Functional morphology of the salivary system in some Reduviidae (Insecta—Heteroptera)

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Abstract. The salivary system in Reduviidae is organised into a multilobed principal gland and a vesicular accessory gland, the different lobes of the principal gland exhibiting distinct histological differences as well as variation in secretory activity. While the secretions of the anterior lobe have zootoxic effects used by the predator in the immobilization and capture of the prey, the posterior lobes secrete enzymes used for the digestion of the prey. In haemophagous Triatominae the principal gland is without anterior and posterior separations and their unilobed gland produces only anticoagulants that assure an uninterrupted flow of blood from the vertebrate hosts. In all reduviids there is a well-developed accessory gland that is concerned with the production of a watery saliva, the water being recycled from the gut and haemolymph, and used to help the predatory insects to flush-feed and suck up the predigested food. The junction of the various lobes of the principal glands in these predaceous insects shows a well-developed hilus and the valves of this region provide an efficient regulating system for the independent flow of secretions from the different lobes of the salivary system.

Keywords. Reduviidae; principal gland; accessory gland; hilus; zootoxic; anticoagulant; watery saliva.

1. Introduction

The structure and function of the salivary system of phytophagous Heteroptera have attracted increasing attention because of their cecidogenetic and disease transmitting ability (Bronskill et al 1958; Miles 1959, 1964a, b; 1967, 1968, 1972; Salkeld 1960; Miyamoto 1961; Saxena 1963; Hori 1969). An extensive study in relation to their structural diversity in different groups of Hemiptera has been made by Baptist (1941). Southwood (1955) indicated that the salivary system in terrestrial Heteroptera has characteristics sufficient enough to distinguish Cimicomorpha and Pentatomomorpha groups within it. Louis and Kumar (1973), while establishing the inter-relationships among Reduvoidea, observed interesting variations in the salivary system among Reduvidae. With the exception of blood sucking Triatominae (Baptist 1941; Barth 1954), the salivary system of predatory reduvids has not been given due consideration.

The salivary system of the carnivorous Reduviidae, as in most other Heteroptera, is organised into a principal gland and its closely associated accessory gland. The principal gland is made up of one to many anterior and posterior lobes with definite structural and functional differences, and the latter is of the vesicular type. In order to understand the variations in the structure and functions of the different lobes of the salivary system, and also the regulation of the secretions from these glands, detailed studies were made utilizing the species, Haemator-rhophus nigroviolaceus (Reuter)-(Ectrichodiinae), Pirates affinis Serville (Piratinae), and Triatoma rubrofasciata (De Geer)-(Triatominae), which have been shown to have diplopodophagous, insectivorous and haemophagous food habits respectively (Haridass and Ananthakrishnan 1980). In addition the anatomy of the salivary system in 16 species of reduviids, belonging to seven subfamilies (table 1), was also studied to enable a better understanding of the variations in the salivary system.

2. Materials and methods

Parts of the salivary system were dissected out from freshly killed insects in insect Ringer, using microneedle and watch-maker's forceps. These parts were fixed

Table 1. Species of reduviids studied and the nature of the principal and accessory glands in them.

Make 2.79 May	Species	Sub-family	Principal gland lobes			- Accessory gland
Sl. No.			No.	Ant.	Post.	· Accessory gianti
1.	Haematorrhophus nigrovio-				1.1.	Diamontod vegicle
	laceus (Reuter)	Ectrichodiinae	. 3	+	++/	Elongated vesicle with triradiate
2.	Guionius nigripennis					
	(Fabricius)	Ectrichodiinae	3	+	++	tubular
3.	Ectrychotes pilicornis		_			branches
	(Fabricius)	Ectrichodiinae	3	十	++/	
4.	Pirates affinis Serville	Piratinae	2	+	+)	
5.	Ectomocoris vishnu Distant	Piratinae	2	+	+ (Elongated
6.	Catamiarus brevipennis				* (vesicle
	Serville	Piratinae	2	+	+ /	
7.	Triatoma rubrofasciata				٠.	
	(De Geer)	Triatominae	1	• •	• •	Saccular vesicle
8.	Linshcosteus costalis Ghouri	Triatominae	1	••	••)
9.	Acanthaspis siva Distant	Reduviinae	2	+	+	
10.	Acanthaspis pedestris Stal	Reduviinae	2	+	+	
11.	Acanthaspis quinquespinosa					
	Fabricius	Reduviinae	2	+	+	
12.	Lizarda annulosa Stal	Salyavatinae	2	+	+	Elongated vesicle
13.	Petalochirus indicus Reuter	Salyavatinae	2	+	+	with tubular
14.	Rhaphidosoma atkinson i					extension
17.	Bergroth	Rhaphidoso-	2	+	+	
	Bergroun	matinae				
15.	Sycanus collaris (Fabricius)	Harpactorinae	2	+	4	
16.	Sphedenolestes bowring i					
10.	Distant	Harpactorinae	2	+	4 /)

in alcoholic Bouin or Carnoy's fluid and later stored in 70% alcohol. These were processed through usual methods of dehydration and embedding. Sections were cut $(8-10\,\mu)$ and stained with Delafield's haematoxylin and eosin.

The anticoagulatory property of the salivary secretions of T. rubrofasciata was tested with 10 main and 10 accessory glands that were separately homogenised with 0.5 ml of distilled water and three drops of such homogenates were added to three drops of freshly drawn out human blood in a clean tube and immediately sealed with ester wax. These tubes were thoroughly agitated and observed under microscope for signs of clotting of the blood. Gland homogenates prepared in a similar manner but boiled in hot water (100° C) for 10 min were used as controls. The time taken for the clotting of the blood by the gland homogenates was taken as the efficiency of the anticoagulatory function of these glands.

The zootoxic effects of the salivary glands of P. affinis were also tested. Gland homogenates were prepared from four adult insects separately for the anterior and posterior lobes of the main glands and accessory gland. Using a microsyringe, 0.2 ml of each of these homogenates was separately injected into the body cavity of a live carabid beetle, Omphora pilosa Klug, through the pleural membrane of the neck region. The time taken for the stoppage of all the twitching movements of the antennal and tarsal segments was taken as an index of the toxic effects of the various salivary lobes. Similar experiments were made with the anterior, posterior dorsal, and posterior ventral lobes of the main gland and the accessory gland of H. nigroviolaceus and the homogenates were tested by injecting them separately into the neck region of the millipede, Trigoniulus sp. Boiled homogenates were used as controls in both these experiments. The results thus obtained, along with that for the salivary glands of T. rubrofasciata, are tabulated in table 2.

Vital dye (neutral red) in dilute concentrations (0.001%—dissolved in insect Ringer) was injected into the bodies of P. affinis and H. nigroviolaceus and T. rubrofasciata to determine the possible sites of absorption of the pigments (after Bahadur 1963). The 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 which was later closed with ester wax. These test insects were dissected in their blood, at intervals of 30 min, 90 min, and 180 min to observe the absorption of the dye in the various parts of the salivary system.

For observations on the nature of the contents in the lumen of the different lobes of the salivary system, as well as of their differential secretory activity in terms of feeding, test insects were dissected (i) when they were starved for 5-6 days, (ii) immediately after killing the prey, (iii) immediately after cessation of feeding, and (iv) 2 hr after feeding.

3. Observations and results

3.1. Morphology of the salivary glands

The salivary glands of Reduviidae, despite their constancy of form in related species, exhibit variations. They consist principally of (i) paired unilobed or

Table 2. The effects of salivary gland homogenates of H. nigroviolaceus, P. affinis, and T. rubrofasciata on test animals.

• •	Predator	Test animal/source of salivary gland homogenate	Effects on test animal	Time taken
1.	P. affinis Omphora pilosa	(i) Anterior lobe	Immediate stoppage of all body movements and total paralysis	12-16 sec
		(ii) Posterior lobe	No ill-effects. Insects die after long duration	2-3 hr
•		(iii) Accessory gland	No effect	•.•
		(iv) Control (boiled gland homogenate)	No effect	••
2.	H. nigrovio- laceus Xenobolus	(i) Anterior lobe	Quick stoppage of antennal and leg movements. Total paralysis	48–52 sec
	carnifex	(ii) Dorsal post. lobe	No appreciable ill-effects. Millipede dies after long duration	3–5 hr
	•	(iii) Ventral post. lobe	No ill-effects. Millipede dies after long duration	3-4 hr
		(iv) Accessory gland	No effect	• •
		(v) Control (boiled gland homogenate)	No effect	••
3.	T. rubro-	Human Blood:		
	fasciata	(i) Main gland	Coagulation of blood after long duration	43–53 min
		(ii) Accessory gland	Coagulation of blood	8–11 min
		(iii) Control (boiled gland homogenate)	Coagulation of blood	7–8 min

multilobed principal glands, located in front or on either side of the fore part of the first midgut extending into the abdominal cavity and rarely extending into the head; and (ii) paired vesicular accessory glands, usually located on either side of the saccular first midgut in the abdominal cavity, the tubular extensions of which, in many cases, reach as far as the rectal region. From the mid-region of the accessory gland arises the accessory salivary duct traversing forwards. Behind the level of the hind margin of the compound eye in the neck region, it takes a 'U' turn, running posteriorly to join the principal salivary gland at the hilus. The hilus is located at the junction of the different lobes of the principal gland. Where the accessory duct joins the hilus, the main duct of the principal gland emerges, taking a forward course, usually following the contour of the alimentary canal. The principal ducts from both sides enter the neck and, a little distance beyond the 'U' turn of the accessory salivary glands, unite to form a common salivary duct that ultimately finds its way into the lumen of the salivary pump as the efferent salivary duct.

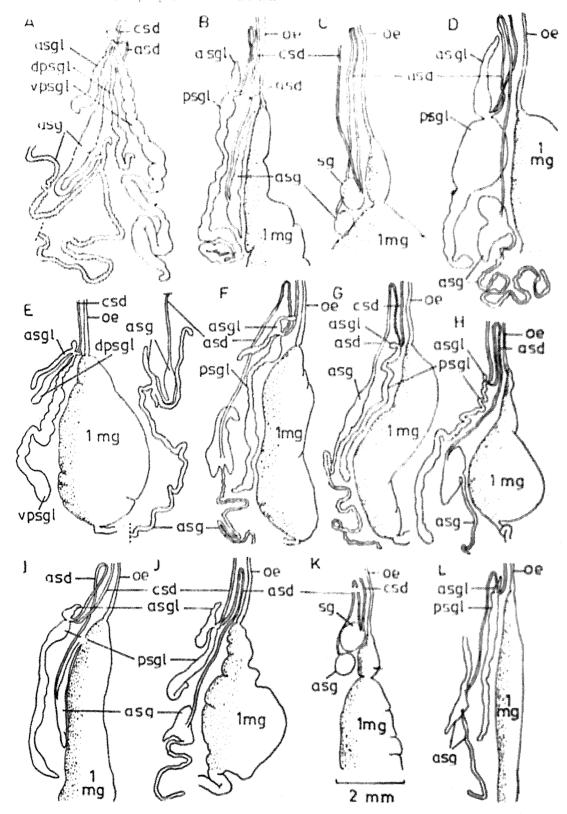


Figure I. Salivary system in Reduviids. A. H. nigroviolaceus (Reuter) - (Ectrichodiinae). B. P. affinis Serville - (Piratinae). C. T. rubrofasciata (De Geer) - (Triatominae). D. S. collaris (Fabricius) - (Harpactorinae). E. G. nigripennis (Fabricius) - (Ectrichodiinae). F. A. siva Distant - (Reduviinae). G. P. indicus Reuter - (Salyavatinae). H. L. annulosa Stal - (Salyavatinae). I. E. vishnu Distant - (Piratinae). J. A. pedestris Stal - (Reduviinae). K. L. costalis Ghouri - (Triatominae). L. R. atkinsoni Bergroth - (Rhaphidosomatinae). (The principal glands, the accessory glands and their salivary ducts are shown only on one side.)

The principal gland is highly variable in different groups of reduviids (figure 1). In T. rubrofasciata and L. costalis it is unilobed. In P. affinis, E. vishnu, C. brevipennis, S. collaris, R. atkinsoni, L. annulosa and P. indicus it consists of a small anterior lobe and a very long lobulated posterior lobe that extends into the abdominal cavity. In A. siva, A. pedestris and A. quinquespinosa, the salivary gland is also bilobed but the anterior lobe shows anterior and posterior extensions. In H. nigroviolaceus, E. pilicornis, and G. nigripennis the principal gland is three-lobed. The small anterior lobe sometimes extends into the head. Of the two posterior lobes, the smaller one is dorsally placed while the other is highly lobulated and ventrally placed. The latter extends well into the abdominal cavity. In all the reduviids the anterior lobe, whenever present, is always transparent in contrast to the posterior lobe or lobes, which have milky-white secretions.

Tissue homogenates prepared from the principal gland of *T. rubrofasciata* required as long as 43-53 min to bring about coagulation, while those prepared from the accessory gland and that of controls showed no such anticoagulatory property and the blood clotted in 7-10 min (table 2).

Zootoxic effects of the salivary system appear to be confined to the secretions from the anterior principal gland lobe in *P. affinis* and *H. nigroviolaceus*. The anterior salivary gland homogenates of *P. affinis* cause total paralysis and complete stoppage of all the twitching movements of the antennal and tarsal segments of the carabid beetle in 12-16 sec. The posterior and accessory gland homogenates and the controls did not show such effects. Similarly the anterior principal gland homogenates of *H. nigroviolaceus* produced total paralysis and stoppage of all body movements in the millipede in about 48-52 sec. The posterior dorsal and ventral as well as the accessory gland homogenates and controls failed to bring about such drastic effects on the millipedes (table 2).

The vesicular accessory glands of all reduviids appear to be always filled with a watery fluid. This gland is spherical in T. rubrofasciata and L. costalis, but elongated antero-posteriorly in P. affinis, E. vishnu and C. brevipennis. In most other reduviids the saccular accessory gland, in addition to having two or three blind projections, invariably produces a long tubular appendage from its middle and this process extends in a convoluted manner (figure 1BL). The most complicated type of accessory gland occurs in the members of Ectrichodiinae in which there is a well-developed membranous sac-like region that is applied to the fore part of the first midgut which subsequently narrows to a tubular region. The apex of this tubular part is connected with yet another triradiate tubular part and one of the tubular extensions of it is fused with its counterpart on the opposite side, thus providing a link between the accessory glands on both sides. The tubular extensions of the accessory glands have many convolutions, being spread out on the alimentary canal (figure 1AE).

Observations of the state of salivary gland activity at different stages of feeding showed interesting variations in test animals. In starved as well as those with a time lapse after feeding, the lobes of the principal and accessory glands were completely filled with secretions. The anterior lobes alone were in a flaccid state in *P. affinis* and *H. nigroviolaceus*, when the predators successfully completed immobilizatior of their prey. The posterior and accessory gland lobes in these were filled with secretions. In insects dissected soon after cessation of the feeding

activity, the anterior lobes were found to be almost full, while the posterior lobe in P. affinis, both the posterior lobes in H. nigroviolaceus and the unilobed principal gland in T. rubrofasciata, appeared considerably reduced in size, evidently with secretions spent during feeding. In all the three insects the accessory gland appeared like a collapsed bag with very little fluid inside them and their tendency to concentrate the neutral red solutions injected into the body cavity was equally evident.

3.2. Histology of the salivary glands

The unilobed principal gland of T. rubrofasciata comprises of a single layer of cuboidal cells, each with two spherical nucl-i. These cells enclose a spacious cavity, where the secretions are stored before being discharged. Their cytoplasm is highly viscous with numerous secretory granules and vacuoles. In P. affinis the cells of the two principal gland lobes show variations. Those of the anterior lobe are smaller and flattened with less viscous cytoplasm, having fewer secretory granules and vacuoles. Their nuclei are flattened and clongated. In contrast, the cells of the posterior lobe are larger and cuboidal with a highly viscous cytoplasm and with numerous granules and large collecting vacuoles. There are two spherical nuclei in every cell showing many chromatin granules. The histology of the anterior lobe of H. nigroviolaceus is similar to that of P. affinis, the posterior lobe having cells of the same type. But the posterior ventral lobe cells have more secretory granules and vacuoles than the dorsal lobe. In both these insects the lobes of the principal salivary glands enclose a spacious lumen. The secretions of the unilobed principal gland of T. rubrofasciata and the anterior principal gland lobe of P. affinis and H. nigroviolaccus are always viscous and transparent and the secretions of the posterior lobe's of the last two insects are milky-white and highly viscous. All the cells of the salivary system are characterised by apocrine or merocrine secretory activity (figure 2 GHI). The cells of the vesicular accessory gland in all the three insects are uninucleate and extremely flattened enclosing a wide lumen. Their cytoplasm lacks sceretory granules and vacuoles. The tubular region of the accessory gland of H. nigroviolaceus has cuboidal cells enclosing a narrow canal, their cytoplasm exhibiting no secretory granules.

3.3. Hilus of the salivary glands

The junction of the anterior and posterior lobes of the reduviid salivary gland has a well-developed, compartmentalised hilus, provided with valvular openings for the regulation of secretions sent out from the different lobes of the main and accessory glands. Even in T. rubrofasciata, which has a unilobed principal gland, there is a well-developed two-chambered hilus. The outer chamber of this hilus receives the incoming accessory salivary duct and sends out the main salivary duct, the respective openings of these ducts being guarded by valve-like flaps. The outer chamber communicates with the inner one, the latter receiving the secretions from the principal gland. This opening is also guarded by valves (figures 3C, 4A to F). The hilus of P. affinis is more complicated and divided into two highly selerotised inner and outer chambers. The outer chamber gives off the

main salivary duct and receives the accessory salivary duct at the distal end, and communicates with the inner chamber at the proximal end. The openings of the outer chamber into the salivary and accessory ducts as well as into the inner one are provided with separate valves. The inner chamber, in addition, receives independent openings of the anterior and posterior lobes of the principal salivary gland and these openings are also provided with valves made up of uninucleate

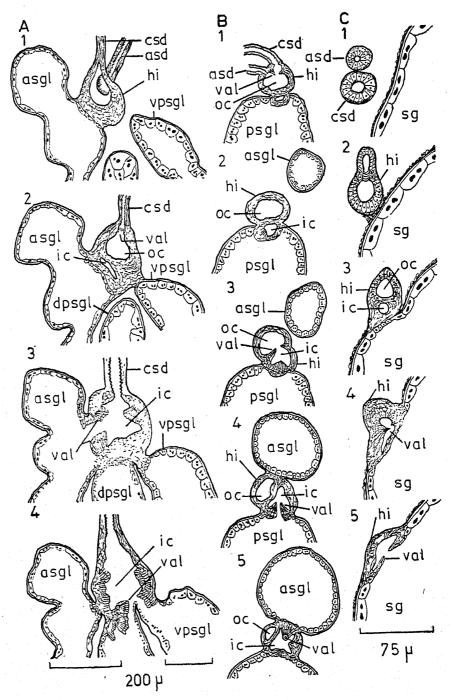


Figure 3. Histology of the salivary system in Reduviids. A. 1-4. L.S. through the hilus of the salivary gland of *Haematorrhophus nigroviolaceus*. B. 1-5. L.S. through the hilus of the salivary gland of *Pirates affinis*. C. 1-5. L.S. through the hilus of the salivary gland of *Triatoma rubrofasciata*.

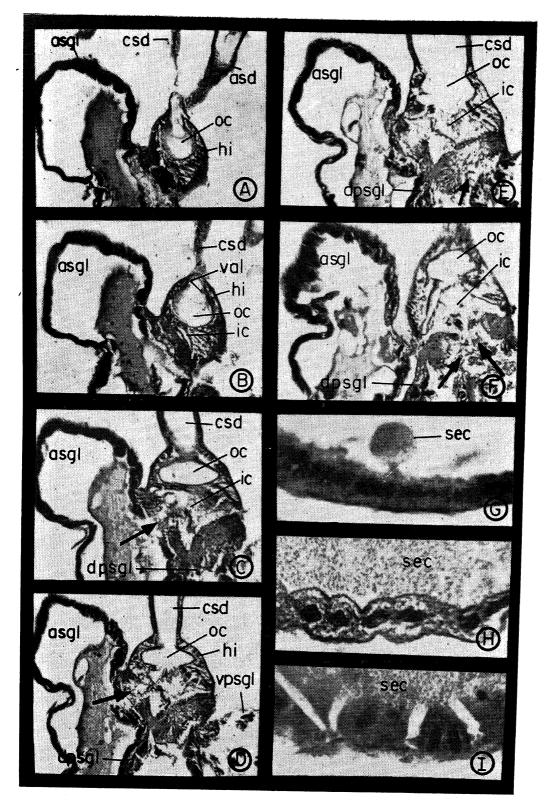


Figure 2. Histology of the salivary system in *Haematorrhophus nigroviolaceus*. A-F—L.S. through the hilus of salivary lobes (arrow indicates salivary lobe opening into the hilus, guarded by valves) (× 500). G—Apocrine secretion from the anterior main salivary lobe (× 4200). H—Non-secretory phase of the posterior dorsal main salivary lobe cells (× 3200). I—Merocrine secretions from the posterior dorsal main salivary lobe cells (× 3200).

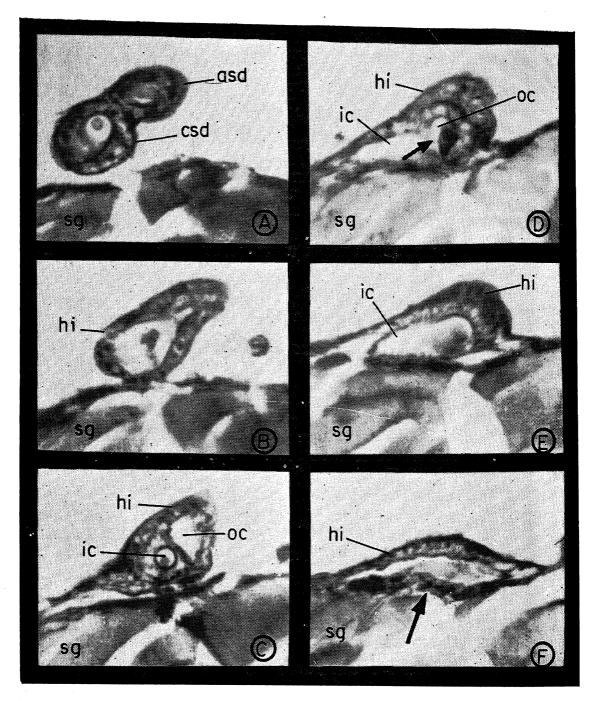


Figure 4. Histology of the salivary system in *Triatoma rubrofasciata*. A-F-L.S. through the hilus of the salivary lobe (arrow indicates the salivary lobe opening into the hilus) (× 1800). Abbreviations used: asd—accessory salivary duct; asg—accessory salivary gland; asgl—anterior lobe of principal gland; csd—common salivary duct; dpsgl—dorsal posterior lobe of principal gland; 1 mg—first midgut; oe—oesophagus; psgl—posterior lobe of principal gland; sg—principal salivary gland; vpsgl—ventral posterior lobe of principal gland.

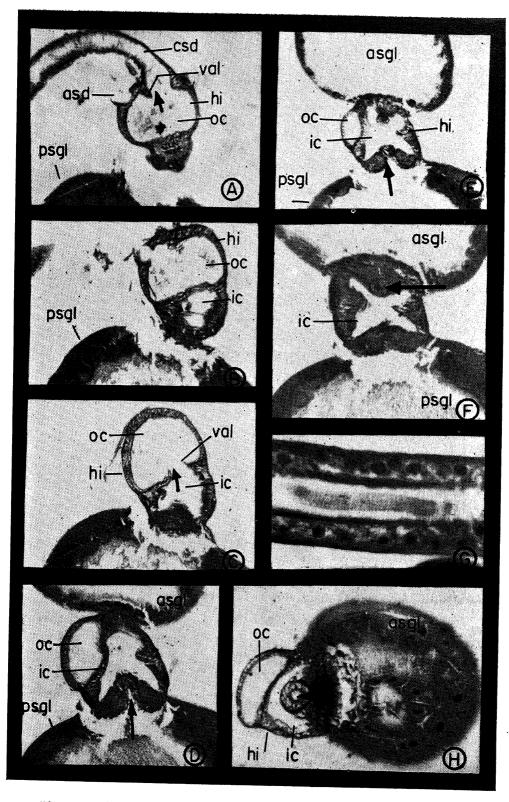
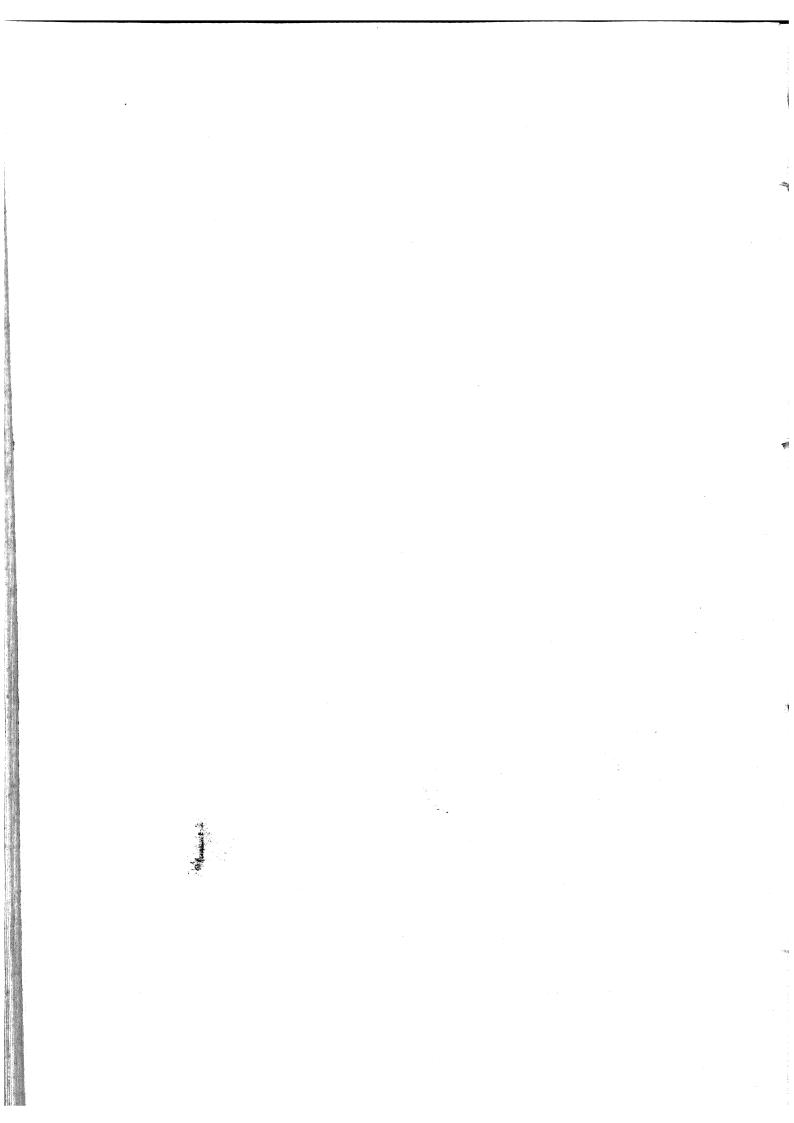


Figure 5. Histology of the salivary system in *Piratesa ffinis*. A-F—L.S. through the hilus of salivary lobes (arrow indicates salivary lobe opening into the hilus, guarded by valves) (\times 500). G—L.S. of the common salivary duct (\times 1500). H—T.S. through the hilus of the salivary lobes (arrow indicates the opening of the anterior salivary lobe opening into the hilus) (\times 960).



columnar cells (figures 3B, 5A to F, H). The hilus in the salivary system of H. nigroviolaceus is also two-chambered and the structure of the outer chamber is very similar to that of P. affinis. The inner chamber differs in that it receives two independent openings, one coming from the anterior lobe and the other, a common opening for both the dorsal and the ventral posterior lobes. All these openings are also provided with valves consisting of uninucleate columnar cells (figures 2A to E, 3A).

The ducts of the main and accessory glands are made up of a single layer of cuboidal cells, the diameter of the former is always greater. The cuticular lining of these ducts is thrown into spiral thickening as in the tracheal tubes (figure 5G).

4. Discussion

The salivary system of most reduviids studied typically conforms to the general heteropteran plan of principal and accessory glands with their ducts, their vesicular gland being similar to those found in other Cimicomorpha families. But the structure and the number of lobes of the principal glands are found to be specific to different subfamilies. The maximum number of lobes (one anterior, one posterior dorsal, and one posterior ventral) is seen in the members of Ectricho-In Piratinae, Reduviinae, Salyavatinae, Rhaphidosomatinae, Harpactorinae, the principal gland is only bilobed (one anterior and one posterior). The least number is found only in Triatominae. Louis and Kumar (1973), while discussing the interrelationships of certain subfamilies of Reduviidae based on their anatomical characters, suggest that the trilobed condition of the salivary system is primitive and its reduction to a bilobed condition in other groups is an advanced character. The unilobed salivary system finds no mention in their study. If the view that reduction of salivary lobes is an advanced character is accepted, then among the subfamilies of Reduviidae, Ectrichodiinae is the most primitive and Triatominae—the most advanced. Analysis of the pyloric region and the rectal glands in Reduviidae (Haridass and Ananthakrishnan 1980) also points to the primitive organization of this subfamily.

The separation of the principal salivary gland into an anterior and a posterior lobe, also found in other Heteroptera irrespective of their feeding habits, suggests the differential function of these lobes involving division of labour. Though Baptist (1941) believed that there is no such difference in the secretory activity of the salivary glands of Heteroptera, numerous investigations have shown the existence of such differential secretions. In Pentatomomorphid families the secretions of the anterior lobes are primarily concerned with stylet-sheath formation and those of the posterior lobe involve production of digestive enzymes (Miles 1967, 1968, 1972; Hori 1969). Salkeld (1960) has also reported such differential function in the anterior and posterior salivary lobes of *Oncopeltus* sp.

In Reduviidae too while the anterior lobe secretes zootoxic substances which the predators use to immobilise their prey, the posterior lobes are concerned with the secretion of digestive enzymes. This is contrary to the results obtained by Edwards (1961), who analysed the salivary secretions in *Platymeris rhadhamanthus* Gaerst. and found the presence of zootoxic substances both in the anterior and posterior lobes besides digestive enzymes secreted by the posterior lobe. The

division of labour among the different salivary lobes of Reduviidae is further substantiated by the fact that the anterior and posterior lobes show distinct histological variations. Moreover, the secretion of the former lobe always appears to be less viscous and is produced in smaller quantities while that of the posterior lobe is highly viscous and secreted in large quantities. The nervous supply to the salivary system is very complex, the nerve branches coming from the sub-oesophageal ganglion and from the stomatogastric system (Baptist 1941; Miles and Slowiak 1976). There is always a double nerve supply separately to the anterior and posterior lobes facilitating the discharge, either of the anterior or posterior and accessory lobes (Miles 1972). In addition to all these, a histological analysis of the hilus region of three species belonging to three sub-families indicates the existence of a common valvular system in this region. The hilus provides a regulatory system for sending out secretions from different lobes of the salivary system. In T. rubrofasciata the secretions from the accessory gland flow into the main salivary duct separately and independently of those coming from the main gland. In P. affinis and H. nigroviolaceus the valves in the hilus make it possible not only to send the secretions independently from the accessory glands but also to send separately the secretions issued from the anterior and posterior lobes of the principal glands.

When such a functional difference is involved in the salivary system, it is not surprising to find three lobes in the salivary system of Ectrichodiinae as their food always consists of large-sized primitive arthropods namely millipedes. From this primitive condition the two posterior lobes undergo fusion resulting in a bilobed principal gland as found in most of the reduviid subfamilies whose prev records are restricted to various insect groups (Haridass 1978). In the extreme condition of such reduction of salivary lobes into a single one as seen in certain members of Triatominae there is no distinction of anterior and posterior lobes. It should be explained that in these insects the need for the immobilization of the prey through zootoxic secretions is not felt as they have taken up a haemophagous habit on the vertebrates and the absence of an immediate reaction by the vertebrate will be an added advantage to such haematophagous insects. As shown by the present experiments and also by those of Baptist (1941) and Barth (1954). the salivary secretions of Triatominae have anti-coagulants which help them not only to suck an uninterrupted flow of blood but also to store this blood in the sac-like first midgut for long periods for gradual digestion. Baptist (1941) has also shown the complete absence of digestive enzymes in the salivary glands of Rhodnius sp. and Triatoma sp. It is also interesting to observe that only in T. rubrofasciata the principal gland is single lobed as in Rhodnius prolixus Stal (Wigglesworth 1973), while in all other species of Triatoma so far known T. protracta (Barth 1954) and T. infestans (Baptist 1941) the principal gland is divided into anterior and posterior lobes.

The accessory glands in all reduviids are typically of the vesicular type (Baptist 1941; Southwood 1955; Edwards 1960) and exhibit variations in different subfamilies. In Ectrichodiinae it is fused and branched while in Piratinae it is an elongated sac; in related subfamilies of Piratinae too, it is an elongated sac, but with tubular extensions. In Triatominae it is typically a spherical sac. Histologically the accessory glands differ distinctly from the principal glands and

always produce a watery saliva as has been shown by many other heteropterists. Miles (1972) has suggested that feeding in predatory insects is very similar to the lacerate-flush mode of feeding of Pentatomomorpha and the watery saliva is useful in flushing out the food from its source. Miles and Slowiak (1976) have recently shown in pentatomids and a coreid that the accessory gland is the main source of watery saliva. Injection of dilute vital dyes into the body cavity of live reduviids has shown that there is absorption of the body fluid through the surface of the accessory salivary gland in these predaceous insects. The accessory salivary glands recirculate water from the gut to ensure a copius flow of watery saliva which helps the predators to flush out the predigested food from the body of the prey.

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