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Morphology of the Reproductive System of *Tetrix arenosa angusta* (Hancock) (Orthoptera, Tetrigidae)

By RICHARD E. WIDDOWS and JAMES R. WICK

Abstract. The internal reproductive organs of the male include a pair of testes, each composed of about 37 follicles and connected to a short vas efferens; a pair of vasa deferentia; about 12 paired accessory glands; a twice folded ejaculatory duct and a membranous, extensible intromittent organ. The external structures of the male include a chitinous collar, pallial complex and ninth abdominal sternum. The internal reproductive organs of the female include a pair of ovaries, each composed of 11 ovarioles; paired lateral oviducts; a short median oviduct; a terminal genital charaber; a trilobed spermatheca attached to a spermathecal gland, and a pair of median glands. The external structures of the female include the ovipositor and its related sclerites and apodemes.

Recent studies of the genitalia of insects have been directed towards the correlation of terminology and the homologizing of structures (Ander, 1956; Snodgrass, 1957). In the Tetrigidae, a better understanding of the reproductive system is needed to determine the relationship of their reproductive structures to those of other Orthoptera. The research reported here provides an account of the reproductive structures of one tetrigid, *Tetrix arenosa angusta* (Hancock).

Members of the family Tetrigidae are commonly known as grouse locusts or pygmy grasshoppers. *Tetrix arenosa angusta* is a widely distributed sub-species of the family. It is a desirable insect for study because of its accessibility and gregarious habit during the spring and fall months. The tetrigids closely resemble the short-horned grasshoppers, the Acrididae, in many morphological respects. The grouse locusts, however, may be distinguished externally from the acridids by the extension of the pronotum nearly to or beyond the tip of the abdomen, the rudimentary tegmina, the prolongment of the prosternum into a chin piece, the lack of arolia on the tarsi, and the absence of a tympanic apparatus. They may be distinguished internally by the lack of posterior prolongations of the gastric caeca and by the differences in genitalia. For an account of the taxonomy of this grouse locust, one may refer to a recent publication of Rehn and Grant (1956).

MATERIALS AND METHODS

The specimens were collected within a seven mile radius of Ames, Iowa. Living specimens used for dissection were kept in quart fruit

jars with perforated lids and stored in a refrigerator at about eight degrees Centigrade. Moss and muck from the collecting sites were put into the jars with the specimens to serve as food and to provide a more natural habitat. The jars were kept moist to prevent desiccation. Under these conditions, specimens were easily maintained in good condition for future use. Because of the close proximity of the collecting areas, no attempt was made to rear the tetrigids.

A number of specimens were killed in 70 percent alcohol and stored in glycerin alcohol (20 parts of 70 percent alcohol to one part glycerin). This preserved their flexibility and caused them to become distended, both conditions being desirable for study of the abdominal sclerites. One disadvantage found in this method of preservation was that some of the fragile internal organs were not adequately preserved for dissection purposes.

The legs, wings, and pronotum were removed from specimens to be dissected and the specimens partially embedded ventral side down in paraffin lined watch glasses. Living specimens were dissected in physiological saline solution and preserved specimens in 70 percent alcohol. It was necessary to stain certain structures for determining the position of openings, the course of ducts, and the shapes of cuticular parts. The material to be stained was taken from 70 percent alcohol and put into acid fuchsin for about 30 seconds, rinsed in a basic alcohol followed by a rinse in acidic alcohol. Stains produced in this manner are temporary.

Excess tissues on heavily sclerotized structures were removed by immersing the structures in a hot potassium hydroxide solution for about one minute. The action of the potassium hydroxide was arrested by transferring the structures to acidulated water. The acidulated water was replaced with 70 percent alcohol and the structure stained according to the procedure given above.

Live spermatozoa in the female grouse locusts were found by dissecting the spermatheca from the live adult. The spermatheca was placed on a glass slide with a drop of saline solution and teased into small portions. A cover slip was placed on the preparation and the slide examined. The spermathecal glands of females and the accessory glands of males were prepared for study in the same way.

DESCRIPTION AND DISCUSSION

General Consideration of Male Reproductive System

The male reproductive system is composed of internal reproductive organs and external reproductive structures. The internal reproductive organs include the testes, vasa efferentia, vasa deferentia, accessory glands, ejaculatory duct and intromittent organ.

The external structures associated with reproduction include the

chitinous collar, pallial complex and ninth abdominal sternum.

Internal Reproductive Organs of Male

Testes. The paired testes of a mature grouse locust lie in the haemocoel between the dorsal diaphragm and the alimentary canal where they are held in position by a dense, interwoven layer of tissue. They extend from the middle of the thorax to about the eighth abdominal segment (Figure 1). Each testis is composed of 30 to 39 individual testicular follicles, 37 being the most commonly occurring number. In a given individual, the number of testicular follicles in each testis is the same. Each testicular follicle possesses a characteristic tear-drop shape. Variation in shape among the follicles is very slight.

Upon close examination each follicle appears segmented or layered. The layers appear as opaque areas lying in transverse planes within each follicle. According to Harmon (1925), the layers in *Paratettix toltecus* (Saussure) (under the name of *Apotettix eurycephalus* Hancock), contain successive stages in the development of spermatozoa. She recognized four zones of development within the testicular follicles: the germarium, the zone of growth, the zone of maturation divisions, and the zone of transformation. A testicular follicle of *Paratettix toltecus* is illustrated by Harmon (1925) which shows the various zones mentioned above. Robertson (1916) also did some work on the general structure of the testicular follicle. His labeled illustration of a follicle of *Tetrix subulata* (Linnaeus) (under the name *Acrydium granulatus* Scudd.) appears in general structure to be like that of *Paratettix toltecus* and *T. arenosa angusta*. A histological study of the testicular follicle of *T. arenosa angusta* would be necessary to establish the events of spermatogenesis in this subspecies.

The number of testicular follicles is variable among species of Tetrigidae according to the records found in literature. Harmon (1925) recorded nine follicles per testis for *Paratettix toltecus* and Carpentier (1942) recorded about 30 follicles per testis for *Tetrix vittatum* Zett. (under the name *Acrydium vittatum* Zett.).

Vasa efferentia. Short, tubular canals lead from the base of each testicular follicle. These are the vasa efferentia (Figure 1). Each vas efferens serves as a connection between a testicular follicle and a vas deferens. Harmon (1925) is the only other author to apply the name "vasa efferentia" to these structures in tetrigids.

Vasa deferentia. The vasa deferentia are the paired tubular canals to which attach the vasa efferentia of the testicular follicles. The posterior end of each vas deferens leads into the ejaculatory duct. Proceeding anteriorly from the ejaculatory duct, the vasa deferentia lead obliquely upward and come to lie above the alimentary canal.

The testicular follicles are attached along the length of the vas deferens except for a short portion near the posterior end. No consistent pattern of attachment of the follicles to the vasa deferentia was observed. Robertson (1916) stated that he found the testicular follicles connected to the vasa deferentia in regular order in the tetrigrids he studied. Harmon (1925) did not mention the arrangement of the follicles in *Paratettix toltecus*. Of the same insect, she mentioned that the vasa deferentia lie very close together and are difficult to separate. In *T. arenosa angusta* the vasa deferentia lie parallel but are widely separated (Figure 1).

Accessory glands. From 11 to 13 pair of large, tubular structures open into the anterior end of the ejaculatory duct near the openings of the vasa deferentia (Figures 1 and 3). These tubes are the accessory glands. The size of the tubes within each specimen varies. The anterior ends of several glands on each side fold back as shown in Figure 1. In specimens in which the accessory glands are not well developed, the glands lie along the floor of the haemocoel from the eighth abdominal segment to about the third abdominal segment. In specimens with well developed glands, the glands may reach anteriorly into the mesothorax. The anteriorly directed portion and the recurved portion of each gland increase in length and diameter as development takes place.

When the glands are well developed, one of the short tubes on each side may be enlarged distally. Dufour (1841) referred to each of the two enlarged glands among the nine to ten glands he found in *Tetrix subulata* as an epididymis. He referred to the other glands as seminal vesicles. Fenard (1896) also found two enlargements among the ten glands he found in *Tetrix subulata* (Linnaeus) (under the name *Tettix subulata* Linnaeus) and *Tetrix bipunctata* (Linnaeus) (under the name *Tettix bipunctata* Linnaeus). He referred to these two enlarged glands as seminal vesicles. Both Dufour (1841) and Fenard (1896) claimed to have found the epididymis or seminal vesicles (as they termed them respectively) filled with spermatozoa. Harmon (1925) found similar enlargements among the nine glandular tubes in *Paratettix toltecus* but found no spermatozoa contained in them. Carpentier (1942) mentioned 12 accessory glands in *Tetrix vittatum* but did not make any distinction among them, except for showing two enlarged tubes in his accompanying illustration. Most of the enlarged glands in *T. arenosa angusta* were found in specimens collected during the spring months. No spermatozoa were observed in the enlarged glands nor in any of the other accessory glands. All were filled with a viscous fluid. The two enlarged glandular tubes are not designated separately in this study since their occurrence was not consistent and their function was not distinguished from the other glandular tubes.

Ejaculatory duct. The ejaculatory duct is a membranous canal

leading from the vasa deferentia to the intromittent organ (Figure 3). The anterior end of the duct is located above the eighth sternum and receives the openings of the accessory glands and the vasa deferentia. It continues posteriorly to near the end of the ninth sternum. Here a heavily membranous structure is found which encloses the duct ventrally and laterally. This is the ventral plate of the ejaculatory duct (Figure 3). Though composed of membrane, the shape of the ventral plate is consistent due to an elastic quality. Its edges are free, but it is not readily detached from the ejaculatory duct.

From the region of the ventral plate, the duct bends back on itself and extends forward to near the bases of the accessory glands. This anteriorly directed portion is dorsoventrally flattened and lies nearly parallel to the lower region of the duct. It terminates its anterior extension in a thick enlargement. This thick region has a dark yellow color which remains even after bleaching in a hot potassium hydroxide solution. The ejaculatory duct continues posteriorly from this region to the intromittent organ as a dorsoventrally flattened tube. It is enclosed in a thick muscular layer which obscures its exact course until the muscle is removed. When the muscle layer is intact, the ejaculatory duct appears as a short, thick tube leading directly to the intromittent organ.

Dufour (1841) and Fenard (1896) mentioned the presence of an ejaculatory duct without further discussion. Harmon (1925) called the ejaculatory duct an irregular membranous bag. She mentioned its general position and that it terminates posteriorly in a conical penis. Carpentier (1942) stated that the accessory glands empty into the ejaculatory duct, but did not discuss it further. The relative lack of information on the ejaculatory duct of tetrigids indicates that its structure has not heretofore been studied in detail.

Intromittent organ. The intromittent organ is a single-walled, entirely membranous structure (Figures 2 and 3). It is impractical to designate its exact place of differentiation from the ejaculatory duct because the membrane of one is continuous with that of the other. In the compressed condition, the intromittent organ lies above the subgenital plate of the ninth sternum. In this condition, the rounded opening of the organ is covered by the pallial valves, but may be seen by extending the valves to a vertical position. When the intromittent organ is extended, the pallial valves are nearly upright and the organ projects in a nearly vertical position from the area between the pallial valves and the anus (Figure 2). The mechanism of extension has not been determined. Figures 7, 8, and 9 are diagrammatic illustrations indicating the process of extension as determined from preserved specimens. The small circles in these figures represent cross sections of the chitinous collar to

which the membrane of the intromittent organ is attached. The membrane comprising the organ is shown compressed in Figure 7, partially extended in Figure 8, and fully extended in Figure 9. Only when the intromittent organ is extended does it possess a double wall.

Because the bases for assignment of the terms "phallus" and "penis" are not evident in the simple copulatory organ of this insect, the term "intromittent organ" is used here to designate the copulatory structure.

Chopard (1920) gave the name "penis" to the membranous intromittent organ found in Tetrigidae. Walker (1922) also referred to a penis in Tetrigidae as having a genital opening with folded, membranous walls. In *Paratettix toltecus*, Harmon (1925) referred to a penis or sac-like intromittent organ as the termination of the ejaculatory duct. Snodgrass (1935b) designated the organ of intromission in *Tettigidea lateralis* a phallus. Carpentier (1942) mentioned an entirely membranous penis in *Tetrix vittatum*. Ander (1956) mentioned the presence of a phallus in the Tetrigidae which is much more simply built than in the other Orthoptera.

External Reproductive Structures of Male

Chitinous collar. A collar-like sclerite is found in the membranous area between the pallial complex and the anus. This sclerite is the chitinous collar (Figure 2). The anterior margin is heavily pigmented, but the posterior or inner margin is transparent and not readily discernible. The inner margin attaches to the membrane of the intromittent organ. The chitinous collar is at the base of the intromittent organ when the organ is extended.

Corresponding structures have been observed and described in other tetrigids by various authors. Chopard (1920) referred to the collar as a small chitinous piece. Walker (1922) termed it a pseudosternite. Harmon (1925) called it a chitinous collar. Snodgrass (1935b) described it as a median process armed with small spines. Carpentier (1942) described it as a chitinous arc.

Pallial complex. The pallial complex is composed of the pallial valves, pallial hooks and pallial membrane (Figures 1 and 2). The pallial valves are a pair of convex sclerotized plates lying between the posterior rim of the subgenital plate and the chitinous collar. The median margin of each valve bears a thickened ridge which terminates anteriorly as a pallial hook. The paired hooks converge medially at their free ends. Between the pallial valves is found the pallial membrane. The membrane continues anteriorly and is continuous with the membrane of the intromittent organ.

The corresponding structures of other tetrigids have been studied

and given similar names by other workers. The pallial valves were called valves or genital pieces by Chopard (1920), pallial plates by Walker (1922) and Ander (1956), and pallial valves by Snodgrass (1935b) and Carpentier (1942).

Ninth abdominal sternum. The ninth abdominal sternum is transversely divided into two separate sclerites. The proximal sclerite is the ninth sternum proper and the distal lobe is the subgenital plate (Figures 2 and 3). Walker (1922) described the divided ninth sternum of tetrigids as a basal sternite and a coxale. He based this terminology on the belief that the coxale is formed by the fusion of two coxites. Since no developmental study has been conducted on this insect, the terminology of Snodgrass (1935b) is followed here.

General Consideration of Female Reproductive System

The female reproductive system is composed of internal reproductive organs and external reproductive structures. The internal reproductive organs include the ovaries, lateral oviducts, median oviduct, genital chamber, spermatheca, spermathecal gland and the median glands. The external reproductive structures are composed of the ovipositor and its related sclerites and apodemes.

Internal Reproductive Organs of Female

Ovaries. The paired ovaries of a mature grouse locust lie in the haemocoel between the dorsal diaphragm and the alimentary canal. They extend from the prothorax to about the middle of the abdomen. Anteriorly the ovaries are tapered and medially appressed. Posteriorly the ovaries increase in size and occupy a position dorsal and lateral to the alimentary canal (Figure 4). In many cases, the ovaries extend anterior to their point of attachment and bend back on themselves forming a loop.

Each ovary usually consists of 11 ovarioles, although, occasionally, one more or less was found. It is interesting to note that this is the smallest number of ovarioles recorded for the family. Dufour (1841) mentioned the presence of 20 ovarioles in *Tetrix subulata*. Fenard (1896) found about 25 ovarioles in each of *Tetrix subulata* and *Tetrix bipunctata*. Harmon (1925) found about 18 ovarioles in *Paratettix toltecus*. Carpentier (1942) found around 13 ovarioles in *Tetrix vittatum*. Voy (1949) listed 13 ovarioles for *Tetrix tenuicornis* J. S. (under the name *Tettix tenuicornis* J. S.).

Each ovariole is comprised of three general regions: the terminal filament, the egg tube, and the pedicel. The most anterior region of the ovariole is the terminal filament (Figure 4). This is a slender strand of tissue which serves to attach each ovariole anteriorly in the region of the first phragma. The terminal filaments do not

unite to form a suspensory ligament like that described in *Dissosteira carolina* (Linnaeus) by Snodgrass (1935a). Harmon (1925) made mention of an ovarian ligament consisting of a bundle of terminal filaments in *Paratettix toltecus*, but she did not imply that the terminal filaments are united or fused. In the absence of a union of terminal filaments, the authors believe that the term "ovarian ligament" does not apply to *T. arenosa angusta*.

Posterior to the terminal filament of each ovariole is the egg tube which contains the germ cells in various stages of development. The egg tube is comprised of two regions: a short, anterior germarium and a more extensive, posterior vitellarium (Figure 4). The exact limits of the germarium cannot be ascertained in gross dissections, but temporary slides of the ovarioles show the germarium to occupy a very short region of the egg tube. In such preparations, the cells in the anterior part of the germarium appear smaller than those more posteriorly located. Harmon (1925, p. 221) wrote about the germarium of *Paratettix toltecus*, "It is the multiplication zone. It includes the primordial germ cell, the oogonia, and cells of the early part of the growth period."

The vitellarium, the extensive posterior region of the egg tube, consists of a linear series of follicles, each containing a developing oocyte. Each mature ovariole contains an average of 15 follicles. The vitellarium extends posteriorly from the germarium to its attachment with the pedicel (Figure 4). As the developing follicles become located more posterior to the germarium, they change in size and proportion from very small, thin and disc-shaped follicles, to large, elongate and ovoid follicles. Increase in the size of each follicle accompanies an increase in the size of the oocytes. According to Harmon (1925), this increase of oocyte size is due to the accumulation of yolk. The most mature follicle of an ovariole occupies the most posterior position within the vitellarium. In mature females, the follicles may reach three millimeters in length.

In fresh specimens, the large oocytes are a brilliant yellow. This is probably due to the accumulation of yolk. The color is less pronounced in the smaller follicles. The very small follicles at the anterior end of the vitellarium are opaque white.

At the base of the egg tube immediately posterior to the vitellarium is the pedicel. The pedicel is a tubular, cup-shaped structure which is easily seen by making temporary slides of the egg tubes. The posterior ends of the mature oocytes fit into the concave ends of the pedicels. Harmon (1925) called a similar structure in *Paratettix toltecus* the calyx. Fenard (1896) indicated that the ovarioles are attached to lateral and external egg cases, but no illustrations are included in his publication to clarify this terminology.

The author deems the term "pedicel" more consistent with the present morphological interpretation of the structure which connects the last follicle of an ovariole with the lateral oviduct. A study of the postembryonic development of the ovary is needed to resolve this problem in tetrigids.

Lateral oviducts. The tubular canals leading posteriorly from the ovarioles are the lateral oviducts (Figure 4). Each lateral oviduct forms a calyx at its anterior end. The calyx is the expanded region which is continuous with the pedicels of the ovarioles (Figure 4). It tapers gradually as the more anterior ovarioles are attached along its length. The calyx is capable of stretching to accommodate several mature oocytes following their emergence from the pedicels.

The posterior portion of each lateral oviduct is a simple tube which serves as a passageway for mature oocytes. The lateral oviducts converge and unite medially beneath the alimentary canal in the region of the fifth abdominal segment. Corresponding structures in tetrigids studied by Fenard (1896), Harmon (1925) and Carpentier (1942) were not designated separately from the oviduct. The designation "lateral oviduct" more adequately describes the condition found in *T. arenosa angusta*.

Median oviduct. The median, tubular passageway leading posteriorly from the united lateral oviducts is the median or common oviduct. It extends from about the fifth abdominal segment to the middle of the eighth abdominal segment and lies on the floor of the haemocoel (Figures 4 and 6). When no oocytes are present in the median oviduct, it is dorsoventrally flattened from the sixth segment through the eighth segment. The opening of the median oviduct into the floor of the genital chamber is the female gonopore (Figure 6). Harmon (1925) and Carpentier (1942) have designated the posterior region of the oviduct as the vagina in the tetrigids which they studied. They apparently have not taken into consideration the different origin of the median oviduct and the genital chamber in assigning terminology. The term "vagina" usually applies to a modification of the genital chamber. According to Snodgrass (1935a, p. 563), "the vagina is a direct derivative of the genital chamber and not a continuation of the oviduct." It seems advisable, therefore, to term the entire median tube leading from the lateral oviducts to the gonopore, the median oviduct. Since there is no anatomical modification of the genital chamber between the gonopore and the exterior of the insect, there is no vagina present in *T. arenosa angusta*.

Genital chamber. The median oviduct opens into the genital chamber which is a pouch-like cavity lying above the eighth abdominal sternum (Figure 6). The gonopore of the median oviduct opens into the floor of the genital chamber near the vulva, the

posterior opening of the genital chamber. The chamber is formed by folds of membrane attached to the posterior rim of the eighth abdominal segment and to the first valvulae of the ovipositor. The part of the genital chamber anterior to the opening of the gonopore constricts abruptly to form a narrow tube leading to the spermathecal gland. A pair of median glands lead into the dorsal wall of the genital chamber. These glands will be discussed later.

Spermatheca. In dissections of freshly killed specimens and specimens preserved in glycerin-alcohol, the spermatheca can be distinguished easily as a purplish, lobate structure lying to the left of the rectum and above the sixth abdominal sternum. In dried specimens, the structure remains dark but loses its color. The spermatheca is a trilobed, Y-shaped structure (Figures 4 and 6). The longest lobe of the spermatheca is directed downward. The two short lobes are usually directed obliquely upwards and to the rear. The more ventral of the two short lobes constricts distally and continues as a small spermathecal canal. The canal curves ventrally and crosses the left side of the spermatheca. It terminates on a large, sac-like structure, the spermathecal gland. A perceivable amount of variation occurs in the shape of the dorsal lobe of the spermatheca.

Spermathecal gland. The spermathecal gland is constricted into two lobes, a large dorsal lobe and a small ventral lobe (Figures 4 and 6). The dorsal lobe is grooved on the right where it bends upon the alimentary canal. The smaller lobe extends immediately ventral to the dorsal lobe. The spermathecal canal enters the spermathecal gland at the division of the dorsal and ventral lobe. The spermatheca is tightly affixed to the posterior side of the gland by tracheoles and other tissues. In living specimens, the spermathecal gland is opaque white. The gland was divided into two lobes in all specimens studied. The over-all shape of the gland was found to be slightly variable. The dorsal lobe varied in shape from almost spherical to elongate. The ventral lobe was less variable, but was found in slightly elongate conditions.

A tubular canal, the seminal canal of Voy (1949), leads ventrally from the lower lobe of the spermathecal gland (Figure 6). The canal turns abruptly to the rear just above the median oviduct and continues posteriorly to enter the anterior end of the genital chamber. The length of the canal parallel to the median oviduct is dorsoventrally flattened.

Confusion has resulted over the functions and, consequently, the names of the spermatheca and spermathecal gland. Since no post-embryonic study has been employed with the above named structures of the Tetrigidae, there can be no certainty as to their homology

with the corresponding structures of the closely related family, Acrididae.

The only structure in the female found to contain spermatozoa was the spermatheca. A series of dissections was conducted in which the spermathecae and the spermathecal glands were examined for spermatozoa. No spermatozoa were found in the spermathecal gland. In contrast, spermatozoa were found in the lumen of every spermatheca examined. As a result of these observations, the small trilobed structure is called the spermatheca and the canal leading from it, the spermathecal canal. The large, bilobed structure to which the spermatheca is attached is called the spermathecal gland. In all examinations of this gland, a viscous fluid was found.

A review of the literature involving these structures in question gives evidence of the confusion regarding the spermatheca and spermathecal gland. Dufour (1841) referred to the spermathecal gland as a bulky reservoir and the spermatheca as a sebific gland. Fenard (1896) termed the spermathecal gland a copulatory pouch. However, he stated that his dissections showed spermatozoa were stored in the trilobed structure, the spermatheca. The short canal leading from the spermatheca he called the seminal canal. Harmon (1925) stated that she found spermatozoa only in a balloon-shaped sac (spermathecal gland) which she called the spermatheca. She included a drawing of a cross section of this structure in which spermatozoa are shown. The trilobed structure she called the spermathecal gland.

Carpentier (1942) agreed with Harmon (1925) in calling the spermathecal gland the spermatheca but designated the bilobed structure a nourishing gland. He did not give reasons for his terminology, but did have the structures clearly diagrammed and labeled. Slifer (1943) made mention of the confusion of terminology and function of the organs in her publication. She agreed with Fenard (1896) in naming the spermatheca. The spermathecal gland she referred to only as a large sac. Voy (1949) modified the terminology and called the spermatheca an appendicular organ and the spermathecal gland the seminal receptacle. Although his work involved much histological study, no mention is made of the histology of any grouse locusts. To resolve the controversy concerning the functions of these structures, a thorough histological study is needed.

Median glands. Two tubular glands, the median glands, open into the roof of the genital chamber (Figures 4 and 6). Each gland is slightly constricted at its base and is attached to the genital chamber near the mid-line of the body. Their distal ends are unattached but are held in place by tracheae and muscles. The glands are about one millimeter in length. The function of the median glands has not

been determined. Slifer (1943) is the only author to mention the presence of these glands. She stated that she found them in all the tetrigids included in her study. She considered them secretory in nature and also suggested that these glands may represent the spermatheca of certain other Orthoptera. The spermathecae of Acrididae occupy the same position that these median glands occupy in *T. arenosa angusta*. A study of the postembryonic development of the female would be necessary to ascertain the indicated homology.

Carpentier (1942) showed two structures similar to these glands in his drawings of *Tetrix vittatum*, but he neither labeled them nor discussed them.

External Reproductive Structures of Female

Ovipositor. The ovipositor complex consists of three pairs of valves, the first valvulae, second valvulae, and third valvulae, and the related intervalvular sclerites.

The first valvulae are the most ventral of the three sets of valves (Figures 5 and 6). They join with the abdomen immediately dorsal to the vulva. Each of the valves constituting the first valvulae may be divided into two regions, a terminal lobe and a basal region. The terminal lobe is the heavily sclerotized posterior projection. Viewed from the side, it is broadest at its base and tapers to a sharp centrally curved spine. It is laterally compressed and bears a double row of spines along its ventral surface. Each row contains about eight spines. The dorsal margin of the lobe is rounded. The median surface bears minute spines.

The basal region of each first valvula is largely membranous. The dorsal surface of the ventral lobe continues over the membranous part of the base as a basal extension. It forms an articulation with the lateral intervalvular apodeme (Figure 6). The membranes of each valve base contain two separate sclerites. The linear sclerite lying obliquely in the membrane of the basal region serves as a support for the wall of the genital chamber. This linear sclerite is termed a ventral basivalvular sclerite (Figure 5). The other sclerite is located in the membranous area between the extension of the terminal lobe and the ventral basivalvular sclerite. It is the dorsal basivalvular sclerite. Walker (1919) figured two basivalvular sclerites and a distinct valvifer in *Tetrix ornatum* Say (under the name *Acrydium ornatum* Say). No valvifer-like sclerites are present in *T. arenosa angusta*. Slifer (1943) referred to the elongate ventral basivalvular sclerites as anterior basivalvular sclerites.

Chopard (1920) figured a lateral sclerite associated with the first valvulae of *Paramastax laeta* which he termed the pileolus. The location of the pileolus suggests that it is the same sclerite as the dorsal basivalvular sclerite found in the membrane of *T. arenosa angusta*.

The second valvulae are very small in comparison to the first valvulae (Figures 5, 10 and 11). They lie dorsal to the first valvulae and are concealed by the first and third valvulae. They consist of two lateral sclerotized areas with a partially sclerotized membrane between them. The two lateral sclerotized areas are the rami of the second valvulae and membranous area between them is the intervalvular membrane (Figures 10 and 11), after Walker (1919). The membrane forms a hood above the first valvulae and terminates in two fleshy lobes. Anteriorly, the rami and the intervalvular membrane are attached to the anterior intervalvula, a sclerite of the third valvulae.

The third valvulae are the most dorsal of the three pairs of valvulae (Figures 6, 10 and 11). Viewed from the side, they are broadest midway along their length. Each terminates posteriorly in a dorsally projected spine. The dorsal surface of each valvula bears two rows of about eight spines. Anteriorly, the valves connect with the lateral intervalvular apodemes.

The third valvulae articulate with two sclerites. The most posterior of these sclerites is the posterior intervalvula (Figure 10). Its distinctive shape suggests the possibility of its being used in taxonomy. It is easily accessible and heavily sclerotized. The anterior sclerite is the anterior intervalvula (Figures 10 and 11). It is a narrow, transverse sclerite which articulates with the anterior ends of the third valvulae. On its anterior margin is a small median apodeme. The terminology used for the intervalvular sclerites is taken from similar sclerites of Carpentier (1942) and Snodgrass (1935b).

The first and third valvulae function together in oviposition. Their action is forceps-like, pushing back the moss or soft soil into which the eggs are laid. The second valvulae act as an egg guide beneath which the eggs must pass.

The valvulae of Orthoptera have been assigned different names by various authors. The first and third valvulae have been termed ventral and dorsal valvulae respectively by Walker (1919), inferior and superior valvulae by Chopard (1920) and Carpentier (1942), first and third valvulae by Snodgrass (1935a, 1935b), and anterior (ventral) and posterior or dorsal (lateral) valvula or gonopophysis by Ander (1956). The second valvulae have been called an egg guide by Harmon (1925), inner valvulae by Walker (1922) and Ander (1956), internal valves by Carpentier (1942), and second valvulae by Snodgrass (1935a, 1935b).

Lateral intervalvular apodemes. The paired, lateral intervalvular apodemes are hollow, sclerotized rods directed anteriorly from the bases of the valvulae (Figures 4, 10 and 11). The first and third valvulae articulate with the apodemes. The apodemes serve as

attachments for muscles which operate the valves of the ovipositor. Anteriorly, the apodemes extend into the sixth abdominal segment. This type of apodeme is also found well developed in the related family, Acrididae.

Subgenital plate. The sternum of the eighth abdominal segment of the female is termed the subgenital plate (Figure 5). Although not an actual structure of the external genitalia, it does play a part in oviposition. In *T. arenosa angusta*, the posterior margin of the plate is modified slightly to form a median projection, the egg guide (Figure 5). The egg guide is much less pronounced in the Tetrigidae than in certain other Orthoptera. The term "egg guide" as used by Harmon (1925) refers to the second valvulae and not to the structure described here. The egg guide of *T. arenosa angusta* does correspond to the structure designated egg guide in *Paramastix laeta* by Chopard (1920).

SUMMARY

A morphological study has been conducted on the reproductive system of *Tetrix arenosa angusta* (Hancock). The internal reproductive organs of the male were found to include a pair of testes, each composed of 31 to 39 testicular follicles attached to a vas deferens by short vasa efferentia, a twice folded ejaculatory duct into which enter the paired vasa deferentia and 11 to 13 pair of accessory glands, and an entirely membranous and extensible intromittent organ.

The external reproductive structures found in the male were a U-shaped chitinous collar through which the intromittent organ is extended; a pallial complex consisting of a pair of pallial valves, a pair of pallial hooks, and a pallial membrane; and a ninth abdominal sternum transversely divided into a proximal section and a distal subgenital plate.

The internal reproductive organs of the female were found to include a pair of ovaries, each consisting of 11 ovarioles attached to a lateral oviduct by means of an expanded calyx. Posteriorly, the lateral oviducts join with the median oviduct which empties into the floor of the genital chamber. A trilobed spermatheca attaches to a bilobed spermathecal gland which leads into the anterior end of the genital chamber. A pair of median glands open dorsally into the genital chamber, which also receives the openings of the median oviduct and the spermathecal gland. The genital chamber opens to the exterior beneath the first valvulae.

The external reproductive structures of the female consist of an ovipositor composed of the first, second and third valvulae; paired intervalvular apodemes to which the valvulae articulate; and a subgenital plate with the posterior margin modified to form an egg guide.

PLATE I

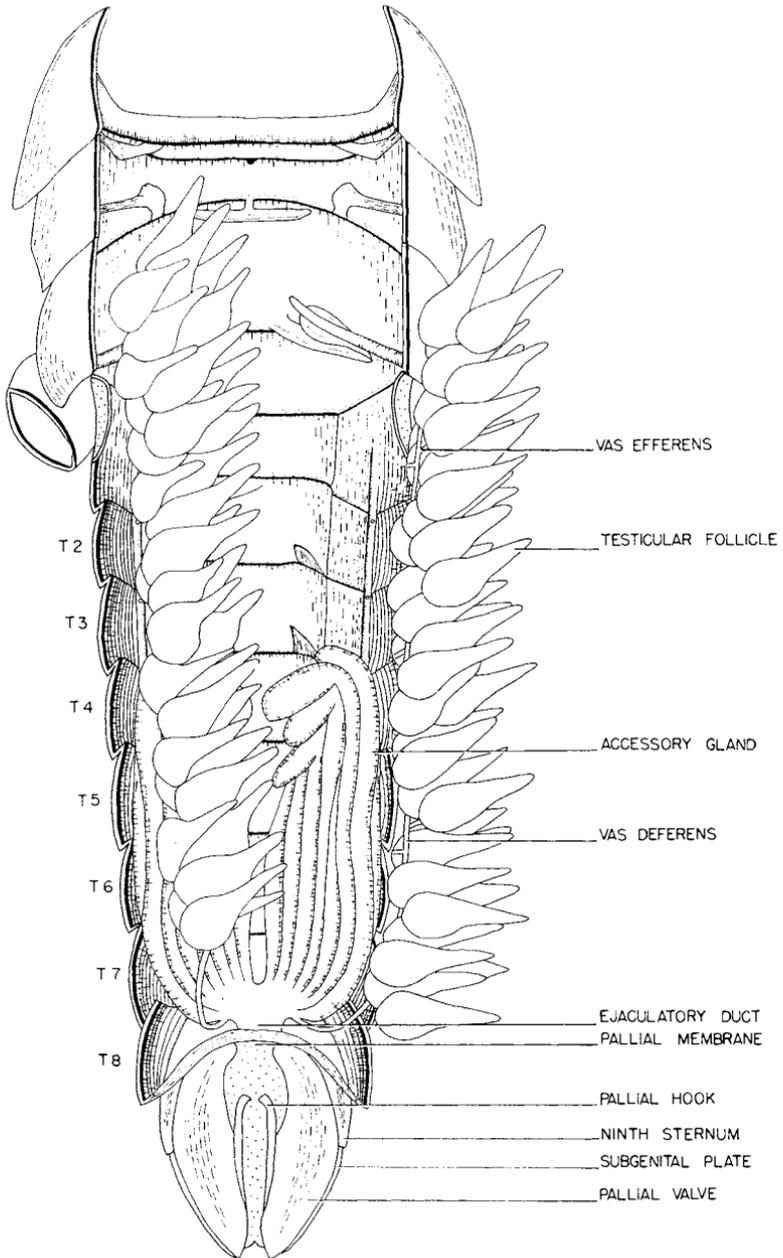
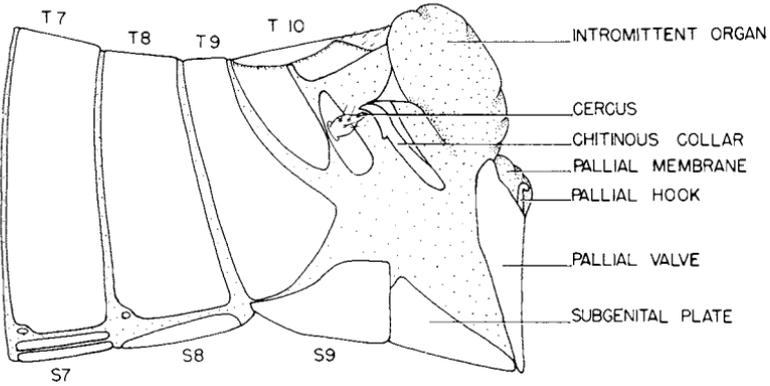
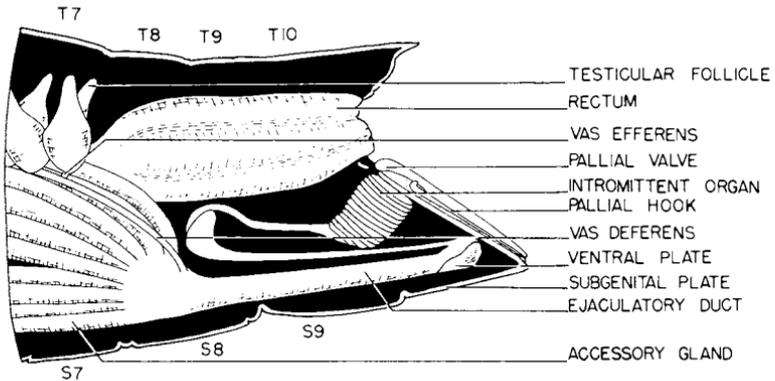


Figure 1. Dorsal view of the reproductive system of a young adult male; T, tergum.

PLATE II



2



3

Figure 2. End of male abdomen, lateral view of external structures; T, tergum; S, sternum.

Figure 3. End of male abdomen, lateral view of internal reproductive structures; T, tergum; S, sternum.

PLATE III

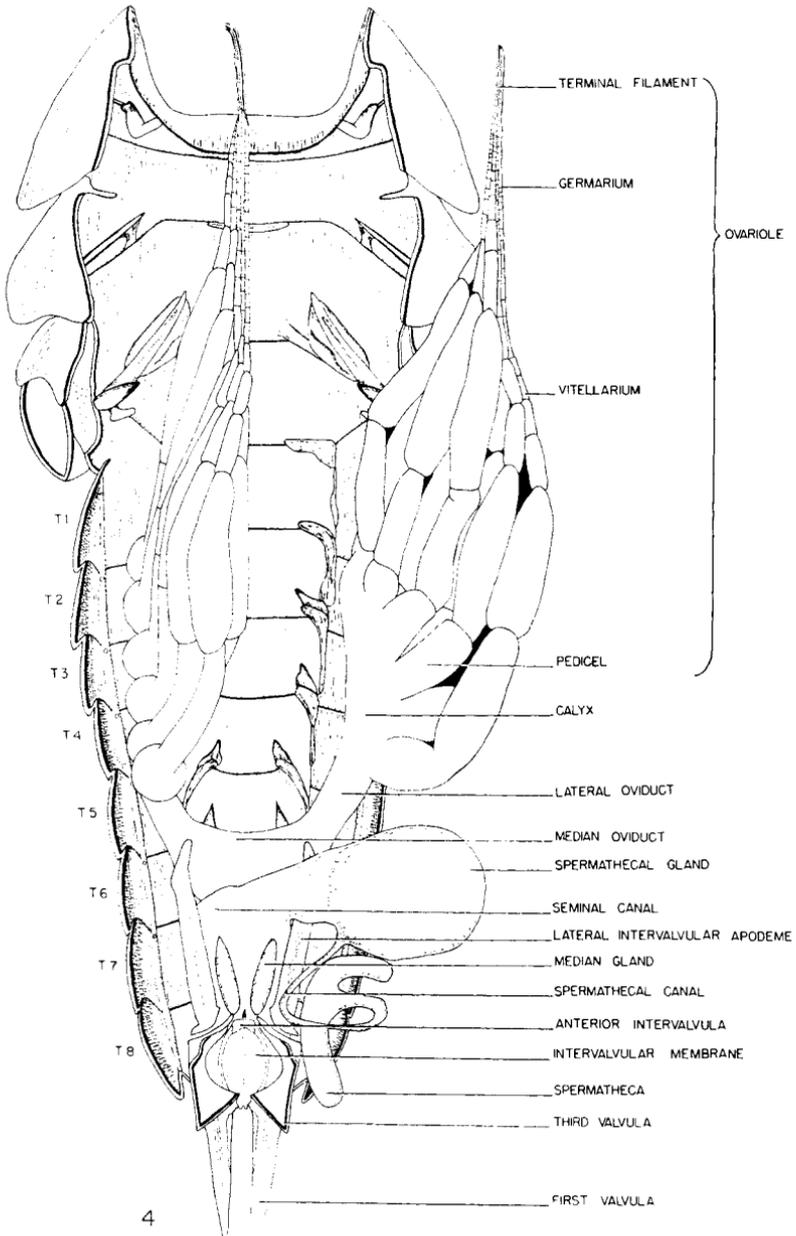
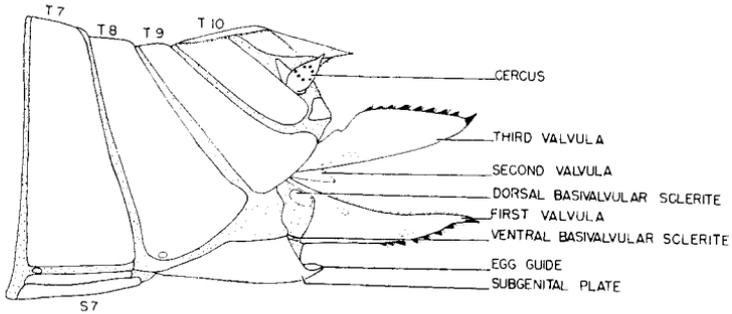
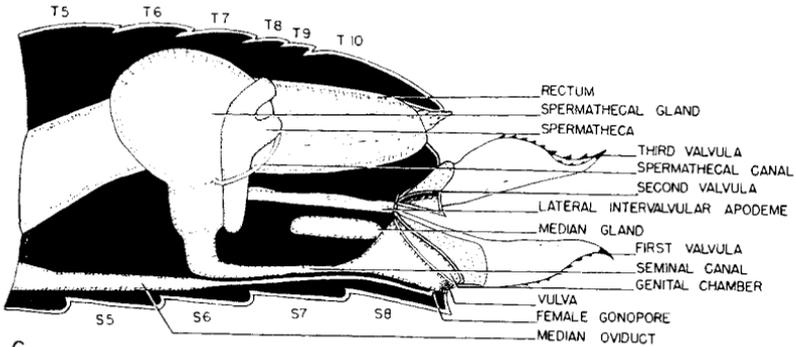


Figure 4. Dorsal view of the reproductive system of a young adult female; T, tergum.

PLATE IV



5



6

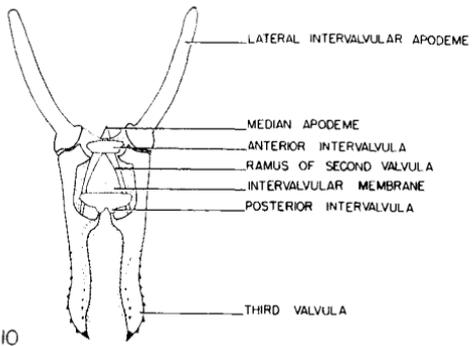
Figure 5. End of female abdomen, lateral view of external structures; T, tergum; S, sternum.

Figure 6. End of female abdomen, lateral view of internal reproductive structures; T, tergum; S, sternum.

PLATE V



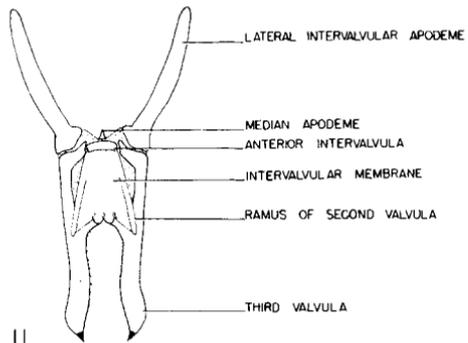
7



10



8



11

Figure 7. Diagrammatic illustration of compressed male intromittent organ.

Figure 8. Diagrammatic illustration of partially extended male intromittent organ.

Figure 9. Diagrammatic illustration of extended male intromittent organ.

Figure 10. Dorsal view of third valvulae, related sclerites and apodemes.

Figure 11. Ventral view of second and third valvulae, and related sclerites and apodemes.

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