THE COPULATORY AND OVIPOSITIONAL APPARATUSES OF SPEYERIA (LEPIDOPTERA: NYMPHALIDAE)

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ABSTRACT

THE COPULATORY AND OVIPOSITIONAL APPARATUSES OF SPEYERIA (LEPIDOPTERA: NYMPHALIDAE)

By

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The morphology of the copulatory and ovipositional mechanisms of Speyeria are described. The myology of the copulatory and ovipositional mechanisms is described, named, and homologized. Finally, the sequential skeleto-muscular events of copulation and oviposition are explained.

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INTRODUCTION

Lepidopterists have relied heavily upon the structural peculiarities of Lepidoptera genitalia to clearly demarcate species. The great diversity in structural detail of the genitalia has proved of inestimable value for the identification of Lepidoptera at the species level. Yet, little effort had been expended to understand the operational mechanism of the genitalia during copulation. Without a functional analysis of the external genitalia, it is difficult to determine how its components are interrelated, to properly assess their adaptive importance, or to deterine their role in the evolution of the species.

This study reports on the morphology of the male and female abdominal segments, the myology of the abdomen, and the operational mechanism of copulation and oviposition in *Speyeria atlantis* (Edwards), *S. cybele* (Fabricius) and *S. aphrodite* (Fabricius).

There have been very few studies on the functional morphology of the external genitalia of insects. Kullenberg (1947) studies the copulatory apparatus in Hemiptera. Bonhag and Wick (1953) studied the common milkweed bug, *Oncopeltus fasciatus* (Dallas) (Hemiptera: Lygaeidae). Kunze (1959) studied the morphology of the genitalia in the Cicadidae. Fischer (1956) reported on the morphology of the male *Megachile fortis* (Say) genitalia (Hymenoptera: Megachilidae).

The morphology of the male copulatory musculature of relatively few species of Lepidoptera has been described and these often inaccurately. Snodgrass (1936 and 1957) briefly described the musculature of *Carpocapsa pomonella* (L.) and *Bombyx mori* (L.). Unfortunately these two species possess rather reduced external genitalia with some structures having been lost, and others apparently coalesced.

Forbes (1939) reported in detail upon the male copulatory musculature of the noctuid, *Septis arctica* (Boisduval), and added some notes on the male copulatory musculature of seven other species. Santer (1956) did the same for *Solenobia*, a psychid. Shirozu and Yamamota (1953) studied the muscles, skeletal and membranous parts of the male external genitalia of the nymphalid *Argyronome laodice japonica* (Menetries). Ehrlich and Davidson (1961) illustrate the musculature of the male and female external genitalia of *Danaus plexippus* (L.).

Hannemann (1954a and 1954b) studied both the male and female abdominal and external genitalia musculature of the Nymphalid, *Argynnis paphia* (L.). He later (1957) described the male musculature for the microterygid, *Micropteryx calthella* L. For each species he described what he believed to be the role of the muscles and components of the male external genitalia and female during copulation. Steklonikov (1965) briefly described the morphology of the copulatory apparatus in both sexes of four moth species.

The terminology pertaining to the structure of the male and female external genitalia of the Lepidoptera has been subject to much confusion. Several nomenclatural systems, many purely descriptive in nature, have previously been set forth. Others have been based upon the comparative morphology of the adults. In this paper, the terminology as set forth by Klots (1970) has largely been followed.

GENERAL STRUCTURE OF THE ABDOMEN

The definitive abdomen of Speyeria consists of ten segments in both sexes. Segments I-VII constitute the pre-genital area of the abdomen. Segments VIII-X, which have been variously modified to house and operate the reproductive apparatus, constitute the genital segments of the abdomen. The first abdominal segment is partially suppressed and can be easily overlooked. The pre-genital area is comparatively rather short, robust, rounded and somewhat depressed ventrally. The genital area is conical, tapering posteriorly (Figs. 1 and 2).

Female Segmentation

In the female, only the tergum of the first segment is clearly present, as the sternum is reduced. Sterna II-VI are similar to one another. Each is more or less rectangular in shape and slightly bowed. Each successive sternum decreases slightly in length and width, until sternum VI which is about half the length of sternum II (Fig. 2). Sterna VII and VIII are elongate and conical caudally. Segments IX and X have fused and become modified to form the anal papillae. The sterna and terga of segments IX and X are not clearly distinguishable (Fig. 8).

A well-defined antecosta is found along the anterior margin of sternal plates II-VII. The acrosternite, which extends anteriorly from the antecosta as a narrow marginal flange in many insects, is lacking on all of the sternal plates.

Between each successive sternum and tergum is the intersegmental membrane, or conjunctiva. The intersegmental membrane is folded upon itself in a non-extended individual, whereas, in an extended individual the membrane becomes taut. This membrane is attached anteriorly to the trailing edge of the sclerite, and posteriorly on the antecosta of the following sclerite, and allows a segment to slide over the following segment upon two opposing sclerotic surfaces.

A pleural membrane extends between each sternum and tergum of the first through seventh segments. The sternum and tergum of segment VIII closely approximate one another due to the extreme reduction of the pleural membrane.

Terga II-VII are similar to the sterna in general organization and appearance. Each tergum is rectangular in shape, successively decreasing slightly in length and width through tergum VI, which is about half the length of tergum II. On the anterior lateral edge of terga VI and VII is a rounded, somewhat produced tergal apodeme, to which the Tertiary lateral dorsal longitudinal muscle attaches.

A conspicuous antecosta, onto which the longitudinal muscles are attached, is found along the anterior margins of terga II-VII. It is lacking in tergum VIII, and difficult to discern in the fused ninth and tenth segments. Tergum VIII possesses the anterior apophyses and segment IX possesses the posterior apophyses (Figs. 2 and 8).

Female Musculature of Segments II-VI

With but minor variations the musculature of the abdominal segments in the females of *Speyeria atlantis*, *S. cybele* and *S. aphrodite* has been found to be essentially the same. Thus if the above sampling of fritillaries in any manner indicates the myology of the group, the following discussion on the mechanism of the pre-genital musculature of these three fritillaries, is likely to be representative of the genus *Speyeria* and possibly other closely related genera. To eliminate the lengthy muscle terminology in the text and possible confusion with figure references, the muscles have been designated by numbers in italics. Each muscle has its own number, which is used throughout the text and figures, and may be referred to in the annotated descriptive list of muscles found at the end of this paper.

The pre-genital musculature of female *Speyeria* follows a definite pattern which is repeated in segments IV through VI of the terga and throughout the II through VI sterna (Fig. 2). Modifications in this general pattern of musculature have occurred in the first abdominal segment, due to its attachment to the thorax, and terga II and III. The copulatory function of segments VII through VI have likewise resulted in modification of the muscular pattern of these segments (Fig. 8). There are 32 paired muscles in the six pre-genital segments of these female fritillaries. The muscles of the pre-genital segments function collectively as contractors of the pre-genital segments, but operate individually as retractors of their respective segments.

While the musculature of a few of the segments is dissimilar, there is enough similarity in the various segments to warrant a discussion of the muscular mechanism of the more generalized segments (segments IV, V, and VI). Thus, only those muscles of segments IV, V, and VI are specifically mentioned. The homologs of these muscles in other segments function in a similar manner, except where otherwise stated. Variations in the general pattern of muscles in other segments are noted later.

The contractors of the pre-genital segments all function in the retraction of the tergal or sternal plates over one another. The retraction of these individual plates results in the decreased length or contraction of the pre-genital region. The *Median dorsal longitudinal muscles* (*12*, *19*, *26*), the *Accessory median dorsal longitudinal muscles* (*13*, *20*, *27*), the *Primary lateral dorsal longitudinal muscles* (*14*, *21*, *28*), the *Secondary lateral dorsal longitudinal muscles* (*15*, *22*, *29*), and the *Tertiary lateral dorsal longitudinal muscles* (*16*, *23*, *30*), all serve as tergal retractors (Fig. 2). The *Ventral longitudinal muscles* (*18*, *25*, *32*), and the *Lateral ventral longitudinal muscles* (*17*, *24*, *31*), serve as retractors of the sternal plates (Fig. 2).

The musculature of terga II and III is similar, except that the *Tertiary lateral dorsal longitudinal muscle* (the homolog of *16*) is lacking in segment III, while in tergum II neither the *Secondary* or *Tertiary lateral dorsal longitudinal muscles* (the homologs of *9* and *16*) are present (Fig. 2).

Male Segmentation

In contrast with the female, the tergum and sternum of the first segment are both present. Sterna II through VIII are similar to one another, although sternum II slopes anteriorly to accommodate the attachment to the thoracic area. Each is more or less rectangular in shape and slightly bowed. Each successive sternum decreases slightly in length and width, until the eighth sternum which is about half the length of sternum II (Fig. 1).

A well-defined antecosta, on which the longitudinal muscles are attached, is found along the anterior margin of the sternal plates. The acrosternite, which extends anteriorly from the antecosta as a narrow marginal flange in many insects, is lacking on all of the sternal plates.

Along the apical margin of segments II through VIII is the intersegmental membrane as is found in the female.

Sterna IX and X have become modified to form components of the external genitalia.

Terga II through VIII are similar in structure and complementary to the sterna in general organization. A conspicuous acrotergite is found on tergal plates V through VII. Terga IX and X have likewise become modified to form components of the external genitalia.

Male Musculature of Segments II-VII

The pre-genital musculature of male *Speyeria* follows a definite pattern which is repeated in segments IV through VII of the terga and sterna II through VII. Modifications in this general pattern of musculature have occurred in the first abdominal segment, due to its attachment to the thorax, and the second and third terga. The copulatory function of segments eight through ten have likewise resulted in modification of the musculature pattern of these segments. There are 34 paired muscles in the pre-genital segments of these male fritillaries. The myology of the pre-genital segments of the male abdomen is quite similar to the female, muscle homologs are numbered similarly, and likewise function in a similar manner.

The contractors of the pre-genital segments all function individually in the retraction of the tergal or sternal plates over one another. The retraction of these individual plates results in the decreased length or contraction of the pre-genital region. The *Median dorsal longitudinal muscles* (*12*, *19*, *26*, *50*), the *Accessory median dorsal longitudinal muscles* (*13*, *20*, *27*, *51*), the *Primary lateral dorsal longitudinal muscles* (*14*, *21*, *28*, *52*) and the *Secondary lateral dorsal longitudinal muscles* (*15*, *22*, *24*, *53*), all serve as tergal retractors, whereas the *Ventral longitudinal muscles* (*18*, *25*, *32*, *55*) and the *Lateral ventral longitudinal muscles* (*17*, *24*, *31*, *54*) serve as retractors of the sternal plates (Fig. 1).

The musculature of terga II and III is similar to that of terga IV through VII. However, in terga II and III, the *Secondary lateral dorsal longitudinal muscle is not present*. In tergum II, the

Accessory median dorsal longitudinal muscle (*2*) is so closely allied with the *Median dorsal longitudinal muscle* (*1*) that they appear to be one muscle rather than two distinct muscles as they do in the succeeding terga.

THE MORPHOLOGY OF SPEYERIA GENITALIA

A great many entomologists have studied the genitalia, particularly the male external genitalia, of the Lepidoptera from a taxonomic viewpoint. Thus, the terminology pertaining to the structures of the male and female external genitalia of the Lepidoptera has been subject to much confusion. In fact, an average of more than six different names have been applied to each separate organ of the male (Beirne, 1942). Several nomenclatural systems, many purely descriptive in nature, have been set forth. Others have been based upon the comparative morphology of the adults. In this paper the terminology set forth by Klots (1970) has largely been followed for naming the components of the external genitalia.

The integumentary genitalic structures used in the taxonomy of the Lepidoptera are derivatives primarily from the tergites and sternites of segments VIII through X.

The Male External Genitalia

Before discussing the morphology of the different parts of the male genitalia, it is necessary to describe the non-genitalic structures of the tenth and eleventh segments. The anus opens at the apex of the abdomen at the end of a membranous tube, the anal tube (Fig. 3). The anal tube is sclerotized dorsally, forming a long narrow plate, known taxonomically as the scaphium. In the male the basal end of the scaphium articulates with the ventral side of the base of the uncus along the posterior and lateral edges (Fig. 3). The anal tube is sclerotized ventrally in a similar manner, the ventral sclerotization being known as the subscaphium (Fig. 3).

Zander (1903) and Mehta (1933) state that ontogenetically, the uncus (Fig. 3) arises as an outgrowth from the base of the scaphium and becomes secondarily attached to the caudal margin of the tegumen (Fig. 3). However, from a study of the male genitalic musculature, Forbes (1939) showed that the base rather than the distal portion of the uncus is the tenth tergum. This interpretation of the parts is probably correct due to the fact that the anal tube is separated from the ninth segment by the basal parts of the uncus, representing the tenth segment. The base of the scaphium articulates with the base of the uncus and is not fused to, nor forms an adherent part of the uncus, as is likely to be the case if the uncus was merely an outgrowth from the scaphium. Presumably, what Zander and Mehta regarded as tergum X was in reality segments X and XI. Therefore, it seems likely that the anal tube is a portion of segment XI, as concluded by both Zander and Mehta. Thus, the scaphium and subscaphium represent remnants of tergum and sternum XI respectively.

The external genitalia may be considered to have been derived from abdominal segments IX and X. The genitalia as a unit are connected to abdominal segment VIII by the intersegmental membrane (the articular membrane or conjunctiva of some authors). It forms a protractile base for the copulatory apparatus.

Ninth Segment

This is the main genital segment and is highly modified bearing the phallic and clasping organs. The sclerites of the ninth abdominal segment together with remnants derived from the tenth segment, form the transverse, sclerotic ring which serves for the attachment of the other parts of the external genitalia. The ring apparently developed primarily to form a supportive structure for the entire external genitalic bulb (Fig. 3).

The dorsal portion of the ring is composed of the ninth tergum and is known as the tegumen (Fig. 3) by lepidopterists. It is quite large, heavily sclerotized, and forms a roof or hood-like shaped structure which tapers caudally. While it is chiefly derived from the ninth tergite, Klots (1970) notes that its more caudal portion may consist of the anterior portion of the tenth tergite. The tegumen is heavily thickened for muscle attachment around its anterior edge. Dorsally, there is a poorly sclerotized area which lacks normal pigmentation in the tegumen, apparently characteristic of the Argynninae (dos Passos and Grey, 1945).

The ventral portion of the ring is composed of the sternite IX which gives rise to a large sclerite known as the vinculum and the saccus (Fig. 3). While it is derived from the ninth sternite, the vinculum actually is situated between the sclerites of the eighth and ninth segments. It is typically in the form of a flattened "U". The dorsal part of the "U" is attached to the tegumen. Midventrally, the vinculum is greatly expanded and is extended cephalad to form a deep trough-shaped inflection known as the saccus. The non-sclerotized ventral wall of the saccus is adnate with the eighth sternal surface. The anterior edge of the gonobase is reflected outwards where it is connected with the intersegmental membrane originating from the eighth segment.

The most caudal components of the male genitalia are paired, movable, clasping structures, known as the valves or gonoforceps (Fig. 3). These are large, flattened, double-walled lobes, interiorly concave, more or less tapering and bluntly pointed distally. Klots (1970) notes that these appear to be derived in part, at least, from the styli, coxites or parameres of the gonopods of the ninth segments. Each valve articulates to the vinculum, from which muscles which operate the gonoforceps take their origin. The dorsal, basal corner of each valve articulates with the corresponding poster-lateral margin of the tegumen. The ventral, basal corner of each valve articulates with the juxta (Fig. 5).

A gonoforcep consists of a number of parts or regions. The nomenclature of these regions and structures of the valves is extremely confused because of the difficulty of homologizing, in the various families, not only the various processes, but also the basic regions themselves. A paper by Sibatani, et al. (1954) is the most complete attempt to delimit the fundamental regions in various families. These authors recognize six fundamental regions as follows: costa (dorso-proximal) ampulla (central and medio-dorsal), cucullus (dorso-distal), valvula (ventro-distal), harpe (central and medio-ventral), and sacculus (ventro-proximal). However, these findings do not agree in part with Forbes' (1939) conclusions. He studied the valval musculature, especially that of the so-called "clasper" (the harpe of Sibatani, et al., and other lepidopterists) which in some groups apparently has a separate musculature which would seem to infer a separate origin.

The expanded sac-like, ventro-proximal region of the gonoforceps is known as the sacculus (Fig. 3). The inner wall is not continued to the lower edge of the valve, but meets the edge of the folded-over part of the outer wall. The portion of the outer wall of the sacculus situated on the inner surface where the inner and outer walls of the gonoforceps meet is widest at its base. A membrane extends to the juxta, and also to the sacculus from the opposite side (Fig. 5).

The harpe is a strongly sclerotized arm in the form of a curving spine, and is provided with independent musculature. It arises from the inner surface of the valve in a central position, extending outwardly and upwardly from the gonoforceps as a free arm.

The terminal, transverse sheet of membrane of the abdomen, known as the diaphragma, is connected to the posterior margin of the gonobase and the reflected free margin of the uncus (Figs. 5 and 6). From this dorsal point of attachment, it extends to the bases of the valves and vinculum ventrally. It is probably in large part derived from the ninth-tenth intersegmental membrane, but according to Klots (1970), may contain elements of the eleventh segment. The lower half of the intermediary area between the tegumen and the anellus is transformed into a pair of fusiform pouches (Fig. 6). Medially, where perforated by the emerging aedeagus, the diaphragma is doubly folded around this organ to form an eversible cone, the anellus (Fig. 5). The inner most layer of this cone, the manica (Pierce, 1914), is shaped like a megaphone and enwraps the subzonal portion of the aedeagus and fastens around the aedeagus at the zone (Fig. 7). It is connected to the inner reflected edge of the juxta, and anteriorly attached to the zone of the aedeagus. This membrane allows for the passage of the genital ducts from the abdomen into the genitalia, for the free flow of body fluids, and the extrusion of the genital bulb at the time of copulation.

The juxta is a sclerite lying on the ventral surface of the anellus, supporting the aedeagus, heavily sclerotized and shield-shaped (Fig. 5). Its ventral corners articulate with the basal portions of the sacculi. The apical margin is connected to the anellus, the inner portion of which serves as the anterior attachment of the manica.

In Speyeria a median membranous penis is nonexistent, rather it has entirely fused with the penis valves to form an aedeagus (Fig. 7). The penis arose developmentally in the median conjunctival membrane (Klots, 1970). In the resting position, the aedeagus lies retracted completely within the manica.

During development, the distal portion of the aedeagus invaginated cephalad, forming in inner tube known morphologically as the endophallus and taxonomically as the vescia. Extending cephalad into the body, this meets the caudal portion of the ejaculatory duct (Fig. 7) along which the components of the spermatozoa travel from the testis and vas deferens. This invaginated endophallic tube is commonly, but erroneously referred to by taxonomists as the distal end of the ejaculatory duct. As the vesica, it is posteriorly continuous with the aedeagus. It is narrow and lies coiled within the aedeagus. During copulation the greater part of the vesica is uncoiled and thrust through the end of the aedeagus. It passes up the bursal duct and opens into the base of the bursal sac. The vesica bears small chitinous teeth, the cornuti. These can be seen shining through the aedeagus in the resting position. In Speyeria, the vesica is evaginated during copulation as far as the cornuti, which thus guards the opening of the vesica into the bursa.

Tenth Segment

The tenth abdominal segment is virtually non-existant in Speyeria. All that remains of the tenth tergite is the uncus (Fig. 3), a very prominent feature of the genitalia. Its anterior edge is broadly ankylosed with the caudal edge of the tegumen. It is heavily sclerotized, with a tapering arm which is sharply accuminate. The ventral margin is reflected inwardly and its free edge is connected to the dorso-caudal part of the diaphragma of the abdomen.

The Musculature of the Male External Genitalia

In the past, the mechanism of the extrusion of the genitalia has not been thoroughly understood. As a result, several possible explanations for the extrusion of the male genitalia have arisen.

Perhaps the most widely accepted theory is similar to Hanneman's (1954a) speculation on the manner of extrusion of the male genitalia. He noted that with a freshly killed male, one can easily protrude the genitalia from the abdomen by applying pressure with your thumb and forefinger to the last abdominal segment. The same effect could be accomplished if one used a pipette to send a stream of water into the first abdominal segment. Thus, Hanneman concluded that it was the rise in interior pressure which effects the evagination. The male butterfly does this on his own by the contraction of his pleura muscles, which connect the side portions of the sternites with the tergites. Thus, the terga and sterna mutually squeeze together to create internal pressure, which extrudes the genitalia.

The fact that the genitalia may be protruded by manipulation by applying pressure upon the abdomen with the finger tips, is apparently not significant. Fischer (1956) pointed out the analogy that a distended balloon will break when additional pressure applied upon the balloon exceeds its elastic limit. Likewise, when pressure is applied to the abdomen of a butterfly by means of the finger tips, it will give at its weakest point to release the pressure when the breaking limit has been attained. Since the weakest point in the body is undoubtedly that of the orifice through which the genitalia are extruded, the genitalia are everted, regardless of the presence or absence of muscles. The assumption that the genitalia in nature are extruded solely by the action of a build up of internal pressure, is not tenable. A definite pattern of musculature accounts for the protraction and retraction of the genitalia.

Since there are no records in the literature which could be found on the mating behavior of Speyeria, the following discussion of the copulatory mechanism must be based in large part upon the musculature of the male genitalia and associated terga and sterna. To determine the probable function of the muscles of the genitalia, three methods have been employed in both living and preserved specimens: deduction, micro-manipulation, and the comparison of musculature of everted and non-everted genitalia.

The *Median dorsal longitudinal muscles* (*26*, *50*), the *Accessory median dorsal longitudinal muscles* (*27*, *51*), the *Primary lateral dorsal longitudinal muscles* (*28*, *52*), and the *Secondary lateral dorsal longitudinal muscles* (*29*, *53*) of the sixth and seventh terga are directly concerned with the extrusion of the genitalia during coition (Fig. 1). When contracted this set of sixteen muscles accounts for the contraction of the terga VI and VII. To a slight extent, they probably also serve to retract tergum VIII. As a result, tergum VIII is uplifted somewhat, leaving a caudal opening for the genitalia to pass through to the outside of the body. Because of the variance in angle of insertion of the *Secondary lateral dorsal longitudinal muscles* (*29*, *53*), there is an increase in the possible movements for opening the orifice through which the genitalia exit. In a like manner, the contraction of the *Ventral longitudinal muscles* (*32*, *55*), pull the sterna forward opening the orifice ventrally (Fig. 1). These are aided by the *Lateral ventral longitudinal muscles* (*31*, *54*).

Thus the contraction of the longitudinal muscles contracts the abdominal terga and sterna. This contraction of the terga and sterna does cause some pressure due to the compression of the abdomen. The diaphragma is folded upon itself before this build up of internal pressure. The hemocoel thus expands the diaphragma which exerts a force on the external genital bulb and causes it to move posterad. Thus the intromittent organ is slightly extruded from the abdomen and ready for copulation. It is interesting to note that the muscles which cause the slight extrusion of the genitalia are not protractors, but retractors and that they do not act upon the genitalia directly to extrude the genitalia, but contract the terga and sterna covering the genitalia.

Extrinsic Muscles

In the Lepidoptera, the male external genitalia is considered to include only the ninth and following segments though the muscles of the eighth segment support the genitalia and are listed as extrinsic muscles. Six pairs of extrinsic muscles have previously been described as associated with the genitalia. All of these muscles originate on the antecosta of segment VII and insert on the sclerotized "ring" of segment IX.

In the genus Speyeria, there are only five pairs of extrinsic muscles all running from the antecostal part of abdominal segment VIII to various areas of the ring of segment IX. Four sets of these muscles, two pairs associated with the terga and two with the sterna, all are involved with the retraction of the genital bulb after copulation. The Median dorsal retractor of the genitalia (56) serves to pull the dorsal area of the tegumen anterad after extrusion, while the Ventral retractor of the genitalia (59) complements this muscle in the sternum pulling the saccus anterad (Fig. 3). The net effect is to retract the entire genital bulb. Two other muscles, the Lateral dorsal retractor of the genitalia (57) and the Lateral ventral retractor of the genitalia (58) also complement this total effect, but in addition have some rotatory effect upon the action because of their angle of insertion (Fig. 3).

A fifth muscle, the *Reflector of the genitalia* (*60*), directs the anterior portion of the saccus posterad and thus indirectly aids in the extrusion of the aedeagus (Fig. 3).

Forbes (1939) and Stekolnikov (1965) have previously referred to these extrinsic muscles as tergal and sternal muscles depending upon their location.

The extrinsic external genital muscles of two other species in the nymphalid subfamily Argynninae have been studied. Hanneman (1954a) studied *Argynnis paphia* and in addition to the *Median dorsal retractor of the genitalia* (T_1 of Hanneman) and the *Lateral dorsal retractor of the genitalia* (T_2), found a third tergal muscle (T_3), which originated near the origin of the lateral dorsal retractor muscle of the genitalia and inserted upon the anterior edge of the tegumen. This third muscle has not been found in *Speyeria*, nor did Shirozu and Yamamota (1953) locate it in their study of *Argyronome laodice japonica*.

Speyeria possesses three extrinsic sternal muscles. Each is attached to the anterior portion of sternite VIII. Forbes (1939) states that the three sternal muscles are attached in a group to the anterior lateral angle of the sternite. The *Median ventral retractor of the genitalia* is absent in *Argyronome laodice japonica* (Shiroza and Yamamota, 1953). Hanneman (1954a) found a *Median ventral retractor of the genitalia* in *Argynnis paphia*, just as there is in *Speyeria*.

Intrinsic Muscles

Ten paired muscles are found within the external genitalia of male *Speyeria*. Eight of these function in the movement of the tegumen, uncus, valves, and the aedeagus. It is difficult to assign arbitrarily any one function to a particular muscle because of the possible effect any muscle or set of muscles may have upon the net effect of another. Thus the muscles have been named with what is presumed to be their primary function, but the reader must keep in mind that these various functions may be materially altered by the effect of other muscles. The supposed effect of many of these muscles is outlined in the text along with the primary result of the contraction of any individual muscle.

The *Depressor of the uncus* (*61*) depresses the ankylosed tegumen and uncus (Fig. 3).

In *Speyeria* as well as in *Argyronome* (Shirozu and Yamamota, 1953), the *Retractor of the anal tube* (*62*) is represented by only a few stray fibers (Fig. 3). It is more developed in *Argynnis* (Hanneman, 1954a). In other Lepidoptera, this muscle originates on the swollen anterior edge of the tegumen, loops around the *Depressor of the uncus* (*61*), and inserts as a large bundle on the sclerotized subanal plate with several finer fibers inserting on the membranous sides of the anal tube (Forbes, 1939). It will retract and thus raise the anal tube. Forbes (1939) suggests that perhaps it was originally a muscle of the gnathos, a structure which is not present in *Speyeria*.

Forbes (1939) gives no name to the *Extensor of the tegumen* (*63*). This muscle would appear morphologically to be an extensor of the valve. Yet upon contraction, it raises the tegumen in such a way that the longitudinal axis of the tegumen occupies an almost vertical position (Fig. 3).

According to Forbes (1939) the *Extensor of the valve* (*64*) has its origin and insertion different from that of other lepidoptera (Fig. 3). Forbes (1939) and Stekolnikov (1965) report that in other lepidopteran species the *Extensor of the valve* originates on the base of the tegumen and inserts on a narrow process which is a continuation of the inner region of the costal margin of the valve. It is interesting to note that the other Argynninae which have been studied, *Argynnis paphia* and *Argyronome laodice japonica*, also have their *Extensors of the valves* originating and inserting in the same manner as it does in *Speyeria*.

The *Flexor of the clasper* (*65*) aids the *Flexor of the valve* (*68*) since the clasper is fused to the valve (Fig. 3).

The *Protractor of the aedeagus* (*66*) is responsible for the extrusion of the aedeagus during copulation, and the *Retractor of the aedeagus* (*67*) returns the aedeagus to its normal position after copulation. The saccus thus serves as an apodeme for the *Retractor of the aedeagus* (*67*). Insofar as the saccus and vinculum constitute a single whole, the vinculum has the same importance for the muscles which extrude the aedeagus as the saccus has for the muscles which retract it (Fig. 3).

Mechanically, the valves are levers and their fulcra are situated between the planes of the valves so when the *Flexors of the valves* (*68*) contract, the valves open. In the case of the *Extensors of the valves* (*64*), the fulcra are situated outside the valves and contraction of the extensors causes the valves to close.

SKELETO-MUSCULAR MECHANISM OF COPULATION

There have been several brief descriptions in the literature of different Lepidoptera species copulating. Unfortunately, there is rarely any mention of the skeleto-muscular mechanism involved. One of these brief descriptions was made by Bayard (1944) on a copulating pair of *Dryas* (now *Argynnis*) *paphia*. Hanneman (1954a and 1954b) described the operational mechanism of *Argynnis paphia*, and Steklonikov (1965) described the operational mechanism of four moths.

The Female

No true morphological ovipositor, derivatives of podites, as may be found in many insects, is present in this butterfly. Female *Speyeria*, as well as other female Lepidoptera of the suborder Ditrysia, possess two separate genital openings (Fig. 2). The ovipositional opening, the oviporus, is situated below the anus, posterior to the ninth segment. The copulatory opening, the ostium bursae, has moved ventro-cephalad to a position anterior of the eighth venter, and is the equivalent of the vulva in those insects having a common opening for egg deposition and the copulatory function (Fig. 2). The ostium bursae opens internally into a large, blind sac, the bursa copulatrix, in which the spermatophore is initially stored after copulation. Thus, the understanding of the copulatory mechanism in the female is not based upon the morphology of an ovipositor, but rather on the manipulative maneuverability of the abdominal segments themselves. The functions of egg laying and copulation are restricted to the operability of segments VII through X.

The seventh segment is not unlike preceeding segments except that it is longer and tapers caudally giving it a cone-like appearance. The sternal plate is especially strongly sclerotized (Fig. 8). This strengthening is understandable due to the stress brought about by the penetration of the aedeagus.

The close approximation of the eighth tergum and sternum has been attained by the extreme reduction of the membranous pleuron to a tergal-stergal conjunctiva more typical of most insects with secondary segmentation. It is a specialization for both oviposition and copulation. The reduction of the amount of membrane has increased the ability of the segment to work as a unit rather than as separate sclerites, in effect increasing maneuverability for the copulatory and egg laying functions (Fig. 8).

The eighth tergum is larger than the sternum and has its anterior corners produced as a pair of rods, the anterior apophyses (Fig. 8). The anterior lateral margin of the eighth tergum has a greatly expanded lateral tergal apodeme, a homolog of similar but much smaller apodemes found in segments VI and VII.

The fused ninth and tenth segments are very much reduced. The sterna of these two segments presumably have evanesced, indistinguishably fused with the terga, or perhaps because of the nature of the musculature, have expanded dorsally to include what has previously been termed the terga. At any rate, fusion has occurred to form the anal papillae (Fig. 8). These form a pair of large, setaceous bearing lobes, one on either side of the anus and oviporus. The lobes are more or less separate, soft, and somewhat kidney shaped.

From the lateral edges of the ninth segment extend cephalad, paired, sclerotized, rod-like apodemes. These are the posterior apophyses used for muscle attachment (Fig. 8).

The intersegmental membrane between the eighth segment and the fused ninth and tenth is extra long (Fig. 8). This allows the anal papillae the extra flexibility required during oviposition.

The tergal musculature of segment VII is homologous with previous segments but highly modified for the copulatory function and to a lessor degree egg laying. Four elongate muscles serve collectively as retractors of tergum VIII (Fig. 8). These are the *Median dorsal longitudinal muscle* (*33*), *Primary lateral dorsal longitudinal muscle* (*34*), *Secondary lateral dorsal longitudinal muscle* (*35*), and *Tertiary lateral dorsal longitudinal muscle* (*36*). Upon their contraction, tergum VIII moves anterad causing the retraction of the tergum. Muscles *33* and *34* however are extremely long and because of their origin, have a differentially greater pull on the anterior apophysis, uplifting the apex of tergum VIII. With the contraction of the wide banded *Compressor of segment* VIII (*41*), coupled with the action of *33* and *34*, sternum VIII is likewise uplifted apically (Fig. 8). This action is further enhanced by the complete lack of any sternal muscles antagonistic to the four tergal retractors (*33*, *34*, *35*, *36*). Retractors of the ninth segment, the *Median retractor of segment* IX (*45*) and the *Lateral retractor of segment* IX (*46*), contract pulling the ninth segment anterad (Fig. 8). The contraction of the *Anterior retractor of the posterior apophysis* (*42*) raises the anal papillae through the leverage action upon the posterior apophysis (Fig. 8). These three sets of muscles thus retract and raise the fused IX and X segments removing it from interfering with the copulatory process. But, what the combined action of these muscles have thus far done is to uplift the eighth sternum exposing the ostium bursae. Further exposure of the ostium bursae and most importantly the dilation of the bursa copulatrix, which readies the female for the reception of the male intromittent organ, is brought about by contraction of six additional muscles which insert directly on the bursa copulatrix. These six sets of muscles are involved in the dilation of the bursa copulatrix (Fig. 8). Two of these originate anteriorly on the venter and include the *Lateral ventral dilator of the bursa copulatrix* (*37*) and *Median ventral dilator of the bursa copulatrix* (*38*); a third which also originates ventrally but posteriorly is an extremely large powerful muscle, the *Posterior ventral dilator of the bursa copulatrix* (*39*). All three of these muscles insert ventrally on the bursa copulatrix. Complementary muscles which originate dorsally and posteriorly include the *Dorsal dilator of the bursa copulatrix* (*43*), *Dorso-lateral dilator of the bursa copulatrix* (47), and *Dorso median dilator of the bursa copulatrix* (*48*). The combined action of these six muscles is the dilation of the bursa copulatrix and to a lessor extent the greater exposure of the ostium bursae. A total of 20 muscles are thus involved with the exposure of the ostium bursae and the dilation of the bursa copulatrix -- all in preparation for reception of the male.

The Male

With the extrusion of the external genital apparatus, the male raises its tegumen and its ankylosed uncus by the *Extensor of the tegumen* (*63*) upon approach to the female. As the tegumen and uncus cover the rear of the female's abdomen, the *Depressor of the uncus* (*61*) contracts lowering the uncus and tegumen upon the anal papillae of the female. The *Flexors of the valves* (*68*) and the *Flexors of the claspers* (*65*) contract and spread the valves laterally. The flexors then relax and the *Extensors of the valves* (*64*) contract and move the bases of the valves which embrace the anal papillae, while the claspers embrace the anterior of the anal papillae. The anal papillae thus rest in the membranous fusiform pouches of the male (Fig. 6). This movement of the valves enables the uncus to move anterad onto the eighth tergum of the female, where the sharply accuminate tip of the uncus is able to hook into the intersegmental membrane.

The female is thus secured at three points: the uncus of the male secures the tergum of segment VIII, the claspers of the male secure the lateral portions of the anal papillae, and the posterior portion of the valves secure the seventh sternum of the female.

During the anchoring of the uncus, the anus is also retracted and somewhat raised by the contraction of the *Retractors of the anal tube* (*62*). At this time, the *Protractors of the aedeagus* (*66*) contract and direct the aedeagus caudally. Simultaneously, the *Reflector of the male genitalia* (*60*) contracts, tipping the anterior portion of the saccus dorsally, and thus also directing the aedeagus somewhat dorsally. The combined action of *66* and *60* direct the aedeagus dorso-caudally and introduce the aedeagus into the female's bursa copulatrix. As this happens, the male is able to grip the female still more securely with his valves.

The circular *Ejaculator muscles* (*70*) squeeze the pouch-like ejaculatory bulb (Fig. 7). The contraction of this muscle is also employed to evaginate the vesica as the ejaculate passes through it, after the aedeagus has been introduced into the bursa copulatrix.

Once copulation has been completed, the evaginated vesica is retracted into the aedeagus by the contraction of the *Retractors of the vesica* (*69*) (Fig. 7). The aedeagus is then returned to its resting position by the contraction of the *Retractors of the aedeagus* (*67*) and relaxation of *60* (Fig. 3).

The restoration to the resting position of the remainder of the copulatory apparatus is due to the combined effect of the relaxation of the external genital muscles and the retractors of segment VIII. While the retractors of segment VIII (*56*, *57*, *58* and *59*) contract, thus pulling back the male external genitalia, the *Depressor of the uncus* (*61*) relaxes which unhooks the uncus. Then, the *Extensor of the tegumen* (*63*) contracts, thus raising the combined uncus and tegumen. Simultaneously, the *Extensors of the valves* (*64*) relax, releasing the anal papillae. Then, the *Flexors of the valves* (*68*) and the *Flexors of the claspers* (*65*) contract, spreading the valves laterally. The relaxation of the *Retractors of the anal tube* (*62*) returns the anal tube to its normal position. The dorsal and ventral longitudinal retractors of the pre-genital segments relax, which returns the tergal and sternal coverings over the external genitalia and decreases the haemolymph pressure against the diaphragma.

In the female, the dilators of the bursa copulatrix (*37*, *38*, *39*, *43*, *47* and *48*) relax closing the ostium bursae. The relaxation of her *Retractor of the posterior apophysis* (*42*) lowers her anal papillae. It is further lowered and returned to its normal position by the contraction of the *Protractor of the posterior apophysis* (*44*), the relaxation of the dorsal longitudinal muscles (*33*, *34*, *35* and *36*) of the eighth segment, and the retractor muscles (*45* and *46*) of the ninth segment. The combined effect of these eight pairs of muscles re-conceals the ostium bursae.

SKELETO-MUSCULAR MECHANISM OF OVIPOSITION

Whoever has had the opportunity to observe a female butterfly during egg laying is amazed at the maneuverability of its abdominal segments. A variety of movements including protraction, retraction, depression, and lateral movements of the abdomen may be explained on the basis of the anatomical structure of the terga and sterna, and their associated muscles.

The skeleto-muscular operational mechanism of oviposition has been described by Hanneman (1954b) for *Argynnis paphia*. Unfortunately, his description is not entirely accurate because he inaccurately named some of the muscles involved with oviposition. Most notable are his segmental and genital protractors which in reality are retractors.

At the time of oviposition, a fertilized egg lies in the posterior portion of the membranous common oviduct (Fig. 2). The combined action of the muscles of the female abdomen literally squeeze the egg out of the abdomen.

The contraction of the abdomen is brought about by several factors. The contraction of the dorsal and ventral longitudinal retractor muscles in the pre-genital abdominal segments, supported by the drawing together of the muscularis of the pleura, whose threads run dorsoventrally, has a reciprocal approach of the terga and sterna and thus increases the interior pressure of the abdomen. This forces the haemolymph posterad against the supporting membrane of the common oviduct, and the last intersegmental membrane. The *Compressor of segment* VIII (*41*) achieves the same effect in the eighth segment (Fig. 8). This dorsal-ventral compression results in the extension of the anal papillae.

The fused ninth and tenth abdominal segment is especially moveable. This is attained by the greatly lengthened last intersegmental membrane and by the posterior apophysis with its assemblage of muscles. The anterior apophysis of segment VIII and the posterior apophysis of segment IX play a special role as the point of departure for the muscles which cause the telescope-like in and out pushing of the segments, as is manifested during egg laying (Fig. 8). The contraction of the *Protractor of the posterior apophysis* (*44*), moves segments IX and X caudally. This fused segment is thereby thrust out and the intersegmental membrane, which lies inside on the caudal edge of the eighth abdominal segment, evaginates.

The lifting of the last segment occurs by means of the *Anterior retractor of the posterior apophysis* (*42*). Contraction of this muscle exerts a diagonal (oblique) pull ventrally oriented on the anterior portion of the posterior apophysis. Since this functions as a lever, the final segment is raised (Fig. 8). Muscles *45* and *46* function with the movement of the anal papillae similar to their combined action involved with copulation. In addition, muscle *46*, inserting on the inner wall of the anal papillae, tends to draw the papillae together upon contraction, contrasting to *45* which pulls the papillae away from one another. The lowering of the last segment is brought about, namely by the contraction of the depressors of segments VIII and IX (*49* and *40*). At the same time, in addition to this ventrally oriented movement, the final segments experience a somewhat lateral shift through the contraction of muscles of 49 and 40 (Fig. 8). It is therefore, moveable in all directions and can perform the demands which are required during oviposition.

The flexibility of segment VIII is by far not so great as that of the final segment. The eighth segment can also be pulled apart from the seventh segment somewhat during the everting of the final segment. Also, its lengthening is probably somewhat attributable to the effect of the intra-abdominal pressure and the peristaltic movements of the lateral oviducts. The main function of muscle 42 is to aid the median and lateral retractors of segment IX (45 and 46) retract the evaginated final segment into the eighth segment, while the eighth segment itself is retracted by the combined contraction of 33, 34, 35, and 36.

In summary, the sequential events involved in oviposition begin with the contraction of the combined efforts of the dorsal and ventral longitudinal retractor muscles, and the muscularis of the pleura. The anal papillae are extruded by the combined effect of the increased intra-abdominal pressure, the peristaltic contractions of the lateral oviducts, and the *Protractor of the posterior apophysis* (44).

Since the female often oviposits on the underside of a *Viola* leaf, the apical end of her abdomen must bend and curve under while she is standing on the upper surface of the leaf. This is accomplished by the depressors of segments VIII and IX (49 and 40).

Since the female does not possess a true ovipositor, the combined effect of the compression of the anterior segments, the extension of segments IX and X, the increase in intra-abdominal pressure, the peristaltic movements of the oviducts, plus the compression of segment VIII by muscle *41*, all combine to literally squeeze each egg out of the common oviduct.

With the conclusion of each egg being laid, the abdomen returns to its normal position. The depressors of segments VIII and IX (*49* and *40*) relax thus raising the rear of the abdomen to its pre-ovipositing position. The *Compressor of segment* VIII (*41*) relaxes and allows segment VIII to restore its normal expansion. The dorsal and lateral longitudinal muscles of the first six abdominal segments relax, thus decreasing the intra-abdominal pressure, and allowing the terga and sterna to return to their normal position. The *Anterior retractor of the posterior apophysis* (*42*), plus the *Median* and *Lateral retractors of segment* IX (*45* and *46*) contract, and thus restore the anal papillae to their normal position.

ANNOTATED LIST OF MALE AND FEMALE ABDOMINAL MUSCLES

Muscles of Segment II

1. Median dorsal longitudinal muscle (Figs. 1 and 2). A short muscle arising posteriorly on the dorsum of tergum II, extending somewhat dorso-caudally in the female, but only caudally in the male, and inserting on the antecostal ridge of tergum III.

2. Accessory median dorsal longitudinal muscle (Figs. 1 and 2). A short muscle arising posteriorly on tergum II, extending caudo-mesally in the female. In the male, although it is lateral of 1, it appears to be contiguous and part of 1. In both sexes it inserts on the antecostal ridge of tergum III.

3. Primary lateral dorsal longitudinal muscle (Figs. 1 and 2). A short muscle arising posteriorly on tergum II, extending ventro-caudally in the female, while in the male it is an elongate muscle, arising mid-anteriorly on the sloping face of tergum II, and extends caudo-ventrally. In both sexes it inserts on the antecostal ridge of tergum III.

4. Lateral ventral longitudinal muscle (Figs. 1 and 2). A short muscle arising posteriorly in the female (latero-posteriorly in the male) on sternum II, extending dorso-laterally in the female (caudally in the male), and inserting on the antecostal ridge of sternum III.

5. Ventral longitudinal muscle (Figs. 1 and 2). A short muscle arising posteriorly on sternum II in the female. In the male it is a short muscle but longer than 4, arising medially on the sloping face

of sternum II. In both sexes it extends caudo-mesally, inserting on the antecostal ridge of sternum III.

Muscles of Segment III

6. Median dorsal longitudinal muscle (Figs. 1 and 2). A short, fan-shaped muscle in the female, arising posteriorly on the dorsum of tergum III, extending caudo-dorsally, and inserting on the antecostal ridge of tergum IV. In the male it is similar to 1.

7. Accessory median dorsal longitudinal muscle (Figs. 1 and 2). Similar to 2, but wider in the female, while it is more extensive and distinctly separated from 6 in the male.

8. Primary lateral dorsal longitudinal muscle (Figs. 1 and 2). An elongate muscle arising medially on the lateral wall of tergum III, and extending caudo-ventrally in the female. In the male it is an elongate, robust muscle, arising mid-laterally on tergum III and extending caudally. In both sexes it inserts on the antecostal ridge of tergum IV.

9. Secondary lateral dorsal longitudinal muscle (Fig. 2). A short muscle arising posteriorly and ectally of 8 on the lateral wall of tergum III, extending caudo-ventrally, and inserting on the antecostal ridge of tergum IV in the female. Not present in the male.

10. Lateral ventral longitudinal muscle (Figs. 1 and 2). Similar to 4, but more elongate, and origin partially hidden beneath 11 in the female. Similar to 4, but extending more dorso-caudally in the male.

11. Ventral longitudinal muscle (Figs. 1 and 2). Similar to 5, but arising more medially in both sexes, and more elongate in the female.

Muscles of Segment IV

12. *Median dorsal longitudinal muscle* (Figs. 1 and 2). Similar to *6* in both sexes, but more robust in the female.

13. *Accessory median dorsal longitudinal muscle* (Figs. 1 and 2). Similar to *7* in both sexes, but arising on the mid-dorsal wall of tergum IV, more robust and elongate, extending caudo-ventrally, and inserting on the antecostal ridge of tergum V in the female.

14. *Primary lateral dorsal longitudinal muscle* (Figs. 1 and 2). Similar to *8* in both sexes, but more robust, and arising more anteriorly in the female.

15. *Secondary lateral dorsal longitudinal muscle* (Figs. 1 and 2). Similar to *9* in the female. An elongate robust muscle in the male, arising mid-laterally on tergum III, extending caudally, and inserting on the antecostal ridge of tergum IV.

16. *Tertiary lateral dorsal longitudinal muscle* (Fig. 2). An elongate muscle arising anteriorly on the lateral wall of tergum IV, extending caudally, and inserting on the antecostal ridge of tergum V in the female. Not present in the male.

17. *Lateral ventral longitudinal muscle* (Figs. 1 and 2). Similar to *10* in both sexes.

18. *Ventral longitudinal muscle* (Figs. 1 and 2). Similar to *11* in both sexes, but arising more anteriorly in the female.

Muscles of Segment V

19. *Median dorsal longitudinal muscle* (Figs. 1 and 2). Similar to *6* and *12* in both sexes, but much smaller in the male.

20. Accessory dorsal longitudinal muscle (Figs. 1 and 2). Similar to 7 and 13 in both sexes.

21. Primary dorsal longitudinal muscle (Figs. 1 and 2). Similar to 14 in both sexes, but more elongate in the male.

22. Secondary lateral dorsal longitudinal muscle (Figs. 1 and 2). Similar to 15 in both sexes.

23. Tertiary lateral dorsal longitudinal muscle (Fig. 2). Similar to 16, but inserting on the tergal apodeme in the female. Not present in the male.

24. Lateral ventral longitudinal muscle (Figs. 1 and 2). Similar to 10 and 17 in both sexes.

25. Ventral longitudinal muscle (Figs. 1 and 2). Similar to 11 and 18 in both sexes.

Muscles of Segment VI

26. Median dorsal longitudinal muscle (Figs. 1 and 2). Similar to 12 and 19 in both sexes, but less robust in the female.

27. Accessory median dorsal longitudinal muscle (Figs. 1 and 2). Similar to 13 and 20 in both sexes, but more elongate in the male.

28. Primary lateral dorsal longitudinal muscle (Figs. 1 and 2). Similar to 14 and 21 in both sexes.

29. Secondary lateral dorsal longitudinal muscle (Figs. 1 and 2). Similar to 15 and 22 in both sexes.

30. Tertiary lateral dorsal longitudinal muscle (Fig. 2). Similar to 23 in the female. Not present in the male.

31. Lateral ventral longitudinal muscle (Figs. 1 and 2). Similar to 17 and 24 in both sexes, though smaller in the male.

32. Ventral longitudinal muscle (Figs. 1 and 2). Similar to 18 and 25 in both sexes.

Male Muscles of Segment VII

50. *Median dorsal longitudinal muscle* (Fig. 2). Similar to *19* and *26*.

51. *Accessory median dorsal longitudinal muscle* (Fig. 2). Similar to *27*.

52. *Primary lateral dorsal longitudinal muscle* (Fig. 2). Similar to *28*.

53. *Secondary lateral dorsal longitudinal muscle* (Fig. 2). Similar to *29*.

54. *Lateral ventral longitudinal muscle* (Fig. 2). Similar to *31*.

55. *Ventral longitudinal muscle* (Fig. 2). Similar to *32*, but because of reduced size of sternum VII, virtually extends intersegmentally.

MUSCLES ASSOCIATED WITH THE FEMALE GENITALIA

Segment VII

33. Median dorsal longitudinal muscle (Fig. 8). Similar to 11 and 19, but extending caudally and inserting on the anterior apoplysis.

34. Primary lateral dorsal longitudinal muscle (Fig. 9). Similar to 21, but thin and elongate.

35. Secondary lateral dorsal longitudinal muscle (Fig. 8). Similar to 22, but inserting on the greatly expanded lateral tergal apodeme of segment VIII.

36. Tertiary lateral dorsal longitudinal muscle (Fig. 8). Similar to 23, but inserting on the greatly expanded lateral tergal apodeme of segment VIII.

37. Lateral ventral dilator of the bursa copulatrix (Fig. 8). Similar to 31, but inserting on the latero-ventral portion of the bursa copulatrix.

38. Median ventral dilator of the bursa copulatrix (Fig. 8). Similar to 32, but inserting on the medio-ventral portion of the bursa copulatrix.

39. Posterior ventral dilator of the bursa copulatrix (Fig. 8). A massive muscle originating on the antecostal ridge of sternum VIII and extending latero-ventrally, and inserting on the posterior venter of the bursa copulatrix.

Segment VIII

40. Depressor of segment IX (Fig. 8). An elongate muscle arising mid-laterally on tergum VIII, extending ventrally, and inserting on the ventral extension of segment IX.

41. Compressor of segment VIII (Fig. 8). A wide muscle arising just posterad and ventrad of 40, extending caudo-ventrally, and inserting on the posterior of sternum VIII.

42. Anterior retractor of the posterior apophysis (Fig. 8). A short muscle originating on the greatly extended lateral tergal apodeme, extending meso-caudally, and inserting on the anterior portion of the posterior apophysis.

43. Dorsal dilator of the bursa copulatrix (Fig. 8). It originates mid-laterally on sternum VII, extends antero-ventrally, and inserts on the dorsum of the bursa copulatrix.

44. Protractor of the posterior apophysis (Fig. 8). An elongate muscle originating on mid-dorsally on the posterior apophysis, extending meso-caudally, and inserting on the caudal portion of segment VIII.

45. Median retractor of segment IX (Fig. 8). An elongate muscle originating ventro-anteriorly on the posterior apophysis, extending meso-caudally, and inserting on the median portion of segment IX.

46. Lateral retractor of segment IX (Fig. 8). An elongate muscle originating medially on sternum VII, extending meso-caudally, and inserting on the ventral portion of segment IX.

47. Dorso-lateral dilator of the bursa copulatrix (Fig. 8). A short muscle originating medially on sternum VIII, extending antero-ventrally, and inserting on the bursa copulatrix.

48. Dorso-median dilator of the bursa copulatrix (Fig. 8). A short muscle originating postero-ventrally on sternum VIII, extending anteriorly, and inserting on the bursa copulatrix.

49. Depressor of segment VIII (Fig. 8). An elongate muscle originating ventro-posteriorly on the posterior apophysis, extending caudo-ventrally, and inserting on the posterior portion of sternum VIII.

MUSCLES ASSOCIATED WITH THE MALE GENITALIA

Extrinsic Muscles (Segment VIII)

56. Median dorsal retractor muscle of the genitalia (Fig. 3). This is a flattened, several fibered muscle originating near the medio-dorsal edge of the eighth antecosta and inserts on the anterior edge of the tegumen just laterad of the medio-dorsal line. It is probably homologous with the median dorsal longitudinal muscles of the preceeding segments.

57. Lateral dorsal retractor muscle of the genitalia (Fig. 3). Resembles 56 with fibers originating on the eighth antecosta, but inserting on the extreme upper angle of the vinculum. It is probably homologous with the secondary lateral dorsal longitudinal muscles of the preceeding segments.

58. Lateral ventral retractor muscle of the genitalia (Figs. 1 and 3). This is a slender and long muscle originating on the lateral angle of the eighth sternite and inserting on the vinculum near the insertion of 37 at the base of the tegumen.

59. Ventral retractor muscle of the genitalia (Fig. 3). This is a small, short muscle, inserting on the venter of the saccus, posterior to the origin of the large retractor muscle of the aedeagus (67).

60. Reflector muscle of the genitalia (Fig. 3). This is a short, massive muscle inserting on the posterior ventral area of the saccus.

Intrinsic Muscles (Segment IX)

61. Depressor of the uncus (Fig. 3). A pair of massive, fan-like muscles originating on the swollen anterior ring edge of the tegumen and inserting on the inwardly reflected flange of the ventral margin of the uncus.

62. Retractor of the anal tube (Fig. 3). Represented by only a few stray fibers. A median fiber originates from the medio-dorsal point of the swollen leading edge of the tegumen and terminates at the medio-dorsal points of the anal tube. Two lateral fibers originate just laterad of the base of the median fiber and insert on the subanal plate.

63. Extensor of the tegumen (Fig. 3). Originating on the tegumen near the depressor of the uncus (61) but more dorsally. It runs directly under the articulation of the tegumen and pleuron to insert in the tip of the valve where it articulates with the vinculum.

64. Extensor of the valve (Fig. 4). Originating on the mid- to upper part of the vinculum, it inserts on a serrate internal ridge of the valve known as the crista (dos Passos and Grey, 1945) and crowds the flexor of the clasper (65).

65. Flexor of the clasper (harpe) (Fig. 4). It originates in the swollen saccular portion of the valve, mostly along the ventral posterior edge, but also partly from the ental surface, and inserts on the lower portion of the sclerite bearing the clasper of the valve.

66. Protractor of the aedeagus (Fig. 3). This is the most massive of all of the intrinsic muscles. Originating on the anterior margin of the vinculum from its dorsal articulation with the tegumen ventrally to the saccus, it inserts on the extreme basal half of the subzonal

portion of the aedeagus, almost completely enwrapping the latter.

67. Retractor of the aedeagus (Fig. 3). This muscle lies ental to 66 and is almost equally as massive. It originates on the tip of the saccus, enwrapping it on both sides, and runs up around the aedeagus on each side and inserts on the dorsum of the aedeagus just anterad of the attachment of the ejaculatory duct.

68. Flexor of the valve (Fig. 4). It originates on the basal edge of the juxta and runs longitudinally and parallel to insert mostly on the anterior part of the invaginated inner surface of the saccus with only a few fibers inserting in the extreme base of the valve. It lies mesad of the flexor of the clasper (65).

Endophallic Muscles

69. Retractor of the vesica (Fig. 7). This is enclosed by the tubular aedeagus, originating on the extreme basal portion of the inner surface of the aedeagus, and circumscribing the cup-shaped invaginated vesica.

70. Ejaculator muscle (Fig. 7). This muscle is telescoped in the pouch-like ejaculatory bulb and is composed of circular fibers, surrounding the ejaculatory duct.

SUMMARY

The morphology of the copulatory and ovipositional mechanisms of Speyeria are described. The myology of the copulatory and ovipositional mechanisms is described, which aids in explaining the skeletomuscular operational mechanisms of copulation and oviposition.

The male and female copulatory apparatuses of Speyeria do not have to be appreciably everted, as do some other insects, to be ready for mating. The male's genitalia are everted by the sequential contraction of the pre-genital segments by the dorsal and ventral longitudinal muscles of each segment which also creates an increased intra-abdominal pressure and pushes the haemolymph posterad against the diaphragma.

No true morphological ovipositor, nor external genitalia are present in the Speyeria studied. Thus, the understanding of the copulatory mechanism in the female is not based upon the morphology of an ovipositor, but rather on the manipulative maneuverability of the abdominal segments themselves. The female prepares herself for the reception of the male by raising and retracting the apical portion of her abdomen. This exposes her ostium bursae, which has dilated through the action of six muscle pairs and is ready for the intromittent organ of the male.

With the extrusion of the male external genital apparatus, he extends his tegumen and then lowers it and the ankylosed uncus upon the dorsum of the anal papillae. The valves spread laterally, allowing the anal papillae to rest in his membranous fusiform pouches and then

extend to securely fix the position of the female. The aedeagus is then introduced into the bursa copulatrix and the vesica everted as the ejaculate passes through it.

At the time of oviposition, a fertilized egg lies in the posterior portion of the membranous common oviduct. Since the female does not possess a true ovipositor, the combined effect of the compression of the anterior segments, the extension of segments IX and X, the increase in intra-abdominal pressure, the peristaltic movements of the oviducts, plus the compression of segment VIII, all combine to literally squeeze each egg out of the membranous common oviduct.

LITERATURE CITED

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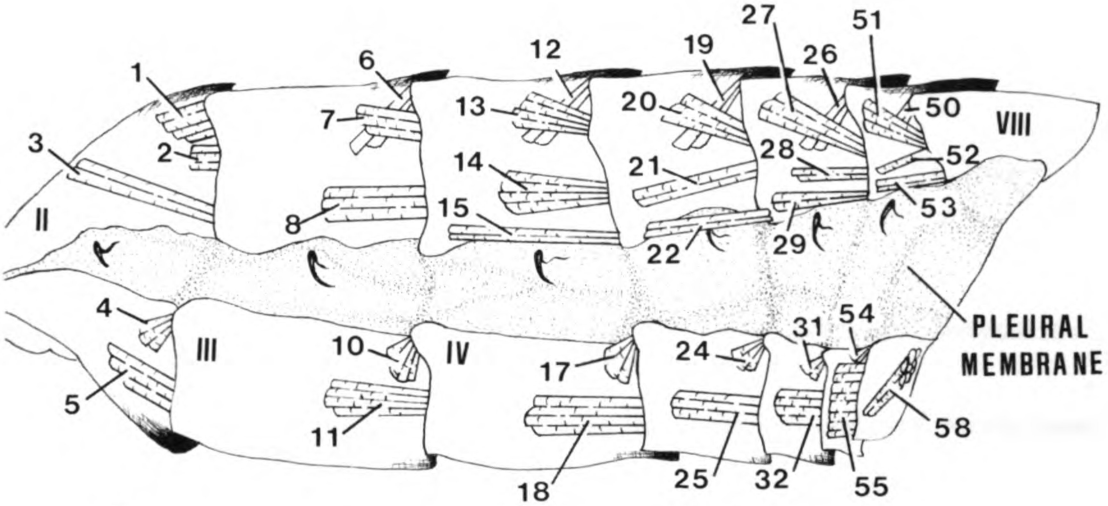
FIGURES

Figure 1. Internal Right Lateral View of the Male Abdominal Segments II-VIII and Associated Musculature

Figure 2. Internal Right Lateral View of the Female Abdominal Segments II-X, Associated Musculature and Reproductive Structures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VIII
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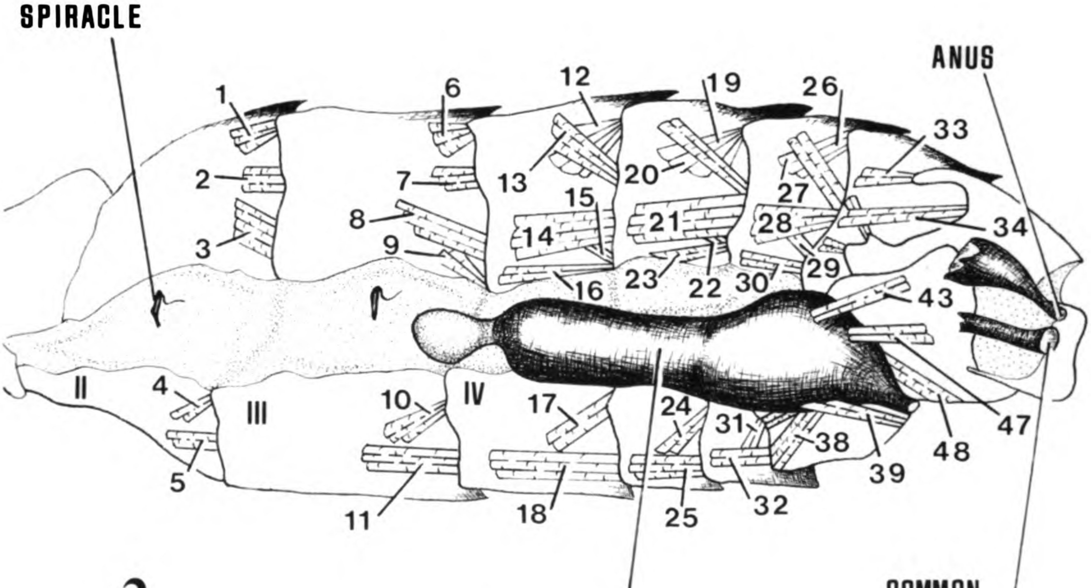
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ANUS
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BURSA COPULATRIX
COMMON OVIDUCT

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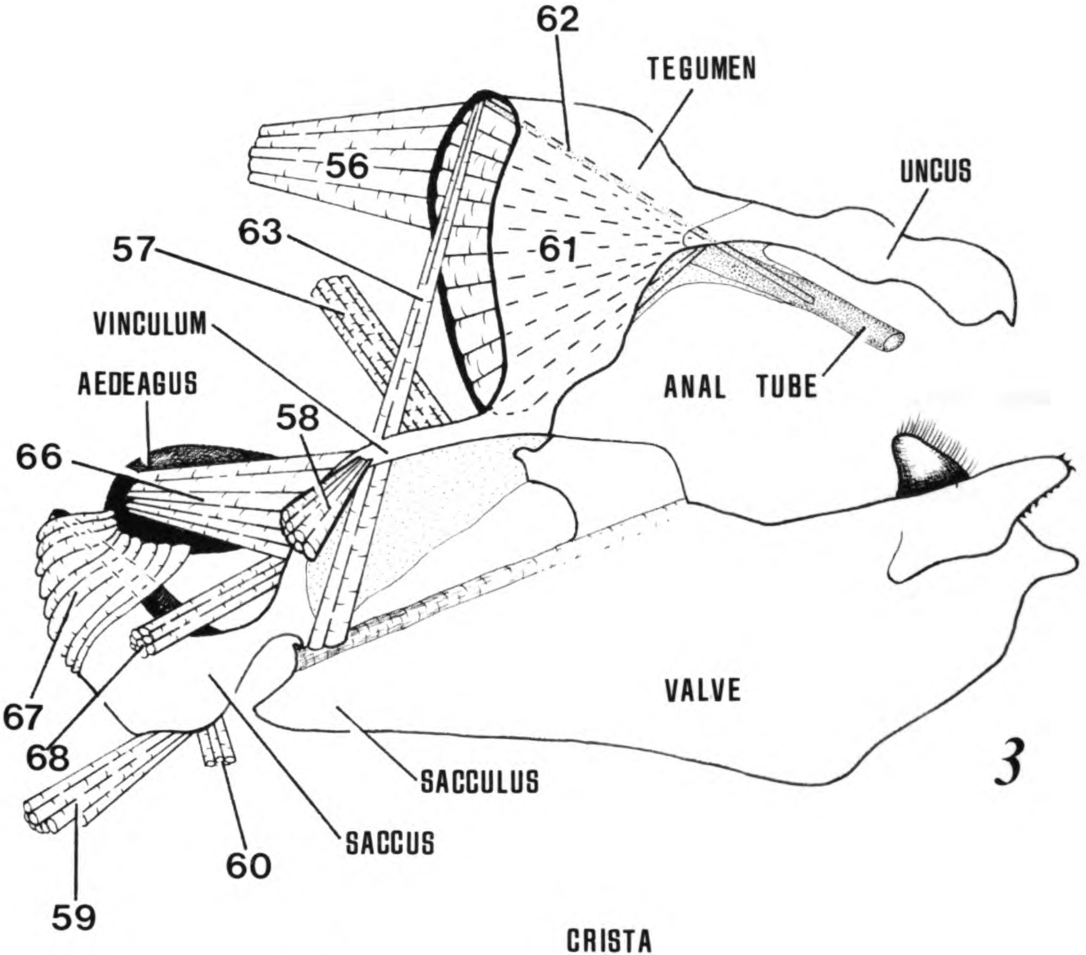
Figure 3. External Left Lateral View of the Male External Genitalia and its Associated Musculature

Figure 4. Internal Lateral View of the Right Valve and its Associated Musculature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TEGUMEN
UNCUS
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57
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VINCULUM
AEDEAGUS
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ANAL TUBE
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VALVE
SACCULUS
SACCUS
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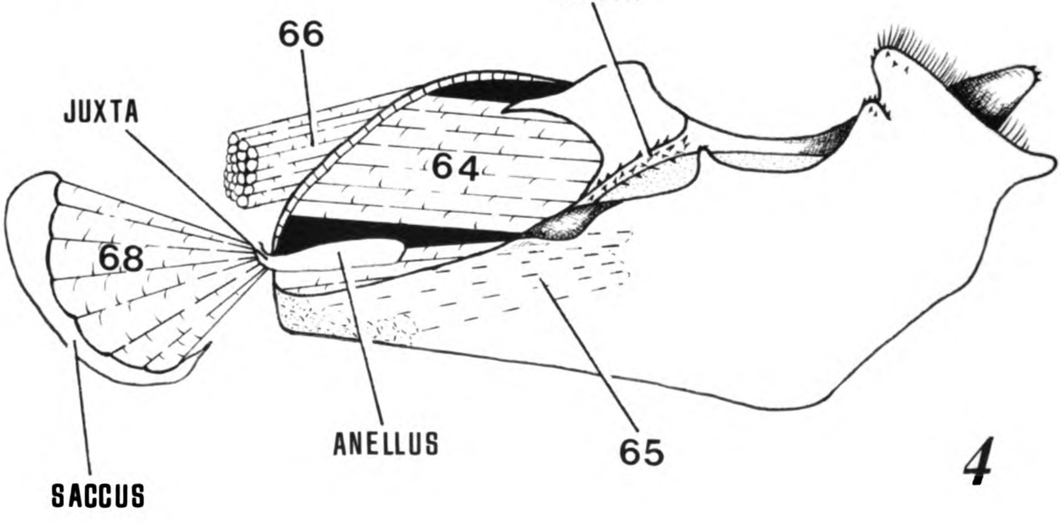
3

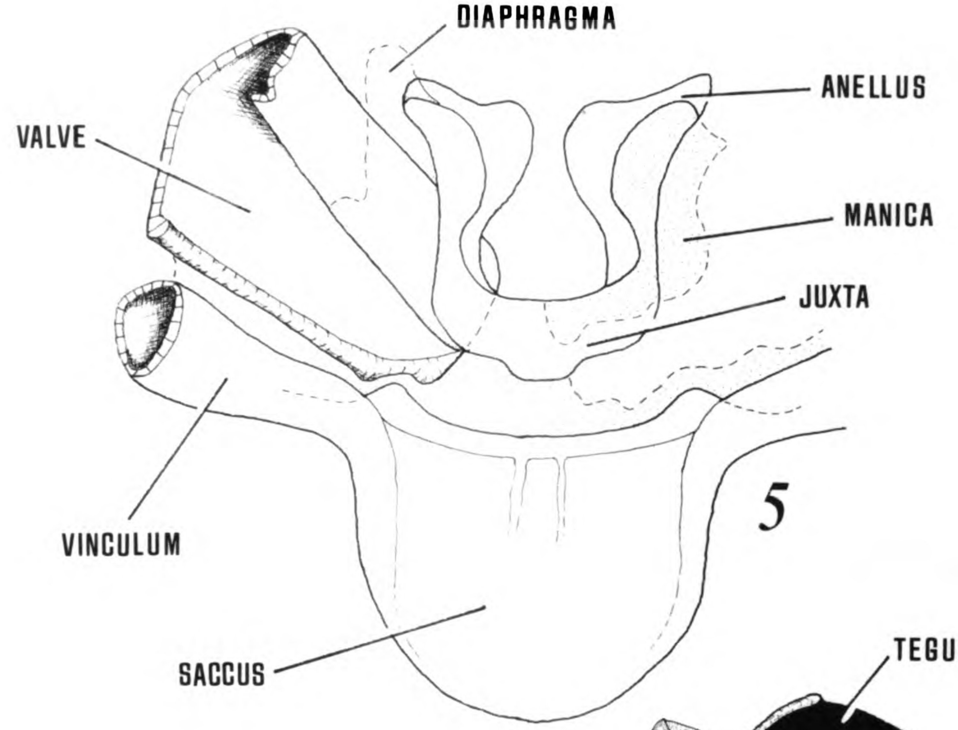

CRISTA
66
JUXTA
64
68
ANELLUS
65
SACCUS

4

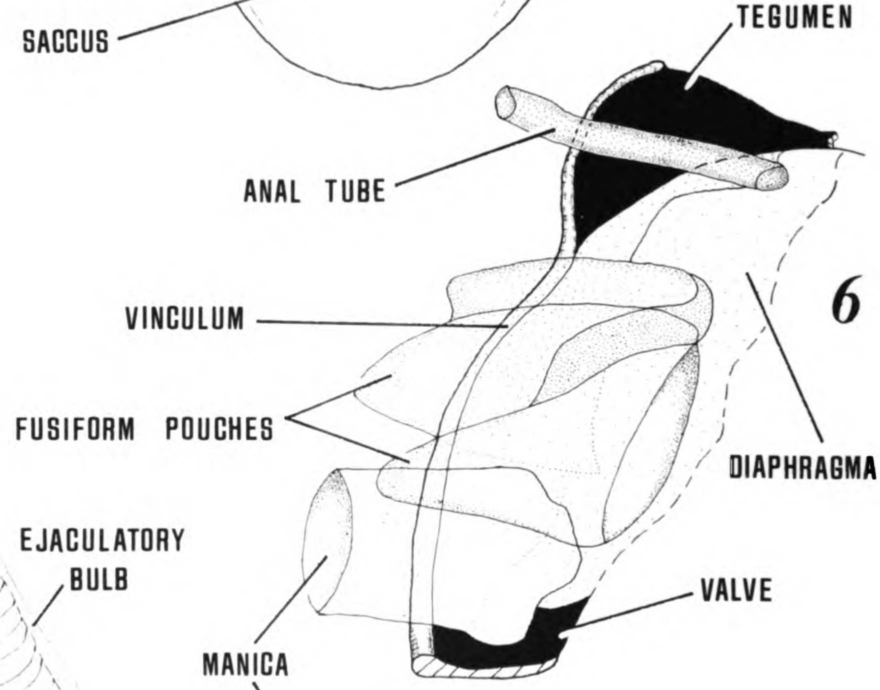
Figure 5. Dorsal View of the Articulations of the Juxta, Valve, and Saccus

Figure 6. Left Lateral View of the Membranous Areas of the Male Genitalia

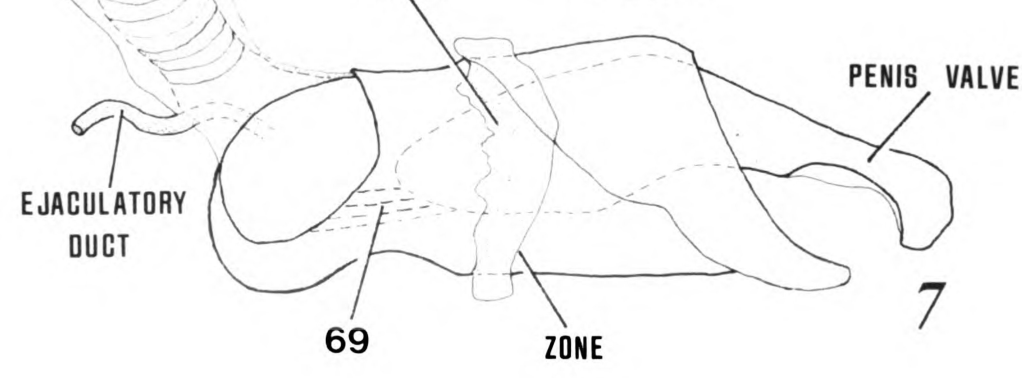
Figure 7. Left Lateral View of the Aedeagus and its Associated Musculature


DIAPHRAGMA
ANELLUS
VALVE
MANICA
JUXTA
VINCULUM
SACCUS

5

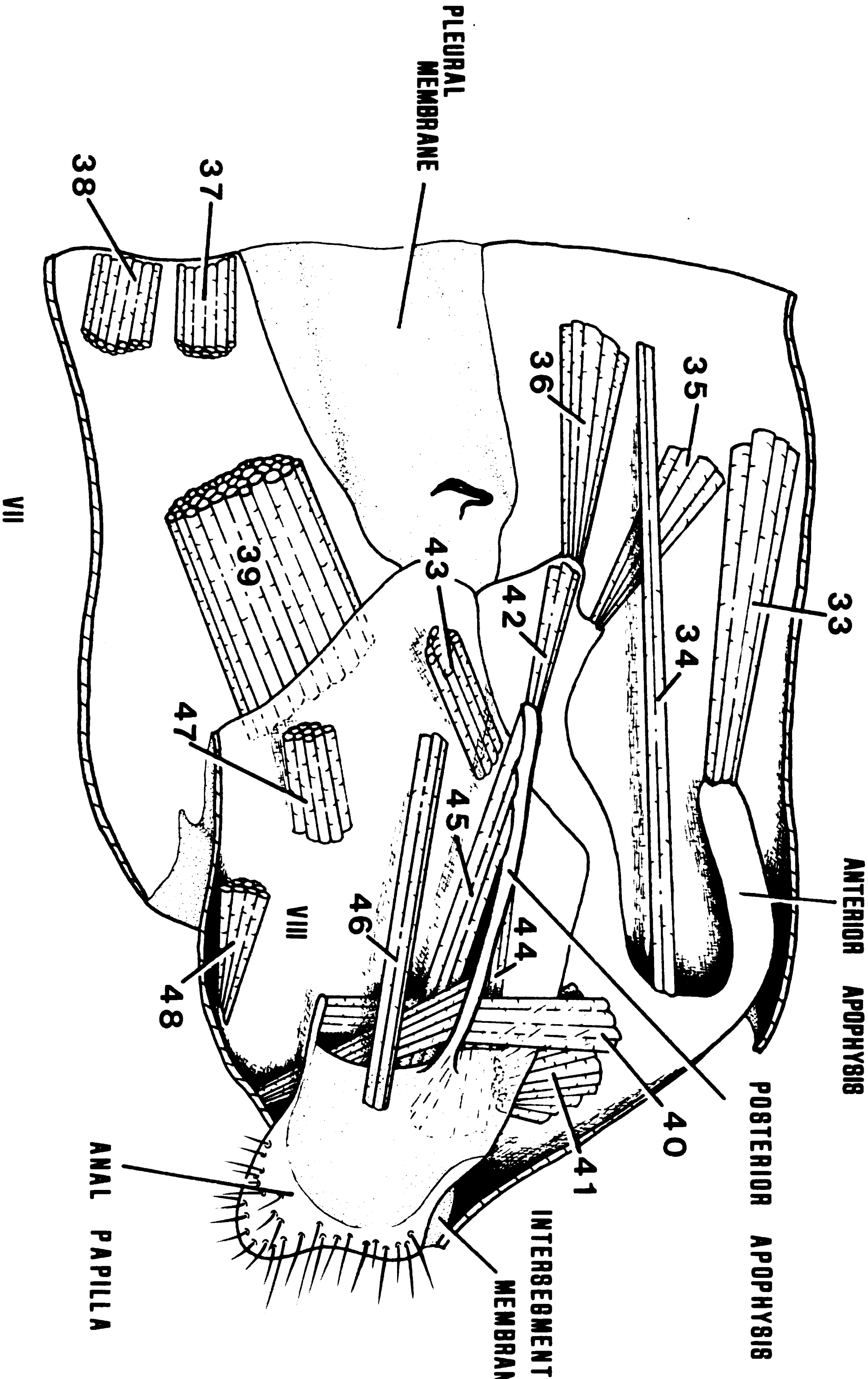

TEGUMEN
ANAL TUBE
VINCULUM
FUSIFORM POUCHES
DIAPHRAGMA
VALVE

6


EJACULATORY BULB
70
MANICA
PENIS VALVE
EJACULATORY DUCT
69
ZONE

7

Figure 8. Internal Right Lateral View of the Posterior Segments (VII-X) of the Female Abdomen with Associated Musculature


PLEURAL MEMBRANE
38
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VII
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ANTERIOR APOPHYSIS
POSTERIOR APOPHYSIS
ANAL PAPILLA
INTERSEGMENTAL MEMBRANE

8