging to seven subfamilies, and three species belonging to subfamilies Ectrichodiinae, Piratinae, and Triatominae, with diplopodophagous, insectivorous, and haemophagous food habits (Haridass and Ananthakrishnan 1980) are discussed in detail.

2. Materials and methods

The following reduviids were dissected for the study of the alimentary canal and those marked (*) were taken for detailed investigation:

1.	Haematorrhophus nigroviolaceus (Reuter)*		Ectrichodiinae.
2.	Guionius nigripennis (Fabricius)		' do
3.	Ectrychotes pilicornis (Fabricius)		do
4.	Pirates affinis Serville*	_	Piratinae.
5.	Ectomocoris vishnu Distant		do
6.	Catamiarus brevipennis Serville		do
7.	Triatoma rubrofasciata (De Geer)*		Triatominae.
8.	Linshcosteus costalis Ghouri		do
9.	Acanthaspis pedestris Stal		Reduviinae.
10.	Acanthaspis siva Distant		do
11.	Acanthaspis quinquespinosa Fabricius		do
12.	Lizarda annulosa Stal		Salyavatinae.
13.	Petalochirus indicus Reuter	-	do
14.	Rhaphidosoma atkinsoni Bergroth		Rhaphidosomatinae.
15.	Sycanus collaris (Fabricius)		Harpactorinae.
1 6 .	Sphedenolestes bowringi Distant		do

Dissection of the parts of the alimentary system were made in insect Ringer from freshly killed specimens, fixed in alcoholic Bouin or Carnoy's fluid, stored in 70% alcohol and processed through the usual methods of dehydration and embedding. Sections were cut $(8-10\,\mu)$ and stained with Delafield haematoxylin and cosin.

To determine the possible sites of absorption of dyes, neutral red in dilute concentrations (0.001%—dissolved in insect Ringer) was injected into the bodies (after Bahadur 1963a) of Haematorrhophus nigroviolaceus, Pirates affinis and Triatoma rubrofasciata. 0.5 ml of vital dye was introduced with a microsyringe into the posterior abdominal cavity of the test insects by cutting a small window on the second abdominal tergum, later closed with ester wax. Care was taken not to inject the dye into any part of the alimentary canal. Similarly, 0.5 ml of the same dye was injected into the saccular first midgut of starved test insects. Both categories of insects were dissected at intervals of 30, 90, and 180 min. to note the site of concentration and absorption of the dye in the various parts of the alimentary canal.

3. Observation

3.1. Gross structure of the pylorus-rectum complex

The structure and arrangement of the posterior part of the alimentary organs appear similar in all the reduviids studied (figures 1, 2 and 3) and the generalised alimentary structure observed is in agreement with the descriptions of Wigglesworth (1931, 1936), Yanai (1952), Miyamoto (1961), and Goodchild (1963, 1966). In all reduviids the last part of the tubular midgut is always swollen and its permanent nature is evident by its constant bulbous shape, both when full or empty. This region has a distinct cellular composition and it is designated here as the third midgut (figures 1, 2, 3 and 4B, 4C). The third midgut opens into the pear-shaped rectum alongside with the malpighian tubules. The flask-shaped ampulla at the bases of the malpighian tubules converge into a short pylorus. The opening

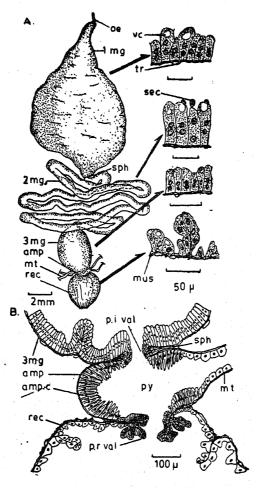


Figure 1. Alimentary canal of *Haematorrhophus nigroviolaceus* (Reuter) A. Histology of the alimentary canal. B. L.S. through the junction of third midgut, pylorus and rectum.

Amp—Ampulla; amp.c—Ampullary cell; bc—Bacterial chamber; 1 mg—First midgut; 2 mg—Second midgut; 3 mg—Third midgut; mt—Malpighian tubules; mus—muscle; Oe—Oesophagus; p.i. val.—Pylorus-intestinal valve; p.r.val—Pylorus-rectal valve; Py—Pylorus; re-Rectal epithelium; rec—Rectum; rec.g—Rectal gland; sec—Secretions; sph—Sphincter; tr—Trachea; vc—Vacuole.

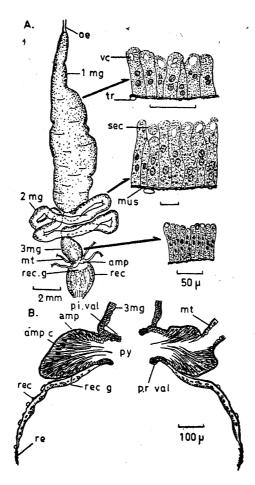


Figure 2. Alimentary canal of *Pirates affinis* Serville. A. Histology of the alimentary canal. B. L.S. through the junction of third midgut, pylorus, and rectum.

of the third midgut into the pylorus and that of the pylorus into the rectum are provided with well-developed pyloric-intestinal and pyloric-rectal valves respectively (figures 1B, 2B, 3B, 4D, 4E, 5A, 5E and 5F).

Of the four highly convoluted malpighian tubules, two are dorsal and two are ventral to the rectum. One dorsal and one ventral tubule of each are always connected to each other at their distal ends. The malpighian tubules have proximal and distal regions as indicated by Wigglesworth (1931) in *Rhodnius*. These tubules spread over most of the midgut region, especially above the dorsal part of the rectum, where they form a compact and twisted knot, preventing the pericardial space from coming into contact with the rectum.

A distinct rectal gland, restricted to the anterior apical 1/3 or 1/4, is evident in the pyriform rectum in the reduviids examined. In most of the freshly dissected specimens this gland is seen as a clear, inverted cup-like area. In none of the members of the Ectrichodiinae examined, there is any indication of such a distinct glandular area, and the rectum is uniformly simple. In reduviids with a distinct rectal gland, the lumen of the rectum is always filled with a clear, transparent watery fluid surrounding the glandular region, and with a viscous, creamish or blackish-brown faecal material in the rest of the rectum.

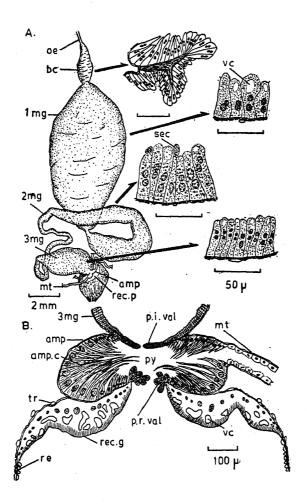


Figure 3. Alimentary canal of *Triatoma rubrofasciata* (De Geer). A. Histology of the alimentary canal. B. L.S. through the junction of third midgut, pylorus, and rectum.

3.2. Histology

The saccular third midgut is composed of binucleate cells that are distinctly shorter than the second midgut cells $(32\cdot4-43\cdot3\,\mu$ in *H. nigroviolaceus*; $4\cdot1-6\cdot2\,\mu$ in *P. affinis*; $3\cdot1-3\cdot9\,\mu$ in *T. rubrofasciata*). The cytoplasm of these cells shows many vacuoles but without any secretory granules, so characteristic of the tubular second midgut cells. The free ends of the third midgut cells possess brush border. Also, apocrine and merocrine nature of the secretions of the second midgut cells are lacking in these cells (figures 1A, 2A, 3A, 4A, 4B and 4C).

The cells of the ampulla, in *H. nigroviolaceus*, *G. nigripennis* and *E. pilicornis*, are columnar with pointed apex and with a large nucleus (figures 1B and 4F). Each ampulla beers 20-28 of these cells and their apices project into the lumen of the ampulla, hardly reaching that of the pylorus. The ampullary cells of all other reduviide, including those of *T. rubrofasciata* and *P. affinis*, have their apices modified into long filamentous processes that freely project into the pylorus, sometimes even into the rectum (figures 2B, 3B, 5B and 5F). The cytoplasm of these uninucleate cells has many fibrillar processes without any granules.

The anterior pyloric valve, i.e. the pyloric-intestinal valve, is poorly developed in the members of Ectrichodiinae being composed of a single layer of flattened uninucleate cells. This valvular region has a well developed sphincter. In all other reduviids this valve has regularly arranged single layer of cuboidal or columnar binucleate cells. The posterior valve of the pylorus—the pylorus reatal valve—is uniformly well-developed in all reduviids (figures 1B, 2B, 3B, 4E and 5E), consisting of regularly arranged cuboidal or columnar binucleate cells. Both the ampullae and the pylorus do not show any chitinous intima.

The apical part of the rectum of most reduviids reveals a distinct rectal gland the relative size of which alone varies in different species. This gland has eosinophilic cells with large nucleus, without distinct cell boundaries between adjacent cells. The free margins at the apex bear many parallel striations. This glandular area gradually tapers off and abruptly from the posterior middle of the rectum it is replaced by small rectal epithelial cells with chitinous intima. The rectal gland cells retain their shape even when the rectum is empty, while the rectal epithelial cells get infolded into the lumen in groups along with their basement membrane (figures 5C, 5D and 5G). Unlike other reduviids, members of Ectrichodiinae possess a rectum which is very peculiar and not reported so far among Reduviidae. The rectum of there species is composed throughout of large, uninucleate, globular or dome-shaped cells, without rectal gland-rectal epithelial demarcations. When the rectum is empty these single layer of cells gets inpushed and folded into the lumen in clusters. However, the muscular layers of the rectum remain distinct and do not take part in such infoldings (figures 4G and 4H).

3.3. Absorption of vital dye

Injection of neutral red into the body cavity and first midgut of *H. nigroviolaceous*, *P. affinis*, and *T. rubrofasciata* shows absorption of this dye at different places. When injected into the body cavity, the distal parts of the malpighian tubules first absorb the dye, from where it gradually extends into their proximal parts. After 90 min the dye is concentrated in the ampulla of the tubules and after 180 min the dye is finally located around the rectal gland areas in *P. affinis* and *T. rubrofasciata*. But in *H. nigroviolaceous*, the concentration of neutral red is noticed throughout the rectum.

Vital dye injected into the first midgut accumulates in the third midgut first and by 90 min it reaches the pylorus and ampullae. After 180 min the concentration of the stain is centred around the rectal gland (in *P. affinis* and *T. rubrofasciata*) or throughout the rectum (in *H. nigroviolaceous*).

4. Discussion

The posterior part of the first midgut of all reduviids studied terminates in a permanent swollen region. Goodchild (1963) has suggested this to be only temporary owing to the accumulation of undigested food residue and reported (Goodchild 1966) that such swelling is not evident in most species of Cimicomorpha. Miyamoto (1961) also has reported this bladder-like swelling in Reduviidae, but maintains this to be indistinct in some forms. The histology of this region and the secretory activity of their cells differ considerably from those of preceding tubular

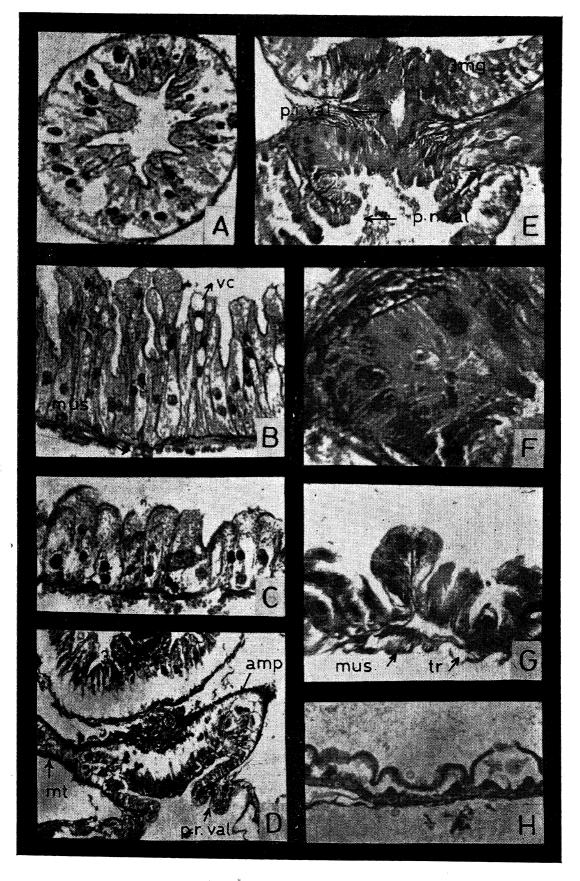


Figure 4. Histology of the alimentary canal of Haematorrhophus nigroviolaceus (Reuter). a. T.S. of second midgut when empty (\times 250). b. Third midgut cells when lumen is empty (\times 420). e. Third midgut cells when lumen is full (\times 420). d. L.S. through the junction of third midgut, pylorus, and rectum (\times 120). e. Cells of the ampulla (\times 800). f. Cells of the rectum when empty (\times 500). g. Cells of the rectum when full (\times 500).

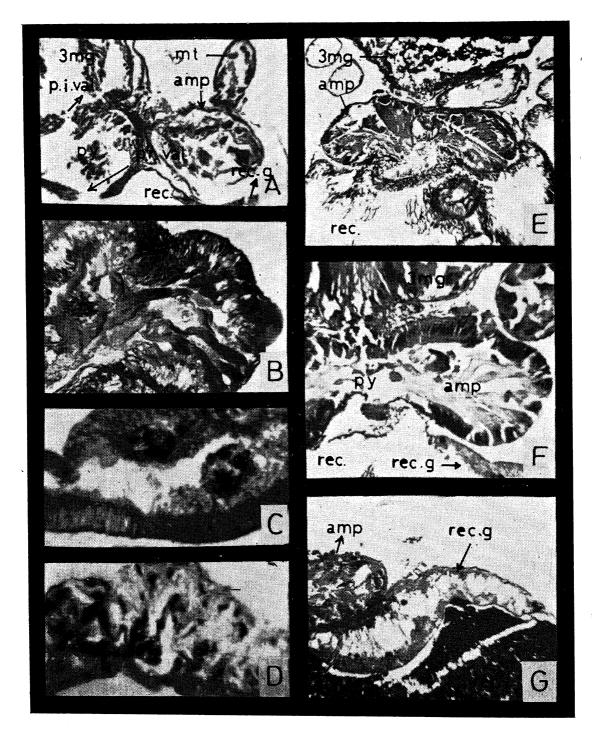


Figure 5. Histology of the alimentary canal of *Pirates affinis* Serville and *Triatoma rubrofasciata* (De Geer). **a-d.** *Pirates affinis*. **a.** L.S. through the junction of third midgut, pylorus and rectum (× 500). **b.** Cells of the ampulla (× 620). **c.** L.S. of rectal gland area (× 2,200). **d.** Rectal epithelium cells when lumen is empty (× 3,700). **e-g.** *Triatoma rubrofasciata*. **e.** L.S. through the junction of third midgut, pylorus, and retum (× 540). **f.** Cells of the ampulla (× 520). **g.** L.S. of rectal gland area (× 540).

second midgut. Moreover, the swollen nature of this part is always retained, whether it is full or empty. Their secretory activity is similar to that of the saccular first midgut cells (Haridass 1978). It is possible, therefore, that this region is a distinct part of the midgut, concerned with the absorption of nutrients from he digested food. Hence it is designated as third midgut.

In all reduviids, the four and highly convoluted malpighian tubules separate the rectum and the posterior midgut from the rest of the abdominal cavity. The histology of these is the same as described by Wigglesworth (1931) in *Rhodnius*, consisting of a proximal part with brush border and a distal part with honeycomb border. The network of these tubules will be able to remove water efficiently as it flows from the anterior midgut. But as Ramsay (1952) has shown in *Rhodnius prolixus* Stal, the malpighian tubules are not so efficient in osmoregulation, for they also excrete large quantities of sodium, potassium, amino acid, and other useful substances which should be necessarily reabsorbed.

The reduced and narrow pylorus is a characteristic feature of Reduviidae and other Cimicomorphid families, in contrast to the phytophagous Pentatomomorphid families which have a distinct tubular or saccular pylorus (Yanai 1952; Yanai and Iga 1956; Miyamoto 1961; Goodchild 1966). In Desdercus koenigii Fab. the pylorus has been shown to be formed by the fusion of vesicles developed at the base of the malpighian tubules (Srivastava and Bahadur 1961). The absence of intima points to an endodermal origin and the use of the term 'ileum' for this region is not in agreement with the ileum of other insects where it forms part of the proctodaeum. The cells of the pylorus-intestinal and pylorus-rectal valves are also binucleate like those of the midgut cells and this provides further proof of the endodermal nature of the reduviid pylorus.

The elongate ampullary cells in P. affinis and T. rubrofasciata, as in most other reduviids studied, have filamentous apices and many fibrillar processes in the cytoplasm. Such cells have been reported in many other reduviids like Rhodnius, Sphedenolestes, and Petalochirus (Wigglesworth 1931; Goodchild 1963). Members of Ectrichodiinae have simple columnar ampullary cells with tapered apices, confined only to the lumen of the ampulla, and lack the long cytoplasmic fibrillar processes. Wigglesworth (1931) has experimentally shown that the ampullary cells are concerned with active water absorption from the nitrogenous waste products sent out by the malpighian tubules. This is confirmed in the present study where the cells of the ampulla have been shown to have great affinity for absorbing vital dye injected into the body cavity. As Goodchild (1963) has suggested, the predaceous zoophagous insects, because of their high protein metabolism, must necessarily cope with a high rate of uric acid production and, to precipitate these acids produced in large quantities, the ampulla is provided with special cells which absorb as much water as possible from the excretory products effluxed from the malpighian tubules. It is, therefore, not surprising to find the ampullary cells so very well-developed and specialised in most Reduviidae. The presence of simple and unspecialised ampullary cells of Ectrichodiinae only reflects its primitive organization.

Reduviids are also characterised by the possession of a well-developed rectal gland that is restricted to the anterior part, immediately behind the pylorii-rectal valve, distinct from the rest of the rectal epithelium. Bahadur (1963b) who made an extensive survey of this region in different Heternptera and proposed a classi-

fication based on their location, has noted the frequent and common occurrence of rectal pads in Heteroptera. The present study and those made earlier on these predaceous insects (Wigglesworth 1931; Bahadur 1963b; Miyamoto 1961; Goodchild 1963, 1966) have clearly established the common nature of this gland, always occupying the anterior apical end of the rectum of all reduviids.

A distinct rectal gland is absent in all the species of Ectrichodiinae studied. Instead, there are large dome-shaped or globular cells distributed evenly throughout the rectum, similar to those reported only in Homoptera (Goodchild 1963) and in some terrestrial phytophagous Heteroptera (Breakey 1936; Bahadur 1963b). Wigglesworth (1932) suggested that such uniformly scattered rectal cells perform the function of rectal glands. Based on his observation on the histology and function of these glands, Goodchild (1966) concluded that in Hemiptera the domeshaped cells of the hindgut are concerned with the solute absorption while rectal gland cells with striated border have a water absorbing function. This observation gains further support from the fact that in freshly dissected reduviids, the rectal gland area shows accumulation of clear watery fluid while the rest of the rectum is filled with dark pasty faecal matter. Besides, dilute stains injected into the body cavity get accumulated only in this part of the rectal gland. Stained sec tions show the existence of numerous clear fluid filled vesicles immediately beneath the striated border of such rectal gland cells. Though they are not faced with the problem of excess water, the terrestrial reduviids need some mechanism to conserve water which is in excess at the time of their feeding. This water could be safely stored in the highly distensible intima-lined rectum, from which water could be absorbed by the gland cells as and when there is a need. The simple nature of the ampullary cells and the diffused rectal gland cells in Ectrichodiinae may be taken as the characters of the primitive organization of this subfamily. The salivary system of this subfamily also indicated their primitive nature (Haridass and Ananthakrishnan 1981). It is interesting to note that Louis and Kumar (1973), based on the study of digestive and reproductive organs of Reduviidae, came to the same conclusion that Ectrichodiinae is a primitive subfamily near the basal stock of Reduviidae.

Acknowledgement

The University Grants Commission's research grant for college teachers (F. 25-5 (9014)/77) to one of the authors (ETH) is gratefully acknowledged.

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