THE MORPHOLOGY OF THE GENITALIA AND ASSOCIATED ABDOMINAL SEGMENTS OF MONOCHAMUS CAROLINENSIS (OLIVIER)

(COLEOPTERA: CERAMBYCIDAE)

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By

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I. INTRODUCTION

The present paper deals with the structure of the genitalia and associated abdominal segments of one of the North American species of long-horned beetles, Monochamus carolinensis (Olivier). Those who have previously figured the genitalia of certain groups of Coleoptera have usually made no attempt to homologize the structures with those of the related groups. Workers have unfortunately used their own special terms without regard to previous terminology. This has resulted in a system of terminology which is complex and confused. An attempt is made to elucidate concepts pertaining to the structure of the genitalia of coleopterous insects.

Little has been published concerning either the morphological or ecological aspects of the long-horned beetles. The structure of the genitalia is important in both the fields of morphology and taxonomy. Representatives of the subfamilies and tribes should be studied in detail throughout the family Cerambycidae. As time was limited only this species was studied, the results of which are presented.

II. REVIEW OF LITERATURE

In the literature there is limited information on the muscular mechanism of the abdominal segments of the cerambycids and only a few important papers on the genitalia of beetles can be found. In addition, most of the papers were published in the second half of last century or early in the 20th century. Their points of view are usually beyond the scope of homology and phylogeny and are inadequate for the present.

The most outstanding paper of these is that of Tanner (1927), who has done considerable work on the morphology of female genitalia of coleopterous insects. He has advanced our knowledge of the female genital apparatus considerably, but like many others has failed to homologize the structures and was mislead as to the segmentation and interpretation of the structure of genitalia. He has treated the whole structure that retracted into the body including the genital and post-genital segments as the female genitalia.

Another remarkable paper is that of Sharp and Muir (1912). They divided the male genitalia of coleopterous insects into two main portions, the zygotic and azygotic. The azygotic portion was further subdivided into the eurazygotic and stenazygotic portions. As they explained these terms, the azygotic portion, or azygos, comprises all the unpaired portion of the tube from the body wall to the divergence of the ends of seminal ducts; the zygotic portion, or zygos, is formed by the two seminal ducts preceeding from the testes; the eurazygotic portion, or eurazygos, is the enlarged portion of the genital tube; and the

stenazygotic portion or stenazygos, is the slender portion of the azygos.

It is very clear that the zygotic portion (the zygos), is the seminal duct or the vasa deferentia; the stenazygotic portion (the stenazygos) is the ejaculatory duct, or the ductus ejaculatorius; and the eurazygotic portion (the eurazygos), is the phallus with internal sac. The whole apparatus is rather simple in structure. To divide the genital apparatus into so many portions and establish so many special terms seems unnecessary and merely adds to the confusion in terminology.

III. THE GENERAL MORPHOLOGY OF THE ABDOMEN

A consideration of the functional aspects of the insect genitalia must be based upon adequate understanding of the morphology of the abdomen. Thus, a brief description of the abdomen of Monochamus carolinensis (Olivier) (which this study deals with) follows.

In general, the insect abdomen may be divided into three divisions:

First, the pregenital or visceral segments, including the first to seventh segments, are usually of simple form and structure and differ but little from one another.

Second, the genital division, including the eighth and ninth segments, usually bears the genital aperture and genital appendages.

Third, the postgenital division includes segments ten and eleven. This region usually bears the anus and terminal appendages, such as the cerci and the telson, and in certain forms the median caudal filament.

In Monochamus carolinensis (Olivier) as well as other long-horned beetles, the abdomen is rather simple. Only seven segments are visible on the dorsal surface (Figure 2) and five on the ventral (Figure 1). All the terga, except the last one, are similar in size, shape and weakly sclerotized, as they are covered by the hardened elytra. Some forms with narrow elytra as Thranius spp., with short elytra as Molorchus spp., and Stenopterous spp., and certain others are exceptions. The last visible tergum, the seventh, is larger than the preceding and unlike others is strongly sclerotized, as it is usually beyond the cover of the elytra, especially in the female. The sterna are five in number, as

the first two are concealed and overlapped by the hind coxae. All of the sterna are strongly sclerotized. Only the last visible sternum, the seventh, differs in shape from the preceding.

The eighth, the ninth, and the post-genital segments are all retracted into the abdomen and concealed by the seventh tergum and sternum.

IV. THE ASSOCIATED ABDOMINAL SEGMENTS

The abdominal segments associated with the genitalia are the seventh segment (the last visceral segment), the eighth segment (the first genital segment), the ninth segment (the second genital segment), and the tenth segment (the periproct).

The male

The seventh segment.--The seventh tergum is much more sclerotized than the preceding, setiferous along the posterior margin, and with a broad projection on the anterior margin which projects forward into the body cavity under the preceding tergum. This projection functions as an apodeme and increases the area of attachment for muscles. This tergum is termed the pygidium in taxonomic literature, visible externally and usually extending beyond the cover of the elytra.

The sternum of the seventh segment is taxonomically known as the subgenital plate. Its posterior margin is much narrower than its anterior margin. Along the posterior margin there are many bristles and a thin triangular region demarked by darker color and larger hairs.

The eighth segment.--This segment, as well as the ninth, is retracted within the body in its usual condition. It is much reduced in size. The tergum of the eighth is complete, with the same shape as the seventh tergum only much smaller in size (Figure 15). The sternum (Figure 16) is much reduced and present as a broad band-like sclerite with a thin Y-shaped and strongly sclerotized apodeme at the base

(the anterior portion). This apodeme projects forward and functions for support of muscles which evert and retract this segment (Figure 11).

The ninth segment.--The structure of this segment (Figure 17) is greatly modified. The entire tergum and sternum are pliable and toughly membranous. When the ninth segment retracts inwardly it successively ensheathes the genitalia in its usual state, and forms the so called genital chamber. On the ventral basal margin there is a slightly larger Y-shaped apodeme similar to that of the eighth sternum.

The tenth segment.--This segment has been called the periproct which bears the epiproct and paraprocts surrounding the anus. But in this insect, it appears only as a small projection from the dorsal wall of the entrance chamber.

The female

The seventh segment.--The subgenital plate (Figure 3) and tergum or the pygidium (Figure 4) are similar to those of the male. The posterior margins are slightly broader when compared with the anterior.

The eighth segment.--This segment (Figures 7, 8, 9) is extremely modified in shape and structure. Its tergum is complete but much reduced, with long hairs on its posterior angles, and its lateral margins extended to the ventral aspect involving the lateral portions of the sternum. The sternum is membranous, in great part, with a wing-like and slightly sclerotized plate at the basal portion and a large and strongly sclerotized plate mesally. A very long and strongly sclerotized apodeme arises from the mesal plate and projects forward through the abdominal cavity with its tip into the metathorax. This extremely long apodeme serves for the attachment of muscles which evert the eighth,

and the following segments, and genitalia at the time of copulation. Muscles are connected to the tip of this apodeme and the anterior margin of the seventh sternum ventrally. When contracted, these muscles result in the eversion of the eighth segment, the following segments, and genitalia. In the dorsum, there are muscles arising from the tip of the apodeme which connect to the oviductus communis directly. When contracted these same muscles indirectly pull the ninth segment within the abdomen proper. Thus they also function as retractors of the ninth segment and the genitalia.

In its usual condition, the eighth segment as well as those posterior to it are retracted within the body.

The ninth segment.--This segment is notable by its entirely complicated folding membranous condition with the dorsal anus and the external genitalia ventrally at its terminal end. In the usual condition, the terminal-half retracts into the basal-half with the apex of the tube forming a double-walled tube (Figure 9). The cavity of the double-walled tube is the genital chamber. The retracted ninth segment with the genitalia in its cavity retracts into the eighth segment. It everts only during the period of copulation or egg-oviposition.

The tenth segment.--This segment is markedly reduced, only the proctiger, a portion of the tenth tergite, is visible. It bears the anus which is located on the dorsal base of the genitalia and beneath the proctiger. The epiproct and paraprocts are lacking.

V. THE GENITALIA

The male

The male genitalia (Figures 11-14) of this species consists only of the phallic structures, the aedeagus, and the phallobase. All the structures are derived from the appendages of the ninth abdominal segment.

The aedeagus has developed from the second gonapophysis and contains the phallus and the internal sac. The two united gonapophyses form the phallus proper, which invests the internal sac. The bases of two parameres connect to the phallobase with membrane. These continue anteriorly to form the struts. At the terminal end of the phallus there is an opening, the median orifice, along the edge of which it connects with the membrane of the internal sac, and through which the internal sac may evert during copulation.

The internal sac (terminal vesica of Snodgrass) connects to the median orifice at its basal end, to the ejaculatory duct with its apical end. It is retracted into the ninth abdominal segment in the usual condition and everted through the median orifice during copulation. When it is evaginated the opening at its terminal end is the genital aperture or gonopore.

The phallobase (tegmen of Sharp and Muir) is developed from the coxites of the ninth abdominal segment and well differentiated from the aedeagus. It bears a pair of valves called the parameres or lateral lobes and a median dorsal lobe called the epimere or the basal piece.

From its base, an apodeme called the terminal strut projects into the body cavity and serves as the attachment of muscles.

In coition, only the aedeagus is the intromittent organ, namely only the phallus with the internal sac inserts into the female genitalia and the latter when everted is the only functional part. The phallobase is left outside of the female genitalia but in the genital chamber with its terminal end against the ventral chamber wall and its struts against the dorsal chamber wall. It maintains the position of the aedeagus in the female genitalia and is similar to that of the claspers in other male insects. Thus it functions for the aedeagus during copulation not only as a support but as a guide and also as a sustaining apparatus.

The female

The female genitalia (Figures 5-9) of this insect consists of two main parts, the genitalia proper and the genitalia valvae or egg guides. The former is presumed to have developed from the ninth gonapophyses which united together to form a completely membranous tube-like structure. It bears the anus dorsally at its base, and the valvae on its sides.

The latter are presumed to have developed from the ninth gonocoxites. Apically each valva bears a small stylus which internally is supported by the baculum, a rod-like sclerotized structure. This functions as a stiffening structure for the valva and a support for the genitalia. The valvae serve as a guide for copulation as well as for oviposition.

VI. DISCUSSION

An attempt should be made to establish a common understanding regarding the morphological concepts of pterygotan insect genitalia. For the sake of convenience, the interpretation of Michener (1944) is quoted:

Origin	Female	Male
Coxites of eighth abdominal segment	First valvifer	Absent in Pterygota
Gonapophyses of eighth abdominal segment	First valvae	Absent in Pterygota
Coxites of ninth abdominal segment	Second valvifer	Gonocoxites
Gonapophyses of ninth abdominal segment	Second valvae	Penis valves (?)
Styli of ninth abdominal segment	Third valvae	Gonostyli

This table shows that the higher female insectan genitalia is composed of the coxites and the gonapophyses of the eighth abdominal segment, and the coxites, the gonapophyses, and styli of the ninth abdominal segment. In the male, only the coxites, gonapophyses, and styli of the ninth abdominal segment are involved.

Gustafson (1949) stated that, "The appendage rudiments develop into the coxites and their styli; while the ampullae from the gonapophyses of both male and female and the phallus of the male. The genitalic patterns of all insects are derived from a common plan." He states

further that, "Evolutionary tendencies of the ovipositor are demonstrated in the complete loss of the structure, in the reduction in size of the inner valvae (gonopophyses of the ninth segment) with the concurrent development of gonocoxites of segment nine to form a pair of valves greatly resembling the gonopophyses of segment eight, and in the general reduction of all component structures. The latter condition is best demonstrated in the Coleoptera.

"The males show a great stability in the retention of the gonocoxites of the ninth abdominal segment and to a lesser degree the styli of that segment. There is a strong tendency for the gonapophyses (Parameres) of the male to fuse with the phallus.

"The primitive phallus of the insects is primarily a paired structure.

"The genitalic appendages of all insects may be directly compared with the basic pattern as demonstrated in the Thysanura.

"No completely new structures have arisen, all variations from the basic pattern occurring by the modifications of existing appendages and sclerites or by loss".

In fact, there is a common tendency in the evolution of the insectan abdomen to gradually simplify it from the abdomen of lower groups to those of the higher groups.

The number of the abdominal segments is gradually reduced,,as in the Order Protura where the number of abdominal segments is twelve. The Order Collembola is an extreme exception, for the abdomen of this group has only six segments, even in embryonic stages. In the lower groups of ptergotan insects, such as the orthopteroid and hemipteroid orders, the visible abdominal segments are always less than twelve,

usually nine or ten in number. In higher groups, the neuropteroid orders, the number of visible abdominal segments is even more reduced. It is not rare that six or seven abdominal segments may be found in Coleoptera, five in Hymenoptera, and three in the Diptera.

Abdominal appendages borne on the pregenital segments (one to seven) are found only in the apterygotan orders, such as Protura, Collembola, Diplura, and Thysanura, and have never been found in the pterygotan orders. As for those appendages borne on the genital or postgenital segments, though they may be found throughout the orders, they have disappeared or are concealed in the abdomen in higher groups.

Because the insect abdomen and its appendages are reduced in sum and form in the higher groups, there is no reason to think of the genitalia which developed from the appendages of the eighth, and ninth abdominal segments as being more complex than those of the lower insects.

In this species as well as its allies and even in the whole order of Coleoptera, the female genitalia consists only of the appendages of the ninth abdominal segment. However, former workers have used various terminologies reflecting their opinions concerning the structures of the female genitalia of coleopterous insects. Stein (1847) considered the structures of the female genitalia of coleopterous insects as the divided ninth sternum. Verhoeff (1894) considered them as the tenth sternum. Wheeler (1893) considered them as rudimentary abdominal appendages and designated them as ninth valvae which consist of the valvifers, coxites, and styli. Peytoureau (1895) thought that they were the eighth sternum in the Dytiscidae and the seventh in the

Hydrophilidae. Wandollek (1905) considered them as the tergum or sternum of ninth segment. MacGillivray (1923) contended that the "Octopophyses" have migrated caudad from the eight segment to their present position, the posterior margin of the ninth segment. Crampton (1925) considered them as rudimentary abdominal appendages and designated them as ninth valvae, including the valvifers, coxites, and styli, the same as that of Wheeler, and suggested that the paraproct of the beetles may be a part of the ninth tergite called the surstylus in other insects, as in Trichoptera. Tanner (1927) considered them as the coxites and styli of the ninth segment, and that the valvifer are a sclerotized portion of the adjacent end of the ninth sternite which bears the coxites and styli, and some sclerotized remnants of the tenth sternite in some species, and proposed to call the rod like structures of the paraprocts, valvifers and coxites, the baculi which are lying in the integument and serving as stiffening structures for the long membranous expanses of the ovipositor.

From all the evidence obtainable, there seems to be no reason for considering parts of the female genitalia of coleopterous insects as the structures of the eighth or tenth segment. Some aspects in Tanner's paper (1927) are worthy of considerable attention. His statement that "The genitalia consist of the eighth, ninth, and tenth abdominal segments and their appendages" is not true in the Cerambycidae. The associated eighth, ninth, and tenth abdominal segments are not included in the composition of the genitalia. The genitalia are developed from the appendages of the ninth abdominal segment only. In addition, the appendages of the tenth segment, the cerci, which have functions related to reproduction are only found in Embioptera or other very rare

cases. So the statement, "the genitalia consist of eighth, and tenth segments and their appendages" is to inclusive. The statements that "The proctiger is a part of the tenth tergite. The paraprocts are probably parts of the ninth tergite." is not true in any case. The paraprocts are always accompanied with the epiproct, if they are present, and the epiproct is always located on the proctiger. Since the proctiger is a portion of the tenth tergite, the paraprocts should also belong to the tenth segment. To think of the proctiger as an upper genital valvae is also a misleading concept, because it is always located above the anus.

VII. CONCLUSION

From a morphological study of the structure of the genitalia and abdomen of Monochamus carolinensis (Olivier), it has been shown that seven visible abdominal terga and five sterna are present. The structure of the external genitalia is much simpler than that of the lower pterygotan insects. The male genitalia consists only of the phallus and phallobase, but the former with an internal sac and the latter with the modified valvae. Both of these structures are developed from the appendages of ninth abdominal segment. The phallobase functions similarly to those of the claspers of other insects, but serves to prevent its forward movement instead of holding. The female external genitalia consists of the genitalia proper and the genital valvae. Both of these structures are developed from the appendages of the ninth abdominal segment. The modified genital valvae with styli on or near their terminal end have the functions of support for the genitalia and guide for copulation and oviposition. The seventh abdominal tergum, the dorsogenital plate, is well developed, with one (in male) or two (in female) expansions (the apodeme) along the anterior margin and long bristles along the posterior margin, the bristles at the angle being much longer. The seventh abdominal sternum, the subgenital plate, is also well developed, with long bristles along the posterior margin and conceals the genital and postgenital segments within the body. The eighth abdominal segment is much reduced in size and retracted within the body in its usual condition. In the ventral area there is a rod-like

structure, the apodeme, which serves as an attachment for muscles and has the functions of supporting, everting, and retracting this segment and the others succeeding to it. This rod-like apodeme in the female is especially long and retracted through the abdominal cavity into that of the metathorax. The ninth abdominal segment is much modified in shape and much reduced in size. The tergum and sternum of this segment are entirely membranous. When its terminal half retracts inwardly it successively ensheathes the genitalia and forms the genital chamber. In the male, there is a similar apodeme to that of the eighth sternum, in the ventral region. The tenth abdominal segment, which bears the anus, is located dorsally on the base of the external genitalia and behind the ninth segment. It is very reduced, but in the female its epiproct and paraprocts seem to be sclerotized. The external genitalia both of the male and female is developed only from the appendages of the ninth abdominal segment. The terminal abdominal segments are not included in the composition of the external genitalia but merely associated with it.

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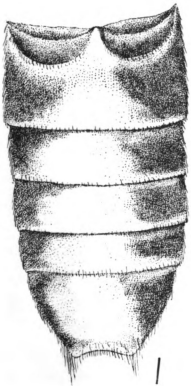
EXPLANATIONS OF PLATES

Figure 1. Ventral aspect of the female abdomen.

Figure 2. Dorsal aspect of the female abdomen.

Figure 3. Ventral aspect of the female seventh sternum.

Figure 4. Dorsal aspect of the female seventh tergum.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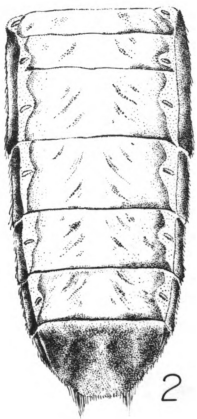
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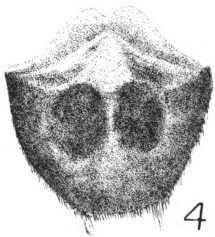
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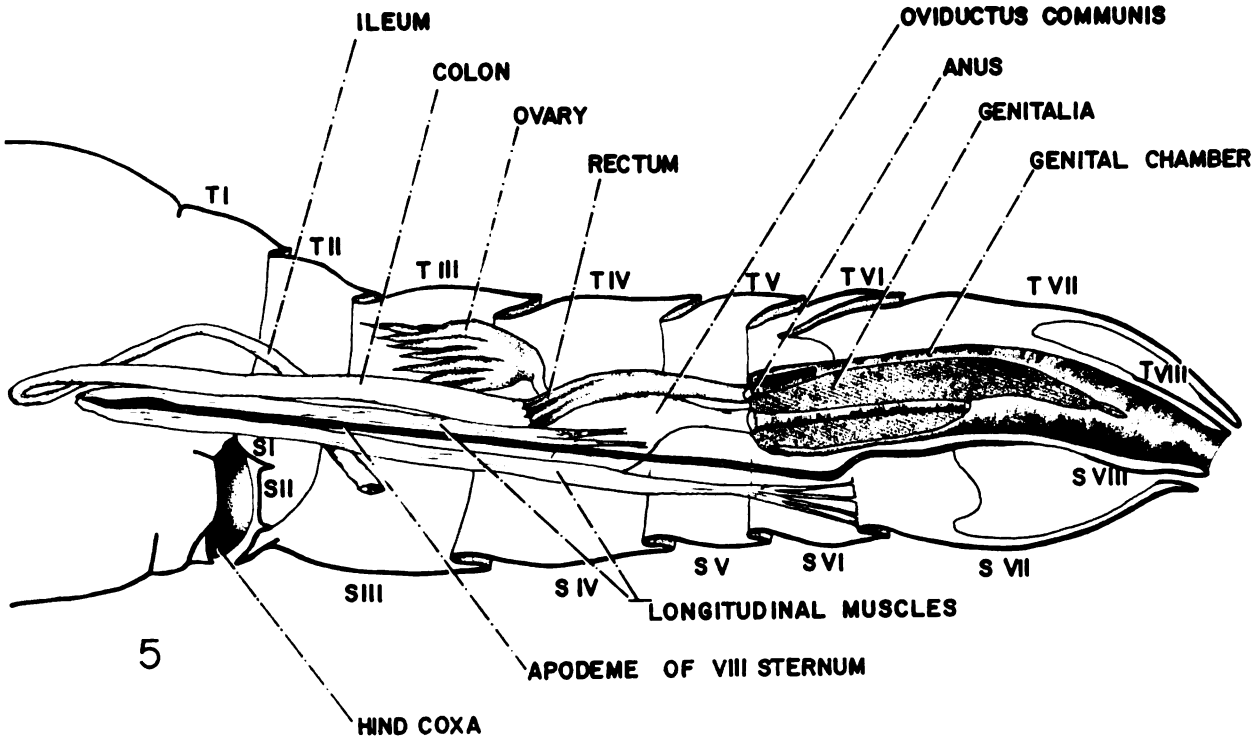
Figure 5. Longitudinal section of the female abdomen.

Figure 6. Enlarged parasagittal view of the brain and posterior segments of the female.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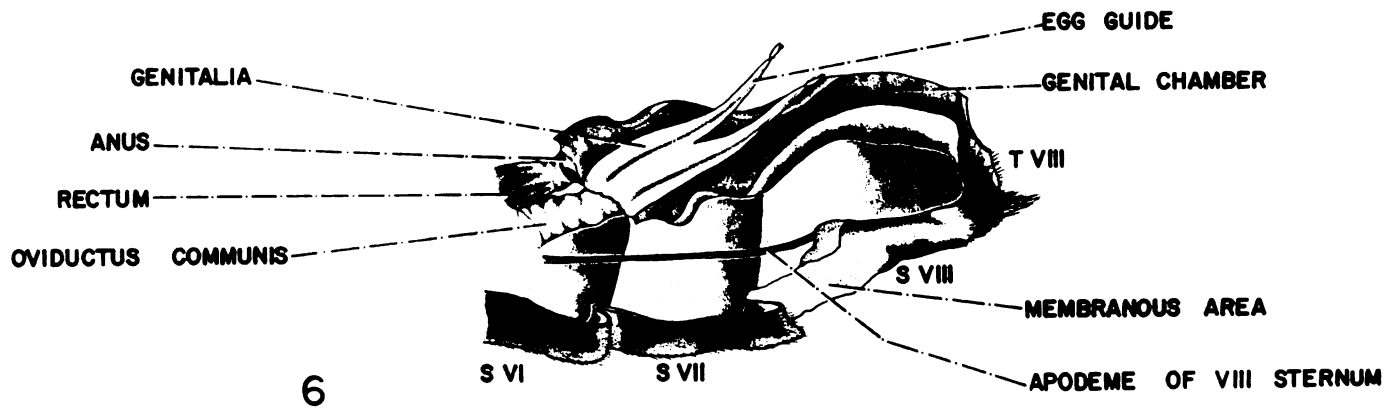
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APODEME OF VIII STERNUM

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Figure 7. Dorsal view of the eighth and ninth segments showing the relation of the female genitalia.

Figure 8. Ventral view of the eighth and ninth segments showing the relation of the female genitalia.

Figure 9. Dorsal view of the eighth and ninth segments showing the female genitalia protruded.

Figure 10. Ventral view of the eighth and ninth segments showing the female genitalia protruded.

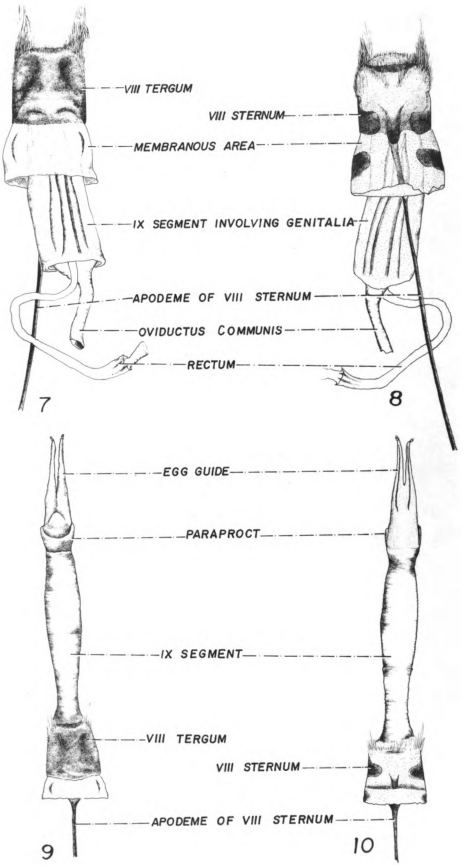
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Figure 11. Dorsal view of the eighth and ninth segments showing the relation of the male genitalia.

Figure 12. Ventral view of the eighth and ninth segments showing the relation of the male genitalia.

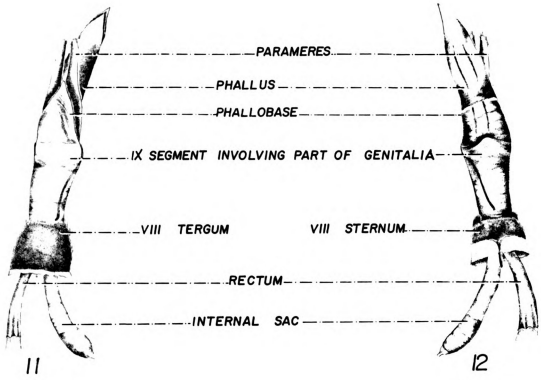
Figure 13. Enlarged dorso-lateral view of the external male genitalia.

Figure 14. Enlarged latero-ventral view of the external male genitalia.

Figure 15. Eighth tergum of male.

Figure 16. Eighth sternum of male.

Figure 17. Ninth segment of male.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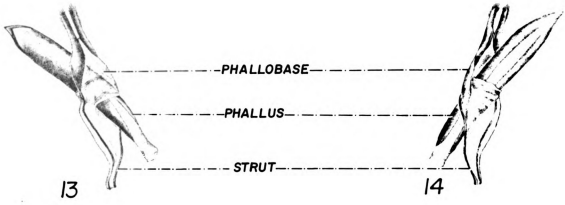
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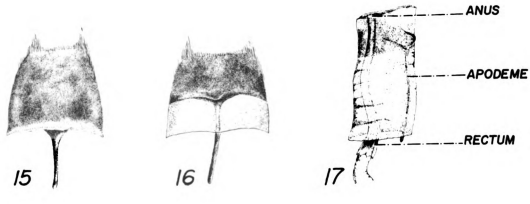
ANUS
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