

# MORPHOLOGY OF THE FEMALE ORGANS OF REPRODUCTION IN THE MIRIDAE (Hemiptera)<sup>1</sup>

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This investigation was undertaken in order to provide a more complete understanding of the structure and function of the parts of the female reproductive system in Miridae. Special emphasis has been given to the structure of the genital chamber and to the possible homologies of its parts. Since certain structures of the genital chamber are now becoming important as taxonomic characters, there exists a definite need for a morphological study so that these structures may be adequately understood. When possible, it is highly desirable that names of structures used in taxonomy be standardized by determining the existing homologies in various groups of insects. This must be done to avoid adding to the abundant synonymy and excessive number of morphological names. Of course, in many instances structures apparently become differentiated out of relatively unspecialized areas and, therefore, no particular homologies exist. To such structures descriptive names can be applied. However, basing such descriptive names on the location relative to structures which can be homologized should avoid needless complexity in morphological names.

The study of the female reproductive system of Miridae is also of great interest from a purely morphological point of view. In Miridae, as well as in Reduviidae, Nabidae, and Anthocoridae, the arrangement of the genital organs and genital ducts appears to be distinctly different from the arrangement in other Hemiptera as well as from insects in general. In so far as is known, the definitive spermatheca of insects arises posterior to the opening of the median oviduct. In Miridae the sperm receiving organ lies anterior to the median oviduct opening, but it is not known whether this organ is homologous to the spermatheca of other insects or if it is an organ peculiar to this group.

Final determination of the homologies of certain structures of the female genitalia of mirids must await more extensive studies of the genitalia of other Hemiptera. However, it is felt that the present investigation will at least provide a useful link in the eventual establishment of a complete knowledge of the female genitalia of the various groups of Hemiptera.

Four species, *Lygus lineolaris* (Palisot de Beauvois)\*, *Miris dolabratus* (Linnaeus), *Lopidea staphyleae* Knight, and *Plagiognathus albatus* (Van Duzee), were studied in detail during the course of this investigation. These species were selected because it was felt that each was representative of one of the several types of modifications of the female genitalia found in Miridae and these species were readily available to the author during certain parts of the spring and summer.

## REVIEW OF LITERATURE

Although thorough studies have been made of the genitalia of some Hemiptera, there was almost no knowledge of the anatomy of the female genitalia of Miridae until extensive investigations were made by Kullenberg (1946, 1947). His first paper was concerned primarily with the biology of Swedish species, but in connection with his biological studies he investigated the mating positions and egg laying habits of various species and described the general anatomy of the external genitalia of the mirid female. In his second paper Kullenberg published the results of an extensive investigation of the anatomy and function of the various parts of the male and female reproductive systems of Miridae. This study included a general description of the anatomy of the genitalia and of the copulation process of twenty four species. In another phase of this study Kullenberg has described the tissues of the reproductive organs.

Kullenberg made his studies largely from a standpoint of functional anatomy rather than of comparative morphology. Consequently the names which he has applied to many of the structures of the genital chamber are primarily descriptive and without basic morphological significance. However, it should be noted that the extensive scope of Kullenberg's studies and his emphasis on functional anatomy provide a most valuable guide in establishing homologies.

The next important study concerned with the female genitalia of Miridae was by Slater (1950). His investigation of the structure of the female genitalia for taxonomic characters successfully demonstrated that certain sclerotized parts in the

<sup>1</sup>A thesis submitted to the Graduate Faculty of Iowa State College in partial fulfillment of the degree of Master of Science.

\**Lygus lineolaris* (P.B.) has recently been shown by Slater and Davis (1952) to be the valid name of the Nearctic *Lygus* known in the economic literature as the Tarnished Plant Bug.

genital chamber were of value as a basis for determining phylogenetic relationships between the various genera and subfamilies of Miridae.

Where applicable, Slater used the terminology established by Kullenberg. However, in many instances he employed structures whose functional and morphological significances were unknown and which, therefore, he believed could not then be adequately named. Slater felt that any names which were purely descriptive might later have to be discarded for more suitable names when more was known of the function and phylogenetic relationships of these parts. Therefore, in anticipation of terminology arrived at by more detailed morphological studies, he referred to these structures only by alphabetical letters.

In 1952, Slater and Davis used structures of the female genitalia to show specific differences between *Lygus pratensis* (L.), *Lygus rutilans* Horvath, and *Lygus lineolaris* (P.B.).

Several works which included a study of the female reproductive system of various Hemiptera other than mirids have aided in understanding the function and morphology of the organs studied in this investigation. The genital apparatus and method of copulation of *Pyrrhocoris apterus* (L.) and *Lygaeus equestris* (L.) were studied by Ludwig (1926). Ekblom (1926) published an investigation which included studies of the anatomy of the female genitalia of species belonging to several families of Hemiptera. Galliard (1935) investigated the anatomy of the female reproductive system of reduviids, and this was followed by an extensive study of the reproductive system and the copulation of many aquatic Hemiptera by Larsen (1938). In 1953, a very detailed study of the functional anatomy of the reproductive organs of the milkweed bug, *Oncopeltus fasciatus* (Dallas) was published by Bonhag and Wick. Carayon (1946, 1952, 1953) has in recent years published a number of papers on the reproductive organs of Hemiptera, especially of cimicids, anthocorids, and nabids. His work has contributed considerably to the knowledge of these insects.

The problems of the evolution and the establishment of the homologies of the parts of the female genitalia of insects have interested various insect morphologists for many years. Heymons (1899) made substantial contributions to an understanding of the hemipteran abdomen by his embryological studies. Newell (1918) and Crampton (1929) published studies of the comparative morphology of the genitalia of various groups of insects including Hemiptera. The second of three publications by Snodgrass (1933) on the morphology of the abdomen of insects was concerned with the genital ducts and ovipositor. More recently Michener (1944) made a comparative study of the genitalia of insects which included some consideration of Hemiptera.

## DESCRIPTION AND DISCUSSION

### *The Abdomen of the Female*

The abdomen of the mirid female is generally rather boatlike in shape and relatively broader and more pointed than the abdomen of the male (Figs. 1, 2). The lateral portions of the tergal plates are apparently inflexed on each side along ridgelike margins, the *connexiva*, so that parts of the terga lie on the ventro-lateral surfaces of the abdomen below the *connexiva* (Fig. 2, *Cnx*). Reasons for this view are presented below. The terga of the pregenital segments, or segments one through seven, are not clearly demarked from the sternal or pleural regions by a suture or membranous area. Since a portion of each abdominal tergum is so closely associated with the sternopleural region, reference to the definitive dorsum and venter of the mirid abdomen is somewhat confusing. Therefore, in order to avoid this confusion the surface regions of the mirid abdomen are referred to in this study as the *dorsal plate* and the *ventral plate*, which include the dorsal and ventral surfaces, respectively, and which meet dorso-laterally at the *connexiva*.

The second through eighth abdominal segments contain spiracles. The spiracles are in the ventral plate near its dorsal margins (Fig. 2, *sp*). Snodgrass (1931) has generalized that though spiracles are subject to migration, they lie above the region of the limb bases in the typical segment in most insects. He further points out that tergal sclerotization commonly invades the spiracular areas and that the spiracles are, therefore, commonly found in the tergal or paratergal plates. He believes that in cases where the spiracles appear in the sternal sclerite this is probably because paratergal sclerites containing the spiracles have fused with the sternal sclerites. Kullenberg (1947) suggested that this condition occurs in the mirid abdomen and that the latero-ventral margins of the tergum can be represented by hypothetical lines running just ventral of the abdominal spiracles. Therefore, sclerites of the ventral plate in the pregenital region consist of paratergites laterally and pleuro-sterna medially.

The genital segments, or segments eight and nine, give a further indication of the position of the paratergites. In this part of the abdomen the ventral plate is divided by the elongated second valvifers (Fig. 1, *2Vlf*). Michener (1944) has pointed out that the valifers are now generally regarded as the remains of primitive limb bases of abdominal appendages. Therefore, the portions of the genital segments which are dorso-laterad of the valvifers may be considered to be parts of the terga. These plates extending from the *connexiva* to the valifers are, therefore, referred to as *paratergites* (Figs. 1, 2, *ptg*).

Eleven segments, the number considered basic to the insect abdomen, may be identified in the abdomen of the female mirid although some of

these are considerably modified. The portion of the first segment included in the ventral plate is reduced to an elastic membrane which joins the abdomen to the thorax (Fig. 2, *mb*). The ventral region of the second segment is also membranous except for sclerotized bands which may run along its anterior and posterior margins. In the remainder of the pregenital region, the broadly arched sclerites of the ventral plate are more or less uniform.

The seventh segment has a pointed, flap-like piece extending posteriorly from the caudal margin in the mid-ventral region. This flap covers the vulva and base of the ovipositor and has, therefore, been named the *subgenital plate* (Fig. 1, *SgP*).

In Miridae, as in other pterygota, the eighth and ninth segments are the genital segments of the female. The sternal regions of these segments are apparently inflexed and form the walls of the chamber and vestibulum (Fig. 7, *GC*).

The remaining external sclerites of the eighth and ninth segments in the ventral plate region overlap ventrally the sclerites of the ovipositor sheath. The ovipositor sheath is composed of the greatly elongated second valvifers and the small, lobe-like third valvulae (Fig. 2, *2Vlf*, *3Vl*). The ovipositor sheath is sometimes incorrectly referred to as the *vagina exterior* in taxonomic literature.

The tenth segment is annuliform and is sclerotized in all but the mid-ventral region which lies immediately dorsad of the lobes of the third valvulae (Fig. 7, *X*). The dorso-lateral margins are not differentiated into connexiva.

Except during defecation, the eleventh segment is drawn into the annulus formed by the tenth segment. The tergum and sternum of the eleventh segment are small arcuate sclerites. They are flexibly joined to each other at their narrow lateral margins. The caudal edges of these sclerites when at rest are in apposition so that a valve over the anal opening is formed (Fig. 7, *XI*). The eleventh segment bears no appendages.

A series of broad median abdominal tergites constitute what is known as the dorsal plate of the abdomen. In this region the first and second segments are not reduced as they are in the ventral plate. Therefore, eleven tergal sclerites may be identified, but it must be remembered that the eleventh tergum is covered by the tenth. Two membranous bands extending from the anterior margin of the abdomen continue through the eighth segment and join the tergal sclerites to the connexiva. These membranous bands allow the abdomen to increase considerably in diameter as it does in the case of the abdomen of the gravid female or the abdomen of species which accumulate a large store of body fat prior to hibernation.

As noted above, the membranous strips extending posteriorly between the dorsal plate and the connexiva do not extend into the ninth tergum. It may also be noted that the ninth segment is differentiated into only very slight connexiva, and that part of it which lies in the ventral plate is rather rigidly attached to the second valvifers on each side. As a result of this structural arrangement, the ninth tergum is able to serve as a rather firm attachment for several powerful muscles concerned with the movement of the valves of the ovipositor. This unit consisting of the ninth segment plus the valvifers and valvulae and their processes is referred to as the *genital frame* in this study.

#### The Valvulae and Valvifers

The mirid ovipositor consists of a median and two lateral blades (Fig. 6, *Ovp*). The median blade of the ovipositor is formed by the *second valvulae* (Fig. 4), which are fused together along their dorsal margin, except for a short divided portion at their distal ends whereby they still retain some of their identity as separate pieces (Fig. 12B, *2Vl*). Proximally, the median blade is somewhat expanded into a bulbous base. From the two ventral edges of this base sclerotized arms, known as *rami*, extend in an arc which passes dorsally and then posteriorly where the rami are fused to the anterior dorsal margins of the *second valvifers* (Fig. 13C, *2Ra*, *2Vlf*). As pointed out above, the second valvifers are elongated plates which lie on each side of the ovipositor and ensheath it when it is not extended.

At the distal region of the ovipositor the lateral surfaces of the second valvulae are covered by the broad, saber-like portion of the first valvulae (Fig. 6, *1Vl*). Basally the first valvulae become more narrow and gradually become confined to the ventral edges of the second valvulae. Near the base of the ovipositor the first valvulae branch into large *anterior* and small *median rami*. The median rami are weakly developed and may even be imperceptible. They extend anteriorly and slightly mesad of the reduced sclerites of the first valvifers. The anterior rami are curved dorsally in an arc which is contiguous with the

#### EXPLANATION OF PLATE I

FIG. 1. Ventral aspect of the abdomen of the female of *Lygus lineolaris*. X 28.

FIG. 2. Lateral aspect of the abdomen of the female of *Lopidea staphyleae*. X 38.

FIG. 3. Lateral aspect of the first valvula from the left side of the ovipositor of *Lygus lineolaris*. X 45.

FIG. 4. Lateral aspect of the left second valvula of the ovipositor of *Lygus lineolaris*. X 45.

*Cnx*, connexiva; *mb*, membranous area of the venter of the first and second segments; *Ovp*, ovipositor; *ptg*, paratergites of the eighth and ninth segments; *rg*, ridge on which the first valvulae slide along the second valvulae; *SgP*, subgenital plate; *sp*, spiracles; *3Vl*, third valvulae; *2Vlf*, second valvifer; I-X, abdominal segments.

FIG. I

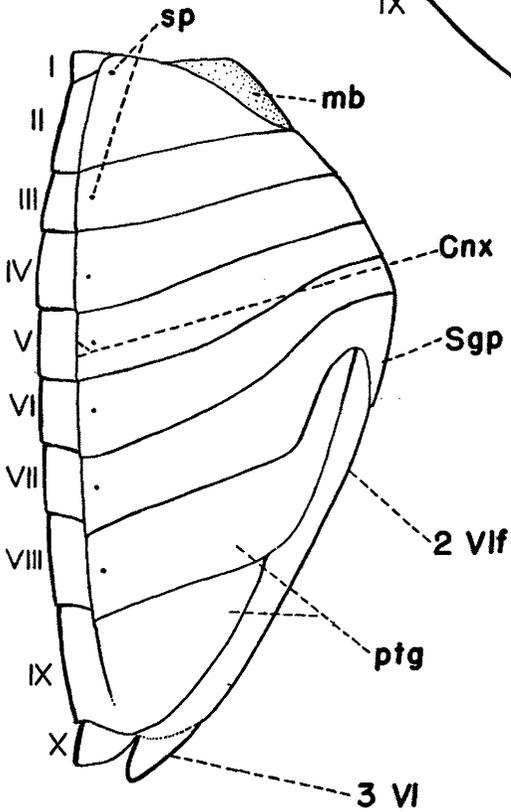
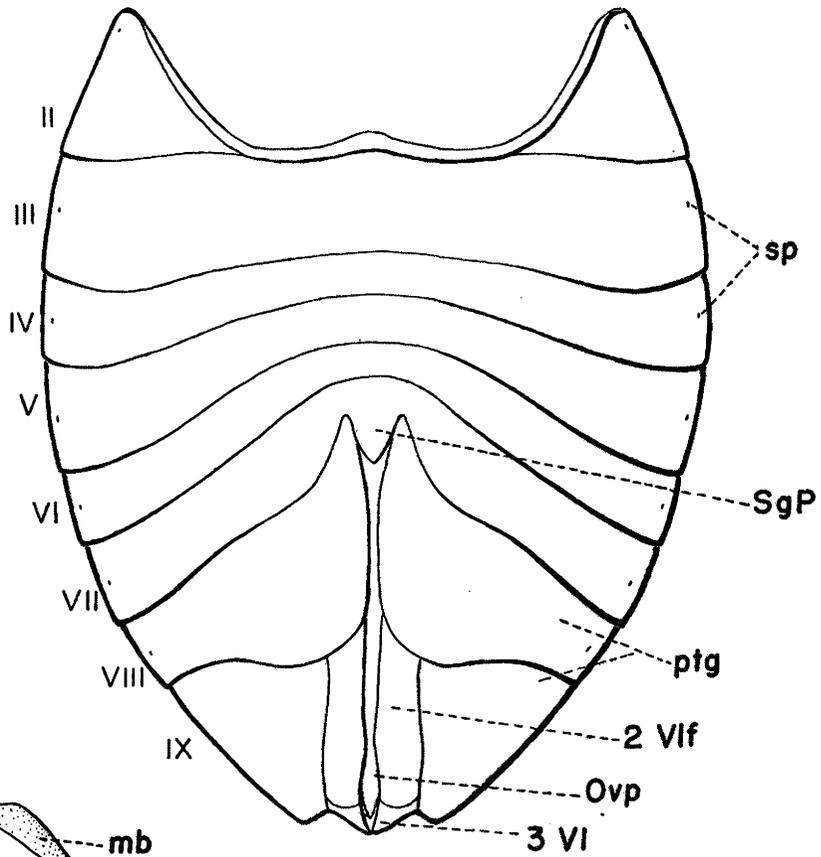


FIG. 2

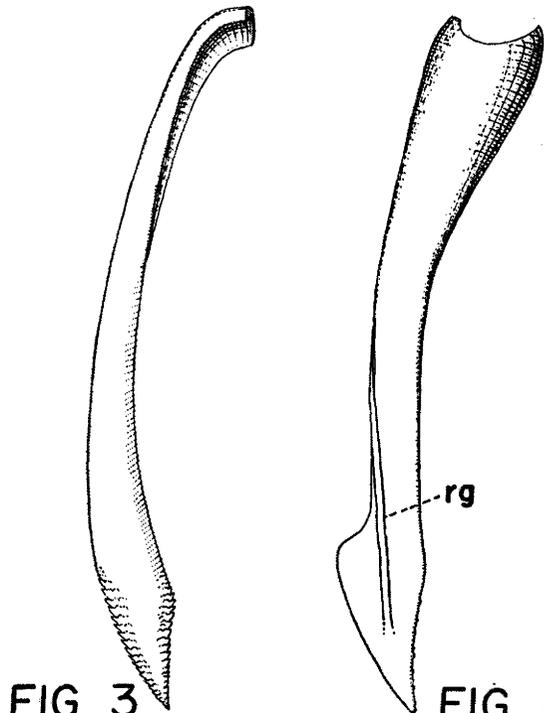


FIG. 3

FIG. 4

arch of the rami of the second valvulae (Figs. 6, 13B, *1 Ra*). From here these rami extend dorso-caudally in a straight line to the apodemes formed by the inflected anterior margins of the ninth paratergites (Fig. 5, *RP*). These apodemes are referred to in this study as the *ramal plates* since the fan-like proximal ends of the rami are fused to them.

Kullenberg (1947) referred to the anterior rami as each consisting of two pieces. The first piece was designated as a short extension from each first valvula called the *fibula* and this was said to be joined to the long rod-like piece extending to the ninth tergum. He called the second part the *connecting piece* (*Verbindungsstück*). Anatomically, there seems to be no basis for considering each of these rami as two pieces since there are no joints or sutures in them which would indicate a division. Furthermore, consideration of each of the anterior rami of the first valvulae as two pieces does not seem to be justified from the standpoint of comparative anatomy. Judging from the generalizations made by Snodgrass (1933) regarding the genital segments and ovipositor of Hemiptera, it can be assumed that the anterior rami of hemipterons are simple elongations of processes from the bases of the first valvulae.

When viewed from the dorsal aspect, a ridge is seen to extend along the surface of each ramus of the second valvulae (Fig. 15, *rg*). These ribs continue from the rami onto the ventral edges of the anterior portion of the second valvulae. From here the ribs extend distad and gradually pass on to the lateral surfaces of the second valvulae, terminating near their apices (Fig. 4, *rg*). These ribs fit into grooves which lie along the inner surface of the first valvulae (Figs. 12A-B, *rg*). By means of this structural arrangement, the first valvulae are closely held alongside of the second valvulae but are free to slide back and forth, making it possible for the cutting action of the blades to be coordinated in one common path and preventing the first valvulae from buckling when pressure is exerted on them.

The extent to which the cutting teeth are developed on the ovipositor blades varies and probably reflects the oviposition habits of the various species. Judging from those species studied, the dorsal and ventral margins of the first valvulae are lined with rows of teeth which extend somewhat out on the lateral surfaces of these blades (Fig. 3). The teeth lying between the apex and the broadest part of each of the first valvulae are relatively strong and scale-like. Anterior to this region the teeth abruptly become much finer and as they extend toward the bases of the second valvulae they gradually become almost invisible. The only teeth found on the second valvulae are those on their ventral margins near the apices (Fig. 4). These teeth

are very fine and, unlike those of the first valvulae, they are directed posteriorly.

Soft infolded strips from the ventral margins of each of the first valvulae extend posteriorly from the ventral margins of the first valvifers through the egg-channel of the ovipositor (Fig. 12A, *mbf*).

The sclerotized inner surfaces of the first and second valvulae which form the egg-channel are compactly lined with microscopically fine wrinkles whose crests are directed posteriorly.

The dorsal portions of each of the second valvifers are inflexed mesally so that a broad ledge is formed on each. These edges serve for the attachment of the muscles of the ovipositor (Fig. 5, *VIA*). In this study these ledges have been named the *valviferal apodemes*. The ventral ends of the ramal plates are articulated to the mesal portion of the valviferal apodemes. The apodeme of each valvifer is reinforced at this point of articulation by a short ridge extending across the inner surface of the angle of inflection of each of the second valvifers (Fig. 7, *r1*). Another strengthening ridge just anterior to the articulation of the ramal plate and valviferal apodeme extends over the outer surface of the angle of inflection of each valvifer (Fig. 14, *r2*).

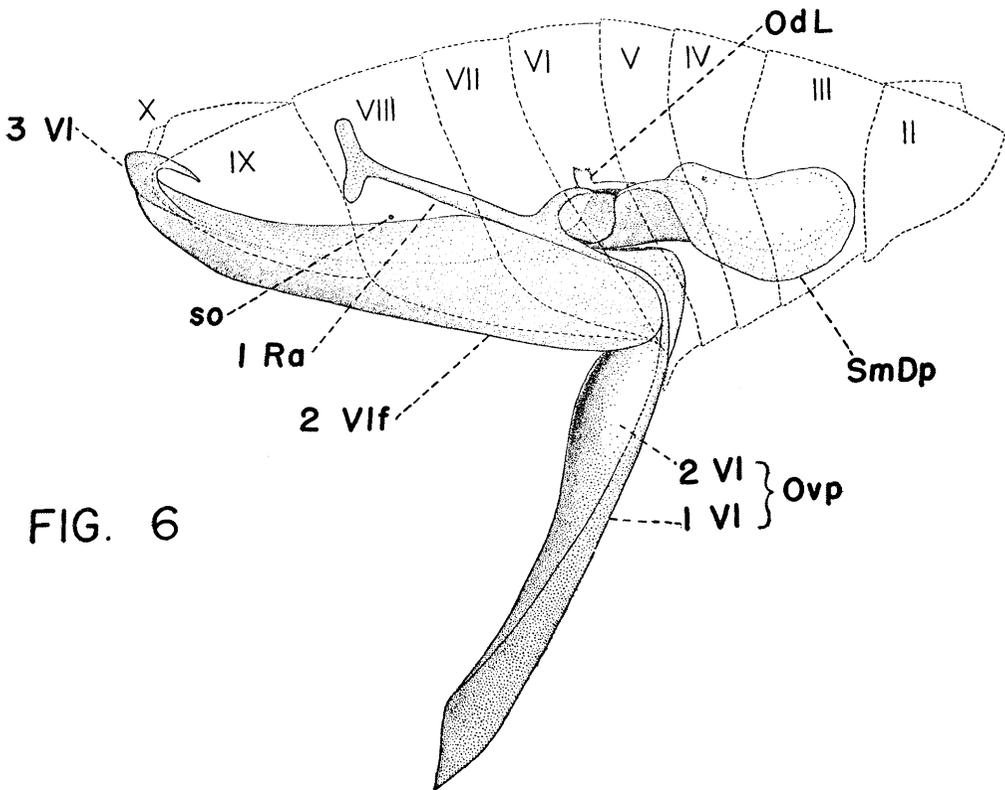
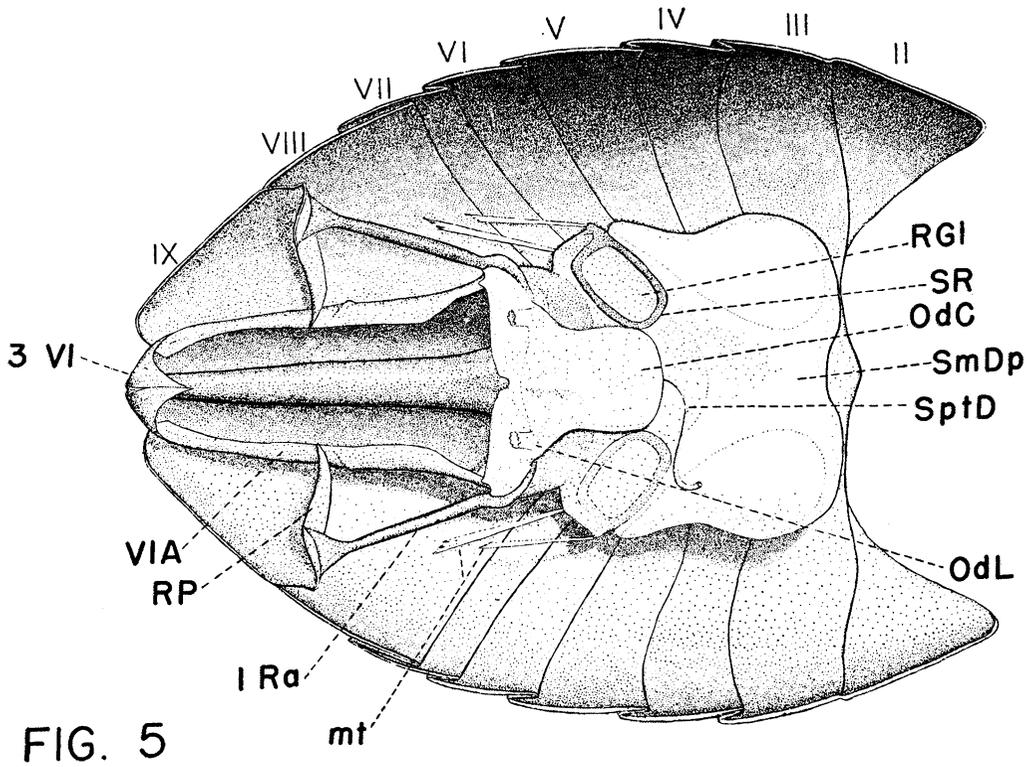
Anteriorly, the valviferal apodeme narrows considerably and merges with the portions of the second valvifers which are fused to the rami of the second valvulae. A third ridge extends from the ventral surface of each valviferal apodeme in the anterior region where the apodeme begins to narrow. This ridge extends ventrally and somewhat anteriorly to the anterior ventral margin of each of the second valvifers (Fig. 7, *r3*). Although these ridges do strengthen the anterior region of the valviferal apodemes they probably serve a more important function by acting as braces for the extended ovipositor. The ventral margins of the second valvifers are drawn into apposition when the ovipositor is extended so that the anterior ventral margins of the valvifers close about the base of the ovipositor. In this position the ridges mentioned above run almost perpendicular to the ovipositor base.

#### EXPLANATION OF PLATE II

FIG. 5. Dorsal view of the ventral abdominal wall and genital apparatus of *Lygus lineolaris*. X 28

FIG. 6. Lateral aspect of the genital apparatus of *Lygus lineolaris* with the segments of the abdomen indicated by broken lines. X 28.

*mt*, cuticular muscle tendons; *OdC*, the modified common oviduct; *OdL*, the cuticular lining of the bases of the lateral oviducts; *Ovp*, the extended ovipositor; *Ra*, ramus of the first valvula; *RGl*, area in which the ring gland occurs; *RP*, ramal plate of the ninth paratergite; *Smdp*, seminal depository; *so*, a sensory organ; *SptD*, cuticular portion of the spermathecal duct; *SR*, sclerotized ring; *1Vl*, first valvula; *2Vl*, second valvula; *3Vl*, third valvula; *VIA*, valviferal apodeme of the second valvifer; *2Vlf*, second valvifer.



Therefore, when the ovipositor is cutting into the plant tissue, these ridges brace against the pressure which tends to fold the ovipositor back into the ovipositor sheath.

Immediately anterior to the articulation of the ramal plate and the valviferal apodeme on each side, there is a very small button-like patch which bears about twenty compactly arranged sensory bristles. These patches are set in the thin inter-segmental membrane extending between the eighth and ninth paratergites and are very close to the ventral margin where this membrane is attached to the second valvifer (Fig. 6, *SO*). It should be noted that although these patches are on the external body surface, they are covered by the overlapping posterior edge of the eighth segment. The bristles on these patches fit into sockets and, possibly they have a sensory function. However, the exact nature of such a sensory function is not at all evident. These patches may not be related to the reproductive processes, but since they occur on the genital segments they have been so considered here.

Similar integumental organs on the abdomen of various nabids have been described by Carayon (1950).

The third valvulae are fused to the ventro-posterior margins of the second valvifers and form the lobe-like apical pieces of the ovipositor sheath (Figs. 2, 7, *3VI*). The dorsal portion of each of the third valvulae extends anteriorly as a narrowing, pointed strip (Fig. 7), which lies ventrad to the sternal region of the tenth and eleventh segments. This portion of each of the third valvulae serves as an attachment for muscles which extend to the anterior margin of the tenth tergum (Fig. 7).

The body wall between the second valvifers is completed by a soft, semitransparent membrane which enfolds the ovipositor in repose (Fig. 12A, *IvM*). In the present study this has been called the *inter-valviferal membrane*. This membrane apparently represents the sternal region of the ninth and tenth segments. The anterior extensions of the dorsal portions of the third valvulae support the inter-valviferal membrane in this region in an arch over the distal portion of the ovipositor (Fig. 12B, *3VI*, *IvM*). Anteriorly, this membrane is joined to the dorsal anterior margin of the fused second valvulae. The mid-dorsal region of the anterior margin of the base of the second valvulae is also joined to the membranous middle portion of the ventral margin of the posterior wall of the genital chamber.

Laterally, the membranous ventral portions of the posterior wall of the genital chamber are not attached to the base of the second valvulae but extend into its lumen and form the dorso-lateral lining of the egg-channel. On each side between the dorso-lateral lining of the egg-channel and the sclerotized wall of the second valvulae there is thus an extension of the body cavity into the

ovipositor (Fig. 11, *bc*). Each of these extensions of the body cavity becomes a narrow tubular passage into the base of the second valvulae (Figs. 12A-B, *bc*). Distally, these passages are very slightly dilated and terminate within the apices of the second valvulae. For most of their length these tubular passages lie between two sclerotized ridges which extend along the inner surfaces of the second valvulae (Fig. 12A). Presumably these ridges prevent the collapsing of the tubular extensions of the body cavity as the egg passes between the valvulae to the outside. Many fine ducts from these extensions of the body cavity pass through the walls of the second valvulae to the outer surfaces (Fig. 12A, *dt*). These ducts open only on the surfaces of the second valvulae which are not covered by the first valvulae. Therefore, basally the ducts extend to the dorsal and lateral surfaces, while distally they extend only to the dorsal and apical surfaces.

Study of the histological components of the lining of these extensions of the body cavity was hindered because the sclerotized parts of the ovipositor made it difficult to obtain a satisfactory series of microtome sections. The occasional satisfactory microtome sections and microscopic dissection of the second valvulae indicate that the tubular extensions of the body cavity are lined with squamous epidermis, and that a nerve and a trachea extend through the body cavity on each side (Figs. 12A-B, *nv*, *tr*). It seems very probable that each nerve gives rise to nerve fibers which pass into the ducts extending to the surface of the second valvulae. These ducts at the surface open into a small cup-like depression each of which appears to contain a small papilla. These papillae are presumably sensilla.

### The Genital Chamber

The *vulva*, or *secondary gonopore*, is covered by the subgenital plate of the seventh sternum. The anterior margin of the vulva is formed by the inter-segmental membrane from the caudal margin of the sternal region of the seventh seg-

### EXPLANATION OF PLATE III

FIG. 7. Optical sagittal section of the posterior portion of the abdomen of *Miris dolabratus*. X 40.

FIG. 8. Dorsal aspect of the genital apparatus of *Miris dolabratus* with the abdominal segments indicated by broken lines. X 51.

*DlbP*, dorsal labiate plate; *GC*, genital chamber; *M1*, 2, 3, 4, 5, 8, genital muscles; *mt*, cuticular muscle tendon; *OdC*, the modified common oviduct; *OdL*, lateral oviduct; *Ovp*, ovipositor; *r1*, 3, strengthening ridges of the second valvifer; *IRa*, ramus of the first valvula; *RP*, ramal plate of the ninth paratergite; *Rt*, rectum; *SgP*, subgenital plate; *SmDp*, seminal depository; *SplG*, spermathecal gland; *VLP*, ventral labiate plate; *1VI*, first valvula; *2VI*, second valvula; *3VI*, third valvula; *2Vlf*, second valvifer.

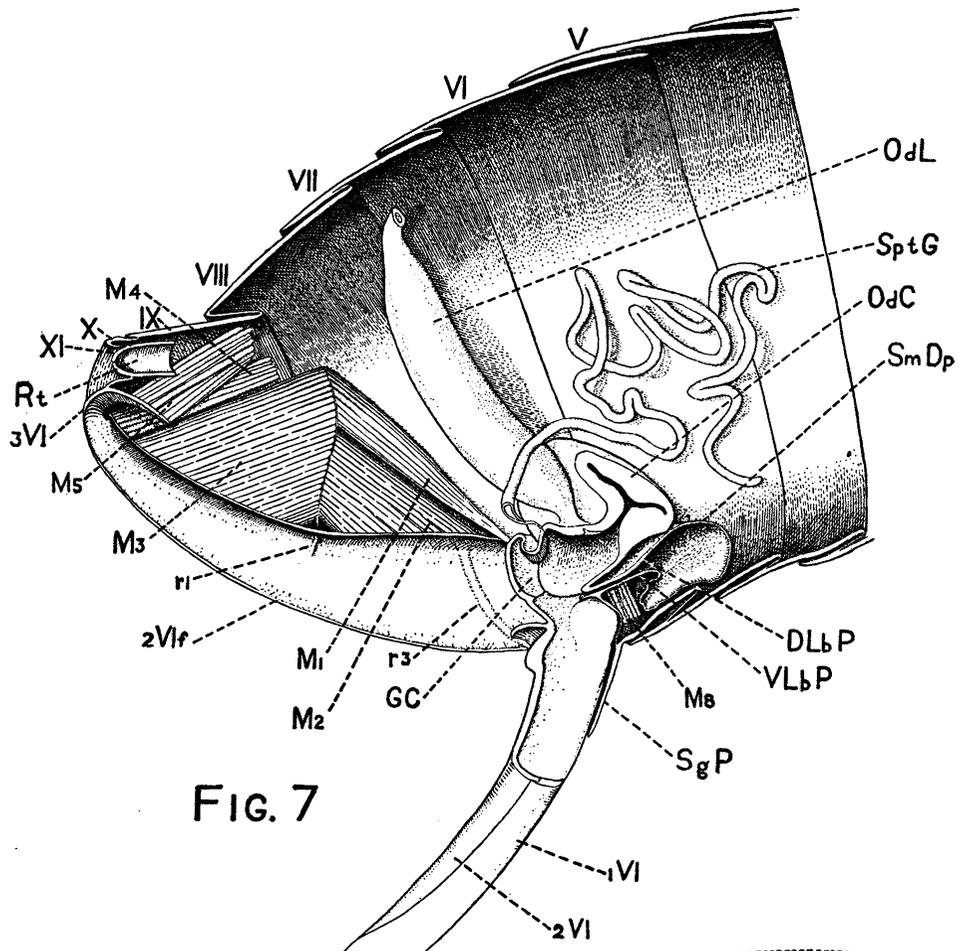


FIG. 7

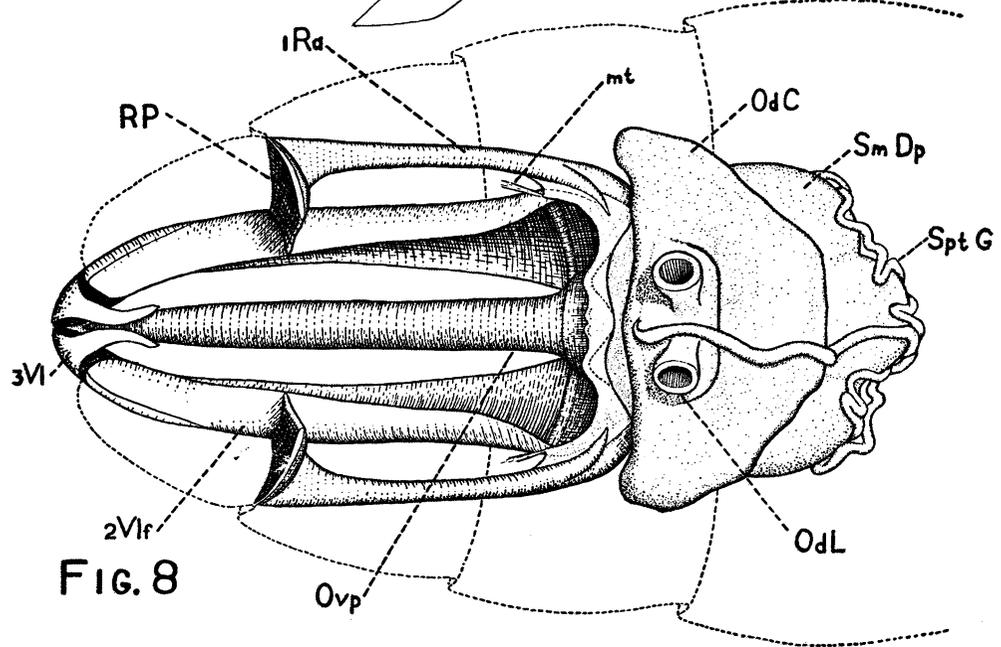


FIG. 8

ment. This membrane forms a part of what has been designated as the anterior wall of the genital chamber. The posterior margin of the vulva is formed by the base of the ovipositor, especially the ventral surfaces of the first valvulae (Fig. 19A, *Vu*). Kullenberg (1944) designated the secondary gonopore as the "*Vulvamündung*" and the passage extending dorsally from it as the "*vulva*". This usage is not entirely satisfactory since "*vulva*" when applied to insects generally refers to an opening. The passage which he calls the vulva may more properly be called the *vestibulum* (Fig. 19A, *Vst*). Snodgrass (1933) defines the vestibulum as a chamber formed by the extension of the seventh sternum beyond the eighth; this is essentially what is found in Miridae. Therefore, in this study the external opening of the genital chamber is termed the vulva, while the short passage extending dorsally into the genital chamber from the vulva is termed the *vestibulum*. It should be emphasized that the vestibulum is not chamber-like in Miridae, as it often is in other insects. It is a narrow passage although it may be stretched considerably during the time that the intromittent organ of the male is inserted into it.

In his study of the female reproductive system in Miridae Kullenberg (1947) designated three anatomical regions of the genital chamber. These are the *forward wall* (*vorger Wand*), the *posterior wall* (*hinter Wand*), and the *roof* (*Dach*). In some respects these designations are inappropriate, nevertheless, they are at least convenient terms to use as a basis for introduction of description and discussion of specific portions of the genital chamber.

The anterior wall, as designated by Kullenberg, lies between the anterior rami and extends dorsally from the caudal margin of the sternal region of the seventh segment (Figs. 13B, 16B, *AWVst*). The dorsal portion of the anterior wall is directed cephalad as a broad plate-like area (Figs. 7, 16B, *VLbP*). Thus designated, the ventral portion of the anterior wall is seen to be the anterior wall of the vestibulum, not the genital chamber. The dorsal plate-like portion of the anterior wall is usually somewhat sclerotized and has been designated in this study as the *ventral labiate plate*. It lies in a horizontal plane and extends anteriorly and laterad beyond the anterior rami. Its anterior margin forms the ventral lip of a membranous sac referred to here as the *seminal depository* (Figs. 7, 8, *SmDp*).

Folds which vary in different species may extend into the genital chamber from the anterior wall. The posterior margin of the ventral labiate plate forms one such fold (Fig. 19A, *VLbP*). In *Lopidea staphyleae* and *Plagiognathus albatrus* there are lateral lobes which extend into the genital chamber ventrad of the ventral labiate plate. These lobes converge medially to form an asymmetrical, sclerotized protuberance which extends

ventrally into the vestibulum. This structure probably serves as a place for attachment of the male copulatory organs during the mating process.

The portion of the genital chamber referred to as the roof is the more or less flat dorsal surface. The posterior portion of the roof extends between the rami of the first valvulae and is supported by sclerotized areas which vary considerably in different species (Figs. 5, 8, 14, 17). In the anterior region of the genital chamber the roof is formed by a broad plate (Figs. 5, 13A, *DLbP*). This somewhat sclerotized area constitutes the *dorsal labiate plate* of the seminal depository. It is appressed to the ventral labiate plate and they are continuous at their lateral margins (Fig. 13A). The work of Kullenberg (1947) and of Slater (1950) has shown that in most mirids the dorsal labiate plate has a pair of low ridges on its dorsal surface. These ridges encircle patches of cuboidal epidermal tissue and are thus in the form of bilateral, sclerotized loops (Figs. 5, 13A, 17, *SR*). These structures were referred to by Kullenberg as the *Chitinschlinge* and by Slater as the *sclerotized rings*. The name of these structures used by Slater has been adopted in the present investigation and the areas of tissue which they encircle are here referred to as the *ringed glands*.

A pouch-like structure is attached to the roof of the genital chamber in many species of Miridae. This structure was referred to by

#### EXPLANATION OF PLATE IV

FIG. 9A. Cross section of the spermathecal gland of *Lygus lineolaris*.

FIG. 9B. Longitudinal section through the spermathecal chamber of *Miris dolabratus*.

FIG. 10A. Cross section through the wall of the seminal depository of *Lygus lineolaris* showing the modified epidermis.

FIG. 10B. A section through the ringed gland of *Lygus lineolaris* showing the modified epidermis.

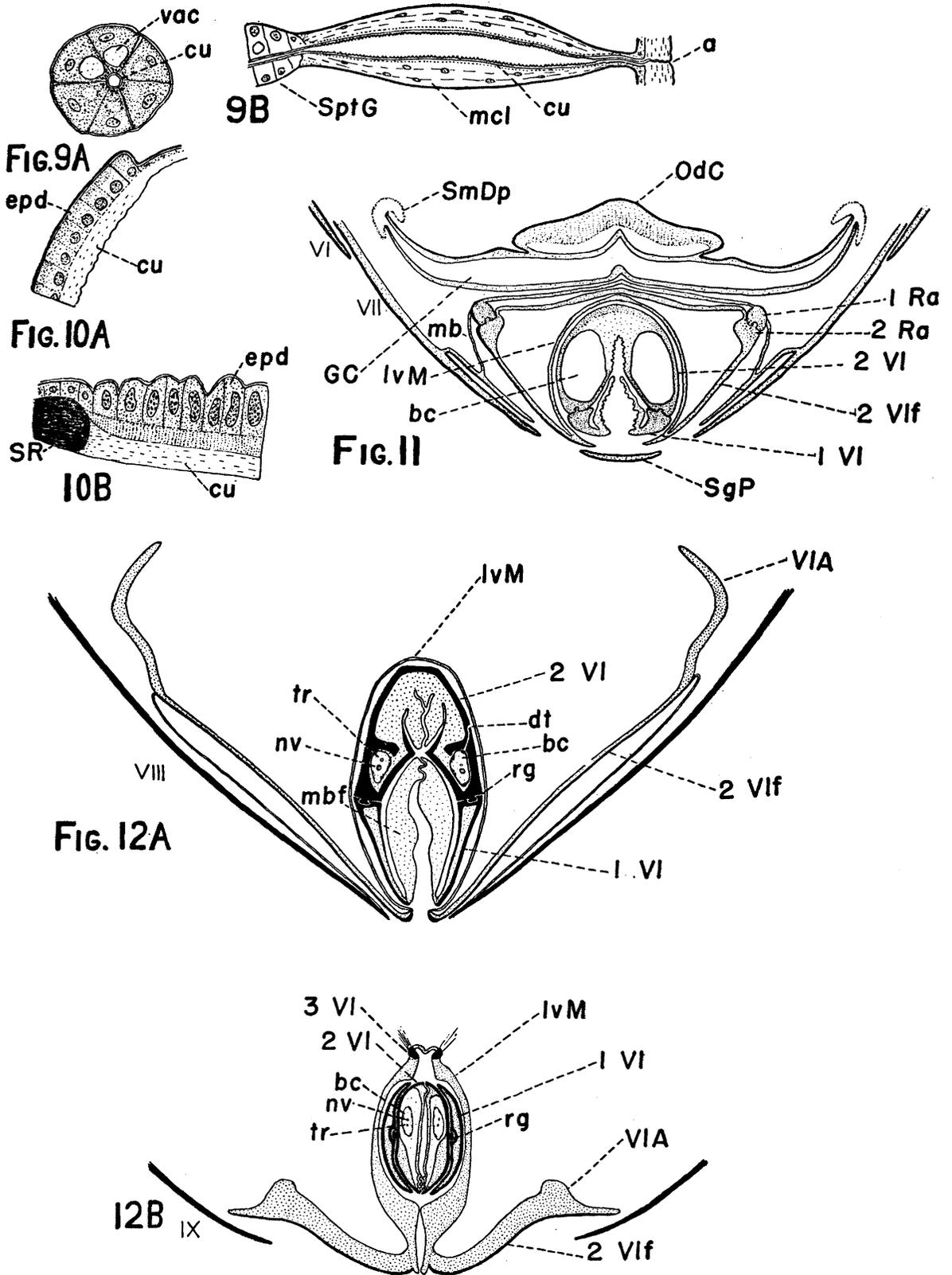
FIG. 11. Cross section through the genital chamber and base of the ovipositor of *Lygus lineolaris*. X 56.

FIG. 12A-B. Cross sections through the ovipositor and second valvifers of *Lygus lineolaris*. X 103.

FIG. 12A. A section just posterior to the genital chamber showing the fused portion of the second valvulae.

FIG. 12B. A section near the tip of the ovipositor showing the separate portion of the second valvulae.

*a*, opening of the spermatheca into the genital chamber; *bc*, a portion of the body cavity extended into the second valvula; *cu*, cuticle; *dt*, duct from the body cavity to the surface of the second valvula; *epd*, modified epidermis; *GC*, genital chamber; *IvM*, intervalviferal membrane; *mb*, membrane between the eighth segment and anterior wall of the genital chamber; *mbf*, membranous fold in the egg-channel of the ovipositor; *ncl*, muscularis of the spermathecal chamber; *nv*, nerve; *Odc*, common oviduct; *1Ra*, ramus of the first valvula; *2Ra*, ramus of the second valvula; *rg*, ridge on which the first valvulae rest; *SgP*, subgenital plate; *SmDp*, seminal depository; *SpIG*, basal portion of the spermathecal gland; *tr*, trachea; *1Vl*, first valvula; *2Vl*, second valvula; *3Vl*, third valvula; *VIA*, valviferal apodeme; *2Vlf*, second valvifer.



Kullenberg as the *dorsal sack* and he considered it to be derived from the *common oviduct* (Figs. 5, 14, 17, *OdC*). This view is supported in the present study.

Membranous margins of the paratergites of the eighth segment are continuous with the anterior wall and roof of the genital chamber at the rami of the first valvulae (Fig. 11, *mb*). Also the anterior wall lies posterior to the seventh sternum. Therefore, these portions of the genital chamber may be considered to have been derived from the sternum of the eighth segment.

The posterior margin of the region designated as the roof of the genital chamber is marked by a ventral inflection. The surface of the genital chamber extending from this inflection ventrally to the base of the second valvulae is the posterior wall (Figs. 13C, 15, 16A). Laterally, the posterior wall extends between the rami of the second valvulae. The dorsal portion of the posterior wall is membranous. The ventral portion, in general, consists of a median sclerotized process and a pair of bilateral sclerotized plates. The plates are referred to in this study as the *inter-ramal sclerites*. The dorsal margin of the inter-ramal sclerites in *Miris dolabratus* and *Lygus lineolaris* is turned anteriorly and a membranous fold extends from them (Figs. 13C, 16A, *IrS*). In *Lopidea staphyleae* the dorsal portion of each inter-ramal sclerite gives rise to a pair of prominent biramous processes (Fig. 15). In *Plagiognathus albatu*s the inter-ramal sclerites are simple, oblong plates and in *Lopidea staphyleae* they are not clearly differentiated from the remainder of the posterior wall (Fig. 15, *IrS*). Between the dorsal portions of the inter-ramal sclerites the posterior wall is differentiated into a sclerotized process which has an s-shaped form when viewed laterally. This is referred to here as the *sigmoid process*. Its development is elaborate in *Miris dolabratus* and *Lygus lineolaris* (Fig. 19A, *SmP*), whereas it is rather simple in *Plagiognathus albatu*s and *Lopidea staphyleae* (Fig. 15, *SmP*).

The posterior wall is continuous with the second valvifers at the rami of the second valvulae (Fig. 11, *2Ra*). For this reason the posterior wall may be considered to have been derived from the sternum of the ninth segment.

#### The Seminal Depository

Of particular interest in mirids is the relatively large membranous bladder which opens into the anterior wall of the genital chamber (Figs. 5, 7, *SmDp*). This organ apparently serves to receive and store sperms and is, consequently, referred to as the *seminal depository* in this investigation. It is of integumental origin and evidently derived from the venter of the eighth segment. The lumen of the seminal depository is lined with a thin, very pliable cuticle. The internal surface, that is the surface facing the

haemocoel, is lined with epidermis. On the dorso-lateral surfaces of the seminal depository the epidermis appears to be differentiated into two large patches of glandular epidermis consisting of cuboidal cells with nuclei which are almost opaque when stained with hematoxylin (Fig. 10A, *epd*). Large secretory vacuoles were not found in these cells so it is assumed that their secretion passes through pores in the cuticle as it is slowly formed.

In the virgin female this bladder is collapsed and contains almost no fluid (Fig. 18, *SmDp*). After insemination it is completely filled by the seminal fluid and by clumps of semi-solid material.

Though the seminal depository appears to function as an organ for the storage of sperms, there is not sufficient reason for considering it to be homologous to the spermatheca of other insects. The first indication that it is not a spermatheca is that it is not in the proper position relative to the gonopore. Johannsen and Butt (1941) have pointed out that embryological studies indicate that the median oviduct of higher insects arises in early development by invagination of the posterior region of the seventh venter. This is followed by the formation of a groove extending posteriorly on the venter of the eighth segment. The groove is gradually transformed into a tubular extension of the common oviduct. The external opening of the common oviduct, or *gonopore*, thus comes to lie in the posterior region of the venter of the eighth segment. The spermatheca arises as a median

#### EXPLANATION OF PLATE V

FIG. 13A. Dorsal aspect of the genital chamber of *Miris dolabratus* with the common oviduct and seminal depository removed. X 56.

FIG. 13B. Ventral aspect of the roof and anterior wall of the genital chamber of *Miris dolabratus* with the first valvulae removed at the first valvifers. X 56.

FIG. 13C. Dorsal aspect of the posterior wall of the genital chamber of *Miris dolabratus*. X 56.

FIG. 14. Dorsal view of the genital chamber of *Plagiognathus albatu*s. X 100.

FIG. 15. Dorsal aspect of the posterior wall of the genital chamber of *Lopidea staphyleae*. X 46.

FIG. 16A. Dorsal aspect of the posterior wall of the genital chamber of *Lygus lineolaris*. X 61.

FIG. 16B. Ventral aspect of the anterior wall and roof of the genital chamber of *Lygus lineolaris* with the left valvula removed at the left first valvifer and the right valvula removed at its rami near the posterior margin of the roof. X 61.

*AWVst*, anterior wall of the vestibulum; *BODC*, margin of attachment of the common oviduct; *brp*, biramous process; *DLbp*, dorsal labiate plate; *IrS*, inter-ramal sclerite; *mb*, membranous fold on the posterior-dorsal portion of the inter-ramal sclerite; *mt*, cuticular muscle tendon; *OdC*, the modified common oviduct; *OdL*, lateral oviduct; *Ovp*, ovipositor; *r2*, strengthening ridge of the second valvifer; *1 Ra*, ramus of the first valvula; *2 Ra*, ramus of the second valvula; *rg*, ridge; *RGI*, area in which the ringed gland occurs; *SmDp*, seminal depository; *SmP*, sigmoid process; *SR*, sclerotized ring; *VLP*, ventral labiate plate; *2Vlf*, second valvifer.

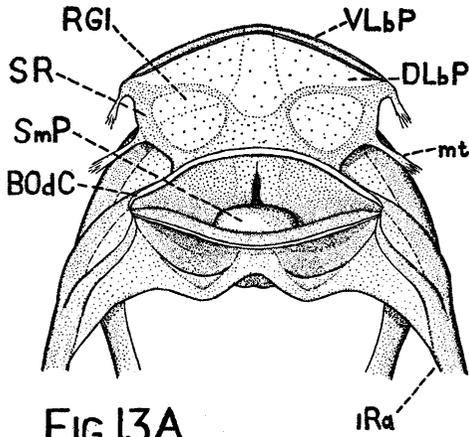
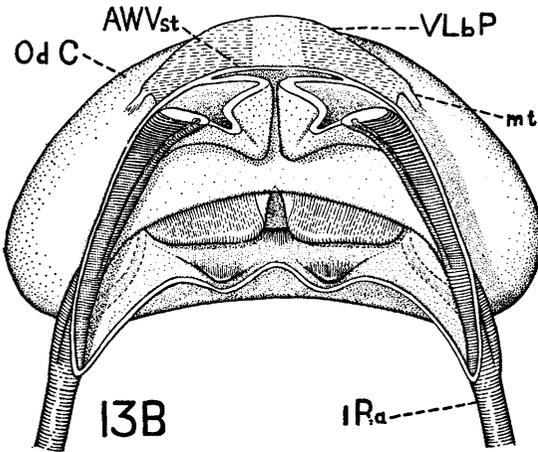
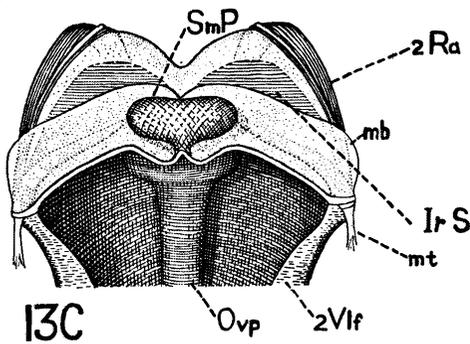


FIG. 13A



13B



13C

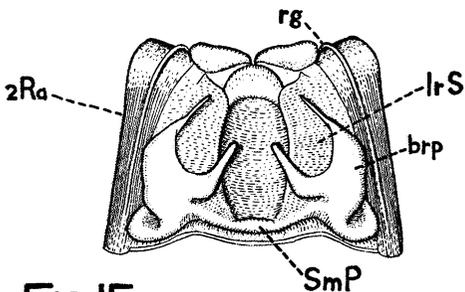


FIG 15

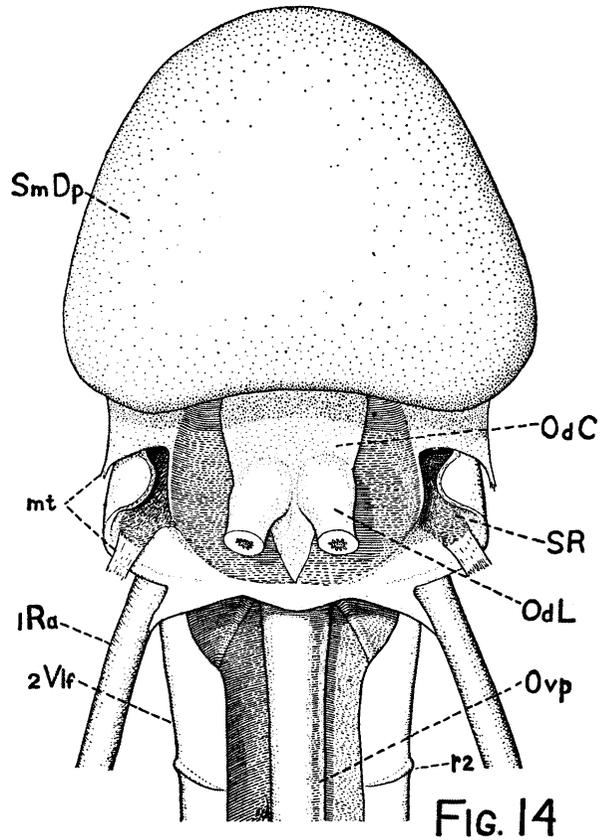


FIG. 14

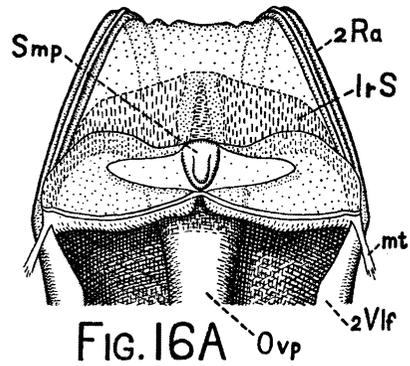
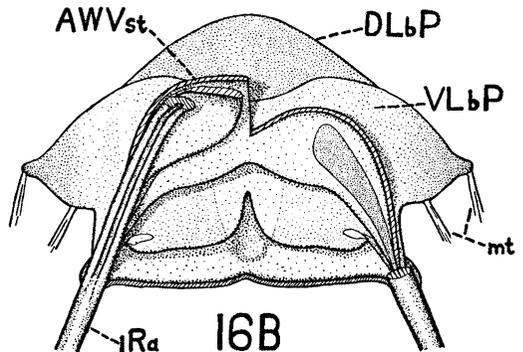


FIG. 16A



16B

invagination in the eighth sternum just posterior to the gonopore.

Johannsen and Butt (1941) have pointed out that in later development the gonopore and opening of the spermatheca may be carried inward by the formation of a copulatory pouch. Snodgrass (1933) has pointed out that the gonopore may shift with changes in the genital chamber but that morphologically it opens anterior to the opening of the spermatheca.

In giving a generalized description of the structure of the spermatheca of insects Snodgrass (1935) has noted that the spermatheca is typically a single sac-like structure with a muscular wall and a slender duct. Spermathecae which are of the general form indicated by Snodgrass have been described in various species of Hemiptera such as *Lygaeus equestris* (L.) (Ludwig, 1926), *Nezara viridula* (L.) (Malouf, 1933), and several species of aquatic hemiptera (Larsen, 1938).

The opening of the seminal depository of Miridae can in no sense be considered morphologically posterior to the gonopore. Its walls contain no muscularis and it opens into the genital chamber by means of a broad slit-like orifice rather than a tubular duct. These facts seem to indicate that the seminal depository of mirids is unquestionably not homologous to the spermatheca of other insects. This conclusion is supported by the fact that mirids do have an organ which is apparently homologous to a spermatheca even though it does not store sperms.

According to Reuter (1910), Nabidae, Anthocoridae, Cimicidae, and Reduviidae are relatively closely related phylogenetically to the family Miridae. The female genital organs of these families are, therefore, of particular interest in this investigation. Verhoeff (1893) has described a sac-like structure (*umpaare Skelettstück*) at the base of the ovipositor of Anthocoridae. This structure is apparently homologous with the seminal depository of mirids. Kullenberg (1947) has shown that a seminal depository is also found in Nabidae. Galliard (1935) has noted that a pair of pouch-like organs which receive sperms are attached to the ventro-lateral surfaces of the genital chamber of reduviids. Since these organs are paired they may not be homologous to the seminal depository of mirids, but more study is needed to answer this question.

In *Cimex lectularius* L. there are (Cragg, 1920) paired "spermathecae" on each side of the common oviduct. Cragg has shown that these organs do not have a cuticular lining. Their structure, plus the fact that they are paired and have a different function makes it seem very unlikely that these organs could be considered homologous with the seminal depository of Miridae.

#### The Ringed Glands

A portion of the epidermis covering the dorsal

labiate plate of the seminal depository is differentiated into a specialized tissue in two bilateral patches which apparently are glandular. Each of these plate-like patches of tissue is encircled by a low, somewhat sclerotized ridge in the sub-jacent cuticle (Fig. 5 10B, SR).

The tissue of these glands consists of a single layer of cuboidal cells. The cell nuclei are more or less elliptical and they are almost opaque when stained with hematoxylin. The cytoplasm is moderately granular and it does not appear to contain any secretory vacuoles (Fig. 10B, *epd*). The structure of these glands seems to indicate that they do not produce a great quantity of secretion. Since they are closely associated with the seminal depository, their secretion may be assumed to be in some way associated with maintenance of the sperms. It seems rather unlikely that these glands could function as colleterial glands since they could not store and release sufficient secretion at the time the egg passes through the genital chamber.

In *Lopidea staphyleae* the sclerotized rings appear to be considerably modified. In this species the sclerotized areas equivalent to the sclerotized rings have their lateral portions twisted dorsally and the areas encircled by this structure are invaginated finger-like projections in the seminal depository. The function of this arrangement is not understood.

Similar glands have been described in other Hemiptera. Kullenberg (1947) noted that flat epidermal glands encircled by sclerotized rings are found on the dorso-lateral surfaces of the genital chamber of *Nabis*. Ludwig (1926) described very similar glands on the genital chamber of *Lygaeus*. He regarded these as accessory glands and stated that they produce egg-cement.

#### EXPLANATION OF PLATE VI

FIG. 17. Dorsal view of the genital chamber of *Plagiognathus albatius*. X 100.

FIG. 18. Dorsal aspect of the ventral plate of the abdomen of *Lygus lineolaris* showing some of the genital muscles. X 17.

FIG. 19A. Parasagittal optical section of the genital chamber of *Lygus lineolaris*. X 37.

FIG. 19B. The same as above but showing the ovipositor extended and an egg entering the genital chamber.

FIG. 20. Dorsal view of the ovaries and lateral oviducts of *Lygus lineolaris* with the left ovary as it normally occurs and the right ovary dissected out to show the individual ovarioles. X 18.

*Clx*, Calyx; *DLbP*, dorsal labiate plate; *E*, egg; *GC*, genital chamber; *IvM*, intervalviferal membrane; *M1*, 2, 3, 6, 7, genital muscles; *ml*, cuticular muscle tendon; *OdC*, common oviduct; *OdL*, lateral oviduct; *Ovp*, ovipositor; *IRa*, ramus of the first valvula; *RP*, ramal plate; *SgP*, subgenital plate; *SL*, suspensory ligament; *SmDp*, seminal depository; *SmP*, sigmoid process; *Sph*, sphincter of oviduct; *SptC*, spermathecal chamber; *SptD*, spermathecal duct; *SptG*, spermathecal gland; *SR*, sclerotized ring; *TF*, terminal filament; *VLbP*, ventral labiate plate; *IVlf*, first valvifer; *2Vlf*, second valvifer; *Vst*, vestibulum; *Vu*, vulva.

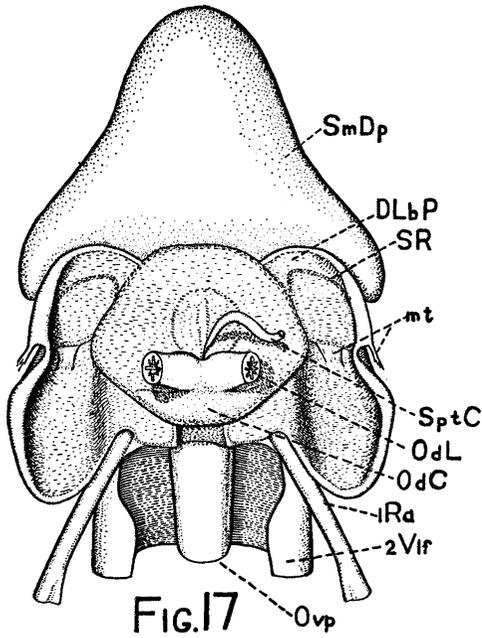


FIG. 17

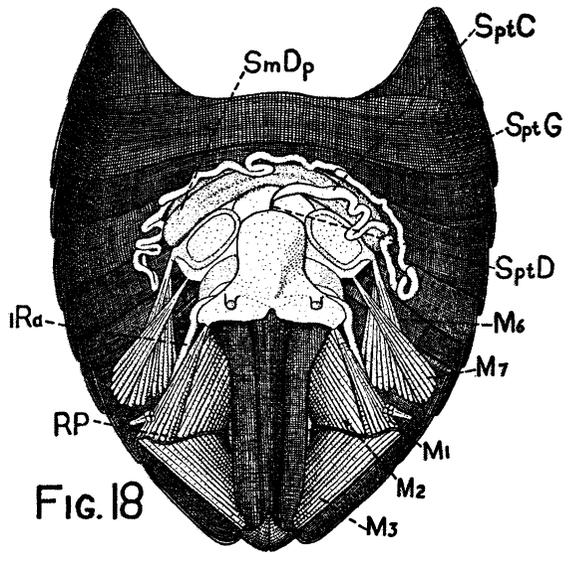


FIG. 18

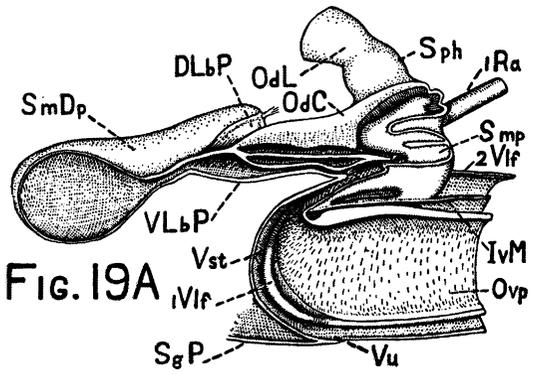


FIG. 19A

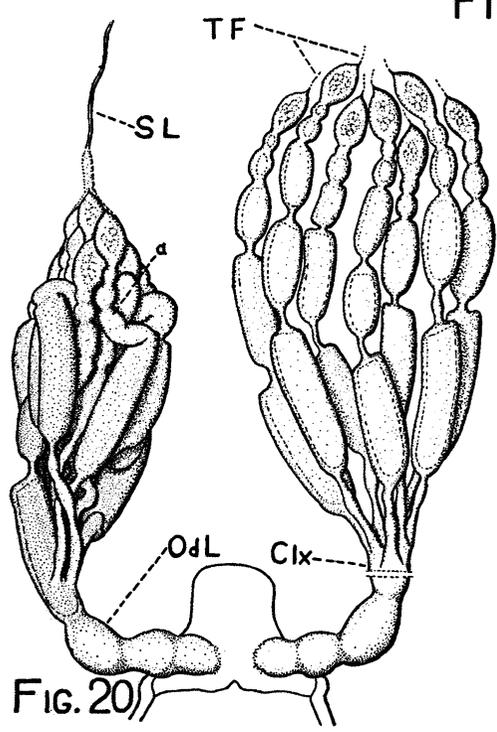
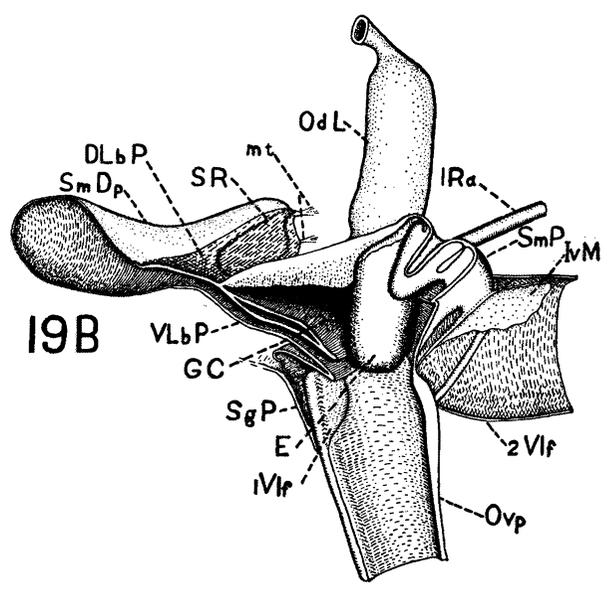


FIG. 20



19B

Larsen (1938) has described an unpaired, plate-like gland on the dorsal surface of the genital chamber of *Aphelocheirus* and *Micronecta*. The gland in these genera is also encircled by a sclerotized cuticular ring. Larsen believes that they produce a colleterial fluid.

#### The Spermatheca

The well developed, tubular organ referred to as the *spermatheca* in this paper opens medially into the genital chamber in the vicinity of the lateral oviducts (Figs. 8, 18, *SptG*). Three regions can be recognized in this organ. The first is the narrow *spermathecal duct* which opens into the genital chamber (Fig. 18, *SptD*). This is followed by the tubular *spermathecal chamber* (Fig. 18, *SptC*) which distally gives rise to the *spermathecal gland* (Fig. 18, *SptG*).

The lumen extending through these three regions is lined with a non-sclerotized, cuticular intima. The lumen of the basal portion of the spermathecal duct is very fine. In *Lygus lineolaris* the spermathecal duct is not straight but is convoluted as it passes through the genital chamber. Distally the spermathecal duct gradually widens as it opens into the spermathecal chamber (Fig. 9B). The cuticular intima of the spermathecal chamber is characterized by many encircling, ridge-like folds (Fig. 9B, *cu*). The spermathecal chamber is ensheathed by a relatively thick muscularis (Fig. 9B, *mcl*). The muscle fibers extend longitudinally and are attached on the distal and proximal marginal zones of the spermathecal chamber. Apparently the folds in the cuticular wall serve to enable a shortening and lengthening of the spermathecal chamber with the corresponding contraction and expansion of the muscularis.

The lumen of the spermathecal chamber gradually narrows distally as it passes into the spermathecal gland. In the glandular portion the cuticular intima is very fine. It is surrounded by large, wedge-shaped, glandular cells. In cross section a vacuole can be seen in various stages of development in the basal part of each cell (Fig. 9A). When fully formed these vacuoles are rather large. The cytoplasm has a strong tendency to retain the hematoxylin stain so that it is almost as dark as the nuclei. The nuclei when stained were granular and they were rather large and spherical.

It is of particular interest to note that sperms are not found in the spermatheca. However, comparison of this organ to the spermatheca of other Hemiptera leaves little doubt that it is at least homologous to a spermatheca.

The studies which have included the internal female genital organs of *Lygaeus*, *Pyrrhocoris* (Ludwig, 1926), *Naucoris*, *Notonecta*, *Aphelocheirus*, *Corixa* (Larsen, 1938), and *Nezara* (Malouf, 1933) indicated that the spermatheca of each of these genera has the same basic structure.

Three general regions are recognizable in the spermatheca of each, although the form of each region may vary considerably in the different genera. The spermatheca of each has an efferent duct which opens dorsally into the genital chamber. The duct leads from a muscular portion and apically there is a glandular portion.

In the reduviid genera *Rhodnius* and *Triatoma* an entirely different type of sperm-receiving organ has been described by Galliard (1935). This organ consists of paired sac-like structures which open ventro-laterally into the genital chamber. They are of integumental origin. It seems quite unlikely that these are homologous to the spermatheca of other insects because their structure is not like the typical spermatheca and because their openings are not in the proper relationship to the median gonopore. However, a tubular gland opening dorsally into the genital chamber of reduviids has been described by Galliard. He referred to this as the accessory gland and stated that the function of this gland is to cover the eggs with a secretion which will permit them to adhere to the substratum. Larsen (1938) has pointed out that the structure of this so-called accessory gland is very similar to the spermatheca of many aquatic hemiptera, such as species of *Naucoris*, *Aphelocheirus*, *Notonecta*, and the corixid species.

The so-called accessory gland of reduviids is also very similar to the spermatheca of Miridae. The similarity between the two is particularly marked in the basal tubular chamber found in each. As illustrated by Galliard (1935), the inner surface of this chamber contains a series of ring-like folds in the cuticular lining. The external surface of this chamber is covered by a layer of longitudinal muscles. This is essentially the same as the structure of the spermathecal chamber of mirids. The glandular distal portion of each is also very similar, and neither stores sperms in its lumen.

Last of all, it should be pointed out that the presence of muscles on this gland of reduviids is a further indication that it is a spermatheca rather than an accessory gland. The presence of muscles on the spermatheca of other insects is a characteristic commonly mentioned but, aside from Galliard's description, the author has found no mention in entomological literature of a muscularis associated with the accessory gland.

In *Cimex* there are also paired sac-like structures arising laterally from the genital chamber and they commonly are referred to as the spermathecae. Cragg (1920) and Abraham (1934), who have studied the structure of these pouches, indicated that they do not have an inner cuticular lining and that their function is the absorption of excess sperms. Neither of these workers regarded these organs as homologous to the true spermatheca of other insects. Since they lack an inner cuticular lining and have a different

function, they are probably not homologous to the sperm-receiving organ of reduviids. Abraham has stated that *Cimex* does not have an organ which could be considered to be a spermatheca.

#### *The Accessory Glands*

In this study the author has not found any glands in the mirids which are unquestionably homologous to the accessory glands of the female reproductive system of other insects. However, Kullenberg (1947) has pointed out that the eggs of mirids are usually coated with egg-cement when deposited. He attributed the secretion of this cement to glandular tissue at the base of the second valvulae. This is an assumption based on his observation that this tissue is more prominent in species in which the egg-cement is produced in greater quantities. Kullenberg suggested that when the ovipositor is extended the egg-cement is secreted into the egg-channel of the ovipositor. He did not provide illustrations of the gross anatomy or histology of this tissue.

In the present investigation the region at the base of the second valvulae has been carefully studied and the tissue believed to be that described by Kullenberg has been located. This tissue is found lining the inner surface of the anterior portion of each of the second valvifers. In young adult females of *Lygus lineolaris* this tissue is thin and indistinct but becomes thicker and more clearly differentiated from the adjacent epidermis when the female becomes gravid. When these patches of tissue are fully developed they are composed of large columnar cells which are stained very deeply by hematoxylin. Secretory vacuoles were not found in this tissue nor were there found any ducts or chambers.

In describing the typical form of the female accessory gland of insects, Snodgrass (1933) has noted that it develops as a median invagination of the ectoderm of the ninth-segment and that it is usually bifurcate. These patches of tissue in Miridae are associated with the ninth segment only in so far as they are on the second valvifers. They are bilateral rather than median. They are not tubular nor do they appear to be associated with any integumental invagination. It would probably be impossible to determine if this tissue has an important glandular function without detailed cytological study. However, since these patches of tissue lack cuticular lined ducts opening into the genital tract, it is doubtful that they are homologous to the female accessory gland or that they could function as colleterial glands.

It has been mentioned previously in this study that the spermathecae of certain reduviids apparently serve for the production of egg-cement (Galliard, 1935; Larsen, 1938). It is possible that the spermathecae of mirids have the same function.

In the discussion of the ringed glands in this paper it was noted that glands similar to these have been described in certain other Hemiptera in which they were considered to be the accessory glands and to produce egg-cement (Ludwig, 1926; Larsen, 1938). The ringed glands of mirids may be homologous to these but probably do not produce egg-cement.

#### *The Common Oviduct*

The lateral oviducts do not lead into a tubular common oviduct but enter separately into the genital chamber (Figs. 17, 20, *OdL*). The portion of the genital chamber through which the lateral oviducts enter is a clearly differentiated, non-sclerotized structure (Figs. 5, 19A, *OdC*). Kullenberg's (1947) study shows that this structure is commonly pouch-like. It appears to have been formed, at least partly, by the incorporation of the common oviduct into the roof of the genital chamber and is, therefore, referred to in the present study, as the *common oviduct*. The form and probably the function of this structure may vary considerably in different species. In *Miris dolabratus* (Figs. 7, 8, *OdC*) the common oviduct is a broad, flat pouch. In *Lopidea staphyleae* and *Phagiognathus albalus* the common oviduct is reduced to a flat membranous area in the roof of the genital chamber (Figs. 14, 17, *OdC*).

The epidermis of the common oviduct is well developed and may be glandular.

#### *The Lateral Oviducts*

The *lateral oviducts* arch dorso-anteriorly from the genital chamber (Fig. 20, *OdL*). A cuticular portion evidently derived from the common oviduct, extends a short distance into the lumen of each (Fig. 5, *OdL*). The lateral oviducts are enclosed by a thin layer of circular and longitudinal muscles. The circular muscles are especially well developed near the point of attachment of the lateral oviducts to the genital chamber, and in *Lygus lineolaris* they may be seen as swollen sphincters in this region (Fig. 19A, *sph*). The calyx (Fig. 20, *Clx*) of each lateral oviduct is not enlarged for the storage of accumulated eggs as it is in some insects.

#### *The Ovaries*

Each ovary consists of seven *ovarioles* extending serially from the calyx (Fig. 20). Apically the ovarioles are drawn out into *terminal filaments* (Fig. 20, *TF*) which join together into a suspensory ligament (Fig. 20, *SL*) extending anteriorly from each ovary. The suspensory ligaments extend into the thorax where they are separately attached to the anterior phragma of the mesonotum. The ovarioles are the acrotrophic type which according to Snodgrass (1935) is the usual type in Hemiptera. As the ovaries mature there is an accumulation of eggs in successive stages

of development in the ovarioles, the ovarioles become considerably longer and double up on themselves (Fig. 20, *a*). When fully mature each ovary is relatively large and occupies much of the space of the abdominal cavity.

#### *The Genital Muscles*

Eight pairs of muscles are directly associated with the female genitalia. Since the homologies of these muscles have not been established they are referred to here by numbers only. The most conspicuous of these are the three pair of muscles which are inserted on the ramal plates. The most anterior of these is a pair of muscles originating at the posterior lateral margins of the genital chamber and inserted on the dorsal anterior faces of the ramal plates (Figs. 7, 18, *M1*). These are designated as the *number one muscles*. Caudo-ventrad of these muscles there is another pair of muscles which originate on the valviferal apodemes and are inserted on the ventral portion of the anterior faces of the ramal plates (Figs. 7, 18, *M2*). These are referred to here as the *number two muscles*. The third pair of large muscles originates on the posterior portion of each of the valviferal apodemes and each is inserted on the posterior face of a ramal plate (Figs. 7, 18, *M3*). These are referred to here as the *number three muscles*.

A pair of small muscles originates on the median tergite of the ninth segment and each is inserted on the most posterior portion of a valviferal apodeme (Fig. 7, *M4*). These are designated here as the *number four muscles*. Slightly mesad of these muscles there is another pair of muscles which originate on the median tergite of the ninth segment and are inserted on the third valvulae (Fig. 7, *M5*). These are referred to here as the *number five muscles*.

The remaining muscles are attached on the labiate plates. Two pairs of fan-shaped muscles originate on the eighth paratergites and are inserted by tendons extending to the fused lateral margins of the labiate plates (Fig. 7, *M6*, *M7*). The muscles of the pair with the most anterior insertion on the labiate plates are referred to as the *number six muscles*. The muscles of the other pair are referred to as *number seven muscles*. A short pair of muscles which originate on the seventh sternum, and are inserted on the ventral labiate plates, (Fig. 7, *M8*) are referred to as the *number eight muscles*.

#### *The Mechanics of Oviposition*

The sheath of the ovipositor which is formed by the second valvifers and third valvulae is probably opened and closed by the action of the number one, two, three and four muscles which are inserted on the valviferal apodemes and by each of the number five muscles which are inserted on the third valvulae (Fig. 7, *M*). When the ovipositor is to be extended the sheath opens

until the ovipositor is erect and then closes behind it, locking the ovipositor in position. The extension of the ovipositor seems to be brought about by the contraction of the number four muscles. This produces a pull on the rami of the first valvulae and thus extends the ovipositor. As the ovipositor is extended the entire genital frame rocks so that the anterior end (that is, the base of the ovipositor) moves caudo-ventrad, and the posterior portion of the genital frame moves cephalo-dorsad (Fig. 7). This shift of the genital frame is brought about by the contraction of the number five and six muscles posteriorly and by the number eight muscles anteriorly. Probably this shift is also aided considerably by the dorsal longitudinal muscles of the eighth segment. Simultaneously, the entire abdomen is depressed so that the ovipositor is almost perpendicular to the substratum and the drilling movements of the ovipositor blades begin. Presumably these movements are essentially the same as those which may be observed shortly after decapitation of a gravid female. When such a female is placed ventral side up in a dissecting pan and covered with physiological saline, the ovipositor may be teased into the erect position and a series of distinct, rhythmical movements of the ovipositor blades observed. The primary drilling movements are alternate extensions and retractions of the first valvulae. These movements are occasionally interrupted by two or three movements of a different type. In this case the first valvulae work in unison and they and the second valvulae are alternately extended and retracted. This second type of movement probably serves to move the second valvulae down into the hole as it is drilled by the first valvulae.

The number one, two, and three muscles are responsible for the extension and retraction of the ovipositor blades. When they move the ramal plate posteriorly, this movement is transmitted through the rami of the first valvulae, retracting them. Similarly, when the ramal plate is pulled anteriorly, the first valvulae are extended. When the first valvulae are working alternately, the second valvulae are neither extended nor retracted, since they are fused into one piece and the pull of the muscles on one side is counteracted by the pull of the muscles on the other side. When the first valvulae are moved in unison the muscles of each side act to pull the second valvulae up at the same time they are extending the first valvulae and vice versa.

The number six and seven muscles (Fig. 18) serve to regulate the folds of the genital chamber so that the egg can pass through it. In *Lygus lineolaris* and *Miris dolabratus*, for example, contraction of these muscles bows the labiate plates and at the same time draws their anterior portion dorso-caudad. This causes the posterior margins which extend into the genital chamber to move

cephalo-ventrad, opening the passage between the oviducts and the egg-channel of the ovipositor. The shift in these parts can best be seen by comparison of the position of the labiate plates in Figs. 19A and 19B.

Meanwhile the muscles of the lateral oviduct begin to move the egg into the genital chamber. The alternate movements of the valvulae are transmitted through the genital chamber and these movements apparently serve to move the egg through the genital chamber. There are various special structures in the genital chamber of different species which facilitate the movement of the eggs. In *Lygus lineolaris* many of the parts bear fine wrinkles and spines. The apices of these structures are all directed distally, and as the parts of the genital chamber rub against the egg the friction moves the egg down into the egg-channel of the ovipositor. In *Lopidea staphyleae* there are biramous processes derived from each of the inter-ramal sclerites of the posterior wall (Fig. 15, *brp*). Each of these structures lies ventrad to the openings of the lateral oviducts. As the egg passes into the genital chamber the prongs of the biramous process on the side where the egg enters fits against each side of the egg. These prongs are lined with little teeth and as they move back and forth with the movements of the ovipositor blades they push the egg down into the egg-channel of the ovipositor.

The inner surfaces of the egg-channel of the ovipositor of mirids is lined with fine wrinkles. The crests of the wrinkles are directed distally; their friction against the egg as the valvulae move, causes the egg to move down and out of the egg-channel.

#### *The Terminology of Taxonomic Characters*

The more important structures used as taxonomic characters by Slater (1950) have been considered in this investigation. The sclerotized areas encircling the ringed glands were used extensively by Slater who referred to them as the *sclerotized rings* (Fig. 5, *SR*). Since little is known at present of the homologies and function of these glands, it is felt that a more adequate name for the structures encircling them cannot be suggested. Slater has referred to the plate on which the rings occur as the *F* structure. In the present study this structure has been named the *dorsal labiate plate* (Fig. 13A, *DLbP*). The subcent structure designated as structure *G* by Slater is referred to here as the *ventral labiate plate* (Fig. 13B, *VLbP*).

In the posterior wall of the genital chamber Slater referred to the two lateral sclerotized areas as the *A* structures. In the present paper these have been named the *inter-ramal sclerites* (Fig. 13C, *IrS*). The prominent mesal thickening of the posterior wall was referred to by Slater as the *B* structure. This structure is called the *sigmoid process* in the present study (Fig. 19A, *SmP*).

Various parts of the inter-ramal sclerites such

as the soft folds (Fig. 13C, *mb*) or the biramous processes (Fig. 15, *brp*) extending from the posterior margin were given alphabetical designations by Slater. Such designations were also applied to various regions of the sigmoid process. In the present study these regions have been referred to only by descriptive terms. It is felt that such descriptive terms plus specific names of the parts on which they occur will be adequate for taxonomic purposes.

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#### SUMMARY AND CONCLUSIONS

In the female mirids eleven abdominal segments may be distinguished. The sternum of the first segment is greatly reduced. The sternum of the seventh segment is produced caudally to form a subgenital plate. Spiracles are found on segments two through eight. The terga are inflexed on each side forming connexiva. Clear boundaries between the terga and sterna of the pregenital segments are lacking. Therefore, in order to avoid confusion resulting from this lack of boundaries the abdominal regions above and below the connexiva are referred to as dorsal and ventral plates.

The ovipositor is formed by the first and second valvulae. The second valvulae are fused into one piece except near their apices. The first valvulae are the blades active in drilling and have fine, saw-like teeth. They shuttle on ridges of the second valvulae which fit into grooves in the first valvulae.

The first valvifers are apparently represented by small lobes at the base of each of the first valvulae. The second valvifers are elongated plates forming a sheath enclosing the ovipositor when not in use. The third valvulae are small, lobe-like sclerites at the posterior end of each of the second valvifers.

From the base of each of the first valvulae a rod-like ramus extends back and is attached to the inflexed anterior margin of each of the ninth paratergites. The inflexed portions of the ninth paratergites are called the ramal plates. Ventrally the ramal plates are articulated to the second valvifers.

A small patch of bristles is found on each side of the abdomen in the intersegmental membrane between the eighth and ninth paratergites and near the point of articulation of the ramal plates to the second valvifers. These patches are probably sensory organs.

The sternal portion of the eighth and ninth segments is apparently turned inward forming a vestibulum and genital chamber. The vulva of the vestibulum lies beneath the subgenital plate.

A membranous cuticular sac extends anteriorly from the genital chamber. This sac evidently serves to receive and store sperms and has therefore been named the seminal depository. The orifice of this sac is formed by broad dorsal and ventral sclerotized pieces called the labiate plates. On the dorsal labiate plate there is a pair of sclerotized rings encircling modified epidermal tissue which is apparently glandular. These two plates of epidermal tissues have been termed the ringed glands. The secretion of these glands is believed to be related to the maintenance of the sperms. They appear to be homologous to accessory glands which have been described in other Hemiptera but which have been reported to have a different function.

The posterior wall of the genital chamber may be differentiated into a pair of sclerites termed the inter-ramal sclerites and a median sclerotized process which is typically s-shaped and has been termed the sigmoid process.

The spermatheca is a long, vermiform organ which opens on the roof of the genital chamber. It consists of a basal duct portion, a median chamber, and an apical gland portion. The chamber is provided with a muscularis. This organ evidently does not serve for the storage of sperms. Possibly its secretion is spermatophilous or it serves as an egg-cement.

It has been shown that structures described as the accessory glands in an earlier study are not true accessory glands and do not produce the egg-cement. The source of the egg-cement remains undetermined.

The common oviduct appears to be modified to form a pouch or membranous area on the roof of the genital chamber. The lateral oviducts open separately into the genital chamber through the common oviduct.

The ovaries each consist of seven acrotrophic ovarioles and are suspended by separate ligaments which are attached to the anterior thoracic phragma.

There are eight pairs of genital muscles. These variously serve to erect the ovipositor, extend and retract the blades of the ovipositor, and to open the genital chamber so that the egg may pass through.

The drilling movements of the ovipositor consist primarily of alternate extensions of the first valvulae. These movements are interrupted at intervals and the first valvulae move in unison.

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