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THE MALE GENITALIA OF ORTHOPTEROID  
INSECTS

BY

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## I. INTRODUCTION

The order Orthoptera as here understood includes at least the Mantoidea, Blattoidea, Tettigonioidae, and Acridoidea. The group

unity of these forms is attested in the structure of the male reproductive system by the compounding of the so-called accessory genital glands that appear, in the adult condition, to arise from the inner end of the ductus ejaculatorius, but which in their development are outgrowths of the mesodermal coelomic ampullae into which the vasa deferentia discharge. Closely associated with the true Orthoptera by the same feature of the male genitalia are the Termitidae, Embiidae, Grylloblattidae, Phasmatidae, and probably the Zorotypidae. On the other hand, the Plecoptera and the Dermaptera would appear to be distinct orders having no close relationship with the Orthoptera, since in each of these groups the male reproductive system is specialized in its own way, and shows none of the features characteristic of the orthopteroid insects. Concerning Dermaptera, Favrelle (1934) says, not only the structure of their reproductive organs, but also the cytology of their spermatogenesis shows that they are entirely distinct from Orthoptera.

*Development of the male gonads.*—The primary germ cells of Orthoptera, so far as their history is known, are differentiated from the somatic cells at a relatively late stage of development as compared with those of insects in which they appear at the time of blastoderm formation. In *Blatta*, *Blattella*, *Gryllus*, and *Melanoplus* the germ cells have been first recognized as such after the differentiation of the inner germ layer, but before the formation of the coelomic sacs (Heymons, 1895; Nelsen, 1934), in *Conocephalus* and *Locusta* not until the coelomic cavities have been formed in the mesoderm (Wheeler, 1893; Roonwal, 1937). The germ cells of *Melanoplus differentialis*, according to Nelsen (1934), are first distinguishable from the ectoderm of the germ band when metamerism is about to begin in the abdomen; they now appear as bands of weakly staining cells bordering the abdomen (fig. 1 A, *GCLs*) from the region of the first to that of the ninth prospective somite, and are seen in sections (B, *GCLs*) as masses of cells at the sides of the abdominal ectoderm projecting laterad of the bases of the ammotic folds (*Am*). The mesoderm rudiment (*Msd*) has already been formed as a solid band of cells lying above the midline of the ectoderm. During the subsequent growth of the embryo the mesoderm spreads laterally to the edges of the ectoderm (C), and the germ cell bands are now folded inward upon the mesoderm. When the coelomic sacs are later formed (D, *Coel*), the germ cells (*GCLs*) have come to lie on their dorsal walls, and from this position they soon invade the mesoderm and intermingle with the mesoderm cells in the upper parts of the splanchnic

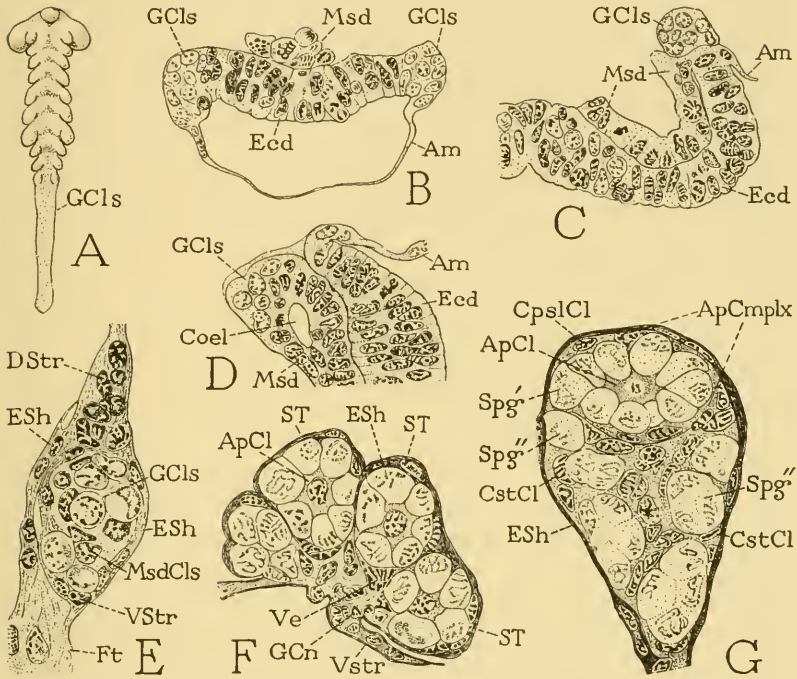


FIG. 1.—Development of the testis of *Melanoplus differentialis* (Thomas). (From Nelsen, 1931, 1934.)

A, an embryo at age when the germ cells are first distinguishable as such lying along sides of ectoderm of abdomen. B, transverse section of unsegmented part of abdomen at stage of fig. A, showing masses of germ cells (GCLs) proximal to amniotic folds (Am) at sides of abdominal ectoderm (Ecd). C, transverse section of lateral half of germ band at later stage, with germ cells folded inward upon upper end of mesoderm. D, still later stage, germ cells now transferred to splanchnic wall of mesoderm. E, transverse section of testis just after revolution of embryo, showing group of germ cells (GCLs) and undifferentiated mesoderm cells (MsdCls) in germinal area of gonad, with dorsal strand of mesoderm cells above (DStr) and ventral strand (VStr) below, the whole surrounded by a mesodermal epithelial sheath (ESH) continuous with a body of fat tissue (Ft) below. F, transverse section of testis near close of first postembryonic instar, showing rudiments of sperm tubes (ST), each containing an apical cell (ApCl) surrounded by primary spermatogonia, with vasa efferentia (Ve) forming from germinal center (GCn). G, section of young sperm tube during latter part of second instar, with apical complex (ApCmplx) in its distal end, and encysting spermatogonia (SpG'') in its proximal part.

Am, amnion; ApCl, apical cell; ApCmplx, apical complex; Coel, coelomic cavity; CpslCl, capsular cell; CstCl, cyst cell; DStr, dorsal strand; Ecd, ectoderm; ESH, epithelial sheath of testis; Ft, body of fat tissue; GCLs, germ cells; GCn, germinal center; Msd, mesoderm; MsdCls, undifferentiated mesodermal cells of gonad; SpG', primary spermatogonia; SpG'', secondary spermatogonia; ST, rudiments of sperm tubes (testicular "follicles"); Ve, vas efferens; VStr, ventral strand.

layers. Roonwal (1937) questions whether Nelsen properly identified the supposed early germ cells of *Melanoplus*, and suggests that they are probably cardioblasts.

After the successive coelomic cavities have merged into a continuous coelome by the dissolution of the separating walls, the germ cell areas of the splanchnopleure form two long genital strands, or ridges. These ridges in the young embryo of *Melanoplus*, Nelsen says, extend from the first to the eighth abdominal segment; in *Conocephalus*, Wheeler (1893) observes, germ cells may lie as far back as the tenth segment, though ordinarily they extend only into the sixth, and in *Locusta*, according to Roonwal (1937), they can be traced back to the tenth segment. As each ridge enlarges it protrudes into the coelome and comes to have the form of a free fold suspended from the upper part of the splanchnopleure in the neighborhood of the cardiac rudiments; in *Melanoplus* (fig. 1 E) the fold supports ventrally a mass of fat tissue (*Ft*). A transverse section of the male gonad at this stage, as described by Nelsen (1931) in *Melanoplus*, shows the following elements (fig. 1 E): dorsally is the membranous attachment of the gonad to the splanchnopleure; below this runs a dorsal strand of mesodermal cells (*DStr*); next is a central mass of germ cells (*GCls*) and undifferentiated mesoderm cells (*MsdCls*); and finally, a ventral strand of mesodermal cells (*VStr*), which forms the lower wall of the gonadial rudiment and supports the mass of fat tissue (*Ft*) beneath it. The entire organ, from the suspensory membrane to the ventral fat body, is invested in a mesodermal epithelial sheath (*ESh*), the "outer limiting membrane" of Nelsen.

The later history of the male genital rudiment consists of a differentiation of the inner cellular elements, the formation of the definitive sperm tubes, or so-called testicular "follicles" (it should be noted that an ovarian follicle is a subdivision of an egg tube), the establishment of the sperm tube ducts (vasa efferentia), and the formation of the gonadial part of the vas deferens. The following account of the processes involved is a brief summary of the excellent description of the development of the testis in *Melanoplus differentialis* given by Nelsen (1931), which adds much in the way of concise information to our previous knowledge of the subject in other insects.

At the beginning of the post-revolution period in the development of the *Melanoplus* embryo, the genital rudiments have somewhat shortened, reaching now only to the end of the seventh abdominal segment. By the middle of this period, the indifferent mesodermal

cells of each gonad begin to differentiate into connective tissue elements that form intratesticular partitions among the germ cells, thus segregating the latter into groups of one or more cells each (fig. 1 F). The partition-forming cells are probably generated from cells at the junction of the gonad proper with the ventral cell strand. The actively proliferating area here located is termed by Nelsen the "germinal center" (*GCn*). Each cell group, or cell nest, thus secondarily isolated, marks the nucleus of a definitive sperm tube, or "follicle."

By the time of hatching, the gonads have the form of two cords lying immediately below the heart, extending from the rear half of the third abdominal segment into the anterior half of the sixth. The germ cells have multiplied until there are about four or five cells in each group. Now an "indifferent mesoderm cell", Nelsen observes, leaves the periphery of the gonad and pushes into the center of each germ cell group, where it sends out cytoplasmic processes that fill the spaces between the germ cells. This interpolated cell becomes the apical cell of the group (fig. 1 F, G, *ApCl*); the entire nest of cells is surrounded by a capsule of connective tissue cells (G, *CpslCl*). The whole formation, which will be retained in the apex of each sperm tube, Nelsen calls the *apical complex* (*ApCmplx*).

The growth of the apical complexes causes a series of lobes to appear on the dorsal surface of the gonad, which are the beginnings of the definitive sperm tubes (fig. 1 F, *ST*). Undifferentiated cells now grow upward from the germinal center against the lower end of each apical complex (*Ve*), while at the same time the outer epithelial sheath grows inward between the dorsal lobes of the gonad until it invades the germinal center. In this manner the young sperm tubes are formed, each consisting of a germarium, which is the apical complex, and of a duct, or vas efferens (*Ve*), derived from the germinal center, the whole structure invested in a fold of the outer epithelial sheath (*ESh*).

The next phase of activity in the gonad, which begins during the second nymphal instar, is the formation of the sperm cysts, and the further differentiation of internal cellular elements. The germ cells surrounding the apical cell, and in immediate contact with it, are the primary spermatogonia (fig. 1 G, *Spg'*). During division, however, some of the germ cells are crowded away from the apical cell, or they are excluded from it by a tangential plane of division. These displaced cells become secondary spermatogonia (*Spg''*). As the latter leave the sphere of primary spermatogonia they take with them some of the capsular cells investing the apical complex, which,

attaching themselves to the secondary spermatogonia, become the cyst cells (*CstCl*) that give rise to the sperm cysts. The encysted secondary spermatogonia by subsequent divisions produce the cell groups that eventually form the spermatocytes and spermatozoa. The formation of the cysts from mesoderm cells, as described by Nelsen, seems much more reasonable than the idea that the cyst cells are derived from the spermatogonia, as some writers have claimed. The cyst cells of the testis are thus seen to be entirely analogous in their origin to the follicle cells of the ovary. During the formation of the cysts the sperm tubes increase in size, and the interstices between the cysts become occupied by a continuously growing interfollicular framework of connective tissue cells derived mostly from the germinal center. A central core of cells also is produced from the same source. Since the cysts first formed lie between the apical complex and the rudiment of the outlet duct, these cysts remain in the neighborhood of the duct as younger ones are formed in the upper part of the tube, which later elongates in the apical direction to form a zone of growth to accommodate the increasing number of cysts.

Finally, there is formed from the ventral strand and the germinal center beneath the sperm tubes the gonadal part of the vas deferens, which is continuous with a cell strand proceeding posteriorly that becomes the free part of the duct. The lumen is formed as an internal cleavage space between the cells of the strand. The individual ducts of the sperm tubes, or vasa efferentia, which are connected with the vas deferens, Nelsen says, do not acquire distinct lumina until just before the last moult. The mature testis of *Melanoplus differentialis*, according to Nelsen, includes about 188 sperm tubes.

The mature testes of the Orthoptera in general vary in size and shape according to the number, form, and arrangement of the sperm tubes. In the more generalized condition the testicular tubes are small pear-shaped or oval bodies arranged in series on the gonadal parts of the ducts (figs. 7 B, 11 A, B, *Tes*); in *Blattella* (fig. 16 A) each organ is reduced to four globular bodies on the end of the duct. Generally, however, the testis is a large oval compact mass of elongate tubules enveloped in a common peritoneal sheath (figs. 9 A, 20 A, 34 A, 39 A). An exceptional condition occurs in some of the Phasmatidae, in which the testes are long cylindrical organs having no subdivision into sperm tubes (fig. 7 A, *Tes*).

*The male genital ducts.*—The embryonic vasa deferentia of Orthoptera (fig. 2 A, *Vd*) end posteriorly with hollow terminal enlargements, or *anpullae* (*Amp*), inserted into the appendage rudiments of the tenth abdominal somite (*XApd*). This condition has long been known



from the work of Heymons and of Wheeler on *Periplaneta*, *Blattella*, *Gryllus*, and *Conocephalus*, and recently has been shown to occur in Acrididae by Else (1934) and by Roonwal (1937). The cavities are present in the ampullae long before the lumina appear in the other parts of the ducts. The ampullar cavities are ventral remnants of the coelomic sacs of the tenth abdominal somite, and similar though transient ampullae of coelomic origin may occur in the preceding abdominal somites. To the ampullae of the tenth segment of the male,

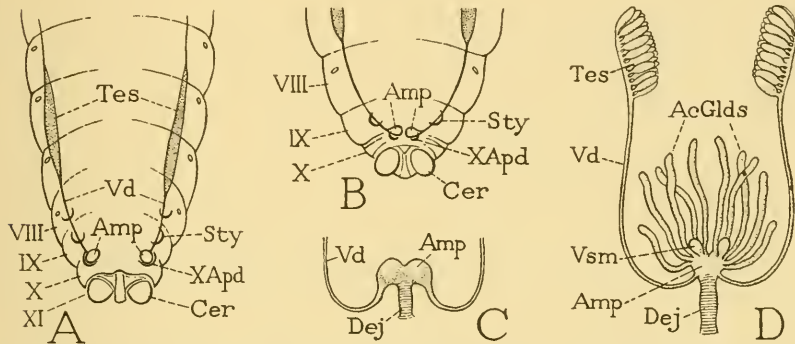


FIG. 2.—Development of the male genital ducts and accessory glands of Orthoptera. (A, B, simplified from Wheeler, 1893; C, D, diagrammatic.)

A, abdomen of embryo of *Conocephalus brevipennis* (Scudder) with vasa deferentia ending in ampullae contained in appendage rudiments of tenth abdominal segment (*XApd*). B, same, later stage, ampullae dislodged from appendages and approximated medially. C, diagram of usual condition of genital ducts in an orthopteran nymph, ampullae (*Amp*) united with each other and with anterior end of an ectodermal ductus ejaculatorius (*Dej*). D, diagram of typical structure of internal male genitalia of adult Orthoptera, in which the accessory glands (*AcGlds*) and vesiculae seminales (*Vsm*) are outgrowths of the united mesodermal genital ampullae (*Amp*).

*AcGlds*, accessory genital glands; *Amp*, coelomic ampullae of genital ducts; *Cer*, cercus; *Dej*, ductus ejaculatorius; *Sty*, stylus of ninth abdominal segment; *Tes*, testis; *Vd*, vas deferens; *Vsm*, vesicula seminalis; *VIII*, *IX*, *X*, eighth, ninth, and tenth abdominal segments; *XApd*, appendage rudiment of tenth abdominal segment.

however, are attached the posterior ends of the genital strands that become the vasa deferentia (fig. 2 A). The ampullae persist, first as terminal parts of the lateral ducts, but later united as an anterior part of the definitive median ejaculatory duct (C, D, *Amp*).

Inasmuch as the gonadial parts of the embryonic genital ridges shorten during their development, with a complementary lengthening of the parts forming the ducts, it seems very probable that each entire ridge was primarily a gonad, and that the terminal ampullae alone represent the primitive coelomic outlet ducts. If this is true, as the occurrence of germ cells as far back as the tenth abdominal somite

would suggest, the primitive genital ducts of insects are then quite comparable with the outlet ducts of Onychophora and of those arthropods in which they are known to be of coelomic origin. The lumen of the gonad and of the definitive lateral genital duct of insects and of some other arthropods appears to be a secondary cleavage space formed in the originally solid genital ridge. However, the observation of Heymons (1892) that the embryonic germ cells of *Blattella* are overgrown by folds of the splanchnic mesoderm, might be interpreted as evidence of the closure of a dorsal gonadial compartment of the coelome, and thus give the insect gonad the same morphological status as that of Onychophora and Chilopoda (see Snodgrass, 1936, pp. 7-12).

The terminations of the embryonic genital ducts of the male in the appendage rudiments of the tenth abdominal segment (fig. 2 A) would seem to imply that the primitive ducts, represented by the coelomic ampullae, opened on the bases of these appendages when the latter had a more leglike form. The gonopores have a similar position in many other arthropods, though on different pairs of appendages. It might be assumed also that the ducts discharged through a pair of papillae or short tubular penes arising from the appendage bases, though such organs are not reproduced in the embryo; but it seems improbable that the appendages themselves containing the duct exits ever formed an intromittent organ, since in other arthropods the intromittent organs, if present, are formed from neighboring appendages that have no direct relation to the genital ducts.

As the development of the male exit system of the Orthoptera progresses toward the mature condition, the appendage rudiments of the tenth abdominal segment shift toward the median line (fig. 2 B), but the enlarging ampullae (*Amp*) leave the appendages and independently migrate forward and mesally into the posterior part of the ninth abdominal segment. Here the ampullae unite with each other to form a bilobed mesodermal vesicle into which open the two vasa deferentia (*C*, *Amp*). At the same time a median, tubular ingrowth of the ectoderm has formed between the ninth and tenth segments, which is the primary ejaculatory duct (*Dej*). The ectodermal duct unites with the mesodermal vesicle, and the lumina of the two organs eventually become continuous. The definitive median genital exit passage in the Orthoptera, commonly called the "ductus ejaculatorius", is therefore a composite structure formed of a posterior ectodermal part, and an anterior mesodermal part (*D*, *Dej*, *Amp*).

The outgrowth of numerous vesicular or tubular diverticula from the ampullar part of the definitive ductus ejaculatorius is a feature characteristic of all the true Orthoptera and of most of the orthop-

teroid insects (fig. 2 D). These structures, being produced from the mesodermal part of the median outlet duct, are necessarily themselves mesodermal, and are therefore to be classed as *mesadenia*. They include tubular *accessory glands* of various lengths (D, *AcGlds*), producing in most cases materials for the formation of spermatophores, and saclike or tubular *vesiculae seminales* (*Vsm*) serving for the storage of the spermatozoa. These organs do not usually appear until the adult moult, and sperm vesicles may not be formed at all in some families. The male accessory glands of insects of certain other orders appear, from ontogenetic and structural evidence, to be of ectodermal origin, and therefore properly classed as *ectadenia*.

*The external genitalia.*—The external genital structures of male orthopteroïd insects are principally phallic organs. Accessory copulatory structures, or periphallic organs, are but little developed, and when present they are mostly secondary formations having no apparent relationships in the different groups. Appendage rudiments are commonly present on all the abdominal somites of the embryo, but in the male those of the somites anterior to the ninth disappear before hatching. The appendages of the ninth segment of the male, however, are retained in many families as a pair of small, nonmusculated styli borne on the posterior margin of the definitive ninth sternal plate, their coxopodites supposedly in most cases being incorporated in the sternal plate. According to Else (1934) the embryonic appendages of the ninth abdominal segment of the male of *Melanoplus differentialis* merge completely with the posterolateral parts of the primitive sternum of this segment, even the styli being thus obliterated in Acrididae. It is only in the Grylloblattidae that the ninth segment appendages retain a two-segmented structure, the coxopodites being here large, free lobes bearing the styli (fig. 6 A, B, C).

The phallic organs of the Orthoptera are highly variable and often very complex structures. In most cases their principal modifications are not adaptations for the direct intromission of the sperm, but for the production of spermatophores and the transfer of the latter to the genital chamber or the sperm receptacle of the female. The phallic structures of Blattidae, Tettigoniidae, and Acrididae can be traced in their nymphal development from small lobes that grow out around the mouth of the ejaculatory duct. These phallic lobes, or *phallomeres*, of Grylloblattidae, Blattidae, and Mantidae retain their independence and take on various forms in the adult; in the other families they unite to form a single phallic structure, or *phallus*, which contains an open endophallic cavity into which discharges the ejaculatory duct.

It should be observed that the median penis as formed in certain Ephemeroptera and some Dermaptera is quite a different structure from the median penis, or phallus, of Orthoptera, because it is clearly a product of the union of two separate penes each containing an outlet duct. A median penis of this type the writer (1936) has designated a *penis conjunctus*; it frequently recurs in Crustacea and Diplopoda. The median penis of Orthoptera, and probably that of most pterygote insects, on the other hand, is a *penis communis*, since, however formed, it is not produced by the union of two primary organs containing each the outlet of a primitive lateral duct. The definitive median duct, or ductus ejaculatorius, of the phallus is an independent structure, single in its origin—it is a *ductus communis*, not a ductus conjunctus, nor a persistent branch of conjoined ducts as in some Dermaptera.

Since in some cases there are only two primitive phallic lobes in the nymph, or a pair of lateral lobes take a predominant part in the formation of the adult phallic structure, it might be supposed that these lobes are derived from the segmental appendages of the tenth abdominal somite. According to Wheeler (1893) the embryonic tenth appendage rudiments of the male of *Conocephalus*, after the ampullae have withdrawn from them, disappear. It is claimed by Else (1934), however, that the appendage rudiments of the tenth segment in *Melanoplus* persist and continue their migration toward the median line until they take a position at the sides of the point where the ejaculatory duct invagination is being formed. Here, he says, they grow out into lobes that unite about the mouth of the duct, and eventually form the complex phallic organ of the adult, which contains the gonopore.

An origin of the acridid phallus from appendage rudiments is described also by Roonwal (1937) in *Locusta migratoria*, but Roonwal claims that the appendages both of the tenth and the ninth segments are involved. He says: "the tenth abdominal appendages shift forwards and fuse with the ninth, and together they form the aedeagus and its duct (ejaculatory duct) and associated structures." Inasmuch as the ninth segment appendages of most other orthopteroid families become the styli of the definitive ninth sternum, it seems hardly credible that they should take part in the formation of the phallus in an acridid, and, as above noted, the appendage rudiments of the ninth segment of *Melanoplus* are said by Else to disappear. Otherwise, the accounts of the development of the acridid phallus as given by Else and by Roonwal are in essential agreement.

If the acridid phallus is a direct product of the united appendages of the tenth abdominal segment, a similar origin for the organ has not been observed in any other insect. The embryonic appendages of the tenth segment are known otherwise to be retained only as larval "legs" in Neuroptera, Trichoptera, Lepidoptera, and lower Hymenoptera. The phallic rudiment of Lepidoptera is said by Mehta (1934) to appear during the fourth larval instar as a small conical outgrowth in the base of an ectodermal genital pouch formed earlier on the venter of the ninth abdominal segment. Toward the end of the larval period the single rudiment splits into a pair of phallic lobes, which, before pupation, come together and unite about a central depression of the integument that becomes the unpaired part of the ejaculatory duct. The final development of the phallus takes place in the pupal stage. In Mehta's account there is certainly nothing to suggest any possible relation of the primitive phallic lobes to the larval appendages of the tenth segment. In Blattidae, there may be three distinct phallic lobes (fig. 15 B), and in Tettigoniidae as many as six in a young nymph (fig. 23 B). We may question, therefore, whether the two primary phallic lobes of Acrididae are not independent outgrowths of the genital integument that might be confused with the simultaneously disappearing appendage rudiments of the tenth abdominal segment.

The phallic components have usually been attributed on theoretical grounds to the appendages of the ninth abdominal segment, supposedly endites or "endopodites" of these appendages, thus making the male organ partly equivalent to the female ovipositor; but of this there is certainly no evidence from ontogeny. It is shown by Mehta (1934) that the phallic lobes of Lepidoptera have no anatomical relation to the integumental outgrowths of the ninth segment that give rise to the clasping appendages, or valvae, of the adult genital apparatus. It seems most probable, therefore, that the insect phallus is either an independent product of the genital integument around the mouth of the ejaculatory duct, or a product of the tenth pair of abdominal appendages. If the primary phallic components really are lobes of the tenth abdominal segment that converge from a lateral position and join with each other, it might be supposed, judging from the facts in other arthropods, that these lobes are primitive paired penes derived from the limb bases, rather than that they are the appendages themselves, for in no case does a genital duct traverse an entire appendage. The original presence within the lobes of the terminal ampullae of the primary ducts would suggest such an interpretation, but in this case it is evident that the ampullae leave the

penes, and that the definitive median outlet duct is a secondary invagination formed between the penes as the latter unite, and which makes a secondary connection with the conjoined ampullae.

The embryonic appendages of the eleventh abdominal segment (fig. 2 A, B, *Cer*) persist as the cerci of the adult. These organs are usually sensory in function, but in some of the Orthoptera they are modified for clasping or other copulatory purposes (fig. 8 K), and may be armed with basal lobes or hooks (fig. 4 G, *d*, 8 B, *a*, *b*, 17 C, *a*, *b*), or with processes of the distal parts (figs. 25 C, 26 B, 27 A, 28 A).

## II. ISOPTERA

The reproductive system of the Isoptera is unquestionably of the orthopteroid type of structure. The internal genital organs have been described by Grassi and Sandias (1893, 1897-'98) in *Termes lucifugus*, by Bugnion and Popoff (1912) in *Termes obscuriceps*, by Imms (1920) in *Archotermopsis wroughtoni*, by Light (1934) in *Zootermopsis nevadensis*, and by Bonneville (1936) in *Neotermes aburiensis* and *Bellicositermes natalensis*. The testes consist each of a group of small digitate, fusiform, or pyriform sperm tubes (fig. 3 A, B, D, *Tes*), apparently not invested in a common peritoneal sheath, arising from the end of the vas deferens. The vasa deferentia (*Vd*) open into a short ductus ejaculatorius (*Dej*). In *Archotermopsis* and *Zootermopsis*, as shown by Imms and by Light, a group of glandular tubules (*A*, *AcGlds*) arises from the inner end of the ejaculatory duct anterior to the junction of the vasa deferentia. These tubules, though designated "vesiculae seminales", are clearly the homologs of the accessory glands of Orthoptera, as stated by Imms, who observes that no spermatozoa are present in them. The tubules of *Archotermopsis* are separated into two lateral groups. A simpler condition appears to occur in *Termes*, since in *T. obscuriceps* Bugnion and Popoff find only a pair of small vesicular diverticula given off from the posterior ends of the vasa deferentia (fig. 3 B, *AcGld*), and in *T. lucifugus* Grassi and Sandias show but two large sacs (*C*) in a similar position. Grassi and Sandias note, as does Imms, that the "vesicles" do not contain spermatozoa. According to Bonneville (1936), however, a pair of similar vesicles in *Neotermes aburiensis*, consisting of pouchlike enlargements of the posterior ends of the vasa deferentia, are true vesiculae seminales, since they are filled with spermatozoa; in *Bellicositermes natalensis* the vesicles are reduced to simple enlargements of the ducts. In addition to the sperm vesicles, Bonneville says, *Neotermes aburiensis* has a median diverticu-

lum of the ejaculatory duct receiving a pair of united tubes, which are probably accessory glands. Hence it is evident that the Isoptera may have both accessory glands and seminal vesicles arising from the vasa deferentia, or from their conjoined ends united with the ejacula-

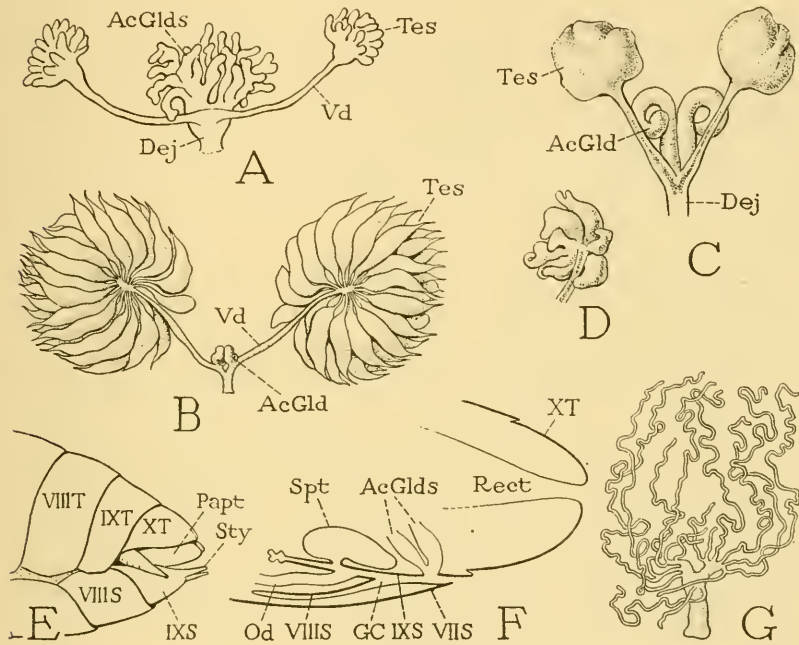


FIG. 3.—Isoptera: male and female genitalia.

A, *Archotermopsis wroughtoni* (Desneux), internal male reproductive organs of an adult soldier (from Imms, 1920). B, *Odontotermes obscuriceps* (Wasmann), internal reproductive organs of a king (from Bugnion and Popoff, 1912). C, *Reticulitermes lucifugus* Rossi, internal reproductive organs of a perfect male before loss of wings (from Grassi and Sandias, 1897). D, same, testis of perfect insect before loss of wings (from Grassi and Sandias, 1897). E, *Mastotermes darwiniensis* Froggatt, end of abdomen of winged male (from Crampton, 1920). F, *Archotermopsis wroughtoni* (Desneux), diagrammatic median section of posterior part of abdomen of female soldier (from Imms, 1920). G, same, accessory genital glands of female soldier (from Imms, 1920).

AcGld, accessory gland; Dej, ductus ejaculatorius; GC, genital chamber; Od, oviduct; Papt, paraprot; Rect, rectum; Spt, spermatheca; Sty, stylus; Tes, testis; Vd, vas deferens.

tory duct. A phallic ("prostate") gland, such as that present in Blattidae and Mantidae, has not been observed in the Isoptera.

The ovaries of Isoptera have the generalized type of structure that occurs also in some Orthoptera, in which the ovarioles arise serially from the distal parts of the lateral oviducts. The terminal filaments unite in a common median suspensory ligament. The accessory genital

glands of the female of *Archotermopsis*, as shown by Imms (fig. 3 G), consist of two groups of long tubules arising from short lateral branches of a large common outlet duct opening on the venter of the ninth abdominal segment.

External genitalia appear to be nonexistent in male termites, and nothing has been recorded concerning the manner of sperm transfer. A complete ovipositor consisting of three pairs of small valvulae is present in *Mastotermes darwiniensis* (see Crampton, 1920, 1923, and Browman, 1935), which closely resembles the ovipositor of nymphal blattids, except for the absence of styli on the third valvulae. In various other species apparent rudiments of first valvulae have been observed, but the valvulae of the ninth segment have been completely lost.

There is little ground for disputing the currently accepted view that the termites are closely related to the roaches and mantids, but the idea often expressed or implied that these three groups of insects are separated from other Orthoptera by having the female genital opening between the seventh and eighth abdominal segments clearly arises from an error of anatomical interpretation (see Snodgrass, 1933, p. 76). In the Isoptera the eighth abdominal sternum of the female, as shown by Imms (fig. 3 F, *VIIIS*), is concealed above the extended seventh sternum (*VII*S), as it is in the blattids and mantids, in which the eighth sternum is much reduced. In all cases, however, the opening of the oviduct in the adult is morphologically *behind* the eighth sternum, since it is either on the reflected dorsal surface of the sternum (F, *Od*), or on a fold or lobe above the sternal rudiment. If, therefore, it is found that in a young termite nymph the median oviduct arises between the seventh and eighth abdominal sterna, such a condition would be but a recapitulatory stage of development common to various insects, including Orthoptera.

### III. EMBIOPTERA

The Embiidae, in the structure of the internal reproductive organs of the male, resemble the Orthoptera, and have no characteristic feature of the Plecoptera. The male organs have been studied in three species, namely, *Haploembia solieri*, described by Grassi and Sandias (1897-'98), *Embia minor* by Mukerji (1928), and *Embia major*, illustrated in the present paper. The testes are soft elongate bodies (fig. 4 A, *Tes*) situated laterally in the anterior part of the abdomen. Each testis is composed of a large number of small vesicular bodies opening separately into the anterior part of the vas deferens.



The embiid testis thus resembles the testis of the primitive phasmid *Timema* (fig. 7 B) and the nymphal testis of *Blatta orientalis* (fig. 11 A, B). Grassi and Sandias, and Mukerji describe the testis of *Embia* as being imperfectly divided into five consecutive lobes; a

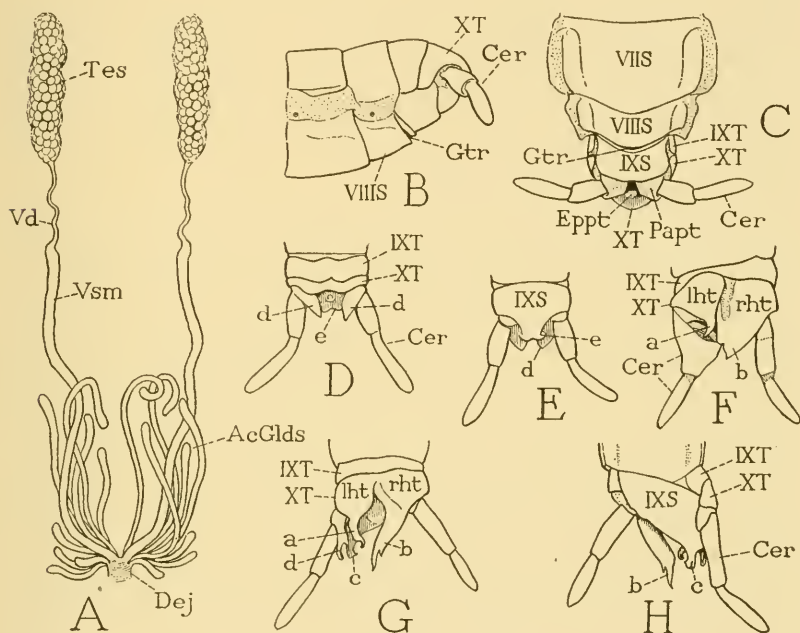


FIG. 4.—Embioptera: male and female genitalia.

A, *Embia major* Imms, internal organs of male, dorsal view. B, same, end of female abdomen, lateral view. C, same, end of female abdomen, ventral view. D, *Clothoda nobilis* (Gerstaecker), end of male abdomen, dorsal view (from Enderlein, 1912). E, same, end of male abdomen, ventral view (from Enderlein, 1912). F, *Embia major*, end of male abdomen, dorsal view (from Crampton, 1918). G, *Oligotoma saundersii* Westwood, end of male abdomen, dorsal view (from Walker, 1922). H, same, end of male abdomen, ventral view (from Walker, 1922).

a, distal process of left half of tenth abdominal tergum; AcGlds, accessory glands; b, distal process of right half of tenth tergum; c, distal process of ninth sternum; Cer, cercus; d, basal endite of cercus; e, terminal lobe of ninth sternum; Eppt, epiproct; Gtr, gonotreme; lht, left hemitergite of tenth segment; Papt, paraproct; rht, right hemitergite of tenth segment; Tes, testis; Vd, vas deferens; Vsm, vesicula seminalis.

distinct lobulation was not observed in *Embia major*, but the single specimen available for dissection had been long preserved in alcohol. Each vas deferens (fig. 4 A, Vd) is somewhat enlarged throughout most of its length to form a long slender "vesicula seminalis" (Vsm), and the two ducts unite posteriorly in a short ductus ejaculatorius

(*Dej.*). From the anterior end of the last there are given off in *Embia major* about 16 slender accessory-gland tubules of different lengths (*AcGlds*) arranged in two lateral groups. In *Embia minor*, as shown by Mukerji, there is a similar number of tubules, but one tube on each side is particularly long and is much thickened in its anterior half. Grassi and Sandias find only four tubules in *Haplocmbia solieri*, which they describe as "glandular sacs." Though the number of accessory-gland tubules in *Embia* is thus variable and always small as compared with the usual number in Orthoptera, the number of tubules may be greater than in *Grylloblatta* (fig. 6 E) and in some of the Phasmatidae (fig. 7 A, C).

The external genital structures of male Embiidae are well known from the general works of Verhoeff (1904) and Enderlein (1912), and from the description of individual species by Grassi and Sandias (1893, 1897-98), Imms (1913), Crampton (1918), Walker (1922), and Mukerji (1928). A true phallic organ apparently is absent or but little developed. The eleventh abdominal segment is suppressed in the male, except for the large two-part cerci, which are generally asymmetrical, and may have large basal lobes (fig. 4 D-H). The external genital structures consist of asymmetrical modifications of the sternum of the ninth abdominal segment and the tergum of the tenth segment, and of lobes and processes developed from these parts and from the bases of the cerci. The least modified condition occurs in *Clothoda nobilis* (D, E), in which there is but a small degree of asymmetry. The ninth and tenth terga are narrow transverse sclerites (D), and the sternum of the ninth segment (E) is an entirely symmetrical plate extended posteriorly in a median lobe (*e*) beneath the genital opening. The bases of the cerci are produced mesally as large endite processes (D, E. *d*). In most other forms the tergum of the tenth segment is subdivided into two asymmetrical lateral plates, or hemitergites (F, G, *lht*, *rht*), bearing irregular apical processes (*a*, *b*), and the ninth sternum (H) is more or less asymmetrically produced to the left. In some forms the base of the left cercus is armed with a large irregular endite (G, *d*). It is to be noted that all the accessory genital structures converge to the left, and that it is the left cercus that bears a basal lobe or is otherwise modified. The sinistral development of the genital parts is an adaptation to the relative position of the male and female during copulation.

The mating habits of embiids have been noted by Melander (1903) in *Oligotoma texana*, and more fully described by Friederichs (1934) in *Oligotoma nigra* and *Monotyloa ramburi*. The male of *Embia* or *Oligotoma* places himself on the back of the female, with his abdomen

turned to the right and its apex bent to the left beneath the abdomen of the female (see figure by Friederichs). In the case of *Monotyloa ramburi* the male grasps the fore part of the head of the female with his mandibles, curves his body to the right of the female, still holding the latter by the head, and directs the end of his abdomen to the left beneath that of the female to effect a union of the genital parts. The genital region of the female (fig. 4 B, C) is entirely unarmed. The gonotreme (*Gtr*) opens into a tubular genital chamber above the eighth sternum, which is continuous with the short median oviduct anteriorly, and has the aperture of the spermatheca in its dorsal wall just within the gonotreme. The male organs, therefore, are probably inserted into the genital chamber of the female in order to expose the mouth of the spermatheca. The presence of compound accessory glands in the male (fig. 4 A) would suggest the formation of a spermatophore, and Friederichs records that a male was observed a few minutes after copulation to double upon himself and eat something (possibly a spermatophore) projecting from his genital opening. Copulation with *Monotyloa ramburi*, Friederichs says, lasts about 15 minutes.

The question of the relationships of the Embiidæ has given rise to much discussion, some writers holding that the embiids have affinities with the Plecoptera and others that they are related to the Isoptera. The structure of the internal genital organs of the male shows definitely that the Embiidæ belong to the orthopteroid group of insects and not to the Plecoptera, but the embiids lack some of the characteristic features of the termites. The eighth abdominal sternum of the female, for example, is a well-developed external plate (fig. 4 B, C, *VIIIS*), and the genital opening (*Gtr*) is exposed behind it. Styli are never present on the ninth sternum of the male. On the other hand, the tenth tergum forms the apical dorsal plate of the abdomen (B, *XT*), as in Isoptera and Blattidæ, and the epiproct is a rudimentary lobe, present in the female (C, *Eppt*), on its ventral surface. That the accessory genitalia of the male have been developed within the Embiidæ is apparent from the relatively simple terminal parts in the primitive genus *Clothoda*.

#### IV. ZORAPTERA

The Zoraptera are here included with the orthopteroid insects, not implying that their relations to the Orthoptera can be demonstrated, but because the insects cannot be satisfactorily placed anywhere else. Crampton (1922) expressed the opinion that psocids, Zoraptera, and embiids have been derived from a common ancestral source, and

Imms (1934) associates the Zoraptera with the Psocida in a common order Psocoptera. Crampton (1922) points out a similarity in the wing venation between *Archipsocus* and *Zorotypus*, but in an earlier paper (1920 a) he regarded the Zoraptera as intermediate between Plecoptera and Isoptera, with perhaps closer affinities on the side of the Isoptera.

The general outlines of the body of a wingless *Zorotypus hubbardi* (fig. 5 A) suggest those of a newly hatched cockroach, and the aspect of the insect as a whole, especially when seen in side view,

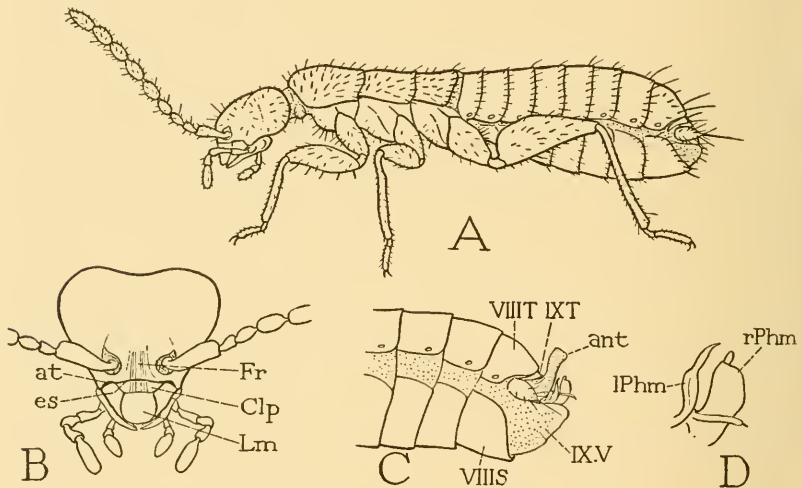


FIG. 5.—Zoraptera: *Zorotypus hubbardi* Caudell.

A, wingless adult ( $\times 33$ ). B, head, anterior view, showing orthopteroid type of structure in frons, clypeus, and labrum. C, posterior end of male abdomen. D, male genital lobes.

at, anterior tentorial pit; ant, anal tube; Clp, clypeus; es, epistomal suture; Fr, frons; Lm, labrum; lPhm, left phallomere; rPhm, right phallomere.

has a rather striking resemblance to that of a grylloblattid. The features of the head of *Zorotypus*, except for the specialized form of the antennae and palpi, and the absence of parietal sutures, are those of *Grylloblatta*, and have no likeness to the head characters of Psocidae. There is, for example, no upward enlargement of the postclypeus, a prominent characteristic of the psocid head, and the maxillary rods of the psocids are absent in *Zorotypus*. The only well-marked head suture in *Zorotypus hubbardi* is the epistomal suture (fig. 5 B, es); it cuts straight across the lower edge of the face below the antennal bases, and contains laterally the tentorial pits (at). Beyond the epistomal suture, as shown by Crampton, is a narrow

clypeus (*Clp*) and a fairly large labrum (*Lm*). The labral muscles arise on the cranial area between the bases of the antennae, demonstrating that this area is the frons (*Fr*). In the Psocidae the enlarged postclypeus intervenes between a small anteclypeus and the reduced frontal region, and the labral muscles, as shown by Badonnel (1934), traverse the postclypeus from their dorsal origins on the frons.

The internal reproductive organs of *Zorotypus* are difficult to study, and the writer has not been able to make a satisfactory dissection of them. In mature males, however, there are always to be found three very delicate membranous sacs containing coiled bundles of enormous spermatozoa. The spermatozoa were observed by Silvestri (1913), and also by Crampton (1920 a), who refers to them as "wavy" or "crinkly" fibers. The bundles of spermatozoa are very similar to those of the mantid *Tenodera*, and when a single sperm thread is straightened out it is actually as long as or longer than the entire insect. In the psocid *Stenopsocus*, according to Badonnel (1934), there is a pair of huge sperm vesicles, each vesicle subdivided into two chambers with thick glandular walls. The testes of *Zorotypus*, Silvestri says, are situated dorsally in the third and fourth abdominal segments, and the vasa deferentia unite to form a long, variously folded ejaculatory duct.

The abdomen of the male of *Zorotypus hubbardi* has eight well-defined segments (fig. 5 C). The tergum of the ninth segment, however, is reduced to a narrow sclerite (*IXT*) with a small median tooth, and the venter of this segment is unsclerotized, though it forms a large subgenital lobe (*IX.V*). Dorsally the abdomen terminates with a small anal tube (*ant*), from beneath which projects a pair of genital lobes. The genitalia of *Zorotypus hubbardi* have been described by Crampton (1920 a) and by Walker (1922). The genital lobes (phallomeres) lie side by side, one right, the other left, but the position of the gonopore has not been determined. The left genital lobe (*D*, *lPhm*) tapers distally to a point; the right one (*rPhm*) is flattened, bears distally a small papilla, and proximally a slender process directed posteriorly.

## V. GRYLLOBLATTOIDEA

The relationships of the grylloblattids has been a subject of discussion and difference of opinion ever since the insects have been known, and the very name of the first described genus and species, *Grylloblatta campodeiformis* Walker (1914), seems to provide for most any taxonomic eventuality. There is no question that the grylloblattids are orthopteroïd insects; it is their position within this

group that is uncertain. Crampton (1927), after several changes of opinion, finally settled to the conviction that the Grylloblattidae are related to the Tettigoniidae and Gryllidae, while Imms (1927) contended that the weight of evidence justifies their retention in the Cursoria, with which they were first associated. From a study of the general body musculature Ford (1923) concluded that *Grylloblatta* belongs to the blattid and mantid line of descent rather than to that of the saltatorial Orthoptera, though she showed that the musculature of the ovipositor is much like that of Tettigoniidae and Gryllidae. Walker (1933), however, finds that the musculature of the head and head appendages of *Grylloblatta* is also nearest that of the Saltatoria. The structure of the external male genitalia, on the other hand, clearly suggests a relationship with the mantids and blattids, while the internal genital organs, as here shown from sketches by Walker, undoubtedly present a very generalized type of orthopteroid structure.

The following brief description of the external and internal genitalia of *Grylloblatta campodeiformis* is to be accredited entirely to Dr. E. M. Walker, who has most generously sent the writer notes and sketches from his as yet unfinished work on the anatomy of the species.

The most evident generalized feature of the grylloblattids is the entire lack of union between the sternum and the appendages of the ninth abdominal segment of the male (fig. 6 A, B, C). This character is unique among the Orthoptera, though common in Thysanura and Ephemeroptera on the one hand, and in many holometabolous insects on the other. The genital coxopodites of the adult are large, free, triangular plates, asymmetrical in size and shape (B, C, *Cxpd*), each bearing a small apical stylus (*Sty*). The asymmetry of the coxopodites is less pronounced in younger instars (A). Though both coxopodites are freely hinged on the ninth sternum, only the right one, Walker says, is provided with a muscle, which arises on the ninth tergum. Neither stylus, however, is muscled.

The narrow tenth tergum is continued ventrally on the sides around the bases of the cerci into a pair of free asymmetrical processes (fig. 6 D) that nearly meet beneath the venter. The left tergal process (*tpl*) is a sclerotic arm terminating in a flattened disk; the right process (*tpr*) is of simpler form and is unsclerotized except at its base. The epiproct (*Epppt*) is small, entirely free from the tenth tergum, but concealed beneath the margin of the latter.

The external male genitalia of *Grylloblatta* consist essentially of two phallic lobes (phallomeres) arising from the genital surface, with the gonopore between them, or on the base of the right lobe.

In a young nymph, Walker (1922) says, the ventral intersegmental membrane between the ninth and tenth abdominal segments presents “two oval, slightly elevated areas (fig. 6 A, *r, l*), which are the rudiments of the genital lobes.” In an older nymph “the genital lobes are much larger and are separated by an oblique fissure, as in the adult, but there are as yet no chitinous processes nor eversible sac.” The genital lobes remain distinct in the adult (B, C, D, *rPhm, lPhm*),

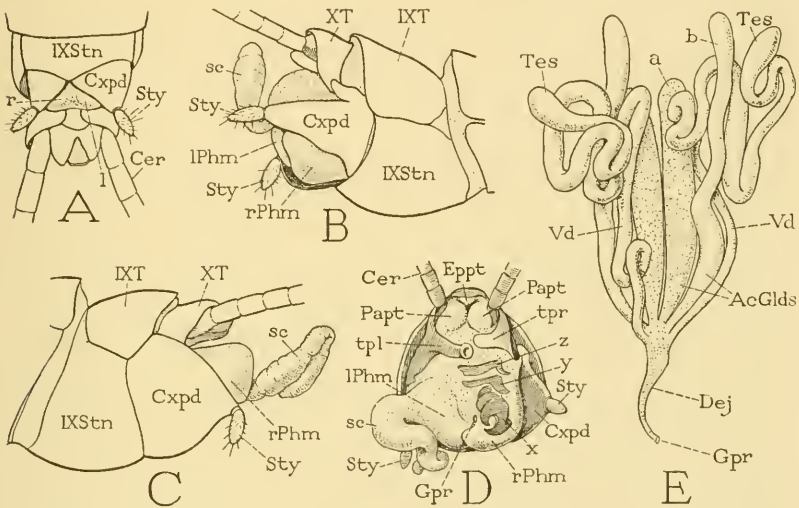


FIG. 6.—Grylloblattoidea: Male genitalia of *Grylloblatta campodeiformis* Walker. (A, B, C, from Walker, 1922; D, E, from unpublished sketches by Walker.)

A, half-grown male nymph, showing rudiments of phallic lobes, and approximate symmetry of coxopodites of styli. B, C, adult male, end of abdomen, right and left sides. D, adult male, end of abdomen, posterior view, showing genital structures. E, internal reproductive organs of adult male.

*a, b*, thick median, and more slender lateral accessory glands (*AcGlds*); *Cer*, cercus; *Cxpd*, coxopodite of stylus; *Dej*, ductus ejaculatorius; *Eppt*, epiproct; *Gpr*, gonopore; *l*, rudiment of left phallic lobe (*lPhm*); *Papt*, paraproct *r*, rudiment of right phallic lobe (*rPhm*); *sc*, saclike phallic lobe; *Sty*, stylus; *Tes*, testis; *tpl, tpr*, left and right ventral processes of tenth abdominal tergum; *Vd*, vas deferens; *x, y, z*, phallic sclerites.

and the gonopore now appears as a small aperture (D, *Gpr*) on the inner margin of the right lobe. The latter contains three prominent sclerites on its upper surface (*x, y, z*); the left lobe (*lPhm*) is unsclerotized except for a small setigerous area on its base, but it is produced into a long, twisted sac (B, C, D, *sc*).

The internal genital organs of the male are shown by Walker to have a very simple structure as compared with those of most other Orthoptera. “The testes”, Walker writes, “are simple tubes (fig.

6 E, *Tes*), lying freely in the abdominal cavity on each side of the intestine, and are irregularly convoluted. They pass insensibly into thick vasa deferentia (*Vd*), which are coiled back and forth a few times. Their junction with the ejaculatory duct (*Dej*) occurs in the ninth segment, and at the point of union two pairs of accessory glands (*AcGlds*) are given off. The outer pair of glands (*b*) consists of long tubes extending forward almost as far as the testes, but are not coiled. They are thickened at their anterior ends, which are bluntly rounded. The inner pair (*a*) are much shorter and stouter than the outer glands and appear to have a lobulated inner structure." It is possible that one pair of these "glands" will be found to be sperm vesicles.

The structure of the genital organs of *Grylloblatta*, both external and internal, suggests that the grylloblattids are simply generalized Orthoptera. A generalized orthopteron should have a generalized ovipositor, such as that of the female of *Grylloblatta*. According to Ford (1926) *Grylloblatta* (in confinement) deposits its eggs in the soil, the ovipositor being held at right angles to the abdomen, and the eggs passed through it. This primitive egg-laying habit has been but little modified in Tettigoniidae and Gryllidae, and consequently the ovipositor in these families retains the generalized structure. In Mantidae and Blattidae, on the other hand, the ovipositor has acquired a specialized form in adaptation to the acquired habit of enclosing the eggs in a cocoon or ootheca. The external male genitalia of *Grylloblatta* are generalized in that they consist of separate phallic lobes; though they acquire a specialized structure in the adult, as they do in Mantidae and Blattidae, the lobes do not unite to form a composite phallic organ enclosing the terminus of the ejaculatory duct as in other Orthoptera. Ford (1926) says the type of spermatheca found in *Grylloblatta* indicates the formation of a spermatophore; but from what we now know it is probable that most Orthoptera produce spermatophores. The internal male genitalia of *Grylloblatta* are unquestionably generalized, and most closely resemble those of Phasmatidae, in which there is a relatively small number of accessory gland tubules (fig. 7 A, B, C, *AcGlds*) and the testes may be simple tubes (A, *Tes*). The freedom of the genital appendages of the male from the sternum of the ninth abdominal segment is a primitive feature found nowhere else in the Orthoptera. The reduction of the epiproct occurs in Embioptera and Phasmatidae as well as in *Grylloblatta*, and suggest an approach to the almost complete elimination of the epiproct in Mantidae and Blattidae.



## VI. PHASMATOIDEA

The general structure of the reproductive organs of the Phasmatidae shows that the phasmatids are to be classed among the more generalized groups of orthopteroid insects. The external genitalia of the male consist either of irregular lobes surrounding the gonopore, or of a single phallic structure containing the genital opening, and thus resemble the nymphal organs of either Blattidae or Tettigoniidae. The female is provided with a small ovipositor, which differs but little from the ovipositor of Mantidae and Blattidae. Few studies have been made on the internal reproductive organs of the phasmatids, but the several examples here given show that the testes may have a generalized compound structure, though usually they are simple tubes without external subdivisions, and that the accessory glands consist of a group of tubules, though the latter are never so numerous as in Mantidae and Blattidae, or in the saltatorial Orthoptera.

*The testes.*—A generalized type of testicular structure occurs at least in *Timema californica*, in which each testis (fig. 7 B, *Tes*) consists of two long rows of small but distinct globular bodies opening serially into the anterior part of the vas deferens. Siebold and Stannius (1854) included the Phasmatidae among Orthoptera having a multitude of round testicular follicles, but they mentioned no particular species, and Suckow (1828), cited as authority in a footnote reference of the English translation, gives no examples of phasmatid genital organs. De Sinéty (1901), finding the testes to be simple continuous tubes in species studied by him, as in *Bacillus rossii* described by Heymons (1897), dismissed the earlier idea of a compound structure in the phasmatid testis as one of the "légendes traditionnelles" of entomology. However, if *Timema* is truly a phasmatid, there would appear to be in this case some basis for the legend.

With most of the Phasmatidae in which the internal reproductive organs have been examined, the testes are found to have the form of long tubes showing no subdivision into sperm tubules, or "follicles." Heymons (1897) described the testes of an immature male of *Bacillus rossii* as two long strands of genital and epithelial cells continuous posteriorly with the outlet ducts. Adult organs of the tubular form are described by De Sinéty (1901), particularly in *Leptyniella attenuata* (fig. 7 A, *Tes*), and by Pehani (1925) in *Carausius morosus*. The testes of *Anisomorpha buprestoides* are of the same type, as are probably also those of *Diapheromera femorata* in an active condition, but the specimens of this species examined by the writer had

evidently passed the functional stage, for the testes consisted of long, delicate, threadlike tubes having no evident cellular structure.

The long tubular testis of *Leptyniella* (fig. 7 A), according to De Sinéty (1901), consists of a mass of cysts, containing spermatozoa in different stages of development, enclosed in a cellular envelope.

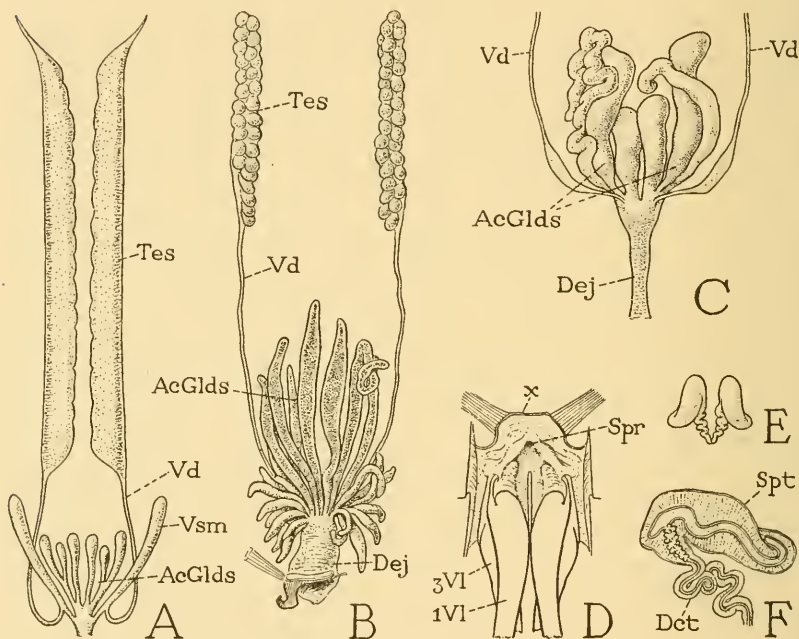


FIG. 7.—Phasmatoidea: male and female genitalia.

A, *Leptyniella attenuata* (Pantel), male internal reproductive organs (combined from De Sinéty, 1901). B, *Timema californica* Scudder, male, internal reproductive organs. C, *Diapheromera femorata* (Say), male, internal reproductive organs except testes. D, same, female, base of ovipositor and dorsal wall of genital chamber with spermathecal opening. E, same, spermathecae and ducts. F, same, single spermatheca and duct, optical section.

AcGlds, accessory glands; Dej, ductus ejaculatorius; Dct, duct of spermatheca; Spr, spermathecal aperture; Spt, spermatheca; Tes, testes; Vd, vas deferens; 1VI, 3VI, first and third valvulae of ovipositor; Vsm, vesicula seminalis; x, cut edge of genital chamber wall.

The spermatogonial cysts lie along the dorsal crest of the testis, which presents a series of low elevations, while the cysts containing mature spermatozoa occupy the ventral part of the organ, which is traversed by the vas deferens. The testes of *Carausius* are said by Pehani (1925) to have the same structure as that described by De Sinéty for *Leptyniella*. The simple tubular form of phasmatid testis might be supposed to represent a primitive gonadial structure

comparable with the testis of Chilopoda; but since the usual compound type occurs in *Timema*, it seems more probable that the common form of the testis in the Phasmatidae has been produced secondarily by an amalgamation of the primitive sperm tubes.

*The accessory genital glands.*—Tubular diverticula of the ejaculatory duct, most of which are probably genital accessory glands, are present in each of the several species of Phasmatidae that have been studied. In *Timema californica* the tubules are relatively numerous and of different sizes (fig. 7 B, *AcGlds*). In *Leptyniella attenuata* a pair of long lateral tubules (*A, Vsm*) are described by De Sinéty (1901) as vesiculae seminales, and a group of six median tubules (*AcGlds*) as accessory glands. A compact mass of tubules is present in *Diapheromera femorata* (*C*) lying against the ventral wall of the eighth abdominal segment. The individual tubes are difficult to separate, but careful manipulation reveals six of them. At least four are thick, orange-yellow sacs (*AcGlds*), but the tubule on the right is always longer and more coiled than the others, and has a pale pink color (in alcoholic specimens). The accessory tubules of *Carausius morosus* as shown by Pehani (1925) are similar to those of *Diapheromera*; two lateral tubules of the group are much larger than the others, and are regarded by Pehani as seminal vesicles. In a specimen of *Auisomorpha buprestoides* only two saclike diverticula were found (fig. 8 F) arising from the vasa deferentia, but the specimen may have been immature. A phallic gland corresponding with that present in Mantidae and Blattidae has not been observed in the Phasmatidae.

*The external genitalia and associated structures.*—The terminal parts of the male abdomen, as well as the phallic organs themselves, are highly variable in different species of the Phasmatidae. A relatively generalized structure of the abdomen is found in *Timema californica* (fig. 8 A, B), though associated here with a very specialized development of the cerci. In most of the phasmatids the first abdominal segment is as completely incorporated into the metathorax as it is in the higher Hymenoptera, but in *Timema* the tergum of this segment is entirely free from the metatergum, though the narrow sternum is united with the metasternum. The genital segments of *Timema* are not particularly modified (*A, B*); the ninth sternum is somewhat prolonged beneath the genital organs, but there is no distinct subgenital plate differentiated from it. In the typical phasmatid structure, the ninth abdominal sternum is completely divided into an anterior sternal plate (*C, J, L, IXS*) and a free posterior subgenital lobe (*IXSL*). The sternal plate is more or less displaced anteriorly, and may come to be associated with the eighth segment

(L, *IXS*); the venter of the ninth segment posterior to the sternum is mostly membranous, being formed possibly by an extension of the intersegmental membrane. The large subgenital lobe (C, J, L, *IXSL*) is scoop-shaped, its dorsal concavity forming the floor of the genital chamber, in which is lodged the phallic organ. An extreme development of this type of structure is seen in *Diapheromera* (L), in which the sternal plate (*IXS*) forms a small supporting stalk for the subgenital lobe (*IXSL*), and is provided with two pairs of large muscles arising on the tergal plates of the eighth and ninth segments.

The phallic organs of the Phasmatidae are said by Chopard (1920) to consist of several highly variable lobes, and of a very much reduced penis entirely concealed by the lobes. From a comparative study of the more simple types of phallic structures, and from a study of the development of the genitalia in *Cyphocrania gigas*, Chopard arrives at the following generalization: Fundamentally there are four very asymmetrical genital valves, but the upper two are often united in a single lobe; the valves in most cases are membranous, particularly the lower ones, containing only small sclerotic areas usually near their bases; sometimes, however, the valves are strongly sclerotized, and in such cases they have a tendency to unite in two large lobes, one dorsal, the other ventral, or rarely in a single structure.

The illustrations here given of the phasmatid intromittent organ include examples only of the type in which the phallic lobes are more or less united to form a single structure (fig. 8 G, H, I, M, N); the writer is not familiar with forms in which the lobes are entirely distinct. In an unidentified species (I) the phallus is a soft, ovate body composed of several irregular lobes of different sizes united only at their bases. In *Anisomorpha buprestoides* (G, H) the lobes are mostly united, being free only at their tips, which converge about the gonotreme on the ventral surface (H). In the dorsal wall of the phallus is a weak median sclerite (G, *e*) projecting distally in a small, free process on the left. The phallus of *Diapheromera femorata* (M, N) is a thick cylindrical structure, divided apically by a median cleft into short right and left lobes, between which is a third flat, median lobe. The ejaculatory duct opens here between the bases of the lobes; in *Anisomorpha* it opens on one of the lobes just within the lower lip of the gonotreme. The "penis," said by Chopard to be concealed within the phallic lobes, the writer has not observed.

Chopard points out that the lobiform structure and asymmetry of the phasmatid male genitalia give the organs a resemblance to the genital lobes of male Blattidae. The likeness is more particularly evident when the comparison is made with the simpler lobes of

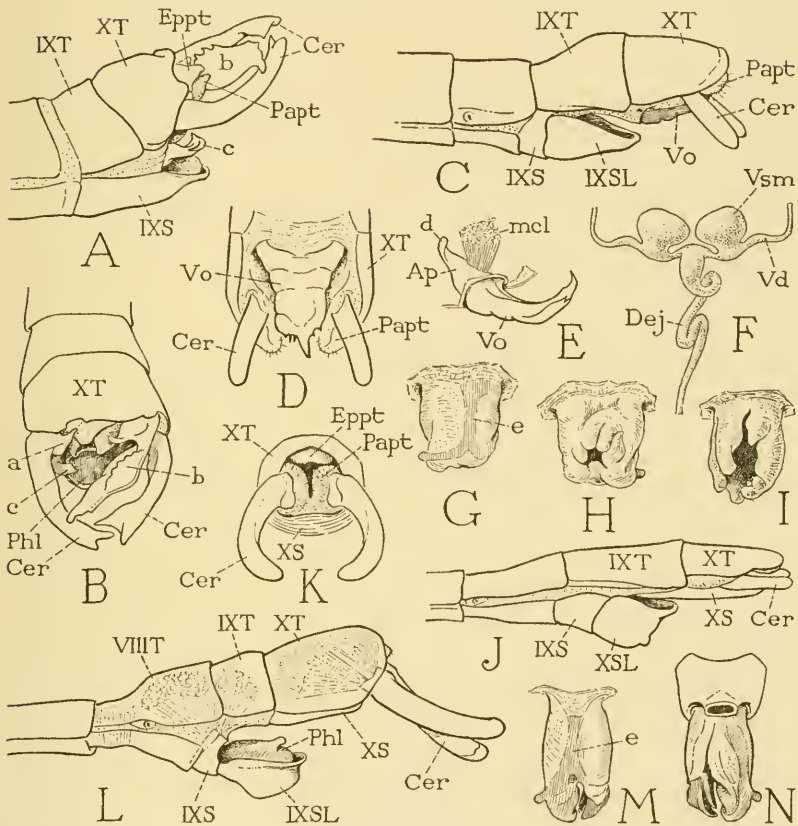


FIG. 8.—Phasmatoidea: male genitalia.

A, *Timema californica* Scudder, end of abdomen, lateral view. B, same, dorsal view. C, *Anisomorpha buprestoides* (Stoll), end of abdomen. D, same, ventral view of end of abdomen, showing vomer (*Vo*). E, same, lateral view of vomer with left apodeme and muscle. F, same, genital ducts and vesiculae seminales. G, H, same, phallus, dorsal and ventral views. I, unidentified species, ventral view of phallus. J, same, end of abdomen. K, *Diapheromera femorata* (Say), end of abdomen, posterior view. L, same, distal part of abdomen. M, N, same, phallus, dorsal and ventral views.

*a*, basal lobe of left cercus; *Ap*, apodeme of vomer; *b*, basal lobe of right cercus; *c*, left genital process; *Cer*, cercus; *d*, articular point of apodeme of vomer; *Dej*, ductus ejaculatorius; *e*, dorsal sclerite of phallus; *Eppt*, epiproct; *mcl*, muscle of vomer; *Papt*, paraproct; *Phl*, phallus; *Vd*, vas deferens; *Vo*, vomer; *Vsm*, vesicula seminalis.

nymphal blattids (fig. 12 E); but in the forms in which the lobes are partly united (fig. 8 H, I), the phallic organ of an adult phasmatid comes near being a replica of the nymphal organs in Tettigoniidae (fig. 23 E).

The tenth abdominal segment is always well developed and usually extends beyond the genital parts as a conical or oval end-segment of the body bearing the cerci and the anus (fig. 8 C, J, L, X), but in *Timema* (A) it is relatively short and the ninth sternum projects beneath it. The tenth sternum may be a simple plate extending backward to the anal region (J, L, XS); its posterior margin is sometimes cleft, the two points being continuous dorsally with the paraprocts. In many of the phasmatids, however, the venter of the tenth segment of the male abdomen bears a large sclerotic lobe extended horizontally backward from its anterior margin, and is otherwise membranous. This ventral lobe of the tenth segment is known as the *vomer* (C, Vo). The vomer varies greatly in size and shape in different species of phasmatids; an elaborate account of its numerous modifications is given by Pantel (1915), and both De Sinéty (1901) and Pantel show that the organ is developed during nymphal stages as a fold of the venter of the tenth abdominal segment. In the example here given, *Anisomorpha buprestoides*, the vomer is a broad, strongly sclerotic plate (D, Vo) armed distally with several small spines, and ending with an asymmetrical point curved upward between the paraprocts (C). Its basal angles are produced into inflexions of the body wall as a pair of strong divergent apodemes (E, Ap), each provided with a thick muscle (*mcl*) arising on the tenth tergum. The ends of the apodemes appear to be fulcral points applied against the tergal walls. The vomer might be supposed to be an instrument for depressing the subgenital plate of the female, but its asymmetry and the spinous armature of its distal part do not appear to adapt it to such a purpose.

The eleventh segment is inconspicuous, though it bears the cerci, which are usually large and prominent. It consists of a small epiproct (fig. 8 K, *Eppt*) projecting above the anus from beneath the margin of the tenth tergum (XT), and of two soft paraproctial lobes (*Papt*) lying at the sides of the anus, either vertical or more or less horizontal in position. The cerci are generally of a simple cylindrical form (C, D, *Cer*), but they vary much in size, and may be long, falcate clasp ing organs (K, L), or sometimes foliaceous or branched structures. They are movable by large muscles arising on the tergum of the tenth segment (L). In *Timema californica* the cerci have an exceptional development, being strong, asymmetrical appendages curved toward

each other distally (A, B, *Cer*); each cercus, moreover, has a mesal lobe arising from its base (*a, b*), the left one of which is a small recurved process (B, *a*), the right (A, B, *b*) a large irregular lobe larger than the cercus itself.

The females of most Phasmatidae, including *Timema*, have a small though fully developed ovipositor consisting of the usual three pairs of valvulae. The valvulae are weak and flexible, and enclose between them a cavity the size of an individual egg. The ovipositor is mostly concealed by the long subgenital eighth abdominal sternum, which forms the floor of an ample genital chamber extending anterior to the base of the ovipositor. The opening of the oviduct is a median cleft in the genital chamber floor below the base of the ovipositor, and the spermathecal opening is a small aperture in the dorsal wall of the chamber just anterior to the bases of the first valvulae (fig. 7 D, *Spr*). The sperm receptacle of *Diapheromera femorata* consists of two small spermathecal sacs (E) with convoluted ducts opening through the common exit. Each sac is a thick-walled structure having a tubular lumen connected with the duct near its anterior end (F). The histology of the spermathecae has been described by Marshall and Severin (1906).

During mating the male takes a position on the female's back and curves his abdomen downward and forward beneath that of the female (see Stockard, 1908; Grimpe, 1921). The exact use of the copulatory apparatus has not been recorded, and no observations suggest that the phasmatids produce spermatophores. Parthenogenesis is of common occurrence in the family. Each egg may be held for some time in the ovipositor before being liberated. Ordinarily the eggs are dropped casually, but according to Grimpe (1921), the female of *Phyllium bioculatum* by a strong swing of the abdomen throws each egg a considerable distance from her.

## VII. MANTOIDEA

The male genitalia of the mantids are very similar in general structure to those of *Blatta* and *Periplaneta* among the Blattidae, and differ but little among the mantid genera. In *Tenodera sinensis*, the species here illustrated (fig. 10), the slender male abdomen tapers to the apex of the slightly asymmetrical sternum of the ninth segment (A, IXS), which bears two small terminal styli (*Sty*), and projects far beyond the cercus-bearing proctiger composed of the tenth and eleventh segments. Resting in the shallow cavity on the dorsal side of the large ninth sternum, fully exposed beyond the proctiger, are the

external genital organs, consisting of three thick lobelike phallomeres with various accessory prongs (*lPhm*, *rPhm*, *vPhm*). The short tenth segment presents dorsally a small triangular tergum (*XT*) with lateral condyles on which articulate the bases of the long slender cerci (*Cer*). The venter of the tenth segment is membranous and forms the short dorsal wall of the genital chamber. The eleventh segment is much reduced; it consists principally of the two paraprocts (*Papt*), which are mostly concealed beneath the tenth tergum,

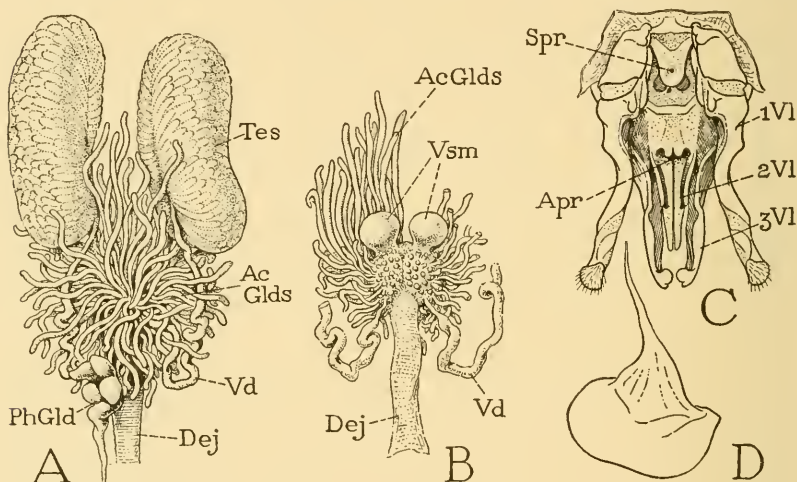


FIG. 9.—Mantoidea: male and female genitalia and a spermatophore.

A, *Tenodera sinensis* Saussure, male, internal genitalia, dorsal view. B, same, seminal vesicles exposed by removal of most of accessory glands. C, same, female, ventral view of ovipositor, spermathecal aperture, and opening of accessory glands. D, *Mantis religiosa* Linnaeus, spermatophore (from specimen furnished by K. D. Roeder).

*AcGlds*, accessory glands; *Apr*, aperture of accessory glands; *Dej*, ductus ejaculatorius; *PhGld*, phallic gland; *Spr*, aperture of spermatheca; *Tes*, testis; *Vd*, vas deferens; *1VI*, *2VI*, *3VI*, valvulae of ovipositor; *Vsm*, vesiculae seminales.

but the epiproct is present as a soft median lobe projecting from the under surface of the tenth tergum. The tenth and eleventh abdominal segments thus have the same structure in the mantids as in the blattids.

*The internal genitalia.*—The internal male reproductive organs of *Tenodera* (fig. 9 A, B) include a pair of large testes (A, *Tes*), the vasa deferentia (*Vd*), a mass of tubular accessory glands (*AcGlds*), a pair of vesiculae seminales (B, *Vsm*) in which the spermatozoa are stored, the ejaculatory duct (*Dej*), and a phallic gland (A, *PhGld*). The testes, which lie laterally in the fifth, sixth, and seventh abdominal



segments, consist each of numerous sperm tubes invested in a delicate peritoneal sheath. The vasa deferentia run caudad from the testes as simple tubes with a few convolutions, turn mesad beneath the cercal nerves, and then go forward to the ductus ejaculatorius, which they enter at the base of a bilobed anterior swelling of the latter (B). This anterior enlarged part of the ejaculatory duct probably represents the united mesodermal ampullae of the primitive exit system; from it are given off the tubules of the accessory glands (*AcGlds*), and the pair of globular sperm vesicles (*Vsm*), which normally are concealed among the gland tubules. The numerous tubules of the accessory glands are of different lengths, but are approximately of the same diameter, and appear to be all of a like nature functionally. The ectodermal part of the ductus ejaculatorius is a wide tube extending straight backward to the base of the ventral phallomere, on the dorsal surface of which it opens between membranous folds (fig. 10 F, *Gpr*). The phallic gland (A, *PhGld*) lies on the posterior part of the mass of accessory gland tubules, at the left of the ejaculatory duct; it is subdivided into several irregular lobules, but posteriorly is continued as a tapering duct into the left phallomere to open on the distal part of the latter.

*The external genitalia.*—The external genital organs of *Tenodera sinensis*, as already noted, consist of three large irregular genital lobes, or phallomeres (fig. 10 A, *lPhm*, *rPhm*, *vPhm*), which, as in *Blatta* and *Periplaneta*, enclose the gonopore between them but do not form a unified phallic structure. Two of the phallomeres arise respectively right and left above the genital opening, the third is median and ventral.

The right phallomere (fig. 10 B) is a wide flat appendage of triangular form with a long transverse base extending to the left above the base of the left phallomere in the anterior wall of the genital chamber. The distal margin is produced into a large lobe (*a*) on the right and a smaller lobe (*c*) on the left. On the under surface of the appendage, along the proximal part of the lateral margin of the ventral wall, is a slender, strongly sclerotized bar forming a serrated ridge (C, E, *d*), from the proximal end of which an arm (*e*) extends laterad and supports a large apodeme (B, C, E, *Ap*). The apodeme projects forward on the right into the body cavity of the ninth and eighth segments of the abdomen, and expands into a flat plate (E) over the anterior end of the eighth sternum. Just mesad of the proximal end of the serrated ridge there arises from the wall of the genital chamber a strong hooklike process (C, E, *f*) articulated basally on the ridge and having its apex opposed to the latter. The

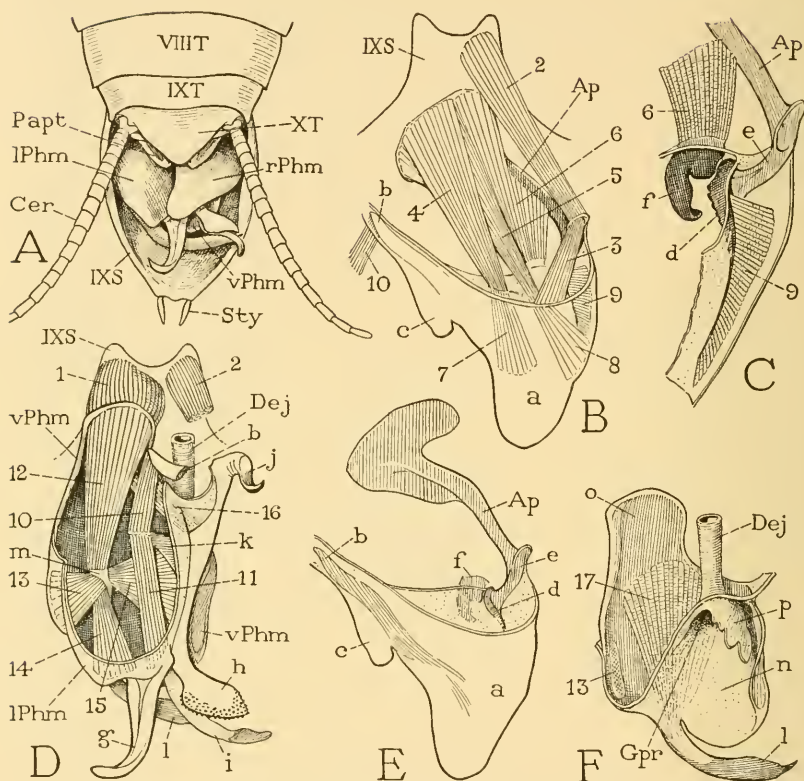


FIG. 10.—Mantoidea: external male genitalia of *Tenodera sinensis* Saussure.

A, end of abdomen, dorsal view, phallomeres in place within genital chamber. B, right phallomere and muscles, dorsal view. C, latero-proximal part of ventral wall of right phallomere, dorsal view, showing movable hook (*f*) beneath the phallomere. D, left phallomere and underlying ventral phallomere, dorsal view. E, right phallomere and its apodeme, muscles removed, dorsal view. F, ventral phallomere and terminus of ejaculatory duct, dorsal view.

*a*, dextral lobe of right phallomere; *Ap*, apodeme of right phallomere; *b*, left extremity of base of right phallomere; *c*, sinistral lobe of right phallomere; *Cer*, cercus; *d*, serrated ridge of ventral surface of right phallomere; *Dej*, ductus ejaculatorius; *e*, basal support of apodeme of right phallomere; *f*, movable hook beneath right phallomere; *g*, *h*, *i*, distal processes of left phallomere; *Gpr*, gonopore; *j*, proximal mesal process of left phallomere; *k*, mesal apodeme of left phallomere; *l*, distal arm of ventral phallomere; *IPhm*, left phallomere; *m*, ventral apodeme of left phallomere; *n*, exposed part of ventral phallomere; *o*, ventral plate of ventral phallomere; *p*, membranous fold enclosing gonopore; *Papt*, paraproct; *rPhm*, right phallomere; *Sty*, stylus; *vPhm*, ventral phallomere. 1-17, muscles of phallomeres; for explanation, see text, pages 34, 35.

hook is movable by a large muscle (C,  $\delta$ ) inserted on its base. This pincerlike structure is said by Walker (1922) to serve as a clasper in copulation, the remnant of a male abdomen of *Stagmomantis carolina* having been found attached by it to the female.

The left phallomere (fig. 10 D, *lPhm*) has a more complex structure than the right phallomere. It consists of a broad, thick basal lobe and of three large terminal processes (*g*, *h*, *i*). The dorsal wall of this appendage is derived directly from the anterior wall of the genital chamber, but its ventral wall is reflected into the dorsal wall of the ventral phallomere (D, *vPhm*), which lies beneath it. Of the terminal processes, one (D, *g*) is a strongly sclerotic arm extending posteriorly and ending in an upcurved hook, the second (*h*), arising from the distal end of a plate in the mesal wall of the appendage, is a broad flat lobe turned mesally, the third (*i*) is a weaker, slender process arising beneath the second and curving to the right and dorsally. Arising proximally from the mesal plate is a strong hooklike process (*j*) that normally lies in a pocket on the under surface of the right phallomere. A broad tapering apodemal inflection (*k*) extends inward from the dorsal margin of the mesal plate to give attachment to muscles within the appendage, but the left phallomere has no basal apodeme corresponding with that of the right phallomere (E, *Ap*). A short apodemal process from the floor of the left phallomere (D, *m*) gives insertion to several convergent muscles.

The ventral phallomere (fig. 10 F) is a flat appendage of irregular outline, bearing a large distal process (*l*) curved to the right. Its long, smooth under surface fits snugly upon the concave floor of the genital chamber; the shorter membranous dorsal wall is reflected into the ventral wall of the left phallomere (D), so that the basal parts of the two appendages have a common inner cavity. The ventral wall contains a large plate (F, *o*). The distal part of the ventral phallomere is expanded to the right, forming a large oval lobe with a smooth concave surface (*n*) lying usually to the right of the distal part of the left phallomere, where normally it is covered by the major lobe of the right phallomere (B, *a*). At the base of the concave dorsal surface of the ventral phallomere is the wide funnel-shaped opening (*FGpr*) of the ejaculatory duct (*Dej*) beneath a large fimbriated membranous fold of the integument (*p*). At D of figure 10 the ventral phallomere is shown retracted to the left, in which position it is almost completely covered by the left phallomere, but ordinarily its distal lobe (F, *n*) is exposed on the right of the latter.

The phallic musculature of *Tenodera* is highly developed, as in *Blatta* and *Periplaneta*, but its chief interest from the standpoint of

comparative anatomy lies in the fact that it has little in common with the phallic musculature of Blattidae. Aside from several sheets of muscle fibers inserted dorsally at the base of the right phallomere, which appear to arise on the tenth segment, the muscles of the three appendages are as follows:

1. *Retractor of the ventral phallomere* (fig. 10 D).—A short thick muscle arising to the left on the anterior lobe of the ninth abdominal sternum (IXS), inserted on the base of the ventral plate of the ventral phallomere.

2. *Retractor of the right phallomere* (fig. 10 B, D).—A corresponding but much longer muscle on the right from the anterior lobe of the ninth sternum to the base of the apodeme of the right phallomere (B).

3. *Levator of right phallomere* (fig. 10 B).—A short muscle from the base of the apodemal stalk to the dorsal margin of the base of the right phallomere.

4, 5. *Depressors of the right phallomere* (fig. 10 B).—Two flat sheets of fibers arising on the distal expansion of the apodeme, inserted ventrally on the base of the right phallomere.

6. *Muscle of the ventral clasper of the right phallomere* (fig. 10 B, C).—A broad flat muscle arising on the stalk and lobe of the apodeme (B), inserted on the base of the movable ventral hook (C, *f*) of the right phallomere.

7, 8, 9. *Intrinsic muscles of the right phallomere* (fig. 10 B).—Two of these muscles (7, 8) are divergent bundles of fibers on the ventral wall of the right phallomere, the third (9) is a lateral series of short fibers inserted on the serrated ridge (C, *d*) of the ventral wall of the phallomere.

10. A short muscle (fig. 10 B, D) from the mesal extremity of the base of the right phallomere (*b*) to the mesal apodeme (D, *k*) of the left phallomere.

11. An intrinsic muscle of the left phallomere (fig. 10 D) extending from the mesal apodeme of the latter (*k*) to the base of the apical process (*g*).

12, 13, 14, 15.—A group of four intrinsic muscles of the left and ventral phallomeres (fig. 10 D) converging upon the apodemal process (*m*) of the ventral wall of the left phallomere, one muscle (12) from the anterior end of the ventral plate of the ventral phallomere, another (13) from the distal lateral angle of the same plate (F, 13), the third (14) from the base of the apical process (*g*), and the fourth (15) from the mesal plate of the left phallomere. Muscles 12 and 13 of this group evidently serve to move the left and ventral phallomeres

on each other; muscles 14 and 15, together with 11, probably effect a change in the shape of the left phallomere that gives a movement to the distal processes.

16. An oblique muscle (fig. 10 D) from the mesal sclerite of the left phallomere to the ventral plate of the ventral phallomere.

17. *Intrinsic muscle of the ventral phallomere* (fig. 10 F).—A wide fan of fibers arising on the ventral plate of the ventral phallomere and converging to the base of the distal arm (*l*).

*Mating habits and spermatophores.*—The mating habits of the mantids is a subject on which writers seldom fail to become emotional; it furnishes the high point in the curve of literary entomology. The female mantis is frequently observed to attack and more or less completely devour the male before or during copulation, an act which, of course, can be made to seem highly sensational. A recent analysis of the sexual behavior of the mantis by Roeder (1935), however, puts the matter on a physiological basis. The principal sense organs of the mantids are the eyes, but the only visual perception is motion. Any moving object, therefore, is to the mantid an article of food and calls forth the attack response. The male mantis, preliminary to copulation, leaps upon the back of the female and normally grasps her by the mesothorax and the edges of the wings. If the male attains this hold at the first attempt, according to Roeder, the female is completely negative, giving no sign that she recognizes the presence of the male, and making no attack on him. In any other position, however, the male mantid is to the female only another insect. Thus, Roeder says, "if the male approaches the female from the side, landing on her back at right angles, or instead of clasping the mesothorax with his raptorial arms, grips her by the head or only by the tips of the wings, the female then immediately wheels and grabs him." The numerous records of cannibalism on the part of the female mantis, Roeder suggests, are largely the result of disturbance of the insects by the observer, or of the limited space in cages in which the insects are confined.

If, however, the female for any reason does attack and partially eat the male during copulation, the sexual act is not prevented or arrested, since, as Roeder demonstrates, the copulatory apparatus is controlled entirely by the last nerve ganglion of the abdomen. Furthermore, by decapitation the copulating movements are greatly increased because the activating mechanism is now released from the inhibitory stimulus that normally arises in the suboesophageal ganglion of the head. Decapitated insects, under any circumstances, Roeder shows, make con-

tinuously the copulating movements of the abdomen, which in the male are stimulated normally only by the contact of his body with the back of the female.

To effect copulation the male mantis, as described and shown in photographs by Roeder, lowers his abdomen on the right side of the female and bends the end around in an acute curve to the left beneath the female's wings, so that the phallic organs are directed forward toward the genital chamber of the female, into which eventually they are inserted between the ovipositor and the subgenital sternum. The exact use of the male organs has not been observed, but the only response of the female is an elevation of the ovipositor. Copulation, once effected, continues a varying length of time. Binet (1931) says that out of doors in an afternoon sun it is completed in about 15 minutes, according to Przibram (1907) it lasts usually about 2½ hours with specimens in cages, Roeder (1935) observes that it continues 4 or 5 hours. Insemination is finally accomplished by the transfer of a spermatophore, formed in the genital organs of the male, into the genital chamber of the female. The production of a spermatophore by mantids during copulation has been recorded by Przibram (1907) and by Gerhardt (1914). The spermatophore of *Mantis religiosa* here shown at D of figure 9 was furnished by Prof. K. D. Roeder, of Tufts College, who says it was produced by a male not in copulation with a female, but having the suboesophageal ganglion removed. The specimen when received projected from the right side of the male genitalia, but evidently it had been formed in the shallow dorsal cavity of the ventral phallomere, for the long tapering neck was still held in the end of the ejaculatory duct. The opening of the female spermatheca of *Tenodera sinensis* is a minute pore on the under surface of a large lobe of the body wall between the bases of the ventral valvulae of the ovipositor (fig. 9 C, *Spr*). Evidently the tip of the spermatophore neck, or duct, must be inserted into the spermathecal aperture.

#### VIII. BLATTOIDEA

The male genital organs of the cockroaches differ in no essential respect from those of the mantids. The external genitalia appear in an early nymphal stage as two or three small phallic lobes close to the gonopore, and the lobes retain their individualities in the adult stage. The mature phallomeres are either relatively simple structures, widely separated, or they form groups of highly complex processes, which in *Blatta* and *Periplaneta* are very similar to the phallic organs of Mantidae. A phallic gland is present, which in *Blatta* and *Periplaneta* opens as in the mantids on the left phallomere.

*The testes.*—The testes of Blattidae are of the compound type of structure, the sperm tubes being small globular or fusiform bodies, either projecting freely from the vas deferens, or enclosed in a common peritoneal sheath. In *Blattella* each testis consists of only four rounded or oval sacs placed radially on the end of the duct (fig. 16 A, *Tes*). In *Cryptocercus punctulatus*, Cleveland (1934) says, "the testis is composed of many rounded follicles or lobes attached by short tubes to the vas deferens" (in his figure the "follicles" are fusiforme tubes). The testes of *Blatta orientalis* are functionally mature at the end of nymphal life, when each consists of an elongate mass of small globular sacs arising from the axial duct (fig. 11 A, *Tes*, B). In the imago, however, the testes become degenerate (C, *Tes*) and are to be found only with much difficulty. For this reason some of the earlier students of roach anatomy mistook the mass of accessory genital glands for the testes; even Fénard (1896) fell into this error and asserted that the Blattidae differ from other Orthoptera in lacking accessory glands, though the true condition in *Blatta* had already been described by Miall and Denny (1886).

*The genital ducts.*—The vasa deferentia proceed posteriorly from the testes to the rear part of the abdomen, where they turn mesally beneath the cercal nerves (fig. 11 C, *CerNv*) and then go forward and dorsally to open into the upper surface of the ejaculatory duct at the base of the accessory glands (figs. 11 C, 15 D, 16 A, *Vd*). The vasa deferentia of *Blatta* divide and shortly reunite at two places in the course of each (fig. 11 A, C), but there are no permanent convolutions or dilatations of the ducts in any of the Blattidae that have been described. In nymphal instars, however, the vasa deferentia end in a pair of saclike ampullae broadly joined to each other and united with the inner end of the ejaculatory duct (figs. 11 A, 12 F, 15 C, *Amp*). Since these ampullae of the vasa deferentia later give rise to the tubular accessory glands, the ampullae themselves become functionally an anterior mesodermal part of the definitive ejaculatory duct. The distal ectodermal part of the latter (fig. 12 F, *Dej*) becomes a wide muscular tube (figs. 11 C, 15 D, *Dej*), which opens either between the bases of the phallomeres (fig. 15 D), or into an endophallic sac (fig. 16 A, C, E, *Enph*). In *Blattella* the anterior part of the ejaculatory duct forms a large pouch behind the bases of the accessory glands (fig. 16 A, C, *SP*).

*The accessory genital glands.*—The accessory glands of the male genital system of Blattidae consist of numerous tubules forming the characteristic oval mass of "utriculi" seated upon the anterior end of the ejaculatory duct (figs. 11 C, 15 D, 16 A, *AcGlds*). In *Blatta*

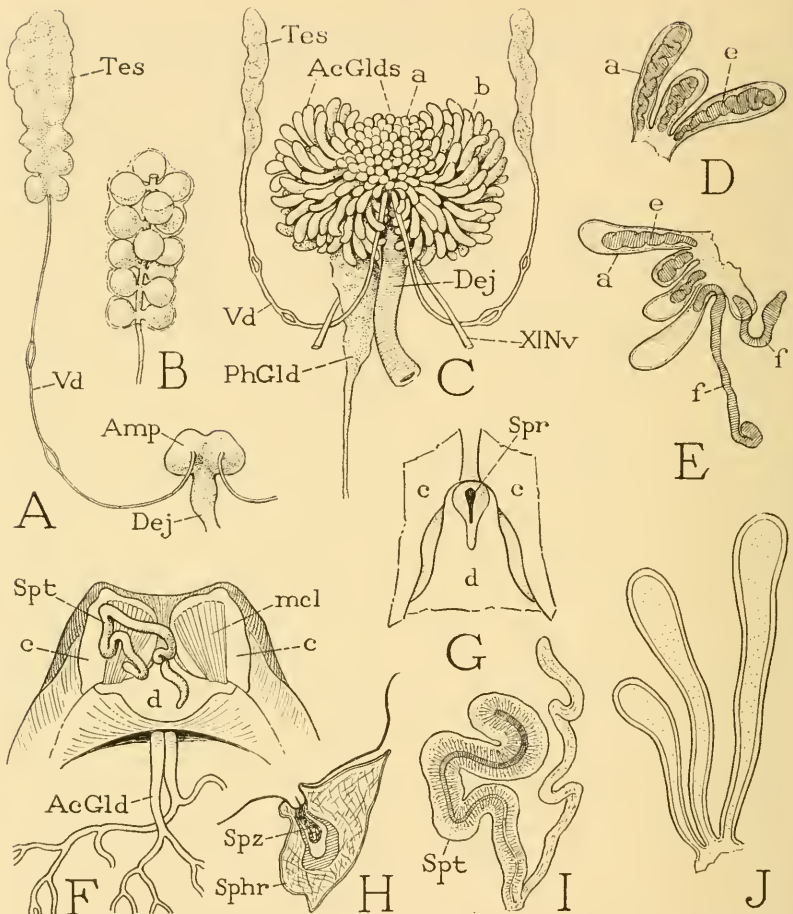


FIG. 11.—Blattoidea: male and female genitalia of *Blatta orientalis* Linnaeus.

A, male nymph, 22 mm long, internal genitalia. B, same, detail of testis, more enlarged. C, adult male, internal genitalia, dorsal view. D, small tubules of accessory glands, characteristic appearance. E, same, under pressure. F, adult female, floor of body cavity above ovipositor, showing spermatheca and accessory glands. G, same, external aperture of spermatheca. H, section of spermatheca attached to papilla of spermathecal aperture (from Zabinski, 1933 a). I, spermatheca, showing ductules in glandular wall of sperm-receiving tube. J, larger tubules of male accessory glands, same enlargement as D and E. *a*, smaller tubules of accessory glands (utriculi breviores); *AcGld*, female accessory gland; *AcGlds*, male accessory glands; *Amp*, mesodermal ampullae of nymphal ejaculatory duct; *b*, larger tubules of accessory glands (utriculi majores); *c, d*, sclerites of dorsal wall of female genital chamber; *Dej*, ductus ejaculatorius; *e*, inner tube of smaller accessory gland tubules; *f*, same, extruded by pressure; *mcl*, muscle of spermathecal sclerite (*d*); *PhGld*, phallic gland; *Sphr*, spermatophore; *Spr*, spermathecal aperture; *Spt*, spermatheca; *Spz*, spermatozoa; *Tes*, testis; *Vd*, vas deferens; *XINv*, cercal nerve of eleventh abdominal segment.



(fig. 11 C) and *Periplaneta* (fig. 15 D, E) the glands are differentiated into a median group of short tubules (*a*) and lateral groups of longer tubules (*b*), the "utriculi breviores" and "utriculi majores" of Miall and Denny (1886). In *Blattella germanica* (fig. 16 A) and in *Cryptocercus punctulatus* (Cleveland, 1934) a group of tubules corresponding with the larger tubules of *Blatta* and *Periplaneta* forms the usual compact cluster on the end of the ejaculatory duct, but projecting forward far beyond the latter is a group of long, thick, chalky white tubes. In *Blattella* those long glands are usually six in number (fig. 16 A, C, *d*) though some are united at their bases, and they arise from the left branch of the bifurcate anterior end of the ejaculatory duct (C). These tubes lie in the ventral part of the abdomen, where in freshly killed specimens they show through the integument as a conspicuous white mass extending from the posterior part of the seventh segment to the anterior edge of the fourth.

The secretion of the male accessory glands of Blattidae has been but little studied, and the function of the secretion cannot be definitely stated until the method of insemination of the female is better known. Ito (1924) says the male accessory glands of *Blatta orientalis* form a spermatic fluid, which stimulates the activity of the spermatozoa. The corresponding glands of other Orthoptera furnish the material of the spermatophores. A spermatophore has been observed among the roaches only in *Blatta orientalis* (fig. 11 H), described by Zabiniski (1933 a) as consisting of several layers, the first of which he believes must be formed by the small median tubules of the accessory glands, and the other outer coats by the larger tubules. The two sets of gland tubules of *Blatta* differ in appearance in a manner suggestive of a functional difference. The larger peripheral tubules (fig. 11 J) are turgid and opaquely white when freshly dissected in water, but they quickly become clear in glycerine. Most of the smaller tubules contain each a dark inner tube (D, *c*) compressed into irregular folds, which under pressure slides out of its sheath (E, *f*) and may expand to a length double or more that of the outer gland wall. When crushed, some of the inner tubes are seen to contain innumerable dark granules. The writer at first suspected that these inner tubes of the smaller glands might have some relation to the spermatophores, but no evidence of their nature or function was obtained. Miall and Denny (1886) say that in the adult of *Blatta orientalis* "the utriculi are usually distended with spermatozoa, and are of a brilliant opaque white." The writer has failed to discover spermatozoa in any of the glandular tubules of *Blatta*, *Periplaneta*, or *Blattella*.

*The seminal vesicles.*—The presence of special vesicles for the storage of the spermatozoa appears to have been overlooked by other students of the reproductive organs of the roaches. Ito (1924) states there are no seminal vesicles in *Blatta orientalis*, and that the sperm is stored in the anterior enlarged part of the ejaculatory duct. Miall and Denny, as above noted, believed that the accessory gland tubules

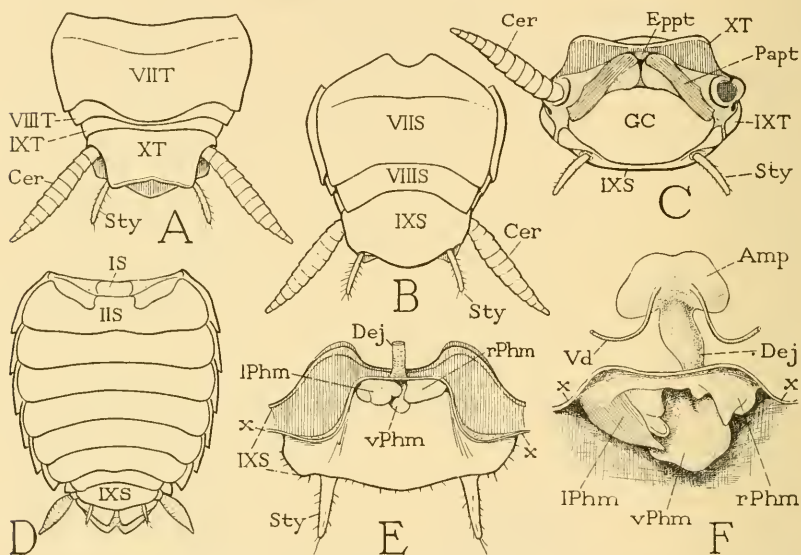


FIG. 12.—Blattoidea: adult and immature structure of the male abdomen, and nymphal genitalia of *Blatta orientalis* Linnaeus.

A, end of abdomen of adult male, dorsal view. B, same, ventral view. C, same, posterior view. D, nymph 11 mm long, ventral surface of abdomen. E, same, genital chamber exposed from above, showing three simple phallomeres arising from anterior wall around gonopore. F, nymph 22 mm long, showing later stage of phallomeres, and mesodermal ampullae united with anterior end of ectodermal ejaculatory duct.

*Amp*, mesodermal ampulla of ejaculatory duct; *Cer*, cercus; *Dej*, ductus ejaculatorius; *Eppt*, epiproct; *GC*, genital chamber; *lPhm*, left phallomere; *Papt*, paraproct; *rPhm*, right phallomere; *Sty*, stylus; *Vd*, vas deferens; *vPhm*, ventral phallomere; *x-x*, cut wall of genital chamber.

are filled with spermatozoa. However, in *Blatta*, *Periplaneta*, and *Blattella*, at least, there are special sperm-containing vesicles arising from the anterior end of the ejaculatory duct among the gland tubules. The seminal vesicles of *Blattella* are two small oval sacs arising close together from the end of the right branch of the ejaculatory duct (fig. 16 C, *Vsm*), where ordinarily they are concealed by the accessory gland tubules. They are filled with spermatozoa, and are similar to the sperm vesicles of the mantid *Tenodera* (fig. 9 B) except that both

are dextral in position. In *Blatta* and *Periplaneta* the seminal vesicles consist of two groups of small pyriform sacs, six or seven on each side, arising from the ventral surface of the ejaculatory duct at the base of the area of the small median gland tubules (fig. 15 E, *Vsm*). The vesicles are distinguishable from the smaller glands by their slightly larger size and more opaque whiteness; they are clearly shown in *Blatta* by Miall and Denny (1886, fig. 99, 1), who did not recognize their function. The sacs are filled with spermatozoa, which must be stored in them by the time the testes go into a state of degeneration. The spermatozoa of Blattidae are very small as compared with those of Mantidae, and are not attached to one another in bundles.

*The phallic gland.*—A large gland of unknown function, the "conglobate gland" of Miall and Denny, or "prostate gland" of some other writers, is associated with the external genital organs of male Blattidae. It lies beneath the accessory glands and ejaculatory duct, and opens on the phallic region. The phallic gland of *Blatta orientalis* is an elongate sac (fig. 11 C, *PhGld*) tapering posteriorly into the base of the left phallomere (fig. 14 A), where it terminates in a duct that opens on a membranous space between the two middle distal lobes (*r*, *s*) of the appendage. Ito (1924) mistakenly says that the duct of the gland opens into the posterior extremity of the ejaculatory duct. The phallic gland of *Periplaneta americana* is similar to that of *Blatta* except that it is subdivided into several compact lobes. In *Blattella germanica* the phallic gland consists of a mass of coiled tubules (fig. 16 B); its long slender duct opens on the phallic integument mesad of the mouth of the sac containing the left phallomere (E, *z*).

*The phallic organs.*—The external genital apparatus of male roaches, as of the mantids, consists of genital lobes, or phallomeres, associated with the mouth of the ejaculatory duct, which do not unite to form a single phallic organ comparable with that of other Orthoptera. Two distinct types of phallic structure are found in the Blattidae; one is characteristic of the Blattinae; the other, judging from various published accounts, but principally from Chopard's (1920) comparative study of the blattid genitalia, would appear to occur, with various modifications, in most of the other subfamilies. Presumably intermediate forms are to be found between the two types, but it is not necessary to suppose that one has been derived from the other, since both types have a similar origin in nymphal instars. The descriptions of two representative species of each type here given can serve only as a basis for a more extensive study, which might lead to a better understanding of the natural classification of the blattid subfamilies.

The type of phallic structure pertaining to the Blattinae consists of a highly integrated complex of parts belonging to three phallic organs, which appear in the nymph as three simple lobes of the genital chamber wall immediately surrounding the gonopore. This type of structure is illustrated in the following descriptions of *Blatta orientalis* and *Periplaneta americana*.

The abdomen of an adult male of *Blatta orientalis* (fig. 12 A) ends with the broadly truncate and somewhat emarginate tenth tergum above (*XT*), and the large rounded ninth sternum below (*B, IXS*), which latter bears the elongate styli (*Sty*). Beneath the margin of the tenth tergum are the paraprocts (*C, Papt*), and a small membranous area or lobe (*Eppt*) representing the epiproct. Between the paraprocts and the ninth sternum is the mouth of a deep cavity, the genital chamber (*GC*), containing the phallic organs. In a nymphal male the abdomen is relatively short and broad (*D*) and the small ninth sternum does not completely conceal the paraprocts. If the genital chamber of a median-sized nymph is opened (*E*) there will be seen three small, soft lobes projecting from its anterior wall around the opening of the ejaculatory duct (*Dej*). These lobes are the left phallomere (*lPhm*), the right phallomere (*rPhm*), and the ventral phallomere (*vPhm*). In a later nymphal instar (*F*) the phallomeres have increased in size and the lateral ones show the development of accessory lobes. The ejaculatory duct (*Dej*) opens above the base of the broad ventral phallomere. From this simple beginning are evolved the extraordinarily complex genital organs of the adult roach.

The mature phallomeres of *Blatta orientalis*, as seen from above in their usual position within the genital chamber, are shown at *A* of figure 13. The right phallomere (*rPhm*) has taken a more median position above the genital opening, the elaborately subdivided left phallomere (*lPhm*) forms a group of lobes and horny processes on the right, and the broad ventral phallomere (*vPhm*) projects to the right from beneath the other two. The base of the right phallomere is produced forward on the right into a deep pocket (*y*) of the genital chamber wall, and the base of the left phallomere is sunken into a similar but shallower pocket on the left (*z*). Beneath the right phallomere is a deep, transverse, oval cavity (*C*) within a large, strongly convex capsular sclerite (*A, B, C, m*), which is normally closed from below by a flat valvular sclerite (*C, n*). Between the dorsal right phallomere and the left phallomere is an obliquely transverse fold, which, beginning on the left (*A, fd*), goes downward to the right and expands on the dorsal surface of the ventral phallomere (fig. 14 *B, fd*). Within the lower end of this fold above the base of the ventral

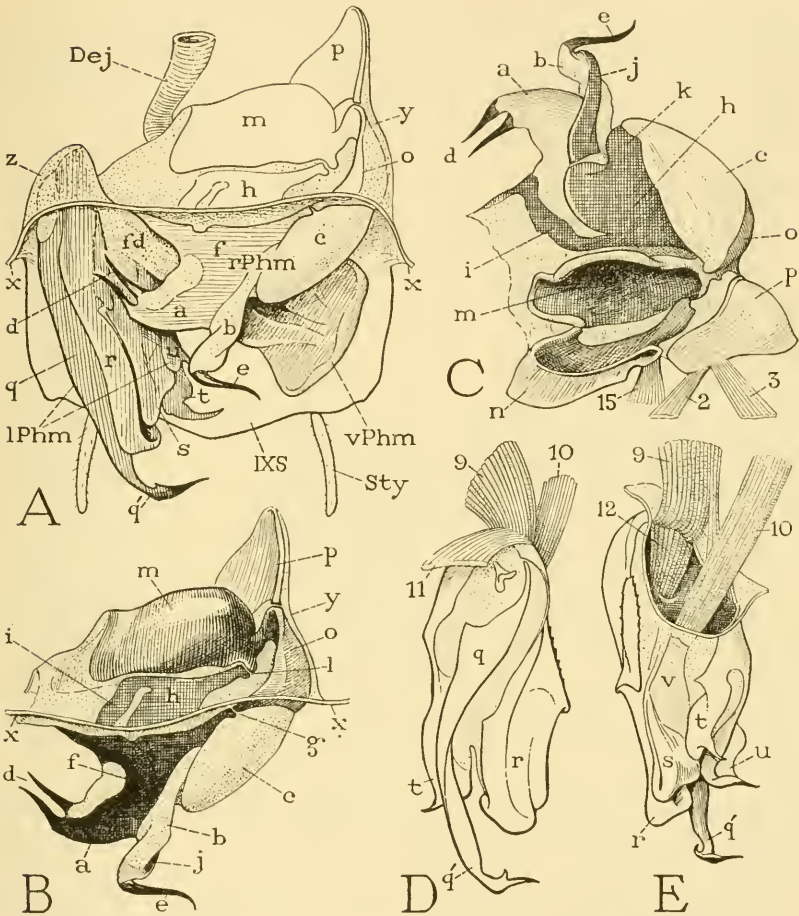


FIG. 13.—Blattoidea: external male genitalia of *Blatta orientalis* Linnaeus.

A, genitalia in place within genital chamber distal to anterior wall of latter (*x-x*), and parts invaginated into body cavity, dorsal view. B, right phallomere, dorsal view. C, same, posterior view with distal lobes turned dorsally. D, left phallomere, dorsolateral view. E, same, ventromesal view.

*Parts of Right Phallomere.*—*a, b, c*, left, median, and right lobules of free dorsal lobe; *d*, sinistral prongs; *e*, dextral hook; *f*, dorsal plate of dorsal lobe; *g*, articulation of dorsal plate with apodemal plate (*o*); *h*, ventral plate of dorsal lobe; *i*, left arm of ventral plate; *j*, distal arm of ventral plate; *k*, right lobe of ventral plate; *l*, articulation of ventral plate with capsular sclerite; *m*, capsular sclerite; *n*, ventral valvular plate; *o*, basal plate of apodeme; *p*, apodeme; *y*, pouch of genital chamber wall (*x-x*) containing base and apodeme of right phallomere.

*Parts of Left Phallomere.*—*q, q', r, s, t, u*, distal subdivisions and free processes; *v*, ventral sclerite; *z*, pouch of genital chamber wall containing base of left phallomere.

Other lettering as on preceding figures. For explanation of muscles, see fig. 14.

phallomere is the large genital opening, or phallotreme (*Phtr*). Since the terminal part of the genital exit passage contains a sclerotization (*es*) in its wall, it is probably a phallic invagination, or endophallic sac (*Enph*), rather than the end of the true ductus ejaculatorius (*Dej*), which is continuous with it.

The exposed part of the right phallomere comprises an oval membranous lobe on the right (fig. 13 A, B, *c*), and a flat extension on the left (*f*), which is subdivided into a sinistral lobe (*a*) bearing two strong prongs (*d*), and a dextral lobe (*b*) bearing a curved spine (*e*) turned to the right. From the base of the phallomere a basal plate (*o*) extends into the dextral pocket (*y*) of the genital chamber wall, where it becomes continuous with the capsular sclerite (*m*) of the ventral cavity, and supports an apodemal plate (*p*). The under surface of the right phallomere (C) contains an irregular sclerotization (*h, i, j, k*). Proximal to the latter is the cavity of the capsular sclerite (*m*), which is closed in the usual position of the right phallomere by the valvular sclerite (*n*) hinged to its lower lip.

The left phallomere (fig. 13 A, *lPhm*, D, E) is a fascies of irregular, elongate lobes (*q, r, s, t, u*), free at their extremities but having a common base sunken into the sinistral pocket (A, *z*) of the genital chamber. A large oval foramen opens into the base of the phallomere (E) from the body cavity. The outermost lobe (A, D, *q*) terminates in a strong spearhead-shaped process (*q'*) turned to the right, and two smaller more proximal prongs arise from the median lobes (*t, u*).

The ventral phallomere is a simple broad lobe projecting to the right from beneath the right phallomere (fig. 13, A, *vPhm*). The interphallic fold (*fd*) containing the phallotreme ends on its upper surface (fig. 14 B, *fd*); its lower surface is a flat plate (*w*) with a basal arm projecting to the left.

The phallic musculature of *Blatta* is quite different from that of the phasmid *Tenodera* (fig. 10), notwithstanding the evident identity of the phallomeres in the two genera. The muscles of the right phallomere of *Blatta* (fig. 14 C) include the following: 1, a short thick muscle from the left side of the ninth abdominal tergum to the left extremity of the phallomere base; 2, 3, right and left retractors of the phallomere, arising on the anterior lobes of the ninth sternum and converging to their insertions on the apodemal plate (fig. 13 A, *p*) near its mesal end; 4, a muscle arising posteriorly on the ninth sternum, inserted anteriorly (fig. 14 C) on the apex of the apodemal plate; 5, a large muscle from the apodemal plate to the capsular sclerite (*m*); 6, a long muscle from the apodemal plate to the basal plate (*o*) of

the phallomere; 7, a long flat muscle, probably a levator of the phallomere, from the apodemal plate to the dorsal plate (*f*) of the free part of the phallomere; 8, a thick mass of fibers in the right lobe (*c*), arising on the basal plate (*o*), and inserted on the distal process (fig. 13 C, *k*) of the ventral plate (*h*) of the phallomere.

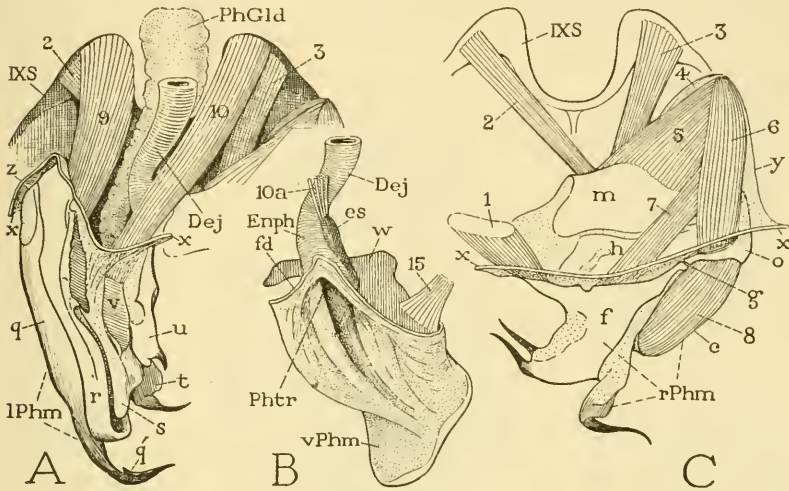


FIG. 14.—Blattoidea: the phallomeres and phallic musculature of *Blatta orientalis* Linnaeus.

A, left phallomere (*lPhm*) and muscles, phallic gland (*PhGld*), ejaculatory duct (*Dej*), and anterior lobes of ninth abdominal sternum (*IXS*), dorsal view. B, ventral phallomere (*vPhm*), with phallotreme (*Phtr*) on its base opening from endophallic pouch (*Enph*) continuous with ejaculatory duct, dorsal view. C, right phallomere (*rPhm*) with muscles, and base of ninth abdominal sternum, dorsal view.

*es.* sclerite of endophallic wall; *fd*, fold containing phallotreme; *v*, ventral plate of ventral phallomere; *x-x*, cut edge of anterior wall of genital chamber. Other lettering as on fig. 13.

1, tergal adductor of dorsal lobe of right phallomere; 2, 3, sternal adductors of right phallomere; 4, sternal protractor of same; 5, retractor of capsular sclerite; 6, muscle of basal plate; 7, apodemal adductor of dorsal lobe of right phallomere; 8, dextral abductor of same; 9, 10, sternal retractors of left phallomere; 10*a*, branch of 10 inserted on endophallic sclerite; 11, sternal protractor of left phallomere; 12, inner muscle of left phallomere; 13, 14, internal muscles of left phallomere not shown in figures; 15, muscle of ventral phallomere. (See text, pages 44-46.)

The muscles of the left phallomere are as follows: 9, 10, two large retractors of the phallomere, arising right and left on the anterior lobes of the ninth sternum (fig. 14 A), extending into the basal foramen of the phallomere (fig. 13 E), where the right is inserted dorsally and the left ventrally; 10*a*, a few fibers from 10 inserted on the endophallic sclerite (fig. 14 B, *es*); 11, a protractor of the phallomere

arising posteriorly on the ninth sternum, inserted ventrally on the phallomere base (fig. 13 D); *12*, a large bundle of fibers within the left phallomere (fig. 13 E), arising in the base of the appendage and inserted distally in the lateral lobe (*q*), giving independent movement to the distal process of the latter; *13*, *14*, two small muscles within the left phallomere (not shown in the figures).

The ventral phallomere has but one muscle attached upon it; this is a short muscle (fig. 14 B, 15) attached to the right margin of the

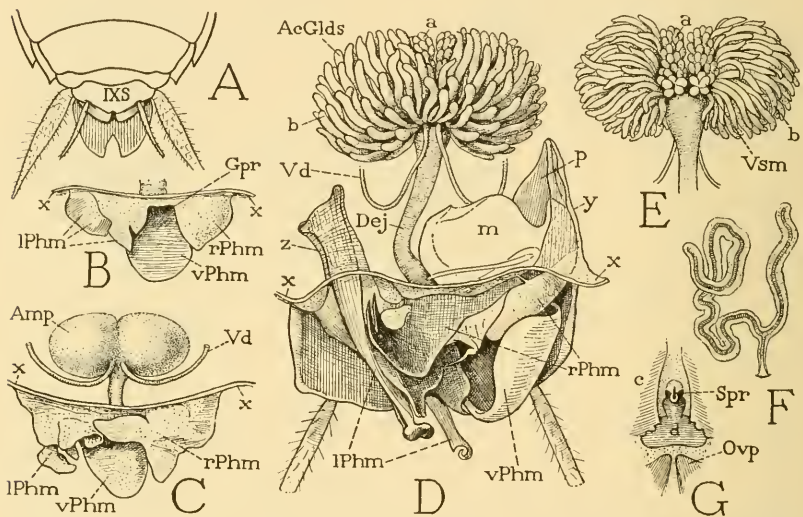


FIG. 15.—Blattoidea: male and female genitalia of *Periplaneta americana* (Linnaeus).

A, male nymph, 31 mm long, end of abdomen, ventral view. B, same, external genitalia, dorsal view. C, genitalia of following nymphal instar taken from within cuticle of B. D, adult male, external and part of internal genitalia, dorsal view. E, same, accessory glands and vesiculae seminales, ventral view. F, spermatheca. G, spermathecal aperture and surrounding structures in dorsal wall of female genital chamber.

*a*, *b*, smaller and larger tubules of accessory glands; *c*, *d*, sclerites in dorsal wall of female genital chamber associated with spermathecal aperture (*Spr*); *Ovp*, base of ovipositor; *Vsm*, vesiculae seminales. Other lettering as on fig. 13.

ventral plate (*τ*), which extends downward from the right marginal angle of the valvular plate (fig. 13 C, *n*) beneath the right phallomere.

The external genitalia of *Periplaneta* (fig. 15 D) differ only in details from those of *Blatta*. The three phallomeres have essentially the same structure and the same relations to one another in the two genera, but in minor characters they present many differences. The left phallomere of *Periplaneta americana* is somewhat more deeply sunken into its basal pouch (*z*) than in *Blatta orientalis*, but the right phallomere has the same basal structure as that of *Blatta*, and beneath



it is the same cavity within a large capsular sclerite (*m*). This interphallic cavity of the Blattinae, with its strongly developed walls and closing valve, must have some important function connected with the insemination of the female. According to Zabinski (1933 a) *Blatta orientalis* produces a spermatophore (fig. 11 H), though nothing is known of the place or manner of its formation. Structural details of the phallic organs in several species of *Periplaneta* are shown by Walker (1922), and Crampton (1925) gives a complete nomenclature for all the phallic parts of *P. americana*. The right and left phallic lobes are the "parameres" of Walker, who calls the ventral lobe the "penis." Crampton, however, designates as the "penis" a small lobe on the base of the ventral phallomere, which is evidently a part of the interphallic fold containing the phallotreme. *Eurycotis*, as described and figured by Chopard (1920), would appear to have the same type of phallic structure as *Blatta* and *Periplaneta*, and the same is true of *Blaberus atropos* described by Walker, though the phallomeres of this species are not of the typical blattine form.

The immature phallomeres of *Periplaneta americana* consist of three small lobes similar to those of *Blatta*. In a nymph 31 millimeters long (fig. 15 A) the left phallomere is already partly subdivided into accessory lobes (B). If a specimen of this instar is in a premoult condition, the phallomeres of the next instar (C), contained within the loosened cuticula, will be found to have a shape more suggestive of that of the adult organs.

The second type of blattid phallic structure, which is well exemplified in *Blattella germanica*, is characterized by the absence of the ventral phallomere, by a simplification of the other two phallomeres, which are mostly invaginated into right and left pouches of the genital chamber wall, and by the development of an eversible median lobe containing the opening of the genital exit passage. The median lobe appears to be a secondary evagination at the mouth of an eversible endophallic sac; when protracted it forms an intromittent organ, and may therefore be termed the *penis*, in a functional sense.

In *Blattella germanica* the external genital organs and the proctiger are concealed between the long tenth tergum and the shorter, asymmetrical ninth sternum (fig. 17 A). The proctiger is a membranous cone (C, *Ptgr*) arising beneath the base of the tenth tergum; it bears the anus at its apex and a pair of lateral hooks (*a*, *b*) on its base, but it shows no differentiation into epiproct and paraprocts. The subgenital sternum (A, *IXS*) bears two small styli (*Sty*) on its distal margin, and has a pair of long apodemes (*IXSAp*) projecting into the body cavity from its concealed anterior margin. On the left side of its

free part is a deep marginal notch. In some specimens there projects from this notch a long sclerotic process with a terminal hook and a membranous base (B, *lPhm*). This process is called the "penis" by Chopard (1920); it is the "titillator" of Wille (1920), the "left

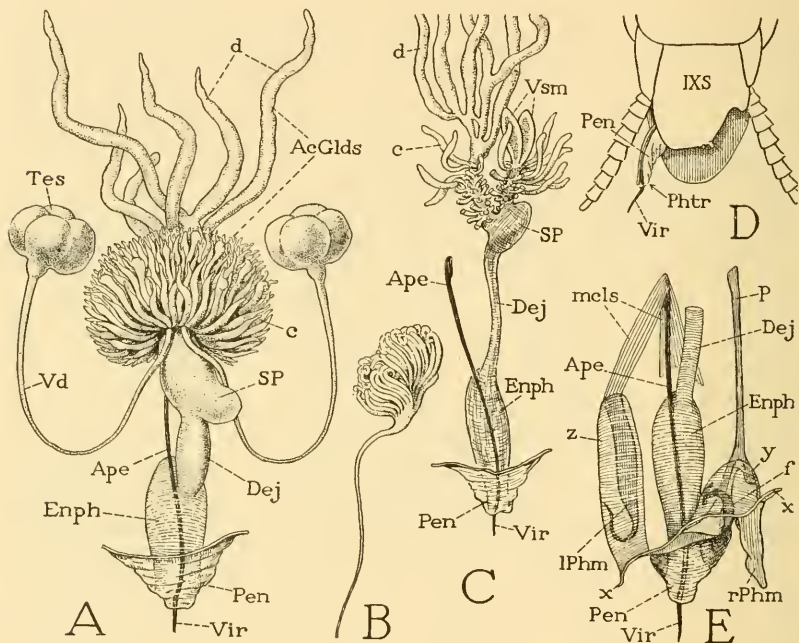


FIG. 16.—Blattoidea: male genitalia of *Blattella germanica* (Linnaeus).

A, internal reproductive organs, dorsal view. B, phallic gland. C, ejaculatory duct and associated structures, with most of smaller accessory gland tubules removed to expose the seminal vesicles. D, end of abdomen with penis projected, ventral view. E, external genitalia and endophallic pouch in retracted position, dorsal view.

*AcGlds*, accessory glands; *Ape*, endophallic apodeme; *c*, smaller tubules of accessory glands; *d*, long white tubules of accessory glands; *Dej*, ductus ejaculatorius; *Enph*, endophallus; *f*, sclerotic fold of wall of right phallic pouch; *lPhm*, left phallosome; *mcls*, muscles of endophallic apodeme; *p*, apodeme of right phallosome; *Pen*, penis; *Phtr*, phallosome; *rPhm*, right phallosome; *SP*, pouch of ejaculatory duct; *Tes*, testis; *Vd*, vas deferens; *Vir*, virga; *Vsm*, vesiculae seminales; *x-x* cut edge of anterior wall of genital chamber; *y*, right phallic pouch; *z*, left phallic pouch.

paramere" of Walker (1922), or the left phallosome according to the nomenclature here used. In other specimens, again, there is sometimes seen a conical or slender membranous organ terminating in a spine projecting from the right above the genital sternum (fig. 16 D, *Pen*). This is the penis, which is more usually concealed within the genital chamber.

The phallic organs of *Blattella* in the retracted state are shown as seen from above at E of figure 16. The anterior wall of the genital chamber ( $x-x$ ) runs obliquely forward from left to right. On the left it is produced into a deep pouch ( $z$ ) containing the hooked left phallomere ( $lPhm$ ); on the right it forms a wider but shallower pocket ( $y$ ) containing the right phallomere. The right phallomere consists principally of a flattened sclerotic arm ( $rPhm$ ), which, though never seen projecting from the genital chamber, is evidently protractile, since it is provided with a long basal apodeme ( $p$ ) on which muscles are inserted. The apodeme forks in the wall of the pouch, giving one branch to the base of the phallomere arm, and sending the other through the mesal wall of the pouch to an external sclerite above the base of the penis ( $Pen$ ). On the inner wall of the pouch is a thick rounded fold ( $f$ ) with a heavy, dark, crescentic, marginal sclerotization. The retracted penis appears as a conical, membranous lobe or fold (A, C, E,  $Pen$ ) projecting from between the phallomere pouches, and bearing at its apex a free spine, or virga ( $Vir$ ). Ventral to the base of the virga is an irregular opening, the phallotreme, leading into a large endophallic sac ( $Enph$ ), which receives the ejaculatory duct ( $Dej$ ) near its anterior end. The endophallic sac of *Blattella* apparently is equivalent to the terminal part of the genital exit passage of *Periplaneta* and *Blatta* (fig. 14 B,  $Enph$ ) opening in the membranous fold on the dorsal side of the base of the ventral phallomere. The phallotreme of *Blattella* is on the ventral surface of the penis, which fact would make it seem improbable that the penis represents the ventral phallomere of the Blattinae. From the base of the virga a long slender apodeme runs forward through the dorsal wall of the endophallus and projects anteriorly as a free rod (fig. 16 A, C, E,  $Ape$ ), on which protractor muscles (E,  $mcls$ ) are inserted.

In a young male nymph of *Blattella germanica* the ninth abdominal sternum is a simple, symmetrical, narrow plate (fig. 17 D,  $IXS$ ), bearing two widely separated styli ( $Sty$ ). At a later stage (E) it is larger and produced posteriorly in a truncate extension on which the styli are closer together, but it still shows none of the irregular features of the adult subgenital plate (A). At this stage the phallic structures are distinct lobes (F) arising from the anterior wall of the genital chamber above the ninth sternum. The left lobe ( $lPhm$ ) unquestionably represents the left phallomere of the adult because in the premoulting period a hooked structure ( $G$ ) may be found within it, which is clearly the beginning of the mature form of the organ (H). The right phallomere is a small simple lobe ( $rPhm$ ) on the right. Between the two phallomere lobes is a sclerotic point ( $Vir$ ), which is

the rudiment of the virga, and evidently cannot represent the median ventral phallomere of *Blatta* or *Periplaneta* because of its position dorsal to the genital opening.

The external genitalia of *Ectobius lapponicus* have the same type of structure as those of *Blattella*, but in most respects they are simpler. The exposed part of the ninth abdominal sternum of the adult male

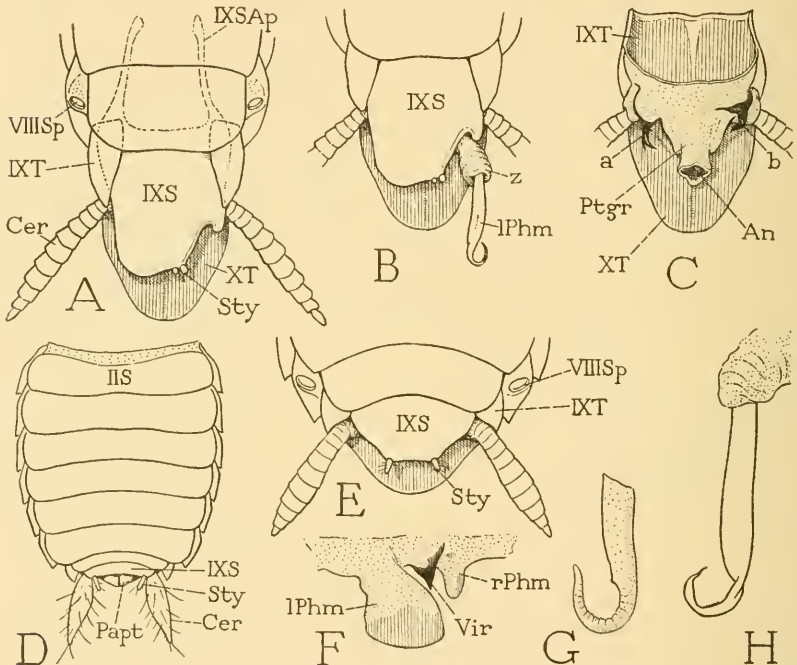


FIG. 17.—Blattoidea: abdomen and external male genitalia of *Blattella germanica* (Linnaeus).

A, adult male, end of abdomen, ventral view. B, same, with left phallomere projected. C, same, proctiger and basal hooks (*a*, *b*) beneath tenth tergum, ventral view. D, nymph 3 mm long, abdomen, ventral surface. E, nymph 22 mm long, end of abdomen, ventral view. F, same, phallic lobes removed from genital chamber, dorsal view. G, left phallomere of following nymphal instar taken from within cuticula of left lobe of F. H, left phallomere of adult.

For letter explanation, see preceding figures.

forms an asymmetrically triangular subgenital plate (fig. 18 A, B, IXS) projecting far beyond the short tergum of the tenth segment (A, XT), and bearing the coalesced rudiments of the styli (B, Sty) at its apex. The anterior invaginated part of the ninth sternum (E) is produced into two long apodemal arms (IXS*aps*) extending far forward in the abdomen, the left arm being longer than the right. Above the external part of the ninth sternum is the genital chamber,

within which may be seen the short membranous penis (A, E, *Pen*), but the phallomeres are usually entirely concealed in their lateral pouches (E, *y*, *z*). The much-reduced right phallomere (D, E, *rPhm*) consists of two small superposed lamellae at the bottom of the right pouch (*y*), with a short apodeme (*p*) projecting from the wall of the latter. The left phallomere is a long, thick, strongly sclerotized rod with a hooked extremity (E, *lPhm*), contained in a correspondingly deep pouch (*z*). By the complete eversion of the pouch, however, the left phallomere can be protracted far beyond the end of

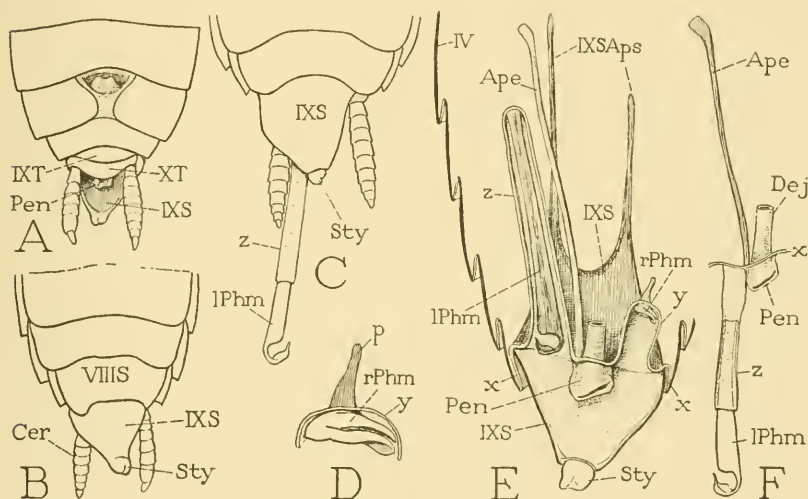


FIG. 18.—Blattoidea: abdomen and external male genitalia of *Ectobius lapponicus* (Linnaeus).

A, end of abdomen, showing penis (*Pen*) in base of genital chamber, dorsal view. B, same, ventral view. C, same, ventral view, with left phallomere projected on everted pouch (*z*). D, right phallomere in right phallic pouch (*y*). E, general view of retracted genitalia, somewhat diagrammatic, including ninth sternum and its apodemal arms (*IXSAps*), dorsal view. F, left phallomere projected, penis (*Pen*), and endophallic apodeme (*Ape*).

For letter explanation, see fig. 16.

the abdomen (C, F). The penis is a short membranous lobe (E, F, *Pen*) with a small endophallic cavity opening at its extremity. The penis is unarmed, but from the endophallic wall there arises a long apodeme (*Ape*), which extends forward and to the left into the fourth abdominal segment.

The type of phallic structure here shown in *Ectobia* and *Blattella*, representing the Ectobiinae and Pseudomopinae, occurs in many other forms, certainly including, as is evident from the descriptions and figures of Chopard (1920), the Nyctiborinae, Epilamprinae, Panchlorinae, and Perisphaerinae.

*The female genitalia.*—The external genital structures of female Blattidae include the opening of the median oviduct, the aperture of the spermatheca, the ovipositor, the opening of the accessory glands, and the oöthecal mold; they involve the seventh abdominal sternum and the ventral parts of at least the eighth and ninth abdominal segments. The genitalia are completely concealed in a large cavity above the seventh sternum, which latter is prolonged beneath the ventral parts of the succeeding segments. The short ovipositor arises (in the adult) from the venter of the ninth segment in the dorsal wall of the cavity. The small anterior part of the cavity lying before the ovipositor and above a fold representing the eighth sternum corresponds with the usual genital chamber of the eighth segment (see Snodgrass, 1933, fig. 23); the much larger posterior part, or vestibule, lying above the seventh sternum contains the ovipositor anteriorly, and forms distally a mold and container for the oötheca. The opening of the oviduct (gonopore) lies on a fold or lobe of the venter of the eighth segment, the spermatheca opens somewhere between the gonopore and the ovipositor, and the accessory glands discharge behind the base of the ovipositor.

The spermatheca of Blattidae is a two-branched structure (figs. 11 I, 15 F), one branch, which is usually thicker than the other or enlarged at the end, being the true sperm receptacle, the other apparently a glandular accessory. In *Blatta* and *Periplaneta* there is but one spermatheca; in *Blattella* there are two complete spermathecae (fig. 19 B), each with a separate opening and a glandular branch. According to Cleveland (1934) two spermathecae are present also in *Cryptocercus punctulatus*. The larger branch of the spermatheca of *Blatta orientalis* (fig. 11 I, *Spt*) is traversed by a narrow axial canal with strongly sclerotic walls, from which are given off numerous fine canaliculi into the cells of the thick glandular epithelium. In a preliminary study the writer mistook these threadlike ductules for spermatozoa, and made the foolish statement that the supposed spermatozoa are attached to a long spermatophore (Snodgrass, 1936, p. 90). Ito (1924), however, has shown the true nature of the structures radiating from the central canal. He says, moreover, that the lumen of the spermatheca, after copulation, is filled with spermatozoa and fine granules of secretion. The spermatheca of *Blatta* and of *Periplaneta* opens upon a small papilla on a median sclerite in the dorsal wall of the genital chamber (figs. 11 F, G, 15 G, *Spr*) proximal to the base of the ovipositor. In *Blattella* the spermathecae have quite a different position, as will be shown later, and their openings have a very special relation to the gonopore.

The structural details of the female genital region are well known in *Blatta* and *Periplaneta*; they have been but little studied in forms in which the male organs have the type of structure exemplified in *Blattella* and *Ectobia*, though Wille (1920) has given an account of the female genitalia in *Blattella germanica* that is deficient in only one essential point.

Most of the external genital organs of the female of *Blattella germanica* are exposed by depressing the seventh abdominal sternum. When the subgenital sternum is carefully cut away from its basal connections, it is to be seen that the lateral and anterior walls of the cavity above it (fig. 19 A) are formed by thick membranous folds (VIII V) converging downward and forward from the spiracular plates of the eighth tergum (VIII T). The folds, therefore, evidently represent the venter of the eighth segment, and the several asymmetrical sclerites contained in them (A, C, D, *h, i, j, k*), as well as a large crescentic sclerite (A, *l*) in the roof of the chamber before the ovipositor (*Ovp*), must be remnants of the eighth sternum. Immediately behind the crescentic dorsal sclerite (A, *l*) are the bases of the first, or ventral, valvulae of the ovipositor, with the accompanying first valvifers (*IVlf*). The second and third valvulae arise from the venter of the ninth segment, in which are several small sclerites linked with the ninth tergum by a pair of long sclerotic bars (*o, o*) extending forward and mesally from the lateral extremities of the tergum. The area behind the ovipositor includes the venter of the tenth segment and the under surfaces of the paraprocts (*Papt*).

The mouth of the median oviduct of *Blattella* (fig. 19 A, *Gpr*) is situated on the end of a soft triangular lobe (*m*) projecting from the anterior wall of the genital chamber. The dorsal surface of this genital lobe is marked by a deep median groove (C, D, *sg*), in the anterior end of which are the apertures of the two spermathecae (D, *Spr, Spr*). Beneath the genital lobe is a flat fold of the integument (A, C, *n*) that contains the ventralmost sclerite (*h*) referable to the eighth sternum. Another sclerite (D, *k*) lies dorsally on the left side of the lobe, and two sclerites converge above it (A, *i, j*) from the lateral ventral folds of the eighth segment. The general conformation of the region of the genital opening is thus quite different in *Blattella* from that in *Blatta* and *Periplaneta*, in which the gonopore is on the dorsal surface of a simple fold of the venter of the eighth abdominal segment, and the spermathecal aperture is located on a small sclerite in the dorsal wall of the genital chamber immediately before the base of the ovipositor (figs. 11 G, 15 G, *Spr*). The two spermathecal apertures of *Blattella* are far in advance of the base of the ovipositor, and,

as above noted, they lie in the anterior end of a groove (fig. 19 D, *sg*) on the dorsal surface of the genital lobe (*m*) that contains the gonopore (*C*, *Gpr*) in its free posterior margin. The groove of the genital lobe, therefore, is clearly a sperm conduit serving to convey the spermatozoa from the spermathecal apertures at its base (*D*, *Spr*, *Spr*) to the eggs issuing from the gonopore at its posterior end (*C*, *Gpr*).

The oötheca of *Blattella* is molded in the cavity of a large triangular,

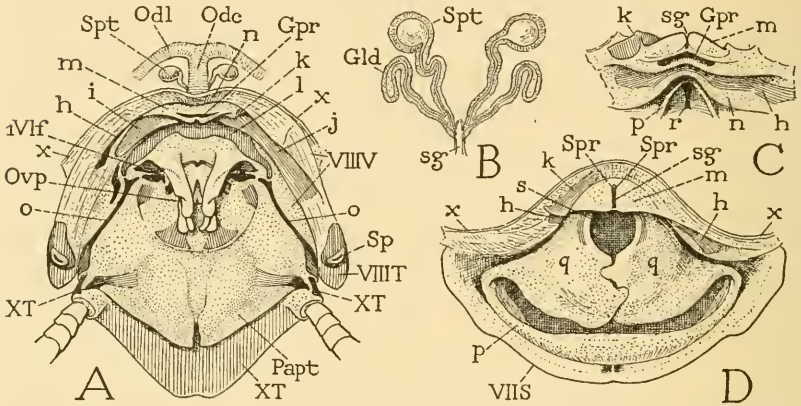


FIG. 19.—Blattoidea: female genitalia and associated structures of *Blattella germanica* (Linnaeus).

A, general view of external genitalia and associated inner structures exposed by removal of seventh abdominal sternum, ventral view. B, spermathecae. C, genital lobe (*m*) containing gonopore projecting from anterior wall of genital chamber, posterior view. D, genital lobe (*m*), and oöthecal fold (*p*, *q*) on floor of vestibulum.

*Gld*, spermathecal gland; *Gpr*, gonopore; *h*, *i*, *j*, *k*, sclerites in ventral folds (*VIII V*) of eighth abdominal segment; *l*, transverse sclerite in roof of genital chamber proximal to ovipositor; *m*, genital lobe; *n*, subgenital fold; *o*, *o*, ventral arms of ninth tergum; *OdC*, oviductus communis; *OdI*, oviductus lateralis; *Ovp*, ovipositor; *p*, oöthecal fold on dorsal surface of seventh sternum; *Papt*, paraproct; *q*, *q*, lateral flaps of oöthecal fold; *r*, median anterior sclerite in floor of oöthecal chamber; *s*, foramen admitting end of ovipositor into oöthecal chamber; *sg*, spermatic groove; *Sp*, spiracle; *Spr*, spermathecal aperture; *Spt*, spermatheca; *VII S*, sternum of seventh segment; *VIII V*, venter of eighth segment; *VIII T*, tergum of eighth segment; *x-x*, cut edge of anterior wall of genital chamber; *XT*, tergum of tenth segment.

calyxlike fold (fig. 19 D, *p*, *q*) arising submarginally on the floor of the vestibulum. The apex of this fold (*C*, *p*) lies anteriorly beneath the subgenital fold (*n*) of the eighth segment, and encloses a small median sclerite (*r*) of the vestibular floor. The lateral parts of the oöthecal fold are produced in two broad irregular flaps (*D*, *q*, *q*), which overlap medially, but leave between their bases a round foramen (*s*), through which the end of the ovipositor projects posteriorly and downward into the oöthecal chamber. The genital lobe of the eighth



segment (*A, m*) evidently is protractile against the ovipositor base; the short ovipositor, therefore, serves as an egg conduct leading from the gonopore (*Gpr*) on the end of the genital lobe into the chamber of the oöthecal fold, and it also conveys into the latter the formative material of the oötheca discharged from the accessory glands opening between the bases of the second valvulae. With the formation of the oötheca, the lateral flaps of the oöthecal fold are pressed upward against the roof of the vestibulum, and thus shut off the oöthecal chamber from the cavity containing the ovipositor, except for the foramen that admits the end of the ovipositor.

*Copulation and insemination.*—There can be little doubt that many of the differences in the male genital structures between *Blatta* and *Periplaneta* on the one hand, and *Blattella* and related genera on the other are correlated with the differences in the genital apparatus of the females, but we have no exact information on the interrelated functions of the genital organs. Considering how intimate some of the cockroaches are with us, it is disconcerting to find how little we know of the private lives of cockroaches. Several investigators, however, have revealed something of their mating habits.

It has long been known that male roaches are provided with glands opening on the back of the abdomen; the secretion of some of these glands is attractive to the female at the time of mating, and assists the male in effecting a union with the female.

The first observation on dorsal abdominal glands in cockroaches was made by Gerstaecker (1861), who described two pairs of small, eversible, glandular vesicles found in a species of *Corydia* between the dorsal and ventral plates of segments *I* and *II*, present in adult males and females, but not in nymphal instars. The function of these glands is unknown, and the occurrence of similar glands in other species has not been determined. In *Blatta* and *Periplaneta* a pair of small glandular pouches occur in the infolded membrane between the tergal plates of segments *V* and *VI*. These glands were first described in *Periplaneta* by Minchin (1889, 1890), whose observations were confirmed by Haase (1889), and their histology has been further studied by Oettinger (1906), and by Koncěk (1924). The walls of the pouches contain glandular cells, and their inner surfaces are covered with small hairs. The dorsal glands of *Blatta* and *Periplaneta* are present in both sexes of the adult, and, according to Oettinger, in all stages of the nymph. They are regarded as odor-producing organs by Haase and Oettinger. It is possible that their secretion has a sex attraction during mating. In *Blattella* and related genera the back of the male abdomen is marked by two deep irregular

depressions of the integument at the bases of the seventh and eighth tergal plates (see Oettinger, 1906; Wille, 1920). Into each of these depressions opens a pair of glands, the first between segments *VI* and *VII*, the second between segments *VII* and *VIII*. The glands of *Blattella*, according to Oettinger and Konček, are similar to those of *Periplaneta*, though located on different segments, but they are present only in adult males. The secretion of the male glands in *Blattella*, as suggested by Sikora (1918) and demonstrated by Wille (1920), is attractive to the females at the time of mating and induces the female to mount the back of the male preliminary to copulation. The glands thus have a function similar to that of the back glands of certain male crickets.

Wille (1920) describes the mating and copulation of *Blattella germanica* as follows: When a male encounters a prospective mate he takes a position either face to face with her or at her side. After a short interplay of the antennae, the male raises his wings at right angles to his body, turns himself about, and brings the end of his abdomen close to the head of the female. The depressions on the back of the male are thus exposed to the female, who, being soon attracted to them, first explores them with her palpi and then proceeds to lick them with her mouth parts. When the female becomes absorbed in this occupation, the male suddenly makes a backward movement, thrusting his abdomen under that of the female, until the female's head is almost against the bases of his upstanding wings. From the abdomen of the male, already extended at its tip, there is now projected the long, hooked left phallomere ("titillator") and the penis. The first grasps and pulls down the subgenital plate of the female, while the second is turned upward and forward and thrust into the female's genital chamber. In the following discussion of the act of insemination, Wille appears to assume that the spermatozoa are discharged into the oviduct; he describes the means by which the penis might be guided toward the "vaginal" orifice in such a manner that the genital openings of the two sexes would be pressed together; he makes only an incidental mention of a sperm receptacle, and does not observe the separate spermathecal openings in the spermathecal groove above the gonopore. It would seem more probable, therefore, that the virga of the penis is laid in the seminal groove of the female genital lobe, and that the spermatozoa are thus guided from the exit orifice of the penis to the spermathecal apertures.

Zabinski (1933), who studied the mating habits of several common species of roaches, claims that the male, after having secured a hold on the genitalia of the female, turns end to end from her, and that

insemination is normally completed in this position. Copulation in the reversed position, he says, continues about a half hour with *Blattella*, perhaps an hour with *Periplaneta*, and two or three hours with species of *Blaberus*. The preliminary mating of *Blatta orientalis*, as described by Rau (1924) and by Zabinski (1933), is accomplished in the same manner as with *Blattella germanica*. There appears, however, to be no positive evidence that the females of *Blatta* are attracted to the males by any gland secretion of the latter, though Rau says that when a male has partly inserted his body under the female, the latter "slowly walks on top of his back, touching and feeling the segments of his abdomen with her jaws and palpi."

Little is known of the exact function of the numerous phallic structures of the Blattinae. Rau (1924) observes that a male of *Blatta orientalis* attempting to copulate with a female opens and closes the genital claspers like a pair of tongs. Zabinski (1933 a) found that after removal of the long hooked process of the left phallomere (fig. 13 A, q') the male of *B. orientalis* is entirely unable to copulate with the female, and likewise, after removal of the ventral valvulae of the female's ovipositor, a normal male cannot retain his hold on the female. The curvature of the left phallomere hook to the right, Zabinski points out, must compel a grasping of the female on this side, and for this reason the male always turns to the right in taking the reversed position, in which insemination of the female is finally accomplished.

The method of sperm transfer in Blattidae has been but little studied. In most other Orthoptera the spermatozoa are enclosed in a spermatophore formed from the secretion of the male accessory genital glands, and the high development of these glands in the Blattidae would suggest that the glands have the same function in this family. Yet, Zabinski (1933 a) is the only observer who has reported the occurrence of a spermatophore among the roaches; his record pertains to *Blatta orientalis*. Copulation in this species, Zabinski says, results in the attachment of a spermatophore on the papilla of the female containing the spermathecal orifice (fig. 11 H). The spermatophore, about the size of pin head, is at first pear-shaped but later becomes deformed by pressure; when fresh it is white and has the consistency of hard butter. It consists of outer and inner walls with an intervening layer of vacuolated material. The inner wall, Zabinski believes, is formed by the secretion of the smaller tubules of the accessory glands, and the outer parts by that of the longer tubules. The spermatophore is carried by the female for 2 or 3 days, and is then rejected. Wille (1920) found no evidence of spermatophore

formation in *Blattella germanica*. Free spermatozoa, he says, are present in the seminal receptacles of females examined the morning following mating that took place during the night, but no trace of spermatophore capsules is to be seen.

#### IX. TETTIGONIOIDEA

The external genital apparatus of the adult male of tettigoniid, gryllid, and acridid Orthoptera differs from that of the Blattidae and Mantidae in that it consists of a single phallic structure which encloses the opening of the ejaculatory duct. The organ is developed in the nymph, however, from primitive genital lobes (phallomeres) that grow out from the genital integument around the gonopore.

The mature phallus of the Tettigonioidea has a distinctive type of structure, which fact can leave no doubt of the close relationship of the several families included in this group (Tettigoniidae, Gryllidae, and related forms variously classified by taxonomists). Unquestionably a wider comparative study of the organ would give valuable evidence on the natural classification of the families. Since the structure of the phallus is adapted to the formation of a spermatophore, the nature of the spermatophore itself should be an index to relationships. Judging from what is known concerning the spermatophores of members of several families, it seems probable that the families will be found to fall into two series, according to whether the spermatophore contains a single sperm capsule, or two sperm capsules.

The internal reproductive organs of male Tettigonioidea exemplify the typical orthopteran structure of these parts in a highly developed condition (figs. 20 A, 27 C, 34 A, 39 A). The testes (*Tes*) are compact bodies, each composed of a large number of sperm tubes (fig. 27 D, *ST*) surrounded by a peritoneal sheath (*PSh*). The vas deferens (*Vd*) penetrates into the testis and the sperm tubes converge upon its anterior end, which may be much enlarged. Beyond the testis each vas deferens is thrown into numerous loops, forming an epididymis-like body (figs. 20 A, 27 C, 34 C, 39, *Epdm*) that attains a particularly large size in the Gryllotalpidae (fig. 39). Posteriorly the vasa deferentia turn mesad and ventrally, going beneath the large cercal nerves of the eleventh abdominal segment (figs. 20 A, 34 A, 39 B, *XINv*), and then forward to enter the anterior part of the ductus ejaculatorius.

The ejaculatory duct (if the name is given to the entire median genital exit passage of the adult) is clearly composed of both ectodermal and mesodermal parts. The mesodermal section is formed of the united embryonic ampullae of the vasa deferentia (figs. 21 E, 31 E,

*Amp*), and gives rise to the accessory glands and seminal vesicles of the adult. From each ampulla in a late nymphal stage there may be a single diverticulum, but the great mass of tubules appears only in the imaginal stage. The ampullar part of the definitive ejaculatory duct may be bilobed (fig. 25 G) or single; in *Gryllotalpa* it forms a large median sac (fig. 39 A) from which the accessory gland tubules arise. The accessory glands always consist of numerous tubules (figs. 20 A, 27 C, 34 A, 39 A, *AcGlds*), which differ in length, and may be differentiated into several groups by differences in size and probably in the nature of their secretions. In *Phaneroptera furcata* (fig. 20 A) there are four distinct, paired groups of tubules, including two anterior groups of long thick tubes (*a*), lateral clusters of shorter and more slender tubules (*b*), a dense ventral mass of still smaller ones (*c*), and finally two large, compact bodies of fine, closely interwoven tubules (*d*) projecting laterally and posteriorly. Bodies of tubules similar to the last, but much smaller, are present also in *Gryllotalpa* (fig. 39 A, *d*). Sperm-containing vesicles comparable with those of Mantidae and Blattidae appear to be absent in Tettigoniidae and Gryllidae, but in *Gryllotalpa* two large tubular diverticula (fig. 39 A, *Vsm*) arise laterally from the ejaculatory duct near the terminations of the vasa deferentia, which, as noted by Ito (1924), are found to be filled with mature spermatozoa, their heads buried in the vesicular walls.

The posterior ectodermal part of the ejaculatory duct is wide and usually very short. Its walls are continuous posteriorly with those of the endophallus (figs. 25 F, 32 E), but the termination of the duct is always marked by the orifices of two globular vesicles (*ejv*) that open into it. These vesicles of the ejaculatory duct are characteristic features of the Tettigoniodea (figs. 20 A, 25 F, C, 27 C, 32 E, 34 A, 39 A). They have been termed "prostate glands", and should have a better claim to this name than the phallic glands of Blattidae and Mantidae, but nothing is known of their function. According to Ito (1924) the lumen of each vesicle is lined by a thick chitinous intima and contains a granular mass with large globules. The vesicles usually have a pale yellow or orange color.

The accessory glands, the ejaculatory duct, and the phallic muscles are innervated by branches given off from the common basal trunks of the nerves to the tenth and eleventh segments (figs. 34 D, 39 B). This fact suggests that the ectodermal phallus and ejaculatory duct, as well as the mesodermal ampullar part of the latter, are derived from the tenth abdominal somite.

The female genital organs of the Tettigoniodea, aside from the ovipositor, are simple and of a generalized type of structure. The

external genital opening, or vulva (female gonotreme), lies between the base of the ovipositor and the posterior margin of the eighth sternum, or a differentiated subgenital lobe of the latter (fig. 20 B, F, *Vul*). It leads into a small genital chamber into which open both the median oviduct and the spermatheca. The opening of the oviduct (female gonopore) lies ventrally, either in the anterior wall of the

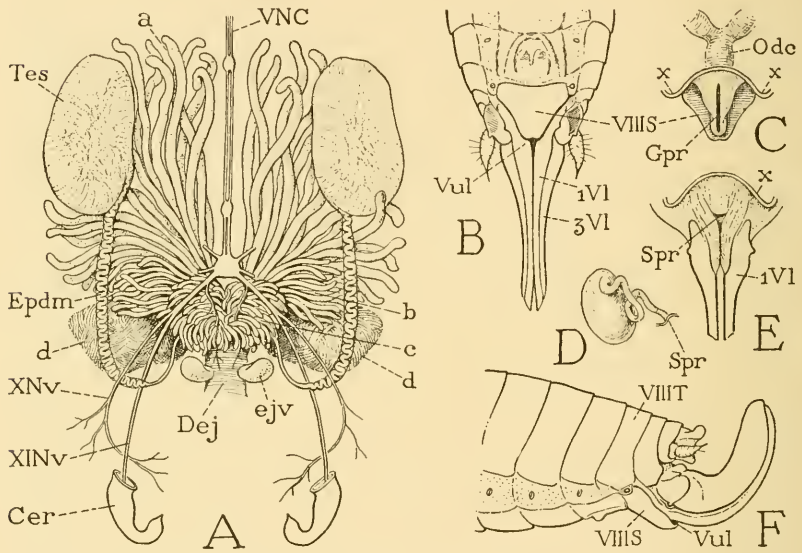


FIG. 20.—Tettigonioidae—Tettigoniidae: male and female genitalia of *Phaneroptera furcata* (Brunner).

A, internal reproductive organs of adult male, ventral view. B, end of abdomen of female, ventral view. C, opening of oviduct (*Gpr*) on fold of upper surface of eighth abdominal sternum. D, spermatheca. E, spermathecal aperture at base of ovipositor in dorsal wall of genital chamber. F, end of female abdomen, lateral view.

*a, b, c, d*, four paired groups of accessory gland tubules; *Cer*, cercus; *Dej*, ductus ejaculatorius; *ejv*, vesicle of ejaculatory duct; *Epdm*, epididymis; *Gpr*, gonopore; *Odc*, oviductus communis; *Spr*, spermathecal aperture; *Tes*, testis; *1VI*, *3VI*, first and third valvulae of ovipositor; *VNC*, ventral nerve cord; *Vul*, vulva (female gonotreme); *x-x*, cut edge of anterior wall of genital chamber; *XNv*, *XINv*, nerves of tenth and eleventh abdominal segments.

genital chamber, or on a median fold of the floor (fig. 20 C, *Gpr*). The spermathecal aperture is in the dorsal wall of the chamber (E, *Spr*); it may be concealed in a pocket of the latter, or, as in *Gryllus*, it may be situated on a large spoutlike projection. The spermatheca is a single oval or elongate sac (figs. 20 D, 29 B), and its duct has no diverticulum. The short median oviduct (fig. 40 A, *Odc*) unites with the lateral oviducts (*Odl*) in the ventral part of the abdomen, the

lateral ducts turning downward and mesally between the principal nerves of the seventh and eighth segments (B). Compared with the male, in which the vasa deferentia turn downward between the nerves of the tenth and eleventh segments, it is seen that the nerves of three segments intervene between the positions of the ends of the ducts in the two sexes, from which it is evident that two segments intervened between the primary female genital segment (VII) and the primary male genital segment (X).

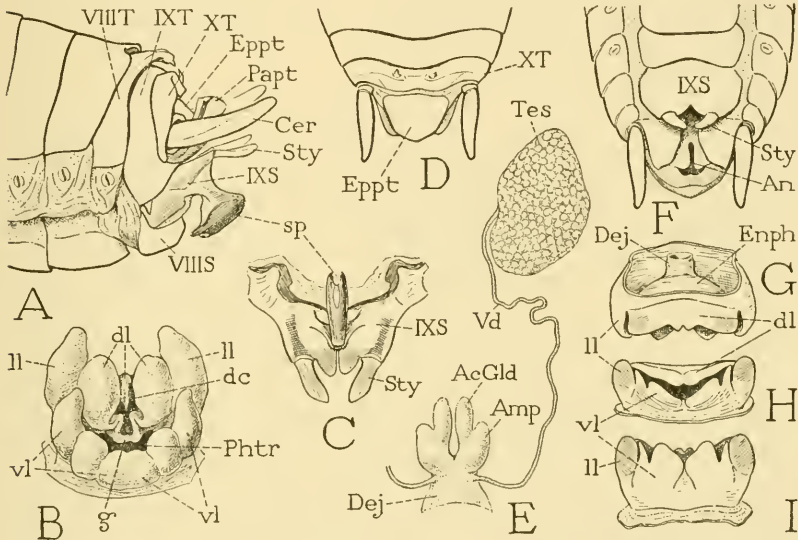


FIG. 21.—Tettigonioida: male genitalia of *Cyphoderris monstrosa* Uhler.

A, adult male, end of abdomen, lateral view. B, phallus of adult, posterior view. C, ninth abdominal sternum, ventral view. D, male nymph, probably full grown, end of abdomen, dorsal view. E, same, internal reproductive organs. F, same, end of abdomen, ventral view. G, H, I, same, phallus, dorsal, posterior and ventral views.

*AcGld*, first rudiment of accessory glands; *Amp*, mesodermal ampulla; *dc*, dorsal cavity of phallus; *Dej*, ejaculatory duct; *dl*, dorsal lobe of phallus; *Enph*, endophallus; *g*, posterior margin of dorsal lobe of phallus; *ll*, lateral lobe of phallus; *Phtr*, phallotreme; *sp*, sternal process; *Sty*, stylus; *Tes*, testis; *vl*, ventral lobe of phallus; *Vd*, vas deferens.

*Cyphoderris monstrosa*.—This insect, of uncertain taxonomic status, would appear to belong to the Tettigoniidae because of the presence of well-developed styli on the ninth abdominal sternum of the male in both adult and nymphal stages (fig. 21 A, F, *Sty*), and because of the more complete separation of the epiproct from the tenth tergum (A, D) than is characteristic of the Gryllidae. The phallus, moreover, very well represents a generalized condition of the tettigoniid type of phallic structure, and certainly does not have the special features of the organ developed in Gryllidae and related families. The ninth

sternum of the adult male has a very unusual form (A, C, *IXS*); it folds up against the end of the abdomen and bears a large hammer-shaped process (*sp*) on its under surface. Walker (1922) gives a good illustration of the terminal aspect of the abdomen of *Cyphoderris monstrosa*, and he says the only representative of the penis are the folded membranous lips of the genital passage. This statement is entirely true, but when the membranous folds are inflated, as shown at B of figure 21, drawn from a dried specimen boiled in water, they take the form of a definite organ, the lips of which are produced into a number of lobes surrounding the gonotreme, which opens from a spacious endophallic cavity.

The structure of the phallus of *Cyphoderris* is easily understood on examining the organ in a late nymphal stage. The nymphal phallus (fig. 21, G, H, I) is a broad, flat structure with weakly sclerotized walls, arising by a wide base from the wall of the genital chamber. It contains a large endophallic cavity, to the anterior wall of which is attached the ejaculatory duct (G, *Dej*). The lips of the phallostreme are subdivided into several distinct lobes; above is a broad dorsal lobe (G, H, *dl*), at the sides a pair of oval lateral lobes (*ll*), and below a pair of ventral lobes (H, I, *vl*), each subdivided into two parts. The structure of the nymphal phallus of *Cyphoderris* is typical of that of the Tettigonioidae in general (figs. 23 B-F, 31 F-H). The differentiation of the organ into its various adult forms takes place principally with the change to the imago.

In the phallus of the adult *Cyphoderris* (fig. 21 B) the various lobes of the nymphal organ (H) have expanded into large vesicular processes, which are probably distended by pressure from within the abdomen. The ventral lobes (*vl*) now include five subsidiary lobes, but the median one is evidently the small median part between the ventral lobes of the nymph (I). At the sides of the phallostreme are the greatly expanded lateral lobes (*ll*). The dorsal lobe (*dl*) carries two marginal vesicles, and its median part is deeply depressed, forming a dorsal cavity (*dc*), but its distal margin (*g*) is still the upper lip of the phallostreme. The latter leads into an ample endophallic cavity that receives the ejaculatory duct.

*Tettigoniidae*.—The phallus of the tettigoniids in its essential structure and immature form is identical with that of *Cyphoderris*, but in its adult development it is subject to greater modifications. The structural variations of the adult organ, however, are but little divergent and closely follow a single line of evolution.

The mature tettigoniid phallus in its usual retracted condition is mostly concealed within the genital chamber, where it appears as a



large, thick, soft body arising from the anterior wall of the chamber. Its general structure may be represented diagrammatically as at C, figure 22. The posterior part of the organ presents ventrally a wide transverse opening, the phallotreme, which leads into a large ventral endophallic cavity (*Enph*) continuous anteriorly with the ejaculatory duct. The part of the organ above the phallotreme constitutes a large,

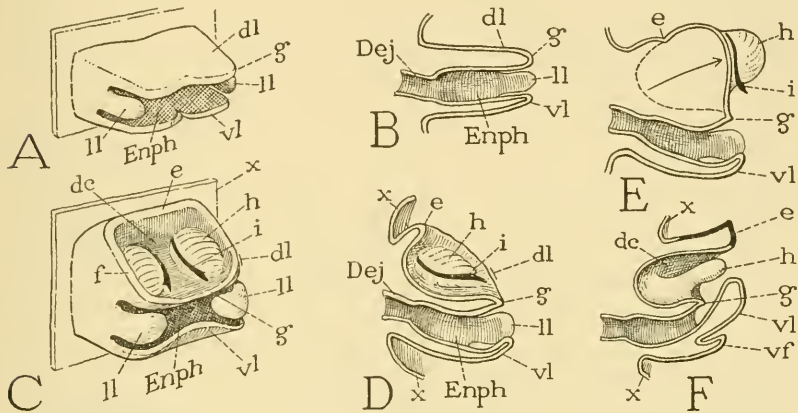


FIG. 22.—Diagrams showing the fundamental structure and the evolution of the tettigonioid type of phallus in Tettigoniidae and Rhabdiphorinae.

A, nymphal structure of the phallus, postero-lateral view. B, same, median section. C, adult structure of the phallus in Tettigoniidae, postero-lateral view. D, same, median section. E, same, dorsal cavity and its armature everted. F, adult structure of the phallus in Rhabdiphorinae, median section.

The following letter explanations apply to figs. 22 to 28, inclusive. *An*, anus; *AcGlds*, accessory glands; *Cer*, cercus; *dc*, dorsal cavity of phallus; *Dej*, ductus ejaculatorius; *dl*, dorsal lobe of phallus; *e*, anterior margin of dorsal cavity of phallus (produced posteriorly at F); *ejv*, vesicle of ejaculatory duct; *Enph*, endophallus; *Epdm*, epididymis; *Eppt*, epiproct; *f*, lateral margin of dorsal cavity of phallus; *g*, posterior margin of dorsal lobe of phallus; *h*, membranous lobe or fold on floor of dorsal cavity of phallus; *i*, sclerotic armature associated with *h*; *j*, dorsal fold of body wall above base of phallus; *k*, dorsal pouch of phallus formed by posterior reflection of anterior margin (*e*) of dorsal phallic cavity (*dc*); *ll*, lateral lobe of phallus; *mcl*, muscles; *Papt*, paraproct; *Phl*, phallus; *Phtr*, phallotreme; *PSh*, peritoneal sheath of testis; *rpd*, *rpv*, dorsal and ventral retractor muscles of phallus; *ST*, sperm tube of testis; *Sty*, stylus; *Tes*, testis; *Vd*, vas deferens; *vf*, ventral fold of phallus; *vl*, ventral lobe of phallus; *x-x*, cut edge of anterior wall of genital chamber; *X.V*, venter of tenth abdominal segment.

thick *dorsal lobe* (*dl*), the part beneath projects as a broad, flaplike *ventral lobe* (*vl*), while at each side of the opening is a *lateral lobe* (*ll*). The upper or posterodorsal surface of the dorsal lobe is usually depressed or deeply sunken, forming a *dorsal cavity* (*dc*), the margins of which (*e*, *f*, *g*) are often prominent folds. The distal margin (*g*) appears as a transverse septum between the dorsal cavity and the mouth of the endophallic cavity. The floor of the dorsal cavity is

generally produced in a pair of soft lateral folds or rounded lobes (*h*), and associated with these structures is usually a pair of sclerotic bars or plates (*i*), the ends of which may project as free processes. The anatomical relations of the various parts of the phallus in the ordinary retracted state are best seen in a median longitudinal section (D), from which it becomes evident that the entire organ is merely an outgrowth from the genital chamber wall (*x-x*), enclosing a large endophallic cavity (*Enph*), into which opens the ejaculatory duct (*Dej*). Disregarding the modification of the dorsal lobe, therefore,

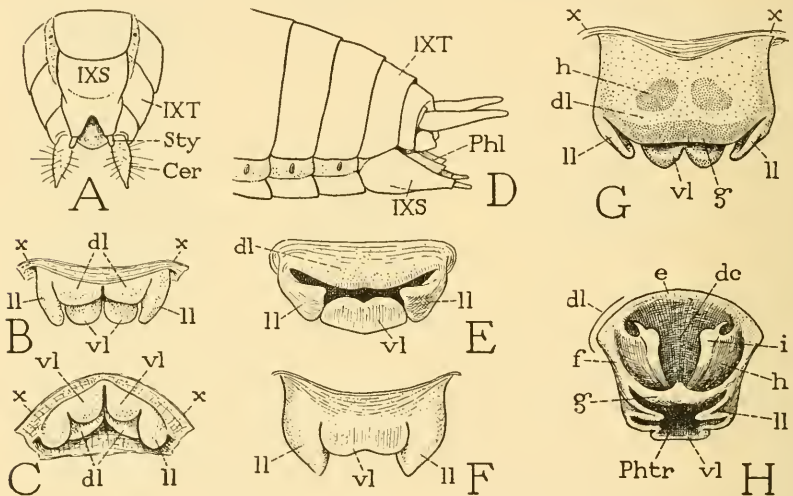


FIG. 23.—Tettigonioidae—Tettigoniidae: external male genitalia of *Conocephalus fasciatus* (Degeer).

A, nymph, 9 mm long, end of abdomen, ventral view. B, C, same, phallus in dorsal and ventro-posterior views. D, nymph, 11 mm long, end of abdomen. E, F, same, phallus in posterior and ventral views. G, nymph, 14 mm long, phallus, dorsal view. H, adult, phallus, posterior view.

For letter explanation, see fig. 22.

the essential structure of the phallus may be expressed as in the diagram at A, or in section as at B. This simplified concept of the adult phallic structure is the actual structure of the organ in late nymphal stages of its development (fig. 23 E, G).

The male organs of the Tettigoniidae have been well described by Walker (1922), though in terms somewhat different from those used here because based on a different idea concerning the origin and evolution of the phallus. The paired processes or armature of the dorsal phallic lobe Walker calls the "parameres", the dorsal cavity the "paramere sac", and the endophallic cavity the "spermatophore sac."

The so-called parameres of the Tettigoniidae are supposed to represent the paired right and left phallic lobes of Blattidae, but, as will presently be shown, the development of the tettigoniid phallus does not warrant the assumption of a close homology between any of its minor parts and the phallic structures of Blattidae.

Though the tettigoniid phallus is ordinarily concealed within the genital chamber, the entire organ is protractile. In the protracted condition (fig. 22 E) the dorsal cavity with its armature is everted, and all parts of the phallus may be so greatly distended by blood pressure that the organ assumes an entirely different appearance from that of its passive state. The principal muscles of the phallus are a pair of dorsal retractors (fig. 24 B, *rpd*) arising on the lateral parts of the tenth abdominal tergum, and a pair of ventral retractors (*rpv*) arising on the ninth sternum.

The development of the tettigoniid phallus in nymphal instars shows that the adult organ is a composite structure formed by the union of several primary lobes of the genital integument that grow out around the gonopore, or mouth of the invagination that gives rise to the ectodermal part of the ejaculatory duct. In a young nymph of *Conocephalus fasciatus*, 9 mm in length (fig. 23 A), the gonopore is surrounded by six small phallic lobes (B, C), two of which are dorsal, two lateral, and two ventral. These simple lobes, or phallomeres, enclose between them a shallow endophallic cavity, to the base of which is attached the ejaculatory duct. The early nymphal phallomeres of *Conocephalus* thus resemble the nymphal phallomeres of *Blatta* or *Periplaneta* (figs. 12 E, 15 C), except that there are six of them instead of three. At this stage, therefore, it is impossible to identify any particular pair of lobes in *Conocephalus* with any particular pair in *Blatta* or *Periplaneta*. At a later stage in the development of *Conocephalus*, in a nymph 11 mm long (fig. 23 D), the two primary dorsal phallomeres have united in a single broad dorsal lobe (E, *dl*), and the two ventral phallomeres have united in a single ventral lobe (E, F, *vl*), the lateral lobes (*ll*) retaining their independence. All the lobes, moreover, are now carried out on a common basal ring, and the endophallic cavity is correspondingly deepened. Thus is established the typical four-lobed structure of the adult phallus, but the special features of the dorsal lobe are not yet in evidence. At a still later stage, in a nymph 14 mm in length, the basal part of the phallus has greatly lengthened (G), so that the primary phallomeres now appear as relatively small terminal lobes, with the wide phallotreme between them. The dorsal lobe (*dl*) still presents a broad flat upper surface, but there are differentiated upon it two oval thickenings (*h*), which

evidently are the rudiments of the adult armature (H, *h*, *i*). The mature structure of the phallus (H) apparently is attained at the last moult; it involves principally the thickening of the dorsal lobe, the invagination of the upper surface of the latter, and the development of the dorsal armature characteristic of the species.

The adult modifications of the tettigoniid phallus consist principally of variations in the relative size of the several terminal lobes, and in the form and development of the armature of the dorsal lobe. In the Decticinae, however, the cavity of the dorsal lobe becomes converted into a pocket by the posterior extension of its anterior margin, which condition leads into that characteristic of the Rhabdophorinae (fig. 22 F), and finally to an extreme type of modification that distinguishes the Gryllidae from the Tettigoniidae.

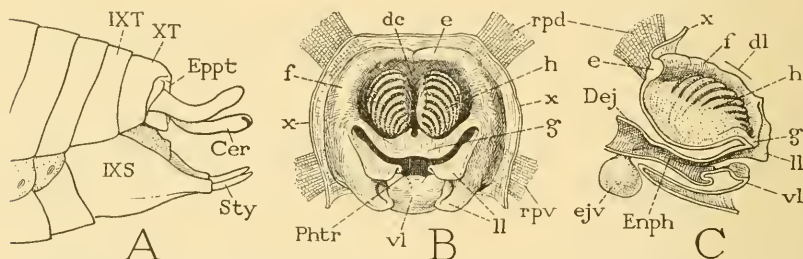


FIG. 24.—Tettigonioidae—Tettigoniidae: external male genitalia of *Microcentrum retinerve* (Burmeister).

A, end of abdomen, lateral view. B, phallus, posterior view. C, same, median longitudinal section.

For letter explanation, see fig. 22.

For a concrete example of a phallic structure that comes close to the hypothetical generalized structure shown at C of figure 22 we may select the genus *Microcentrum*. The phallus of *M. retinerve* (fig. 24 B) is a low, rounded organ with a basinlike cavity (*dc*) in the dorsal wall, a pair of folded lateral lobes (*ll*), and a thick, bifurcate ventral lobe (*vl*). The phallotreme (*Phtr*) is a wide, transverse opening between the distal lip (*g*) of the dorsal lobe above, and the lateral and ventral lobes below. The dorsal cavity contains two large, oval, strongly convex protuberances (*h*), transversely ribbed on their lateral surfaces with finely toothed ridges, but there is no other accessory armature. Attached on the inner surfaces of these dorsal organs are large masses of muscle fibers converging from the lateral parts of the base of the phallus. The dorsal and ventral retractor muscles (*rp<sub>d</sub>*, *rp<sub>v</sub>*) have the typical arrangement and are inserted on the phallic base. A median section of the organ (C) shows clearly the

simple anatomical relations of its parts, including the endophallic cavity (*Enph*) that receives the ejaculatory duct (*Dej*). In the closely related *M. rhombifolium* the phallus has the same general structure as that of *retinerve*, but the organs of the dorsal cavity are absent.

A nymphal condition of the phallus appears to be retained in the adult of *Amblycorypha oblongifolia*, since the phallic organ is here a small, soft, compact body presenting a broad, flat dorsal surface without the usual dorsal cavity and armature. The endophallic cavity, however, contains a flat, tongue-like fold that divides it into a dorsal

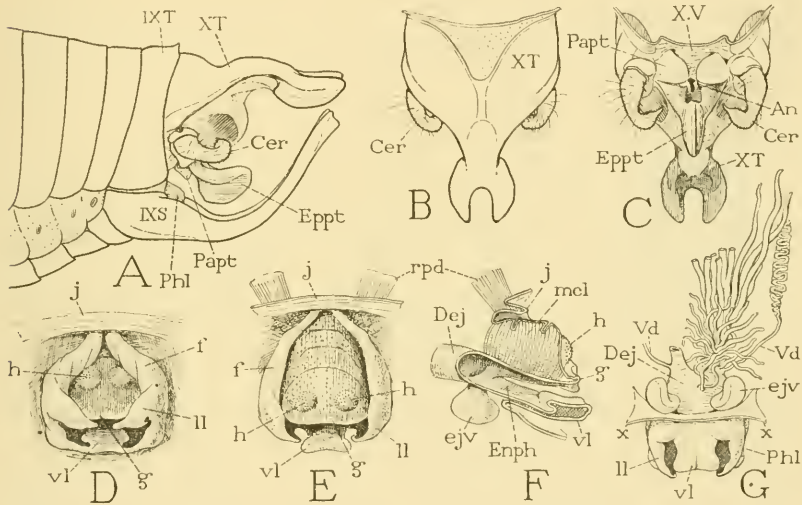


FIG. 25.—Tettigonioidae—Tettigoniidae: abdomen and genitalia of male of *Phaneroptera furcata* (Brunner).

A, end of abdomen, lateral view. B, tenth tergum and cerci, dorsal view. C, tenth and eleventh abdominal segments, ventral view. D, phallus, posterior view. E, same, dorsal view. F, same, median longitudinal section. G, phallus and associated internal organs, ventral view.

For letter explanation, see fig. 22.

and a ventral compartment. The fold arises by a narrowed base above the gonopore, and ends with two small divergent lobes projecting from the phallotreme.

In the genus *Phaneroptera* the male "terminalia" include numerous modifications of the ninth, tenth, and eleventh abdominal segments. In *S. furcata* (fig. 25 A) the tergum of the ninth segment resembles the tergal plates preceding it, but the ninth sternum (*IXS*) is produced posteriorly in a long, slender, tapering, trough-shaped extension, strongly curved upward, ending in a narrow truncate margin. Styli are absent unless they are represented by two small nodules on the

distal angles of the sternal process. The concave dorsal wall of the ninth sternum becomes proximally a deep concavity in which the phallus (*Phl*) is lodged. The tenth tergum (A, B, *XT*) is a large triangular plate with its apex produced into a thick median stalk bearing two strong terminal lobes that embrace the process of the ninth sternum when the tenth tergum is depressed. The venter of the tenth segment is a narrow membranous area proximal to the paraprocts (C, *XV*). The eleventh segment projects ventrally from beneath the broad basal part of the tenth segment (A, C); the epiproct is produced into a prominent, laterally compressed lobe (*Eppt*); the paraprocts (*Papt*) are two small, soft lobes at the base of the epiproct. The anus (C, *An*) lies in the anterior end of a deep depression on the under surface of the epiproct. The falciform cerci (A, B, C, *Cer*) are articulated by their basal sclerites to the proximal parts of the lateral margins of the tenth tergum (A).

The phallus of *Phaneroptera furcata* is a thick, padlike organ arising from the anterior wall of the genital chamber. In its usual condition it is contained in the dorsal concavity on the base of the ninth sternum (fig. 25 A, *Phl*), where it is concealed by the overhanging lobe of the epiproct. The broad, sloping posterior surface of the phallus (D, E) presents a median depression dorsally between prominent marginal folds (*f*) that terminate distally in the lateral phallic lobes (*ll*). The ventral lobe is a tongue-like extension of the ventral lip of the broad phallotreme (E, *vl*), which may be folded back into the latter (D). The floor of the dorsal cavity is roundly convex and is crossed by four, narrow, dark-lipped grooves. Distally, it bears a pair of prominent oval swellings (*h*), conspicuous by their darker color, which results from a dense covering of small spines such as are more sparsely distributed on the surrounding surface. The interior of the dorsal lobe of the phallus is occupied by two dense masses of muscle (F, *mcl*) the fibers of which arise laterally within the phallus and curve medially and dorsally to their insertions on the arched floor of the dorsal cavity. In the retracted condition the base of the phallus is covered dorsally by a transverse fold of the genital chamber wall (D, E, F, *j*).

The apparently abrupt change in the structure of the phallus from the simple nymphal condition to the complex adult form, as illustrated in *Conocephalus fasciatus* (fig. 23 G, H), is of course more gradual than it appears. The adult modifications take place during the last nymphal instar within the cuticula of the nymphal phallus, and are completed at ecdysis. The mature phallus of *C. fasciatus* (fig. 23 H) much resembles that of *C. brevipennis* described and figured by Walker (1922). In the retracted condition the phallus projects but

little from the wall of the genital chamber. The upper surface of the dorsal lobe contains a wide, cuplike depression, the dorsal cavity (*dc*), from the lateral walls of which arise a pair of folds (*h*) with sclerotized margins (*i*) that end in free horny processes. The sclerotized parts are the "parameres" of Walker, the supporting folds the "bases of the parameres." The phallotreme (*Phtr*) is a large opening in the ventral part of the phallus between the thickened posterior margin of the dorsal lobe above (*g*), the lateral lobes at the sides (*ll*), and the ventral lobe below (*vl*). When the phallus is protracted the whole organ forms a grotesque vesicular body (fig. 26 B) projecting between the epiproct and the depressed ninth sternum (A). The cavity of the dorsal lobe is entirely everted (B, *dl*), and the folds of its floor are

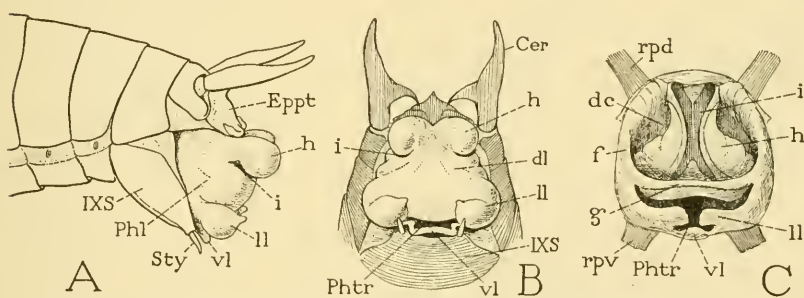


FIG. 26.—Tettigonioidae—Tettigoniidae: external male genitalia of *Conocephalus fasciatus* (Degeer) and *Neoconocephalus ensiger* (Harris).

A, *Conocephalus fasciatus*, end of abdomen with phallus everted, lateral view. B, same, posterior view. C, *Neoconocephalus ensiger*, phallus in retracted condition, posterior view.

For letter explanation, see fig. 22.

inflated to form two protruding dorsal vesicles (*h*), beneath which the sclerotic bars (*i*) curve to the sides. The lateral lobes likewise are distended as pair of vesicles (*ll*) at the sides of the phallotreme; but the ventral lobe (*vl*) is not changed from its usual form (fig. 23 H, *vl*).

The phallus of *Neoconocephalus ensiger* (fig. 26 C) resembles that of *Conocephalus fasciatus*. In the retracted condition the organ is scarcely more than a low, oval fold projecting from the genital chamber wall. The dorsal lobe is occupied by a deep, open cavity (*dc*), on the floor of which is a median X-shaped sclerotization (*i*) without projecting points, which is flanked by two large, soft folds (*h*). The phallotreme is a large transverse opening (*Phtr*). The lateral lobes (*ll*) and the ventral lobe (*vl*) are present as usual, but the ventral lobe is very small.

In *Orchelimum minor* the phallus is characterized by the great development of the ventral lobe (fig. 27 B, *vl*), which projects as a large flap from beneath the phallotreme. The shallow dorsal cavity (*dc*) contains two thick lateral folds (*h*), each of which is armed with a long, curved, sclerotic band (*i*) arising on the median side of the fold and curving laterally around its distal end. The sclerites are bifurcate at their terminations, but only the outer points project as

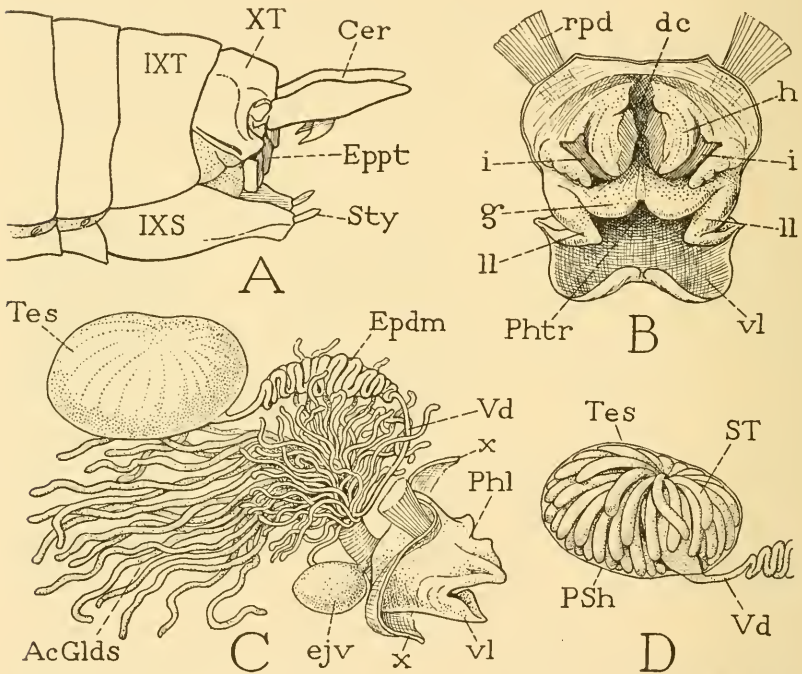


FIG. 27.—Tettigonioidae—Tettigoniidae: male genitalia of *Orchelimum minor* Brunner.

A, end of abdomen, lateral view. B, phallus, posterior view. C, internal genitalia and phallus, lateral view. D, testis and adjoining part of vas deferens. For letter explanation, see fig. 22.

free processes. The posterior margin of the floor of the dorsal cavity forms a wide, bilobed lip (*g*) above the phallotreme, at the sides of which project the triangular lateral lobes (*ll*).

The Decticinae present several important modifications of the phallic structure that are not found in the other tettigoniid families, but which prefigure some of the characteristic features of the phallus in Rhaphidophorinae and Gryllidae. The dorsal cavity of the phallus, for example, is converted into a deep pouch (fig. 22 F, *dc*), apparently



by a posterior extension of its anterior margin (D, *e*), which latter thus comes to form a free dorsal fold (F, *e*) at the distal end of the phallus, where its upper surface is reflected into the genital chamber wall above (*x*). Furthermore, the armature of the dorsal cavity takes the form of two processes projecting from the mouth of the cavity.

The decticine type of phallic structure is illustrated by Walker (1922) from *Nebdula carinata*. Walker also regards it as intermediate between the ordinary tettigoniid structure and the rhabdophorine structure, but he takes the latter to represent the more generalized form. Just the opposite view is adopted here, because there can be no question that the type of structure progressively developed through the Decticinae, Rhabdophorinae, and Gryllidae

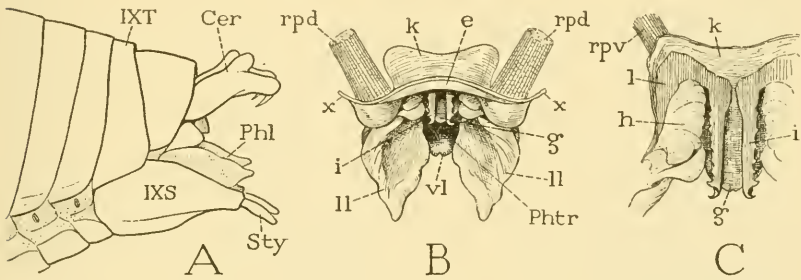


FIG. 28.—Tettigonioidae—Tettigoniidae—Decticinae: external male genitalia of *Anabrus simplex* Haldeman.

A, end of abdomen, lateral view. B, phallus, posterior view, showing also internal pouch (*k*) and muscles exposed before cut wall (*x-x*) of genital chamber. C, floor of dorsal phallic pouch and its armature.

For letter explanation, see fig. 22.

is successively more and more removed from the primitive structure of the phallus shown in all nymphal forms.

*Anabrus simplex* (fig. 28) gives a good example of the decticine type of phallic structure. When the phallus is viewed from behind (B) it appears to consist principally of two large, prominent lateral lobes (*ll*), between which are the mouths of two cavities, one dorsal, the other ventral, separated by a horizontal partition (*g*). The upper cavity, from which projects a pair of serrate, sclerotic arms (*i*), is roofed over by a membranous fold (*e*); the floor of the ventral cavity is formed by the ventral phallic lobe (*vl*). If the phallus is removed from the body, it will be seen that the dorsal cavity ("paramere sac" of Walker) forms a large internal pouch (B, *k*). On opening the membranous dorsal wall of the latter, it is at once evident that the floor of the pouch (C) is the floor of the usual dorsal cavity of the

phallus. From it there arise laterally two thick, membranous folds (C, *h*), and closely associated with the base of each fold is a large U-shaped sclerite (*l*), the inner arm of which is prolonged posteriorly as one of the free serrate processes (*i*) above noted. The distal margin of the floor of the dorsal pouch (*g*) forms the upper lip of the phallosome (B, *Phtr*). That the roof of the dorsal sac is formed by the posterior extension of the anterior margin of the usual dorsal cavity (fig. 22 D, *e*) is shown by the fact that the insertions of the dorsal retractor muscles (fig. 28 B, *rpd*) are carried posteriorly to points laterad of the mouth of the sac. The fold (*e*) forming the upper lip of the dorsal sac is, therefore, not the same as the fold over the base of the dorsal cavity in *Phaneroptera furcata* (fig. 25 D, E, F, *j*), for here the dorsal muscles (E, *rpd*) are attached on the base of the phallus and not on the fold. The rest of the phallus of *Anabrus* (fig. 28 B) has the usual tettigoniid structure. The ventral cavity ("spermatophore sac" of Walker) is the endophallic cavity, the large expanded lobes at its sides (*ll*) are the lateral lobes, and the small median lobe beneath it (*vl*) is the ventral lobe.

There would seem to be no question that the Decticinae are true tettigoniids, since, according to Gerhardt (1913), the spermatophore contains two sperm capsules, as in all other members of the Tettigoniidae.

The mating habits of the Tettigoniidae are well known (See Gerhardt, 1913). The male at first takes a position beneath the female and inserts into the genital chamber of the latter the neck of a large, bilobed spermatophore, the principal part of which hangs outside the vulva (fig. 29 A, *Sphr*), and generally is later eaten by the female. With some species the male assumes a reversed and inverted position before copulation is completed.

The tettigoniid spermatophore (not including that of Rhabdophorinae) is said by Gerhardt (1913) to contain always two sperm capsules, thus differing from the spermatophores of members of related families, which, so far as known, have but a single capsule. A typical tettigoniid spermatophore (fig. 29 C) consists of two oval, thick-walled sperm capsules (*a, a*) more or less enveloped in a bilobed mass of white albumenlike substance (*c*). The two capsules are united on a cylindrical stalk, or neck (*b*), which projects through the outer covering and is inserted into the female genital chamber (A) at the time of copulation. Each capsule contains a relatively small inner cavity (C, *d*) filled with spermatozoa, from which a slender duct enters the base of the spermatophore stalk. In the species here illustrated, *Amblycorypha rotundifolia*, the two primary ducts appear to

unite in a single duct (*e*) that traverses the stalk and ends in a free terminal point (*f*). According to Gerhardt, however, the tettigoniid spermatophore characteristically has two separate ducts.

The substances that form the outer and inner parts of the spermatophore are undoubtedly secreted in different sets of the accessory gland tubules of the male. The outer covering is said by Gerhardt to vary in different tettigoniid species from a semifluid, slimy consistency to the more usual, fairly solid texture resembling coagulated egg albumen. The walls of the sperm capsules are dense, laminated, and of

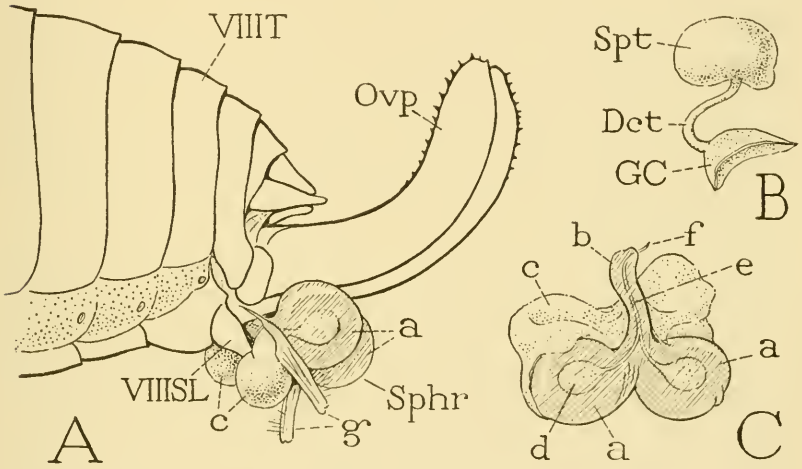


FIG. 29.—Tettigoniodea—Tettigoniidae: female genitalia and a spermatophore of *Amblycorypha rotundifolia* (Scudder).

A, end of abdomen with spermatophore attached. B, spermatheca, duct, and pocket of genital chamber. C, spermatophore.

*a*, sperm capsules of spermatophore; *b*, stalk of spermatophore; *c*, albuminous covering of spermatophore; *d*, sperm chamber of sperm capsule; *Dct*, duct of spermatheca; *e*, *f*, duct of spermatophore; *g*, flower bracts adhering to spermatophore; *GC*, pocket of genital chamber receiving spermathecal duct; *Ovp*, ovipositor; *Sphr*, spermatophore; *Spt*, spermatheca; *VIIIISL*, subgenital lobe of eighth abdominal sternum.

a brown color. According to Ito (1924) the secretions of the two sets of accessory gland tubules differ in their staining reactions, and the outer covering of the spermatophore shows the staining properties of the secretion of the larger tubules. Gerhardt says also that the secretion taken from the long tubules is clearly the substance of the outer spermatophore covering. The relative size and anterior position of the larger tubes of the accessory glands (fig. 20 A, *a*) would suggest that these tubes furnish the more abundant material and the last to be discharged. The capsular substance of the spermatophore, therefore, is to be referred to the smaller tubules, but where there are

several sets of the latter, as in *Phaneroptera furcata* (fig. 20 A, b, c, d), it must have either a differentiated structure or a mixed composition.

No studies have been made on the manner by which the tettigoniid spermatophore is formed, but inasmuch as only the necklike stalk is introduced into the genital chamber of the female, it is evident that the sperm capsules at least are produced in the genital tracts of the male. After the capsules are ejected from the endophallus, they are covered by a discharge of gelatinous or albuminous material from the large anterior tubules of the accessory glands.

In effecting copulation with the female, the male tettigoniid, as described by Gerhardt (1913), clasps the female at the base of the ovipositor with his cerci. The phallus is then everted and introduced into the genital chamber of the female. The sperm-containing capsules are now ejected, and, as the male organ is withdrawn, the outer covering of the spermatophore is discharged upon them. While the function of the various parts of the phallic apparatus are not described, it is evident that the exposed structures have no role in the formation of the spermatophore.

*Rhaphidophorinae*.—In the camel crickets the dorsal cavity of the phallus is entirely closed over by a posterior extension of its anterior margin as in Decticinae (fig. 22 F, *dc*), but the free margin of the covering fold (*e*) is strongly and variously sclerotized, forming a conspicuous plate (fig. 30 B, *e*) arched over the genital opening. The form of this plate ("epiphallus" or "pseudosternite") is characteristic of different species; Hubbell (1936) says its modifications in structure are of utmost taxonomic value in the study of the genus *Ceuthophilus*, and he gives seven plates illustrating its variations of form in this genus. Most unfortunate it is, therefore, that the sclerite has no appropriate name. The term "pseudosternite", commonly now given to it, suggests a sternal derivation, which the sclerite in question certainly does not have, and the alternative "epiphallus" would relate it to the sclerite so called in Acrididae (fig. 41 A, *Epph*). The latter is situated dorsally on the base of the phallus, where it is developed in the nymph (fig. 42 D, H, *Epph*). Since the sclerite in Rhaphidophorinae is evidently derived from the basal fold of the dorsal cavity of the phallus (fig. 22 D, F, *e*), it has a certain analogy at least with the epiphallus of Acrididae, and, for want of a better term, is here called the *epiphallus*. The same sclerite is highly developed in Gryllidae.

The dorsal sac of the phallus of Rhaphidophorinae lacks the sclerotic armature present in Decticinae, but in place of it there is usually a pair of soft, eversible, fingerlike papillae (figs. 22 F, 30 F, *h*). The

usual lateral phallic lobes appear to be absent; the ventral lobe, however, is well developed (figs. 22 F, 30 B, *vl*), and beneath it is a subsidiary ventral fold (*vf*).

In *Ceuthophilus gracilipes* (fig. 30 A) the genital region of the abdomen is concealed above the large hemispherical sternal plate of the ninth segment (*IXS*). When the subgenital sternum is depressed or removed the phallus may be seen projecting from the anterior wall of the genital chamber as a large body (B) with a deep central cavity, the mouth of which is partly occluded by a thick, tongue-like, ventral lobe (*vl*). Arched above the opening is the epiphallus. This structure, as seen from behind (B), presents an elevated, bilobed median part (*e*), with a reflected marginal flange (*o*), which is produced downward at the sides of the phallic opening as two tapering arms. On the dorsal surface of the phallus (C) the epiphallus includes a large median plate (*m*) with divergent basal extensions, and a pair of smaller lateral plates (*n*). There are no lateral phallic lobes, such as those always present in Tettigoniidae, but the ventral lobe (B, D, *vl*) is well developed and projects upward over the mouth of the phallic cavity. Beneath the ventral lobe is an accessory ventral fold (*vf*) of the under wall of the phallus. The phallic mouth leads into an ample, sac-like, dorsal cavity (D, *dc*), and a smaller, ventral endophallic cavity (*Enph*), the two separated by the distal margin (*g*) of the floor of the dorsal cavity. From the floor of the dorsal cavity there arises on each side a large, thick, soft fold (*h*), which is probably distended when the phallus is protruded. The inner structure of the phallus of *Ceuthophilus* is thus seen to be the same as that shown diagrammatically at F of figure 22, and is clearly a derivation from the usual tettigoniid type given at D. That the dorsal fold (*e*), containing the epiphallus, is a production of the anterior margin of the dorsal cavity (fig. 22 D, *c*) is evident from the fact that in *Ceuthophilus* the dorsal retractors of the phallus (fig. 30 C, D, *rpd*) are inserted on the epiphallus.

The genitalia of *Ceuthophilus uhleri* (fig. 30 F) are only partially concealed by the ninth abdominal sternum, which here is a large, soft, bilobed structure (*IXS*) little resembling an ordinary sternum. Between the sternal lobes are seen the ventral phallic lobe (*vl*), and below this the edge of the accessory ventral fold (*vf*). Arched over the mouth of the phallus is the epiphallus (*e*), beneath which projects a pair of soft, cylindrical papillae (*h*) that arise on the floor of the dorsal cavity.

Walker (1922) describes the genitalia of *Ceuthophilus lapidicola*, *C. aridus*, and *C. maculatus*, and Gurney (1936) those of *C. brevipes*.

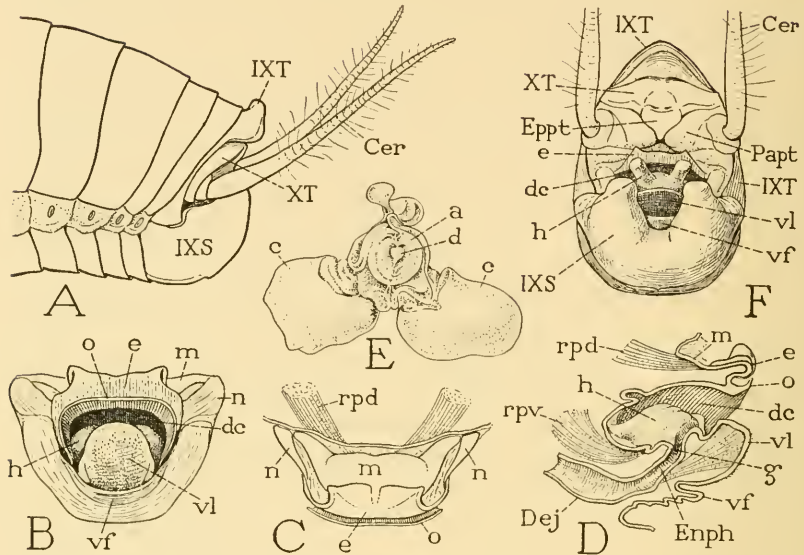


FIG. 30.—Tettigonoidea—Rhaphidophorinae: male genitalia and a spermatophore.

A, *Ceuthophilus gracilipes* (Haldiman), end of abdomen, lateral view. B, same, phallus, posterior view. C, same, phallus, dorsal view. D, same, phallus, median longitudinal section. E, *Diestrammena marmorata* de Hahn, spermatophore (from Gerhardt, 1913). F, *Ceuthophilus uhleri* Scudder, end of abdomen, posterior view.

The following letter explanations apply to figs. 30 to 37 inclusive. *a*, sperm capsule of spermatophore; *aa*, sclerite in base of grooved lobe *v*; *AcGlds*, accessory glands; *Amp*, mesodermal ampulla of ejaculatory duct; *bb*, apodemes of plate *aa* in base of grooved lobe *v*; *c*, albuminous lobes of spermatophore; *Cer*, cercus; *Con*, nerve connective; *d*, sperm chamber of spermatophore; *dc*, dorsal cavity of phallus; *dct*, duct of spermatophore; *Dej*, ductus ejaculatorius; *dl*, dorsal lobe of phallus; *e*, anterior margin of dorsal phallic cavity produced posteriorly and sclerotized as the epiphallus; *eju*, vesicle of ejaculatory duct; *Enph*, endophallus; *Epdm*, epididymis; *Eppt*, epiproct; *g*, posterior margin of floor of dorsal phallic cavity; *Gpr*, gonopore; *Gng*, ganglion; *h*, eversible lobe on floor of dorsal cavity of phallus; *k*, dorsal pouch of phallus; *ll*, lateral lobe of phallus; *m*, proximal plate of epiphallus; *n*, lateral sclerite of epiphallus; *o*, marginal flange of epiphallus; *p*, lateral arm from epiphallus in base of phallus; *Papt*, paraproct; *Phl*, phallus; *q*, median process of epiphallus; *r*, *s*, lateral processes of epiphallus; *rpv*, dorsal and ventral retractors of phallus; *sl*, terminal lobe of ninth sternum; *Sphr*, spermatophore; *t*, sclerite in dorsal wall of dorsal phallic pouch; *Tes*, testis; *u*, median grooved fold in wall of dorsal phallic pouch; *v*, grooved rod or lobe serving to guide spermatophore duct; *Vd*, vas deferens; *vf*, ventral fold of phallus; *vl*, ventral lobe of phallus; *w*, phallic mold of attachment plate of spermatophore; *x-x*, cut edge of anterior wall of genital chamber; *XNv*, *XINv*, nerves of tenth and eleventh abdominal segments; *xt*, arm of tenth tergum; *y*, attachment plate of spermatophore; *z*, pouch of ventral wall of genital chamber.

These species apparently do not differ essentially in their genital structure from the species described above, but on the dorsal surface of the phallus of *C. lapidicola* Walker notes the presence of two small openings leading into a pair of partly glandular tubules. In Gryllotalpidae a single long tube opens in a similar position (fig. 38 B, D, *PhGld*).

In a half-grown nymph of *Ceuthophilus* the phallus is a simple flattened structure, resembling that of a nymphal tettigoniid; it consists of a broad smooth dorsal lobe, and a smaller bilobed ventral lamella, with a flat cavity between them.

Judging from the structure of the male genital organ, the Rhabdophorinae would appear to be related on the one hand to the Decticinae, and on the other to the Gryllidae. The enclosure of the dorsal sac and the development of an epiphallus on the margin of the covering fold are features highly evolved in the true crickets, though with more important accompanying modifications that set the gryllids entirely apart from the camel crickets. Again, the spermatophore of the rhabdophorine *Dicstramuena* (fig. 30 E), as shown by Gerhardt (1913), is of the gryllid and not of the tettigoniid type, in so far as it contains only one sperm capsule (and the same should be true of other genera since all have the same general structure of the phallus), but the spermatophore otherwise has no resemblance to a typical gryllid spermatophore (figs. 32 F, 35 E), and is covered during copulation with a bilobed mass of albuminous substance as in the tettigoniids, including Decticinae. If we might assume, as Walker (1922) does, that the rhabdophorine type of phallus is generalized, we could then suppose that the gryllid type has been produced from it by elaboration, and the tettigoniid type by simplification. As already pointed out, however, the nymphal development of the phallus leads directly into the simpler phallic structures found in the Tettigoniidae.

*Stenopelmatus fuscus*.—*Stenopelmatus* is inserted here not because its genital structures show any close similarity to those of the Rhabdophorinae, but because they do not include the characteristic genital features of the Gryllidae. The true crickets have a well-developed epiphallus, and the dorsal wall of the dorsal phallic sac bears a distal lobe or long process with associated supporting sclerotizations, which serves to guide the slender duct of the spermatophore into the receptacle of the female. However, *Stenopelmatus* has such general grylloid characters as the close union of the epiproct with the tenth tergum (fig. 31 A), the presence of a dorsal phallic pouch, though the latter is relatively very small (D, *dc*), and the absence of eversible processes or other armature on the floor of the dorsal sac.

On the other hand, a typical epiphallic sclerotization is not present in *Stenopelmatus*, but a pair of long transverse sclerites (B, *p*) are seated on the upper lip of the dorsal phallic sac, and curve laterally and ventrally in the outer walls of the phallus. These sclerites are present in the Gryllidae as lateral arms of the epiphallus (fig. 32 B, *p*).

The nymphal phallus of *Stenopelmatus* (fig. 31 F, G, H) much resembles that of *Cyphoderris* (fig. 21, G, H, I). It is a flattened structure with an undivided basal part, presenting distally a broad dorsal lobe (fig. 31 F, G, *dl*), a pair of tapering lateral lobes (*ll*), and a wide,

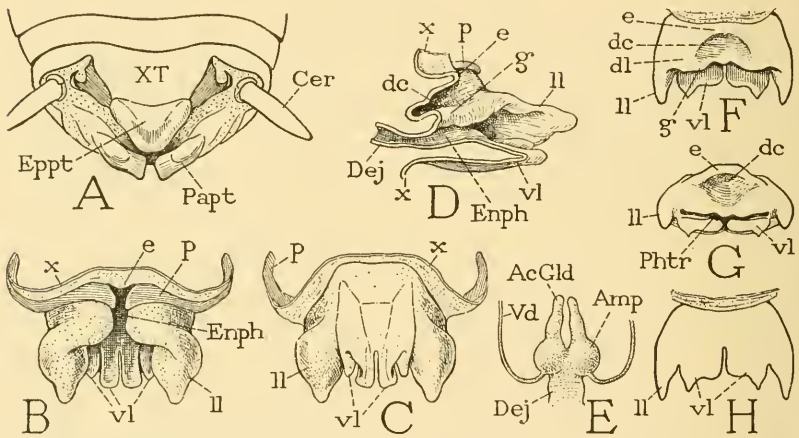


FIG. 31.—Tettigonioidae—*Stenopelmatus*: external male genitalia of *Stenopelmatus fuscus* Haldeman.

A, end of abdomen, dorsal view. B, mature phallus, dorsal view. C, same, ventral view. D, same, median section. E, ejaculatory duct and ampullae of nymph. F, G, H, immature phallus, dorsal, posterior, and ventral views.

For letter explanation, see fig. 30.

medially subdivided ventral lobe (H, *vl*). The dorsal lobe shows on its upper surface a slight but distinct median depression (F, G, *dc*), which is the beginning of the dorsal cavity. In the mature phallus the dorsal cavity becomes a small pocket (D, *dc*) between the extended anterior margin of the dorsal lobe (D, *e*, cf. F, *e*) and the retracted posterior margin (*g*). The lateral lobes of the mature organ are large, soft, folded structures (B, C, D, *ll*), suggestive that they serve to hold the body of a spermatophore. The ventral lobe (C, *vl*) is flat and subdivided into four parts. The small endophallic cavity (D, *Enph*) is directly continuous with the ejaculatory duct (*Dej*). In a late nymphal stage the short ejaculatory duct is surmounted by two small



globular ampullae (E, *Amp*), each of which is produced into a single diverticulum (*AcGld*), evidently a rudiment of the definitive accessory gland tubules.

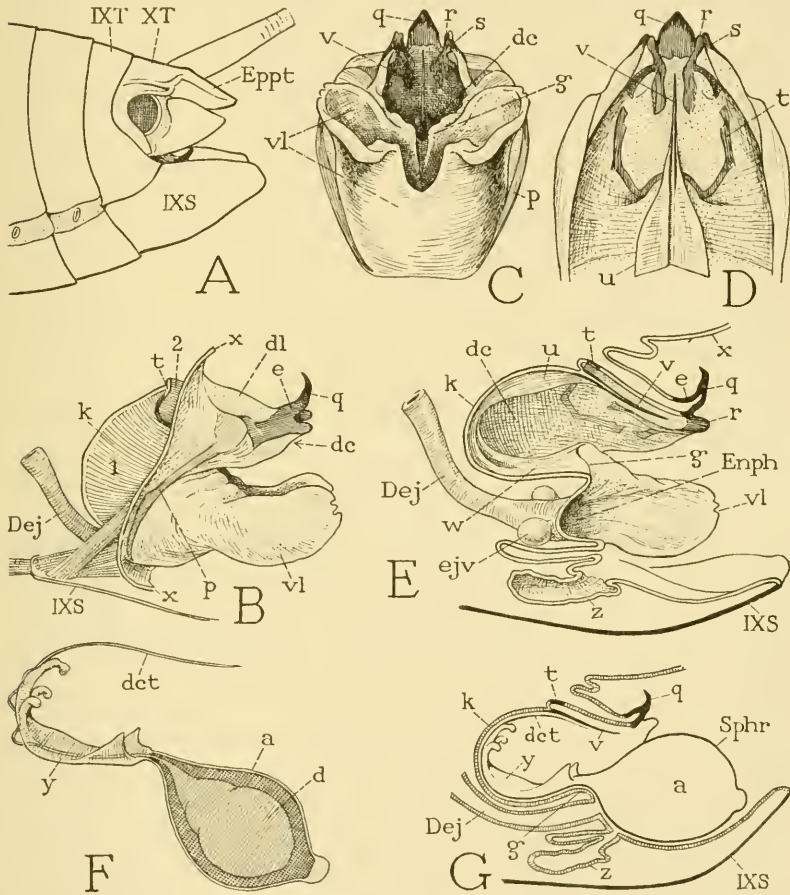


FIG. 32.—Tettigonioida—Gryllidae: external male genitalia of *Gryllus assimilis* Fabricius.

A, end of abdomen, lateral view. B, phallus, lateral view, showing ectophallus to right of anterior wall of genital chamber (*x-x*), and internal parts to left. C, phallus, ventral view. D, distal part of dorsal wall of dorsal cavity of phallus (C, *dc*), ventral view. E, semidiagrammatic median section of phallus and ninth abdominal sternum. F, spermatophore. G, spermatophore in phallus.

For letter explanation, see fig. 30.

*Gryllidae*.—Characteristic of this family, in the terminal structure of the abdomen, is the union of the epiproct with the tenth tergum (figs. 32 A, 35 A, 36 A). The phallus attains a highly specialized form, which is an extreme modification of the tettigoniid type of

phallic structure, and is entirely an adaptation of the latter to the formation of the gryllid type of spermatophore and the insertion of the tip of the spermatophore duct into the spermathecal aperture of the female. The gryllid spermatophore (fig. 32 F) contains a single, large sperm capsule (*d*), and has a long, slender duct (*dct*), at the base of which is usually an irregular plate (*y*) for attachment in the genital chamber of the female. A more generalized condition of the phallic structure is found in *Gryllus* and *Gryllodes*, the opposite extreme occurs in *Nemobius*. The nymphal development of the genital organs shows that the phallus of the crickets is formed from the usual dorsal and ventral phallic lobes only, lateral lobes being absent, and that the principal modifications pertain to the dorsal lobe, on which an epiphallic sclerotization is highly developed. The dorsal cavity (fig. 32 E, *dc*) is entirely concealed beneath the posteriorly extended epiphallic region (*e*), and the ventral endophallic cavity (*Enph*) is enclosed by the ventral lobe (*vl*), which, in *Gryllus* and *Gryllodes*, is subdivided into two large lateral valves. The spermatophore and its duct are molded in the two cavities of the phallus (G).

The phallus of *Gryllus assimilis* (fig. 32 B) presents externally a large dorsal lobe (*dl*) capped by the epiphallus (*e*), and a soft ventral lobe (B, C, *vl*) divided into two valvelike lateral flaps, the form and size of which may be quite different in different specimens according to the state of expansion or the presence or absence of a spermatophore. The sclerotic epiphallus is produced into a broad, recurved median lobe (B, C, *q*), and two lateral lobes each subdivided into two points (*r*, *s*). From the dorsal epiphallic plate (B, *e*) a long arm (*p*) extends downward on each side in the base of the phallus. Beneath the epiphallus is the entrance to the dorsal cavity (B, C, *dc*), which latter extends forward as a large, thin-walled pouch (B, E, *k*). The ventral lip of the pouch (E, *g*) lies far anterior to the epiphallic extension of the dorsal lobe, but its position in *Gryllus* is relatively the same as in *Ceuthophilus* (fig. 30 D, *g*). *Gryllus* thus differs from *Ceuthophilus* in the greater development of the epiphallus, and in the enlargement of the pouchlike dorsal phallic cavity; but it should be noted also that in *Gryllus* (as in all members of the Gryllidae) there are no eversible lobes or other armature arising from the floor of the dorsal cavity corresponding with the structures here located in Tettigoniidae and Rhabdophorinae (fig. 22 D, F, *h*, *i*). The endophallic cavity of *Gryllus* (fig. 32 E, *Enph*) is enclosed by the proximal part of the ventral lobe of the phallus (*vl*), and is directly continuous with the wide terminus of the ejaculatory duct (*Dej*). The floor of the genital chamber beneath the phallus is inflected to form a large median pouch (*z*).

The musculature of the phallus comprises intrinsic muscles of the dorsal pouch (figs. 32 B, 34 D, 1, 2) and the ventral lobe, and several pairs of extrinsic muscles. The latter (fig. 34 D) include two pairs of muscles arising from the anterior angles of the ninth abdominal sternum, one pair (3) inserted on the lower ends of the lateral sclerites in the base of the phallus, the other (4) on the base of the lateral walls of the dorsal lobe. Dorsal phallic muscles from the tenth tergum, such as are present in the tettigoniids, appear to be absent in *Gryllus*. The phallus is innervated from a nerve trunk (D, *XNv*) that branches from the base of the large cercal nerve (*XINv*), and appears to belong to the tenth abdominal segment, since it certainly does not pertain to either the ninth or the eleventh segment.

The dorsal phallic pouch of *Gryllus assimilis* has a thin, membranous inner wall, but it is covered externally by a muscular sheath of transverse fibers (figs. 32 B, 34 D, 1). Though, as above noted, it has no armature arising from its floor as in Tettigoniidae and Rhabdophorinae, it has other structures adapting it to its function of forming and holding the spermatophore and inserting the spermatophore duct. On the floor of the pouch is a thickened median plate (fig. 32 E, *w*), having its proximal angles at the ventral lip of the pouch (*g*) produced as a pair of triangular lateral expansions, and its distal part furrowed by a median depression and two lateral grooves. The distal end of the plate is continued in a troughlike fold (*u*) with a median groove that extends upward and then posteriorly in the anterior and dorsal walls of the pouch, and ends with a long, free, tapering, virgalike rod (E, D, *v*) that projects from the wall of the pouch beneath the epiphallus. The axial groove of the fold is continuous from the distal depression of the ventral plate to the tip of the terminal rod (D, *v*). The base of the rod is supported by a **W**-shaped sclerite in the dorsal wall of the pouch (figs. 32 B, D, 34 D, *t*), on the median part of which is inserted a pair of broad muscles (fig. 34 D, 2) converging from the lateral parts of the epiphallus. The inner structures of the dorsal sac are clearly the molds of the attachment plate and the duct of the spermatophore, since the shape and contour of the attachment plate (fig. 32 G, *y*) fit exactly the form and depressions of the ventral plate of the pouch, and the long, recurved, tapering duct of the spermatophore (*dct*) follows the groove of the fold (D, *u*) and the terminal rod (*v*).

Walker (1922) in his description of the phallic structure of *Gryllus* calls the dorsal cavity the "spermatophore sac", though he observes that it would appear at first sight that the dorsal sac of *Gryllus* is the paramere sac (i. e., dorsal sac) of Tettigoniidae. This view, which

Walker discards, seems to the writer the only logical interpretation of the gryllid structure, since the latter is so clearly but an adaptation of the structure of the phallus in *Ceuthophilus* (fig. 30 D), which in turn is derived from the more primitive tettigoniid structure (cf. figs. 22 D and F with fig. 32 E).

The endophallic cavity, together with the space between the lateral flaps of the ventral phallic lobe and the floor of the genital chamber, forms the mold of the large, oval ampulla of the spermatophore (fig. 32 G, *a*). When the fully formed spermatophore is still in place within the phallus, the ampulla is almost entirely enclosed by the flaps of the ventral lobe, and the mouth of the ejaculatory duct (*Dej*) is pressed close against the anterior part of its ventral surface; the narrow neck connecting the ampulla with the attachment plate (*y*) curves over the lower lip (*g*) of the dorsal sac and expands upon the ventral plate of the latter.

The development of the phallus of *Gryllus* can be followed in the nymph, but the phallic development of each instar begins in the preceding instar long before there is any evidence of ecdysis on other parts of the body. On removal of the cuticula from the genital region of any instar there is hence usually found beneath it the phallus of the next instar, which already has taken on quite a different form. In a half-grown male nymph (fig. 33 A) the phallic rudiments are slightly embossed on an oval area of the genital chamber wall (B); they include a pair of oval dorsal swellings (*dl*), a pair of similar ventral swellings (*vl*), and a somewhat depressed central disk (*dc*) with a faint median groove. At the lower end of the last is the gonopore rudiment (*Gpr*). By removing the cuticula there will probably be exposed the phallus of the next instar developing beneath it (C). At this stage the dorsal elevations are united in a large dorsal lobe (*dl*) with a prominent median projection (*q*), which will become the median lobe of the epiphallus of the adult (fig. 32 C, *q*). The ventral swellings of the preceding instar (fig. 33 B, *vl*) are likewise united to form an emarginate ventral lobe (C, *vl*). The central area is still more depressed, but shows no distinction between a dorsal cavity and a ventral cavity. At a later stage (D, E) the dorsal lobe is clearly taking on the form of the epiphallus of the adult, and a thick, tapering grooved process (*v*) projects from the dorsal wall of the median depression below it. Again, by removal of the cuticula, there is exposed the phallus of the succeeding instar (F), which is perhaps the beginning of the imago, for the organ now has distinctly adult characters. The epiphallus has become differentiated into three apical lobes, and the ventral process (*v*) has taken the form of a slender rod

arising from a flaring base. Proximal to the latter is the mouth of a deep dorsal cavity (*dc*), the ventral lip of which (*g*) appears as a septum between the upper cavity and a lower endophallic cavity above the ventral lobe (*vl*). The ventral lobe itself is much enlarged, deeply cleft, and has several marginal lobules. Whether a stage intervenes between this one (F) and the fully mature adult (fig. 32 C) was not determined, but the specimen appeared to be a pre-imaginal nymph.

The internal reproductive organs of the male cricket (fig. 34 A) are characterized by the large size of the testes, the relatively uniform

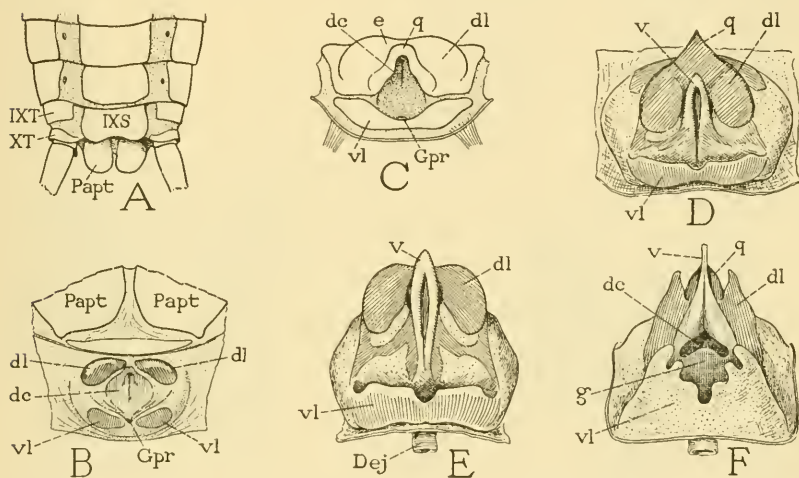


FIG. 33.—Tettigonioidae—Gryllidae: nymphal development of the phallus of *Gryllus assimilis* Fabricius.

A, half-grown nymph in premoult condition, end of abdomen, ventral view. B, same, phallic rudiments in genital chamber wall beneath bases of paraprocts, posterior view. C, phallus of succeeding instar exposed by removal of cuticula from B, posterior view. D, phallus of later nymphal instar, posterior view. E, same, ventral view. F, phallus of succeeding instar (perhaps immature adult) exposed by removal of cuticula from E, ventral view.

For letter explanation, see fig. 30.

size of the accessory gland tubules, and the absence of sperm vesicles. The mature testes (*Tes*) lie against the lateral and dorsal walls of the second, third, and fourth abdominal segments, where they overlap the rear end of the crop, and almost meet along the midline of the back. Each testis consists of a large number of slender sperm tubules (B), approximately 280, according to Spann (1934), which overlie one another in concentric layers diverging posteriorly from the anterior end of the testis, and are enveloped in a delicate peritoneal sheath. The tubules discharge through narrow efferent ducts into the enlarged intra-testicular part of the vas deferens. Beyond the testis

the vas deferens takes a straight course to the ninth abdominal segment, where it loops beneath the large cercal nerve (A, *XINv*), and then turns forward to enter the mass of accessory gland tubules. Here it becomes much thickened and forms a compactly coiled epididymis (C, *Epdm*), beyond which it again tapers to a narrow tube and opens ventrally into the ejaculatory duct near the bilobed anterior end of the latter.

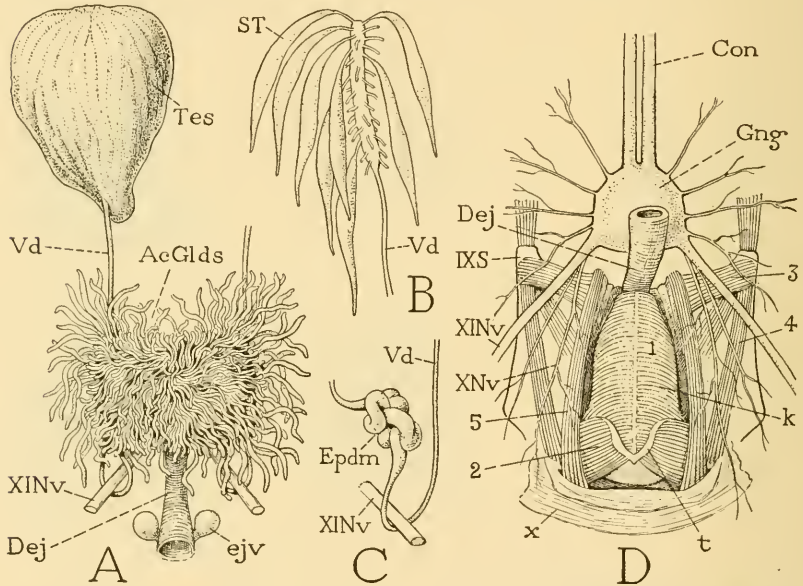


FIG. 34.—Tettigonioidea—Gryllidae: internal male genitalia of *Gryllus assimilis* Fabricius.

A, general view of internal reproductive organs, dorsal view. B, anterior intratesticular part of vas deferens and group of sperm tubes. C, posterior loop of vas deferens beneath nerve to cercus, right side, dorsal view. D, dorsal pouch of phallus (*k*) invaginated into body cavity, the phallic muscles, and associated last ganglion of ventral nerve cord, dorsal view.

For letter explanation, see fig. 30; for muscles, see text, page 81.

The accessory glands consist of a mass of slender tubules arising from the bilobed anterior end of the ejaculatory duct (fig. 34 A, *AcGlds*). The dorsal tubules are somewhat smaller than the lateral and more ventral tubules. The smaller tubules, according to Spann (1934), have a glassy appearance because of their clear granular secretion, which takes a nuclear stain, while the larger tubules have a milky-white secretion, which coagulates readily on exposure to air, and takes a cytoplasmic stain. The parts played by the products of the two sets of glands in the formation of the spermatophore will be

noted presently. The ejaculatory duct (*A, Dej*) is a wide muscular tube that turns downward between the last ganglion of the ventral nerve cord and the dorsal sac of the phallus (*D, Dej*); it then goes posteriorly and enlarges at its opening into the endophallic cavity (fig. 32 E). A pair of oval lateral vesicles (*ejv*) opens into the extreme end of the duct.

The spermatophore of *Gryllus assimilis* (fig. 32 F) consists of a thick-walled, ovate or pear-shaped ampulla (*a*), of an elongate attachment plate (*y*) connected with the apex of the ampulla by a narrow neck, and of a slender recurved duct (*dct*) that traverses the plate and extends far beyond it. The wall of the ampulla, as observed by Spann (1934), contains three distinct layers. The innermost layer forms a distinct but thin-walled capsule (*d*) containing the spermatozoa; the middle layer is thick, hard, and usually dark yellow or brown in color; the outer layer is a thin, transparent external covering, which at the posterior end of the ampulla forms a small vesicular papilla. The middle layer, according to Spann, takes cytoplasmic stains and thus shows that its material must be derived from the larger milky tubules of the accessory glands; the outer and inner layers, on the other hand, take nuclear stains, and hence must be formed from the secretion of the smaller clear tubules. The attachment plate of the ampulla is pale or translucent, and its substance, Spann says, shows the same staining reactions as the outer and inner coats of the ampulla; the hard, dark middle layer of the ampulla does not extend into the pliable attachment plate. The extremity of the duct, when the spermatophore is taken from the male, Spann claims, is normally closed, but if the tip is broken off the spermatozoa flow out from it; the inner capsule of the ampulla is then seen to collapse within the more rigid outer walls as air diffuses through the latter to occupy the space around the shrinking capsule. The liberation of the sperm during copulation, Spann suggests, is probably accomplished by a dissolving of the end of the duct in the spermathecal passage. The spermatophore is then emptied of spermatozoa in from 45 minutes to an hour. According to Baumgartner (1911), however, the sperm automatically flows out of the tip of the duct when the spermatophore is placed in normal salt solution, and the capsule may be emptied in 15 minutes, but whether the tip was presumably perfect or not Baumgartner does not say.

The mating habits of *Gryllus* and *Liogryllus*, the structure of the male genital organs and the spermatophore, have been described by Lespés (1855, 1855 a), Baumgartner (1911), Gerhardt (1913), and Regan (1924). At the time of mating, the male takes a position below the female. Copulation is said to be effected by the thrusting

of the epiphallic armature into the genital chamber of the female; probably the median recurved hook (fig. 32 B, *q*) holds in the fold of soft tissue on the floor of the genital chamber posterior to the gonopore, while the tip of the rod (G, *v*) carrying the spermatophore duct is inserted into the spermathecal opening, situated on the end of a thick process projecting downward and backward from a pouch in the dorsal wall of the genital chamber (see Snodgrass, 1933, figs. 18, 19). A contraction of the muscular sheath of the dorsal sac of the phallus

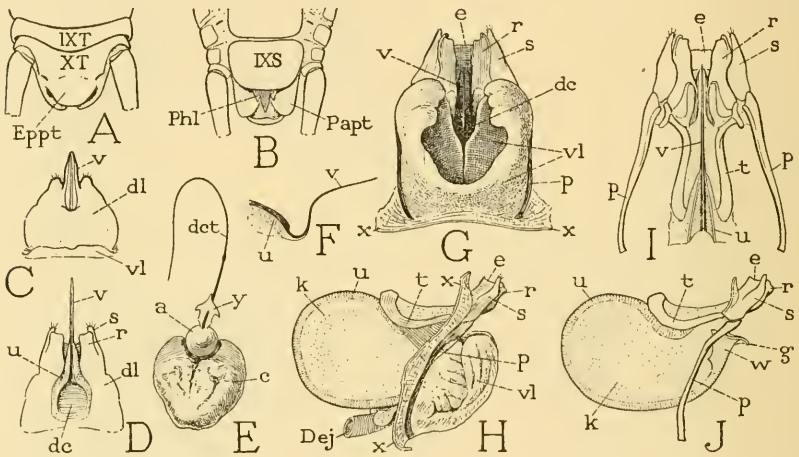


FIG. 35.—Tettigonoidea—Gryllidae: external male genitalia and spermatophore of *Gryllodes sigillatus* (Walker).

A, adult, end of abdomen, dorsal view. B, late nymphal instar (full-grown), end of abdomen, ventral view. C, same, phallus, removed from genital chamber, ventral view. D, phallus of succeeding instar (probably immature adult) taken from within cuticula of C. E, spermatophore, dorsal view. F, end of guide rod (G, I, *v*) for spermatophore duct. G, mature phallus, ventral view. H, same, lateral view, showing ectophallic parts to right of genital chamber wall (*x-x*), and internal parts to left. I, distal part of dorsal wall of dorsal pouch of phallus, together with epiphallic lobes (*e, r, s*) and basal ectophallic sclerites (*p*), ventral view. J, epiphallus and dorsal pouch of phallus, lateral view.

For letter explanation, see fig. 30.

would now protract the spermatophore duct from the guiding rod, and also force out the attachment plate (fig. 32 G, *y*), which latter, being inserted into the genital chamber of the female, holds the duct in place, and supports the ampulla, which hangs from the neck of the plate mostly outside the genital chamber. After copulation the female carries the spermatophore a varying length of time, but eventually removes it with her jaws or by rubbing against the ground.

*Gryllodes sigillatus* (fig. 35) presents the same type of structure in the genital parts as does *Gryllus*, though there are distinctive minor



differences between the two forms. The epiphallus of *Gryllodes* (G, H, I, *e*) lacks the median recurved process of *Gryllus*, but the two lateral epiphallic lobes (*r*, *s*) are well developed. In the nymphal phallus (B, *Phl*) the large dorsal lobe (C, *dl*) ends in three terminal processes, but the median one (*v*) represents the ventral rod of the adult (I, *v*) that guides the spermatophore duct. An intermediate stage is shown at D, which was taken from within the cuticle of C, and probably represents the beginning of the imaginal instar. The median process is here a slender rod (*v*) at the base of which is forming the dorsal cavity (*dc*) on the under surface of the dorsal lobe. The ventral lobe of the phallus is a small, inconspicuous fold in the nymph (C, *vl*) beneath the base of the dorsal lobe, but in the adult it becomes much enlarged, deeply emarginate, and is ordinarily irregularly folded against the posterior surface of the phallus (H, *vl*). When a spermatophore is present in the phallus, however, it is almost completely embraced by the expanded lateral halves of the ventral lobe (G, *vl*), which enclose a large oval cavity in which is held the body of the spermatophore (E).

The spermatophore of *Gryllodes sigillatus* is similar in shape to that of *Gryllus*, but structurally quite different in some respects. The sperm capsule is a small spherical ampulla (E, *a*) attached by a sunken neck to the upper surface of a large oval supporting body (*c*). A long, slender, recurved duct (*dct*) extends anteriorly from the capsule, and at its base is a small attachment plate (*y*). The single example of the spermatophore was obtained from a male specimen in alcohol. Before removal, the oval body of the spermatophore was held in the pocket of the ventral lobe of the phallus (G, *vl*), the sperm capsule projected dorsally before the mouth of the dorsal phallic cavity (*dc*), and the curved duct followed the median groove of the latter into the ventral channel of the guide rod (*v*). The dorsal sac of the phallus is oval and compressed (H, J, *k*); its lateral walls are formed of a thin, transparent membrane, but are covered by a muscular sheath (not shown in the figures) as in *Gryllus*. At the mouth of the sac, just within the ventral lip (J, *g*) is the mold (*w*) of the relatively small attachment plate of the spermatophore (E, *y*), and from the mold is continued the grooved channel (H, I, J, *u*) to the guide rod (I, *v*). The rod, as seen in lateral view (F), is abruptly curved upward at its base, and then goes posteriorly. The base of the rod is supported by a large, U-shaped sclerite (H, I, J, *t*) in the dorsal wall of the dorsal sac, on which are inserted protractor muscles from the sides of the epiphallus (H).

The genitalia of *Oecanthus* have been described by Walker (1922), who shows that they differ from those of *Gryllus* only in a few unimportant details. The spermatophore of *Oecanthus pellucens* is described and figured by Boldyrev (1913a), Gerhardt (1914), and Hohorst (1937). It resembles the spermatophore of *Gryllus* except in the small size of the "attachment plate" and in the greater thickness of the duct, but Gerhardt and Hohorst show that the plate in the case of *Oecanthus* does not enter the genital chamber of the female, and that the spermatophore is held in place entirely by the duct, which, according to Hohorst, is armed near its tip with a small brush of short bristles. While the spermatophore lies within the phallus the duct is recurved above the ampulla as in *Gryllus*, but after its ejection and insertion in the female the duct is straightened out, as shown in figures by Gerhardt and Hohorst.

A quite different type of phallic structure occurs in *Nemobius*, but it is one clearly derived from that of *Gryllus* and *Grylloides*. In *Nemobius fasciatus* (fig. 36) the epiphallic margin of the dorsal phallic lobe (F, *e*) has been carried so far back, and the ventral lobe (*vl*) set so far forward, that the dorsal cavity (*dc*) is flattened out until it appears as a shallow depression on the ventral side of the dorsal lobe (C, F, *dc*), and the endophallic cavity (*Enph*) comes to lie in front of it above the ventral lobe (*vl*). The two cavities are separated by a U-shaped fold (*g*), which represents the originally posterior lip of the dorsal cavity. The dorsal cavity of the phallus has thus undergone a complete inversion in *Nemobius*, since it now occupies the ventral surface of the dorsal lobe, where it is entirely exposed on removal of the ninth sternum from beneath it (C, *dc*).

When the phallus of *Nemobius* is viewed from above (fig. 36 B), the epiphallic surface of the dorsal lobe is seen to have the form of a long truncate cone with a large V-shaped sclerite (*m*) in its basal half, and a weakly sclerotized, deeply emarginate distal area (*e*). At the sides are two elongate sclerites (*p*) ending distally in two pairs of strong lateral processes (*r*, *s*), and a pair of ventrally convergent mesal processes. The ventral surface of the dorsal lobe (C), as seen by removal of the ninth sternum, presents a long, shallow median depression (*dc*), which is the inverted dorsal cavity, limited anteriorly by the U-shaped fold (*g*) above noted, which corresponds with the ventral lip of the dorsal cavity in *Ceuthophilus*, *Gryllus*, and *Grylloides* (figs. 30 D, 32 E, 35 J, *g*). An elongate plate on the floor of the cavity tapers distally into a groove between the halves of a soft, globular, median lobe (*v*). Since the duct of the spermatophore passes through this groove, the cleft lobe evidently represents the virgalike

rod of *Gryllus* and *Gryllodes* that guides the end of the spermatophore duct. The lobe is set somewhat back from the extremity of the epiphallus (F, *v*), and in its base dorsally is a transverse sclerite (E, F, *aa*), from which a pair of apodemal arms (E, *bb*) projects into the body cavity above the wall of the dorsal phallic cavity. The inner

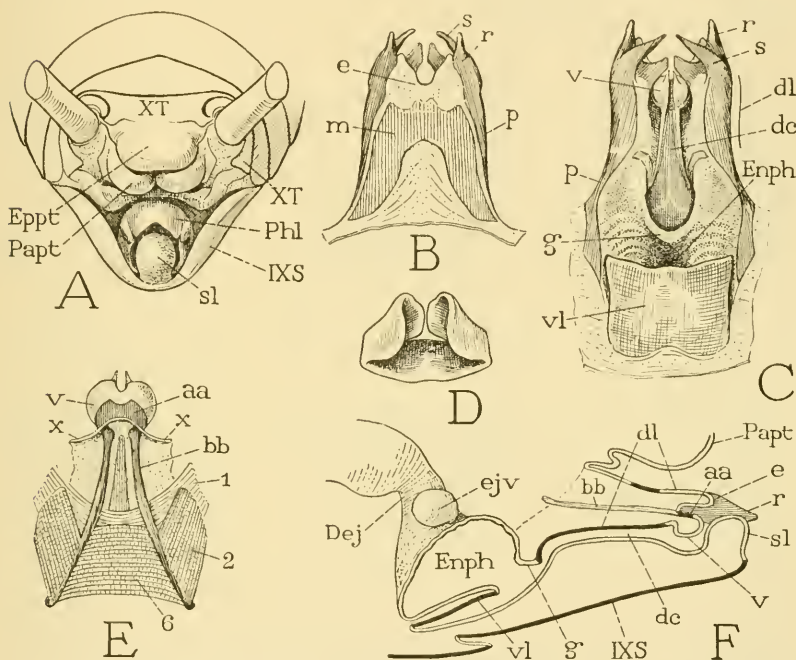


FIG. 36.—Tettigonioidea—Gryllidae: external genitalia of *Nemobius fasciatus* (Degeer).

A, end of abdomen, posterior view. B, epiphallus, or exposed dorsal wall of dorsal lobe of phallus, dorsal view. C, phallus, ventral view, showing dorsal cavity (*dc*) open ventrally beyond ventral lobe (*vl*). D, ventral lobe of phallus, posterior view, showing inflected margins. E, distal part of dorsal wall of dorsal cavity of phallus, and free guide lobe (*v*) for spermatophore duct, dorsal view. F, diagrammatic median section of phallus, base of paraproct (*Papt*), and ninth abdominal sternum (*IXS*).

For letter explanation, see fig. 30.

ends of the apodemes are connected by a broad sheet of muscle fibers (*6*), and on each apodeme is inserted laterally a strong muscle (*2*) from the lateral sclerites of the epiphallus. The apodemes and the supporting plate, therefore, must represent the sclerite of the wall of the dorsal sac in *Gryllus* and *Gryllodes*. Beneath the apodemes and their muscles are the usual transverse muscles (*1*) of the wall of the dorsal cavity.

Proximal to the anterior lip (*g*) of the dorsal cavity is the deep, pouchlike endophallic cavity (C, F, *Enph*), the soft walls of which are thrown into rugose folds. The endophallus is mostly closed below by the wide, quadrate ventral lobe (*vl*), which, when viewed endwise (D), is seen to have its lateral margins inflected as two broad flaps. The ejaculatory duct (F, *Dej*) opens by a funnel-shaped enlargement directly into the endophallic cavity.

In the normal position of the genital parts of *Nemobius* the ninth abdominal sternum entirely conceals the phallus from below (fig. 36 A); a high median fold of its dorsal surface fits closely into the cavity on the ventral surface of the dorsal phallic lobe (F), and a soft end lobe of the sternum (*sl*) plugs the entrance to the dorsal cavity between the terminal processes of the epiphallus (A, *sl*).

The spermatophore of *Nemobius* resembles that of *Gryllus* in that it consists of a sperm-containing ampulla with a long recurved duct, but the attachment plate appears to be an expansion of the duct near its distal end (see Lespés, 1855; Gerhardt, 1913; Baumgartner, 1911; Fulton, 1931). The spermatophore of *Nemobius fasciatus* is described by Fulton as having a spherical ampulla about  $1\frac{1}{3}$  mm in diameter, and a flattened curved tubular duct about  $2\frac{1}{2}$  mm long with an expanded part near the recurved tip. By comparison with *Gryllus* it would seem that the ampulla of the spermatophore of *Nemobius* must be molded likewise in the endophallic cavity, and the duct formed in the median channel of the dorsal cavity (fig. 36 C, F). Fulton gives a figure showing the walls of the dorsal cavity of the phallus evaginated in the form of a large, grooved fold with the ampulla hanging free from its lower end, and the duct lying in the groove of the fold. He describes the formation of the duct in the groove as it appears when the spermatophore is first seen on the male, but this stage must be after the ampulla has been formed in the endophallus and ejected from the latter. The end of the duct at the time of its insertion into the female is probably held in the slot of the terminal lobe of the dorsal cavity (fig. 36 C, *v*) between the epiphallic processes. The spermathecal aperture of *Nemobius*, as in *Gryllus*, is situated on the end of a small knoblike papilla of the dorsal wall of the genital chamber, and Fulton observes that this knob "is about the right size to be grasped by the male claspers (epiphallic armature), which would bring the tip of the spermatophore tube to the hole in the apex of the knob."

The development of the phallus of *Nemobius* is somewhat simpler than that of *Gryllus*, and leaves little doubt that the grillid organ is a modification of the more generalized phallic structure of the Tet-

tigoniidae. In a young nymph of *Nemobius fasciatus*, in which the hind wings do not yet project from the margin of the metatergum, and the subgenital sternum is not enlarged (fig. 37 A), the phallus is a small, simple lobe in the genital pocket above the ninth sternum (B). With its base is connected a pair of slender ventral extensions (*xt*) of the tenth tergum (C), suggestive that the phallus is primarily a derivative of the tenth segment and not of the ninth. The phallic

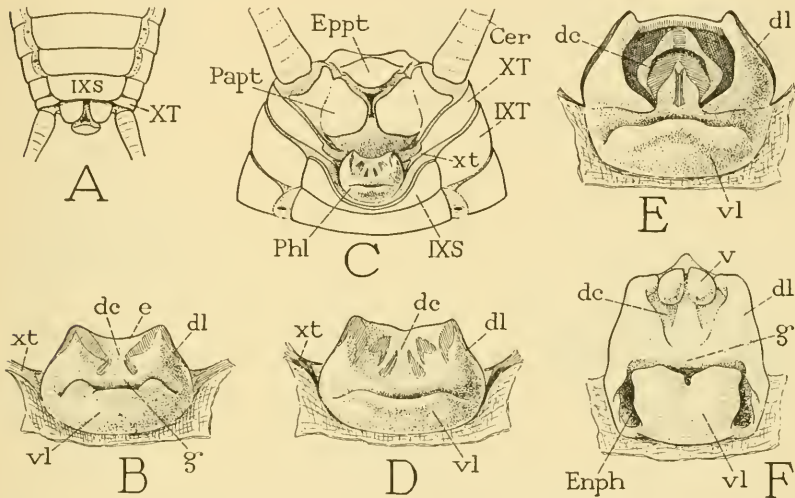


FIG. 37.—Tettigoniodea—Gryllidae: nymphal development of the phallus of *Nemobius fasciatus* (Degeer).

A, young wingless nymph, end of abdomen, ventral view. B, same, phallus, ventral view. C, older nymph with hind wings reaching to end of first abdominal tergum, end of abdomen with subgenital plate (IXS) partly removed to expose phallus (Phl), postero-ventral view. D, same, phallus, ventral view. E, phallus of nymph with hind wings reaching almost to fifth abdominal tergum, ventral view. F, phallus of succeeding instar (perhaps immature adult) exposed by removal of cuticula from E.

For letter explanation, see fig. 30.

rudiment consists of a thick dorsal lobe (B, *dl*), and a short, wide ventral lobe (*vl*). The distal surface of the dorsal lobe presents a shallow depression (*dc*), which is the beginning of the dorsal cavity, the exposed position of which suggests its identity with the dorsal phallic cavity of Tettigoniidae. At a somewhat later stage, when the hind wings extend to the end of the first abdominal tergum, the phallus has changed but little in structure (C, D); but when the wings reach to the fifth abdominal segment, the phallus (E) begins to show some of the adult modifications. If the specimen is in a premoulted condi-

tion, and the cuticula is removed, the organ exposed within (F) is so distinctly of the imaginal type of structure (fig. 36 C) that there is no question of the identity of the parts.

*Gryllotalpidae*.—The abdomen of *Gryllotalpa* has a simple, rounded posterior end (fig. 38 A). The ninth segment is short above and

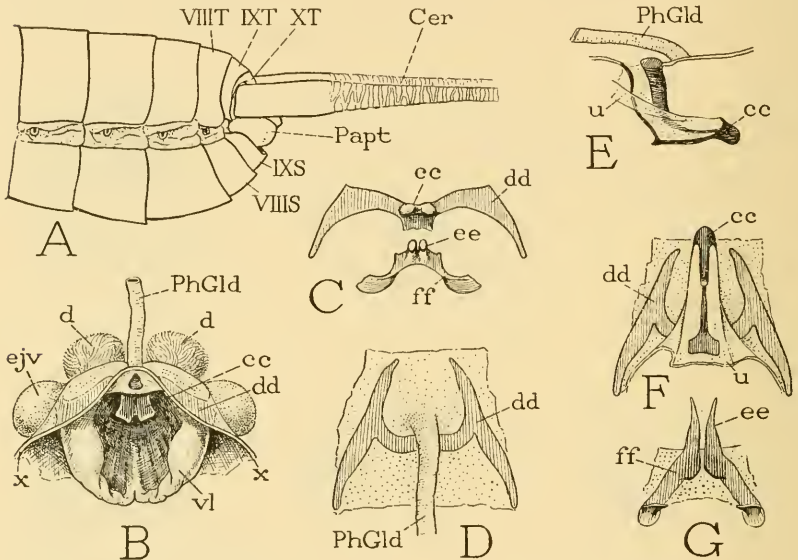


FIG. 38.—Tettigonioidae—*Gryllotalpidae*: external male genitalia of *Gryllotalpa* and *Scapteriscus*.

A, *Gryllotalpa hexadactyla* Perty, end of abdomen, lateral view. B, same, phallus and associated internal structures, dorsal view. C, same, sclerites in dorsal wall of phallic cavity, ventral view. D, *Scapteriscus vicinus* Scudder, dorsal wall of phallic cavity, and terminus of phallic gland, dorsal view. E, same, distal process of dorsal wall of phallic cavity, and terminus of phallic gland, lateral view. F, same, distal process of phallic cavity, and supporting sclerite, ventral view. G, same, proximal processes of dorsal wall of phallic cavity, ventral view.

cc, distal process of dorsal wall of phallic cavity; Cer, cercus; d, mass of small accessory glands (see fig. 39 A); dd, sclerite in dorsal wall of phallic cavity; ee, proximal processes in dorsal wall of phallic cavity; ejv, vesicle of ejaculatory duct; ff, supporting sclerites of proximal processes (ee); Papt, paraproct; PhGld, phallic gland; u, fold of wall of phallic cavity; vl, ventral lobe of phallus; x-x, cut edge of anterior wall of genital chamber.

below, the sternum (IXS) not being enlarged as a subgenital plate. The lateral angles of the small tenth tergum (XT) extend above the bases of the long, tapering cerci. The epiproct is free from the tenth tergum, and together with the paraprocts forms a small conical proctiger.

The male genital organ of *Gryllotalpa hexadactyla* is ordinarily concealed above the ninth abdominal sternum, and has a very simple

structure. As exposed by depressing the ninth sternum (fig. 38 B), the phallus appears as a large, rounded, thick-lipped, membranous fold (*vl*) with a concave upper surface that leads into a deep pouch above it. There is no epiphallic sclerotization, and the dorsal lip of the pouch is reflected directly into the dorsal wall of the genital chamber (*x-x*), but on it there opens a long, median, tubular phallic gland (figs. 38 B, 39 A, *PhGld*). From just within the dorsal lip of the phallic pouch a strong, median, flattened, bilobed process (fig. 38 B, *cc*) projects downward from the dorsal wall, in which it is supported by a wide, transverse sclerite (B, C, *dd*). This sclerite and its median process are termed the "ancre" by De Saussure and Zehntner (1894); Walker (1922) regards it as the "pseudosternite" (epiphallus), but its shape in *Scapteriscus* (E) suggests rather a homology with the guide of the spermatophore duct in *Gryllus*. Concealed in front of the median process, when viewed from behind, and closely appressed to its anterior surface, is a pair of peglike processes (C, *ce*) supported on a second and smaller plate (*ff*) in the dorsal wall of the phallic cavity. These processes are the "titillators" of De Saussure and Zehntner; they are generally longer and slenderer than in *G. hexadactyla* (G). Anterior to the second sclerite the dorsal wall of the phallic pouch presents a median depression, and the ejaculatory duct opens directly into the anterior end of the pouch.

In *Scapteriscus vicinus* the phallus is similar to that of *Gryllotalpa*, but the dorsal armature of the phallic pouch is quite different. The median, posterior process here has the form of a large, descendant, but abruptly elbowed arm (E, F, *cc*) ending in a sclerotic knob, and is contained in a membranous fold (*u*) of the dorsal wall of the pouch. This process would thus appear to represent the median rod or lobe of Gryllidae (figs. 32 D, 36 C, *v*) that holds the end of the spermatophore duct. Its base is supported by an H-shaped sclerite in the dorsal wall of the phallic pouch (fig. 38 D, F, *dd*), just behind the cross-bar of which opens ventrally a long, tubular phallic gland (D, E, *PhGld*) similar to that of *Gryllotalpa*. The anterior dorsal processes of *Scapteriscus* are long and tapering (G, *cc*), and arise from separate basal extensions (*ff*) in the pouch wall.

The gryllotalpid phallus has evidently been derived from an organ having the gryllid type of structure, which has been simplified by the union of the dorsal and endophallic cavities, the former being represented only by the depression of the dorsal wall of the common phallic pouch. The separation of the epiproct from the tenth tergum might be regarded as a character relating the mole crickets to *Stenopelmatus*, but the phallic structure of *Stenopelmatus* (fig. 31) has little in common with that of *Gryllotalpa* and *Scapteriscus*.

The spermatophore of *Gryllotalpa vulgaris* is described by Gerhardt (1913) as an oval body, strongly convex on its upper surface, the shape evidently being such as would fit the phallic pouch, where undoubtedly the spermatophore is molded. The outer surface of the spermatophore, Gerhardt says, is formed of a hard, smooth external coat, which encloses both the sperm capsule and the duct of the latter. The duct, after leaving the capsule, is looped within the spermatophore, and opens on a papilla at one end of the latter between two small lobes that serve for the attachment of the spermatophore in the female. No observations have been made on the manner in which the sperm capsule and duct are formed within the phallic pouch before they are ensheathed in the common outer covering.

The mating habits of *Gryllotalpa* (presumably *hexadactyla*) are described by Baumgartner (1911), who says that two pairs of insects observed in copulation took the very unusual position for Orthoptera of having the abdomens attached end to end, the female standing upright, but the male being on his back. Gerhardt (1913), however, says that the mating habits of *Gryllotalpa vulgaris*, as exhibited by one pair observed, are the same as those of Gryllidae, the male taking the usual position beneath the female, and the bodies of the two insects being in the same direction.

The internal reproductive organs of *Gryllotalpa* (fig. 39 A) differ from those of *Gryllus* (fig. 34 A) in the large size of the anterior part of the ejaculatory duct (fig. 39 A, *Dej*), the greater differentiation among the tubules of the accessory glands (*AcGlds*), the presence of a pair of seminal vesicles (*Vsm*), and of a median tubular phallic gland (*PhGld*). The testes (*Tes*) are elongate oval bodies, each composed of numerous small pyriform sperm tubes within a common peritoneal sheath, attached radially by fine ducts to the vas deferens, which traverses the axis of the testis. The vasa deferentia form each a large, closely coiled epididymis (*Epdm*) before entering the ejaculatory duct. Most of the accessory glands consist of two large lateral masses of tubules, of which the more anterior are longer and thicker, but posteriorly there are two small globular masses of fine tubules (*d*) lying close to the usual vesicular glands (*cjv*) opening into the end of the ejaculatory duct. The vesiculae seminales (*Vsm*) are a pair of large, dilated, lateral diverticula from the posterior part of the ejaculatory duct; at their bases are given off a pair of slender tubes. The long, median, tubular phallic gland (*PhGld*) lies on the dorsal surface of the ejaculatory duct, and, as already noted, opens on the dorsal lip of the phallus (fig. 38 B).



The innervation of the distal segments of the abdomen as shown in *Scapteriscus* (fig. 39 B) illustrates well the typical relation of the segmental nerves to the genital organs in Orthoptera. The last ventral ganglion innervates segments VII to XI. The lateral nerves of the first three of these segments in the male go *beneath* the vasa deferentia (or the epididymes), and the nerves of the tenth segment (*XNv*) would do so if brought forward. The large cercal nerves of the

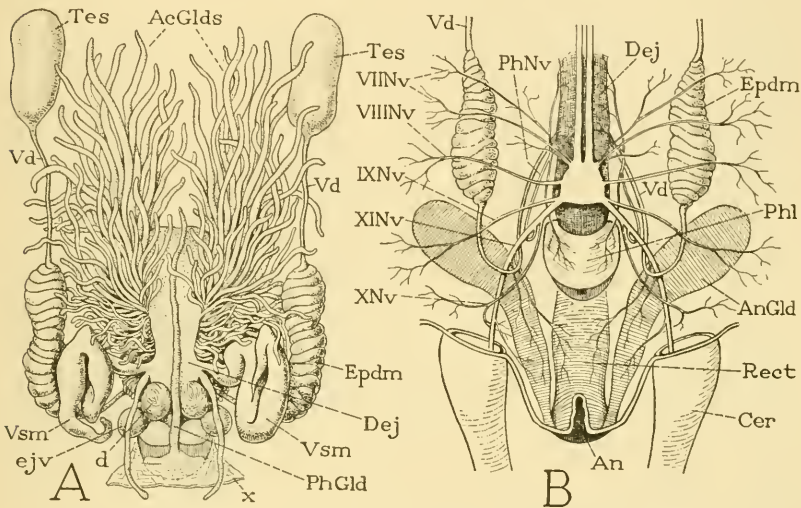


FIG. 39.—Tettigoniodea—Gryllotalpidae: internal male genitalia and associated organs of *Gryllotalpa* and *Scapteriscus*.

A, *Gryllotalpa hexadactyla* Perty, internal organs of reproduction, dorsal view. B, *Scapteriscus vicinus* Scudder, internal organs of terminal part of abdomen, ventral view.

The following letter explanations apply to figs. 39 and 40. *AcGlds*, accessory glands; *An*, anus; *AnGld*, anal gland; *Cer*, cercus; *d*, body of very small gland tubules; *Dej*, ductus ejaculatorius; *ejv*, vesicle of ejaculatory duct; *Epdm*, epididymis; *Eppt*, epiproct; *GC*, genital chamber; *Odc*, oviductus communis; *Odl*, oviductus lateralis; *Ov*, ovary; *Papt*, paraproct; *PhGld*, phallic gland; *Phl*, phallus; *PhNv*, phallic nerve; *Rect*, rectum; *Tes*, testis; *Vd*, vas deferens; *Vsm*, vesicula seminalis; *x*, wall of genital chamber; *VIIINv-XINv*, segmental nerves of seventh to eleventh abdominal segments.

eleventh segment (*XINv*), however, go *dorsal* to the vasa deferentia, which loop forward beneath them to join the ductus ejaculatorius. This relation between the segmental nerves and the male genital ducts is possible only on the condition that the primitive vasa deferentia turned downward and united with the body wall somewhere between the tenth and eleventh nerves, and therefore probably on the posterior part of the tenth abdominal segment. The nerves of the tenth segment branch from common basal trunks with the cercal nerves, and

just beyond them arises from the cercal trunks a pair of phallic nerves (*PhNv*) that go to the phallus and the ejaculatory duct. The phallus and the ectodermal part of the ejaculatory duct, therefore, must be derivatives of the tenth segment, since it is improbable that they belong to the eleventh segment, and they have no connections with the nerves of the ninth segment. The proctiger, the terminal part of the rectum (*Rect*), and the large anal glands (*AnGld*) derive their innervation from branches of the cercal nerves.

In contrast to the condition in the male, the lateral oviducts of the female (fig. 40 A, B, *Odl*) turn downward behind the nerves of the

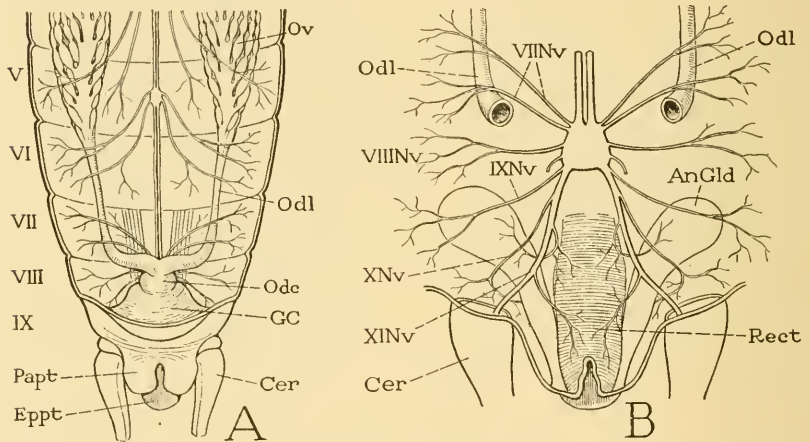


FIG. 40:—Tettigonioidae—Gryllotalpidae: internal female genitalia and associated structures of *Scapteriscus vicinus* Scudder.

A, posterior part of abdomen, showing reproductive organs and nerves, ventral view. B, innervation of posterior abdominal organs from last ganglion of ventral nerve cord, ventral view.

For letter explanation, see fig. 39.

seventh segment (*VIIInv*). The primitive openings of the paired oviducts, therefore, must have been at a position between the nerves of segments *VII* and *VIII*, and hence probably on the posterior part of segment *VII*. The innervation of the following segments in the female of *Scapteriscus* (B) is essentially the same as that in the male except for the absence of phallic nerves. The median oviduct and the genital chamber appear to be innervated from the second pair of lateral nerves in segment *VIII* (A).

#### X. ACRIDOIDEA

The phallic organ of the Orthoptera attains in the Acrididae its highest degree of development and integration into a mechanism of

spermatophoric insemination. Structurally, the acridid phallus belongs to the tettigonioid type, in so far as the primary phallomeres unite to form a single organ; but any closer relationship to either the tettigoniid or gryllid form is not clear, either from the adult structure or the nymphal development.

The mating and copulating habits of the grasshoppers are well known, but only a few studies have been made on the manner of sperm transfer. According to the accounts of different investigators it would appear that some species produce a number of small spermatophores and eject them entirely into the sperm receptacle of the female, while others insert only the end of a long neck from a single bulblike spermatophore into the receptaculum (see Snodgrass, 1935, pp. 71-73). Fedorov (1927) claims that the first type of insemination occurs with *Anacridium aegyptium*; Boldyrev (1929) describes the second for *Locusta migratoria*, the spermatozoa in this case being pumped through the neck of the spermatophore into the receptaculum of the female by the endophallic apparatus of the male, after which the end of the spermatophore neck breaks off and remains in the sperm receptacle. The structure and mechanism of the phallic organ are so nearly the same in all species of Acrididae that we should scarcely expect to find any considerable difference in the manner of insemination: the apparatus appears to be well adapted to the type of action described by Boldyrev.

The acridid phallus consists of a complex ectophallus contained in the genital chamber (fig. 41 A, *GC*), and of a large, strongly muscled, bulblike endophallus (*Enph*) projecting downward and forward into the body cavity beneath the floor of the genital chamber. The ejaculatory duct (*Dej*) ends in a muscularly compressible ejaculatory sac (*ejs*) that opens into the ventral wall of the endophallic cavity between two sclerites (*y*) that, operated by muscles of the endophallic wall, regulate the gonopore.

The ectophallus includes a proximal part, or phallobase (fig. 41 A), and a diversified distal part, which may be termed the aedeagus (*Aed*). The phallobase appears as a membranous elevation of the floor of the genital chamber, having its distal margin produced into a broad basal fold (*bf*) overlapping the base of the aedeagus; on its anterior part is situated a large, irregular sclerite, the epiphallus (figs. 41 A, 42 I, *Epph*). Between the basal fold and the epiphallus there may be a deep depression (fig. 42 I, *c*). The aedeagus (fig. 41 A, *Aed*) is differentiated into several parts, but its major subdivision is into a dorsal lobe (*dl*) and a ventral lobe (*vl*), between which is the phallotreme, or opening from the endophallic cavity. The dorsal lobe itself is

usually differentiated into an irregular basal section (B, *m*) and a cylindrical distal part (*r*), and is cleft posteriorly (or ventrally) by the long, slitlike phallotreme (C, *Phtr*), which may involve also the distal end, and thus divide the apex of the aedeagus into two lateral terminal lobes (fig. 42 I, *r*). One or two pairs of apical processes

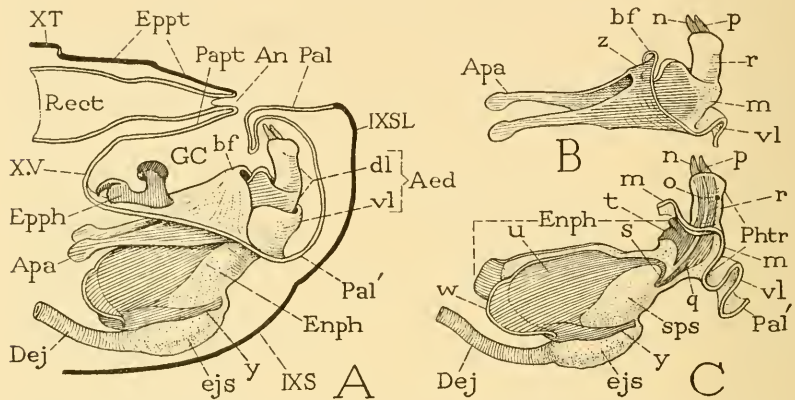


FIG. 41.—Acridoidea—Acridae: structure of the external male genitalia, diagrammatic (from Snodgrass, 1935).

A, section of end of abdomen somewhat to left of median plane, showing organs within genital chamber (GC), and those invaginated into body cavity. B, distal part of ectophallus and apodemal arms. C, aedeagus and endophallus, basal parts of phallus removed.

The following letter explanations apply to figs. 41 and 42: *a*, basal part of nymphal phallus; *Acd*, aedeagus; *Amp*, mesodermal ampulla; *An*, anus; *Apa*, apodeme of aedeagus; *b*, *b*, terminal lobes of nymphal phallus; *bf*, basal fold of phallus; *c*, dorsal depression of phallic base; *Dej*, ductus ejaculatorius; *dl*, dorsal lobe of phallus; *ejs*, ejaculatory sac; *Enph*, endophallus; *Epph*, epiphallus; *Eppt*, epiproct; *GC*, genital chamber; *IXSL*, subgenital lobe of ninth abdominal sternum; *m*, basal part of dorsal lobe of phallus; *n*, dorsal (anterior) apical process of aedeagus; *o*, dorsal (anterior) sclerite of phallotreme wall; *p*, ventral (posterior) apical process of aedeagus; *Pal*, pallium; *Pal'*, inner fold of phallium; *Papt*, paraprot; *Phm*, phallomere; *Phtr*, phallotreme; *q*, ventral (posterior) sclerite of phallotreme wall; *r*, distal part of dorsal lobe of phallus; *Rect*, rectum; *s*, arm connecting posterior phallotreme sclerite (*q*) with endophallic plate (*u*); *sps*, spermatophore sac of endophallus; *t*, dorsal bridge of dorsal phallotreme sclerites; *u*, lateral plate of endophallus; *Vd*, vas deferens; *vl*, ventral lobe of phallus; *x-x*, cut edge of anterior wall of genital chamber; *XV*, venter of tenth abdominal segment; *y*, gonopore process of endophallic plate; *z*, zygoma of aedeagal apodemes.

(fig. 41 B, C, *n*, *p*) may project from the walls of the phallotreme. The basal part of the dorsal lobe (B, *m*) usually contains a sclerotization in its lateral walls, from which a pair of long apodemal arms (*Apa*), the "endapophyses" of Walker (1922), project internally above the endophallus (A). The endophallus is a large laterally compressed sac, with a narrowed meatus leading inward from the

long phallotreme cleft (C). Its lateral walls contain a pair of large plates (*u*), from each of which a slender sclerotic bar (*s*, *q*) is continued through the wall of the meatus, and may terminate in a free apical process (*p*). A second pair of anterior (or dorsolateral)

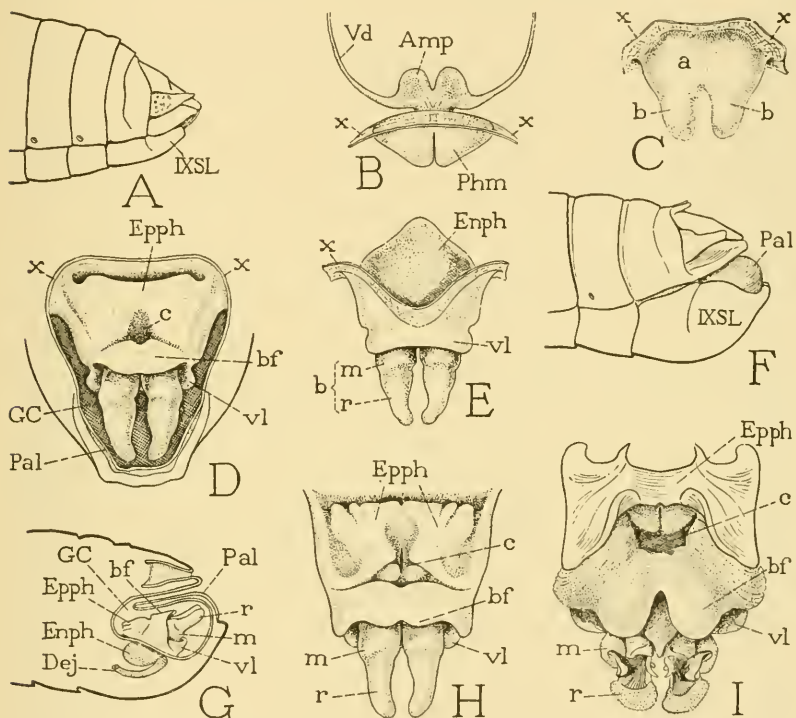


FIG. 42.—Acridoidea—Acrididae: nymphal development of external male genitalia.

A, *Dissosteira carolina* (Linnaeus), end of abdomen of nymph with wings just differentiated from tergal plate. B, same, phallic lobes, connected by short ejaculatory duct with mesodermal ampullae of vasa deferentia. C, *Melanoplus mexicanus* (Saussure), phallus of nymph with wings not extending beyond metatergum, dorsal view. D, same, nymph with wings reaching to middle of first abdominal tergum, phallus in genital chamber beneath outer cuticula, dorsal view. E, same, ventral view, showing endophallic sac. F, same, end of abdomen of nymph with wings extending to middle of third abdominal tergum. G, same, diagrammatic section of end of abdomen of nymph. H, same, phallus of nymph in stage of F, dorsal view. I, same, mature phallus, dorsal view.

For letter explanation, see fig. 41.

bars in the meatus wall (C, *o*), united basally by a dorsal bridge (*t*), runs out into the anterior apical processes (*u*). Further details of the structure of the complex phallic organ of the Acrididae, its musculature and mechanism, and its variations in the several acridid sub-families the writer has described in a former paper (1935).

It is possible to conceive of the acridid phallus as an extreme development of the gryllid type or organ, as does Walker (1922), in which the dorsal cavity and the endophallic cavity have united to form the common inner sac; but the simple development of the organ in the nymph does not bear out this interpretation.

The developing phallus in the various instars of the acridid nymph is always entirely concealed in the genital chamber beneath the covering pallial fold (fig. 42 G, *Pal*); the latter, therefore, must be removed in order to study the growth of the genital organ. In a young nymph of *Dissosteira carolina* (fig. 42 A) in which the wing pads do not yet project from the angles of their tergal plates, the phallus has the form of a simple, bilobed, conical papilla arising anteriorly from the floor of the genital chamber (B). The two lobes, or phallobases (*Phm*), are closely appressed, and from their united bases arises a short ejaculatory duct connected with the ampullae (*Amp*) of the vasa deferentia. This same stage in the development of the phallus of *Melanoplus differentialis* is described and figured by Else (1934). At a somewhat later stage, as shown in *Melanoplus mexicanus* (C), the two phallic lobes (*b, b*) have lengthened and have been carried out upon a common basal part (*a*). In an older nymph having the hind wings reaching slightly beyond the middle of the first abdominal tergum, the phallus shows distinctly the beginning of adult differentiations (D), but the specimen here shown was exposed by removal of the outer cuticula, and therefore belongs to the following instar. Dorsally there is a sharply defined anterior margin of the epiphallus (*Epph*), a central depression (*c*) in the phallobase, and a distinct basal fold (*bf*). On the under side, the ventral lobe (*vl*) appears as a small transverse fold, above which is the opening of an already well-developed endophallic pouch. When the wing pads reach to or slightly beyond the middle of the third abdominal tergum, the end of the abdomen has the adult characteristics (F), and a section (G) shows the phallus in the mature position. The epiphallic region of the phallobase is now well demarked (H, *Epph*), the central depression (*c*) deepened, and the basal fold (*bf*) much enlarged. The two processes of the dorsal lobe, which in *M. mexicanus* remain distinct from the early nymph (C) to the adult (I), are differentiated into proximal and distal parts (E, H, *m, r*), and the ventral lobe (*vl*) projects beneath their bases. Between this stage (H) and the adult (I) the basal structures take on their definitive form, and the various details of the aedeagal lobes are developed.

The development of the acridid phallus thus clearly shows that the complex phallic apparatus of the Acrididae has essentially the same

beginning as the simpler organ of Tettigoniidae, except that at first there are only two phallic lobes instead of six as in *Conocephalus* (fig. 23 B, C). Since a ventral lobe soon appears, however, the phallic rudiments of the acridids might be more directly likened to the latero-dorsal nymphal phallomeres of Blattinae (figs. 12 E, 15 B). Lateral lobes, such as are characteristic of the Tettigoniidae, are absent in Blattidae, Gryllidae, and Acrididae.

The central depression in the dorsal surface of the phallic base of *Melanoplus* (fig. 42 H, I, *c*) suggests the dorsal cavity of the tettigonioid phallus (fig. 22 C, *dc*), particularly as it appears in the nymphal development (fig. 31 F, G, *dc*). The acridid epiphallus, furthermore, is developed from the dorsal wall of the phallus anterior to the median depression (fig. 42 D, H, I, *Epph*), and the so-called epiphallus of the Rhabdiphorinae and Tettigoniidae is a sclerotization of the posteriorly produced anterior margin of the dorsal cavity (fig. 22 C, D, F, *e*). The large inner cavity of the acridid phallus appears to be formed as a direct endophallic invagination, but its strong musculature might be taken as evidence that most of its lumen represents the dorsal phallic cavity of *Gryllus* or *Gryllodes* (figs. 32 E, 35 H, *k*). In the absence of conclusive evidence on homologies between the mature phallic organs of Gryllidae and Acrididae, we may regard the acridid phallus as an independent line of development from phallic rudiments such as are common to the nymphal stages of all the Orthoptera.

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