Chapter III
Female Internal Organs of Reproduction
III.1 **Gross morphology** (Fig: 3,4,5)

The female internal organs of reproduction in *Rhinocoris marginatus* consist of a pair of ovaries (OF) and their ducts (LOD) that unite to form a common oviduct (COD). The common oviduct opens into the vagina. There are a pair of spermathecae (SP), one on either side of the common oviduct, opening independently into the bursa copulatrix (BU). The accessory organs of reproduction consist of a pair of subrectal glands (SRG) lying on either side of the rectum and jointly opening to the exterior close to the anus. A median ventral gland is visible in sections. It opens somewhere into the bursa. It is described here as the subbursal tegumentary gland (TGL) (PL.IX: 1,2).

III.1.i. **The Ovary:**

Each ovary in *R. marginatus* consists of seven telotrophic ovarian tubes. All the tubes are covered by a thin common peritoneal sheath. Each ovarian tube terminates as the terminal filament. All the seven terminal filaments of the same side are enclosed by a common sheath which is attached to the thoracic muscles of the respective side. All the seven terminal filaments of each side then apically unite to form a suspensory ligament in the middle of the mesothorax. This suspensory ligament then runs forward and terminates in front of the principal salivary gland. In a mature insect each ovary has a maximum of five egg nodules.
FIG. 3: RHINOCORIS MARGINATUS - FEMALE INTERNAL ORGANS OF REPRODUCTION

NEWLY EMERGED FEMALE
FIG. 4: RHINOCORIS MARGINATUS - FEMALE INTERNAL ORGANS OF REPRODUCTION

OVIPOSITING FEMALE
FIG. 5: RHINOCORIS MARGINATUS - FEMALE INTERNAL ORGANS, OF REPRODUCTION

SENESCENT FEMALE
In a mature ovary all the basal oocytes ovulate simultaneously. Dissections of several females indicate that when the eggs are ovulated they remain compactly arranged in the calyx in both the ovaries in the same pattern. When the ovulation has occurred, the penultimate oocyte is far from the eggs that have already descended into the lateral oviduct. It appears that in both ovaries, not only does the ovulation occur simultaneously but also the movement of the egg into the rest of the duct occurs almost coinciding with one another. It also suggests that all the eggs that are oviposited at a particular time are those that are ovulated simultaneously. This also suggests that the interoviposition period between two batches of eggs is extended depending on the time taken for the maturation of the next batch of eggs that varies considerably from insect to insect. After the completion of the ovulation the pedicel has elongated considerably and the corpus luteum as the yellow body is clearly visible at the base of the empty follicle. About three to four egg nodules are visible following the ovulation of the basal oocyte.

In a senescent ovary (PL.XIII) the ovarioles show the germarium much elongated and the vitellarium consisting of three or four egg nodules in different stages of development, but none of them show mature oocyte. The pedicel remains highly elongated.

III.1.ii. Pedicel(P)

The hinder part of each ovarian tube is produced into a tube called the pedicel (PL.IX:1) which is very short and hence
not clearly visible externally in a newly emerged adult. In mature and older insects however they are found more elongated (PL.IX:2). All the pedicels converge towards one point and meet at the base and this region is known as the calyx. The lateral oviduct originates from the calyx on each side.

III.1.iii. Oviducts

Lateral Oviduct (LOD)

The lateral oviducts are short and stout. Both the lateral oviducts remain at 180° to one another and their junction remains slightly expanded. It gradually enlarges towards the base and reaches the maximum enlargement and remains as broad as the common oviduct.

The Common Oviduct (COD)

The common oviduct is comparatively longer and thinner in the newly emerged adults and it becomes broader and thicker as the insect attains maturity. It is almost as long as the lateral oviduct but it is bent in the middle and directed postero-dorsally. It's anterior half is slightly larger than the posterior half and then expands into the bursa.

III.1.iv. Bursa copulatrix (BU)

The bursa copulatrix is dorso-ventrally compressed. It forms the terminal segment of the female reproductive tract and is nothing but the expanded terminal part of the common oviduct. In all the three conditions it could be divisible into two halves.
The anterior half that carries the spermatheca is slightly brownish and the posterior half is milky white. It opens to the outside through the genital passage called the vagina which is very brief.

III.1.v Spermathecae (SP)

There is a pair of spermathecae, lying dorsally on either side of the common oviduct and opening independently at the anterior region of the bursa copulatrix, mid dorsally. Each spermatheca has a slightly expanded body that tapers apically and a long almost straight duct by which it communicates with the bursa. Both spermathecae uniformly maintain their shapes, as club shaped bodies that are curved at right angles and their ducts, opening into the bursa middorsally after traversing close to each other for a short distance, remain embedded underneath the muscles of the bursa. The body of the spermatheca is about half as long as the common oviduct and in all the three conditions, it maintains its shape and size. These two are the principal depository of the sperms that are received from the spermatophore which is lodged inside the bursa during copulation.

III.1.vi. The Accessory Glands

III.1.vi(a). The Subrectal Glands (SRG)

There is a pair of subrectal glands which are shaped like the interrogation mark, lying on either side of the rectum. They jointly open to the exterior close to the anus. They are smaller, slender and translucent in a newly emerged adult and gradually grow
larger and attain the maximum size at the time of maturity and remain almost the same thereafter. Their size is correlated with the habit of gluing their eggs to the substratum in compact masses by using large quantum of the gluing material called spumaline secreted by them. The colour also changes gradually to become brownish towards the later stages. In a senescent insect the subrectal gland remains much more elongated and apically curved in the shape of a question mark.

III.1.vi(b) Tegumentary glands

There is a single median branched gland, lying ventral to the bursa. It is not readily visible in dissections. Apparently it communicates ventrally with the bursa. This is a special type of gland present in this insect, hitherto unknown in the female reproductive system of Heteroptera and can be mistaken as a part of the bursa. It is closely applied to the sternite and may claim the status of a tegumentary gland. Its duct is not well defined. It develops to its maximum size as the insect reaches sexual maturity and at this stage the lobes of the gland become visible (PL.XV: 1) even as short digitate white appendages.

III.2. Histology:

III.2.1 Ovarioles

All the ovarioles of each ovary undergo similar stages of development. At emergence the ovarioles are very rudimentary. The germarium(G) or the tropharium is represented by a few minute cells at the apex followed by a region of large trophocytes(TR)
that occupy more than three-fourth the length of the follicle (PL.IX:4,6). The more apical trophocytes are more elongated than the posterior ones. Therefore the delineation of the apical zone of small cells from the rest of the germarium is very easy. These trophocytes representing zone II of the germarium, are arranged in somewhat concentric tiers in the posterior region of the germarium and the central core of nutritive plasma is not yet well differentiated (PL.IX:6).

Posterior to this zone of trophocytes, the head of the pedicel is preceded by a zone of differentiating oocytes, identified by the arrangement of the follicular epithelial cells, around the ooplasm. Immediately in front of this, the vitellarium(V) is demarcated as indicated by the differentiation of a cluster of three to four oocytes. These differentiating oocytes are not supported by the corresponding differentiation of follicular epithelial cells from a mass of prefollicular syncytium that marks the posterior-most zone of the germarium.

All the follicles are enveloped by a tissue which contains clusters of bacteria. In between, the peritoneal tissue (PT) is traversed by numerous tracheal branches. Thus in a newly emerged adult the tropharium alone is properly differentiated and the vitellarium shows signs of differentiation from the tropharium by the arrangement of cells derived from the prefollicular syncytium to form the follicular epithelium. The occurrence of nodules of bacteria within the sheath that surrounds the ovarioles is a special feature.
The basal epithelial plug (BEP) is quite distinctly formed behind a differentiating basal oocyte and the junction of the pedicel and this elongated basal epithelial plug is clearly defined by a patch of cells (to be described later) projecting into the head of the pedicel (PL.IX:8). This tissue is distinctly different from the basal epithelial plug by having small, round, closely packed nuclei appearing as syncytium (PL.X:5,6).

The pedicel has a large lumen with a layer of closely packed nuclei lining the lumen and exteriorly this layer is invested with longitudinal muscle fibres which is followed by a simple layer of peritoneal tissue which is often found to be ensheathed within a fat tissue (PL.IX:7,8). Secretory activity of the epithelium of the pedicel is not recognized at this stage.

In the maturing insect, in each follicle, the germarium and vitellarium are well differentiated (PL.IX:6). A maximum number of four to five egg nodules could be recognised, each nodule having well defined follicular epithelium (FE). The germarium is differentiated into three distinct zones namely the apical zone of minute cells, the middle zone of trophocytes and the basal zone of nutritive plasma or nutritive core (PL.IX:4; PL.X:1). The germarium is distinctly separated from the vitellarium by a transverse septum (ES) (PL.X:7,8) having highly secretory columnar cells, behind which the vitellarium is being differentiated. In front of this septum, the nutritive plasma is connected to the vitellarium by nutritive cords that run through the septum (PL.X:7,2,3). Immediately behind the septum the follicular epithelium of the developing oocyte (OC) is distinctly differentiated and the course
of transformation of the follicular epithelium could be traced readily in the succeeding oocytes (PL.X:2,4).

One of the important features is that in a mature insect all the oocytes are arranged in single file except the first three oocytes. The rest do not have intervening follicular epithelium separating one from the other, though the influx of the follicular epithelium marking the limit of each follicle is identified at the corners. The germinal vesicle occupies different positions in the respective oocytes - concentrically, eccentrically as well as at the poles. It is interesting to record here that one or two ovarioles have their basal oocytes somewhat erratically formed, as indicated by unusual vitellogenic process, as evidenced by unusual behaviour of the follicular epithelium.

When the basal oocyte (BO) progresses in vitellogenesis, the basal epithelial plug begins to expand, with the much elongated cells getting arranged transversely in single file (PL.X: 5,6; PL.XI:2). The space enclosed within is filled with protoplasmic materials. Interiorly, it is lined by the vitelline membrane that envelopes, the developing egg marking the most vitellogenic phase. These cells of the basal epithelial plug do not contribute to the vitellogenic process as much as the cells of the cephalic end.

Immediately behind this active basal epithelial plug, the cells that were not well formed in the beginning become very active and form a mass of tissue with large granular nuclei and highly vacuolated cytoplasm. Mildly eosinophilic homogeneous
secretory material is found in the interstices of these cells. This mass of tissue that intervenes the basal epithelial plug and the head of the pedicel is very active secreting such material, beginning at the onset of vitellogenesis and becoming more massive filling the mouth of the pedicel. Externally it is bound by the peritoneal sheath as well as the tunica propria that continues throughout the entire follicle (PL.XII:4,5,6). A space is formed between the tunica propria and the peritoneal sheath which remains significantly extensive around this tissue. It is this tissue that is marked off earlier as a tiny bit of cells immediately behind that basal epithelial plug in the newly emerged adult, as described earlier.

A close observation of this tissue indicates that its behaviour synchronises with vitellogenesis and its histology is not consistent. As the follicle advances in development, cells of this tissue elongate considerably and their elongated nuclei are directed towards the pedicellar head, but enclosed within the spacious vesicle (PL.XII:4,5) that remains as a plug of the pedicellar head. Subsequently, at the time of ovulation this vesicle ruptures the basal epithelial plug and makes way (0) for the passage of the egg at ovulation (PL.XII:8,9). Meanwhile, one could clearly see that the space surrounding this mass of tissue within the peritoneal tissue is being filled with a light, mildly eosinophilic secretory material that forms a sort of sheath of irregular shape around this region of the tissue.

At this time, the secretory material which accumulated
in the interstices of the mass of tissue described earlier, is no more found even between the elongated cells. A comparison of the material that now occupies the space and the material that accumulated in the interstices initially will clearly indicate that both materials are one and the same. This suggests that the material that is accumulated outside now and closely applied to the exterior of the tissue is nothing but the material that has oozed out from this interstitial tissue. This type of tissue and this kind of behaviour of the tissue including the secretory material that accumulates in the periphery is not found anywhere between oocytes, except at the region immediately in front of the pedicel.

In order to verify the qualitative histology of this tissue and its behaviour, sections of the much older follicles which have ovulated several eggs have been studied. They indicate that this tissue continues to secrete the material that accumulates around this as a massive body of non-cellular mass, and the septum (Wall of the vesicle) that separates the tissue from the pedicel makes an aperture for the eggs to pass (PL.XII:8,9). The basal epithelial plug gradually degenerates while the elongated cells continue to become active and the interstices of these cells contain the secretory material as well. The corpus luteum(CL) is found immediately behind the basal epithelial Plug (PL.XII:7,8,9).

It is clear that this tissue plays a vital role in the physiology of ovulation. It is distinctly a secretory tissue, secreting continuously a material that accumulates within the space
around it, enclosed by the peritoneal tissue. It is neither a part of the pedical head nor a part of the basal epithelial plug. Anatomically and physiologically it is different from both of them. Therefore, this tissue is named as an antepedicellar interstitial tissue (APT). As this tissue begins to function at the onset of vitellogenesis of the basal oocyte and continues to function as a secretory element throughout the active egg producing life of the ovariole it is evident that this tissue is an indispensable component of the reproductive physiology of the female insect.

Regarding the consecutive accumulation of the secretory material around this tissue in successive stages of ovulation, the argument in favour of attributing physiology of secretion in ovulation is as follows: The musculature of the ovarian follicle is weak. Ovulation will tend to cause sagging of the reproductive tract as observed in the case of the pedicels as well as the lateral oviducts. Accumulation of this material around a strategic position, that is immediately behind the basal epithelial plug of the basal oocyte, will provide the ovulating tract a consistency in rigidity, preventing sagging. Further, this material, in the absence of a powerful musculature around this area, provides a sort of constriction that enables the ovulated egg to experience an ejaculatory power exercised by this accumulated material and thus the egg is forcibly ejected into the pedicel. A kind of vacuumatic action that is experienced by this part of the passage, also provides a possible explanation. Since the septum at the floor of the vesicle separates the head of the pedicel which is comparatively much more spacious than the position where the
tissue is found, the rupture of the septum for the release of the egg is brought about by a force generated at this constricted region. Thus the functional importance of this antepedicelllar interstitial tissue is very remarkable.

The biology of the follicular epithelium deserves special consideration since its delineation on the basis of functional organisation forms the basis of this intensive observation. As the egg begins to differentiate in the vitellarium, the follicular epithelium differentiates as well into elongated cells from a mass of minute cells of the pre follicular tissue that occupy the junction of the vitellarium and germarium (PL.IX:4,6; PL.X:2).

The first indication of the differentiation of vitellarium, is the arrangement of prefollicular cells around the germ cell, enclosing a bit of ooplasm, thus constituting the primary oocyte (PL.IX:7). Its posterior and anterior ends are not sealed off since the developing oocytes communicate with one another and with the tropharium through plasmatic cords. As these cells close at the caudal end of the egg by and by, it is separated from the cephalic end of the succeeding egg by the rearrangement of the follicular epithelial cells in the longitudinal axis of the egg.

This arrangement marks the end of a phase in the development of the egg as the plasmatic strand connecting the succeeding egg is shut off and the follicular epithelial cells enter into vitellogenic phase. From now on, the follicular epithelium of the cephalic end of the egg elongates in the longitudinal axis as the egg also elongates in the same direction. There is no indication that these cells at the cephalic end contribute to the vitellogenic
process unlike the other cells which are actively engaged in vitellogenesis. These cells are totally devoid of any secretory vacuole but its basal membranes on its outer surface are continuous with that of the outer follicular epithelium (PL.XI:2).

The nuclei divide and the cells are arranged in two tiers. As this progresses, the cells develop both intercellular and intracellular spaces. On completion of vitellogenesis the oocyte enters the postvitellogenic phase marked by the secretion of the vitello- genic membrane (VM). This is followed by the next phase called choriogenesis involving secretion of the chorion.

The cells of the cephalic end now get engaged in secreting the opercular apparatus (OPA) during choriogenic phase (PL.XI: 2-8). The intercellular space between each row of cells now forms the rib of the hexagons of the chorionic collar (CHC) around the periphery, whereas such ribs constitute the hexagonal impressions of the opercular plate. In between these ribs the intracellular space widens considerably and the secretion fills this space in the form of a very thin sheet marking the hexagonal cells of the chorionic collar. The secretory product of each cell in the middle of the cephalic end is a single elongated hexagonal cell of the opercular plate. Throughout their length the cells are joined and the intracellular space that remains fairly visible initially now becomes compactly arranged by the ribs of the cells.

The longitudinal ribs in fact represent the boundaries of each cell which is apically and basally parted slightly. The
apical parting is more clear as seen in sections of ovulated eggs (PL.XI:8,9) found in the period. It appears apically as a tube. So, in between such cells this type of arrangement is found. This represents the opercular crest (OPC) which is porous apically and basally the opercular plate formed by the fusion of all the cells at the base. The central rows of cells secrete the tall columnella (COL). Thus it is clear that in the formation of the opercular plate and crest and columnella, each hexagonal cell is formed out of a single longitudinally elongated cell having two nuclei. Basally all the cells are united to form the plate and apically each cell remains free leaving an intercellular space forming a honey-comb like meshwork, the intercellular space being eventually filled by secretion to mark the rib (PL.XI:4-9).

As indicated earlier the nucleus of each follicular cell divides into two, peripherally a single layer of cells representing the outer row of cells becomes separated off from the inner row of cells. The outer row of cells remain continuous with the rest of the follicular epithelium enveloping the egg and secrete the chorionic collar (CHC) whereas the inner rows of the cells which are arranged in whorls go to make the opercular cells as well as the opercular crest (OPC) and columnella (COL) (PL.XI:4,5). The marginal cells of the opercular crest that secrete the chorionic opercular plate now remain fused with the base of the chorionic collar to form the sealing bar.

The peripheral cells constituting a single row of several
tiers of cells, reach almost up to the level of the apex of the opercular crest and then deflect inward and merge with the outer row of the cells of the opercular crest, subapically. It is at this point of merging that the chorionic collar gets fused with the outer surface of the opercular crest and the space thus formed is enclosed within, between chorionic collar and the crest. This space extending from the point of the fusion of the opercular plate with the chorionic rim by the sealing bar is the periopercular space. This periopercular space is divided into a lower inner closed periopercular space (IPOS) and an outer open periopercular space (EPOS), both being separated by the deflected flange of the chorionic collar that has fused with the opercular crest (as described earlier).

Thus the cells that are found in the middle of the cephalic end remain tall, binucleate and concentrically arranged, (PL. XI:4) whereas those at the periphery are short consisting of several tiers and concentrically arranged in a single whorl around the central tall cells. Each cell imparts its hexagonal sculpture to the material it secretes. The cells of the opercular plate gradually increase in height, the outermost whorl that lies closer to the sealing bar is the shortest, a few middle whorls being the longest. The cells of the chorionic collar reach beyond the height of the middle cells of the opercular plate and then deflect inward and reach the opercular crest.

The hexagonal sculpture of the chorion (CH) is distinctly formed by the impressions formed by the follicular epithelial cells
while secreting the chorion (PL.XI:7). The inner periopercular space is very spacious. The point at which the peripheral cells fuse with opercular crest cells should communicate with this inner periopercular space through minute pores. It is not clear whether these pores should also serve as the passage for the sperms too, so that the sperms may accumulate around the outer rim of the opercular plate as the sperm groove develops around it making the fusion of the sealing bar with the chorionic rim. The short cells have their rims carrying minute pores that constitute the lowermost whorl of cells of the chorionic collar along the ribs. These pores are directed towards the inner periopercular space. These may constitute the external opening of the aeropyles.

The last function of the follicular epithelium is the secretion of chorion.

Following ovulation, the empty follicle undergoes a lot of changes (PL.XII:1). All the follicular cells that have been reduced to the state of a pavement epithelium, on completion of choriogenesis immediately after the ovulation, undergo drastic changes collectively known as corpus luteum (CL). The cells of the empty follicle from the basal epithelial plug of the penultimate oocyte collapse and the follicular epithelial cells including those of the cephalic end undergo complicated folding and such folds occupy the entire space occupied earlier by the chorionated egg.

The first indication of these changes is the vacuolation of the cells and the fragmentation of the nuclei in the form of a cell mass. The nature of the cell is often referred to as pycnosis (PL.XII:2) and the deterioration of the cell is referred
to as necrosis. Such disintegrating mass of epithelium now comes to occupy the space very close to the epithelial plug which has also undergone drastic reduction synchronising with the corpus luteum formation. The cell mass is the antepedicellar interstitial tissue (APT) that actually secretes the eosinophilic homogeneous material that accumulates around the periphery at the base of the follicle (PL.XII: 4).

Successive ovulations lead to greater accumulation of the disintegrating cells of the corpus luteum close to the basal epithelial plug. This means that the materials of the disintegrating cells of the corpora lutea are resorbed and consequently the remains of the corpora lutea formed by subsequent ovulations come to occupy the same position originally occupied by the basal oocyte. This type of corpus luteum is normally designated as the compound corpus luteum. In all preparations the corpus luteum is distinctly differentiated from the rest in having greater affinity to basic dyes and certain secreting granules are often found in the tissue suggesting that the corpus luteum produces some products which are resorbed at the time when the vitellogenesis of the penultimate eggs is in progress.

Study of the senescent ovariole (PL.XIII) shows that while the ovulated eggs still remain in the lateral oviduct, the corpus luteum of the ovulated follicles has already receded to the base. The penultimate oocyte that has already initiated vitellogenesis has ceased to proceed further in its development and the follicular epithelium begins to disintegrate throughout including the cells of the cephalic end. This disintegration begins with the pycnosis
and fragmentation of the nuclei of the follicular epithelial cells and the cytoplasm of these cells show extensive vacuolations towards the periphery (PL.XIII:5). This event is closely followed by blister formation at the free margin of the cells and the ooplasm being extensively vacuolated. The follicular epithelium with all these changes remains extremely enlarged and the cell content amidst nuclear fragmentation, is filled with large number of eosinophilic globules indicating the sign of oosorption. In a much older specimen disintegrated epithelium shows considerable shrinkage.

While all these changes of disintegration and oosorption take place, the germarium and vitellarium apparently remain least affected. The germarium remains highly extensive and the vitellarium with three or four oocytes. Tunica propria of the germarium and vitellarium remains fairly tough (PL.XIII:1,2). The plasmatic strand also remains extended for a considerable distance into the tropharium but vitellogenesis does not occur in any of the oocytes, while the basal oocyte has already reached a certain stage of oosorption.

III.2.ii. The Pedicel (P)

The pedicel starts with the slightly expanded head (PE) in the form of a cup into which the antepedicellar interstitial tissue projects (PL.XII:8,9). The rim of the cup stops at the base of this tissue that marks the junction of the basal epithelial plug and the pedicel. In the insects immediately after emergence, the pedicel is found to be very short with very narrow lumen. Its single layer of epithelium has compactly set elongated, basophilic, densely granular nuclei, without any sign of secretory activity. There is a thin layer of peritoneal tissue and the musculature is
As the insect grows to maturity, the pedicel elongates considerably and the epithelium gets more clearly defined with the nucleus becoming spherical, finely granular and mildly basophilic (PL.XIV:3). Secretory activity of the cells is more evident at the cephalic end of the pedicel and the muscle fibres, particularly the longitudinal muscle fibres, are very conspicuous. One of the remarkable features of the ducts at this stage is the presence of clusters of bacteria in their lumen (PL.XIV:1).

In a mature insect in which the ovulation is imminent as well as in insects that have ovulated a few eggs, the pedicel enlarges considerably (PL.XIV:2) and the cells become very active with large quantity of cytoplasm. The lumen is filled with a secretory material that provides a viscous appearance. It is probably a viscous fluid. After a few ovulations the epithelium of the pedicel becomes folded longitudinally (PL.XIV:4) throughout the length and all the folds are enclosed by the peritoneal tissue, to allow maximum expansion for subsequent passage of eggs. The epithelium appears cuboidal and the secretion is in the merocrine fashion (PL.XIV:5).

III.2.iii. Oviducts

The lateral oviduct is highly muscular and it is provided with highly padded epithelium whose cells are arranged in several longitudinal rows. The pads are arranged in the form of crypts and the cells are highly secretory. The secretion is of coarsely granular, eosinophilic material. The folds of the lateral oviduct
epithelium continue throughout the common oviduct also. Very fine layer of chitinous intima lines the epithelium and the secretion is poured into the lumen by the interruptions in the chitinous layer. The musculature (M) of the lateral and common oviducts consists of the very heavy outer circular muscles and light inner longitudinal muscles (PL.XIV:6). In between the folds of the epithelium also there are longitudinal muscles.

III.2.iv. Bursa Copulatrix (BU)

The bursa is highly muscular and its lumen is lined with thick chitinous intima and its epithelium is longitudinally folded, the folds continue with those of the common oviduct. The spermathecal ducts on both sides traverse within the musculature of bursa and open into the chamber almost very close to each other on its dorsal aspect, as disclosed by the sections (PL.VII:6).

III.2.v. Spermatheca (SP) (PL.VII; PL.VIII)

Both spermathecae open independently into the posterior end of the bursa (BU) on either side (PL.VII:1). In the newly emerged adults (virgin females) the gland remains highly convoluted and collapsed (PL.VII:2). The histology of the ducts of the spermatheca (SPD) and the body of the spermatheca vary considerably, especially the nature of the lumen (LU). In the duct the epithelium is single layered, the nuclei are round and centrally placed but the lumen is far removed from the epithelium and is lined by a thick intima (PL.VII:4). The outer lining of the basement membrane is invested by thick layer of inner circular and outer longitudinal muscles (M).
In the body of the spermatheca the lumen (LU) is spacious. The wall has a layer of cuboidal epithelial cells with round granular, lightly basophilic nuclei occupying the base of each cell. The inner lining is of chitinous intima which is thrown in the form of regular rows of dentate processes. The space between the nuclei and the lining is cytoplasmic and is mildly granular. The lumen is empty and the musculature is less powerful than that of the duct (PL.VII:2).

In a further stage, the spermatheca shows highly folded epithelium with basally arranged, oval, basophilic densely granular nuclei and the lumen is filled with mildly basophilic finely granular homogeneous substance. The cytoplasm is highly vacuolated with granular secretory material (PL.VII:8,9). In such a condition the spermatheca is said to be highly secretory and the space in between the lumen and the wall of the duct is also filled with a mesh work of cytoplasmic material. The spermatheca at its proximal end and at its junction with the duct is enveloped by fat tissue (FT) (PL.VII:7) which is stuffed with bacteria. Such bacteria are also found as nodules or clusters around this region.

In a fully mature insect, after copulation, the lumen is stuffed with spermatozoa (PL.VII:5). The epithelium of the spermatheca still maintains the nature of the spermatheca of the mature insect before copulation. The secretory activity of the large cells is evident by the presence of secretory vacuoles and the secretion appears to be discharged into the lumen through the rupture of the intimal lining.
The more apical region of the spermathecae has the epithelium not so enlarged as in the proximal region in which the epithelium appears in the form of crypts and such crypts are arranged in longitudinal rows. The intimal lining is obscurely represented.

The epithelium of the duct is highly vacuolated, the nuclei more rounded. The space between the lumen and the epithelium is more evident. The intimal lining of the lumen is thick and is surrounded by a sheath like material that obliterates the space between the epithelium and the lumen (PL.VIII:7). It is not clear whether this sheath material is the secretory product of the epithelium. The lumen is filled with spermatozoa. None of these sections indicate the clusters of bacteria that normally occur in abundance in a teneral insect. Thus it is clear that the epithelium of the spermatheca starts secreting as the insect approaches the stage of maturity, and the secretory activity of the epithelium is more intense from the proximal region towards the distal region. In such a stage when the spermatozoa are received following copulation the secretory materials are clearly visible in between spermatozoa.

The proximal end of the duct of the spermatheca is found embedded within the musculature of the bursa. The two ducts open into the bursal chamber on its dorsal aspect, quite close to one another, suggesting that when the spermatophore is lodged inside the bursa, these openings of the two ducts of the spermathecae closely approximate the dorso-laterally directed aperture
of each half of the spermatophore (PL.VII:6). The spermathecal duct having its own strong circular musculature and the powerful musculature of the bursa that envelops the ducts both aid concurrently in sucking the spermatozoa from the spermatophore capsule. Release of the spermatozoa from the spermatheca is also performed by similar function of these muscles. Ejection of the spermatophore from the bursa after the emptying of the sperms is performed by the powerful muscles of the bursa.

The secretory activity of the spermatheca coincide with the attainment of maturity and its continued secretory activity throughout its reproductive period is clearly understood in the present investigation. The secretion is in the form of eosinophilic granules that accumulate in the form of globular mass and intercellular filling. The vacuoles are very clearly found (PL.VIII: 1, 2, 3 & 4). The release of this material occurs through the rupture of the intima at various points and such release gives the impression of a merocrine form of secretion. The longitudinal foldings of the epithelium towards the proximal end of the gland suggest that they are in the form of longitudinal crypts of the epithelium in an active phase of secretion. The nuclei found at the base of the epithelium are constant in their position but vary in their form—elliptical to spherical. This may be correlated with their secretory activity.

It is interesting to record here that when the spermatheca begins to proceed in its secretory activity the sheath around the
spermatheca is stuffed with cells with large granular nuclei and the intervening space between the sheath and the basement membrane is packed with thick layers of longitudinal muscles (PL. VIII:2). The sheath has got its own sheath membrane which is fairly tough. The sheath is more prominently found at the proximal end of the spermatheca than at the distal end.

In a senescent insect the spermatheca loses its padded nature of its epithelium and the epithelium has been reduced to cuboidal type. The chitinous intima under such condition remains detached in most areas (PL. VIII:5), the cells lose their characteristic vacuolations and the sheath cells have become necrosed. The spermatozoa inside show various stages of disintegration. The space between the intima and the epithelium remains empty and the epithelium now forms its own intimal lining, having almost receded to its basement membrane to give the indication of having receded to its basement membrane. The duct also regains the space between the intima and the epithelium (PL. VIII:9).

III.2.vi. Accessory Glands

III.2.vi(a). The Subrectal Glands (SRG)

The subrectal glands in the newly emerged adults are like interrogation marks, present on either side of the rectum (PL. XV:1). Each gland lying on either side of the rectum jointly open to the exterior close to the anus. The glandular part is in the form of highly folded chitinous folds and ill defined cellular
boundaries and the nuclei are found lining such chitinous folds. The lumen is thus obliterated. Strong longitudinal muscles invest the base of the chitinous wall (PL.XV:3,5). The duct is much more elongated than the gland. It is more muscular than the gland. Posteriorly, both the ducts meet and open to the exterior through a very short common passage (CO) (PL.XV:4).

At the junction of the two ducts, immediately before opening to the exterior, there is a bundle of strong muscles inserted to the anal segment (PL.XV:3) and originating from the wall of the common duct. Fibres of these muscles run along the duct on either side for a considerable distance in the form of a fan. Closely associated with these fibres are the clusters of bacteria (PL.XVI:3,4). There is absolutely no indication of any secretion present in the lumen. The occurrence of these powerful muscles at the junction of the two ducts suggests that the discharge of the material is regulated by these muscles. Therefore, secretion is released at will in the form of spumaline which is released at the time of oviposition. It is also clear that the chitinous nature of the gland explains that it is ectodermal. It is not clear whether the material is released along with the faecal matter or independently. Histological evidence suggests that the gland is not connected to the rectum but opens independently close to it to the exterior.

When the insect attains maturity the subrectal glands increase several fold in size and in its histology. The difference is marked by enormous increase in the cytoplasm of the cells lining
the chitinous folds. The cytoplasm is finely granular and eosinophilic, the nuclei are syncytial and enlarged and become conspicuous but the lumen still remains obliterated due to the folds (PL. XV:6).

The peak activity of the subrectal gland is marked by aciniform types of glands (AC) occurring throughout the periphery of the gland (PL.XV:7,8). Each acinus is composed of three to four nuclei arranged in a circlet and it communicates with the lumen of the gland which has become exceedingly spacious. During this stage the chitinous folds expand and the cytoplasmic contents of the associated cells become vacuolated. The chitin floats in the lumen as wavy pleats, but the nuclei remain attached to them. The acini vary in their shape and size depending on their secretory activity. They are either round or oblong, but the lumen of all of them communicates with the main lumen of the gland. The number of nuclei in the acini also vary considerably.

As the insect approaches senescence the chitinous folds return to their original form as the nuclei remain attached to both sides of the fold. These folds remain hanging into the spacious lumen which contains the remains of the spumaline secreted during the reproductive stage (PL.XV:9).

This cyclic activity of the subrectal glands is a striking feature. The secretory activity starts as the insect advances towards receptivity and the occurrence of the acini throughout the periphery of the gland, marking the peak of its secretory activity,
and the total disappearance of such acini and the depletion of the cytoplasmic contents as the insect reaches senescence, are features that characterise the reproductive physiology of these insects. The occurrence of the acini and the impending secretory activity mark the peak of the oviposition period when large amount of spumaline is required.

III.2. vi(b). Tegumentary Gland (TGL)

One of the striking features of the anatomy of the female reproductive system in R. marginatus is the recording of a special type of gland, hitherto unknown in the female reproductive system of Heteroptera. This gland is named here as tegumentary gland. This tegumentary gland is an ectodermal gland not visible in dissections. In the newly emerged adults, sections of the bursa reveal that, on its ventral aspect, a highly folded gland in the form of a garland is found associated with the posterior end of the bursa (PL.XV:1, PL.XVI:6). In some cases these glands even appear either as small masses of cells or as small vermiform tubes projecting from the wall of the bursa. This garland gland is, chitinous having spacious reservoir which is applied to the ventral aspect at the posterior end of the bursa. The folds of the gland communicate with the reservoir.

The cells of the gland of the newly emerged adult show small dense basophilic nuclei and the gland appears as syncytial (PL.XVI:6,7). As the insect reaches maturity aciniform type of glandular details could be recognised in the form of nodules connected to the reservoir and each nodule having three to four
nuclei which are now much enlarged and granular (PL.XVI:8). In a more advanced condition, on either side of the bursa these glands show pockets of glandular elements with large nuclei, highly granular cytoplasm and the secretion is either stored in this as such or released into the reservoir as mildly eosinophilic homogeneous material. In the senescent insect also these glands remain almost of the same texture.

It is difficult to clearly define the extent of development of the gland since it takes a tortuous course, but still maintaining the garland like character. This could be easily mistaken for a part of the subrectal gland but it differs markedly from the latter by its histology and its disposition. Its activity is clearly related to maturation and reproduction of the insect and it appears to secrete a copious material that accumulates in the reservoir. However, the exact manner of its discharge and its functional role still remains to be confirmed. Since it is purely ectodermal the term tegumentary gland has been given. In some cases mass of fat cells having bacteria as well as patches of bacterial mass have been found to be associated with the gland (PL.XVI:8). The exact nature is not understood.

III.3. Discussion

Ovarioles

The number of ovarioles in Heteroptera has been assessed in a large number of species of different families in general, just in the same way as the number of testis follicles are assessed.
Woodward (1950) maintained that the number of testis follicles and ovarioles remain constant in individual species, but this is not a rule since in Aradoidea, Kumar (1967), found significant variations in the number of testis follicles and ovarioles in individual species. In Termitaphididae, he (Kumar 1967) found two ovarioles and five testis follicles and in Calisiinae he observed six ovarioles and two testis follicles. Similar observations have been reported by Miyamoto (1957). In Tingidae also Livingstone (1967) reported two testis follicles and seven ovarioles.

In majority of cases the ovarioles and testis follicles number have been found to be seven (Woodward 1950, Carayon 1950, Miyamoto 1957 and 1959, Leston 1961, Ramamurthy 1970 and Louis and Kumar 1973). In Cryptocerates (Hamilton 1931, Presswala and George 1936, Poisson 1951) and several species of Cimicomorpha (Miyamoto 1957, Drake and Davis 1960, Kumar 1967 and Davis and Usinger 1970) the ovarioles are known to be five in number. In Reduviidae, Miyamoto (1957) found six to eight ovarioles and in Holoptilinae the number is known to be only three (Miyamoto 1959). According to Pendergrast (1952 and 1957) the ovariole number varies even within a single genus and in Pentatomidae in which the general number is seven, occurrence of four and six ovarioles is not uncommon. In R. marginatus all the seven ovariole present similar stage of development though the number of egg nodules present in each ovariole tend to show minor difference.

The terminal filament in each ovariole is a constant feature though very rarely it is studied in detail. Several workers have
traced the terminal filament up to the thoracic region and reported union of all the terminal filaments of the ovariole of each ovary to form a suspensory ligament that gets associated with the structures of the thorax (Davis 1955 and 1956, Ma and Ramaswamy 1987). Union of these two suspensory ligaments to form a common suspensory ligament and such a ligament entering into the head capsule and getting associated with structures of the head capsule, have been reported in several Heteroptera (Livingstone 1967 in Tingidae and Ramamurthy 1968, 1969a and b and 1970 in several Pentatomidae species). In the present observation there is no common suspensory ligament but the suspensory ligament of each ovary reaches the anterior margin of the prothorax and terminates somewhere near the sub oesophageal ganglion. Though none has given even a suggestion regarding the significance of the association of suspensory ligament with structures of the thorax, it is probable that their association in the proximity of the endocrine glands may be concerned with direct transmission of hormones to the ovarioles.

In Heteroptera, varying degrees of differentiation in the histology of the terminal filament have been reported. Davis (1956) in *Cimex lectularius* described an "end chamber" carrying a series of flattened cells at the junction of the apical filament with the germarium and the peritoneal sheath anteriorly extending from this end chamber to form a sheath of the apical filament. The flattened cells were reported to continue anteriorly forming the core of the apical filament. Syncytial condition of the apical
filament has been reported in several pentatomids (Ramamurthy 1969a and b and 1970, Ramamurthy and Medhi 1970).

While a transverse septum delimiting the terminal filament and the germarium has been recognised by Bonhag (1958), Brunt (1971) and Huebner (1984), such a septum was found lacking in Lygus lineolaris (Ma and Ramaswamy 1987). These authors found the tunica propria continuing over the terminal filament and the flattened cells of the terminal filament having numerous microtubules and less of ribosomes.

Telfer (1975) observed that the question of whether both the oogonial and follicular cells arise from a common stem cell population or from the terminal filament itself that connects the germarial apex to the body wall, still remain unresolved. In R. marginatus the noncellular tunica propria remains extremely thick at the apical region of each ovariole even in the case of newly emerged insects (PL.IX:4). This tunica propria continues as a sheath enveloping the terminal filament and it is not clear whether a septum exists and the terminal filament is cellular.

The most discussed region of the insect ovariole is the region that lies immediately behind the terminal filament, either delimited by a transverse septum or not. This region, originally known as the germarium, is usually described as tropharium. King and Buning (1985) considered that the transverse septum that isolates the terminal filament from the somatic cells of a well developed inner sheath of the tropharium, is the continuation of
the tunica propria which, according to Schreiner (1977) and Huebner (1984), is a product of the inner sheath cells. Bonhag (1958) considered it to be the product of the somatic tissue comprising of the inner sheath cell, prefollicular tissue and follicular tissue. King and Buning (1985) further recognised in each ovariole two regions namely the tropharium or the terminal chamber housing all nurse cells as well as the resting oocytes and the vitellarium in which the growing oocytes are found arranged in a single file in the order of increasing volume. In Dysdercus intermedius, King and Buning (1985) further arbitrarily divided the tropharium into three distinct zones, the first two zones together representing the end chamber of Davis (1956) and the third zone representing the real tropharium.

According to Davis (1956) the end chamber is the more extensive one in which the trophocytes are arranged around an a-cellular core, corresponding to the nutritive core from which the nutritive cords take their origin and the tropharium consisting of the trophocytes of the posterior end of the end chamber itself. Davis (1956) further identified certain undifferentiated nurse cells at the apex of the end chamber representing first zone of Bonhag (1955 a and b) and according to Davis it was a special feature found in bedbugs in comparison with the descriptions given for the germarium by Schrader and Leuchtenberger (1952) and Bonhag and Wick (1953).

Based on the nuclear size, representing the stages in the differentiation of a functional trophic tissue, Bonhag (1955a) in
O. fasciatus recognised the trophic tissue to be composed of three distinct zones. The first zone was named as zone of mitotic activity recognised as the apical zone of the tropharium lying immediately behind the transverse septum and each cell having been separated by its own cell membrane and the nuclei relatively large and spherical. The posterior border of this zone was demarcated by several rows of spherical cells which he called "arrested cells". The second zone that lies behind these arrested cells have been found to have lost their cell boundaries and their nuclei merge with the arrested cells to form a cluster of adnate nuclei. The third zone, that constitutes two third of the trophocyte tissue, has the nuclei arranged in small aggregates round the periphery, leaving a central cylinder of cytoplasm called the trophic core. The nuclei of this third zone are known to be approximately eight times larger than those of the first zone. Bonhag (1955a) further maintained that the increase in the size of the nuclei and nucleoli of this zone was due to the formation of adnate nuclei of individual aggregate and he (Bonhag 1955b) further confirmed that the pseudophilic lipids have been contributed to the oocyte, initially from the apical trophic tissue.

In D. fasciatus, Brunt (1971) recognised four zones in the tropharium. He recognised two zones in the second zone of Bonhag (1955a) and according to him mitotic activity occurs in this second zone and in the third zone the cells by fusion become binucleate. In R. prolixus, Huebner and Anderson (1972a and b) described the cytoarchitecture and development of trophic chamber
and defined the tropharium as a lanceolate structure at the apex of the ovariole having a central area called the trophic core that sends cytoplasmic projections to the periphery that harbour trophocyte nuclei and other organelles.

King and Buning (1985) described the tropharium as a terminal chamber that houses all nurse cells as well as the resting oocytes and according to them the vitellarium is demarcated by the growing oocytes that are arranged in a single file. Mitotic division and binucleate cells characterise the apical zone of tropharium (Bonhag 1955a, Davis 1956, Brunt 1971). Davis (1956) identified symbiotes in the end chamber that are transmitted to the yolk of the developing eggs and such symbiotes were identified earlier as DNA.

Ramamurthy (1970) after having recognised four zones in the germarium in Lygaeidae considered a zone of prefollicular tissue as the fourth zone. According to Buning (1979c) and King and Buning (1985) in a telotrophic ovariole the prefollicular epithelium either develops late in the larval life or soon after final moult. Buning (1979a, b and c and 1980) also found that the prefollicular tissue descends from the tunica propria in the telotrophic ovarioles of Megaloptera and Brunt (1971) traced the origin of prefollicular tissue from a thin layer of interstitial cells that correspond to the somatic mesodermal cells arranged at the base of the end chamber. This thin layer of interstitial cells that are arranged at the base of the terminal chamber are further known to separate
the nurse cells from the oocytes and more basally generating the prefollicular tissue by mitosis (Huebner 1984).

The nuclei of the cells of prefollicular tissue are also known to be diploid, similar to the interstitial cells and they in several layers envelop young oocytes (King and Buning, 1985). Further development of follicular epithelium involves condensation of prefollicular layers around the developing oocyte during previtellogenic phase. From this point onward, mitosis is known to be restricted to the inner follicular region alone, while the nuclei of the cells of the lateral zone of the follicle increases in size.

The follicle cells while incorporating DNA become polyploid and according to Mays (1972), Koeppe et al. (1980), La Pointe et al. (1985) and Dittmann and Maier (1987) polyploidisation is an important step in the differentiation of follicular epithelium from the prefollicular tissue. The prefollicular tissue has been described by King and Buning (1985) to be composed of spindle-shaped cells having one or two nucleoli and closely applied to tunica propria and oriented at right angles to the longitudinal axis of the ovariole.

A close assessment of the tropharium of *R. marginatus* clearly corroborates the end chamber theory advanced by Davis (1956) because of the presence of the distinct epithelial septum, that separates the three zones of the germarium from the prefollicular tissue. This cellular septum, formed by columnar
cells, is a striking feature not recognised by earlier workers in any of the heteropteran insect studied. Further, this septum is not a permanent one since in more advanced ovarioles of a mature insect, such a septum is found wanting. It is also clear that the trophic core differentiates in front of the septum and as the trophic core increases in its extent, the septum disappears. It is also clear that in a senescent insect though the oocytes after having arranged in a single file, fail to proceed to vitellogenic phase. The tropharium and the trophic core continue to persist as a massive structure, the septum having been completely lost. Thus it is evident that the septum that separates the prefollicular tissue from the tropharium represents the initial stage of organisation of the vitellarium and germarium. It is behind the prefollicular tissue the oogonia begin to differentiate. The origin of prefollicular tissue as a primordial tissue that differentiates into germarium and vitellarium has been discussed by several workers (Buning 1979c, 1980, Brunt 1971, Huebner 1984, Koepp et al. 1985, King and Buning 1985). In the present observation in R. marginatus it does not contribute to the differentiation of the tropharium but contribute to the formation of follicular epithelium by migrating, subsequent to the arrangement of the oocytes in a single file. There is no doubt that these spindle shaped small cells have their origin at the time of organisation of germarium itself. In this act, the occurrence of the septum is of great significance.
The organisation and cellular interaction in a nurse cell-oocyte syncytium have been reviewed in the context of providing a comprehensive account on the development and physiology of the so-called oocyte syncytium (Telfer 1975 and Telfer et al. 1981). According to Lutz and Huebner (1980 and 1981), Huebner and Anderson (1970 and 1972a, b & c) and Huebner et al. (1980) the structural basis of this syncytium is offered by the formation of intercellular bridges between the stem cytoblasts and stem cytocytes. The development and maintenance of such a nurse cell-oocyte syncytium has been considered crucial for the ovarian development and function during pre-vitellogenic and vitellogenic phases. The timing of the cellular differentiation in a telotrophic ovariole and the association of ovarioles with one another by intercellular bridge system are regarded as steps of vital importance in the development and structural organisation of nurse cell-oocyte syncytium (Huebner and Anderson 1972a, b & c and Lutz and Huebner 1980 and 1981). The resulting trophic core is the unique feature of the telotrophic ovariole of Hemiptera in which the trophic core mediates nurse cell-oocyte interaction and undergo structural reorganisation, during larva-adult ovarian transformation (Lutz and Huebner 1981). Accordingly, Huebner (1981a and b) maintained that the apex of the adult tropharium consists of discrete cells that do not have syncytial association with the rest of the tropharium and such apical cell represents the mitotic population of the undifferentiating cells which are capable of fusing with the syncytical tropharium that replenishes the nuclear degeneration taking place in the zone three of the tropharium.
In *Dysdercus* Dittmann *et al.* (1984) considered the prefollicular tissue as the site of repeated mitotic division, as reported earlier by Bonhag (1955a), Masner (1968) and Mays (1972) and the binucleate cells are restricted to the vitellogenic follicles, the condition that necessitates synthesis of maximum quantity of DNA by these cells. The DNA content reaches the maximum in the follicle cells of the post vitellogenic oocytes and before chorogenesis, the DNA content of each binucleate cell reaches the maximum and remains twice as high as the mononucleate cells (Dittmann *et al.* 1984). It is on these criteria, that the ovarioles of insects are classified into panoistic and meroistic types, the latter embodies the telotrophic ovarioles of Heteroptera.

Literature pertaining to the differentiation of oocytes in Heteroptera, circumscribes *O. fasciatus* (Bonhag and Wick 1953, Bonhag 1955a and b and 1958 and Johansson 1958), *D. fasciatus* (Brunt 1971) and *R. prolixus* (Huebner and Anderson 1970). The fundamental criterion for the identification of a telotrophic ovariole is the clustering of the cells of the tropharium far away from the developing oocyte and the distension of the nutritive cord of the respective oocyte as it moves farther from the tropharium, consequent to the linear arrangement of the oocytes towards differentiation of the vitellarium.

Active transport of materials to the nutritive cord from the tropharium of a growing oocyte is known to be brought about by a system of microtubules that are arranged in bundles parallel to one another (Huebner and Anderson 1970, MacGregor and Stebbings

When such tubules are absent in a telotrophic ovariole, Buning (1972, 1979b, c and 1980) Dittmann et al. (1981) and Huebner (1984) suggested that transport of materials is brought about by movement of charged molecules, according to the differences in the potential that prevail in the tropharium and the previtellogenic growing oocytes. Huebner (1984) has further suggested that active transport of materials from the tropharium to the oocyte could be brought about by peristalsis caused by the musculature of the epithelial sheath that surrounds the ovarioles. In the present observation, the peritoneal sheath that surrounds the tunica propria lining the epithelium, has a thin fibre lining the longitudinal muscle and the tunica propria itself is known to bring about certain contractile movements. Therefore it is probable that movement of material is brought about by peristalsis in R. marginatus also, as suggested by Huebner (1984).

A number of workers have discussed at length the differentiation, growth and maturation of oocytes and yet there is ample scope for research on the mechanism of differentiation of vitellarium from the tropharium and subsequent course of events that follow till the oocyte has completed choriogenesis and the egg ovulated, followed by corpus luteum formation and final disintegration of follicular epithelium itself. Bonhag and Wick. (1953), Bonhag (1955a), Brunt (1971), Huebner and Anderson (1972b), Schreiner (1977) and Huebner (1984) have maintained that differentiation of oocytes from the prefollicular syncytium occurs
in the similar way as the differentiation of tropharium. In a
generalised insect, Telfer (1975) recognised the population of
oogonia, close to the apex of the tropharium undergoing mitosis
and such a population was considered to be the progeny of the
oogonial stem cells.

As the development progresses such stem cells are
displaced towards the base of the germarium and as they are in
the process of displacement, mitosis is terminated and first meiotic
phase appears. A second population of these cells, then arise
by mitotic division and become prefollicular tissue. It
subsequently generates cells, also by mitosis, to become the cells
of the follicular epithelium. Thus, it is clear that according to
Telfer (1975), all cells of the follicle originate in the germarium.
This suggestion leads to the conclusion that the prefollicular tissue
consists of an actively dividing population of cells, representing
the third zone of germarium which Ramamurthy (1968), called as
aggregation of oocytes.

Bonhag and Wick (1953), Bonhag (1955a and b), Johansson
(1958) and King and Buning (1985), regarded this third zone as
the most extensive zone containing the nutritive core, surrounded
by peripheral aggregates of trophocytes having polytene
chromosomes. In the present observation, in R. marginatus, the
prefollicular tissue distinctly lies behind the epithelial septum
and immediately posterior to this tissue the oocytes differentiate
(PL.X:7). Thus the importance of this septum in demarcating the
germarium from vitellarium cannot be underestimated. Earlier
workers have not recognised such a septum.
After having been arranged in a linear fashion and the migration of the cells of the prefollicular tissue surrounding the developing oocyte, the subsequent stages in the development could be clearly defined as the previtellogenic, vitellogenic, post vitellogenic and choriogenic stages. Bonhag (1955b) recognised the age of the oocytes on the basis of the stages of development of their follicular epithelium. Accordingly, he recognised 4 distinct stages of the oocytes in the previtellogenic stage itself at the anterior end of the vitellarium and behind this previtellogenic phase he further recognised four different stages in the order of maturation, beginning from the basal oocyte to the zone of oocyte differentiation. He called them as alpha(α), beta(β), gamma(γ), and delta(δ) oocytes. The alpha oocytes are recognised by their binucleate follicular epithelium and it represents the oldest oocyte that occurs at the posterior region of the vitellarium. The beta oocytes are recognised by both mononucleate and binucleate cells of the follicular epithelium and number of cells in the process of becoming binucleate cells. The gamma oocytes are recognised by the largest number of mononucleate cells with a few binucleate cells in between. The delta oocytes are the most recently oriented oocytes in single file, representing the anterior end of the vitellarium and forming the junction of the germarium and vitellarium. They are also reported to be surrounded by prefollicular tissue. A similar criteria of identification has also been followed by Johansson (1958) in the vitellarium of O. fasciatus but at the same time he has stated that "germarium contained the apical trophic tissue, young oocytes and prefollicular tissue".
By this conclusion he has included young oocytes as well as the prefollicular tissue under germarium.

In *D. fasciatus*, Brunt (1971) recognised seven stages. The first stage is identified as the oocytes having gained the linear arrangement, and the last stage represents the basal oocyte that has completed choriogenesis. According to him, the binucleate condition of the follicular epithelium, marking the vitellogenic phase, represents the fifth stage, corresponding to the oldest oocyte (alpha oocyte) recognised by Bonhag (1955b) at the posterior end of the vitellarium. This otherwise means that the alpha oocyte is the oocyte of the vitellogenic phase behind which the oocytes of the post vitellogenic phase are arranged.

The oocytes that have entered the post vitellogenic phase have their follicular epithelium increasingly becoming narrower and the cells correspond to those of a pavement epithelium. Brunt (1971) had recognised two such stages, the basal oocyte, representing the seventh stage and the penultimate oocyte, representing the sixth stage. It is also clearly stated by Bonhag (1955b) that the number of follicles that develop in an ovariole before the oldest oocyte is discharged is variable, although the most frequent number is eight.

In *D. fasciatus* Schreiner (1977) recognised eight stages, the first three stages representing the previtellogenic stage and the last two stages, having ceased to synthesise yolk, is the post vitellogenic phase. According to him the first stage represents
the resting oocyte, positioned very close to the basal trophocytes, the second stage represents the youngest growing oocyte lying side by side and the third stage represents the oocyte in the previtellogenic phase, being arranged in a single file. Behind this third stage the oocytes are reported to be engaged in vitellogenesis and represent the vitellogenic stage. Thus the first three stages of Schreiner (1977) together represent the first stage of Bonhag (1955b), Johansson (1958) and Brunt (1971).

In the present observation in *R. marginatus* the delineation of various stages of oocytes, as reported by Schreiner (1977), is found to be more applicable. This is especially confirmed in the context of the present investigation in which the septum separating the vitellarium from the germarium is clearly identified. The previtellogenic phase is distinctly marked by three stages, the third stage being identified by the linear arrangement of the oocytes and at this stage the more apical oocyte as well as one or two oocytes that follow have not yet received their full compliment of cells from the prefollicular tissue, in the organisation of the follicular epithelium. It is only two or three oocytes behind these, will receive the full compliment of the follicular epithelium and the cells being arranged transversely in a single row, the nuclei preparing to enlarge, and the cells here and there showing binucleate condition. These characters mark the first oocyte of the vitellogenic phase but still retaining the nutritive cord running along the periphery of the oocytes that lie in front, to reach the nutritive core. Behind this oocyte there
are one or two oocytes that have elongated considerably in the longitudinal axis and that have severed their connection with the nutritive core by the formation of the basal epithelial plug as well as the opercular apparatus at the cephalic end of the succeeding and preceding oocytes by the arrangement of the epithelial cells in two transverse rows, the first row being the anterior row that forms the basal epithelial plug and the posterior forms the cephalic end. It is after this the oocyte reaches the status of the vitellogenic phase. Therefore, in this description, this stage should represent the fifth stage of Schreiner (1977).

The still posterior oocytes that have completed vitellogenesis and started secreting the vitelline membrane presenting the post vitellogenic phase should be regarded as the sixth stage, characterised by an abrupt termination of vitellogenesis by the switch over of the function of the follicular epithelium to secrete vitelline membrane. The next stage that is, normally the basal oocyte represents the choriogenic phase, in which the follicular epithelium abruptly stops secreting the vitelline membrane and starts to secrete the chorion as well as the opercular apparatus. This should in fact represent the alpha stage of Bonhag (1955b) and Johansson (1958). This in fact represents the eighth stage of Schreiner (1977). The next stage is the complete stoppage of all secretory activities of the follicular epithelium and the egg is ready to ovulate. This stage should represent the ninth stage of Schreiner (1977).
Therefore, in *R. marginatus* the criteria of identification of the various stages of development of oocytes in the vitellarium are closer to the criteria for identification put forth by Schreiner (1977). It is also important to realise that no new oocytes are added once the insect has already reached maturity and each ovariole at this stage comes to possess its full compliment of oocytes and they get arranged in a single file. As a result, the third and the fourth stages of oocytes increase in number, but not indefinitely, subject to the number of oocytes in the first two stages. It is also important to realise that the entry of the oocyte from the previtellogenic phase to the vitellogenic phase is conditioned by several factors such as nutritional, environmental, hormonal, etc. Accordingly, the previtellogenic phase may indefinitely be retained and the vitellogenic phase indefinitely postponed. Even the post-vitellogenic phase could be also indefinitely suspended, as in the case of a senescent insect, in which oosorption terminates all other activities.

In the stages of development of oocytes in the vitellarium, one of the most striking features that hardly escapes the attention of any reproductive biologist is the organisation and fate of the germinal vesicle during oocyte development. This has been closely followed by Bonhag and Wick (1953), Bonhag (1955a and b), Huebner and Anderson (1970, 1972a, b & c), Buning (1979a & b) and King and Buning (1985).

The movement of the germinal vesicle from a concentric to eccentric position heralding the onset of vitellogenesis is of
universal occurrence in the biology of the oocytes. Bonhag (1955a), Huebner and Anderson (1972b), Kozhanova and Gruzova (1975) and King and Buning (1985) have followed this movement in greater detail, focusing their attention mainly on the movement of chromosomes of the nuclei undergoing meiosis. According to them, initially all the chromosomes remain diffused, while the nucleolus generates several similar bodies that also remain attached to the nuclear envelope.

Ray and Ramamurthy (1979), by their radioisotope tracer techniques, found that the germinal vesicle, during the early stage of oocyte growth, incorporates 3H uridine in the nucleiotide as well as in the karyosphere and that ceases in a later stage. Buning (1972) also demonstrated incorporation of 3H uridine in the germinal vesicle of telotrophic ovarioles. According to these authors the germinal vesicle is involved in RNA synthesis during previtellogenic phase. However, Ramamurthy (1963), Bier (1963), Vanderberg (1963) and Bier et al. (1967) in their earlier experiments did not find any supporting evidence to this phenomenon. In panoistic ovarioles Zalokar (1968) found continuous active synthesis of RNA by the germinal vesicle.

In the present observation, the germinal vesicle begins as a small concentrically placed body in the middle of the ooplasm in the oocyte of the first stage of the vitellarium. As the oocytes are arranged in single file, the germinal vesicle continues to be concentric but enormously increases in size, occupying almost one-fourth the area of the cell. As the oocytes enter the last stage of previtellogenic phase, the germinal vesicle, still maintaining
its size, the ooplasm having enormously increased in size begins to occupy different positions towards the periphery as well as cephalic and caudal ends. As it moves, certain darkly staining bodies of various sizes occur, representing the nucleolar material, as reported earlier by King and Buning (1985). These materials also are eccentrically placed on the germinal vesicle closely adhering to the membrane of the vesicle. As the follicular epithelial cells begin to increase in cell volume and become binucleate and the ooplasm gradually displaced by yolk granules as the oocyte progresses in the vitellogenic phase. As the ooplasm recedes, and yolk granules enmass, the germinal vesicle is not traceable. This phenomenon, though universal, is not clearly understood, even by those workers who have used tracer technology to follow its course.

The biology of the tissue representing the tissue that intervenes the basal epithelial plug of the basal oocyte and head of the pedicel has not been clearly followed by those who have studied the phenomenon of ovulation in heteropterous insects. This tissue is reported here as the antepedicellar interstitial tissue whose biology has been traced in the present investigation right from the beginning of its formation to the close of its disintegration. This tissue makes its presence more obvious even earlier than the delineation of the vitellarium and the tropharium (PL IX:8,9). This tissue also has been described earlier in this discourse to have been connected with the peritoneal tissue all around and continues to project into the cup of the pedicellar
head. In front of its connection with the peritoneal sheath there is a space formed in between the peritoneal sheath and the basal epithelial plug. It is into this space, secretions from the antepedicellar interstitial tissue accumulate and as the insect advances in age this secretion that accumulates becomes more and more massive. It is also clear that this secretion accumulates around the basal epithelial plug. It is an acellular mass, the accumulation of which increasingly brings about a characteristic structure that offers certain degree of constriction to the lumen of the basal epithelial plug.

Davis (1956) in Cimex described a similar tissue at a similar position as "Corpus seminalis". Ramamurthy and Medhi (1970) in Cydnus indicus described a similar structure at a similar position as "bacterial chamber" and the same structure in Lygus species was named by Ramamurthy (1970) as "basal epithelial plug". Brunt (1971) however did not recognise a similar structure while describing the follicular epithelium in Dysdercus.

The antepedicellar interstitial tissue occupies a strategic position in the ovulation process since all the ovulated eggs have to pass through this. Davis (1964), while recording the corpus seminalis, described this structure as a development of the basal region of the follicular epithelium that differentiates anteriorly into the epithelial plug having a constriction inbetween. He also reported that this region enlarges considerably shortly before choriogenesis in order to receive large quantity of spermatozoa.
from the peripheral fluid filled space. He (Davis 1956 and 1964) also has described the corpus seminalis as a part of the basal epithelial plug having a central core of nuclei surrounded by a fluid filled space. These nuclei were described as spherical initially and become irregular and disintegrate later.

The same type of tissue, with similar cytological details and fate, has been described by Davis (1964) at the caudal end of the penultimate oocytes also. But Ramamurthy (1964) and Ramamurthy and Medhi (1970), found this tissue as a bacterial chamber to store and transmit bacteria to the developing oocyte, whereas Davis (1956 and 1964) described it as a sperm repository. In _R. marginatus_ though bacterial clusters are found in various regions associated with the reproductive system, the antepedicellar interstitial tissue does not offer any suggestion to assign a sperm storage function. But it is distinctly a tissue that shows considerable growth and secretory activity, synchronising with the oocyte's functional organization and the secretory material oozes out continuously enhancing the mass of material that accumulates around this mass corresponding to the tunica propria. According to Snodgrass (1935) and Ma and Ramaswamy (1987), the tunica propria is a non cellular matrix enveloping the entire ovariole as well as the terminal filament. This non cellular tunica propria has been conventionally considered as a matrix functioning as elastic fibrillar membrane that aids in forcing the oocyte out (Bacetti 1955 and Bonhag and Arnold 1961).
Several workers like Ramamurthy and Medhi (1970), maintain that the tunica propria synonymises the basement membrane of the follicular epithelium. Ma and Ramaswamy (1987), further consider the tunica propria of each ovariole as a mark of demarcation of boundaries between ovariole in the absence of a sheath. Huebner (1984), after having studied the tunica propria of individual ovarioles of the hemipteran species, concluded that each ovariole is lined by an outer sheath and an inner envelope, all ovarioles being collectively enveloped by an ovariolar sheath.

Schreiner (1977) observed that the tunica propria is formed by an inner envelope consisting of pleiomorphic cells constituting a mass of inner sheath cells whose cytoplasmic extensions reach underneath the tunica propria performing nutritive functions. Such extensions are named as peripheral trophocytes by Schreiner (1977). However, Huebner (1984) in *R. prolixus* recognised such inner sheath cells and attributed the function of mechanical support as well as serving the function of a physiological barrier or playing role of nuclei in cell differentiation. Further, Buning (1979 a,b & c and 1980) traced the follicular tissue descending from tunica propria.

In *R. prolixus*, the mass of structureless acellular material that accumulates around the base of basal epithelial plug, as the secretory product of the antepedicellar interstitial tissue, is unequivocally established. It is clear that this tissue under no circumstance, be regarded as an equivalent of the corpus luteum that normally occurs at this region. It is also clear that as the antepedicellar interstitial tissue increases in its secretory activity
and in its volume and it forms a septum that (PL.IX:8) remains as a lid of the mouth of the pedicel. This septum ruptures in the middle due to pressure exerted by the egg that is being ovulated (PL.XII:8,9).

It is evident that the mass of secretion that accumulates forms a sort of tough mass around the posterior area of the basal epithelial plug, constricting the lumen that allows the passage of egg. At the time of ovulation of the penultimate oocyte, the pressure makes the passage through basal epithelial plug reappear and the material, as an analogue of sphincter muscle, ejects the egg forcibly into the head of the pedicel through the ruptured septum of the antepedicellar interstitial tissue (PL.XII:8, 9). This interpretation of the mechanism of ovulation appears to be a logical conclusion based on histological studies. Thus the antepedicellar interstitial tissue plays a significant role in the biology of the ovariole of _R. marginatus._

Even after Singh (1958) paved the way for an active pursuit in the study of the fate of the follicular epithelium after ovulation, progress on this very important aspect of post ovulation physiology has hardly been registered. The corpus luteum that signifies the fate of the follicular epithelium after ovulation, has been observed by Wigglesworth (1936) in _R. prolixus_ who described it as a tissue that undergoes pycnosis, necrosis, resorption and disintegration.
In *Schistocerca gregaria*, Roonwal (1947) first described the corpus luteum as a structure of an orange red mass and later Bonhag and Wick (1953) in *O. fasciatus* described this as an unpigmented structure that discharges its contents before shrinking. Huebner and Davey (1973), in *R. prolixus*, suspected the release of a hormone by the corpora lutea but failed to demonstrate the same. Instead, they suggested that the corpora lutea release certain material that alters the permeability of the follicular epithelium of the penultimate oocyte.

The fact that the follicular epithelium of an empty follicle, while undergoing the process of nuclear pycnosis, cellular necrosis and terminal disintegration, does release certain eosinophilic material, has been unequivocally established. On the basis of the formation and fate of the corpus luteum it is customarily recognised as either simple or compound types. However, in actual practice, it is often found to be difficult to distinguish one from the other. The simple corpus luteum is recognised by the fact that the remnants of the corpus luteum of each follicle are retained throughout, whereas in a compound corpus luteum such remnants of the corpora lutea accumulate at the base of each ovariole at the head of the pedicel. In *R. marginatus*, as described earlier, such a compound or multiple corpora lutea are found in between the antepedicellar interstitial tissue that lies immediately behind, both of them undergoing disintegration process. This condition may tempt one to recognise the antepedicellar interstitial tissue itself
as part of the corpora lutea and this leads Ramamurthy (1969 a and b and 1970) to conclude that the basal epithelial plug and corpus luteum are synonyms and on this concept he defined the corpus luteum as a tissue made up of close fitting mass of cells proliferated from both terminal vitellarian follicle and the upper end of the pedicel. He further stated that presence of the close fitting cellular plug necessitates its repeated dissolution and reformation at the time of ovulation of each ripe egg. This concept of corpus luteum questions the very membership of the follicular epithelium of the empty follicle in the contribution to the corpus luteum formation.

Lusis (1963) described a tubular, transparent corpus luteum as an equivalent of white follicle and according to him the yellow body, that synonymises the corpus luteum, appears in every ovariole after consecutive ovulations are accomplished and certain materials are extruded and deposited at the base of the corpus luteum. In the case of R. marginatus, as the insect grows in age towards senescence the pigmentation of this yellow body is correspondingly intensified.

One of the universal phenomena met with in the biology of the ovarioles is observed in the senescent as well as defective insects, whose neuroendocrinological functioning has been impaired. This phenomenon has been commonly known as oosorption as well as resorption. In a senescent insect it is more commonly found that while the corpora lutea of each ovariole undergo various stages of disintegration and resorption, the oocytes that lie in front undergo various stages of oosorption. While in the former, the materials of the disintegrated follicular epithelium of an ovulated
follicle are actively resorbed, in the latter the follicular epithelium itself disintegrates even though the oocyte has advanced in the vitellogenic phase following the pattern of the process of disintegration of corpus luteum, beginning with pycnosis of the nuclei followed by necrosis of the cells and concluded by disintegration. An oocyte undergoing oosorption has the ooplasm considerably reduced and vacuolated. Interestingly while the process of oosorption is in progress, the tropharium as well as the first two or three stages of oocytes of the vitellarium maintain a steady state.

Oosorption of a degenerating oocyte and resorption of a disintegrating corpus luteum, according to Ahrens (1935) and Singh (1958), are similar because in both cases disintegration occurs in a similar way and the products of such a process are resorbed in the similar way. Lusis (1963) and Bell and Bohm (1975) were of the view that the materials that accumulate in both cases of disintegration are of lipid products, that impart certain pigmentation. Excessive production of such lipid materials with higher concentration of carotene has been considered to be the reason for the yellow colouration of any segment of the ovariole. In a normal white follicle, the lipid metabolism ceases in the epithelial cells but after ovulation, when the follicle cells resume lipid metabolism, yellow colouration appears within two to three days and this process imparts the corpus luteum the yellow colouration and therefore the corpus luteum is said to be yellow body.
Bell and Bohm (1975) considered oosorption as a specific type of reproductive strategy in insects by which oocytes degenerate, instead of being laid as eggs, in response to behavioural, ecological or physiological conditions. When such influences are removed, oosorption may abruptly cease and the ovariole will resume its normal reproductive process. It is considered to be a regulatory mechanism in insect reproduction.

In insects, several factors such as starvation (Johansson 1955, 1958 and 1964; Highnam and Lusis 1962; King 1963; Davis 1964 and Bell 1971); social pressure (Meichner 1965; Barth and Bell 1970 and Bell and Bohm 1975); ovipositional blockage (Johansson 1958, King 1963, King and Richard 1968); adverse conditions of environment such as diapause and aestivation (Singh 1958, DeWilde 1964); parasitism (Phipps 1949, Detinova 1962 and Gordon et al. 1973); ageing (Johansson 1958, DeWilde 1964 and King and Richards 1968); Chemosterilants (Smittle et al. 1966 and Vingelli and Ross 1967) etc. are known to promote oosorption.

In the present observation oosorption occurs in the similar way as in corpus luteum. But in oosorption almost all oocytes of the same stage of development in all the ovarioles of an ovary undergo oosorption and invariably oosorption is noticed in those follicles in which the follicular epithelium has been well organised prior to vitellogenesis. It is also found that in all the oocytes where oosorption occurs, the ooplasm is almost completely resorbed while the follicular epithelium undergoes drastic degenerative
process, almost filling the entire oocyte. Occurrence of darkly staining globules of varying sizes denoting products of disintegration characterise an oocyte undergoing oosorption (PL.XII:1,2 & 3). It is found extensively in degenerating follicles, when the insect has reached the stage of senescence. Interestingly, when the oocytes at the vitellogenic stage undergo oosorption, the other, more young oocytes of the previtellogenic as well as the germarium remain almost unaffected. This suggests that oosorption is the effect of impaired neuroendocrine functioning.

**Pedicel**

Several insect reproductive biologists considered the pedicel as the fourth segment of the ovariole. For that reason this invariably was treated along with the description of the other three segments namely, terminal filament, germarium and vitellarium. Differences in the secretory activity of the epithelium of the pedicel in virgin and mated females have been reported in *R. prolixus* by Huebner and Davey (1973). According to these authors the pedicels, after having received the ovulated egg, secrete and release the factor called antigonadotropin that suppresses egg reproduction. Earlier, Davey and Webster (1967) found that the source of an antigonadotropin was an abdominal neurosecretory organ. In the present observation in *R. marginatus*, the secretory activity of the pedicellar head appears to be more elaborate than the rest of the region, as judged by the nature of the epithelium. The secretory activity is more evident as the insect reaches sexual maturity and becomes receptive to males. It is also found that when the spermathecae are full of sperms, occurrence of bacterial
clusters along the walls of the pedicel, as well as secretory activity of the columnar cells are indications of physiological activity (PL.XIV:1).

In insects in which fertilisation occurs before chorion formation, as reported in Cimex (Davis 1956), Anthocorids (Southwood 1956) and Tingis buddleiae (Livingstone 1967), the pedicels are known to convey sperms to the developing oocytes. In Tingids, Livingstone (1967), recorded a permanent expansion in the middle of the pedicel that receives sperms following copulation and he named such expansion of pedicel as "accessory receptaculum seminis". Similar expansion was also reported by Eguagie (1973) in Tingis ampliata and he regarded this as an annual phenomenon, coinciding with the reproductive cycle, since this European species is known to be univoltine. In R. marginatus however such a differentiation is not found, though Tingidae is said to be closely related to Reduviidae (Pendergrast 1957 and Cobben 1968a).

Oviducts

The lateral oviducts that continue from the calyx in which all pedicels meet, as well as the pedicels, are known to vary in length depending on the length of the egg. The division of the lateral oviduct into anterior and posterior segments, the former without a chitinous intima and the latter with a chitinous intima, is also a common information characterising the nature of origin of the lateral oviduct. Occurrence of bacterial chambers mainly
in the anterior segment of the lateral oviduct is a feature reported by Ramamurthy (1969b and c) and Ramamurthy and Medhi (1970) in pentatomids. In Tingidae, Carayon (1946) and Livingstone (1967) described dilation of the lateral oviduct at the junction of the anterior and posterior segments. Such a dilation has been regarded as a permanent feature and Livingstone (1967) named it as "principal receptaculum seminis".

The lateral oviducts are known to possess stronger longitudinal muscles that invest over the inner circular muscles, are known to develop stronger in gravid females in which the eggs are found irregularly disposed as in Riptortus linearis and other pentatomids (Ramamurthy 1969a, b and c). Such muscles are known to bring about peristalsis in the lateral oviduct that is longitudinally folded and the cells are distinctly columnar, very much similar to those of the common oviduct. The musculature is well developed. The lateral oviduct in insects invariably carries eggs in almost all gravid females examined.

**Bursa**

The bursa copulatrix assumes enormous importance in insects that transmit their sperms through the production of spermatophores. It is an expanded part of the common oviduct and in Reduviidae in which sperm transmission occurs through spermatophores, this part of the common oviduct expands considerably, almost abruptly, as the bursa copulatrix into which the spermathecae open. Pendergrast (1957) observed that when a spermatheca is absent,
as in Miridae, Nabidae, and Velocipodidae, the vagina is modified
to form a chamber called bursa copulatrix which is lined by thick
cuticular intima. In *R. marginatus* the lining of the copulatrix
into which the spermatophore is lodged, is lined with denticulate
chitinous intima.

In Reduviidae it is also known that, successful copulation
is always indicated by the rejection of the empty spermatophore
capsule and the time taken for the reception and emptying,
accomplished by the bursa copulatrix, varies considerably (Ambrose
and Livingstone 1985a). Thus the bursa systematically regulates
the suction of the sperms through the pores of the spermatophore
into the spermathecae and also reject the empty spermatophore
capsule after the suction of the sperms into the spermathecae is
completed, without any lapse of time. The bursa copulatrix also
offers the mechanism to discharge the sperms thus stored in the
spermathecae at the time they are required for release to fertilise
the eggs that descend down into the bursa. In this connection
it is pertinent to report that the openings of the spermathecae,
the openings of the spermatophore capsule and the openings of the
micropyles are all predisposed for effective operation. The two
openings of the spermatophore come into close juxtaposition with
the two openings of the spermathecae on the roof of the bursa,
as the former is lodged inside the bursa during copulation.
Similarly as the egg descends into the bursa, the external openings
of the inner periopercular space present at the point of fusion
of the deflected strip of the chorionic collar with the opercular
crest lie in close juxtaposition with the openings of the spermathecae and get the sperm groove at the chorionic rim filled with sperms. The micropyles that open wide into the sperm groove collect the sperms. This mechanism of filling and emptying of the spermathecae requires precise manoeuvring movements on the part of the bursa and from this point of view the role of the bursa in the biology of reproduction in *R. marginatus* is of great significance. Since the proximal segment of the spermathecal duct is fully embedded within the musculature of the wall of the bursa, the regulatory role of the bursal wall in the reception and discharge of the sperms is highly specialised. This mechanism, as explained here has not been suggested by any of the earlier workers.

In this connection, the size and architecture of the spermatophore capsule and the shape and capacity of the bursa copulatrix require great deal of precision.

The spermatophore capsule moulded inside the spermatophore pouch (SPP) as described herein, (PL.I:8,9,10 & 11), is the basidorsal pouch of the endotheca that lies dorsal to the endotheca with its mouth closely juxtaposed to the opening of the ductus ejaculatorius. This pouch is incompletely divided into two halves and it provides the mould for the casting of the spermatophore capsule into two halves, as described here (PL.1:11). It is also clear that the external opening of each half (OH) is slightly lifted and directed upward and this curvature enables the opening to closely approximate the position of the spermathecal opening on the roof of the bursa when spermatophore is lodged inside the
Davey (1959), while describing the method of spermatophore production in *R. prolixus* coined the term "spermatophore sac" for the first time. It was described as a much folded membranous sac which is composed of both aedeagus and endophallus. Such a sac was described as having two layers of cuticle bounding a blood space, the inner wall was termed as endophallus and outer wall as aedeagus. The spermatophore sac was described as being composed of aedeagus on the outer side and endophallus lining the lumen. It is also described as having three sclerotised plates called "birgae", consisting of a spade like terminal plate and a pair of longer lateral plates. The spermatophore has been described by Davey (1959) as to have been formed within the spermatophore sac. The opening of this sac through which the spermatophore is finally released, is named as 'Phalotremem' meaning gonopore, corresponding to the secondary gonopore of Lent and Jurberg (1967, 1972 and 1984). Davey (1959) further reported that folds of the spermatophore sac that project into the lumen were responsible for the formation of the slit which contains the sperms. This aspect was ignored by Davis (1966) and Lent and Jurberg (1984), while describing the aedeagus of Reduviidae.

Ashlok (1957) named the pouch corresponding to the spermatophore pouch described here as 'vesica' in Lygaeidae while Davey (1959) considered the entire endosoma as spermatophore sac and the ventral wall of the cup of the phallotheca was described by him as vesica. Thus there is great deal of misrepresentation of structures associated with spermatophore production.
The mechanism of release of spermatophore from the spermathecal pouch in which it is moulded is as follows. When the intromittent organ (ITO) consisting largely of the endotheca (endosoma) is pushed into the vagina with the active participation of the parameres and pygophore spine (PYS) as well as the basal plate (BP) (PL.I:8,9) and the dorsal phallic sclerite, distension of the endotheca brings about the tilting of the spermathecal pouch at 180° so that the opening of the spermatophore pouch comes in confluent with the lumen of the endotheca. This tilting reverses the direction of the spermatophore so that its two openings come to be directed forward. When the spermatophore capsule is formed within the pouch that lies on the dorsal wall of the endotheca, these openings are formed, facing backwards in the direction of the ductus ejaculatorius. Now, by the tilting of the pouch by 180°, the two openings of the spermatophore come to lie in front facing the exterior and as the endotheca is pushed into the bursa further, the spermatophore also moves forward, probably through hydrocoelic pressure, and then reaches its destination with its two openings directed forward and turned upward. It is in this position with its two openings juxtaposed with two spermathecal openings on the roof of the bursa, that the spermatophore capsule is lodged inside the bursa. Thus in the biology of reproduction of *R. marginatus*, the biology of the spermatophore, the bursa and the spermathecae are closely interlinked.

Cobben (1978), in his studies on the evolutionary trends in Heteroptera, was tempted to exclude Reduviidae from the
Cimicomorpha for the sole reason that the members of Reduviidae produce spermatophores and possess corresponding structural features of intromittent organ for the production of spermatophore. He considered spermatophore production as a plesiomorphic condition, and suggested to erect a separate taxonomy for Reduviidae, to be known as Reduviiomorpha. In the present discussion the functional significance of production of such a spermatophore in a specialised pouch of the endotheca for the transfer of sperms in a special way is highlighted.

Accessory glands

There is a great deal of confusion in the assessment of female accessory glands in Heteroptera. The confusion is mainly due to the recognition of certain structures associated with the bursa copulatrix in different species. Very often the spermathecae are also mistaken for accessory glands and vice versa (Davis 1955 and 1956). This confusion was greatly aggravated by the introduction of the term pseudospermatheca by Carayon (1954) in heteropteran literature, in order to designate structures whose sperm storage function was not certified.

Wygodzinsky (1966) and Cobben and Wygodzinsky (1975) introduced several conflicting terminologies, enough to confuse a beginner in the pursuit of female accessory glands in Reduviidae. Kershaw (1909) recognised in *Sycanus croceovittatus* paired ectodermal glands associated with a common oviduct and named them as colleterial glands having a common duct opening dorsally into
the bursa at its posterior region. These same glands were later described by Scudder (1959) in *R. prolixus* as median spermathecal gland. Later, Davis (1955) homologised a spermathecal gland with the vermiform gland which he described as a sperm depository. The same gland was described earlier by Galliard (1935) as median tubular accessory gland opening dorsally into the genital chamber and functioning as a cement gland, secreting material to cement the eggs to the substratum.

In several aquatic Heteroptera, Larsen (1938) described certain accessory glands which were later homologised with the spermathecae by Davis (1955) in Miridae. Pendergrast (1957) described a single accessory gland in *Rhodnius* which was later compared with the median spermathecal gland by Scudder (1959). He maintained that occurrence of such median spermathecal gland was not common in Reduviidae and whenever it was found in some, it was present in paired condition.

Davis (1966) located the opening of such glands between the second valvulae and the styloids. Later Davis (1969) more correctly traced the exit of a large bilobed sac in the membrane between styloids and anus and named it as "subrectal glands" and he further considered it as repugnatorial gland having the function of scent production. Later, Cobben (1968a), Cobben and Wygodzinsky (1975) and Hinton (1981) and more recently George (1988b) confirmed the function of this pair of glands to produce egg cementing material called "spumaline". Glands of similar position,
but opening independently to the exterior without having any connection to the genital tract, have been described in *Oncopeltus fasciatus* as "paragenital glands" by Johansson (1958). A pair of yellowish accessory glands opening independently into the common oviduct has been further reported in a Harpactorine reduviid *Pisilus tipuliformis* by Louis and Kumar (1973). In another Harpactorine species *Margasus afzelli* these authors further described another elongated pink accessory gland.

Subrectal glands are reported to be absent in several genera of Harpactorinae (Davis 1969 and Cobben and Wygodzinsky 1975) as well as in most non harpactorine species (Davis 1969 and George 1988 a and b). Scudder (1959) in a species of Ectrichodiinae traced a pair of voluminous sacs lying on either side of the genital chamber and named them as pseudospermathecae. The same structures in another species of Ectrichodiinae were described by Haridass (1987) as lateral expansions of the bursal wall used for storing of numerous eggs prior to oviposition. But George (1988b) named the same enormously expanded structures as subrectal glands without confirming their functional role, since these insects do not oviposit in batches.

In all the species of Harpactorinae examined by George (1988 a and b), *Lophocepha lguerini* alone was found to possess an additional pair of glands opening into the bursa which was designated as "bursal glands". Such a bursal gland is reported by George (1988a) as being developed as a median gland in those species of the scrub Jungle and semiarid zones that deposit their
eggs individually, without smearing any cementing material. In *R. marginatus*, the pair of subrectal glands are clearly found to open just close to the opening of the vagina to the exterior and they have no connection with the rectum. They do not lie beneath the rectum but on either side of the rectum. Therefore, the name of the glands as subrectal glands would be better to "paragenital glands" as rightly named by Johansson (1964) in *O. fasciatus* and Gupta (1951) in *D. cingulatus*.

Haridass (1985a) named both bursal glands and subrectal glands as accessory glands without any distinction between both and it was George (1988 a and b) who recognised the difference between such accessory glands and after having studied these glands in more than sixty species of Reduviidae, she used the term bursal gland for the median accessory gland found in nonharpactorine reduviids and subrectal glands for the paired accessory glands found in all species of Harpactorinae and Ectrichodiinae.

Regarding the histology and secretion of the subrectal glands there is no doubt that this gland is ectodermal. Histological details of this subrectal glands of this Reduviid *Arilus carinatus* has been detailed by Barth (1961). But none has given details regarding the secretory activity of the gland in different phases of reproduction, as well as the mechanism of discharge of spumaline from these glands at the time of oviposition. In the present observation it is clear that at the height of secretory
activity when the vitellogenesis is in progress, the cytoplasmic contents of the cells of the various folds of the glands increase considerably (PL.XV: 6,7,8) whereas during the immature stage and senescence the nuclei become small, the cells lose their identity and the entire gland appears as folds of chitin with nuclei studded on either side of the folds (PL.XV:5,9). In other specimens, as described earlier, the gland remains enormously swollen and filled with light brownish material, the spumaline. The occurrence of the muscles (PL.XV:3) at the short common duct of the glands clearly indicates that the opening is regulated and discharge of secretory materials is at will.

It is observed that the first material that is expressed at the genitalia at the onset of oviposition is the spurring of the spumaline. Subsequently after the extrusion of the first egg, the material is spurted out at intervals coinciding with the extrusion of each egg.

Thus it is clear that the subrectal gland should be appropriately called as paragenital gland that secretes an enormous amount of material when the insect has reached maturity and the material is discharged by the active participation of the musculature present at the junction of the two lobes. It is also clear that the material that oozes out is light brownish in colour and that it is the spumaline that facilitates the gluing of the individual eggs together as well as the eggs in batches. It is probable that this material has some deterrent that deters parasitoids from attacking the eggs. Not a single parasitoid has been raised in the laboratory.
from any of the large number of egg batches collected from the field and brought to the laboratory for culturing. Literature does not offer any information regarding the association of bacteria bearing nodules in this gland. In *R. marginatus* a distinct arborescent structure bearing nodules of bacteria has been described here but it is not clear whether these bacteria are also discharged along with the spumaline though clusters of bacteria, are also found attached to the folds of the gland. Further investigation is required to confirm the function of these bacteria.

There is nothing in the literature on the description of a highly branching gland associated with the bursa, as described here (PL.XV:1). It is distinctly found as a secretory arborescent gland that characterises secretory activity as the insect reaches sexual maturity (PL.XVI:6). Aciniform type of secretory units actively secrete homogeneous mildly eosinophilic material into the lumen (PL.XVI:8). But it is not clear about the manner of discharge of the material and also it is not clear whether this secretory material serves as a sex attractant. Further investigation is required to ascertain the biology of this gland. Since it is more like a chitinous arborescent gland like that of a subrectal gland but not having any connection with it, a tentative term tegumentary gland has been proposed here.

Spermatheca in Heteroptera is a highly controversial structure. Paired sacs functioning as sperm depository have been found to be structurally different from the conventionally known
spermatheca (Kullenberg 1947) and structure described as true spermatheca arising from the bursal wall is known as cement gland, instead of sperm depository (Davis 1955 and 1957). Sometimes a true spermatheca in Heteroptera is also recognised as a colleterial gland.

Snodgrass (1935) defined the typical spermatheca as a simple sac-like structure having a muscular wall and a slender duct. Most of the earlier workers were guided by this definition. While describing various structures of the bursa in several species of Heteroptera (Ludwig 1926; Hamilton 1931; Malouf 1933 and Larsen 1938), Snodgrass (1933) and Johannsen and Butt (1941) further emphasised that the true spermatheca opens into the genital tract at the dorsal wall of the region of the common oviduct called vagina that possesses ectodermal lining.

Pendergrast (1957), after having recognised this part of the vagina being enlarged, called it as bursa copulatrix. Earlier authors placed the genital opening anterior to the opening of the spermatheca, based on the concept that genital opening lies at the origin of the common oviduct formed by the union of the two lateral oviducts. This concept was later reaffirmed by Plout (1970) and Mastuda (1976).

In Reduviidae, Scudder (1959) identified a glandular organ on the genital chamber and named it as median spermathecal gland and Dupuis (1955) maintained that the receptaculum seminis, concerned with sperm storage, has changed its function as accessory
gland in Cimicomorpha and Reduviidae. Following this assumption of Dupuis (1955), Wygodzinsky (1966) and Cobben and Wygodzinsky (1975) in Emesinae described the vermiform gland as true spermatheca. Further, Larsen (1938), Carayon (1954), Davis (1955 and 1956) and Matsuda (1976) described a tubular gland in Reduviidae and homologised it with the spermatheca. The same tubular gland was regarded by Galliard (1935) in Triatoma and Pendergrast (1957) in Rhodnius as accessory gland.

To further complicate the existing confusion in the designation of the spermatheca and the accessory glands, the term "Pseudospermatheca" was introduced into heteropteran literature by Carayon (1954) by describing a pair of sperm receiving ectodermal organ and homologised them with true spermatheca of other insects. Subsequently, most heteropterists like Scudder (1959), Wygodzinsky (1966), Davis (1969), Louis and Kumar (1973), Cobben and Wygodzinsky (1975) and Matsuda (1976) followed the same terminology to describe a pair of diverticulae arising at the base of the common oviduct in Reduviidae. Subsequently, Davis (1969), after having studied the morphology of numerous species for his contribution on the phylogeny of harpactoroid complex, confirmed that a pseudospermatheca is absent in several members of Harpactorinae, whereas they are present in certain species. Carayon (1952a, b and c, 1953 a and b, 1954 and 1961), after having studied some Cimicidae, Anthocoridae and Nabidae suggested that in these families, in which haemocoelic insemination occurs, a pseudospermatheca is wanting and the spermathecae are modified into vermiform gland.
Absence of spermathecae has been reported in Vianaidinae, a subfamily of Tingidae (Darke and Davis, 1960) whereas in the same family Carayon (1954) described a pair of diverticula as extensions from the base of the lateral oviducts functioning as sperm receiving organs and named them as "Saccus seminalis" or sperm sac. The same structure was sketched by Drake and Davis (1960) on the lateral oviduct of another Cantacader sp. of Tinginae and called it as spermathecal organ. In Tingis ampliate, Eguagie (1973 and 1976) described a pair of spermathecae corresponding to the position of the "spermathecal organ" of Drake and Davis (1960) and 'Saccus seminalis' of Carayon (1954) and reported the presence of sperms in them. He has further described a median accessory gland from the vagina in addition to the paired spermathecae. Livingstone (1967) however, in Tingis buddleiae found no evidence of occurrence of a spermatheca and confirmed that the sperms are stored directly in the expansions of the lateral oviducts and pedicels, the expansions of the former was named as "principal sperm reservoir" and the expansion of the latter as "accessory sperm reservoir".

In Reduviidae spermathecae have been described in several species in different names. Pendergrast (1957) described a single spermatheca as an elongate narrow tube in Empicoris vagabundus, Emesinae and Scudder (1959) in another species of Emesinae, Ishnobaena species recognised a pair of bulbus spermathecae each having a short duct. Wygodzinsky (1966) described a similar pair of sub globular, apically ampullate structures as Pseudospermathecae.
in addition to a vermiform apically bifid structure arising from the ventral surface of the common oviduct, also storing sperms. This vermiform structure was later confirmed by Cobben and Wygodzinsky (1975) as pseudospermatheca.

As discussed earlier, the two openings of the spermathecae, each representing one of the spermathecae, are closely applied to the two openings of the spermatophore so that by the sucking action brought about by the muscles of the bursa, the sperms from each half of the spermatophore enter into each of the spermatheca. It is a special anatomical mechanism of sperm transmission.

Thus it is clear that the spermatheca has undergone a series of assessments. However, the description of paired spermathecae, each having a long duct that remains embedded inside the muscles of the wall of the bursa and opening dorsally close to one another into the lumen of the bursa as described here in *R. marginatus* clearly dispels the doubt regarding the term pseudospermatheca a misnomer.

Regarding the histology of the spermatheca in Heteroptera, contributions of various workers offer varying levels of information, making generalisation very problematic. Very rarely the reproductive and neuroendocrinological status of the insects are taken into consideration while describing the histomorphology and secretory activity of the spermatheca. Often, the descriptions are very sketchy and far fetched. For example, Malouf (1933) in *Nezara viridula* described a thick intima lining the spermatheca
and suggested that the secretion of the epithelium escapes outwards into the haemolymph through the thin peritoneal layer. A few years after, Bonhag and Wick (1953) in *O. fasciatus*, reported that intracellular ductules of the hypodermal gland cells penetrate through the intima and open into the cavity of the spermathecal bulb. Subsequently, Ramamurthy (1969a, b and c) and Ramamurthy and Medhi (1970), described two types of secretory cells surrounding the apical bulb, the first type consisting of a single layer of regularly arranged small epithelial cells lining the thick intima and the second type consisting of irregular mass of conspicuous large cells lying external to the first type of cells. Both types of cells are known to be derived from the hypodermal layer during immature stages and undergo specialisation as the insect reaches maturity. The large cells are externally lined by the peritoneal sheath and remain uninucleate with very few vacuoles in the cytoplasm. Later certain of these cells became binucleate, the nuclei being polyploid with coarsely granular chromatin and the cytoplasm highly vacuolated containing granules. The secretions by intracellular channels are emptied into the lumen of the knob through minute pores present in the intima. On this basis Ramamurthy (1969b) analogised such mass of cells to the spermathecal glands reported by earlier workers.

Pendergrast (1957) in *O. fasciatus*, Ramamurthy (1969b) in *Nezara viridula*, Ramamurthy (1970) in *Lygaeus* sp. and Ramamurthy and Medhi (1970) in *Cydnus indicus*, have described in detail large granular cells that ensheath the body of the
spermathecae as well as part of the duct. They are often considered as unicellular glands, each cell having intracellular ductules that penetrate in the chitinous intima and discharge the secretion into the lumen of the spermatheca. Such large cells remain inactive and small in newly emerged adults and these cells get enlarged and remain highly active as the insect reaches sexual maturity.

In the case of *R. marginatus*, in a newly emerged teneral insect the spermatheca, as described earlier, is like a convoluted tube and apically tapers (PL VII:1). The peritoneal sheath is very thin and the epithelium is cuboidal. The intima lining the lumen is denticulate (PL.VII:2). The cells enveloping the peritoneum are not conspicuous, but as the insect advances in age and reaches maturity the cells ensheathing the peritoneum, especially towards the middle exposed part of the duct (rest of the duct being ensheathed within the muscles of the bursa) become greatly enlarged and the nuclei become large and the cytoplasm remains vacuolated. But it is not clear whether these cells have any intracellular canaliculi because of the fact that the original cuboidal epithelium of the teneral insect has now become greatly enlarged and remains columnar and the chitinous lining loses its denticulate nature. Secretions accumulate in the form of eosinophilic mass within these epithelial cells. It is not clear whether the inner sheaths of smaller cells envelop the peritoneal sheath as described by Ramamurthy (1969 b and 1970) and Ramamurthy and Medhi (1970).
In the senescent insect however, when the intima becomes free due to the contraction of the epithelial cells, this mass of cells enveloping the peritoneal sheath also dwindles to mere pycnotic nuclei, suggesting that these cells are distinctly active secreting materials contributing to the spermatic fluid that accumulates in the lumen. It is also probable that the secretion of these cells may accumulate in the epithelial cells before getting discharged into the lumen by disruption of the intima. There is no information regarding the denticulate intimal lining in the teneral insect.

Ramamurthy (1968, 1969a and b) and Ramamurthy and Medhi (1970), have reported a barrel at the junction of the distal bulb and the basal stalk of the spermatheca. Such a barrel has been described by them to be composed of three concentrically arranged tubes each having its own investing cellular layer, the outer tube being covered with columnar epithelial cells which is thrown into folds, lined, by thick serrated intima which is loosened from the cellular layer when secretion accumulates between both. This secretion has been found to diffuse through the intima gradually. In the immature insects the cellular layer is villiform, closely invested by muscles. The proximal end of the barrel has been found to contain coarsely granular secretion of the mesadene gland, while the distal end contains finely granular secretion of the mesadene gland. The middle region contains a mixture of both the types of secretions. The middle tube has the epithelium inside and the intima outside. The secretion of the epithelium accumulates between the middle and the inner tube. The inner tube
is histologically similar to the outer tube and contains the spermatozoa in a mature insect.

The barrel, as described by Ramamurthy (1969a and b), Ramamurthy and Medhi (1970), in their insects, corresponds to the first segment of the spermathecal duct, the second segment being completely embedded in the tissue of the bursa in *R. marginatus*. Though the detailed histology of the three distinct tubes of this part of the spermathecal ducts are not clearly identified, at least two distinct tubes are clearly found (PL.VII: 4,5), the inner tube containing the sperms, the outer tube containing the secretion. The space between the inner and outer tubes remain filled with secretion in the mature insect, whereas, in the immature and senescent insects, the lumen between the inner and outer tubes remain vacuolated (PL.VII:6,7,8 & 9). In a senescent insect the wall of the inner tube remains more thick (PL.VII:9) while the epithelium of the outer tube is almost obliterated. This condition is seen when the cells enveloping the peritoneal sheath at the junction of the tube and the body of the spermatheca become necrosed.

In *R. marginatus* there is no region which could be strictly named as bulb as in the case of other heteropterous bugs, as described by Ramamurthy and Medhi (1970). It is clear that the body of the spermatheca becomes highly secretory during maturity. It is also clear that in an immature insect the body of the spermatheca is lined by a dentate intima which gradually gets
thinned out as the cells increase in size and the secretions accumulate in the cells. The spermatheca therefore is tripartite, as described by Ramamurthy and Medhi (1970), but it is not so complicated as reported by Pendergrast (1957), Ramamurthy (1969 a, b and c), Ramamurthy and Medhi (1970) in other Heteroptera. There is no pump at the base of the spermathecae, as reported in several other Heteroptera by Pendergrast (1957), Ramamurthy (1969 a, b and c) and Ramamurthy and Medhi (1970). But the pumping action as well as the sucking action are brought about by the musculature of the bursa since the second segment of the spermathecal duct is embedded underneath the musculature.
R. marginatus

Fig. 1 Female internal organs of reproduction showing the spermatheca (SP) opening into the bursa (BU)

Fig. 2 Section through the apical region of the spermatheca of a newly emerged adult showing chitinous intima (IT), denticulate empty lumen (LU) and oval nuclei at the base (400 x)

Fig. 3 T.S. through the more basal region of the spermatheca showing secretory activity of the cells (400 x)

Fig. 4 Section through the spermathecal duct showing musculature (M), narrow lumen (LU), thin layer of epithelium and the space surrounding the central lumen (400 x)

Fig. 5 L.S. through the duct showing the vacuolated epithelium and the lumen containing sperms soon after copulation (400 x)

Fig. 6 Section at the region of the bursa showing the spermathecal duct (SPD), traverse into the muscular wall on both sides running close to one another opening almost close to one another at the dorsal roof of the bursa (BU) (100 x)

Fig. 7 Section through the spermatheca of the mature insect showing actively secreting epithelium surrounded by a layer of fat tissue (FT), and finely granular homogeneous secretory material in the lumen (200 x)

Fig. 8 A segment of the actively secreting spermatheca showing merocrine form of secretion - the denticulate intima having lost its form (400 x)

Fig. 9 Another segment of the spermatheca of a mature insect showing the secretory activity of the epithelium (400 x)
PLATE VIII

**R. marginatus**

Fig. 1 A section of spermatheca showing extensive vacuolation and musculature (M) in the beginning of secretory activity (400 x)

Fig. 2 A segment of the spermatheca during secretory activity showing highly active fat tissue (FT) and secretory vacuoles (VA) in the epithelium of the spermatheca - muscle fibres (M) become very prominent (400 x)

Fig. 3 A magnified view of the epithelium showing secretory material (SM) within the cells and vacuolations of the epithelium (400 x)

Fig. 4 Spermatheca of a fairly advanced insect showing secretory materials and vacuolations of the epithelium (200 x)

Fig. 5 Section through the spermatheca of a senescent insect showing atrophy of fat tissue (FT) and detachment of intima (IT) due to contraction of the epithelium (400 x)

Fig. 6 T.S. of the spermatheca of an actively secreting insect showing the secretory activity of the spermathecal duct (400 x)

Fig. 7 Another section of the spermathecal duct of an advancing insect with the space being reduced and the intima being surrounded by a non cellular material (400 x)

Fig. 8 T.S. of the spermathecal duct showing the space being filled up (400 x)

Fig. 9 T.S. of a senescent insect showing empty space and the space between the intima and the wall obliterated (400 x)
**PLATE IX**

*R. marginatus*

Fig. 1 Internal organs of reproduction of a maturing female showing ovarian follicles (OF), pedicel (P), lateral oviduct (LOD), common oviduct (COD), spermatheca (S), bursa (BU) subrectal gland (SRG) and tegumental gland (TGL)

Fig. 2 A) Internal organs of reproduction of an ovulating female  
   B) Internal organs of reproduction of a senescent female showing ovarioles having ovulated several eggs and highly extended subrectal glands (SRG)

Fig. 3 Single ovary showing several ovulated eggs in the pedicel, calyx and lateral oviduct

Fig. 4 L.S. through a very immature ovariole showing thick tunica propria (TP) and germarium (G) — the vitellarium (V) is not well differentiated (200 x)

Fig. 5 L.S. through the tip of follicle showing trophocytes (TR), tunica propria (TP) and peritoneal tissue (PT) (400 x)

Fig. 6 L.S. of a follicle showing differentiation of vitellarium (V) and large trophocytes (TR) of the germarium (G) with large nuclei, the trophic cord being formed (400 x)

Fig. 7 T.S. through two follicles showing massive fat tissue (FT) surrounding each follicle, thick peritoneal tissue (PT) and oocyte (OC) being differentiated by the formation of follicular epithelium (400 x)

Fig. 8 Posterior region of a follicle showing basal epithelial plug (BEP), pedicellar head (PE) and antepedicellar interstitial tissue (APT) being differentiated from the basal epithelial plug (400 x)

Fig. 9 T.S. of the pedicel head showing the differentiating antepedicellar interstitial tissue (APT) (400 x)
PLATE X

R. marginatus

Fig. 1 Germarium of a developing follicle, tunica propria (TP) enveloping it and trophocytes arranged along the side, the trophic cord (TC) in the middle (400 x)

Fig. 2 The developing vitellarium showing nutritive cord (NC) connecting the trophic cord (TC) with the developing oocyte (OC) and the follicular epithelium (FE) getting differentiated as very small cells (200 x)

Fig. 3 The nutritive cord (NC) running through the centre of the differentiating vitellarium connecting the germarium (G), tunica propria (TP) loosely investing the follicle (200 x)

Fig. 4 A developing vitellarium showing the nutritive cord passing through the periphery connecting the apical trophic cord (TC) with the basal oocyte (BO) and the penultimate oocyte (PO) (400 x)

Fig. 5 L.S. of a basal oocyte and the pedicel (P) of a newly emerged adult showing the differentiation of the antepedicellar interstitial tissue at the head of the pedicel, behind the basal epithelial plug (BEP) (100 x)

Fig. 6 L.S. of the basal oocyte of the newly emerged adult showing the starting of vitellogenesis and activity of the antepedicellar interstitial tissue behind the basal epithelial plug (BEP) (200 x)

Fig. 7 L.S. of a maturing follicle showing an epithelial septum (ES) separating the vitellarium (V) and germarium (G) and the nutritive cord (NC) traversing (200 x)
Fig. 8 Enlarged view of the epithelial septum (ES) between the germarium and vitellarium (400 x)

Fig. 9 A developing oocyte showing the eccentric arrangement of the germinal disc (GD) and the follicular epithelium differentiating fully to vitellogenic eggs (400 x)
PLATE XI

R. marginatus

Fig. 1 A mature oocyte showing the arrangement of the cells of the follicular epithelium (FC) that secretes the chorion (CH) after the completion of the secretion of yolk (Y) and vitelline membrane (VM) (400 x)

Fig. 2 Section through the basal (BO) and penultimate oocytes (PO) showing the differentiation of basal epithelial plug (BEP) as transversely arranged cells and opercular apparatus (OPA) (400 x)

Fig. 3 Junction of the basal and penultimate oocyte showing the arrangement of basal epithelial plug (BEP) and the opercular apparatus (OPA) (400 x)

Fig. 4 Cephalic end of a vitellogenic oocyte showing binucleate condition (BN) of the follicular epithelium and the differentiation of the follicular epithelium into the opercular apparatus (OPA) (400 x)

Fig. 5 Cephalic end of the oocyte nearing completion of vitellogenesis showing the opercular plate differentiating from the chorionic collar (CHC) by inner and outer whorls of cells respectively (400 x)

Fig. 6 Section through the cephalic end of the egg showing the manner of secretion of the opercular crest by the single row of elongated cells (200 x)

Fig. 7 Section of chorion (CH) in the form of hexagonal area (400 x)
Fig. 8  Cephalic end of the ovulated egg within the pedicel showing the hexagonal cells of a chorionic collar (CHC) and opercular crest (OPC), developing inner peri-opercular space (IPOS) and outer peri-opercular space (EPOS), enclosed by the chorionic collar, cell attached to the opercular crest and the apical region of the crest (columella) having intercellular space (100 x)

Fig. 9  Enlarged view of the apex of the columella (COL) showing tubular arrangement (TA) of the intercellular space (ICS) (400 x)
R. marginatus

1. Two follicles of a senescent insect showing massive secretions of the tunica propria (TP) having been accumulated on either side of the head of the pedicel.

2. Section through the cephalic end of the egg showing the manner of secretion of the opercular crest by the single row of elongated cells.

3. Cephalic end of the ovulated egg within the pedicel showing the hexagonal cells of a chorionic collar (CHC) and opercular crest (OPC) developing inner periopercular space (IPOS) and outer periopercular space (EPOS) enclosed by the chorionic collar, cell attached to opercular crest. The apical region of the crest (columella) with intercellular spaces.

PLATE XII

R. marginatus

Fig. 1 Section through the basal oocytes of a premature ovariole showing oosorption taking place at the basal oocyte (BO) and the penultimate oocyte and the penultimate oocyte undergoing development with the germinal disc (GD) occupying central position (200 x)

Fig. 2 L.S. of the basal oocyte of a premature follicle undergoing oosorption and extensive pycnosis of the follicular epithelium (100 x)

Fig. 3 An enlarged view of the cephalic end of the basal oocyte showing opercular apparatus undergoing oosorption (200 x)

Fig. 4 Basal region of the oosorbing egg and premature oocyte showing the basal epithelial plug and the septum (ST) separating the pedicel (P) and the antepedicellar interstitial tissue (APT), the latter secreting a homogeneous tunica propria (TP) material that accumulates in the space enclosed by the peritoneal tissue (PT) (200 x)

Fig. 5 Enlarged view of an antepedicellar interstitial tissue actively secreting material similar to tunica propria (TP) accumulating within the space enclosed by the peritoneal tissue (400 x)

Fig. 6 Another section of the basal epithelial plug (BEP) and the pedicellar tissue undergoing active secretory phase (400 x)
Fig. 7  L.S. of the old ovariole showing the ovulated eggs and the corpus luteum (CL) that lies immediately behind the antepedicellar tissue (APT), and the tunica propria (TP) being secreted along the side (50 x)

Fig. 8  An enlarged view of the corpus luteum (CL), antepedicellar interstitial tissue (APT) and the tunica propria (TP) being secreted along the side (50 x)

Fig. 9  An enlarged view of the corpus luteum (CL), antepedicellar interstitial tissue (APT) and the tunica propria (TP) and the pore (O) being formed in the septa for the release of the egg and the basal epithelial plug (BEP) behind (200 x)
R. marginatus

1. L.S. of a follicle showing differentiation of vitellarium (V) and large trophocytes (TR), tunica propria (TP) and peritoneal tissue (PT)

2. L.S. of the old ovariole showing the corpus luteum (CL), antepedicellar interstitial tissue (APT) and the pore being formed in the septa for the release of the egg and its basal epithelial plug (BEP) behind

3. L.S. of a basal oocyte and the pedicel (P) of a newly emerged adult showing the differentiation of the antepedicellar interstitial tissue at the head of the pedicel behind the basal epithelial plug

4. The basal region of the senescing ovariole showing folding of the tunica propria (TP), disintegrating corpus luteum (CL), antepedicellar interstitial tissue (APT). The basal epithelial plug (BEP) of the basal oocyte being almost gone
PLATE XIII

R. Marginatus  HISTOMORPHOLOGY OF A SENESCENT OVARIOLE

Fig. 1  Apical region of the germarium showing thick tunica propria (TP) and disintegrating tropharium (TR) (400 x)

Fig. 2  A segment of the vitellarium (V) and tropharium (TR) showing vacuolating oocyte (OC) and other sections showing normal development (100 x)

Fig. 3  Section of the basal oocyte showing oosorption in progress, the germinal vesicle (GV) along with the fraction of the ooplasm still present (200 x)

Fig. 4  Almost completely oosorbed basal oocyte (BO), resorbed corpus luteum (CL) and basal epithelial plug (200 x)

Fig. 5  The penultimate oocyte having well formed follicular epithelium and the vacuolations in the ooplasm signifying oosorption (200 x)

Fig. 6  A segment of the cephalic end of the senescent basal oocyte showing vacuolations in the ooplasm and disintegrating follicular epithelium (400 x)

Fig. 7  The basal region of the senescing ovariole showing folding of the tunica propria (TP), disintegrating corpus luteum (CL), antepedicellar interstitial tissue (APT), the basal epithelial plug (BEP) of the basal oocyte, being almost gone (400 x)

Fig. 8  Two follicles of a senescent insect showing massive secretions of the tunica propria (TP) having been accumulated on either side of the head of the pedicel (100 x)
Fig. 9 An enlargement of the basal region of basal oocyte (BO) of a senescent insect showing disintegrating follicle being resorbed, the corpus luteum (CL) being almost resorbed and the tunica propria (TP) remaining massive and the basal epithelial plug (BEP) remaining in the stage of disintegration (400 x)
PLATE XIV

*R. marginatus*

Fig.1 L.S. through the pedicels of the maturing insect showing bacterial bodies (BB) in the lumen as well as in the fat tissue surrounding them (400 x)

Fig.2 L.S. of a repeatedly ovulated pedicel showing the nature of its expansion (200 x)

Fig.3 Magnified view of the wall of the pedicel showing the arrangement of the epithelium (EP) (400 x)

Fig.4 Section through the pedicels after the release of the egg (200 x)

Fig.5 An enlarged view of the pedicels of a mature insect showing secretory vacuoles in the epithelium and secretory materials in the lumen (400 x)

Fig.6 A segment of the common oviduct showing folds of the epithelium, its musculature(M) of the wall and intimal lining(IT) (400 x)

Fig.7 Spermatophore capsule showing two halves and opening of the two halves (OH) - These openings approximate the openings of the spermatheca (50 x)

Fig.8 Another spermatophore capsule showing gelatinous covering (JC) and cephalic appendage (CAP) (50 x)

Fig.9 Enlarged view of the cephalic end of the capsule showing cephalic appendage (CAP) and the two external openings of the hemisphere(OH) - the curved nature of this opening is significant (200 x)
R. marginatus

Fig. 1 Subrectal glands (SRG) and tegumentary glands (TGL) of a mature insect

Fig. 2 Subrectal gland (SRG) of a senescent insect - notice the sclerotisation near the posterior end of the bursa (BU)

Fig. 3 Section passing through the two subrectal glands (SRG) showing the muscle attachment (M) at the junction and the cluster of bacteria (200 x)

Fig. 4 Common opening (CO) of the glands to the exterior (200 x)

Fig. 5 Subrectal glands of a newly emerged adult showing the arrangement of the epithelium along the folds, deprived of cytoplasm (400 x)

Fig. 6 Enlarged view of a segment of subrectal gland of a maturing insect showing the increased quantity of cytoplasm and secretory material in the lumen (400 x)

Fig. 7 A segment of the subrectal gland of a mature insect showing aciniform secretory unit (AC), each unit having numerous nuclei (400 x)

Fig. 8 Enlarged view of the same with strong muscles (M) and acini (AC) actively secreting material into the spacious lumen (LU) (400 x)

Fig. 9 A segment of a senescent subrectal gland showing non active epithelial fold (400 x)
PLATE XV.A

R. marginatus

1. Section of the spermathecal duct.

2. Subrectal gland of a newly emerged adult showing the arrangement of the epithelium along the folds, deprived of cytoplasm.

3. Enlarged view of the subrectal gland of the mature insect, showing the aciniform secretory unit, each unit having numerous nuclei.

4. A segment of the spermatheca during secretory activity showing highly active fat tissue (FT) and secretory vacuoles (VA) in the epithelium of the spermatheca. Muscle fibres (M) become very prominent.
PLATE XVI

*R. marginatus*

Fig. 1 Section at the region of the bulbus ejaculatorius showing the glandular structure having bacteria in it (100 x)

Fig. 2 Enlargement of the bacterial mass adjacent to the bulbus ejaculatorius (200 x)

Fig. 3 Section at the region of the duct of subrectal gland (DSRG) showing a gland (GL) having bacteria (BB) (200 x)

Fig. 4 An enlargement of the gland (GL) showing the bacterial bodies (BB) inside (400 x)

Fig. 5 Section through a spermathecal duct (SPD) of a senescent insect showing bacterial bodies (BB) on its sides (400 x)

Fig. 6 A section of the tegumentary gland (TGL) of a newly emerged female showing the wide lumen (LU) (200 x)

Fig. 7 An enlarged view of the same showing the arrangement of the nuclei (400 x)

Fig. 8 An enlarged view of the wall of the gland showing aciniform type of secretory units opening into the lumen (LU), the bacteria at its vicinity (400 x)

Fig. 9 A section of the tegumentary gland of a mature insect showing the lumen (LU) in the middle (200 x)