SMITHSONIAN MISCELLANEOUS COLLECTIONS
VOLUME 89, NUMBER 8

MORPHOLOGY OF THE INSECT ABDOMEN

PART II. THE GENITAL DUCTS AND THE OVIPOSITOR

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(Publication 3219)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
OCTOBER 20, 1933

The Lord Baltimore Press
BALTIMORE, MD., U. S. A.

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INTRODUCTION

Mythologies usually begin with the bringing of order out of chaos. From this, however, it should not be hastily concluded that the results of all attempts to establish order where confusion has prevailed belong to the realm of mythology, even though they may deal with things by their nature unknowable. Particularly, the writer hopes, at least, that there may be seen some ground of plausibility in the scheme set forth in this paper, and in others of the same series that have preceded it,

Smithsonian Miscellaneous Collections, Vol. 89, No. 8

for analyzing an insect in an orderly way from one end to the other. Incidentally it should be observed that the results come out the same regardless of which end is taken first, and this in itself is presumptive evidence of the soundness of the proposed solution. Of course, it may not be claimed that an orderly concept of the structure of an animal has, in itself, greater claim to truth than one that is prolix, unless it can be demonstrated that orderliness, and consequently simplicity is a fundamental law of animate nature. It is possible that the value of simplicity has been overestimated, and that too much confidence is raised in its favor by its mere reputation. We may concede that simplicity is the soul of wit, the essence of art, a distinguishing mark of virtue, etc., but when simplicity comes to be regarded even as an index of truth itself, we must look upon its claims with some suspicion. Simplicity, however, does have in all things a convincing manner.

Segmented animals, as every zoologist admits, are composed of a series of segments, and there is no dispute that the segments were most probably at one time alike. Hence, it follows that each segmentally composite section of the animal's body has the same basic and fundamental structure, a principle which also no one denies. Diversities of opinion concerning the correspondence of parts in different body sections, then, are merely matters of difference of interpretation.

In the study of insect anatomy entomologists have examined the insect's head as if it were a thing in itself, having only a cervical continuity with the rest of the body; they have minutely explored and topographically mapped the thorax, but have for the most part looked upon it also as a discrete entity; they have painstakingly investigated the abdomen, but without giving much thought to aligning its parts with those of the thorax and the head. Students in entomology are taught in this sectional manner, textbooks are written in the same disjointed style. In short, the first principle of insect anatomy is that an insect is *divided* into head, thorax, and abdomen. As a consequence, ideas concerning the unity of the insect are vague at best, and collectively are little short of chaotic.

For a number of years the writer has been attempting to discover the basic plan of arthropod organization that is repeated through the segments, and to see how the special modifications in the several body regions of the insect may conform with the structure of a theoretically generalized segment. The results are quite simple, and are derived from following the horizontal constructional lines through the entire segmental region of the trunk. This scheme for studying the insect as a whole recognizes dorsiventrality as a primary factor in structural differentiation, and accepts the series of limb bases along the sides of the body as marking the anatomical distinction between dorsum and venter. The plan, in the abstract, can scarcely be questioned as morphologically sound. It is only in its practical application that questions of interpretation come up, and if, as applied by the writer, the scheme here and there conflicts with current local interpretations based on former opinions, justification for the interpretive alterations proposed must be found in the degree of improvement given to the general or perspective view of insect structure as a whole. The application of the plan, as carried out in this series of papers, will at least open a way by which the teacher in entomology may conduct his students at once straight through the insect without giving the impression that the head, the thorax, and the abdomen are each a region foreign to the others; if followed in descriptive entomology it would furnish a basis for a common nomenclature. The plan gives at once a unified and a simplified concept of insect morphology, and many facts unquestionably are in its favor; but there is no pretense here made to decree that order and simplicity in any particular pattern are synonymous with truth.

I. GENERAL STRUCTURE OF THE ABDOMEN

In the study of the abdomen it is highly important to be able to identify the several morphologically distinct surface regions. These regions are the *dorsum* (fig. 1 A, B, *D*) lying above the region of the primitive limb bases; the *venter* (*V*) lying below the limb bases, and the *podial,* or *pleural, regions* (*P*) which are the areas of the limb bases themselves (*LB*). The dorsum is separated from the pleural region by the *dorso-pleural line* (*a-a*)*;* the pleural region is separated from the venter by the *pleuro-ventral line* (*b-b*). Much confusion exists in descriptive works on entomology because the positions of these lines have not been clearly perceived, and, as a consequence, names have been applied to certain parts that do not properly belong to them. By observing whatever landmarks are present, however, it is usually possible to determine the limb base areas on the abdominal segments; the rest of the surface is then apportioned to the dorsum and to the venter.

The dorso-pleural line (fig. 1 B, *a-a*), beginning on the head (fig. 2 A), separates the lower edge of the cranium from the bases of the gnathopods (mandibles and maxillae); on the thorax (figs. 1 C, 2 B), it goes dorsal to the subcoxal plates of the leg bases, dipping down between them where necessary to pass beneath the spiracles;

on the visceral region of the abdomen it extends below the series of spiracles (fig. 1 C) and above the limb bases where the latter are present (fig. 2 C); and finally it runs out above the bases of the gonopods, pygopods, and uropods, or cerci (figs. 1 C, 2 D, E, F).

The pleuro-ventral line (fig. 1 B, *b-b*) begins anteriorly between the bases of the gnathopods and the ventral wall of the head (fig. 2 A); on the thorax (figs. 1 C, 2 B) it separates the leg bases from the true venter; on the abdomen it runs ventrad or mesad of the limb bases, where the latter are distinct (fig. 2 C, D, E, F), but where appendages are absent it must be assumed to follow the line of fusion between the limb bases and the primitive sterna (fig. 1 C).

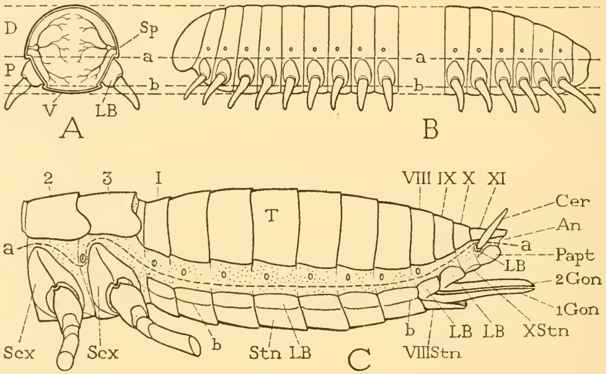

FIG. 1.—Diagrams showing the lengthwise division of the body surface of an insect into dorsal, ventral, and podial regions by the series of limb bases along the sides.

A, cross section, B, lateral view, of theoretically primitive condition in which the podial, or pleural, region of the body (*P*) consists of the segmental areas containing the limb bases (*LB*), the dorsum of the region (*D*) above the dorsopleural line (*a-a*), and the venter (*V*) of that below the pleuro-ventral line (*b-b*). C, generalized structure of thorax and abdomen of an adult female insect, with position of dorso-pleural line as indicated (*a-a*), and in which the limb bases form the coxae and subcoxae (*Scx*) of thorax, but unite with the sterna of abdomen, except in the genital segments (*VIII, IX*) and the eleventh segment (*XI*).

Surface regions of the abdomen.—The dorso-pleural line is frequently marked on the abdomen by a distinct longitudinal fold or groove of the integument running ventrad of the spiracles (fig. 14 A, *a-a*), the dorso-pleural nature of which is shown by the fact that the area above it corresponds with the dorsum of the thorax containing the tergal plates and the paratergal wing bases, while the area immediately below it (*P*) corresponds with the region of the subcoxal pleural plates of the thorax (*Scx*). The pleuro-ventral line of the abdomen is also frequently indicated by the presence of a groove or other structural feature, as in certain Thysanura and in some holometabolous larvae. Where abdominal limb rudiments are present, their bases always occupy the areas between the folds or grooves marking the dorso-pleural and pleuro-ventral lines; but in most adult insects in which the abdominal appendages have been entirely suppressed, the limb base areas are continuously sclerotized with the primitive sterna in the definitive sternal plates, and, unless styli or other representatives of the free parts of the appendages are present, there is usually no indication in the definitive structure as to the primitive position of the pleuro-ventral line.

The dorsum of an abdominal segment may be occupied by a single tergal plate, which in some insects encloses the spiracles laterally, though the spiracles often lie in membranous paratergal areas; or the sclerotization of the dorsum may consist of a principal dorsal sclerite, and of one or more lateral paratergal sclerites. The abdominal pleural areas contain the appendage bases, where appendages are present, but the limb bases are commonly reduced to plates or lobes forming a part of the body wall, or they are entirely suppressed as individual structures, and their areas then become merely a part of the general pleural integument. In the last case the limb base area may be entirely membranous, or it may contain one or more pleural sclerites; when fully sclerotized, it is usually continuous with the primitive sternal sclerotization in a pleurosternal definitive sternum. The venter is the lower surface between the bases of the appendages, and contains the primitive sternal plates. The latter may retain their individuality, but, as just noted, the primitive sternum of each abdominal segment is more commonly united with the pleural sclerotizations. The definitive sternal plate thus formed, finally, may be still further enlarged by a fusion with paratergal plates on each side of the dorsum. It becomes evident, therefore, that the sclerotization of the abdomen is not necessarily an index to the primary regional divisions of the abdominal surface.

The abdominal appendages.—The appendages of the insect abdomen fall into three principal groups, namely, those of the pregenital, or visceral, segments, those of the genital segments (or segment), and those of the postgenital segments. The pregenital appendages take on such a variety of shapes and functions that it is impossible to give them collectively a distinctive name. The genital appendages are the *gonopods.* The postgenital appendages are the *pygopods* on the tenth somite, represented by the postpedes of certain holometabolous larvae, and the *uropods,* or *cerci,* of the eleventh somite.

The pregenital appendages occur as distinctly appendicular organs principally in the Apterygota and in pterygote larvae. They never take the form of the thoracic pereiopods, but in a few cases they are multiarticulate and suggest that they are derived from jointed legs. Each appendage, when well developed, consists of a basis (fig. 2 C, *LB*) and of a movable appendicular part (*Sty*), and the basis frequently bears, mesad of the latter, an eversible and retractile vesicle (*Vs*). The appendicular process, which commonly takes the form of a stylus, a gill, or a tapering process, is usually provided with muscles, and the muscles always have their origins in the basis. The vesicle may be a small eversible sac, as in the Thysanura, a gill-bearing tubercle, as in certain sialid larvae, or a lobe serving for locomotor purposes, as in the larvae of Lepidoptera and chalastogastrous Hymenoptera; it also is provided with muscles, which in Thysanura arise within the limb basis, but which in the other forms may take their origins on the dorsum of the body wall. The limb basis usually has the form of a plate or lobe broadly implanted in the pleural area of its segment; it is generally immovable, but in the Thysanura and in the genital segments of female Pterygota it is provided with muscles arising on the body wall.

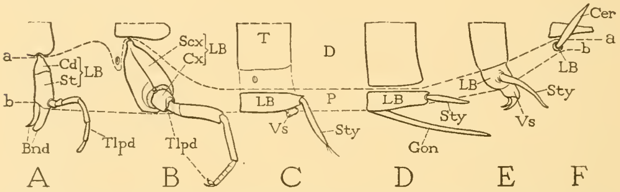

FIG. 2.—Diagrams suggesting the homologies of the basal parts of the appendages and the position of the dorso-pleural and pleuro-ventral lines (*a-a, b-b*) relative to them.

A, a head appendage, with basis subdivided into cardo and stipes (*Cd, St*), the latter bearing a pair of endites (*Bnd*) and the telopodite (*Tlpd*).
B, a thoracic appendage, with basis divided into subcoxa and coxa (*Scx, Cx*), the latter bearing the telopodite (*Tlpd*).
C, a thysanuran abdominal appendage, with limb basis undivided, and bearing a stylus (*Sty*) and vesicle (*Vs*).
D, a typical gonopod, with undivided basis (valvifer) bearing a stylus (*Sty*) and gonapophysis (*Gon*).
E, a generalized larval appendage of tenth segment (pygopod) or of other segments, bearing a stylus and vesicle.
F, a cercus (uropod) of eleventh segment, with small or rudimentary basis, and unsegmented distal shaft.

The gonopods in their more generalized form (fig. 2 D) resemble the pregenital appendages of the Thysanura (C), but they lack eversible vesicles, and each is characterized by the presence of a genital process, or *gonapophysis* (D, *Gon*) arising from the proximal mesal angle of the basis. Typically the distal process, or stylus (*Sty*), and the gonapophysis (*Gon*) are each movable by muscles arising in the basis; and the basis is movable on the body by muscles arising on the tergum of the supporting body segment. In the female, the bases of the gonopods (fig. 1 C) become the supporting plates of the ovipositor (first and second valvifers), and retain their dorsal muscles arising on the eighth and ninth abdominal terga. The female gonapophyses form the first and second valvulae (*1Gon, 2Gon*), the basal muscles of which persist in Thysanura, but are generally lost in Pterygota. The distal processes (styli) of the gonopods are retained in Thysanura and on the second gonopods in some of the more generalized Pterygota.

The pygopods, or appendages of the tenth abdominal segment, are always absent in postembryonic stages of exopterygote insects, though they may be present in the embryo. In many endopterygote larvae, however, they are well developed as the "anal legs", or postpedes (fig. 2 E), which usually resemble the appendages of the pregenital segments. The distal process (stylus) is retained on the pygopods only in certain Neuroptera, but in some Neuroptera and in Lepidoptera and chalastogastrous Hymenoptera the vesicle (*Vs*) forms a retractile lobe generally provided with claws.

The uropods, or cerci (fig. 2 F, *Cer*), belong to the eleventh abdominal segment. Each appendage arises typically from a membranous area behind the tenth tergum between the basal angles of the epiproct and the paraproct. In certain orthopteroid insects, the principal part of the cercus is supported on a small but distinct basal segment (*LB*). Most of the muscles that move the cercus are muscles of the tenth segment, but in some insects a muscle of the cercus arises on the epiproct. The cerci never have muscles arising on the paraprocts.

From this brief review of the various forms of appendages that occur on the insect abdomen it will be seen that the appendages all have a common type of structure, and that the gonopods differ from the others only in the presence of proximal processes (the gonapophyses) arising from the mesal angles of their bases. The bases of the abdominal appendages form a series of lobes, plates, or integumental areas occupying the pleural region on each side of the abdomen, which is continuous anteriorly with the regions of the limb bases on the thorax and the head.

II. MORPHOLOGY OF THE GONADS AND THE GENITAL DUCTS

The embryonic genital ducts of insects are simple mesodermal tubes continuous with the mesodermal walls of the gonads. The primitive ducts had separate openings to the exterior of the body, the apertures in the male being located probably on the tenth abdominal segment, those of the female on the seventh. In the majority of modern insects, however, a median ectodermal exit apparatus, together usually with accessory structures, has been added to the primitive ducts, and in many cases the latter even are largely replaced by ingrowths from the ectodermal parts. The definitive median exit duct of the male (except possibly in Collembola) opens in the ventral membrane between the ninth and tenth abdominal segments, which membrane probably belongs to the ninth primary somite. The definitive median egg passage of the female varies in its extent and point of opening from the posterior part of the seventh abdominal segment to the posterior part of the ninth, or it may open in common with the rectum into a small cloacal pouch on a terminal segment of the abdomen representing the combined ninth and tenth somites.

The gonads are mesodermal structures developed in the dorsal parts of the splanchnopleure as ridges of the latter extending continuously through several abdominal segments to enclose the germ cells here finally located. The gonadial ducts arise from ridges of cells extending posteriorly from the gonads. The subsequent compound structure of the gonads results from a secondary subdivision of each organ into a series or group of egg tubes or sperm tubes. There is no evidence from ontogeny that these gonadial tubes ever had separate openings or ducts to the exterior, and yet much theoretical speculation has been based on the idea that the component tubes of the ovaries and testes represent primitively segmental organs. The following discussion of the subject, therefore, may not be superfluous as an introduction to a study of the appendicular structures associated with the definitive genital apertures.

Early history of the germ cells.—In many insects, representing widely separated groups, the germ cells and the somatic cells are differentiated at the time of cleavage; and in such cases the germ cells are distinguishable when the blastoderm is formed as a group of special cells at the posterior end of the germ band. From this position the germ cells later migrate into the interior of the embryo, and are eventually associated with the dorsal part of the splanchnic wall of the mesoderm in the abdominal region of the body. Since it is not possible in all cases to recognize the germ cells as such prior to their enclosure in the abdominal mesoderm, some of the earlier, otherwise reliable works on insect embryology contain explicit descriptions of the supposed origin of the germ cells from the mesoderm.

The most detailed account of the history of the insect germ cells after their appearance in the mesoderm is that given by Heymons (1892) in his description of the development of the female reproductive organs of *Blattella* (*Phyllodromia*) *germanica.* The germ cells of *Blattella,* according to Heymons, appear as a few large cells scattered in the posterior parts of the mesoderm at the time when the germ band consists only of ectoderm and a simple underlying mesodermal layer. At the time the appendages are formed the germ cells are arranged in two lateral series behind the first segment of the abdomen, and most of them occur above the intersegmental grooves. With the development of the coelomic sacs, therefore, the germ cells are situated in the dorsal parts of the dissepiments between the coelomic cavities. They extend now from the first to the seventh abdominal segments.

Within the coelomic septa the germ cells multiply, and soon, Heymons says, many of them are crowded out posteriorly into the coelomic cavities. The extruded cells remain in contact with the coelomic walls and migrate posteriorly upon them to the splanchnic walls of the sacs. Here they penetrate between the epithelial cells, and thus become again imbedded in the mesoderm. Wheeler (1893) has observed that at this stage in *Conocephalus* (*Xiphidium*) some of the germ cells may become detached and fall into the coelomic cavities.

Origin of the gonads.—The surface of the splanchnic epithelium, where the latter is penetrated by the migrating germ cells, becomes broken, and its cells grow out irregularly about the germ cells (fig. 3 A), which eventually they enclose in a loose mesodermal covering. The germ cells of *Blattella,* Heymons says, now form a continuous series on each side of the body, extending from the second into the sixth abdominal segment, the cells that remained in the dissepiments filling the gaps between those that were extruded and which later took a position in the segmental areas of the coelomic walls. The series of germ cells and their mesodermal coverings, projecting slightly into the body cavity, constitute the *genital ridges* of the embryo, which are the primitive rudiments of the gonads.

Wheeler (1893), in his study of the development of the gonads in *Conocephalus,* was not able to distinguish the germ cells from the mesodermal cells until the germ cells are clustered in segmental groups in the splanchnic walls of the coelomic sacs, where they are partially covered by a mesodermal epithelium. In *Conocephalus* at this stage the paired gonad rudiments occur in the first to the sixth abdominal

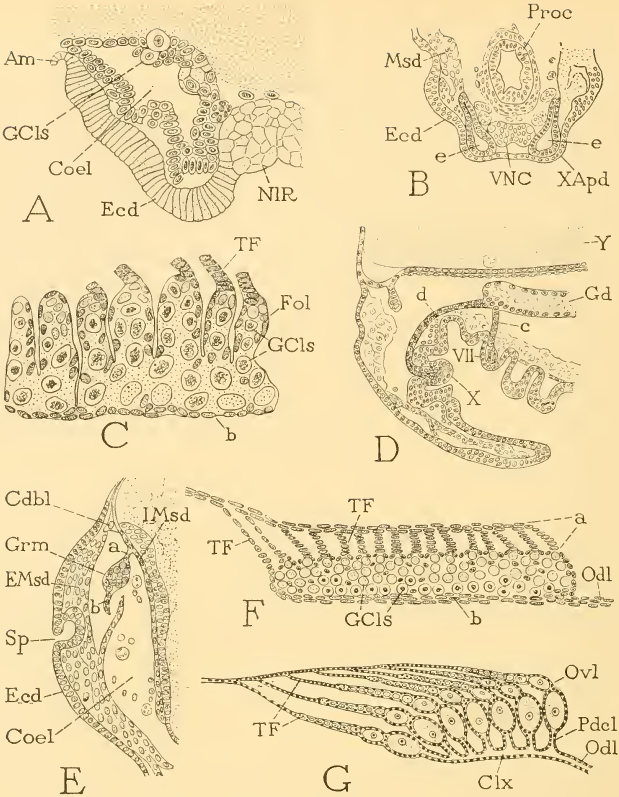

FIG. 3.—Development of the gonads and the genital ducts of insects.

A, cross section through an abdominal coelomic sac of *Blattella germanica* (from Heymons, 1892), showing group of germ cells (*GCls*) in splanchnic wall of mesoderm.

B, section through posterior end of embryo of *Conocephalus* (from Wheeler, 1893), showing termination of male genital ducts in ampullae (*e*) in appendages (*XApd*) of tenth segment.

C, differentiation of female gonad of *Blattella* into ovarioles (from Heymons, 1892).

D, showing branching of the gonadial duct (*c, d*) in embryo of *Forficula* to seventh and tenth segments (from Heymons, 1895).

E, section through a coelomic sac of *Leptinotarsa* (from Wheeler, 1889), showing embryonic gonad differentiated into a dorsal suspensorium (*a*) attached to splanchnopleure (*IMsd*), a germinal region (*Grm*), and a ventral strand (*b*) continuous with the duct.

F, later stage in development of female gonad of *Blattella* (from Heymons, 1892), with dorsal suspensorium (*a*) differentiated into terminal filaments (*TF*), germ cells (*GCls*) in undivided middle part, and ventral strand (*b*) continuous with duct (*Odl*).

G, subsequent stage in development of ovary of *Blattella* (from Heymons, 1892), with gonad completely divided into ovarioles (*Ovl*).

segments, and Wheeler points out that " the reproductive organs of *Xiphidium* are therefore truly metameric in their origin." Later, however, with the rapid multiplication of the germ cells, the successive gonad rudiments on each side of the body elongate and unite, resulting in the " formation of a continuous strand of germ cells with their accompanying epithelial cells ".

The recent account by Lautenschlager (1932) of the development of the female gonads in *Solenobia triquetrella* (Psychidae) is in essential agreement with the observations of earlier writers on Orthoptera. The paired segmental groups of germ cells, lying in the fourth, fifth, and sixth abdominal segments, condense and unite on each side into a single group having the position of the definitive gonad in the fifth segment. Here each composite group of germ cells becomes enclosed in a layer of small mesodermal cells. The latter form a thin sheath about the germ cells dorsally and laterally, but ventrally they form three thick cellular masses, which later give rise to the ovarial pedicles and the lateral ducts of the ovaries. According to Lautenschlager the follicle cells of the definitive egg tubes of *Solonobia* also take their origin from the cells of the mesodermal sheaths of the gonads.

Seidel (1924), on the other hand, finds that in *Pyrrhocoris apterus* the segmental groups of germ cells, formed at an early embryonic stage, become surrounded individually by mesodermal epithelium, and remain thus, up to a relatively late period of development, as a series of distinctly separated gonadial rudiments segmentally distributed on each side of the body in somites *II* to *VIII* of the abdomen. Eventually, the posterior rudiments migrate forward until all are assembled in segments *II* and *III,* where those of each lateral group develop directly into the seven genital tubes of the adult organ. The only union that takes place between them is in the lower tubular parts of the primary elements, which unite to form the lateral duct. Seidel claims that this condition in *Pyrrhocoris apterus* demonstrates the direct origin of the definitive genital tubes from the segmental gonadial rudiments of the embryo. However, since the case appears to be exceptional, and since the Hemiptera are in many ways specialized insects, the suspicion is created that the facts observed are to be interpreted as the result of elimination in some of the earlier stages of development. Yet, as we shall see, there is evidence to suggest that the definitive egg tubes and sperm tubes were first formed as segmental outgrowths from continuous gonads produced by the union of the primitive segmental gonads.

With most of the higher insects the reproductive organs appear from the beginning as continuous genital ridges. In the honey bee, as described by Nelson (1915), the genital ridges of the female at first extend along the splanchnic walls of the mesodermal tubes from the second to the seventh abdominal segments, inclusive. Later they become shorter and thicker, and finally reach only from near the anterior end of the fourth abdominal segment into the anterior end of the seventh.

Beyond the region of the germ cells the genital ridges are continued posteriorly, but they are here much reduced in size and consist of simple cellular strands. These parts of the ridges will form the mesodermal parts of the lateral genital ducts. It has been observed in many insects that the primitive ducts of the female in embryonic and larval stages turn downward posteriorly and are attached to the ectoderm at the posterior end of the ventral wall of the *seventh* abdominal segment. The male ducts of Orthoptera, as described by Heymons and Wheeler, extend into the *tenth* segment and are here similarly attached to the ectoderm.

Comparison with Annelida.—The early segregation of the germ cells in *Blattella* into groups within the dorsal parts of the intercoelomic septa is highly suggestive, as Heymons (1892) points out, of the similar arrangement of the germ cells in many adult Annelida, in which the gonads are simple swellings of the dissepiments, retaining the germ cells beneath a thin mesodermal epithelium. The gonads of Annelida, however, may occur on almost any part of the coelomic walls, but wherever they are formed, the germ cells are not long retained within them, being soon thrown out into the body cavity, where they mature, and from which they are eventually discharged through the nephridia, through special genital ducts, or by way of a pore or rupture in the body wall. The liberation of the germ cells into the body cavity in Annelida, Heymons claims, is represented in *Blattella* by the extrusion of the germ cells from the dissepiments before their reentrance into the mesoderm, the only difference being that in the cockroach the germ cells are not detached from the mesoderm, but migrate upon its surface to their definitive positions in the genital ridges. In *Conocephalus,* however, Wheeler (1893) observed that some of the primitive germ cells of the segmental clusters " show a tendency to leave the wall of the somite and to drop into the coelomic cavity." These cells, he says, " sometimes enlarge considerably, become vacuolated and take on the appearance of young ova."

If the condition described by Heymons in *Blattella* is truly a primitive one, it becomes evident that the definitive gonad of the Arthropoda is a secondary structure produced by the enclosure of the previously liberated germ cells in folds of the splanchnic mesoderm, which folds close over the germ cells and afford them a protected coelomic space in which to complete their development. A similar mesodermal envelope surrounds the gonads in some of the Annelida, and may be continuous with an exit duct. On the other hand, if the condition described by Wheeler in *Conocephalus* is primitive, it would appear that the segmental clusters of germ cells in the splanchnic mesoderm are the primary gonads; and even in *Blattella* Heymons observes that some of the germ cells remain within the intercoelomic septa, where they become later a part of the continuous series of germ cells contained in the genital ridges. In most other insects in which the origin of the reproductive organs has been studied, it is found that the gonads are formed as mesodermal ridges which from the beginning contain the germ cells.

By whatever method the germ cells may become aggregated in the coelomic walls, it is clear, at least, that the primary paired gonads of insects are segmentally arranged, and that the continuous genital ridges later formed are secondary structures resulting from the fusion of the series of primitive gonads on each side of the body. It would seem scarcely probable, therefore, that the subsequent division of the genital ridges into a series of ovarial or testicular tubes can represent a primitive segmental structure of the reproductive organs, though in a few adult apterygote insects and in the embryo of *Pyrrhocoris apterus* the tubes do coincide with abdominal segments. In some of the other Apterygota, and in Protura, the mature gonad is a single, elongate sac continuous posteriorly with the duct, as it is also in most other members of the Arthropoda. In such cases, however, the gonadial sac has the structure of a single secondary tube and not that of a primitive genital ridge.

Origin of the gonadial tubes.—The definitive ovaries and testes of the majority of insects consist each of a series or group of diverticula arising from the common lateral duct (fig. 3 G). The ovarian tubes are free and end in terminal filaments, which are generally united in a cluster at their distal ends. In the male the testicular tubes usually lack terminal filaments, and those of each organ are generally bound together in an investing sheath; otherwise they do not differ from the egg tubes of the female.

The differentiation of the secondary continuous genital ridges into a tertiary series of tubes has been minutely followed by Heymons (1892) in the female of *Blattella,* and most other accounts of the development of the reproductive organs show that the process is essentially the same in both the female and the male of insects having compound gonads. By a multiplication of the cells along the bases of the genital ridges each gonad in the female comes to be suspended from the splanchnopleure by a cellular sheet (fig. 3 E, *a*). This suspensorial sheet Heymons calls the *Endfadenplatte,* since it is destined to form the terminal filaments (Endfäden) of the ovarioles. A thickening of the fold along the lower border of the ridge forms a *ventral strand* of the gonad (*b*), which gives rise to the ovariole pedicles and the calyx of the oviduct; posteriorly it is continuous with the free part of the lateral duct. The middle part of the gonad (*Grm*) between the suspensional dorsal plate and the ventral strand contains the germ cells, and is therefore the germarium, or region of the primitive ovary from which are formed the egg tubes of the definitive organ.

The germ cells at this state, as described by Heymons in *Blattella,* are evenly distributed throughout the length of the median part of the gonad, and the organ increases in thickness owing to a multiplication of the germ cells. The dorsal plate now separates from the wall of the body cavity, and its flat, elongate cells become arranged in about 20 vertical rows (fig. 3 F, *TF*). These columns of cells form the terminal filaments of the definitive ovarioles. The first appearance of the egg tubes is indicated by a series of dorsal swellings of the middle region corresponding with the columns of filament cells. Then the swellings are converted into definite ovarial lobes by a deepening of the grooves between them (C), until finally the gonad is cut vertically into separate compartments as far as the ventral strand. The compartments are the ovarial tubes, each of which is covered by an epithelial layer of mesodermal cells, and contains a number of egg cells (*GCls*). In the larva of *Cloëon dimidiatum,* Lubbock (1863, 1866) observed that the ovaries are at first long cylindrical organs, each consisting of a central body with short lateral lobules. By the end of larval life the lobules have enlarged and have taken on the form of typical ovarial tubules. The developmental processes in these comparatively generalized insects would seem more probably to represent a primitive condition than that described by Seidel in the specialized hemipteron *Pyrrhocoris apterus,* in which the definitive genital tubes are said to be developed directly from independent segmental gonadial rudiments.

The exit apparatus of the egg tubes is formed from the ventral strand of the gonad, which becomes cleft between the attachments of the tubes upon it, and thus divided into the rudiments of the ovariole pedicles (fig. 3 G, *Pdcl*). The undivided part of the ventral strand and its posterior continuation become the lateral oviduct (*Odl*), the anterior end of which supporting the pedicles is widened to form the calyx (*Clx*). By a shortening of the calyx, the egg tubes of the roach become horizontal and the ovary assumes its definitive form and position. In many insects, however, as in Ephemerida, Dermaptera, Plecoptera, Phasmidae, and Acrididae, the ovarioles preserve their more primitive serial arrangement on the elongate calyx, as at an immature stage of the cockroach (G).

The development of the testes does not differ materially from that of the ovaries. The sperm tubes usually lack terminal filaments, and the division of each testis into compartments is not always apparent externally, and is sometimes incomplete. In the Lepidoptera, according to the studies of Zick (1911) on *Pieris,* the lumen of the testis is undivided until about the time of hatching, when there begins the formation of the septa which will divide the organ into four tubular sections. The septa are infoldings of the testicular wall, which grow inward toward the posterior ventral part of the organ where the duct arises.

The lateral ducts.—The primitive mesodermal exit tubes of the gonads become the lateral oviducts in the female and the vasa deferentia in the male, except in so far as they may be partially replaced by branches of the ectodermal median duct. Since the mesodermal ducts are derived from the coelomic walls, they probably originate as channels between epithelial folds continuous with the epithelial covering of the germ cells, which eventually close to form tubes. The idea that the reproductive ducts of Arthropoda are modified nephridial tubes is purely theoretical, and there is nothing to suggest that they are not, from the beginning, canals of the mesoderm formed specifically for the conduction of the germ cells to the outside of the body. Such ducts exist in some of the Annelida, and they may even unite distally in a common outlet tube (Hirudinea).

The primary mesodermal oviducts of insects undoubtedly opened to the exterior on the seventh abdominal segment, since in embryos and in young nymphal and larval stages of many modern insects they are attached to the ectoderm at the posterior end of the venter of the seventh segment. Heymons and Wheeler were the first to call attention to this condition in the more generalized insects, and the same thing has since been observed in representatives of most of the higher orders by various subsequent investigators. The subject has been so well reviewed by Nel (1930) that nothing further can be added here to substantiate the general conclusion. Nel quotes authorities to show that the termination of the mesodermal oviducts in the seventh segment is now known to occur in Thysanura, Ephemerida, Odonata, Dermaptera, Orthoptera, Hemiptera, Coleoptera, Lepidoptera, Hymenoptera, and Diptera. Though some writers say that the openings are *on* the seventh sternum, and others state that they are *between* the seventh and eighth sterna, the fact probably is the same in each case, since the "intersegmental" membranes of the abdomen are the posterior parts of the primary segments. The mesodermal oviducts retain in the adult stage the primitive position of their openings on the seventh venter, or between the seventh and eighth sterna, only in Ephemerida. The paired female gonopores of the Ephemerida are in some species widely separated, while in others they are approximated and open into a slight median depression of the intersegmental fold. In Dermaptera, however, the lateral oviducts open into a short median ectodermal pouch between the seventh and eighth abdominal sterna.

The history of the male genital ducts of insects has been less studied than that of the female ducts, but according to the elaborate embryological studies of Heymons (1890, 1895) and Wheeler (1893), the mesodermal vasa deferentia in the Orthoptera are first attached to the ectoderm of the ventral wall of the tenth abdominal segment. Paired male gonopores are retained in Ephemerida and in some Dermaptera, but they are situated on intromittent organs, or on a single organ in some Dermaptera, which appear to be evaginations of the ventral wall of the ninth segment. According to Palmén (1884) the vasa deferentia in half-grown ephemerid larvae are attached to the posterior border of the ninth abdominal venter, and the penes are formed later as evaginations of the body wall at the points of attachment of the ducts. Palmén believed that the definitive ducts opening on the penes are the ends of the primitive vasa deferentia, but Wheeler (1893) found in *Blasturus* that a considerable length of each exit tube is lined by an intima which is shed during ecdysis attached to the exuviae of the penis and the body wall. In Dermaptera it is generally conceded that the mesodermal vasa deferentia terminate in ectodermal ejaculatory ducts. In all the higher insects the vasa deferentia come together in a single, median ejaculatory duct of ectodermal origin opening on the posterior part of the ninth venter.

The median ducts.—In all insects but Ephemerida and male Dermaptera the lateral genital ducts discharge through a median outlet tube. In the male the median duct (ductus ejaculatorius) opens on the posterior part of the ninth abdominal segment, usually on an evagination forming an intromittent organ. In the female the opening of the median duct is variable; in some insects (Dermaptera) it is located on the posterior part of the seventh abdominal segment, in others on the eighth, and in still others on the ninth segment. The nature of the median female duct and the relation of the median genital opening to the paired gonopores and the paired ducts have been matters of discussion and diversities of opinion for more than a century. A historical survey of the subject from 1815, when Herold first showed that a part of the female duct system is of ectodermal origin, is given by George (1929).

In the Dermaptera, as we have seen, the lateral oviducts open into a short median ectodermal ingrowth between the seventh and eighth abdominal sterna. Several writers have asserted that the same condition exists in Mantidae and Blattidae, but, as will later be shown, this idea is based on an erroneous interpretation of the anatomical facts in the adult insects of these families. Many insects, however, in their embryonic or postembryonic development, recapitulate the primitive condition found in Dermaptera, in that the first rudiment of the common oviduct appears as a median ingrowth on the posterior part of the seventh venter, with which the approximated lateral ducts become united.

The variable position of the female genital opening in different groups of insects has created a perplexing morphological problem, but the recent work of Nel (1930) on Acrididae, and of George (1929) and Metcalfe (1932a) on the hemipteron *Philaenus* leaves no doubt that the primitive position of the median gonopore in female insects is on the posterior part of the seventh abdominal segment behind the seventh sternum, and that the definitive opening, whether on the eighth or the ninth segment, is a subsequent formation. These writers are not entirely in accord as to how the egg duct is extended from the seventh to the eighth or ninth segment, but their observations lead to the same essential conclusions.

It is agreed that the first rudiment of the median duct is formed in a late embryonic or an early nymphal stage as an ectodermal invagination on the posterior part of the venter of the seventh abdominal segment (fig. 4 A, *Odc'*). According to Nel and George the primitive gonopore (*Gpr'*) here located in Acrididae and *Philaenus* runs out into a median groove on the eighth venter. Later, the edges of this groove, beginning anteriorly, grow together and convert the channel into a cuticle-lined tube. In this way the primary opening on the seventh segment (A, *Gpr'*) is lost as the median duct is extended through the eighth segment (B, *Odc*) and acquires its definitive opening (*Gpr*) behind the sternal plate of this segment.

A second invagination is formed in most insects at the posterior end of the eighth abdominal segment, which gives rise to the sperm receptacle, or *spermatheca* (B, *Spt*). Hence, with the posterior extension of the oviduct, the gonopore and the spermathecal opening come to lie in close proximity, and the eggs may be readily fertilized as they issue from the former. Then the two openings, in the majority of generalized insects, are carried inward by the formation of a copulatory pouch, the *bursa copulatrix,* or *genital chamber* (C, *GC*), invaginated above the eighth sternum.

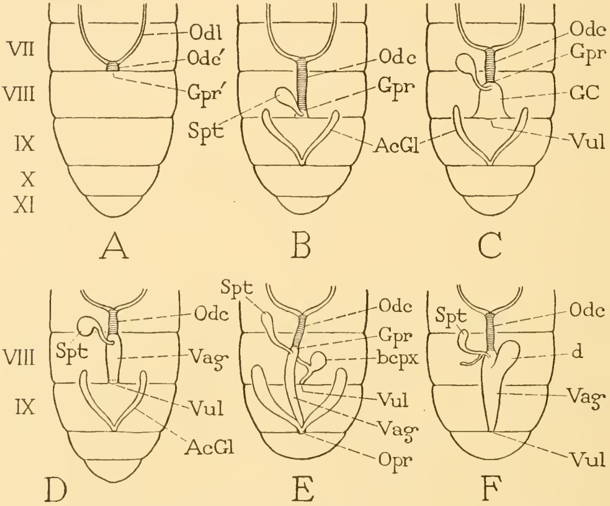

Fig. 4.—Diagrams showing the development of the median oviduct, and the evolution of the secondary copulatory structures added to the duct.

A, origin of primitive median oviduct on seventh abdominal segment.
B, extension of oviduct to end of eighth segment.
C, formation of genital chamber (*GC*) behind eighth sternum to form a copulatory and fertilization pouch receiving the oviduct and the spermathecal duct.
D, genital chamber having form of a tubular vagina (*Vag*).
E, vagina extended to ninth segment, where it opens, but retains the original copulatory opening (*Vul*) on eighth segment.
F, vagina opening only on ninth segment.

AcGl, accessory glands; *bcpx,* copulatory pouch of genital chamber; *d,* diverticulum of vagina; *GC,* genital chamber, or bursa copulatrix; *Gpr,* gonopore; *Gpr′,* primary median gonopore; *Odc,* oviductus communis; *Odc′,* primary median oviduct; *Odl,* oviductus lateralis; *Opr,* oviporus; *Spt,* spermatheca; *Vul,* vulva, ostium vaginae.

The posterior opening of the genital chamber thus becomes both a copulatory entrance, and the final exit for the fertilized eggs. It therefore may be termed the *vulva* (*Vul*). The true gonopore (*Gpr*) is still the opening of the oviduct into the genital chamber. The genital chamber, finally, may take the form of an elongate sac or a slender tube continuous with the oviduct (D). In such cases the median egg passage consists of an anterior part (*Odc*), which is the *true oviduct* (Eiergang), since it serves only for the conveyance of the eggs, and of a posterior section appropriately distinguished as the *vagina* (*Vag*). The two parts are separated approximately by the opening of the spermatheca into the anterior end of the vaginal region of the tube.

On the venter of the ninth abdominal segment there is commonly formed a third median invagination, which gives rise to the *accessory glands* (fig. 4 B, *AcGl*). The opening of these glands may be included in the genital chamber by the posterior extension of the eighth sternum, but it always lies between the bases of the ovipositor blades of the ninth segment when an ovipositor is present.

The observations of Metcalfe (1932a) on the manner by which the median oviduct becomes extended from the seventh to the eighth segment in *Philaenus* are somewhat different from those of George (1929) on the same insect and of Nel (1930) in Acrididae. According to Metcalfe there is formed primarily in *Philaenus spumarius* an oviducal invagination behind the seventh sternum, and a " uterine " invagination behind the eighth sternum. The second extends forward and overlies the first. Then the anterior opening becomes closed, and the opposing walls of the two invaginations come into contact, unite, and eventually break down, thus establishing a continuous median passage opening posteriorly through the primary " uterine " aperture behind the eighth sternum. The anterior end of the " uterine" invagination, which does not unite with the oviduct, becomes the functional sperm receptacle of the adult. It seems probable that the " uterine" invagination observed by Metcalfe represents both the true spermathecal rudiment and the genital chamber invagination of orthopteroid insects, which latter may become a vaginal section of the definitive egg passage.

In all Orthoptera and Hymenoptera and probably in most Hemiptera and Diptera, the egg exit is the secondary opening of the median oviduct established on the eighth segment, or in the intersegmental membrane behind the eighth sternum. This opening, the true gonopore, however, is usually concealed by an extension of the eighth sternum, or of the seventh sternum; and it may be carried inward within a copulatory invagination having the form of an open genital chamber, or of a tubular vagina, in which case the functional genital aperture is the vulva, that is, the external opening of the genital chamber or vagina.

In many of the other orders, however, the egg passage is subject to a further extension in a posterior direction, and its opening may then come to be on the venter of the ninth segment behind the ninth sternum. Thus, in Panorpidae, most Trichoptera and Lepidoptera, all Coleoptera, and apparently in some Hemiptera and Diptera, the median egg passage extends into the ninth segment and has an opening on the venter of this segment in common with that of the accessory glands, if these glands are present. When the egg passage is thus continued from the eighth segment into the ninth, the added part becomes an extension of the genital chamber, or of its derivative, the vagina, having its opening, the vulva, transferred from the venter of the eighth segment to that of the ninth. The primary oviduct remains unaltered; but the vaginal region of the exit tract now receives both the spermatheca and the accessory glands, and in most cases serves as a copulatory pouch.

The morphology of the extension of the efferent passage from the eighth to the ninth segment is not so clear as that of the extension of the oviduct from the seventh to the eighth segment. The ontogenetic processes involved are less simple, and it is difficult to give them a uniform interpretation.

An intermediate condition in the transference of the functional genital aperture from the eighth segment to the ninth occurs in Lepidoptera (fig. 4 E), where, in the majority of families, there is retained a copulatory opening on the eighth segment (*Vul*) leading into a copulatory pouch (*bcpx*) and the spermatheca (*Spt*), while, on the ninth segment (or the combined ninth and tenth somites) there is established a posterior vaginal opening (*Opr*) in common with the aperture of the accessory glands (*AcGl*). The copulatory opening (*Vul*) on the eighth segment is the vulva of orthopteroid insects. The tubular passage in the eighth segment leading to the vagina, with its diverticulum known as the bursa copulatrix (*bcpx*), and the part of the vagina receiving the spermatheca, together represent the genital chamber invagination of the eighth segment. The rest of the vaginal tube (*Vag*) is a secondary extension through the ninth segment. Since the posterior opening serves only for the discharge of the eggs it may be distinguished as the *oviporus* (*Opr*).

According to the account given by Jackson (1889) of the development of the female ducts and associated organs in *Vanessa io*, the definitive egg passage of Lepidoptera is formed, as we should expect, from three sections. The second and third have independent ectodermal origins; the first is formed as an outgrowth from the second. Prior to the appearance of the first rudiment, which is that of the true oviduct, there are produced by invagination of the ectoderm two median bilobed " vesicles ", one on the venter of the eighth abdominal segment, the other on the venter of the ninth segment. The lips of the anterior depression grow out in the form of two longitudinal folds, which unite to form a tube. This is the middle section of the future median passage. Its anterior end is then extended as a cellular growth into the seventh segment, where it unites with the lateral mesodermal ducts. This part becomes the anterior section (the true oviductus communis) of the definitive egg passage. The anterior vesicle gives rise also to the bursa copulatrix and to the spermatheca. The posterior section of the egg passage appears first as a groove on the venter of the ninth segment extending from the anterior vesicle to the vesicle of the ninth segment, which latter forms the accessory colleterial glands. There is thus eventually formed a continuous passage from the lateral oviducts to the ninth segment, communicating with the exterior on the eighth segment through the bursa copulatrix, and having a posterior opening at the end of the ninth segment in common with that of the accessory glands. The spermatheca opens into the dorsal wall of the tube opposite the bursa copulatrix.

In Coleoptera the female genital opening is situated on the venter of the ninth abdominal segment of the adult. According to Heberdey (1931), the rudiments of the unpaired duct and associated organs of *Hydroporus ferrugineus* appear first in a young larval stage as median invaginations on the posterior parts of the seventh and eighth abdominal segments. The bifurcate anterior ingrowth unites with the lateral oviducts ending in the seventh segment, and its median posterior part constitutes the first section (Eiergang) of the definitive outlet passage. The second section (vagina) is formed first as a groove beneath the invagination of the eighth segment, which becomes continuous with the opening of the anterior invagination, and which, by closure of its lips, produces a tube extending posteriorly from the lateral ducts, with the posterior invagination arising as a pouch from its dorsal wall. When the ninth sternal plate is formed it lies anterior to the rear opening of the tube, which latter thus comes to be on the posterior part of the ninth segmental venter. By a peculiar development in *Hydroporus*, as described by Heberdey, the median tube is divided lengthwise into an upper part (*bursa copulatrix* and *receptaculum seminis*) and a ventral part (*vagina*), the two opening separately on the ninth segment.

The development of the median female duct in *Tenebrio molitor*, as described by Singh Pruthi (1924), is somewhat different from that in *Hydroporus*, described by Heberdey. In a young pupa of *Tenebrio*, Singh Pruthi says, the median oviduct ("uterus") begins as an invagination at the posterior margin of the eighth sternum, and a "spermathecal" invagination is formed on the ninth sternum. "Gradually the walls intervening between the two organs (the mid-ventral region of the spermatheca and the mid-dorsal of the uterus) disappear so that their cavities freely communicate with each other." Thus the "uterus", Singh Pruthi says, comes to open "into the spermathecal rudiment and communicates with the exterior through the opening of the latter, behind the ninth sternite". The development of the anterior section of the oviduct from the seventh segment is evidently not recapitulated in *Tenebrio.*

The clear account of the development of the exit apparatus of the female genital system in Coleoptera as given by Metcalfe (1932) is in essential agreement with that of Singh Pruthi. In *Sitodrepa, Gastroides, Anthonomus,* and *Rhagium,* Metcalfe finds that there are formed in the prepupal period two tubular genital invaginations of the body wall (fig. 5 A, *a, b*), one opening between the eighth and ninth abdominal sterna, the other behind the ninth sternum, the second lying immediately dorsal to the first. The anterior, ventral tube (*a*) bifurcates at its anterior end, and the mesodermal oviducts eventually unite with its two arms. The posterior, dorsal tube (*b*) gives off diverticula anteriorly which develop into the sperm receptacle and "accessory" glands of the adult beetle. Finally, during the early part of pupation, the two tubes unite with each other for most of their length (B), the intervening walls disappear, and the opening of the anterior tube on the eighth venter is closed. The definitive

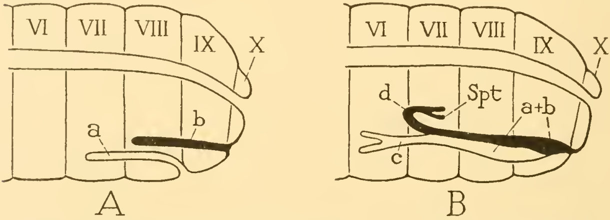

FIG. 5.—Diagrams showing the development of the female exit apparatus in Coleoptera (from Metcalfe, 1932).

A, prepupal stage of *Sitodrepa* with anterior invagination (*a*) behind eighth sternum, and posterior invagination (*b*) behind ninth sternum.
B, union of the two invaginations to form the definitive copulatory pouch and egg passage (*a* + *b*), with spermatheca (*Spt*) opening into diverticulum (*d*) of its anterior end.

egg passage thus comes to be a single median tube opening behind the ninth sternum, receiving the lateral oviducts into its bifurcate anterior section (*c*), and having a dorsal diverticulum (*d*) shortly behind the branches, into which open the sperm receptacle (*Spt*) and associated glands later formed.

If the ontogenetic development of the female exit apparatus in Coleoptera as given by Singh Pruthi and by Metcalfe represents the phylogenetic course of evolution in this order, it would appear that the sperm receptacle of Coleoptera is not homologous with the spermatheca of other insects, which always (except possibly in Diptera) takes its origin at the posterior margin of the eighth segment, and is subsequently associated with the genital chamber invagination found here. There is little in the adult structure of the female organs in Coleoptera, however, to suggest that the exit apparatus in this order is in any way fundamentally different from that of other insects. The large vaginal tube or sac (fig. 4 F, *Vag*) opening on the ninth segment usually has a dorsal pouchlike diverticulum (*d*), generally called the " bursa copulatrix ", which it probably is in function. The sperm receptacle opens either into the anterior part of the vagina (fig. 4 F), or into the diverticulum of the latter (fig. 5 B). Accessory glands are usually absent. Since the genital tract in the mature condition has only the single opening on the ninth segment, this aperture becomes in a functional sense the vulva (*Vul*), though anatomically it corresponds with the oviporus of Lepidoptera (fig. 4 E, *Opr*).

In Diptera it is usually said the female genital opening lies on the venter of the eighth segment behind the eighth sternum, and it apparently does have this position in most families. According to Metcalfe (1933), however, the opening occurs on the ninth segment in the cecidomyid *Dasyneura leguminicola*. The development of the female efferent system in this insect, moreover, is shown by Metcalfe to be closely parallel with that found in Coleoptera. The definitive egg passage, she says, is the product of a union between an ectodermal invagination arising posterior to the eighth abdominal sternum, and another formed posterior to the ninth sternum. The first branches anteriorly, and its arms unite with the mesodermal oviducts; the anterior end of the second gives rise to the spermathecae and the accessory glands. By a closure of the anterior opening, the secondarily continuous passage has its exit through the posterior opening on the ninth segment. Thus, in *Dasyneura*, as in Coleoptera, it would appear that the sperm receptacles are derived from the invagination of the ninth segment, and not from that of the eighth, as in other insects.

When the vaginal opening lies behind the ninth sternum it may come into juxtaposition with the anal opening, particularly when the terminal segments of the abdomen are reduced or partly suppressed, and in some cases, as in Lepidoptera and certain Trichoptera, the vagina and rectum open together into an ectodermal depression, or *cloaca,* which constitutes the extreme posterior extension of the median egg passage.

The position of the functional female genital opening of pterygote insects is now seen to be so variable in different orders, and even within a single order (Hemiptera, Lepidoptera, Trichoptera, Diptera), that it can be given little value as a character for determining the relative positions of groups in classification. Thus, as shown by Busck (1931) in the Lepidoptera, several of the more generalized families in both the Jugatae and the Frenatae have only the posterior opening on the ninth segment, while all the otherwise more specialized families retain the anterior opening on the eighth segment together with an opening on the ninth.

The genital openings of Collembola and Protura.—The unusual positions of the genital openings in Collembola and Protura produce conditions in these groups which are different from those in any of the other Hexapoda.

The abdomen of Collembola contains not more than six segments, and the median gonopore, in both the male and the female, is situated on the posterior part of the fifth segment, or between this segment and the sixth. The Collembola, therefore, in this respect, present either a condition having no relation to that in the other insects, or one produced secondarily by specialization. If we assume that the small number of segments in the collembolan abdomen is the result of a suppression of segments in both the pregenital and postgenital regions, the problem of the position of the genital opening presents no special difficulties. On the other hand, if the six segments of the abdomen represent the maximum abdominal segmentation ever attained in this group, then the common genital opening may be a primitive subterminal aperture. But again, if the Collembola are descended from insects having the usual number of somites in the abdomen, and the posterior segments have been suppressed, then we must assume that the genital apertures have undergone an anterior migration. The general structure of the Collembola suggests a high degree of specialization on a low plane of insect organization.

The Protura present a different kind of problem, relative to the genital openings, from that presented by the Collembola, for here the gonopores, situated in both sexes between the eleventh and twelfth abdominal segments, are evidently the primitive paired openings of the lateral genital ducts, which remain separate in the male, but unite in a median exit in the female. The position of the gonopores in this group might be taken as indicating that at some remote time in the phylogenetic history of the Hexapoda the lateral mesodermal ducts of both sexes opened just before the terminal body segment, as they do in Chilopoda. In this event, the paired openings on the tenth and seventh segments of insects are phylogenetically secondary, and, if so, it becomes an interesting subject for speculation as to how they may have been established on these segments.

Theoretical considerations.—Tillyard (1930) has pointed out that under the term " opisthogoneate " there is included within the Hexapoda a variation of six segments in the position of the genital openings, one extreme being represented by the Collembola with the gonopore on the fifth abdominal segment, the other by the Protura with the gonopores on the eleventh segment. The discrepancy is somewhat exaggerated, however, by including the Collembola, since the collembolan gonopore is a median genital opening, which, as we have seen, is secondary and subject to migration. The variation of the primitive lateral gonopores in Hexapoda is thus only from the seventh to the eleventh segments—a distance of four somites. To account for this variation, and for the greater variation in other arthropods that brings about the " progoneate " condition, Tillyard proposes the assumption that the primitive arthropods had segmentally paired gonads, and that each gonad had an individual segmental duct. The second part of this assumption finds little support in the known facts of the embryonic development of the insect gonads or their ducts. The investigations of Heymons (1892) and of Wheeler (1893), as shown above, have made it clear that the only stage in which the reproductive elements have a segmental arrangement is that in which the germ cells become segmentally arranged in the dorsal part of the splanchnic mesoderm. But at this stage there are no exit ducts. The condition is in every way parallel with that in the Annelida, and it is only at this early ontogenetic period that a comparison can be made between the Annelida and the Arthropoda with respect to the reproductive organs. The definitive gonads and the genital ducts of most insects are formed as continuous mesodermal structures, and the later subdivision of the gonads into tubules is generally a secondary process in ontogenetic development. Though the tubules may take a segmental arrangement, they never have separate, segmental ducts to the exterior of the body.

According to Wheeler's (1893) concise account of the development of the genital ducts in *Conocephalus,* the embryonic male ducts end in hollow enlargements, or terminal ampullae, situated at first in the appendage rudiments of the tenth abdominal segment (fig. 3 B, *e*); the female ducts, which likewise terminate with ampullae, end in the appendage rudiments of the seventh abdominal segment. The female, however, Wheeler observes, has also a pair of ampullae in the tenth segment appendages, which appear to be homologues of the male ampullae. The account given by Heymons (1890, 1895) of the genital ducts in Dermaptera, Blattidae, and Gryllidae is essentially in agreement with that of Wheeler for *Conocephalus* in so far as the male ducts are described as terminating in mesodermal ampullae in the tenth segment, and the female ducts in ampullae of the seventh segment. According to Heymons, however, there is evidence of a primary branching of the ducts in each sex to both the seventh and tenth segments. Wheeler, on the other hand, believes that male insects never have ampullae or branches of the genital ducts in the seventh segment. Heymon's illustration of *Forficula* (fig. 3 D) gives a convincing example of the branching of a genital duct to the two segments, but his identification of the posterior branch (*d*) as the definitive oviduct is evidently wrong, since the definitive female ducts in Dermaptera open on the seventh segment.

From the above we might deduce, as a plausible explanation of modern conditions, the theory that at some period in the phylogenetic history of insects, the mesodermal ducts of the gonads opened in each sex on the bases of the appendages of the tenth abdominal segment, and that later the ducts in the female developed branches to the seventh appendages and lost the primitive connections with the tenth appendages. The reverse assumption, namely, that the openings on the seventh segment are primitive in both sexes, and those to the tenth segment secondary in the male, would appear to be disqualified by the subterminal position of the genital apertures in both sexes of Onychophora, Chilopoda, and Protura. It seems scarcely necessary to accept the view of Heymons (1890) that primitive insects were hermaphroditic. The theory of the branching of the genital ducts offers a possible explanation of the differences in position of the dual genital openings among the Insecta, and makes it possible to derive this condition from the more primitive condition retained in Chilopoda and Protura. The theory at least is in accord with the known facts of embryonic development.

III. THE OVIPOSITOR OF THYSANURA

Among the Apterygota an ovipositor is well developed in the Thysanura. In Dicellura and Collembola the organ is entirely absent; and the female genital armature of the Protura can scarcely be supposed to have any relation to the egg-laying organ of the true Insecta, since it arises from between the eleventh and twelfth segments of the abdomen. No structure homologous with the insect ovipositor occurs in any arthropods other than the insects.

The thysanuran ovipositor is composed of four processes arising from the stylus-bearing lobes of the eighth and ninth abdominal segments. These lobes, commonly designated " plates ", are generally conceded to be the bases (" coxites ") of true abdominal limbs. The pterygote ovipositor differs from that of the Thysanura only in its greater complexity; an essential part of its structure consists of four basal lobes, or plates, that appear without question to be direct homologues of the bases of the thysanuran gonopods. Hence, on the evidence of the limb origin of the component parts of the ovipositor in Thysanura, the parts of the pterygote ovipositor must have had the same origin. Considering, therefore, the many respects in which the Thysanura, particularly the Lepismatidae, show that they are more closely related to the Pterygota than are any other of the apterygote forms, we may reasonably assume that the ovipositor had its inception in the common ancestors of these two groups of insects, and that it has been formed by special modifications of the appendages of the eighth and ninth abdominal segments.

The Machilidae are in many respects more primitive in their structure than are the Lepismatidae; the structure of the abdomen in Machilidae is more generalized even than in any other family of the Apterygota. The relatively primitive condition of the machilid abdomen is shown particularly in the well-known fact that the bases of the appendages, throughout the visceral and genital regions, are distinct from the small median sterna. The abdominal limb bases form a double series of large, stylus-bearing plates intervening between the terga and the sterna, though the two plates of each segmental pair are usually united with each other in the median line posterior to the sternum. Each so-called " plate ", however, is really the ventral wall of a flattened lobe, the membranous dorsal wall of which is reflected into the intersegmental membrane between its segment and the segment following. The stylus is borne in a notch on the distal apical margin of the lobe, and the stylus muscles arise on the anterior margin of the ventral plate. Mesad of the stylus the limb base lobe of most of the pregenital appendages bears on its distal margin also one or two retractile and eversible vesicles, the muscles of which take their origins on the ventral plate. Vesicles are never present on the gonopods.

That the stylus-bearing plates of the Machilidae are the bases of the abdominal appendages is here taken for granted, and is made the basis for all subsequent discussions in this paper on the morphology of the ovipositor. The assumption seems to have ample support from embryology; but, if the plates in question should be shown to be something else than the basal elements of appendages, it will be necessary only to change their names; their relations to structures evolved from them in the Pterygota will not be altered. The abdominal styli of the Thysanura support the abdomen and play an active part in the locomotion of the insect. The writer has elsewhere (1931) discussed the evidence bearing on the morphology of the styli, showing that, while there is much reason for believing that the styli and their homologues in various pterygote larvae are the rudimentary telopodites of the abdominal segments, the question cannot be regarded as settled; the styli may be basal epipodites of the appendages, from which the telopodites have entirely disappeared.

The writer has not been able to make an exact study of the abdominal musculature in the Thysanura, but even with poorly preserved specimens it can easily be seen that each stylus-bearing plate of the abdomen is amply provided with lateral muscles that take their origin on the abdominal terga. In fact, it appears that all the dorsoventral muscles of the abdomen in the Machilidae are attached ventrally on the stylus-bearing plates, there being no muscles of any kind connected with the small median sternal plates. It would thus seem that in the Thysanura the lateral body musculature of the abdomen is formed entirely of the tergal musculature of the limb bases. In studying the abdomen of pterygote insects the writer (1931) was led to make the statement that no evidence was found suggesting the derivation of the lateral abdominal musculature from the muscles of the limb bases; and this is true, since in exopterygote larvae that preserve distinct limb base lobes on the abdomen, none of the body muscles is attached directly on the limb bases. The diversification of the muscle attachments in adult Pterygota, in which some of the lateral muscles may be tergopleural and others tergosternal, cannot be taken as evidence of a primitive condition, since it is evidently an adaptation to the mechanism of respiration and of other body movements. Likewise, in endopterygote larvae a secondary specialization in the musculature may obscure the primitive muscle pattern. The condition in the Machilidae, however, is perhaps more significant; it might be interpreted as indicating a derivation of the lateral body musculature from the primitive leg muscles, though the extreme reduction of the sterna must be taken into account as a factor bringing about a secondary transposition of some of the body muscles to the expanded limb bases.

The gonopods, or appendages of the eighth and ninth abdominal segments, differ in female Thysanura from the appendages of the pregenital segments in that they lack eversible vesicles, and that each is provided with a long genital process, or gonapophysis (fig. 6 B, C, *1Gon, 2Gon*). The basal plates of each segmental pair of gonopods also are not united with each other. The gonapophysis is a slender hollow extension from the dorsal aspect of the median proximal angle of the basis of the gonopod (fig. 7). Its sclerotic wall is continuous with that of the ventral plate of the basis, and the genital process is thus not articulated with the latter, as in the stylus; but, being flexible at its base, the gonapophysis is movable, and it is provided with short muscles (A, *gmcl*) arising on the basal plate mesad of the longer muscles of the stylus (*smcl*). In some of the Thysanura, as in *Nesomachilis* (fig. 7), the four gonapophyses of the ovipositor are individually free structures, except that those of the ninth segment (B) are united at their bases; in others, however, as in *Thermobia* (fig. 6 E), the gonapophyses of the second pair are fused with each other throughout the length of the ovipositor, and only those of

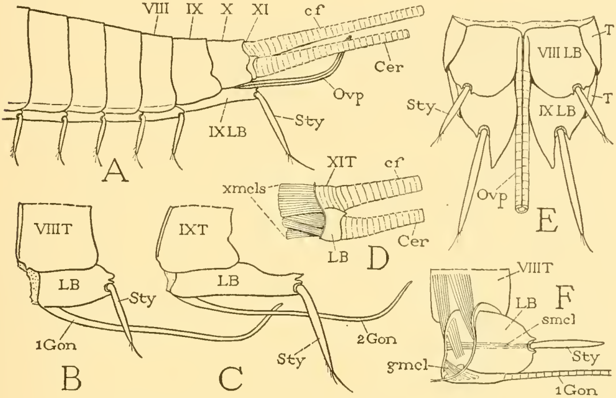

FIG. 6.—The ovipositor and terminal structures of female Thysanura.

A, abdomen of *Machilis*, showing the styli (*Sty*) in position in life.

B, C, genital segments of *Machilis*, showing gonapophyses (*Gon*) arising from limb base plates (*LB*).

D, bases of caudal filament (*cf*) and cercus (*Cer*) of *Machilis*, with muscles of tenth segment.

E, genital segments and base of ovipositor of *Thermobia*, ventral view.

F, diagrammatic figure of the principal muscles of first gonopod of *Thermobia*.

the first pair are free processes. The length and shape of the ovipositor vary somewhat in different Thysanura; in *Machilis* (fig. 6 A) the distal part of the organ is abruptly bent upward.

The morphological origin of the gonapophyses cannot be determined from the evidence at hand. The structures are treated in this paper as being processes of the gonopod bases having the nature of endite lobes. Some writers prefer to regard them as the true telopodites of the genital appendages, but their limitation to the gonopods, their origins from the proximal parts of the latter, their special function, and the fact that they never show a leglike form seem to be suggestive, rather, that the gonapophyses are secondary structures developed on the appendages of the eighth and ninth abdominal segments in adaptation to the special function these appendages have assumed.

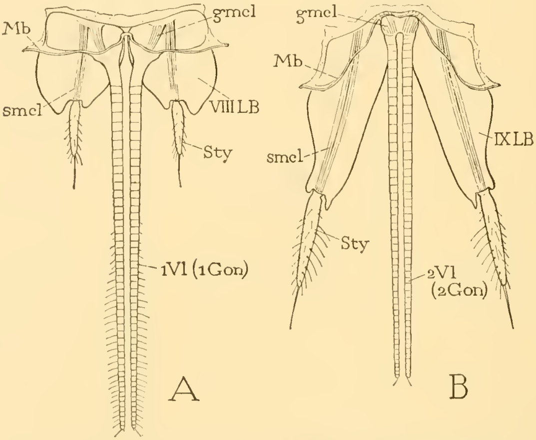

FIG. 7.—Female gonopods of *Nesomachilis maoricus,* dorsal view.

Note in each appendage muscles from basal plate to stylus (*smcl*) and to gonapophysis (*gmcl*).

The bases of the thysanuran gonopods, in conformity with the bases of the pregenital appendages, are well equipped with muscles arising on the terga of their respective segments (fig. 6 F). Some of these muscles of each appendage are inserted on the plate forming the ventral wall of the limb basis, and others at the inner margin of its membranous dorsal wall. Smaller groups of median, longitudinal fibers, apparently intersegmental muscles, are attached near the base of the gonapophysis and evidently act as protractors and retractors of the latter. An exact study of the gonopod musculature could not be made on the material at hand, but there is no doubt that each gonopod, as indicated somewhat diagrammatically at F of figure 6, is movable as a whole by the tergal muscles inserted on its base (*LB*). The gonapophysis, on the other hand, is movable individually on the basis by the group of short fibers (*gmcl*) arising in the latter, and inserted within its proximal end. The stylus (*Sty*), being set in a membranous socket on the distal margin of the basis, is freely movable by its long muscles (*smcl*) arising on the proximal margin of the basal plate. In *Thermobia* the gonapophysis of the ninth segment is attached directly to a small sclerite lying in a notch of the base of the large stylus-bearing plate, but the small sclerite is evidently a secondary subdivison of the larger one.

The postgenital segments of the Thysanura are more generalized in some members of the group than they are in any of the Pterygota. The tenth segment is a complete annulus (fig. 6 A, *X*), but it lacks appendages in postembryonic stages, as it does in all the more generalized Pterygota. The small eleventh segment (A, *XI*) is normally concealed within the tenth segment, but it bears the cerci (*Cer*) and the long median caudal filament (*cf*). In *Nesomachilis* the body of the eleventh segment, when removed from the tenth (D), is seen to consist of a dorsal arch (*IXT*) produced into the caudal filament (*cf*), of two lateral lobes (*LB*), evidently the bases of the cercal appendages (*Cer*) which they support, and of a narrow, membranous venter bearing the two paraproctial lobes. The cerci appear to have no muscles arising in their own bases, but the tenth segment is filled with a mass of intersegmental fibers (D, *xmcls*) attached posteriorly on the anterior margin of the eleventh segment. Some of these fibers, inserted at the bases of the cerci, serve to move the cerci. The twelfth segment, or periproct, is practically obliterated, but in some species of Thysanura there is a small, fleshy dorsal lobe beneath the base of the caudal filament, possibly a remnant of the lamina supra-analis of the telson.

In order better to compare the structure of the pterygote ovipositor with that of the ovipositor of Thysanura, we may briefly summarize the principal features of the simple thysanuran ovipositor as follows:

1. The thysanuran ovipositor consists of two pairs of processes (the first and second gonapophyses), and of two pairs of basal plates belonging to the eighth and ninth abdominal segments, respectively.

2. The gonapophyses are continuous with the mesal proximal angles of the basal plates, and each is provided with a short muscle arising on the supporting plate.

3. The basal plates of the ovipositor are evidently the bases of the appendages (gonopods) of the eighth and ninth abdominal segments. Each bears a gonapophysis proximally and a stylus distally, and is equipped with dorsal muscles arising on the tergum of its segment.

4. The styli of the thysanuran gonopods do not form a part of the ovipositor, but serve to support the end of the abdomen, and are active in the locomotion of the insect. Each is movable by muscles arising proximally in the basal plate on which it is borne.

IV. GENERAL STRUCTURE OF THE PTERYGOTE OVIPOSITOR AND ASSOCIATED ORGANS

There appears to be little doubt that the pterygote ovipositor is an organ formed of the appendages of the eighth and ninth abdominal segments, and that it is, therefore, homologous with the ovipositor of the Thysanura. If, in the embryonic development, the blades of the pterygote ovipositor appear to arise directly from the ventral walls of the genital segments, it is probable that the apparent venter of each segment includes the areas of the limb bases and the sternum. In the definitive condition the limb bases are always distinctly differentiated from the sterna. Associated with the base of the ovipositor are typically three internal organs formed by median invaginations of the ectoderm. The first is the *median oviduct,* the second is the *spermatheca,* the third is a pair of *accessory glands.* Finally, there may be formed cavities at the base of the ovipositor, covered by a posterior extension of the eighth sternum, and of the seventh sternum. These cavities are the *genital chamber* above the eighth sternum, and the *vestibulum* above the seventh sternum.

THE GENITAL INVAGINATIONS

The three median genital invaginations of female insects, namely, the oviduct, the spermatheca, and the accessory glands, have anatomically metameric relations to one another, since primarily they are developed on successive segments (fig. 8 A) ; but it has not been shown that there is any morphological significance in this fact.

The oviductus communis, as shown in section II, first appears in the embryo, nymph, or larva of many insects as a median ingrowth on the posterior part of the venter of the seventh abdominal segment, or in the intersegmental membrane between the seventh and eighth sterna.

We may assume, therefore, that the first of the three median genital invaginations occurred primitively on the posterior part of the seventh venter, and that, by union with the mesodermal oviducts (fig. 8 A, *Odl*), it became the primary median outlet tube of the ovaries, or *oviductus communis* (*Odc′*). The duct retains the primitive position of its opening in adult insects only in Dermaptera.

The second median genital invagination is formed on the posterior part of the venter of the eighth abdominal segment (fig. 8 A, *Spt*), and gives rise to a pouch for the reception of the spermatozoa. This invagination is the *spermatheca,* or *receptaculum seminis.* The spermatheca is usually a single organ, though it may be double or triple. A diverticulum of its duct commonly forms a tubular spermathecal gland.

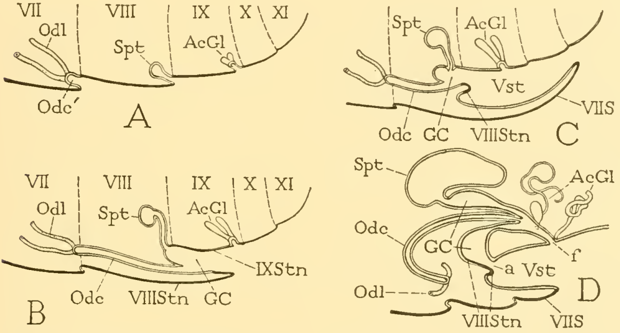

FIG. 8.—Diagrams showing positions of ducts and associated structures of the female genital apparatus.

A, primitive condition, with median oviduct (*Odc′*) opening on seventh segment, spermatheca (*Spt*) on eighth segment, and accessory glands (*AcGl*) on ninth segment.

B, usual condition, with oviduct (*Odc*) extended to end of eighth segment, where it opens together with spermatheca (*Spt*) in a genital chamber (*GC*) formed above eighth sternum.

C, genital chamber (*GC*) enclosed in a vestibulum (*Vst*) formed above seventh sternum (*VIIS*), accompanied by a reduction of eighth sternum (*VIIIStn*).

D, unusual structure in *Magicicada,* in which genital chamber (*GC*) opens from vestibulum by the primary copulatory aperture (*a*), but discharges the eggs through a secondary posterior opening (*f*).

The third median genital invagination is formed on the venter of the ninth abdominal segment (fig. 8 A, *AcGl*). It is typically bifurcate, and gives rise to the *accessory glands* of the female genital apparatus. These glands usually have a colleterial function, since they discharge a substance for attaching the eggs to a support, or for agglutinating the eggs to one another, but the secretion may also be used to form an egg covering, or an egg capsule, and in the stinging Hymenoptera one of the glands produces an irritant or toxic liquid. In some insects the accessory glands are absent, and their function may be assumed by special glandular parts of the oviducts.

The median oviduct and the spermatheca have no homologues in the male insect; but it seems possible, as some writers claim, that the male ejaculatory duct and mucous glands are derived from the same invagination of the ninth segment that forms the accessory glands of the female.

The oviductus communis, in all insects but Dermaptera, becomes extended posteriorly. In most insects the definitive opening of the median oviduct (fig. 8 B, *Odc*) is carried back to the posterior part of the eighth segment, and comes to lie just before the opening of the spermatheca (*Spt*) behind or above the eighth sternum.

Insects having the aperture of the definitive egg passage situated on or behind the ninth abdominal segment include some species of Hemiptera, Parnorpidae, and Diptera, most Trichoptera, and all Lepidoptera and Coleoptera. An opening on the eighth segment in conjunction with that on the ninth is retained in most adult Lepidoptera, and, as we have seen, occurs in immature stages of Coleoptera. A similar opening on the eighth segment is present also in species of Cicadidae in which the genital chamber opens posteriorly on the ninth segment. The trichopterous families Limnophilidae and Phryganiidae preserve the more primitive condition in that the female genital aperture is on the eighth abdominal segment just behind the eighth sternum. In *Panorpa* the oviductus communis, the spermathecal duct, and the duct of the accessory glands discharge into an open cavity in the ventral part of the ninth segment. This cavity is a simple invagination of the body wall widely open laterally and posteriorly above and behind the edges of the somewhat enlarged sternal plate of the ninth segment, and its lumen corresponds with the genital chamber of more generalized insects, though it is closed below by the *ninth* sternum. The anus of Panorpa lies on the ventral surface of the very small eleventh segment of the female. In trichopterous forms having the female genital aperture behind the ninth sternum, the oviduct, the spermatheca, and the accessory glands open likewise into a common chamber, but the latter is here entirely enclosed within the body, and has a small aperture at the base of the terminal (tenth) segment in common with the rectum. In Coleoptera the part of the egg passage beyond that formed of the true median oviduct takes the form of a vaginal tube, and may be produced into a large copulatory pouch.

The egg duct in all Lepidoptera opens at the end of the ninth abdominal segment, or on a terminal segment which is evidently the united ninth and tenth somites. The statement made by Petersen (1900) that the single genital aperture in *Hepialus* and other Jugatae is on the eighth abdominal segment has not been substantiated by subsequent investigators. It has recently been shown by Busck (1931) that the posterior aperture is always on the ninth segment (or on the combined ninth and tenth somites) and that the single, posterior opening is a feature not only characteristic of the Jugatae but occurring likewise in several of the lower families of the Frenatae. It is thus somewhat surprising to find that in the Lepidoptera the more primitive, anterior opening has been suppressed in the more generalized families, but the explanation lies in the fact that the posterior position of the oviporous is correlated with the tubular extension of the abdomen to form an "ovipositor". There is no clear distinction in the egg passage of the Lepidoptera between the true oviducal part of the tube and the vagina, but the opening of the spermatheca into the tube probably marks the anterior end of the secondarily added vagina.

THE GENITAL CHAMBER AND THE VESTIBULUM

The formation of external cavities at the base of the ovipositor concealing the gonopore and the opening of the spermatheca, and sometimes the opening of the accessory glands, results from the invagination of the body wall at the base of the ovipositor, usually accompanied by a posterior extension of the eighth or of the seventh sternum. The sternum concealing the cavity is known as the *subgenital plate;* in some insects it is the eighth, in others the seventh.

The cavity here defined as the *genital chamber,* or *bursa copulatrix* (fig. 8 B, *GC*) is that formed by an invagination of the part of the body wall above the end of the eighth sternum in which are situated the openings of the median oviduct and the spermatheca. The ventral wall of the genital chamber may contain the reflected posterior part of the eighth sternum. The oviductus communis (*Odc*) opens either on the floor of the genital chamber or into its anterior end. The spermatheca (*Spt*) opens typically in the dorsal wall of the chamber, morphologically posterior to the gonopore. The actual relation of the two openings to each other, however, varies on account of the variable position of the gonopore, the latter, when located on the floor of the genital chamber, being below and often behind the point at which the spermatheca opens into the dorsal wall of the chamber.

In some insects the spermatheca appears to arise from the dorsal wall of the median oviduct, but it is probable that in all such cases the part of the median egg passage receiving the spermathecal duct is formed as an extension of the genital chamber. There can be no doubt, for example, that the copulatory pouch of the cicada (fig. 32, *GC*) or of the honey bee (fig. 44 B, *b*), into which the spermatheca opens, is a part of the genital chamber, and it seems equally certain that the so-called " uterus " of viviparous Diptera is likewise a special compartment of the genital chamber. Since in most cases the genital chamber receives the male organ during mating, it is functionally a " bursa copulatrix ". When the genital chamber, or an anterior part of it, however, takes the form of a tubular passage leading back from the true oviduct, it should be called the *vagina,* as by Demandt (1912, Korschelt, 1924) in *Dytiscus,* and by Imms (1930), Heberdey (1931), and others, to distinguish it from the true *oviductus communis* (Eiergang). Much confusion exists in descriptive works as to the distinction between median oviduct and genital chamber, or vagina. A safe rule to follow is that the oviduct lies anterior to the mouth of the spermatheca, and the genital chamber (vagina, or " uterus ") posterior to it.

Morphologically the terminus of the oviductus communis in the genital chamber, or vagina, should be distinguished from the posterior opening of the latter to the exterior. The opening of the oviduct is the true *median gonopore,* whether exposed externally, or concealed in the genital chamber; when the genital chamber is converted into a copulatory pouch or a vaginal tube with a narrowed exit, its posterior opening, whether on the eighth or the ninth segment, is the *ostium vaginae,* or *vulva.*

When the seventh sternum is extended beyond the eighth sternum (fig. 8 C), the latter (*VIIIStn*) is generally reduced in size, and may become rudimentary, or it is retained only as a small plate on the floor of the genital chamber containing the gonopore. This condition is characteristic of Termitidae, Blattidae, Hemiptera, and Hymenoptera.

The extension of the seventh abdominal sternum beyond the eighth produces a second cavity (fig. 8 C, *Vst*) lying above the seventh sternum, which becomes an antechamber to the primary genital chamber (*GC*), or a continuation of the latter, and may be distinguished as the *vestibulum.*

With insects that retain a generalized structure in the genital segments, the base of the ovipositor usually lies in the genital chamber, and the eggs discharged from the gonopore located on the floor of the chamber are passed into the channel of the ovipositor between the bases of the first valvulae. This condition is well illustrated in Acrididae, Tettigoniidae, and Gryllidae. Since the first valvifers, however, are always distinct from the eighth sternum, they may be displaced posteriorly to such an extent that the ovipositor base lies entirely posterior to the genital chamber. This condition is found especially in insects in which the seventh sternum is prolonged, for in such cases the eighth sternum is generally reduced (fig. 8 C, *VIIIStn*) and the genital chamber (*GC*) becomes a mere pocket of the anterior wall of the vestibulum (*Vst*). An unusual condition, to be described in detail later, occurs in some of the Cicadidae, in which the highly developed genital chamber has a second posterior opening on the ninth venter (fig. 8 D).

THE OVIPOSITOR

An ovipositor formed from appendicular processes of the abdomen is in general present only in insects having the female genital opening on the eighth abdominal venter, or between the eighth and ninth sterna. With the transposition of the genital opening to the ninth segment, the ovipositor has been suppressed in all cases (except in Cicadidae having two genital openings, in which the egg passage leads directly into the channel of the ovipositor; and it should be noted also that the female exit apparatus of the Homoptera in general is not well understood). Apparent rudiments of the gonopods of the ninth segment, however, may be retained, as in Panorpidae and Coleoptera. A comparative study of the plates and appendicular structures associated with the female genital opening in Coleoptera has been made by Tanner (1927), who claims that the terminal hooks or spurs are styli; but the general structure and musculature of the organs does not correspond closely with that of the parts of a typical ovipositor belonging to the ninth segment. The principal groups of pterygote insects in which an ovipositor is well developed are the Orthoptera, Hemiptera, Thysanoptera, and Hymenoptera. In various other orders, however, an ovipositor may be present in some members, either as a fully developed organ or in a rudimentary form. The fundamental structure of the ovipositor is always the same, and the wide occurrence of the organ suggests that an ovipositor formed of the appendages of the eighth and ninth abdominal segments was a character of the common ancestors of the Thysanura and Pterygota.

The pterygote ovipositor, in its typical form, consists of a shaft and a basal mechanism, and usually includes a pair of accessory lobes.

The shaft is composed generally of two pairs of bladelike processes, the *first* and *second valvulae* (fig. 9, *1Vl, 2Vl*). The basal mechanism consists essentially of four lobes or plates, the *first* and *second valvifers* (*1Vlf, 2Vlf*), associated with the eighth and ninth segments of the abdomen, together with their connected muscles. The accessory lobes, or *third valvulae* (*3Vl*), are borne at the posterior ends of the second valvifers. In some insects the basal structure of the ovipositor includes median sclerites lying between the second valvifers, known as the *intervalvulae,* and also muscles inserted on these sclerites. The first and second valvulae arise from the anterior ends of the first and second valvifers, respectively. The third valvulae, arising from the posterior ends of the second valvifers, are usually free lobes, but in most Orthoptera they form a third pair of blades in the shaft of the ovipositor. The first valvifers in the Hemiptera are closely associated with the lower margins of the eighth tergum, though they are united by mesal extensions with the ninth tergum; in Orthoptera and Hymenoptera they become more or less displaced posteriorly, and articulated with the ninth tergum, or with the second valvifers. The second valvifers are always associated with the ninth tergum. The dorsal muscles of the first valvifers, regardless of the position of the plates themselves,

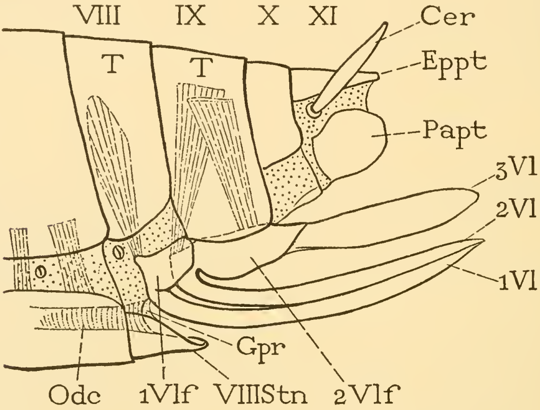

Fig. 9.—Diagram of the basic structure of the pterygote ovipositor.

Each gonopod consists of a basal plate, or valvifer (*1Vlf, 2Vlf*), and a gonapophysis, or valvula (*1Vl, 2Vl*); each valvifer provided with muscles arising on the tergum of its segment; the basis of second gonopod produced distally in a free lobe, the third valvula (*3Vl*); gonopore (*Gpr*) at base of ovipositor above eighth sternum.

invariably take their origin on the eighth tergum (fig. 9); the dorsal muscles of the second valvifers arise on the ninth tergum.

From this sketch of the more generalized structure of the ovipositor in pterygote insects it is clear that the organ may be derived theoretically from a pair of genital appendages having the same structure and the same relations to the eighth and ninth segments of the abdomen as have the female gonopods in the Thysanura. Thus we may conceive that the parts of the pterygote ovipositor belonging to the eighth segment (fig. 10 A) represent the limb bases (*LB*) of a pair of gonopods, which become the first valvifers (B, *1Vlf*), and a pair of corresponding gonapophyses (A, *Gon*), which become the first valvulae (B, *1Vl*). The styli of the first gonopods (A, *Sty*) are absent in all pterygote insects (B). The gonopore (A, *Gpr*) is located typically behind or above the posterior margin of the primitive sternum of the eighth segment (*Stn*), but between the proximal ends of the limb bases. It is, then, but a secondary matter if the limb base plates, or valvifers, of the eighth segment become more or less dissociated from the eighth segment (B) and variously connected with the ninth tergum or with the second valvifers. As above noted, the first valvifers, regardless of their displacement, retain their muscle connections with the eighth segment. The parts of the pterygote ovipositor belonging to the ninth segment may be supposed in the same way to represent corresponding parts of the second gonopods of Thysanura, the second valvifers (fig. 10 C, *2Vlf*) being limb bases, and the second valvulae (*2Vl*) the second gonapophyses.

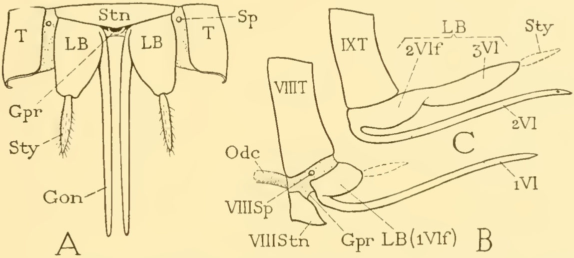

FIG. 10.—Analytical diagrams of the morphology of the pterygote ovipositor.

A, ventral view of theoretical generalized structure of eighth segment and gonopods (cf. fig. 6 E, fig. 7 A).

B, lateral view of generalized eighth segment and first gonopod; stylus absent in all pterygote insects.

C, lateral view of generalized ninth segment and second gonopod; basis of gonopod (*LB*) subdivided into second valvifer (*2Vlf*) and third valvula (*3Vl*), stylus (*Sty*) sometimes present.

The terminal lobes of the second valvifers (figs. 9, 10 C, *3Vl*) might suggest by their usual position that they are the styli of the second gonopods; but, as will be shown presently, it is certain that they are secondary outgrowths of the gonopod bases. They are here termed "third valvulae" because in the Orthoptera they resemble the first and second valvulae, and form a third pair of blades in the shaft of the ovipositor. Usually the third valvulae ensheath the distal part of the ovipositor between their concave inner surfaces.

The sclerites termed intervalvulae, lying between the bases of the second valvifers, evidently belong to the venter of the ninth segment, and probably represent sclerotic remnants of the ninth sternum.

A review of the history of opinion concerning the morphology of the insect ovipositor would occupy more space than its value would justify. The theory here elaborated is essentially that now current with students of insect anatomy, except that it has not been generally recognized that the first valvifers are the bases of the first gonopods. Some writers have claimed that these plates bearing the first valvulae are derived from the eighth sternum, and others that they are a part of the ninth tergum. The difference of opinion has arisen probably from the fact that the position of the first valvifers relative to the surrounding parts differs considerably in different insects according to the mechanism of the ovipositor. In some insects the plates clearly belong anatomically to the eighth segment, since they lie in the pleural areas of this segment between the tergum and the sternum; in others they are dissociated from the eighth segment and are hinged to the second valvifers; in still others they are definitely articulated with, or attached to, the ninth tergum. If, therefore, the first valvifers appear to be derived in their development from the eighth sternum, the ontogenetic facts mean simply that at an early stage the bases of the first gonopods are not distinguishable from the true sternal area of this segment; on the other hand, if the first valvifers appear to be cut off from the ninth tergum, it is probable that their phylogenetic history is not fully recapitulated in their ontogenetic development. The invariable origin of the muscles of the plates in question on the eighth tergum leaves no doubt that the plates belong to the eighth segment, and the fact that the plates always carry the first valvulae would seem to be proof that they are the bases of the first gonopods.

The term "valvifer" was first introduced into the nomenclature of the ovipositor by Crampton (1917) to designate the sclerite here called "first valvifer" supporting the first, or ventral, valvula, and is so used by Walker (1919). A small plate at the base of the first valvula Crampton called the "basivalvula". In a later paper containing a more extensive comparative study of the ovipositor, however, Crampton (1929) repeatedly confused the valvifer and the basivalvula because he did not base his identifications of these sclerites on their relations to the rest of the mechanism of the ovipositor. His " valvifer " in *Grylloblatta, Ceuthophilus, Gryllus,* and Hymenoptera, for example, is the sclerite he calls " basivalvula " in Hemiptera, while in *Periplaneta* he gives the name " valvifer " to a sclerite that belongs to the ninth tergum. The sclerite designated *first valvifer* in the present paper, therefore, is the " valvifer " of Crampton as he applied the term in Grylloblattidae, Tettigoniidae, Gryllidae, and Hymenoptera, and the homologous sclerite in other insects as determined by its muscle attachments and its relation to the first valvula. In his hypothetical diagrams Crampton (1929, figs. 1-4) derives the valvifer from the ninth tergum, probably because the sclerite he calls " valvifer " in Blattidae is a part of the ninth tergum, but he gives it no connection with the first valvula, though this is its most distinguishing and characteristic feature in the mechanism of the adult ovipositor in all insects. Crampton's diagrams, however, do not represent actual anatomical conditions, and it is only by a detailed dissection of the parts in question that the true identities of the various basal elements of the ovipositor can be determined.

Since the term *valvifer* is a very appropriate one when consistently used, inasmuch as it signifies literally a sclerite supporting a valvula, the writer here introduces the innovation of extending it to both pairs of valvula-bearing plates, distinguishing those that carry the first valvulae as the *first valvifers,* and those that carry the second and third valvulae as the *second valvifers* (usually called " coxites " of the ninth segment). The term *basivalvula* fittingly signifies the small sclerites that sometimes occur at the bases of the first valvulae, so named by Crampton (1917, 1929) in *Grylloblatta,* Tettigoniidae, and Gryllidae.

The leading facts in the ontogenetic development of the ovipositor are too well known to be given here more than a brief review. All investigators agree that a pair of processes grow out from the under surface of the eighth abdominal segment, and a second pair from the under surface of the ninth segment, and that each of the processes of the second pair typically becomes double by dividing lengthwise, or by budding an inner lobe from its mesal surface. The processes of the eighth segment in most cases become the first valvulae; the outer processes of the ninth segment form the second valvifers, including the terminal lobes of the latter, while the inner processes become the second valvulae. It is claimed by Nel (1930) that the definitive first valvulae of Odonata and Orthoptera are not the gonapophyses of the first gonopods, but the bases of these appendages. Nel's studies were made principally on Acrididae, in which the ovipositor differs in many respects from that of other Orthoptera, and it is hence possible that his interpretation applies only to this family. His statement concerning the Odonata is based on the observation of George (1929) that there is an inner lobe developed from each of the ovipositor processes on the eighth segment of *Agrion,* which Nel would interpret as being the true gonapophyses of the first gonopods, though George, himself, makes no suggestion that they are other than secondary outgrowths.

While, in general, there is no dispute concerning the ontogenetic development of the first valvulae, the origin of the basal plates, or first valvifers, in connection with them has not been so definitely observed, and, as already noted, these sclerites have been variously ascribed to the eighth and ninth segments. An examination of a nymphal cicada in the last instar shows quite clearly that the genital processes of the eighth segment (fig. 11 A, *1Gon*) arise from a broad plate (*VIIILB*) lying behind the gonopore (*Gpr*) and the small true eighth sternum (*VIIIStn*). This plate bearing the first gonapophyses, which is incompletely divided into lateral halves, can scarcely be anything else than the limb bases of the first gonopods united with each other behind the eighth sternum. It is, on the other hand, clearly the nymphal representative of the first valvifers of the adult (fig. 31 A, *1Vlf*), though this identity could not be verified in the specimens studied by the writer because the imaginal parts were already retracted forward far in advance of the nymphal parts.

The splitting of the primary genital processes of the ninth segment, or the budding of inner lobes from their mesal surfaces, represents the development of the second gonapophyses from the bases of the second gonopods. The result is the formation of four processes on the ninth segment (fig. 11 B). The outer processes (*IXLB*) are the true limb bases, which in the adult are differentiated into the second valvifers and their terminal lobes, or third valvulae (fig. 31 B, *2Vlf*, *3Vl*); the inner processes (fig. 11 B, *2Gon*) are the second gonapophyses, or the second valvulae of the adult (fig. 31 B, *2Vl*). The true ventral region of the ninth segment lies between the limb bases, concealed by the second gonapophyses. In some insects it contains remnants of the ninth sternum forming intervalvular sclerites.

There is not much evidence from ontogeny as to the nature of the distal lobes, or "third valvulae", borne by the second valvifers in the higher insects, but the development of the ovipositor as described by Walker (1919) and others in Blattidae and by Crampton (1927) in *Grylloblatta* appears to show conclusively that the third valvulae are not styli, as is suggested anatomically by their lack of muscles. In a female nymph of a cockroach small processes occur on the ends of the limb base lobes of the ninth segment, which almost certainly are true styli (fig. 25 B, *Sty*); they persist, Walker says, until the last molt, but they are not retained in the imago. In the adult roach, however, the outer processes (limb bases) of the ninth segment are clearly differentiated into a basal part, which is the second valvifer (fig. 24 C, D, *2Vlf*), and into a large, free distal lobe, or third valvula (*3Vl*). In *Grylloblatta* Walker thinks the length of the dorsal valvulae indicates that these processes include the styli, which are distinctly appendicular in the nymph; but Crampton says that the styli of the ninth "coxites" are lost in the adult female, and that, with the suppression of the styli, "the elongate coxite of the nymph becomes the dorsal valve of the adult." It is probable that small processes borne on the third valvulae in the adult stage of some of the lower insects, as in Odonata, are true styli.

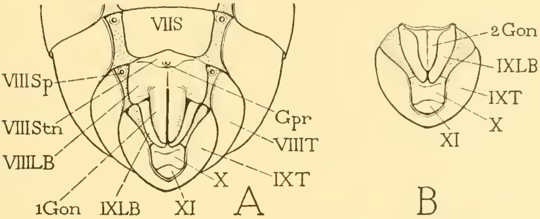

FIG. 11.—Female nymph of *Magicicada septendecim.*

A, ventral view of end of abdomen, showing first gonapophyses (*1Gon*) arising from limb base plates (valvifers) of eighth segment (*VIIILB*) behind small eighth sternum (*VIIIStn*).

B, ninth and following segments detached from eighth segment, showing second gonapophyses (*2Gon*) arising from bases of second gonopods (*IXLB*).

From the above evidence we may conclude that the limb bases of the second gonopods in most adult female insects lose their primitive styli, and that in the Pterygota each becomes secondarily differentiated into a proximal second valvifer and a distal third valvula (fig. 10 C). In an adult cicada the limb basis of the ninth segment is distinctly separated into valvifer and third valvula (fig. 31 B, *2Vlf, 3Vl*), but in the mature nymph the outer ovipositor lobes of the ninth segment are undivided (fig. 11 B, *IXLB*), yet they are mostly occupied by the imaginal third valvulae.

The late, usually postembryonic, development of the external genital processes, often after a complete and prolonged suppression of the embryonic abdominal appendages, as in the larvae of Hymenoptera, is to be regarded merely as a case of retarded development in organs that are used in their secondary function only in the adult stage of the insect. The genital structures in such cases are developed from " imaginal disks ", which are rudiments of primitive limbs. Evidence that the " law " against rehabilitation of a lost structure does not apply in ontogeny seems to be clearly demonstrated by the Acarina, in which, it is said, the fourth pair of legs, present in the early embryo, are suppressed long before hatching, and are fully restored in a late nymphal stage. In some of the lower insects the genital processes, as described by Wheeler (1893) in *Conocephalus,* are derived directly from the persistent rudiments of the abdominal appendages.

The characteristic features of the pterygote ovipositor and the probable correspondence between the parts of the pterygote and thysanuran ovipositors are briefly summarized in the following paragraphs:

1. The pterygote ovipositor consists of two or three pairs of processes (the first, second, and third valvulae), and of two pairs of basal plates (the first and second valvifers) belonging to the eighth and ninth abdominal segments, and sometimes includes intervalvular sclerites of the ninth segment.

2. The first and second valvulae are attached to the anterior ventral angles of the first and second valvifers, respectively; they correspond with the first and second gonapophyses of the Thysanura, and in some insects each has a short muscle inserted on its base, which arises in the corresponding valvifer. The shaft of the ovipositor in most insects is formed of the first and second valvulae alone, but in most of the Orthoptera the third valvulae enter into the composition of the shaft.

3. The first valvifers belong to the eighth segment of the abdomen, and are provided with dorsal muscles arising on the eighth tergum. Typically they are located in the pleural areas of the eighth segment between the tergum and the sternum, but usually they are more or less displaced posteriorly, and may be more closely associated with the ninth tergum, or with the second valvifers. The first valvifers correspond with the stylus-bearing plates of the eighth segment of Thysanura, and are therefore the bases of the first gonopods; in pterygote insects they always lack styli.

4. The second valvifers belong to the ninth abdominal segment, and are provided with muscles arising on the ninth tergum. They are always located between the lower edges of the tergum and the narrow median venter of the ninth segment. The second valvifers, together with the third valvulae, correspond with the stylus-bearing plates of the ninth segment of Thysanura, and are therefore derived from the

bases of the second gonopods. In most pterygote insects each primitive limb base of the ninth segment becomes differentiated into a proximal second valvifer, and a free distal lobe, or third valvula. In some of the lower insects the third valvulae bear small terminal styli, which are usually lost in the adult stage.

5. The third valvulae are secondary differentiations of the limb bases of the second gonopods, forming free lobes at the distal ends of the second valvifers. Usually they ensheath the distal part of the ovipositor between their apposed inner surfaces, but in most of the Orthoptera they resemble the gonapophyses, and form a third pair of blades in the shaft of the ovipositor.

6. The intervalvular sclerites are remnants of the ninth abdominal sternum; in some insects they give insertion to tergosternal and other muscles.

DEFINITIONS

The following terms applied to the ovipositor and associated structures are here defined as used in this paper in order to make the application clear, and to avoid the confusions of synonymy.

Oviductus laterales (*Odl*).—The paired oviducts, formed primarily from the mesodermal strands continuous with the mesodermal sheaths of the ovaries, but their posterior parts may be of ectodermal origin, and in some cases the entire mesodermal ducts are said to be replaced by ectoderm. The ducts are attached to the ectoderm at the posterior border of the seventh segment in young stages of many insects, and open at this position in adult Ephemerida, but in other adult insects they are confluent in the anterior end of the median oviduct.

Oviductus communis (*Odc*).—The median oviduct, of ectodermal origin, opening in Dermaptera just behind the seventh abdominal sternum, but in other insects extended to the eighth segment.

Female gonopore (*Gpr*).—Any of the true oviducal apertures, paired or median. The paired gonopores of Ephemerida and the median gonopore of Dermaptera are on the posterior part of the seventh abdominal segment; the single female gonopore of other insects is on or just behind the eighth sternum, where it is either exposed externally or concealed in the genital chamber (copulatory pouch, or vagina).

Spermatheca, receptaculum seminis (*Spt*).—An ectodermal invagination, usually single, but often double, and sometimes triple, serving for the reception of the spermatozoa; primarily formed on the posterior part of the eighth abdominal segment, opening into the anterior end of the genital chamber, or vagina, when this organ is present.

Accessory glands (*AcGl*).—Typically a bifurcate or paired invagination on the venter of the ninth segment, usually forming glands having a colleterial function.

Gonopods (*Gp*).—The appendages of the eighth and ninth abdominal segments. Each gonopod, when complete, consists of a *basis* (*Lb*) bearing a proximal, medial *gonapophysis* (*Gon*), and a distal *stylus* (*Sty*).

Ovipositor (*Ovp*).—The egg-laying organ formed of the gonopods.

First valvifers (*1Vlf*).—The basal plates or lobes of the ovipositor supporting the first valvulae; derived from the bases of the first pair of gonopods, and provided with muscles arising on the eighth tergum.

Second valvifers (*2Vlf*).—The basal plates or lobes of the ovipositor supporting the second valvulae; derived from the bases of the second gonopods, and provided with muscles arising on the ninth tergum. (Usually called " coxites " of the ninth segment.)

First valvulae (*1Vl*).—The gonapophyses of the first gonopods, forming the ventral blades of the ovipositor.

Basivalvulae (*bv*).—Small sclerites sometimes differentiated at the bases of the first valvulae.

Second valvulae (*2Vl*).—The gonapophyses of the second gonopods, forming usually the dorsal blades of the ovipositor, but the inner blades in Orthoptera having a third pair of valvulae.

Third valvulae (*3Vl*).—The distal lobes of the second valvifers, derived with the latter from the bases of the second gonopods; usually forming a sheath for the shaft of the ovipositor, but in most Orthoptera a third (dorsal) pair of blades in the ovipositor.

Intervalvulae (*iv*).—Sclerotic remnants of the ninth sternum between the second valvifers.

Egg guide.—A median process sometimes present on the end of the eighth sternum behind the invaginated gonopore, serving to direct the eggs into the channel of the ovipositor between the bases of the first valvulae.

Genital chamber (*GC*).—An inflection of the body wall at the base of the ovipositor above the end of the eighth abdominal sternum, forming a pouch containing the gonopore and the opening of the spermatheca; in Panorpidae the genital chamber is closed below by the ninth sternum and opens above the latter.

Vestibulum (*Vst*).—A cavity formed by inflection of the body wall above the seventh sternum when the latter is prolonged beyond the eighth, thus concealing the true genital chamber above the usually reduced eighth sternum.

Subgenital plate.—The exposed sternal plate beneath the genital apparatus; primarily the eighth abdominal sternum, but the seventh when the latter underlies and conceals the reduced eighth sternum, or the ninth sternum when the vaginal opening is transferred to the ninth segment.

Vagina (*Vag*).—The genital chamber when the latter takes on a pouchlike or tubular form with a narrowed posterior opening; in some insects extended into the ninth segment to open on or behind the ninth sternum.

Ostium vaginae, or *vulva* (*Vul*).—The external opening of the copulatory pouch or vagina, on either the eighth or the ninth abdominal segment, serving usually both for copulation and for the discharge of the eggs.

Bursa copulatrix.—Any cavity of the female serving for the reception of the male organ of copulation; usually the genital chamber or its derivative, the vagina; in most Lepidoptera a diverticulum of the genital chamber invagination on the eighth abdominal segment.

V. THE OVIPOSITOR OF ORTHOPTERA

The ovipositor of orthopteroid insects presents three types of structure. It occurs in a reduced and in some cases a more or less modified form in Phasmidae, Mantidae, and Blattidae; it is normally developed in Grylloblattidae, Tettigoniidae, and Gryllidae, and attains its greatest mechanical perfection in the last family; finally, it is most specialized and modified in structure in Acrididae and Tridactylidae. For a general account of the ovipositor in these several families the student is referred to the paper by Walker (1919) on the terminal structures of orthopteroid insects; the comparative musculature of the ovipositor is described by Ford (1923). The morphology and mechanism of the organ will be illustrated here from studies made on *Blatta* and *Gryllus,* forms representing the first and second types of structure noted above; a description of the specialized acridid type will be reserved for a future paper.

The ovipositor of Grylloblattidae, Tettigoniidae, Gryllidae, and Acrididae differs from the ovipositor of other insects in that the third valvulae enter into the formation of the shaft of the organ, which thus consists of three pairs of appendicular blades or lobes, which are the first, second, and third valvulae as here named. Because of their usual positions relative to one another in the Orthoptera, the three pairs of blades are distinguished by Walker (1919) as *dorsal, ventral,* and *inner valvulae,* or correspondingly by Chopard (1920) as *valves* *supérieures, inférieures* and *internes.* The ventral pair are the first valvulae, as designated in the present paper, the inner pair the second valvulae, and the dorsal pair the third valvulae. In Gryllidae and Acrididae the inner, or second, valvulae are rudimentary, and the functional part of the ovipositor thus consists of only two pairs of valvulae. Hence, it must be observed that the four-valve ovipositor of these insects differs from the four-valve ovipositor of Thysanura, Hemiptera, and Hymenoptera in that the shaft is formed of the first and third valvulae, while in the latter groups it consists of the first and second valvulae. The first valvifers are always displaced posteriorly in the Orthoptera and closely associated with the ninth segment; the second valvifers are never distinctly differentiated from the third valvulae.

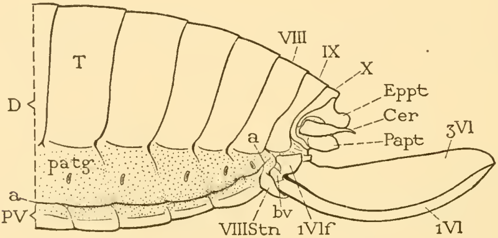

FIG. 12.—Female nymph of *Scudderia.*

Dorso-pleural line of abdomen marked by a fold (*a-a*); ovipositor with small basivalvular sclerite (*bv*) at base of first valvula (*1Vl*); epiproct (*Eppt*) partially surrounding base of cercus (*Cer*).

The six-valve type of ovipositor is typically developed in Grylloblattidae and Tettigoniidae, but the basal parts of the organ are somewhat weak in these families, and in structure they are scarcely representative of that of the highly perfected basal mechanism of the ovipositor of Gryllidae. A brief study of a typical form, such as *Scudderia,* however, will serve as an introduction to the more detailed description of *Gryllus* to follow.

The abdomen of *Scudderia* (fig. 12) presents a wide membranous area on each side in which the spiracles are located. A prominent groove traversing the lower part of the membrane marks the dorsopleural line (*a-a*), which posteriorly extends above the basal plates of the ovipositor. The spiracles lie in the laterodorsal, or paratergal, region of the membrane (*patg*) above the dorso-pleural line. The eighth, ninth, and tenth terga are distinct, and the epiproct (*Eppt*) is well developed. The eighth sternum (*VIIIStn*) forms a small subgenital plate underlapping the base of the ovipositor. The first valvifers (*1Vlf*) are displaced posteriorly, and are thus entirely separated from the tergum of the eighth segment, though they are in closer association with the eighth sternum. The broad ovipositor shows only the first and third valvulae externally (*1Vl, 3Vl*), the second valvulae being concealed between the outer blades.

The mature ovipositor of *Scudderia* is strongly upcurved, and its free margins are toothed (fig. 13 C). The mechanical relations of the parts of the organ to one another can be studied only in fresh specimens, or in specimens preserved in liquid; the parts are best seen when the entire ovipositor is removed from the body. Each of the first, or ventral, valvulae (*1Vl*) is attached to a small, oval lateral plate at the base of the ovipositor (*1Vlf*), which is the first valvifer ("pileolus" of Chopard, 1920). The first valvifer and its valvula are continuous, but they are flexible on each other by reason of the narrowness of their union (*c*). The upper end of the valvifer is connected, also by a flexible union (*b*), with the basal part of the broad third, or dorsal, valvula (*3Vl*), the side of which it overlaps ventrally. From an angle on the anterior margin of the first valvifer there projects internally a strong apodeme (*e*), on which muscles are attached. If the first valvifer is revolved upward on its flexible dorsal attachment (*b*), the ventral valvula is retracted. In some of the Tettigoniidae the proximal part of the first valvula is more or less distinctly differentiated as a basal sclerite, or *basivalvula,* shown in the nymph of *Scudderia* (fig. 12, *bv*).

Each of the dorsal, or third, valvulae of *Scudderia* (fig. 13 C, *3Vl*) is somewhat thickened at its base where the first valvifer is attached, there being differentiated here an area (*2Vlf*) that evidently corresponds with the second valvifer of an ovipositor having a more typical structure (figs. 10 C, 31 B), in which each limb base element of the ninth segment becomes divided into a valvifer (*2Vlf*) and a distal lobe (*3Vl*). The muscles inserted on this basal part of the dorsal valvula in *Scudderia* and other tettigoniids are those of the second valvifer in other insects. The area in question is sometimes called the "basivalvula" of the dorsal valvula, but the term is unnecessary and misleading since the area so designated does not correspond morphologically with the basivalvula of the ventral valvula. A strong apodeme (fig. 13 C, *g*) projects from the anterior margin of the valvifer area. This apodeme is the *superior apophysis* of Walker (1919).

The dorsal and ventral valvulae are rather weakly connected with each other in *Scudderia,* but in the Tettigoniidae and Gryllidae generally the two on each side are interlocked by dovetailing grooves and ridges on their opposing margins (fig. 20), so that they may freely slide upon each other without being separated. Judging from the mechanism of the ovipositor in *Scudderia* it would appear that the principal mobile elements are the ventral valvulae, which are movable by the muscles of the first valvifers.

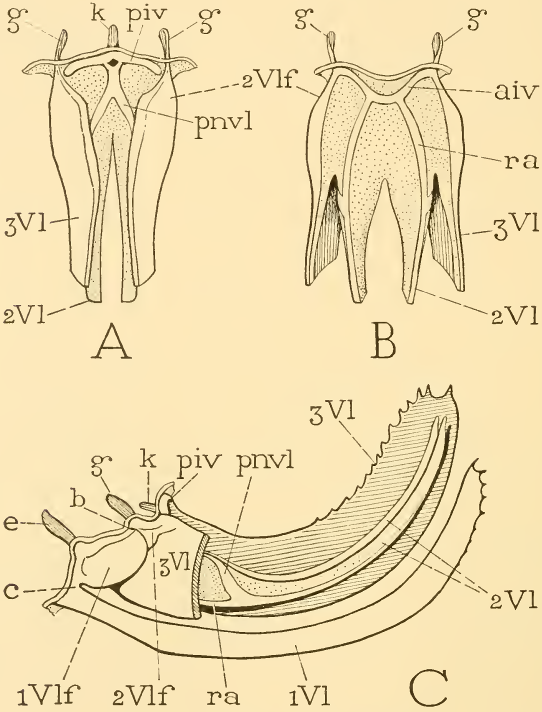

FIG. 13.—Ovipositor of adult *Scudderia*.

A, dorsal view of base of ovipositor.
B, ventral view of same.
C, lateral view of ovipositor, with left third valvula removed near base.
aiv, anterior intervalvula; *b,* articulation of first valvifer with second valvifer; *c,* attachment of first valvula to first valvifer; *e,* apodeme of first valvifer; *g,* apodeme of second valvifer; *k,* apodeme of posterior intervalvula; *piv,* posterior intervalvula; *pnvl,* pons valvularum; *ra,* ramus of second valvula; *1Vl,* first valvula; *2Vl,* second valvula; *3Vl,* third valvula; *1Vlf,* first valvifer; *2Vlf,* second valvifer.

The inner, or second, valvulae of *Scudderia* are narrow, closely appressed blades (fig. 13 C, *2Vl*), upcurved between the broad third valvulae. Their thickened bases are united medially with each other (B, *2Vl*) and laterally with the inner faces of the basal valvifer areas (*2Vlf*) of the third valvulae. The lower edges of the weak inner valvulae are strengthened by narrow sclerotic bands in their walls, the proximal continuations of which, termed by Walker (1919) the *rami* (fig. 13 B, C, *ra*), are united with a transverse intervalvular bar (B, *aiv*) between the ventral margins of the second valvifers. From the ramus of each inner valvula a sclerotic tongue extends upward in the lateral wall of the valvula (C, *pnvl*) into the dorsal wall of the common base of the two inner valvulae (A), and here the two from opposite sides are confluent in a median stem that unites with a dorsal intervalvular bar (*piv*). This Y-shaped dorsal sclerotization in the base of the inner valvulae Walker (1919) calls the *pons valvularum* (*pnvl*).

The dorsal and ventral intervalvular bars above mentioned (fig. 13 A, B, *piv, aiv*) are the " superior intervalvula " and " inferior intervalvula " of Walker (1919). These terms are appropriate in the Tettigoniidae where one intervalvula is dorsal to the other, but the sclerites both belong to the ventral wall of the ninth segment, and are hence morphologically posterior and anterior, as they are anatomically in Gryllidae (fig. 18, *piv, aiv*). For this reason the writer terms the intervalvular sclerites the *anterior intervalvula* (*aiv*) and the *posterior intervalvula* (*piv*), the first being the " inferior " intervalvula according to Walker, the second the " superior ". The posterior intervalvula of *Scudderia* bears a prominent median apodeme (fig. 13 A, C, *k*).

The musculature of the ovipositor in Tettigoniidae and Gryllidae is more complex than in Hemiptera and Hymenoptera. The dorsal muscles of the eighth segment are inserted on the first valvifers; those of the ninth segment on the second valvifers, and on the intervalvulae, the first being tergopleural, the second tergosternal. Besides these there are muscles connecting the first valvifers with the second valvifers and with the posterior intervalvula. In *Scudderia* a large bundle of fibers arises on the inner face of the second valvifer and is inserted on the outer wall of the corresponding inner valvula between the ramus and the arm of the pons. The musculature of the ovipositor and the terminal segments of the abdomen will be fully treated in the description of *Gryllus assimilis*.

The ovipositor of *Grylloblatta*, judging from the descriptions of Crampton (1917, 1927) and Walker (1919), is very evidently of the tettigoniid type. Walker says that " in the external form of the valvulae and their connections with neighboring sclerites *Grylloblatta* is remarkably like a primitive Tettigoniid, such as *Ceuthophilus*." The three pairs of valvulae are well developed, but the dorsal and ventral pairs are not connected, and the median pair is exposed between them. The basivalvulae form distinct sclerites between the bases of the ventral valvulae and the eighth sternum. Crampton believes that the basivalvulae are derived from the " coxites " of the eighth segment of the nymph, but he gives no evidence that the sclerites in the nymph are limb base elements. The presence of well-developed styli on the ends of the dorsal valvulae in the nymph of *Grylloblatta,* which are lost in the adult, is a primitive feature retained likewise in the young of Blattidae.

GRYLLUS ASSIMILIS FABRICIUS

Since the cricket is a good subject for school laboratory work, it is here selected for a detailed study of the orthopteroid abdomen and ovipositor. The abdomen of the cricket gives a fairly generalized example of the typical structure of the abdominal part of the insect body. The ovipositor, however, is by no means generalized; it is specialized in the way the ovipositor of all Orthoptera is specialized, and in addition it is one of the most highly perfected egg-laying mechanisms found among the insects.

The visceral region of the abdomen.—The pregenital segments of the cricket's abdomen are all well developed in both the male and the female (fig. 14 A), and contain distinct tergal and sternal plates. The terga (*T*) are separated from the sterna (*Stn*) by a wide membranous or coriaceous area on each side of the body, containing the spiracles. Running lengthwise through each of these membranous areas, below the spiracles, is a prominent lateral fold (*a-a*). The relations of the parts of the abdomen above and below the lateral fold to each other and to the corresponding parts of the thorax attest that the fold marks the site of the dorso-pleural line. The membranous area above the fold, containing the spiracles, is, therefore, the laterodorsal region, or paratergal area of the dorsum (*ld*), and that below the fold is the true pleural area (*P*). Anteriorly it is seen that the line of the dorso-pleural fold on the abdomen extends into the thorax dorsal to the thoracic pleural plates, or subcoxae (*Scx*), and that the pleural area continued from the abdomen here expands between the metathoracic tergum and sternum (T_3, Stn_3) to include the thoracic pleura, or subcoxal parts of the leg bases. Posteriorly the line of the dorso-pleural fold extends, in the female (B, *a*), between the tergum of the ninth segment (*IX*) and the basal plates of the ovipositor (*Ovp*). This relation is more clearly shown if the dorsum of the abdomen is separated from the pleurosternal parts (C), the dorso-pleural line (*a-a*) being theoretically carried out above the bases of the cerci (*Cer*). It is thus to be seen that the basal plates of the ovipositor (C, *1Vlf*, *2Vlf*) belong to the pleural area of the abdomen (*P*), and that, therefore, they correspond in position, at least, with the subcoxal plates of the thoracic leg bases (A, *Scx*).

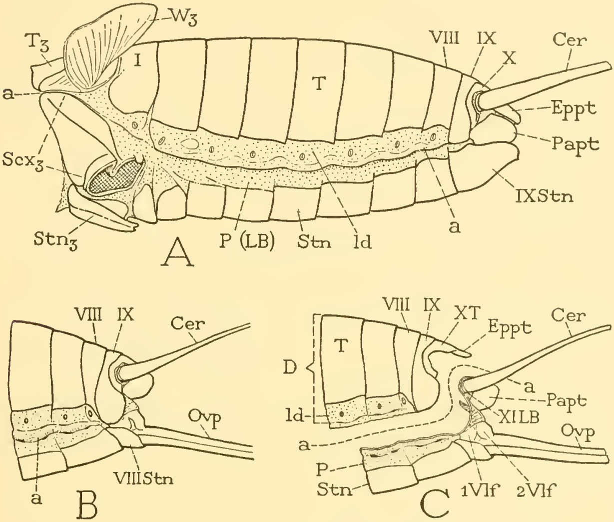

FIG. 14.—Abdomen of *Gryllus assimilis*.

A, lateral view of male abdomen and metathorax, showing groove (*a-a*) along dorso-pleural line above thoracic subcoxae and limb base, or pleural, region (*P*) of abdomen.

B, end of abdomen of female, showing relation of base of ovipositor to eighth and ninth segments.

C, same part of abdomen separated along dorso-pleural line (*a-a*).

A closer study of the membranous lateral areas of the visceral region of the abdomen (fig. 15 A) shows that the dorso-pleural fold (*a-a*) on each side is bordered above by an undulating series of slender sclerotizations, and below by a similar series of somewhat thicker sclerotizations. The upper series evidently marks the lower edge of the dorsum (*D*), and the lower series the upper edge of the pleuro-ventral region (*PV*). The sclerotic thickenings form attachment points for muscles on the inner abdominal wall (B).

The musculature of the visceral segments in the abdomen of *Gryllus* comprises the usual *dorsal, ventral, lateral, transverse,* and *spiracular* muscles. The following muscles may be distinguished in an individual segment, such as the fifth or sixth, shown at B of Figure 15.

The *dorsal muscles* consist of two sets of longitudinal fibers, both of which apparently belong to the internal system, since no muscles lie external to them. The fibers of one set, the median dorsals (*dim*), form in each segment a narrow band of segmental length on each side of the median line of the back, attached to the anterior margins of successive terga. The fibers of the other set, the lateral internal dorsals (*dil*), occupy the wide lateral parts of the terga, but they are confined to the posterior parts of the segments, since they arise behind the middle of the tergal plate before the one on which they are inserted.

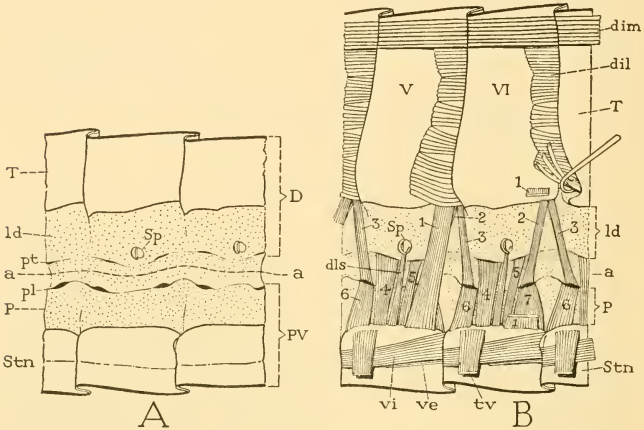

Fig. 15.—Relation of the musculature to the integumental areas in the abdomen of *Gryllus assimilis.*

A, lateral and ventral parts of two consecutive segments, with separation between dorsum (*D*) and pleuroventral region (*PV*) indicated by dorso-pleural line (*a-a*).

B, musculature of right half of segments *V* and *VI.*

a-a, dorso-pleural line; *D,* dorsum; *ld,* laterodorsal area; *P,* pleural region; *pl,* series of pleurites; *pt,* series of paratergal sclerotizations; *PV,* pleuroventral region; *Stn,* sterna; *T,* terga.

The *ventral longitudinal muscles* comprise internal ventrals (*vi*) of segmental length located laterally on the sterna, and external ventrals (*ve*) lying beneath the others, where they arise near the middle of each sternal plate and are inserted posteriorly on the anterior margin of the sternum following. The *transverse ventrals* consist of wide bands of fibers (*tv*) crossing the anterior parts of the segments internal to the longitudinal ventrals, and attached laterally on the edges of the sternal plates. The last transverse ventral in the female is that of the seventh segment (fig. 19 A, *tv*).

The *lateral muscles* include tergosternal, tergopleural, paratergosternal, and pleurosternal muscles. In each segment there is a large tergosternal lateral muscle (*1*) arising on the posterior lateral part of the tergum external to the lateral dorsals, and inserted on the posterior lateral margin of the sternum. Just behind this muscle, and external to it, are two tergopleural muscles (*2, 3*) taking their origin on the lower edge of the tergum. The first (*2*) is attached ventrally on the pleural margin of the same segment; the second (*3*) is intersegmental since it is attached on the pleural margin of the following segment. The paratergosternal muscles comprise two bands of fibers (*4, 5*) on the middle of each segment, one before, the other behind the spiracle dilator (*dls*). The pleurosternal muscles include likewise two bands of fibers, one (*6*) in the anterior part of each segment, the other (*7*) in the posterior part.

The *spiracular muscles* are the usual antagonistic pair inserted on the manubrium of the anterior movable wall of the spiracular atrium. One is a very small occlusor arising on the posterior atrial wall; the other is a large dilator (*dls*) arising ventrally on the edge of the sternum between the attachments of *4* and *5*.

The somatic muscles of the visceral region of the cricket's abdomen are used by the female principally for respiratory purposes, since oviposition is accomplished by the muscles of the genital segments, and ordinarily involves few movements in the rest of the abdomen. The mechanical relation of the lateral muscles to the skeletal parts of the abdomen is shown diagrammatically at A of figure 16. It is to be noted that the muscles can produce only a contraction of the abdomen, brought about mostly by a lifting of the sternal plates, since there is no antagonistic mechanism capable of dilating the abdomen, either dorso-ventrally or longitudinally, such as that developed in the Acrididae. Inspiration with the cricket, therefore, must be accomplished by a passive expansion of the abdominal parts compressed by muscular force.

The genital segments and the ovipositor.—The genital segments of the female cricket (fig. 14 B, *VIII, IX*) are somewhat reduced by comparison with the eighth and ninth abdominal segments of the male (A). The shortened eighth tergum (B, *VIII*) ends below in a point separated by the dorso-pleural fold from the small eighth sternum (*VIIIStn*), which projects beneath the base of the ovipositor as a small subgenital plate. The ninth tergum (*IX*) is narrowed above, but is widened on the sides, and extends downward to the base of the ovipositor. The venter of the ninth segment is not visible externally; it is the narrow, membranous ventral wall of the segment between the basal halves of the ovipositor, containing anteriorly and posteriorly the sclerotic intervalvular bridges (figs. 17 H, 18, *aiv, piv*). In the male the ninth sternum is fully exposed, and forms a large subgenital plate (fig. 14 A, *IXStn*). The inner surfaces of the eighth and ninth terga of the female (fig. 18) are enlarged by thin apodemal extensions from their anterior margins, giving attachment to muscles of the ovipositor. The ninth tergum has a strongly developed antecosa (*Ac*), which terminates in a ventral process bearing a socket (*a*) for articulation with the basal part of the ovipositor.

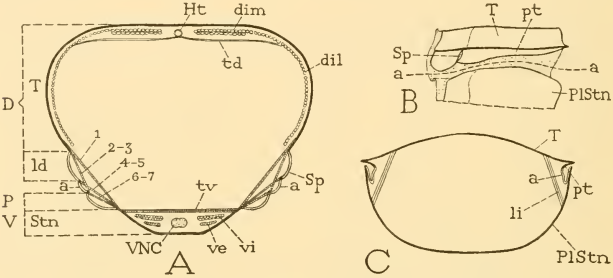

FIG. 16.—Abdominal structures of *Gryllus* and *Blatta*.

A, diagrammatic cross-section through abdomen of *Gryllus assimilis*, showing relation of integumental areas and muscles illustrated in Figure 15.

B, lateral parts of abdominal segment of *Blatta orientalis* with dorsal and ventral plates separated to expose the dorso-pleural fold (*a-a*).

C, diagrammatic cross section of abdomen of *Blatta*, showing infolded dorsopleural membrane (*a*), and position of lateral muscles (*li*).

The musculature of the genital segments is mostly adapted to the mechanism of the ovipositor. The dorsal muscles, however, conform with those of the visceral segments, and in the eighth segment there are one or two pairs of weak lateral muscles inserted below near the margins of the eighth sternum. The other lateral muscles in both genital segments are highly developed as muscles of the ovipositor (fig. 17 E). Ventral muscles are absent in the eighth segment, and those of the ninth segment are of doubtful homology with the ventral muscles of the visceral segments.

The ovipositor of the cricket consists of a small basal part, attached to the ninth abdominal segment (fig. 14 B), and of a long, slender shaft terminating in a sharp-pointed enlargement (fig. 17 B). The shaft is formed of the first and third valvulae (figs. 17 A, E, 18, *1Vl, 3Vl*), which are respectively ventral and dorsal in position relative to each other. The second valvulae are reduced to a pair of small, membranous lobes (figs. 17 E, G, 18, *2Vl*) arising from the venter of the ninth segment between the bases of the dorsal valvulae. The base of the ovipositor consists of the first and second valvifers (figs. 14 C, 17 A, *1Vlf, 2Vlf*), and the anterior and posterior intervalvulae (fig. 17 H, *aiv, piv*). The two valvifers on each side are closely associated with the lower edge of the ninth tergum, but their true segmental relations are shown by the origins of their dorsal muscles (fig. 17 E), those of the first valvifer (*3*) arising on the eighth tergum, those of the second valvifer (*6, 7*) on the ninth tergum. The connection of the first valvifers with the ninth tergum is evidently a secondary association, since it is clearly an adaptation to the special mechanism of the orthopteroid type of ovipositor.

The first valvifer is an irregularly triangular plate (fig. 17 A, F, *1Vlf*). Its only connection with the eighth segment is by the pleural membrane uniting the eighth tergum and sternum; otherwise its associations are entirely with the ninth segment, except for its musculature. By a strongly developed condyle near the middle of its dorsal margin (F, *a*), the first valvifer freely articulates with the lower extremity of the antecosta (*Ac*) of the ninth tergum. Its anterior end is produced into a tapering process (*e*) for the attachment of muscles. At its posterior angle it has a narrow, flexible external connection with the second valvifer (*A, b*), internal to which is a deep notch (*F, d*) by which the first valvifer articulates with a condylar surface (G, *h*) of the second valvifer (figs. 17 H, 21, *dh*). Ventrally the first valvifer is continuous by a narrow, flexible tongue (fig. 17 A, F, *c*) with the first, or ventral, valvula (*1Vl*). From the inner face of the first valvifer, above the inner articulation with the second valvifer, there arises a large flat apodeme (F, H, *f*), giving attachment to a thick, cylindrical muscle (E, H, *9*) from a median apodeme (*k*) of the posterior intervalvula (*piv*).

The second valvifer (fig. 17 A, G, *2Vlf*) is of a more irregular shape than the first, and its ventral part is directly continuous into the third, or dorsal, valvula (*3Vl*). Its posterior end, just before the base of the valvula, is produced upward in a broad dorsal arm (G, *i*), which terminates in an apodeme, the superior apophysis, projecting within the ninth tergum (A, *i*). The anterior extremity of the second

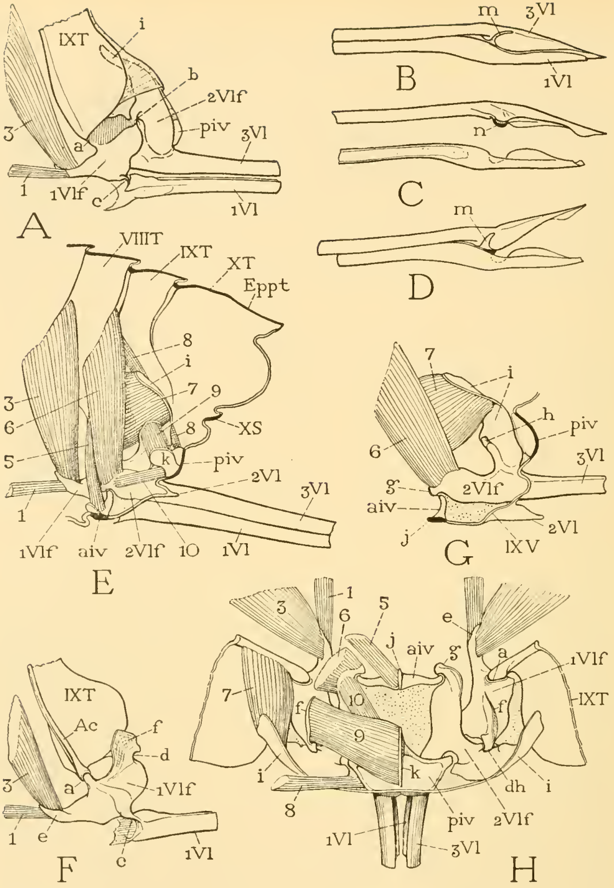

Fig. 17.—Details of structure and musculature of ovipositor of *Gryllus assimilis.*

A, base of ovipositor, showing articulation of first valvifer (*1Vlf*) at *a* with ninth tergum, and at *b* with second valvifer.

B, C, D, apical structure of shaft ovipositor.

E, inner view of genital and tenth segments, with right half of base of ovipositor and muscles of same side.

F, inner view of right first valvifer, showing its articulation (*a*) with ninth tergum, its anterior muscles, and connection (*c*) with first valvula.

G, inner view of right second valvifer and its muscles (*6, 7*), together with anterior intervalvula (*aiv*), rudimentary second valvula (*2Vl*), and base of third valvula (*3Vl*).

H, dorsal view of valvifers and intervalvulae, and their muscles; first valvifers (*1Vlf*) articulated dorsally (*a*) to ninth tergum (*IXT*), posteriorly (*dh*) to second valvifers (*2Vlf*); second valvifers connected anteriorly by anterior intervalvula (*aiv*) and posteriorly by posterior intervalvula (*piv*).

valvifer forms a second strong process, the inferior apophysis (G, H, *g*). The articular condyle by which the second valvifer is hinged to the first is located on the inner face of the anterior margin of the dorsal arm (G, *h*). The second valvifer of the cricket has no direct connection with the ninth tergum.

Two intervalvular sclerites are well developed in *Gryllus*. The first, or anterior intervalvula (fig. 17 H, *aiv*), is a transverse bar between the anterior processes (*g*) of the second valvifers. Medially it bears a small apodeme (*j*). The second, or posterior intervalvula (*piv*), is a broad, externally convex plate exposed above the bases of the dorsal valvulae (A, *piv*). By its produced lateral extremities it articulates with the second valvifers at the deeply notched angles between the dorsal arms of the latter and the bases of the dorsal valvulae (H). Medially the posterior intervalvula bears a high, platelike apodeme (E, H, *k*). In a lengthwise section of the abdomen (figs. 17 E, 18) it is clearly seen that the two intervalvulae (*aiv*, *piv*) belong to the venter of the ninth abdominal segment, and that they have the status of anterior and posterior sternal sclerites lying between the second valvifers. Tergal muscles of the ninth segment are inserted on each of the intervalvulae.

The reduced eighth sternum, which forms a free subgenital plate (fig. 18, *VIIIStn*) beneath the base of the ovipositor, conceals a small genital chamber (*GC*) above its dorsal wall, between the bases of the valvulae. Into the anterior end of the genital chamber the short median oviduct (*Odc*) opens between two membranous folds (fig. 19 B, *l*) on the dorsal surface of the subgenital plate. Dorsal to the opening of the oviduct, the anterior dorsal wall of the genital chamber before the anterior intervalvula (*aiv*) forms a deep pouch (*t*) projecting into the body cavity above the oviduct. The pouch contains a strongly sclerotized, spoutlike organ (*u*) reflected from its anterior wall, which is transversed by the terminal part of the spermathecal duct (*SptD*). The deflected distal extremity of the spout, containing the opening of the sperm duct, projects into the genital chamber a little beyond the opening of the oviduct. The eggs issuing from the gonopore are thus, evidently, fertilized just before entering the channel of the ovipositor between the bases of the valvulae.

The shaft of the ovipositor consists of the slender, elongate first and third valvulae. The two valvulae on each side are firmly but freely interlocked by a ridge with an expanded margin on the lower edge of the dorsal third valvula (fig. 20) that is held in a groove on the apposed surface of the ventral first valvula. The valvulae of opposite sides are not united. The inner walls of the dorsal valvulae are strongly sclerotized throughout, and each is strengthened by a high internal ridge. The ventral valvulae are membranous and flexible on their mesal surfaces, and the inner wall of each is thrown into a longitudinal fold.

The muscles of the ovipositor.—The musculature of the cricket's ovipositor is strongly developed, but is not particularly complex. It includes the ventral muscles of the seventh abdominal segment, and the principal lateral and ventral muscles of the eighth and ninth segments. The muscles attached on, or associated with, the ovipositor are the following, indicated by arabic numerals on figures 17 and 19 A.

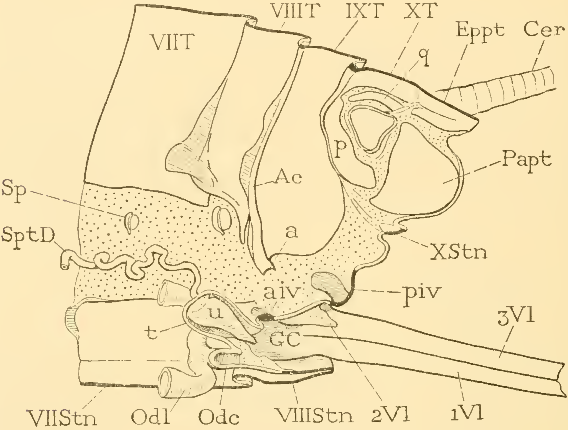

FIG. 18.—Inner view of right half of genital and postgenital segments of *Gryllus assimilis*.

Note genital chamber (*GC*) at base of ovipositor above eighth sternum (*VIIIStn*), with opening of median oviduct (*Odc*) anteriorly, and opening of spermathecal duct (*SptD*) through a spoutlike process (*u*) in a dorsal pouch (*t*) of genital chamber.

1. Retractors of the ovipositor (fig. 19 A).—Origin anteriorly on anterior apodemes of seventh sternum; insertion posteriorly on anterior extremities of first valvifers (fig. 17 A, E, F, H). These muscles of the ovipositor fall directly in line with the internal ventrals of the pregenital segments anterior to the seventh (fig. 19 A, *vi*), and are clearly the corresponding muscles of the seventh segment, though here attached posteriorly on the valvifers of the eighth segment instead of on the eighth sternum.

2. Retractors of the spermathecal pouch (fig. 19 A).—Origins anteriorly on seventh sternum external to *1*; convergent posteriorly to insertions on spermathecal pouch (*t*). These muscles clearly represent the external ventrals of the preceding segments. (Described by Du Porte, 1920, and Ford, 1923, as inserted on the median oviduct.)

3. Tergal muscles of the first valvifers (fig. 17 A, E, F, H).—The largest muscles of the ovipositor. Origins on anterior lateral apodemes and anterolateral surface of eighth tergum (E); insertions ventrally on anterior ends of first valvifers. These muscles, on the assumption that the first valvifers are the bases of the first gonopods, are tergopleural muscles of the eighth segment.

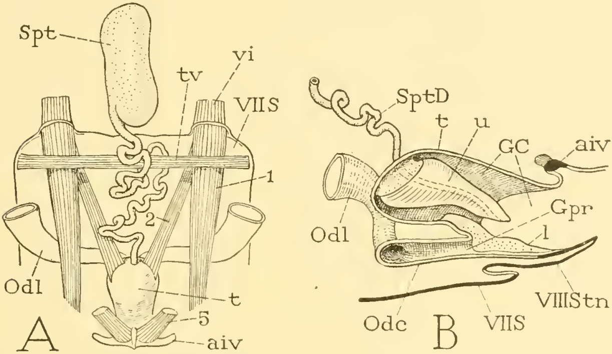

FIG. 19.—The spermatheca and associated structures of *Gryllus assimilis*.

A, dorsal view of spermatheca, lateral oviducts, and base of seventh sternum. B, median section of genital chamber, spermathecal pouch, and median oviduct. *aiv*, anterior intervalvula; *GC*, genital chamber; *Gpr*, gonopore; *l*, fold of membrane at side of gonopore; *Odc*, oviductus communis; *Odl*, oviductus lateralis; *Spt*, spermatheca; *SptD*, spermathecal duct; *t*, spermathecal pouch of genital chamber; *tv*, transverse ventral muscle of seventh segment; *u*, spermathecal spout; *vi*, internal ventral muscle of seventh segment; *1*, muscle from seventh sternum to first valvifer; *2*, muscle from seventh sternum to spermathecal pouch.

4. Ventrolateral dilators of the rectum.—A group of slender, branching fibers arising on inner face of each first valvifer behind articulation with ninth tergum; inserted ventrolaterally on rectum. (Not shown in figures.)

The four following pairs of muscles arise on the lateral parts of the ninth tergum. Two of them (fig. 17 E, *5*, *8*), inserted ventrally on the intervalvulae, are anterior and posterior tergosternal muscles; the other two (*6*, *7*), inserted on the second valvifers, are tergopleural muscles.

5. Tergal muscles of the anterior intervalvula (fig. 17 E, H).—A slender muscle on each side arising on anterior margin of lateral part of ninth tergum; the two converging ventrally to insertions medially on anterior intervalvula (*aiv*).

6. Anterior tergal muscles of second valvifers (fig. 17 E, G, H).—A pair of large vertical muscles, arising on anterior lateral apodemes of ninth tergum, internal to *5*; insertions ventral on anterior processes (inferior apophyses) of second valvifers (G, H).

7. Posterior tergal muscles of second valvifers (fig. 17 E, G, H).—A pair of large, flat, horizontal muscles; each arising anteriorly on anterior margin of ninth tergum (H), external to *6* (E); inserted posteriorly on posterior dorsal apodeme (superior apophysis) of second valvifer (E, G, H, *i*).

8. Tergal muscles of posterior intervalvula (fig. 17 E, H).—A pair of relatively slender muscles, arising on lateral parts of ninth tergum (E) above *5* and external to upper ends of *6;* extend ventrally and posteriorly, ectad of *7,* to insertions in membranes laterad of posterior intervalvula (E, H, *piv*), with a few fibers attached on the latter.

The next two pairs of muscles have a ventral position and connect the valvifers with the posterior intervalvula, but their homology with muscles of the pregenital segments is not clear. They are described by Ford (1923) as primary and secondary " outer sternal muscles " of the ninth segment. An " inner sternal muscle " of the ninth segment, she says, extends from the first valvifer to the paraproct, but the writer did not observe this muscle in the female of *Gryllus,* which, according to Du Porte (1920), occurs in the male only.

9. Intervalvular muscles of the first valvifers (fig. 17 E, H).—A pair of short, thick, cylindrical muscles arising on sides of median apodeme (*k*) of posterior intervalvula (*piv*); extending laterally and a little forward to posterior internal apodemes of first valvifers (H, *f*).

10. Intervalvular muscles of second valvifers (fig. 17 E, H).—Origins medially on apodeme of posterior intervalvula (*k*), ventral to *9;* diverge anteriorly to insertions on anterior ends of second valvifers.

Muscles pertaining to the rudimentary second, or inner, valvulae the writer did not find in *Gryllus,* but Ford (1923) describes a pair of such muscles having their origins on the anterior intervalvula and their insertions in the tips of inner valvulae. In *Scudderia* the well-developed muscles of the inner valvulae have their origins on the inner faces of the second valvifers.

The mechanism of the ovipositor.—The eggs of *Gryllus* are laid in the ground. Before inserting the ovipositor the female often clears a small space on the surface of the earth selected as the oviposition site. The clearing operation is a strenuously performed task, the insect hurriedly scratching away loose surface material with her fore feet as if in desperate haste to prepare the spot, from which she may remove in her jaws pellets and pebbles as large as her body. This done, she reverses her position and jabs the ovipositor at the clearing, or, at least, such is her evident intent, but often as not the aim miscarries, quite unperceived by the impetuous cricket, and the subsequent insertion of the ovipositor is then made at a place entirely untouched in the work of preparation.

At the beginning of oviposition the *Gryllus* female elevates herself on her hind legs, thus raising the abdomen, and depresses the ovipositor until its shaft is directed posteriorly and downward at an angle of about 45 degrees to the surface of the ground, as the tip is inserted into the latter. Within the space of a minute, when working in soft soil, the ovipositor is buried to full length, and the terminal part of the abdomen comes in contact with the ground. During the insertion process the two valvulae of each side glide rapidly back and forth a short distance on each other, the corresponding blades of opposite sides apparently working in unison. The egg enters the channel of the ovipositor at the bases of the valvulae, passes along the entire length of the shaft, and is extruded from the tip into the bottom of the excavation. During the withdrawal of the ovipositor, the organ is repeatedly thrust down into the cavity at successively shorter depths, evidently to pack the soil above the egg. When the ovipositor is fully extracted, the insect gives no further attention to the place where the egg has been intrusted to the earth. These observations on *Gryllus* were made on individuals in confinement. *Nemobius* scratches over the surface where the egg has been deposited before leaving it; *Oecanthus* plugs each egg cavity she makes in a twig with bark chew-

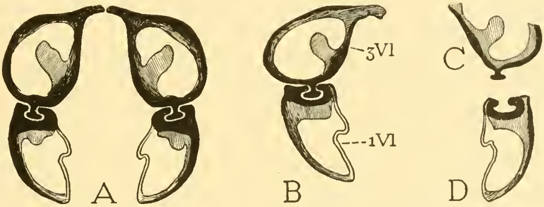

Fig. 20.—Sections of the shaft of the ovipositor of *Gryllus assimilis,* showing groove-and-ridge connections between the first and third valvulae.

ings mixed with a gluey discharge from the ovipositor. As is the usual habit with crickets, *Gryllus* deposits but one egg in each boring.

The movements of the ovipositor made by *Gryllus* during egg laying in soft soil are thus seen to be very simple ones, and there is scarcely any accompanying motion of the abdomen, such as the contortions made by *Oecanthus* while drilling into wood. The ovipositor of *Gryllus* is lowered preparatory to its insertion into the ground, its penetration is accompanied by the rapid back-and-forth movement of the valvulae on each other, and after withdrawal it is elevated again to the usual position, The entire organ is probably capable of a slight protraction and retraction.

The fixed points of movement in the basal parts of the ovipositor are the articulations of the first valvifers with the lower edges of the ninth abdominal tergum (fig. 17 A, F, 21, *a*), the outer and inner articulations of the two valvifers on each side with each other (fig. 17 A, *b,* fig. 21, *dh*), and the weak, flexible unions of the first valvulae with the lower angles of the first valvifers (*c*). Otherwise the ovipositor has a free movement on the abdomen by means of its membranous connections with the latter.

The movements of depression and elevation of the ovipositor affect not only the shaft but the entire basal parts of the organ, and the fulcra are the articulations of the first valvifers with the lower angles of the ninth tergum (figs. 17 A, 21, *a*). The muscles that accomplish these movements are clearly the anterior and posterior lateral muscles of the ninth tergum (figs. 17 E, H, 21, *5*, *8*), the first of which are inserted ventrally on the anterior intervalvula (*aiv*), the second on or near the posterior intervalvula (*piv*). The insertion points of these muscles are anterior and posterior to the articulations of the first valvifers on the ninth tergum (*a*), and pulling upward on these points correspondingly depresses or elevates the ovipositor. Morphologically the levators and depressors of the ovipositor are the tergosternal muscles of the ninth abdominal segment.

The alternating opposite movements of the dorsal and ventral valvulae on each other depend on the articulation of the first valvifers with the ninth tergum (fig. 21, *a*), and on the inner articulation of the two valvifers of each side with each other (*dh*). A depression of the posterior end of either of the first valvifers (B) causes the corresponding ventral valvula, which is flexibly attached to the ventral angle of the first valvifer, to slide proximally on the lower edge of the dorsal valvula. But, since the first valvifer rocks on the fulcrum (*a*) of the ninth tergum, its posterior end, when depressed, describes a short arc of a circle in a downward direction (indicated by the curved arrow on the right), and this movement bears down on the second valvifer and gives this valvifer a thrust posteriorly, which causes the dorsal valvula to slide backward on the ventral valvula while the latter is moving forward. The opposite movement of the first valvifer (indicated by the curved arrow on the left) reverses the movement of the valvulae on each other. Thus, by a simple rocking motion of the first valvifer on its articulation with the ninth tergum, the two valvulae of the same side move lengthwise on each other alternately in opposite directions. This action can easily be demonstrated on a dissected specimen. But also it will be observed that a rocking motion of the second valvifer on its articulation with the first valvifer (*dh*) imparts the same movements to the two valvulae, and increases the degree of movement in the dorsal valvula. The mechanism is extremely delicate, and the least motion, either of the first valvifers on the ninth tergum, or of the second valvifers on the first valvifers, produces the sliding movement of the valvulae on each other. The dorsal valvulae are the stronger of the two pairs of blades forming the shaft of the ovipositor, and end in sharp points which normally project beyond the thin, truncate tips of the second valvulae (fig. 17 B, C).

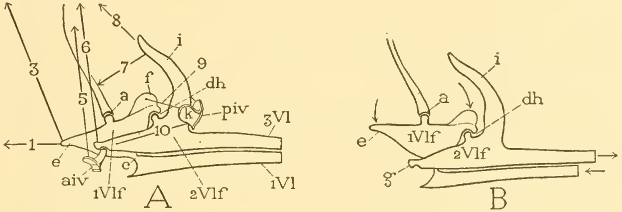

FIG. 21.—Diagrams of the basal mechanism of the ovipositor of *Gryllus assimilis.*

a, articulation of first valvifer with ninth tergum; *aiv,* anterior intervalvula; *c,* attachment of first valvula to first valvifer; *dh,* inner articulation between first and second valvifers; *e,* anterior apodeme of first valvifer; *f,* posterior apodeme of first valvifer; *g,* anterior apodeme of second valvifer; *i,* posterior apodeme of second valvifer; *k,* median apodeme of posterior intervalvula; *piv,* posterior intervalvula; *1Vl,* first valvula; *3Vl,* third valvula; *1Vlf,* first valvifer; *2Vlf,* second valvifer.

The muscles that bring about the movement of the valvulae on each other are the three pairs of large lateral muscles inserted on the valvifers (fig. 17 E, H, *3, 6, 7*). These muscles, morphologically, are the tergopleural muscles of the eighth and ninth abdominal segments. The first on each side (3), arising on the eighth tergum and inserted on the anterior end of the first valvifer, depresses the posterior end of this valvifer by pulling upward on its anterior end (fig. 21 A, B). The muscle, however, has no antagonist inserted on the first valvifer, so that its contraction simply retracts the ventral valvula and protracts the dorsal valvula (B). After this, the principal movement of the valvulae on each other evidently results from the motion of the second valvifer on the first, and there can be no doubt that the muscles effecting this action are those of the ninth tergum inserted on the second valvifers (fig. 17 E, G, H, *6*, *7*). The first of these two muscles (*6*) is attached on the anterior apophysis (*g*) of the second valvifer; the second (*7*), having a horizontal position, is attached on the posterior dorsal arm (*i*) of the same valvifer. The two muscles thus oppose each other from opposite sides of the articular surface (G, *h*) by which the second valvifer rocks on the first valvifer. If the ovipositor were a rigid structure, this mechanism apparently could only move the distal shaft of the ovipositor up and down on the fulcral point (*h*), but as already noted, the demonstrable effect of the rocking of the second valvifer on the first valvifer is an opposite back-and-forth movement of the two valvulae of the same side on each other.

The two pairs of ventral muscles of the ovipositor (fig. 17 E, H, *9*, *10*) uniting the first valvifers and the second valvifers, respectively, with the posterior intervalvula (*piv*), must be tensors in function, since their contraction could only produce a compression of the basal parts of the ovipositor. The muscles of the seventh sternum (fig. 19 A, *1*), inserted on the anterior ends of the first valvifers (fig. 17 A, E, F, H, *1*), are evidently retractors of the ovipositor.

During oviposition, the egg passes through the entire length of the ovipositor in the channel between the valvulae. It appears that the movement of the valvulae on each other is the cause of the progress of the egg, but it is not evident how the effect is produced, since the inner surfaces of the valvulae are smooth and give no suggestion of the means by which the movement of the egg is controlled.

The distal end of the ovipositor is somewhat enlarged and forms a lanceheadlike termination of the shaft with the acute apex slightly depressed (fig. 17 B). The tips of the valvulae are capable of opening upon each other by reason of a hingelike membranous area (*m*) at the base of the enlarged terminal part of each of the dorsal valvulae. In handling narcotized specimens, the observer may be surprised to see the ends of the valvulae suddenly gape widely apart (D), as they sometimes do. There are no muscles in the terminal parts of the ovipositor; the opening of the distal extremities of the blades is produced automatically by an extreme retraction of the dorsal valvulae, which brings a pair of knobs (C, *n*) on their under surfaces against abruptly rising areas on the upper surfaces of the ventral valvulae, with the result that the distal parts of the dorsal valvulae, beyond the membranous hinges (*m*) at their bases, are suddenly thrown upward (D). The opening apparatus probably enables the cricket to hold the egg in the tip of the ovipositor so that it may be thrust securely into the bottom of the hole where it is deposited. This use of the ovipositor the writer has clearly observed in the case of *Nemobius* ovipositing against the wall of a glass jar.

The postgenital segments.—The tenth and eleventh segments of the abdomen together form a conical end piece of the body, which supports the cerci laterally and encloses the anus between its distal lobes (fig. 22 A).

The tenth tergum and the epiproct (fig. 22 A, *XT, Eppt*) are united in a composite supra-anal plate, but the boundary separating the two component parts of the plate is quite evident. The narrowed anterior lateral angles of the dorsal part of the tenth tergum are continued into abruptly widened lateral plates (fig. 18, *p*), which are produced ventrally on the sides of the tenth segment, before the bases of the cerci, to the lower angles of the paraprocts (*Papt*). The venter of the tenth segment is mostly membranous, but it contains a narrow, transversely elongate sternal sclerotization (fig. 22 C, *XStn*). Internally the anterior margin of the tenth tergum is strengthened by a strong antecosta (*Ac*). The dorsal part of the tenth tergum is separated from the base of the cercus on each side by a wide membranous area containing a small crescentic sclerite (*A, q*).

The tergum of the eleventh segment, or epiproct, consists of the distal lobe of the supra-anal plate (fig. 22 A, *Eppt*). Its marginal parts (*s*) are separated from the median shield-shaped region by a narrow, weakly sclerotized or membranous area on each side. The marginal band (*s*) appears to end anteriorly at the transverse folds extending outward from the posterior edge of the tenth tergum to the bases of the cerci. Considering, however, that the cerci belong to the eleventh segment, and observing that in *Scudderia* (fig. 12) the basal angles of the epiproct (*Eppt*) are produced into slender arms extending forward and downward *anterior* to the bases of the cerci, there is reason to believe that the marginal band of the epiproct in *Gryllus* is morphologically continued anteriorly in the narrow crescentic sclerites (fig. 22 A, *q*) lying mesad of the bases of the cerci, which appear to belong to the dorsum of the tenth segment. When the area about the base of the cercus is stretched and flattened out

(B), there is brought to view a weakly sclerotic connection between the sclerites *s* and *q*, and, moreover, there is exposed a distinct third sclerite (*r*) intervening between *q* and the base of the cercus (*LB*), which by an anterior process articulates with the inner margin of the latter. It is to be seen, therefore, that a broken sclerotic continuity exists between the base of the cercus and the epiproct.

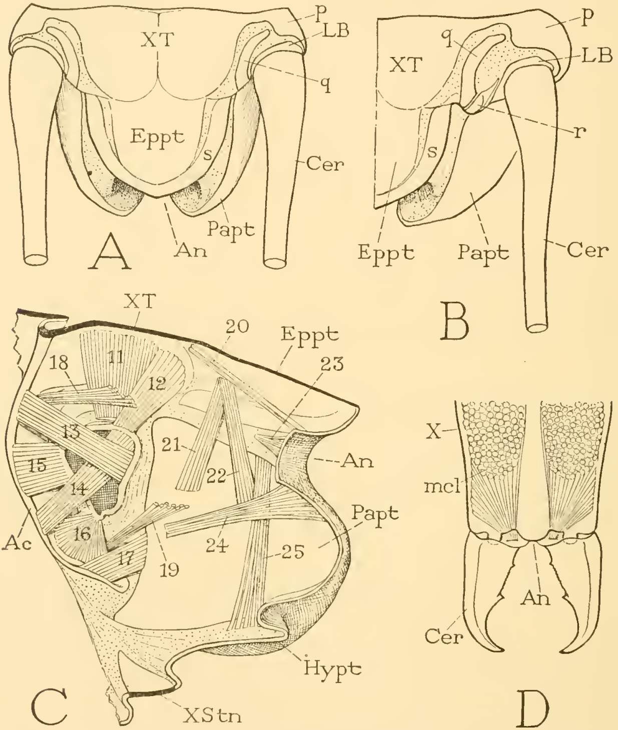

FIG. 22.—Structure of postgenital segments of *Gryllus assimilis,* and muscles of cerci of *Heterojapyx gallardi.*

A, dorsal view of postgenital segments of *Gryllus.*
B, right half of same with membranous parts stretched to show hidden sclerites.
C, muscles of right half of postgenital segments of *Gryllus.*
D, cerci and muscles in tenth segment of *Heterojapyx.*

The paraprocts (figs. 18, 22 A, B, C, *Papt*) are large, half-oval sclerites occupying the ventrolateral parts of the eleventh segment behind and below the bases of the cerci and the lower ends of the lateral plates of the tenth tergum (fig. 18). The dorsal edges of the paraprocts are connected by membrane with the lateral margins of the epiproct (fig. 22 A, C), and their lower edges are united to each other by a median ventral membrane, the posterior edge of which forms a small median flap, or hypoproct (C, *Hypt*). The posterior margins of the several lobes of the eleventh segment are inflected in the circumanal membrane, which is possibly to be regarded as a remnant of the periproct, and which is directly continued into the walls of the rectum.

The cerci are implanted on membranous areas (fig. 18) surrounded by the laterodorsal crescentic sclerites (*q*) above, the lateral plates (*p*) of the tenth tergum anteriorly and ventrally, and the paraprocts (*Papt*) behind. Each cercus has a distinct though narrow annular basis (fig. 22 B, *LB*), which, as already observed, articulates by its inner margin with the anterior arm of the small oval sclerite (*r*) attached to the posterior end of the crescentic dorsal sclerite (*q*). The appendage is provided with six muscles arising on the tenth tergum (C).

The musculature of the postgenital segments has little resemblance to that of the genital and visceral segments and gives little evidence bearing on the morphology of the terminal parts of the abdomen. The tenth segment muscles are mostly inserted on the bases of the cerci; the muscles of the eleventh segment connect the epiproct and paraprocts, and go to the circumanal membrane. The postgenital complex is movable on the rest of the abdomen by the dorsal muscles of the ninth segment inserted on the antecosta of the tenth tergum, and in the male there is a strong ventral muscle on each side from the anterior lateral angle of the ninth sternum to the inner face of the paraproct.

The muscles arising on the tenth tergum include the muscles of the cerci, two pairs of rectal muscles, and a pair of muscles to the paraproct. Du Porte (1920) describes and figures for *Gryllus* a dorsal longitudinal muscle lying " near the median line of the suranal plate, stretching from the anterior to the posterior borders of the sclerite "; but the writer could find no such muscle present, and no corresponding muscle is mentioned by Ford (1923). The muscles of the tenth and eleventh segments, illustrated at C of Figure 22, are the following:

11.—A broad, flat, transverse muscle arising medially on tenth tergum; inserted on anterior arm of the small sclerite (B, *r*) articulating with dorsal margin of base of cercus.

12.—Origin posterior to *11* on extreme posterior part of tenth tergum; crosses internal to outer end of *11* to insertion on dorsal margin of base of cercus. This muscle Ford (1923) regards as a muscle of the epiproct which has shifted forward to the tenth tergum, since the corresponding muscle in some other Orthoptera arises on the epiproct.

13.—Origin anterior on antecosta of tenth tergum above level of cercus; goes posteriorly and downward to insertion on inner (posterior) edge of base of cercus.

14.—Origin on antecosta of tenth tergum before lower end of cercal base; extends upward and posteriorly, ectad of *13,* to insertion on posterior dorsal angle of base of cercus.

15.—A short muscle arising on antecosta of tenth tergum between *13* and *14;* insertion on anterior (outer) margin of base of cercus.

16.—A short, fan-shaped muscle arising on ventral part of tenth tergum; fibers converging dorsally to insertion on ventral angle of base of cercus.

The number of muscles arising in the tenth segment inserted on the bases of the cerci might seem to discredit the embryonic evidence that the cerci are appendages of the eleventh segment. We can only suppose that the muscles which function as motors of the cerci are morphologically the dorsal intertergal muscles between the tenth and eleventh segments that have secondarily become attached on the bases of the cerci. The same assumption must be made for all other insects, except with regard to the cercal muscles from the epiproct, but in the Thysanura it is quite evident that the cercal muscles are the normal longitudinal muscles of the tenth segment (fig. 22 D).

Three muscles take their origin in the tenth segment of *Gryllus* that are not attached on the cerci.

17.—A short intersegmental muscle arising on ventral end of tenth tergum (fig. 22 C); inserted posteriorly on anterior margin of paraproct.

18.—Dorsolateral muscle of the rectum, arising dorsally on tenth tergum above *13.*

19.—Ventrolateral muscle of the rectum, arising ventrally on tenth tergum in angle between *16* and *17.*

The following muscles are confined to the eleventh segment:

20.—A pair of slender, median, dorsal muscles, arising on anterior end of epiproct (fig. 22 C); inserted posteriorly on extremity of dorsal wall of rectum. (The supra-anal muscles of Ford.)

21, 22.—Two lateral muscles on each side, arising together on anterior lateral part of median plate of epiproct; diverging downward to insertions on inner face of upper half of paraproct.

23.—A very small muscle arising in membrane between epiproct and paraproct; inserted on extremity of rectum laterally.

24.—Origin anteriorly on inner face of paraproct; insertion posteriorly on circumanal membrane above posterior end of paraproct.

25.—Origin dorsally on upper edge of paraproct posterior to *22;* insertion ventrally on membrane between lower edges of paraprocts at base of hypoproct.

BLATTA ORIENTALIS LINNAEUS

The Blattidae, the Mantidae, and the Termitidae show a most interesting relationship to one another, especially with respect to the female genital apparatus. The termites are very much like the cockroaches in many of their general features, and particularly in the structure of the ovipositor, though they are placed in a separate order, while, as Walker (1919) says, " in the cockroaches we find many of the peculiarities of the Mantidae in a more pronounced form, as well as special characteristics of their own ". In each of the three families the eighth abdominal sternum of the female is reduced, and the seventh sternum is prolonged backward as a large subgenital plate concealing the eighth sternum and, in the Blattidae, the entire ovipositor as well. In the mantids the seventh sternum forms a troughlike structure with mobile, valvular terminal lobes for manipulating the material of the egg case; in the blattids the lobes of the seventh sternum (fig. 24 A, *VIISL*) enclose a large, distensible vestibular chamber (fig. 23, *Vst*) in which the ootheca is formed, and in some species retained a varying length of time. Hence, we find in the Mantidae, as pointed out by Chopard (1920), " almost the same structure as in the blattids of the subfamily Blattinae, though the rôle of the valves in the two cases may be very different according to the mode of oviposition ". The formation of the egg case in the Mantidae is described by Bugnion (1923).

The definitive female gonopore in both the Mantidae and the Blattidae is located on the reflected dorsal surface of the reduced eighth sternum (fig. 23, *Gpr*), and therefore has the same position as in other members of the Orthoptera. The statement frequently made that the female gonopore in these families lies between the seventh and eighth sterna is based on an error of anatomical interpretation, as will presently be shown. Above the eighth sternum is the true genital chamber

(*GC*) into which opens the spermatheca (*Spt*). The genital chamber of the roach, however, has the appearance of being a mere pocket in the anterior wall of the large vestibulum (*Vst*) lying above the seventh sternum (*VIIS*) and the terminal lobes of the latter (*VIISL*). The accessory glands (*AcGl*) open into the dorsal wall of the vestibular chamber in the region of the ninth venter. The female genital invaginations in the mantids and roaches, therefore, are of the type of structure shown diagrammatically at C of figure 8.

The ovipositor has many points of resemblance in the Mantidae, Blattidae, and Termitidae; it is of small size as compared with the usual ovipositor of other orthopteroid insects, and in some respects it appears to be degenerate, while at the same time, especially in the Blattidae, it shows unusual specializations that obscure the generalized structure of the organ.

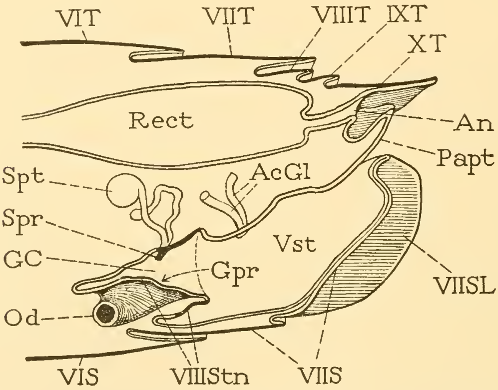

FIG. 23.—Diagrammatic median section through the distal abdominal segments of *Blatta orientalis.*

Note large vestibulum (*Vst*) formed within lobes of seventh sternum (*VIISL*), concealing small genital chamber (*GC*) at its anterior end above invaginated eighth sternum (*VIIIStn*), gonopore (*Gpr*) and spermathecal pore (*Spr*) in walls of genital chamber, and accessory glands (*AcGl*) opening into vestibule.

The visceral region of the abdomen has a simpler mechanism in the Mantidae and Blattidae than in the Tettigoniidae and Gryllidae, allowing much less play between the dorsal and ventral plates. The spiracles are contained in deflected marginal sclerites (fig. 16 B, *Sp*), which belong to the dorsum and are therefore paratergites (*pt*), and not " pleurites " as they are sometimes called.

In *Blatta orientalis* the dorso-pleural line of the abdomen (fig. 16 B, *a-a*, C, *a*) is contained in the narrow, infolded lateral membrane uniting the paratergites (*pt*) and the large ventral plates. Since in the male roach the ventral plate of the ninth segment bears a pair of styli, it is probable that the definitive sterna of all the abdominal segments are composite pleurosternal plates (*PlStn*) formed of the limb base areas and the primitive sterna. The lateral abdominal muscles of the roach are all functionally tergosternal (fig. 16 C), though some may be morphologically tergopleural. Two muscles of each segment are attached above on the median tergite (*T*), and one on the paratergite (*pt*), the last being described by Ford (1923) as a "pleural" muscle. The three are attached below on the lateral parts of the large, strongly convex sternal plate (*PlStn*). The roaches do not make any perceptible breathing movements of the abdomen under ordinary conditions. The well-known diagram by Plateau (1884) purporting to show the respiratory movements of *Blatta orientalis* undoubtedly depicts the kind of movements a roach can bring about between its dorsal and ventral abdominal plates; but since Plateau's subjects were induced to make them after being pinned down by the edges of the prothorax, with the legs and wings cut off, and the abdomen propped up on a bent pin, there is reasonable doubt that the observed contractions and expansions of the abdomen represent normal respiratory movements.

The genital segments of female Blattidae are almost entirely concealed within the seventh segment (fig. 24 A). Beyond the seventh tergum, and above the large terminal lobes of the seventh sternum, is the proctiger carrying the cerci laterally, projecting from the concealed ninth segment (B). The dorsal plate of the proctiger (*XT*) is evidently the tenth tergum alone, as claimed by Walker (1919), the epiproct being represented only by the membranous fold beneath its base. The muscles of the cerci take their origin on the proximal part of the plate, but the weakly developed muscles of the paraprocts are attached dorsally in the ventral membrane. The writer in a former paper (1931), without examining the paraproctial musculature, regarded the terminal dorsal plate of the cockroach as formed of the combined tenth tergum and epiproct, and Crampton (1929) makes the same interpretation. Walker (1919) points out, however, that "the disappearance of the supra-anal plate (epiproct) in the blattids and its substitution by the tenth tergite is the more complete expression of the same tendency indicated in the mantids, where the true supra-anal plate, though present, is reduced and entirely covered by the tenth tergum." In Tettigonidae, Gryllidae, and Acrididae, on the other hand, the epiproct is retained and forms the terminal plate of the abdomen.

The tergum of the seventh segment (fig. 24 A, *VIIT*) does not differ from the terga preceding it. The seventh sternum (*VIIS*), however, is highly modified and specially developed. It consists of a basal, semiannular plate resembling the preceding sterna, and of two large, oval, distal, lateroventral, valvelike lobes (*VIISL*) forming a hoodlike cap concealing the ovipositor. The median ventral edges of these

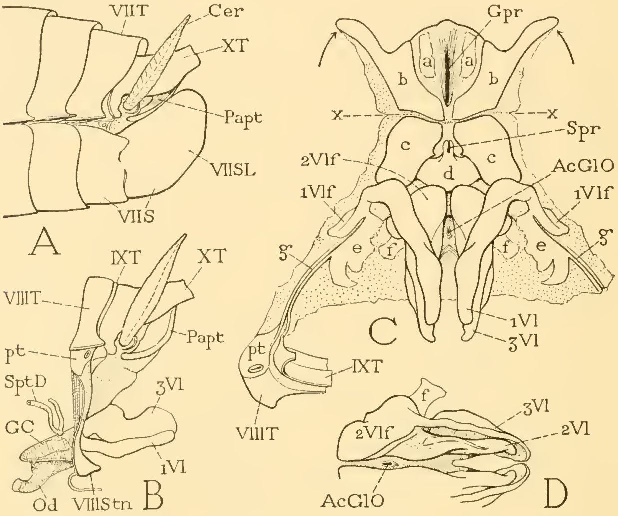

Fig. 24.—The genital segments and the ovipositor of *Blatta orientalis.*

A, end of abdomen, showing large valvular lobes of seventh sternum concealing vestibulum, ventral parts of eighth segment, genital chamber, and ovipositor.

B, genital and postgenital segments detached, showing eighth sternum as small fold beneath entrance to genital chamber (*GC*) into which opens the oviduct (*Od*) and spermathecal ducts (*SptD*).

C, ventral view of ovipositor and associated parts: floor of genital chamber containing gonopore (*Gpr*) turned forward along line *x-x*, exposing sternal sclerites (*a, b*) of eighth segment; spermathecal pore (*Spr*) in median plate (*d*) of roof of genital chamber, flanked by two lateral plates (*c, c*); opening of accessory glands (*AcGlO*) in venter of ninth segment between second valvifers (cf. fig. 23).

D, ventral view of parts of ovipositor belonging to ninth segment.

a, b, sclerites of eighth sternum in floor of genital chamber associated with gonopore; *c, d,* secondary sclerites in dorsal wall of genital chamber associated with spermathecal pore; *e,* ventral part of ninth tergum; *f,* lobe of second valvifer; *g,* intersegmental groove between ventral ends of eighth and ninth terga; *x-x,* line across anterior extremity of genital chamber on which floor of genital chamber is turned forward (C).

lobes are united by a wide inflected membrane, and from their inner surfaces there are produced laterally two high membranous folds. The space between these folds can be greatly expanded by the extension of the ventral membrane, thus forming a pocket in which the ootheca is lodged. All this extension and modification of the seventh sternum is clearly an adaptation for the formation and retention of the egg case. In the structure of the female genital apparatus, therefore, the roach is highly specialized. The oothecal pocket is a part of the vestibulum (fig. 23, *Vst*), at the anterior end of which is the small true genital chamber (*GC*) above the reduced eighth sternum (*VIIIStn*).

When the seventh segment is removed there are exposed dorsally the narrow eighth and ninth terga (fig. 24 B, *VIIIT, IXT*), though the ninth tergum is mostly concealed beneath the eighth. The eighth tergum is somewhat widened laterally, where on each side it forms a sharp marginal ridge as do the preceding terga, and it is then deflected in a small paratergal sclerite (*pt*) enclosing the eighth spiracle. From the paratergite a fold of the integument extends downward and mesally to the lateral arms of the eighth sternum (*VIIIStn*). A lateral tergo-sternal muscle of the eighth segment lies just within the fold uniting the tergum with the sternum.

The sternum of the eighth segment is the sclerotization in the wall of a short fold produced posteriorly from the anterior wall of the vestibulum (figs. 23, 24 B, *VIIIStn*). At the margin of the fold the sternum is reflected dorsally and anteriorly on the dorsal wall of the fold. The fold itself, therefore, is the venter of the eighth segment, and its reflected dorsal wall forms the floor of the genital chamber (fig. 23, *GC*). Upon the latter is situated the gonopore (*Gpr*), a long, narrow, median opening (fig. 24 C, *Gpr*). In *Blatta* the floor of the genital chamber contains four sclerites composing the eighth sternum; two are small median plates (C, *a, a*) lying at the sides of the gonopore, and two are large lateral plates (*b, b*) produced upward on the sides as a pair of arms on which the tergo-sternal muscles of the eighth segment are attached (B). This group of sclerites associated with the gonopore is termed the "vaginal plate" by Vogel (1925). The view of the genital parts given at C of figure 24 shows the roof of the genital chamber and vestibulum, together with the ovipositor, as seen from below; but the floor of the genital chamber is turned forward (as indicated by the arrows) along the transverse line (*x-x*) at its anterior end.

The roof of the genital chamber contains two large, irregularly oval lateral sclerites (fig. 24 C, *c, c*) and a median sclerite (d). These plates must be secondary sclerotizations between the eighth and ninth segments. The median sclerite bears the opening of the spermathecal tubes (*Spr*) on a small projection from its anterior margin (fig. 23, *Spr*), suggestive of the spermathecal spout of *Gryllus,* similarly situated except that it is contained in a pouch of the genital chamber (fig. 18, *u*). The eggs of *Blatta* must be fertilized in the genital chamber, and then passed out between the processes of the ovipositor into the vestibulum, where they are enclosed in the ootheca. The roof of the vestibulum contains the basal parts of the ovipositor (fig. 24 C), between which is the median opening of the large accessory glands (*AcGlO*). An account of the histological structure of these glands, together with a study of their contents, is given by Bordas (1909), and the formation of the ootheca in the vestibular chamber has been described by Kadyi (1879).

The morphology of the female genital segments of the Blattidae as given above, and as interpreted by Miall and Denny (1886), Walker (1919), Ford (1923), Crampton (1929), and Imms (1930), is so strictly in accord with that of the genital segments of other Orthoptera that it is difficult to see why certain recent investigators have not acceded to it. Vogel (1925), Nel (1930), and Heberdey (1931), for example, follow Bordas (1909), who accepted the statement of Peytoureau (1893) that " l'overture du vagin se trouve entre le septième et le huitième " urosternites. Vogel, therefore, disposes of the sclerites of the genital surface (fig. 24 C, *a, b*) surrounding the gonopore (collectively termed the " vaginal plate ") as secondary sclerotizations of the membrane between the seventh and eighth segments, and regards the median plate in the dorsal wall of the genital chamber (*d*), bearing the opening of the spermathecal ducts, or situated behind the latter in some species, as the true eighth sternum. Nel (1930) adopts the same idea, and as a consequence is forced to conclude that the sperm receptacles of Blattidae, since they open on the " seventh " intersternal membrane, are not homologous with the spermatheca of other insects. In describing *Blattella* he says: " The common oviduct is short and opens by means of the gonopore on a raised fold of the floor of the genital cavity very near its anterior end. This raised fold is due to a pocket of the genital cavity extending beneath the part carrying the gonopore. The gonopore is thus on the reflexed inner surface of the seventh sternum, the seventh intersternal or so-called intersegmental membrane." Further, he says of the spermathecal ducts that they open into a short dorsal groove on the fold carrying the gonopore, and he then observes that the position of the spermathecal openings, which are thus on the " seventh intersternal membrane ", constitutes an " aberrant and secondary condition." When it is seen, however, that the fold bearing the gonopore is a part of the eighth sternum, there is then no discrepancy between the Blattidae and other Orthoptera, either with regard to the position of the gonopore or that of the spermathecal opening.

Any doubt that the sclerite (or group of sclerites) on the fold bearing the female gonopore in the Blattidae represents the true eighth sternum is dispelled by observing the muscle connections with the seventh sternum and the eighth tergum. Ford (1923) says convincingly " the sclerite is clearly eighth sternal ", because her statement is based on the fact that the sternal muscles from the seventh segment are inserted on its anterior margin, and that tergosternal muscles of the eighth segment are attached upon it laterally. Hence, the female gonopore of adult Blattidae has the same morphological position as in other adult Orthoptera. It is probable that the female gonopore originates in the Blattidae on the posterior part of the seventh venter behind the seventh sternum, as it is known to do in various other insects, and that the position of the definitive opening is secondary. A migration of the gonopore in the roaches, however, has not been observed. Nel's (1930) statement that the median oviduct of *Blattella* originates on the seventh intersegmental membrane is based on his view that this membrane forms the fold bearing the gonopore, which is here interpreted as the eighth sternum. The female gonopore of adult Blattidae has the usual location on the posterior part of the eighth segment, and is not situated either on the seventh segment, or between the seventh and eighth sterna.

The ovipositor of *Blatta* is reduced and its parts are of irregular form as in other members of the Blattidae, but it retains all the elements of a typical orthopteroid ovipositor, including two pairs of valvifers and three pairs of valvulae.

The first, or ventral, valvulae (fig. 24 C, *1Vl*) are widely divergent proximally, where they are connected with a pair of small basal plates (*1Vlf*). These basal sclerites, though separated by a considerable space from the eighth sternum, are clearly the first valvifers since upon them are inserted muscles from the tergum of the eighth segment, and because they are directly continuous with the ventral valvulae. Each valvifer, however, is fused with an irregular sclerite (*e*) behind it, which belongs to the ninth segment, as shown by the fact that it lies posterior to the intersegmental groove (*g*) and is continuous with the ninth tergum (*IXT*) by a slender sclerotic strip on the posterior margin of the fold. This sclerite (*e*) Crampton (1925, 1929) calls the " valvifer ", but it is not the homologue of the sclerite he terms " valvifer " in Gryllidae and Tettigoniidae; it is evidently the lowermost extremity of the ninth tergum, to which the first valvifer is attached, as it is in most other insects. The eighth tergum has a small paratergal sclerite (B, C, *pt*) enclosing the eighth spiracle, which is extended ventrally (C) in a narrow sclerotic band on the anterior lip of the intersegmental fold (*g*).

The two valvulae of each side belonging to the ninth segment (fig. 24 D, *2Vl, 3Vl*) arise from a common base (*2Vlf*) representing the second valvifer. A small extension (*f*) of the valvifer apparently corresponds with the base of the posterior dorsal arm of the second valvifer in *Gryllus* (fig. 17 G, H, *i*), since it gives attachment to a muscle from the ventral plate (*e*) of the ninth tergum. The large accessory glands of *Blatta* open medially on the ninth venter between the second valvifers (fig. 24 C, D, *AcGlO*).

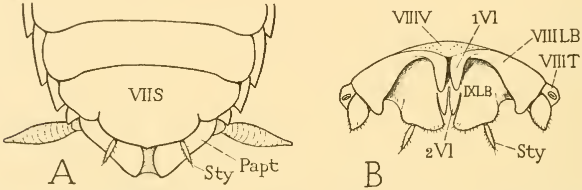

FIG. 25.—Young female nymph of *Blatta orientalis* with styli on ninth segment.
A, ventral view of terminal part of abdomen.
B, eighth and ninth segments exposed from below by removal of seventh sternum, showing styli (*Sty*) borne on basal plates (*IXLB*) of gonopods of ninth segment.

The close correspondence in fundamental structure between the ovipositors of *Blatta* and *Gryllus,* notwithstanding the great differences in size and form of the parts, scarcely needs to be pointed out. Walker (1919) has shown that the ovipositor of the Blattidae is developed in the usual manner from lobes of the eighth and ninth somites. It is particularly interesting to observe that the basal plates of the second gonopods in the female nymph bear small but distinct styli (fig. 25, *Sty*) which, though lost in the adult female, correspond with the styli of the male borne on the definitive sternal plate of the ninth segment.

The female genitalia of the termites, as described by Crampton (1920, 1923, 1929), appear to be the same as those of the Blattidae, except that the parts are more simple in form. In a female soldier of *Mastotermes darwinensis,* Crampton (1920) shows a small subgenital lobe of the seventh sternum underlapping the median part of the eighth sternum, beyond which is the ninth sternum bearing a pair of lobes (limb bases) supporting distally the short styli and basally the rudiments of a pair of inner valvulae. In a winged adult female (Crampton, 1923) the three usual pairs of valvulae are well developed, but the styli, present in the soldier form, apparently are lost. Below the ovipositor the seventh sternum is produced as a subgenital plate, or "hypogenum", and the reduced eighth sternum forms a small lobe beneath the base of the ovipositor. In other termites the ovipositor is rudimentary or completely suppressed. Walker (1919) describes in *Termopsis* a pair of small lobes arising from the eighth sternum, representing the ventral valvulae, but the valvulae of the ninth segment are entirely absent.

VI. THE OVIPOSITOR OF HEMIPTERA

The genital segments and the ovipositor of the Hemiptera present the following characteristic features:

1. The shaft of the ovipositor is formed of the first and second valvulae, the first being external and ventral, the second internal and dorsal. The second valvulae are generally united with each other, either for a part or for most of their length.

2. The sternum of the seventh abdominal segment forms the subgenital plate of the female, and encloses a small vestibular chamber at the base of the ovipositor.

3. The eighth segment is exposed dorsally, but its lateral and ventral parts are mostly concealed within the seventh segment.

4. The first valvifers have a pleural position below the tergum on the sides of the eighth segment, though their posterior angles may be flexibly attached to the ninth tergum. The dorsal muscles of the first valvifers arise on the eighth tergum.

5. The sternum of the eighth segment is rudimentary, being represented generally by a mere fold of the integument below the base of the ovipositor at the anterior end of the vestibulum. The genital chamber is correspondingly reduced in most cases to a small pocket beneath the gonopore; in some of the Cicadidae, however, the genital chamber forms a large pouch into which open the median oviduct and the spermatheca.

6. The first valvulae have each two proximal rami. The outer ramus is flexibly attached to the ventral angle of the first valvifer; the inner ramus expands in a small plate solidly united with the anterior ventral angle of the ninth tergum. A muscle extends from the inner face of the first valvifer to the basal plate of the inner ramus.

7. The ninth tergum is exposed, and usually large. Its anterior ventral angles are produced forward as extensions to which are united the inner rami of the first valvulae.

8. The second valvifers have a pleural position on the sides of the ninth segment beneath the lateral margins of the ninth tergum. Each is movably articulated with the tergum at a point near the middle of its dorsal margin, and is provided with antagonistic muscles from the ninth tergum inserted before and behind the fulcrum.

9. There are generally no intervalvular sclerites in the ninth venter, and tergosternal muscles are absent in the ninth segment.

10. The second valvulae are attached proximally, each by a single arcuate ramus, to the anterior end of the second valvifer, and the ramus slides on the concave margin of the inner ramus of the corresponding first valvula.

11. The third valvulae are well differentiated from the second valvifers; they form a pair of lobes ensheathing the distal end of the shaft of the ovipositor; rarely they are absent.

12. The mechanism of the hemipterous ovipositor is very simple as compared with that of the gryllid ovipositor; its only muscles are those of the first and second valvifers, and the pair of muscles from the first valvifers to the inner rami of the first valvulae.

13. An unusual condition bringing about the discharge of the eggs directly into the channel of the ovipositor exists in some of the Cicadidae, in which the genital chamber forms a large pouch opening above the rudimentary eighth sternum, and has a second posterior exit between the bases of the second valvulae. The relation of this structure to the usual structure in other Hemiptera is not understood, and it appears that the morphology of the terminal parts of the female genital ducts in the Hemiptera is a subject in need of further investigation.

As between the Heteroptera and the Homoptera there is no essential difference in the structure of the ovipositor. In each group, also, the ovipositor is well developed in some forms, and reduced or absent in others. According to the comparative studies of Ekblom (1926, 1930), an ovipositor is present among the Heteroptera in the families Saldidae, Nabidae, Lygaeidae, Veliidae, Gerridae, Mesoveliidae, Corizidae, and Corixidae, and is best developed in the Saldidae and Nabidae; but the organ is well developed also in Notonectidae and Coreidae. The structure of the hemipterous ovipositor will be shown in this paper by examples taken from the Saldidae, Coreidae, Cicadellidae, and Cicadidae. In connection with a study of the ovipositor it is important to understand the segmentation of the abdomen, since students of the Hemiptera are most frequently at fault concerning the identity of the abdominal segments, on account of the partial or complete suppression of the first segment. In order to understand the morphology of the parts of the ovipositor described and figured by Ekblom, the following description of a saldid species, *Pentacora ligata,* is given as an introductory example.

PENTACORA LIGATA SAY

The abdomen of *Pentacora* (fig. 26 A) is broad and flattened, but the genital region, including the seventh, eighth, and ninth segments, forms a terminal enlargement supporting the ovipositor (*Ovp*). The first tergum (*IT*) is well developed, its anterior margin forming a free fold overlapping the narrow notum and postnotum of the metathorax; but the sternum of the first segment is either suppressed or indistinguishably united with the second. Segments *II* to *VII* have large paratergal plates (*pt*) forming the lateral margins of the wide pregenital region of the abdomen. The spiracles of these segments are situated ventrally in the lateral borders of the sternal plates, but those of the eighth segment lie in the paratergal lobes of the dorsum

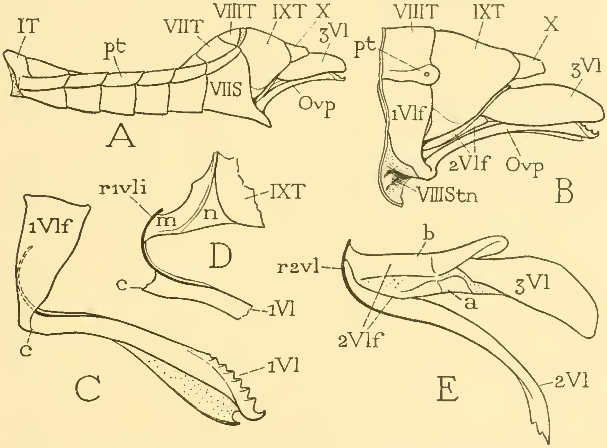

FIG. 26.—Abdomen and ovipositor of *Pentacora ligata* (Saldidae).

A, entire abdomen.

B, genital and postgenital segments and ovipositor, showing rudimentary eighth sternum beneath gonopore.

C, first valvifer and first valvula.

D, attachment of inner ramus of first valvula to ninth tergum.

E, second valvifer with second and third valvulae.

(B, *pt*). The abdomen ends with the small tenth segment, or proctiger (*X*), from beneath which project the wide third valvulae (*3Vl*) with the shaft of the ovipositor (*Ovp*) between them.

The seventh segment is funnel-shaped, expanded posteriorly. Its large sternum (fig. 26 A, *VIIS*) projects ventrally in a median lobe beneath the base of the ovipositor, and its posterior margin is inflected to form the ventral and lateral walls of a vestibulum concealing the lower anterior parts of the eighth and ninth segments, and the base of the ovipositor.

The eighth segment is mostly concealed within the seventh (fig. 26 A). When removed from the latter (B) it is seen to consist of a complete annulus, though the ventral part is reduced and membranous. Dorsally the segment presents a tergal plate (*VIIIT*), with small paratergal lobes (*pt*) containing the eighth spiracles; its lateral walls are formed by large, triangular pleural plates, which are the first valvifers (*1Vlf*); the membranous ventral part forms a small fold (*VIIIStn*) at the base of the ovipositor, representing the rudimentary eighth sternum. The genital opening appears to be situated above the sternal fold between the bases of the first valvulae, but its existence here could not be positively determined in the dried specimens examined.

It is of particular interest to note that the first valvifer (fig. 26 B, *1Vlf*) has a true pleural position on the side of its segment. Crampton (1929) mistakes the valvifer of the eighth segment in Hemiptera for a basivalvula, but the identity of the plate in question is shown without doubt by its musculature, and by the fact that the first valvula is directly connected with its ventral angle (C). The first valvula, however, has an inner ramus (D, *r1vli*) which curves upward from its dorsal margin and is connected with a small plate (*m*) attached to an extension (*n*) of the lower anterior margin of the ninth tergum (*IXT*). This basal sclerite (*m*) of the inner ramus of the first valvula might be regarded as a part of the valvula, inasmuch as it is continuous ventrally with the latter by a fold of the connecting membrane, or it might be supposed to be a part of the ninth tergum; but it is more probable that it is a part of the ramus itself, since there is inserted upon it a short thick muscle arising on the inner face of the valvifer, which would appear to represent the basal muscle of the gonapophysis in Thysanura (fig. 6 F, *gmcl*). In any case, the structure of the first valvifer, and the inner connection of the first valvula with the ninth tergum, as shown in *Pentacora,* are features characteristic of all the Hemiptera. The movements of the first valvula are produced in the usual manner by muscles of the first valvifer arising on the eighth tergum.

The ninth segment has a large tergal plate (fig. 26, A, B, *IXT*) covering the back and sides of the segment; its anterior ventral angles are extended anteriorly within the seventh segment, and, as just noted, they are here fused with the basal plates of the inner rami of the first valvulae (D). Below each lateral margin of the ninth tergum is an elongate lobe (B, *2Vlf*), the outer wall of which is not continuously sclerotized, but presents a dorsal and a ventral plate (E, *a*, *b*). The lobe, however, is unquestionably the second valvifer (*2Vlf*), since it carries the second and the third valvulae (*2Vl, 3Vl*). The second valvula is attached to the anterior end of the second valvifer by an arcuate basal ramus (*r2vl*), which slides on the concave margin of the inner ramus of the first valvula. The large third valvula (*3Vl*) arises from the distal end of the second valvifer; the third valvulae form two broad free lobes embracing the distal end of the shaft of the ovipositor between their concave mesal surfaces. The second valvifer is articulated at a point near the middle of its dorsal margin to the lower edge of the ninth tergum, and muscles arising on the latter, inserted anteriorly and posteriorly on the valvifer, rock the latter up and down and impart a back-and-forth movement to the second valvula attached to its anterior end. The two second valvulae probably work in unison because of their connection with each other. The true sternal region, or venter, of the ninth segment is the narrow membranous wall between the two second valvifers.

According to the terminology used by Ekblom (1926, 1930) for naming the parts of the hemipterous ovipositor, the dorsal plate of the second valvifer (fig. 26 E, *b*) is the "parasternite" of the ninth segment; the small ventral plate (*a*) supporting the third valvula is "sternite *a*" of the ninth segment; and the third valvula is "sternite *b*" of the ninth segment.

The shaft of the ovipositor of *Pentacora* is formed of the first and second valvulae, the first being external, the second internal. Each first valvula consists of a strong outer part (fig. 26 C, *1Vl*) with coarse teeth on the upper margin of its distal part, and of an inner membranous fold. Basally, as already observed, the first valvula is connected externally with the lower angle of the first valvifer (C, *c*), and mesally by an arcuate inner ramus with the lower anterior angle of the ninth tergum (D). The second, or inner, valvulae (E, *2Vl*) are united with each other for most of their length by a narrow membrane between their dorsal margins; their distal parts, however, are free, decurved, and toothed at their extremities. Basally each second valvula is connected by a single curved ramus (*r2vl*) with the anterior end of the corresponding second valvifer. The second valvulae are moved back and forth by the rocking motion of the second valvifers on their points of articulation with the ninth tergum. The mechanism of the hemipterous ovipositor will be more fully explained in the account of the two homopterous species to be described.

ANASA TRISTIS (DEGEER)

The abdomen of female Coreidae consists of 10 segments, all of which are visible and distinct from above (fig. 27 A), though the first tergum is united with the second. The sternum of the first segment, however, is absent (B), and the first ventral plate (*II*), therefore, is the second sternum. It bears laterally a pair of spiracles. The segments following, to the seventh, present no special modifications, and the spiracles are located in the lateral parts of their ventral surfaces. The seventh segment of *Anasa tristis* has a broad tergal plate, emarginate posteriorly (A, *VII*). The seventh sternum (B, *VII*) is deeply emarginate, and bears medially a pair of small lobes (*a*), at the bases of which is a prominent transverse groove. The terga of the eighth and ninth segments are distinct though narrow plates as seen from above (A, *VIIIT, IXT*); their lateral parts appear ventrally (B) as two pairs of marginal lobes at the sides of the genital region. The true sternal parts of these segments are covered by a pair of large triangular plates (B, *1Vlf*), which, as will presently be shown, are the valvifers of the eighth segment. The tenth segment (*X*) projects beyond the genital segments in the form of a short tube containing the anal opening.

The description of the abdomen of *Anasa tristis* by Tower (1913) is wholly misleading, and has been the cause of considerable confusion to systematists in Hemiptera. In the first place, the numbering of the abdominal segments as given by Tower is at fault because the first segment is entirely disregarded, though it is represented by a distinct tergal plate (fig. 27 A, *IT*). The last pregenital segment, therefore, is segment *VII*, not the sixth; and the first pair of subgenital plates (B, *a*) are lobes of the sternum of this segment (*VII*). The second and larger pair of genital plates (*1Vlf*), apparently the "eighth sternum" of Tower, are the valvifers of the eighth segment. The ventral parts of the ninth segment are concealed, and the proctiger, mistaken for the ninth segment by Tower, is the tenth segment, numerically, though anatomically it may represent segments *X* and *XI*.

The ovipositor of *Anasa tristis* is small, and is ordinarily concealed beneath the large first valvifers (fig. 27 B, *1Vlf*). When the valvifers are spread apart, however, the lobes of the ovipositor are exposed (D), and between the bases of the first pair is seen the large, open genital chamber (*GC*), into which the oviduct discharges anteriorly. The ovipositor has the typical hemipterous structure, except that the first valvifers are relatively very large, and the third valvulae are absent. The four lobes associated with the opening of the genital chamber are the first and second valvulae (D, *1Vl, 2Vl*).

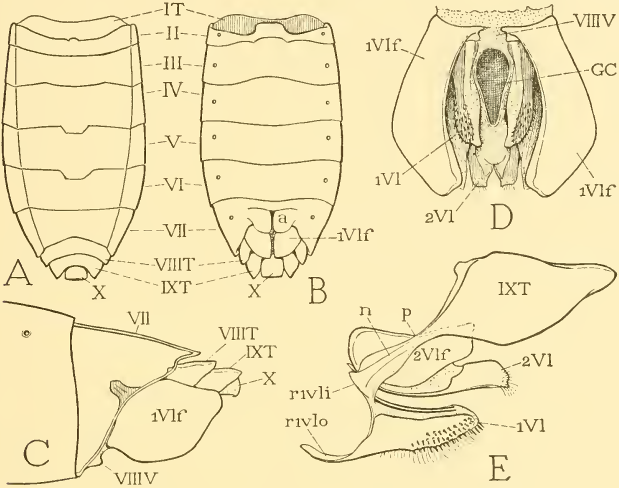

FIG. 27.—Abdomen and ovipositor of *Anasa tristis* (Coreidae).

A, entire abdomen, dorsal view.
B, same, ventral view.
C, lateral view of genital segments, with left wall of segment *VII* removed.
D, ventral view of genital region, with valvifers (*1Vlf*) spread apart, showing lobes of ovipositor (*1Vl, 2Vl*), and large genital chamber (*GC*) opening between anterior pair.
E, left side of ovipositor and ninth tergum, with first valvifers removed, showing basal union of first valvula (*1Vl*) with arm (*n*) of ninth tergum.

The first valvifers, as we have seen, are large triangular plates lying like a pair of valves (fig. 27 B, *1Vlf*) beneath the lobes of the ovipositor. Their bases are attached to the membrane behind the seventh segment (C) ventral to the eighth tergum. On the anterior margin of each valvifer is a strong apodeme for muscle attachments. The venter of the eighth segment is entirely membranous, and is represented only by the membranous bridge between the bases of the first valvifers and the first valvulae anterior to the opening of the genital chamber (C, D, *VIIIV*).

The first valvula is a thick lobe (fig. 27 D, E, *1Vl*) about two thirds the length of the first valvifer. In its outer surface is a plate provided distally with short spines. The proximal ventral angle of the plate is prolonged as the outer ramus of the valvula (E, *r1vlo*), and is attached to the lower basal angle of the first valvifer (B, C, *1Vlf*), thus leaving no doubt of the identity of the latter. The dorsal proximal angle of the first valvula forms the inner ramus (E, *r1vli*), which is attached, in the manner characteristic of Hemiptera, to a process (*n*) from the ninth tergum (*IXT*). The dorsal surface of the first valvula contains two parallel sclerotic ridges, between which is a groove into which fits a ridge on the ventral surface of the corresponding second valvula.

The second valvifer is an oblong plate (fig. 27 E, *2Vlf*) lying mesad of the ventral arm (*n*) of the ninth tergum, and articulated to the ninth tergum at a point (*p*) near the middle of its dorsal margin. Its distal end has a free, truncate edge, representatives of the third valvulae being absent in *Anasa,* though these lobes are usually present in other Hemiptera (fig. 26 E, *3Vl*).

The second valvulae are united with each other, except at their distal ends, which form two short free lobes (fig. 27 D, *2Vl*). The basal part of each has a broad membranous connection with the corresponding second valvifer (E), and the ventral surface bears a strong median sclerotic ridge that slides in the groove of the first valvula.

The mechanism of this ovipositor is evidently such as to cause alternate back-and-forth movements of the upper and lower valvulae on each other. The movable articulations of the second valvifers on the ninth tergum (fig. 27 E, *p*), and the firm union of the first valvulae with the ventral arms (*n*) of the tergum assure an opposite movement in the two pairs of valvulae. The muscles arising on the ninth tergum and inserted on opposite ends of the second valvifers rock the latter up and down and thus move the attached dorsal valvulae; but the same muscles pulling on the tergum impart an opposite movement to the ventral valvulae through the leverlike arms (*n*) supporting the latter.

AMBLYDISCA GIGAS FOWLER

The ovipositor is well developed in the Cicadellidae, and the family is one of considerable economic importance, but since most of the species are very small it is a difficult matter to make a satisfactory study of the egg-laying organ. The Central American species here described, however, has a length of 20 millimeters, and the structure of its ovipositor probably will be found typical of the family in general.

The abdomen of *Amblydisca* is cylindrical, and rigid except at its attachments on the thorax. The first two segments are reduced and their tergal plates are more or less united with each other and with the third tergum. The postnotum of the metathorax is strongly developed laterally, where its ventral ends are fused with the epimera, but dorsally it is reduced to a narrow sclerotic bar beneath the overhanging posterior edge of the metathoracic scutellum. It is entirely separated by membrane from the first abdominal tergum, except for a small, flexible sclerotic bridge on each side, the two points of union forming the fulcra on which the abdomen is movable on the thorax. The sternal plates of the first two abdominal segments are narrow and are concealed in a ventral depression at the base of the abdomen. The distal part of the abdomen (fig. 28 A) is tapering, and ends with the broad tips of the third valvulae (*3Vl*) which normally ensheath the end of the ovipositor (*Ovp*).

The seventh segment of the abdomen is the first that is modified in relation to the genital functions. Its tergum (fig. 28 A, *VIIT*) resembles the tergal plates of the preceding segments, which have prominent marginal paratergites (*pt*) with inflected ventral surfaces containing the spiracles. The seventh sternum (*VIIS*) is a triangular sclerite with a free posterior margin, toothed at the apex, projecting posteriorly as a subgenital plate beneath the base of the ovipositor. Above the seventh sternum is a large vestibular cavity.

The visible part of the eighth segment consists of a principal tergal plate (fig. 28 A, *VIIIT*) exposed behind the seventh tergum, and of a large, triangular paratergite on each side containing the eighth spiracle (B, *pt*). The lower anterior angle of the paratergite is connected with the dorsal posterior angle of the first valvifer (B, *1Vlf*), which is normally concealed within the lower part of the seventh segment by the invagination of the lower parts of the eighth and ninth segments within the seventh (A). The intersegmental membrane (B, *Mb*) between the seventh and eighth segments is reflected from the dorsal (anterior) margin of the second valvifer, and ventrally is continued into the membranous floor of the vestibulum over the seventh sternum. From the anterior wall of the vestibulum there projects beneath the base of the ovipositor a small liplike fold slightly thickened on its dorsal surface (B, *VIIIStn*). This fold is evidently a remnant of the eighth sternum. Above it there is a large, slitlike opening (*a*) between the ventral, or outer, rami of the second valvulae (*r1vlo*), which leads into a small cavity into which the oviduct appears to open, but the internal anatomy could not be satisfactorily studied in the dried specimens on which this description is based. As will be shown later a similar but much larger pouch in *Magicicada* is the genital chamber, receiving the openings both of the median oviduct and the spermatheca (fig. 32, *GC*). In *Magicicada*, however, there is a second, posterior opening from the genital chamber between the bases of the second valvulae. A posterior opening could not be found in *Amblydisca*, and it has not been observed in any homopteron except two species of cicadas. The structure in *Amblydisca*, therefore, so far as can be judged from dried specimens, is the same as that described for Homoptera generally by other writers. (See Holmgren, 1899; Myers, 1928; Weber, 1930.)

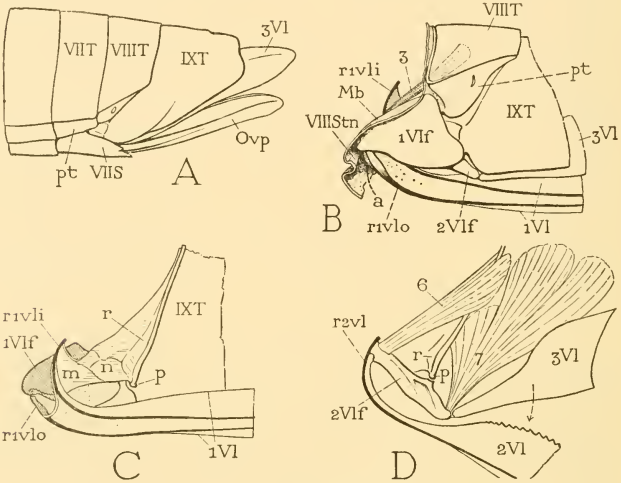

FIG. 28.—Ovipositor of *Amblydisca gigas* (Cicadellidae).

A, genital segments and ovipositor.

B, seventh segment removed, showing first valvifer in pleural position on side of eighth segment, and exposing rudimentary eighth sternum.

C, base of right first valvula, mesal view, showing connection of inner ramus (*r1vli*) with ninth tergum.

D, right second valvifer and basal parts of second and third valvulae, mesal view, showing articulation (*p*) of second valvifer with ninth tergum, and tergal muscles (*6, 7*) of valvifer.

The exposed part of the ninth abdominal segment of *Amblydisca* (fig. 28 A, *IXT*), as in Homoptera generally, consists of the large tergum. The ventral part of the segment is membranous and deeply concave, forming a cavity in which are lodged the proximal parts of the third valvulae and the shaft of the ovipositor.

The ovipositor consists of two pairs of broad, thin valvulae, the first and the second (fig. 29 A, *1Vl, 2Vl*), mostly concealed between the wide third valvulae (*3Vl*). The planes of the valvulae are vertical. The first valvulae lie close against the outer surfaces of the second pair, and the two on each side are firmly but movably attached by the usual interlocking grooves and ridges. The second, or inner, valvulae are conspicuously serrate along their dorsal margins (A, *2Vl*); at their bases they are united with each other by a membranous fold, but for most of their length they are free, though closely appressed. Each first valvula has two proximal rami (figs. 28 C, 29 B), a ventral outer ramus (*r1vlo*) attached to the anterior angle of the first valvifer (*1Vlf*), and a dorsal inner ramus (*r1vli*) which expands in a small triangular plate (*m*) attached to the lower anterior angle of the ninth tergum (fig. 28 C, *n, IXT*). The second

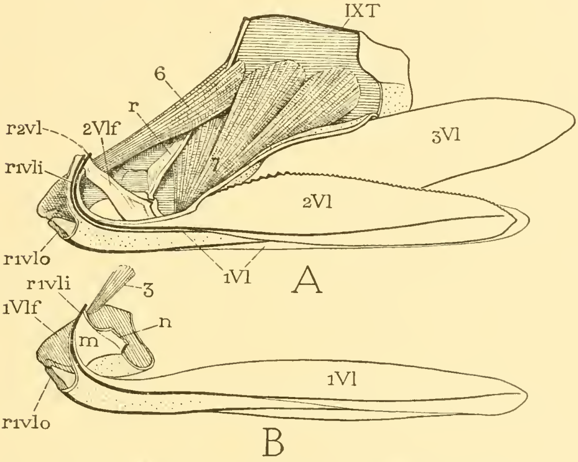

FIG. 29.—Muscles of the ovipositor of *Amblydisca gigas*.

A, right half of ovipositor and ninth segment, mesal view.
B, right first valvifer and first valvula, mesal view.

valvula has a single basal ramus (fig. 28 D, *r2vl*), which is attached to the anterior end of the second valvifer (*2Vlf*), and lies against the concave margin of the inner ramus of the first valvifer (fig. 29 A).

The first valvifer (fig. 28 B, *1Vlf*) is a triangular plate attached posteriorly by membrane to the anterior margin of the paratergite (*pt*) of the eighth segment, and ankylosed with the lower anterior part of the ninth tergum (*IXT*). In the normal position it is concealed by invagination within the seventh segment (*A*). The intersegmental membrane between the seventh and eighth segments (B, *Mb*), therefore, extends forward from the lower end of the eighth tergum along the dorsal margin of the valvifer to the rudimentary eighth sternum (*VIIIStn*) beneath the anterior ends of the valvifers. To the anterior end of each first valvifer is flexibly attached the outer ramus of the first valvula (figs. 28 B, C, 29 A, B, *r1vlo*) ; the inner ramus of this valvula (figs. 28 C, 29 B, *r1vli*), as already noted, is firmly attached by a small plate (*m*) to the lower anterior angle (*n*) of the ninth tergum, mesad of the first valvula. A muscle arising on the eighth tergum (fig. 28 B, *3*) is inserted on the dorsal margin of the first valvifer (fig. 29 B, *3*). The first valvifers are not freely movable because of their posterior ankyloses with the ninth tergum, but they are flexible, and the contraction of their muscles evidently must elevate their anterior ends and produce a depression of the distal part of the ovipositor. A pair of short thick muscles attached laterally on the valvifers and internally on the mesal plates of the inner rami of the first valvulae, are probably antagonistic to the dorsal muscles of the valvifers.

The second valvifer (fig. 28 D, *2Vlf*) is a strong, elongate sclerite having the ramus of the second valvula (*2Vl*) attached to its anterior end, and the base of the third valvula (*3Vl*) movably articulated to its posterior end. In the normal position the second valvifer is mostly concealed, in a lateral view (A), by the first valvifer. The second valvifer is movably articulated at a point somewhat beyond the middle of its dorsal margin to a condyle (D, *p*) on the lower end of a strong anterior ridge (*r*) of the inner surface of the ninth tergum (C, *IXT*). Two large antagonistic muscles arising on the ninth tergum (figs. 28 D, 29 A, *6*, *7*) are inserted on the opposite ends of the second valvifer (*2Vlf*). These muscles evidently rock the valvifer up and down on the fulcrum of the ninth tergum, and thus impart a strong back-and-forth movement to the second valvula attached by its narrow basal ramus (fig. 28 D, *r2vl*) to the anterior end of the valvifer. The second valvulae slide freely on their tracklike connections with the first valvulae, but since the second valvulae are united at their bases with each other, the two inner blades of the ovipositor, which are serrated on their dorsal margins (fig. 29 A, *2Vl*), must work in unison between the outer first valvulae. The first valvulae also may have some independent movement produced by the muscles of the first valvifers, but the writer has not observed the cicadellid ovipositor in action on a living specimen.

An interesting account of the structure of the valvulae in the cicadellid ovipositor, and their relations to one another is given by Balduf (1933). The anterior valvulae, however, are referred to the " seventh sternite ", and the second or inner pair to the " eighth sternite." This error probably arises from overlooking the true first segment of the abdomen, which is partially united with the second, though in no insect are the valvulae connected with the sternal plates of their segments.

MAGICICADA SEPTENDECIM (LINNAEUS)

The well-developed ovipositor of the Cicadidae furnishes an easily studied example of the structure of the ovipositor typical of the Hemiptera. The 17-year cicada here described, however, has a curious and unusual development of the genital chamber, which is provided with a secondary posterior passage giving exit to the eggs directly into the channel of the ovipositor.

General structure of the abdomen.—There has been so much misinformation given out on the subject of the abdomen of the cicada that it will be permissible to devote a little more attention to the general abdominal structure of this insect than would be necessary otherwise in connection with a study of the ovipositor.

The general form of the female abdomen in *Magicicada septendecim* is shown at A of figure 30. At its base the abdomen is broadly but movably joined to the thorax, but the connecting parts are mostly concealed by overlapping parts of the metathorax. When the thorax and the abdomen are somewhat pulled apart, as shown at B of the same figure, it is seen that there lies in the infolded membrane between the metatergum (T_3) and the first abdominal tergum (IT) a well-developed though narrow postnotal plate of the metathorax (PN_3), which bears the large third phragma, and is fused ventrally with the metapleural epimera (Epm_3) in the usual manner. On each side of the dorsum the postnotum retains a flexible sclerotic connection (a) with the first abdominal tergum. The latter (IT) is a narrow, transverse plate united with the second tergum (IIT) ; its lateral part presents an enlarged oval area (*b*), which corresponds with the area of the sound-producing cymbal of the male.

The sternal plates of the first and second abdominal segments are highly modified, and they are separated by a deep inflection that forms a large ventral cavity at the base of the abdomen. This cavity is ordinarily closed to a narrow slit between the sternal plates, and is but little evident in a casual examination of a dried specimen. In the male cicada the cavity is much larger than in the female and contains the so-called "resonance" membranes, or "mirrors", which are now regarded as tympana for the reception of sound vibrations, since it has been shown by Vogel (1923) that chordotonal organs, situated in the lower ends of the second abdominal tergum, are connected with their lateral extremities. The tympanal cavity can be opened and

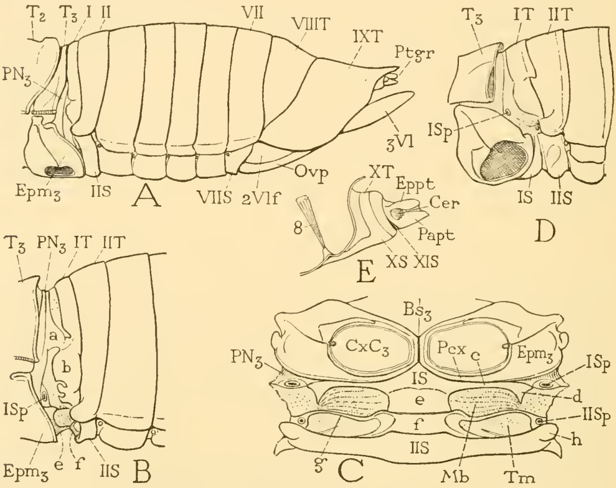

FIG. 30.—Abdomen of *Magicicada septendecim* (Cicadidae).

A, entire abdomen and base of thorax of adult female.
B, details of connection between thorax and abdomen, lateral view.
C, ventral plates of metathorax and first and second abdominal segments.
D, base of abdomen of mature nymph.
E, tenth and eleventh segments of adult.

a, hinge between postnotum of metathorax and first abdominal tergum; *b*, lateral area of first abdominal tergum on which cymbal of male is developed; *c*, lateral arm of first abdominal sternum with expanded end (*d*) on which tergo-sternal muscle is attached; *e*, posterior median plate of first sternum; *f*, anterior median plate of second sternum; *g*, lateral arm of second sternum forming marginal rim of tympanum (*Tm*).

closed by movements of levation and depression of the abdomen on the lateral hinges (fig. 30 B, *a*) between the postnotum and the first abdominal tergum, the movements being produced by the dorsal and ventral muscles of the first abdominal segment. The structure of the first and second abdominal sterna and of the tympanal cavity between them is essentially the same in both sexes, but it is more simple in the female.

The first abdominal sternum of the female cicada lies immediately behind the narrow postcoxal arms of the metathoracic epimera (fig. 30 C, *Pcx*). It consists of two parts. The first is an anterior, median, triangular plate (*IS*) having its lateral angles prolonged as a pair of arms (*c*) fused with the postcoxal bridges (*Pcx*), but each terminating in a lateral expansion (*d*), on which are attached the tergosternal muscles of the first abdominal segment. The second plate is a median, quadrate sclerite (*e*) flexibly hinged to the anterior plate (*IS*), and extending upward from the latter in the anterior wall of the tympanal cavity (B, *e*).

The spiracles of the first abdominal segment (fig. 30 B, C, *ISp*) are contained in peritremal sclerites fused with the lower ends of the metathoracic postnotum (PN_3). They open directly into the great air chamber of the abdomen.

The sternum of the second abdominal segment consists, as does that of the first segment, of two parts, one part exposed, the other concealed in the tympanal cavity. The exposed part of the sternum is in this case the posterior part, which forms a narrow, transverse bridge between the lower ends of the second abdominal tergum (fig. 30 A, B, C, *IIS*), with which it is solidly continuous. The anterior part of the second sternum is a weaker median sclerite (*C, f*) turned upward on the anterior margin of the posterior sclerite in the posterior wall of the tympanal cavity (B, *f*); its dorsal margin meets the posterior plate of the first sternum (*e*) in the transverse fold of the roof of the cavity. The lateral angles of the anterior sclerite of the second sternum (C, *f*) are produced into slender bars (*g*) that extend outward to meet the lateral extremities of the posterior sclerite, where each ends in a small expansion containing one of the second abdominal spiracles (*IISp*). Between the arms (*g*) of the first sclerite and the lateral parts of the second sclerite are the oval glistening tympana (*Tm*), or so-called "mirrors". The chordotonal sense organs connected with the tympana (in the male) are said to be contained in the tubercles (*h*) located at the ventral lateral angles of the second segment where the tergum and the sternum are confluent. The thick corrugated membranes (*Mb*) in the anterior wall of the tympanal cavity are intersegmental membranes between the first and second sterna.

The description of the basal parts of the abdomen of the cicada given by Vogel (1923) in connection with his account of the chordotonal organs, though minute in detail, is not morphologically sound in every respect. The anterior plate of the second sternum (fig. 30 C, *f*) Vogel regards as the first abdominal sternum, and he consequently refers the tympana and the second spiracles to the first abdominal segment. The posterior sclerite of the second sternum (*IIS*), bearing the "auditory capsules" (*h*), he calls the second sternum. Much of this interpretation is clearly in error since it disregards the true first sternum and the first abdominal spiracles, which latter Vogel assigns to the thorax. The difficulty of properly disposing of the first abdominal spiracles in the cicada arises from the fact that the spiracular peritremes in the adult insect are fused with the lower posterior margins of the metathoracic postnotum (fig. 30 B, C, PN_3), the lower ends of which are united with the epimera; but the observation that the spiracles in question lie behind the internal intersegmental ridge bearing the lobes of the third phragma shows conclusively that these spiracles belong to the first segment of the abdomen. The true relations of the basal parts of the cicada's abdomen are unmistakable in the mature nymph of *Magicicada* (D). The first abdominal sternum is here a simple triangular plate (*IS*) lying immediately behind the metathoracic subcoxae, and the first abdominal spiracles (*ISp*) lie in the membranous lateral parts of the dorsum of the first segment. The tergum and sternum of the second segment (*IIT, IIS*) show no particular modifications, and the ventral tympanal cavity is not developed in the nymph.

One of the most curious aberrations in entomological morphology is the tendency to regard the great air chamber of the cicada's abdomen as a part of the digestive system. The chamber is a thin-walled sac always filled with gas, but never containing liquid. Yet, the cicada's stomach may be distended with liquid food. The idea that the air sac is a diverticulum of the stomach was first proposed by Hickernell (1920) on the basis of histological sections, which seemed to show a connection between the two organs. The question was later discussed in the affirmative by Hargitt (1923) and by Myers (1928). If the air sac lacks taenidia and even a chitinous lining these points do not prove that it is not of tracheal origin, since tracheal sacs do not usually contain taenidia, and some investigators have failed to find chitin in their walls. The abdominal air sac of the cicada, as may be more clearly seen in other genera than *Magicicada,* opens directly to the exterior through the first abdominal spiracles; and in various places large, open tracheal tubes are given off from its walls. In

Magicicada there is a tubular extension from the sac that proceeds in the direction of the stomach, but the writer believes it goes into the filter chamber and not into the stomach lumen, though the facts could not be more closely investigated for the lack of fresh material. However, the anatomical incongruity of having a diverticulum of the stomach opening to the exterior through a pair of spiracles suggests a human error rather than a lapse of nature.

Most of the visceral organs of the cicada's abdomen, except the stomach, which lies anteriorly, are crowded into the rear part of the abdomen by the posterior extension of the air chamber, which ends in the seventh segment. The turgid form of the middle part of the abdomen (fig. 30 A), therefore, presents the shape of the air sac. The region between the second and the eighth segments contains a succession of regular tergal and sternal plates. The lateral edges of the terga are inflected to meet the sterna, which are pleurosternal plates, there being no intervening pleurites or other lateral sclerites. In the adult, the spiracles of these segments are contained in small peritremal sclerites united with the anterior lateral angles of the sterna; in the nymph the spiracles have the same position but they lie in membranous areas between the tergal and sternal plates (figs. 11 A, 30 D).

The tergum of the seventh segment does not differ from the terga preceding it. The seventh sternum (fig. 30 A, *VIIS*), however, is shortened, but its deeply emarginate posterior edge underlaps the base of the ovipositor (*Ovp*). Above the seventh sternum is a small vestibular cavity (fig. 32 A, *Vst*), in the anterior wall of which is a large genital opening (*a*) above a small fold (*VIIIStn*), which is the posterior lip of the otherwise invaginated eighth sternum. The genital aperture may be exposed by depressing the seventh sternum, or by pulling the latter forward (fig. 31 A, *a*). It leads into a large copulatory pouch (*GC*), which, as will be shown later, is the true genital chamber.

The eighth segment is exposed dorsally but its ventral parts are normally concealed within the seventh segment. The tergum is declivous behind the seventh tergum (fig. 30 A, *VIIIT*); its lateral parts are narrowed and are widely separated from the sternal region of its segment. The anterior end of the eighth sternum appears as a small fold beneath the opening of the genital chamber (figs. 31 A, 32 A, *VIIIStn*), but most of the sternal plate is reflected anteriorly upon the floor of the chamber (fig. 32 B, *VIIIStn*) and is therefore concealed within the latter. The exposed anterior (anatomically posterior) end of the eighth sternum is connected by membranous folds with the lower ends of the eighth tergum (figs. 31 A, 32 A). The spiracles of the eighth segment (*VIIISp*) lie in these folds behind the lower ends of the eighth tergum. The first valvifers (fig. 31 A, *1Vlf*) are entirely detached from the eighth sternum and are closely associated with the ninth tergum.

The ninth segment forms the large conical, apical part of the abdomen (fig. 30 A). The tergum (*IXT*) ends posteriorly in a median triangular rostrum projecting above the proctiger (*Ptgr*), which is mostly retracted into the rear end of the ninth segment. Between the ventral edges of the ninth tergum is a deep concavity in which is concealed most of the ovipositor and the membranous ventral region of the ninth segment. The latter contains a median sclerotization with strong transverse corrugations lying between the second valvifers. The basal parts of the latter (*2Vlf*) are exposed below the anterior ventral angles of the ninth tergum.

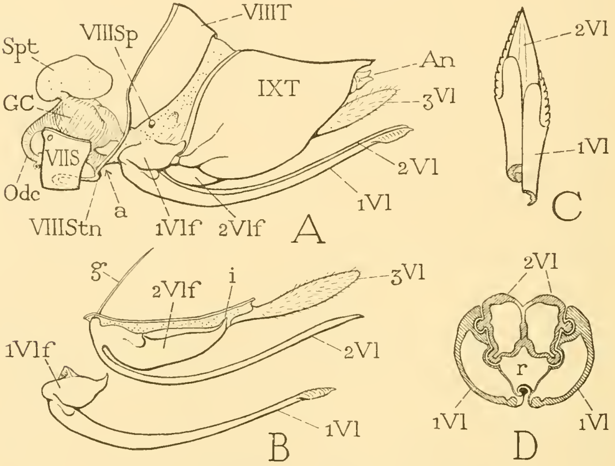

FIG. 31.—Ovipositor of *Magicicada septendecim.*

A, genital segments and ovipositor, with seventh sternum pulled forward exposing genital opening (*a*) leading into pouchlike genital chamber (*GC*).
B, parts of ovipositor separated.
C, tip of ovipositor, ventral.
D, section of ovipositor.

The ovipositor is strongly developed. It consists of two pairs of valvulae (fig. 31 A, *1Vl, 2Vl*), which are the first and second gonapophyses, arising respectively from the first and second valvifers (A, B, *1Vlf, 2Vlf*). The second valvulae are fused by their inner faces (D); the first valvulae are freely movable on flanges of the shaft formed by the united second valvulae, and their lower edges are movably connected with each other. Between the four valvulae is a closed channel (*r*) for the conduction of the eggs. A pair of elongate lobes, the third valvulae (A, B, *3Vl*), arise at the distal ends of the second valvifers, and enclose the distal part of the ovipositor.

The proctiger consists of the tenth and eleventh segments. Ordinarily its tip only is visible projecting from beneath the rostrum of the ninth tergum (fig. 30 A, *Ptgr*). When exposed (E) the proctiger is seen to consist of a basal part representing the tenth segment, and of a distal part representing the eleventh segment. The dorsum of the tenth segment contains a narrow transverse tergal plate (*XT*), which is continuous ventrally with the posterior angles of a long sternal plate (*XS*). The anterior angles of the sternum are produced into a pair of small apodemal processes, on each of which is inserted a muscle (*8*) arising on the ninth tergum (fig. 34, *8*). The small eleventh segment consists of a dorsal and a ventral lobe, apparently representing the epiproct (fig. 30 E, *Eppt*) and the fused paraprocts (*Papt*) enclosing the anal opening (fig. 34, *An*). Between their bases on each side is a small, hairy lobe, evidently the rudimentary cercus (fig. 30 E, *Cer*). At the base of the ventral wall of the eleventh segment is a small sternal sclerite (figs. 30 E, 34, *XIS*). Upon it are inserted short, longitudinal, intersegmental muscle fibers (fig. 34, *9*) from the anterior part of the tenth sternum. From the latter there arise also on each side a group of fibers (*10*) that go to the terminal part of the rectum (*Rect*).

The copulatory and egg-discharging apparatus.—The short seventh sternum of the female cicada ends, as we have observed (fig. 30 A, *VIIS*), in a free posterior margin, and if this subgenital plate is depressed there is exposed above it a large open cavity (fig. 32 A, *Vst*) extending forward into the anterior end of the sixth segment beneath the base of the ovipositor. This cavity clearly corresponds with the vestibulum of the cockroach (fig. 23, *Vst*), though the vestibular space is much larger in the latter insect because of the posterior extension of the seventh sternum (*VIISL*).

In the anterior wall of the vestibulum of the cicada is a wide, thick-lipped opening (figs. 31 A, 32 A, *a*) that leads through a short passage (fig. 32 A, *b*) into a large, strongly muscular pouch (*GC*). The median oviduct (*Odc*) connects with the anterior wall of the pouch, and the spermathecal sac (*Spt*) opens by a narrow neck (*c*) into the dorsal part of the pouch. Posteriorly the pouch has a large funnel-shaped extension (*d*) that terminates in a narrow membranous neck, which opens by a small pore (*f*) between the bases of the second valvulae of the ovipositor. From the base of the neck there arise laterally two small oval sacs (*e*) of a bright yellow color, into each of which opens a long, slender, much-coiled tube. A large, median tubular accessory gland (*h*) lies posterior to the pouch and opens at the rear aperture of the latter (B, *f*) into the channel of the ovipositor.

A section of the genital pouch (fig. 32 B) shows that the oviduct opens into the pouch lumen at the tip of a long, conical inflection of the anterior wall of the pouch (*g*), which projects into the posterior funnel-shaped passage (*d*) leading to the rear exit (*f*). Just dorsal to the base of the oviducal cone is the opening of the spermatheca (*Spr*). The cuticular lining of the pouch is irregularly thickened and corrugated, and is thrown into strong folds, the details of which are not shown in the diagrammatic section (fig. 32 B). All parts of the pouch and the entering oviduct are ensheathed in a thick layer of muscle fibers (*Mcls*), which appear to be so arranged as to force the oviducal cone into the posterior funnel (*d*).

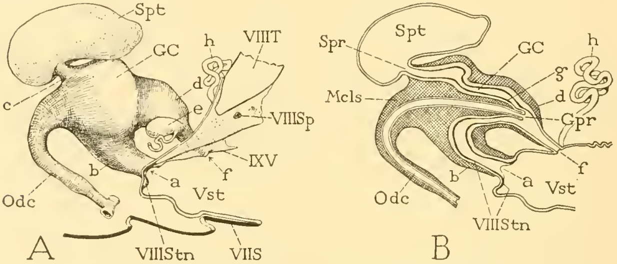

FIG. 32.—Genital chamber of *Magicicada septendecim*.

A, lateral view of genital chamber pouch (*GC*) opening from vestibulum (*Vst*) by copulatory aperture (*a*), but with posterior exit (*f*) for discharge of eggs.

B, diagrammatic median section of genital chamber, oviduct, spermatheca, and vestibulum.

a, copulatory opening to genital chamber; *b*, entrance tube; *c*, duct of spermatheca with opening (B, *Spr*) into genital chamber; *d*, posterior exit tube for discharge of eggs; *e*, reservoir of lateral accessory gland; *f*, posterior opening of egg passage; *g*, evagination of anterior wall of genital chamber with gonopore (*Gpr*) at its extremity; *h*, median accessory gland.

The presence of two genital openings in the female cicada suggests the similar condition in Lepidoptera. Though the structure in the two cases is not identical, yet it is evident that the posterior opening is a secondary one, and that it is located, as in Lepidoptera, at the aperture of the accessory gland.

The morphological nature of the genital pouch of the female cicada is clear when it is considered that it lies above the eighth abdominal sternum (fig. 32 B, *VIIIStn*), and that both the gonopore (*Gpr*) and the spermathecal pore (*Spr*) lie in its walls. The pouch can be nothing else than the genital chamber (fig. 8 C, *GC*) greatly enlarged and modified in an unusual manner. It corresponds exactly with the genital chamber of the Orthoptera (figs. 19 B, 23, *GC*). In the cicada the eighth sternum is mostly reflected forward upon the floor of the genital chamber (fig. 32 B, *VIIIStn*), but its morphologically anterior end projects as a short fold beneath the entrance of the chamber (A, *VIIIStn*). The posterior part turned forward is sclerotized as a small plate surrounding the base of the oviducal cone. The gonopore of the cicada, therefore, lies morphologically in the eighth sternum just as it does in the cockroach (figs. 23, 24 C, *Gpr*). The relation of the terminal genital structures in *Magicicada* to the more usual structure of these parts in other insects is shown in the series of diagrams given in figure 8.

The posterior opening of the genital chamber in *Magicicada septendecim* between the bases of the second valvulae is undoubtedly a special modification to allow the eggs to be discharged directly into the closed channel of the ovipositor. This condition is not peculiar to the 17-year cicada; the same structure was long ago described in *Dundubia* (*Cicada*) *mannifera* by Doyère (1837), but has received little or no attention since, so far as the writer can find. Doyère refers to the genital chamber as the " vestibule copulateur ", and other writers have called it the " bursa copulatrix ". Holmgren (1899) studied the female genital organs of various homopterous forms (Cicadarien), now classed in the families Cercopidae, Cicadellidae, and Fulgoridae, but he says that all species examined by him have but a single genital opening. Myers (1928) gives a review of literature on the female reproductive organs of Cicadidae, including Doyère's paper, and makes no mention of two openings. He describes and figures the female organs of *Carineta formosa,* but the terminal genital structures in this species must be quite different from those in *Dundubia* and *Magicicada.* The single opening shown by Myers is at the point where the accessory glands with yellow sacs open into the " oviduct ", and would therefore appear to be the posterior opening of *Magicicada.* The writer has examined specimens of several other species of Cicadidae, which, though too poorly preserved for reliable dissection, seem to show the same structure as described by Myers for *Carineta.*

The ovipositor.—The ovipositor of the Cicadidae does not differ in any essential respect from that of other Hemiptera. The shaft of the organ is formed by the first and second valvulae (fig. 31 B, *1Vl, 2Vl*) supported at their bases by the first and second valvifers (*1Vlf, 2Vlf*); the third valvulae (*3Vl*) are free distal lobes of the second valvifers. The second valvulae are solidly fused with each other (D, *2Vl*) except at their tips, and the first valvulae (*1Vl*) slide freely on ridges of the united second valvulae. The lower edges of the second valvulae are locked together by a fold on one that grasps a ridge on the other, and the egg passage (*r*) of the ovipositor thus becomes a closed channel. Since the cicadas deposit their eggs in the twigs of trees, the ovipositor is strong and is provided with powerful muscles.

The first valvifer lies at the base of the ovipositor (fig. 31 A, *1Vlf*) where it is normally concealed by the overlapping lateral part of the seventh sternum (*VIIStn,* pulled forward in the figure). When the seventh sternum is removed, the first valvifer is seen to be a small irregularly oval or triangular plate (B, *1Vlf*) bearing the first valvula (*1Vl*). The middle of its dorsal margin is produced into a short wide apodemal plate (fig. 33 A, *e*) for the attachment of muscles. Its somewhat elongate posterior end (*a*) overlaps the anterior part of the second valvifer, and is movably attached to the lower anterior angle of the ninth tergum (fig. 31 A). The first valvifer is separated from the eighth tergum (*VIIIT*) by a much wider space in the cicada than it is in *Amblydisca* (fig. 28 B), or particularly in *Pentacora* (fig. 26 B), owing apparently to a desclerotization of the paratergal region of the dorsum, which in the cicada is represented by the membranous area containing the eighth spiracle (*VIIISp*). The intersegmental membrane between the seventh and eighth segments is continued ventrally on the side anterior to the first valvifer, past the genital opening (*a*), to the subgenital fold formed by the eighth sternum (*VIIIStn*).

The broad base of the first valvula (fig. 33 A) is not differentiated into distinct outer and inner rami, as in the Cicadellidae, but it has the same proximal connections. Its outer wall (B, showing a mesal view) has a membranous union with the lower edge of the first valvifer (*1Vlf*), but it is articulated with the anterior angle of the valvifer (*c*) and is movable on the valvifer at this point. The dorsal wall of the valvula, corresponding with the inner ramus in *Pentacora* and *Amblydisca,* is produced upward and expanded in a small triangular plate (*m*) lying mesad of the valvifer, which is fused with the lower anterior angle (*n*) of the ninth tergum (*IXT*). A thick bundle of short muscle fibers (*4*) extends from the inner face of the first valvifer to the mesal plate (*m*) of the base of the first valvula. The other muscles of the first valvifer are inserted on the dorsal apodeme (*e*). They include a lateral muscle (C, *1*) from the seventh sternum (*VIIS*), and two dorsal muscles (*2, 3*) from the eighth tergum (*VIIIT*).

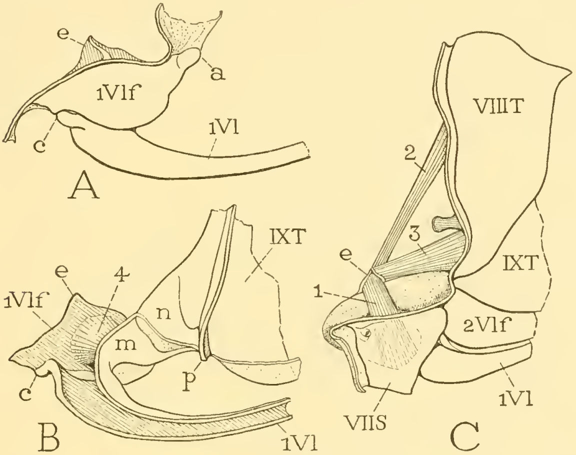

FIG. 33.—Structural details of ovipositor and muscles of first valvifer of *Magicicada septendecim.*

A, left first valvifer and base of first valvula, external view.

B, right first valvifer and base of valvula, mesal view, showing connections with ninth tergum.

C, base of ovipositor and adjoining segmental plates, with seventh tergum removed to show muscles attached on apodeme (*e*) of first valvifer.

a, articulation of first valvifer with ninth tergum; *c,* attachment of first valvula to first valvifer; *e,* apodeme of first valvifer; *m,* mesal plate of base of first valvula; *n,* anterior ventral part of ninth tergum attached to mesal plate (*m*) of first valvula.

The second valvifer (fig. 31 B, *2Vlf*) is an elongate plate, or rather, a fold with a sclerotic outer wall, lying beneath and mostly overlapped by the lower edge of the ninth tergum (A). From its anterior end a slender apodeme (B, *g*) projects dorsally into the body cavity for the attachment of muscles; at its posterior end arises the third valvula (*3Vl*). The second valvula (*2Vl*) is directly continuous with the anterior end of the second valvifer, there being no movement between the two parts except such as is permitted by the flexibility of the narrow base of the valvula. The inner surface of the outer wall of the second valvifer bears a strong longitudinal ridge near its dorsal margin (fig. 34, *2Vlf*). At a point on this ridge anterior to the middle of the valvifer is the articulation of the second valvifer with a fulcral process (*p*) on the lower margin of the ninth tergum near the anterior angle of the latter (fig. 33 B). Two large antagonistic muscles (fig. 34, *6, 7*), arising on the ninth tergum, are inserted anteriorly and posteriorly on the second valvifer at opposite sides of the tergal fulcrum. Tergosternal muscles of the ninth segment are absent in the cicada as in other Hemiptera.

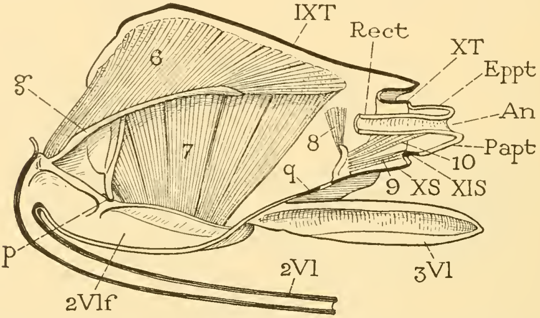

FIG. 34.—Right half of ninth and post-genital segments of *Magicicada septendecim*, mesal view, together with second valvifer and its muscles.

g, anterior apodeme of second valvifer; *p*, fulcrum of second valvifer on ninth tergum between insertions of anterior and posterior muscles (*6, 7*).

The muscles of the ovipositor, or associated with it, are the following:

1. Depressor of the first valvifer (fig. 33 C).—A broad muscle arising on lateral part of seventh sternum; goes dorsally in membranous fold laterad of the valvifer to dorsal apodeme (*e*) of the latter. This muscle, as in *Gryllus* (figs. 17 A, 19 A, *1*), is an intersegmental ventral muscle of the seventh segment attached posteriorly, not on the eighth sternum, but on the valvifer of the eighth segment.

2. First levator of the first valvifer (fig. 33 C).—A long tergopleural muscle of eighth segment, arising dorsally on anterior margin of eighth tergum; inserted ventrally on dorsal apodeme of first valvifer. This muscle rotates the valvifer upward on its posterior articulation with the ninth segment.

3. Second levator of the first valvifer (fig. 33 C).—A tergopleural muscle of the eighth segment, arising on lower part of anterior margin of eighth tergum; inserted anteriorly on dorsal apodeme of first valvifer. This muscle is accessory to the last, and both *2* and *3* are clearly antagonistic to *1*.

4. Muscle of the first valvula (fig. 33 B).—A thick bundle of short fibers arising on inner face of first valvifer (*1Vlf*); inserted posteriorly and mesally on inner plate (*m*) of base of first valvula. This muscle appears to be antagonistic to *2* and *3*, and accessory to *1*.

5. Conjunctival muscle (not shown in the figures).—A short thick muscle arising dorsally on lateral part of eighth tergum; fibers converging downward to insertion on intersegmental membrane between eighth and ninth segments above and posterior to eighth spiracle (fig. 31 A, *VIIISp*). This muscle apparently serves to inflect the wide membrane between the segments.

6. Anterior muscle of the second valvifer (fig. 34).—A flat triangular sheet of strong fibers arising mediodorsally in longitudinal series on ninth tergum; insertion ventrally on anterior apodeme (*g*) of second valvifer and on extreme anterior end of the valvifer. The contraction of this muscle rotates the second valvifer upward anteriorly on the tergal fulcrum (*p*) and retracts the second valvula. It is the homologue of muscle *6* of *Gryllus* (fig. 17 E, G) and of *Amblydisca* (fig. 28 D).

7. Posterior muscle of the second valvifer (fig. 34).—A huge fan of several thick bundles of fibers arising dorsally on ninth tergum, laterad of *6;* inserted ventrally on dorsal part of second valvifer posterior to the tergal fulcrum (*p*). This muscle is antagonistic to the anterior muscle (*6*), and protracts the second valvula by depressing the anterior end of the valvifer. It is the homologue of muscle *7* of *Gryllus* (fig. 17 E, G) and *Amblydisca* (fig. 28 D).

The first valvifers can respond freely to the contraction of the muscles inserted upon them because of the flexible nature of their posterior connections with the ninth tergum. The effect of the muscles inserted on the dorsal apodemes of the valvifers (fig. 33 C, *1, 2, 3*) is only to elevate and depress the anterior ends of the plates. In a dissected specimen these movements of the first valvifer correspondingly depress and elevate the entire ovipositor, and there can scarcely be any question that they serve to unsheath and resheath the ovipositor preceding and following its use in oviposition. The short muscle from each first valvifer to the inner plate of the first valvula (B, *4*) is apparently accessory to the depressor of the valvifer (C, *1*), since, when the ovipositor is depressed, the valvifer and the plate *m* move in opposite directions. The muscles of the first valvifers, however, must also produce independent back-and-forth movements of the first valvulae when the tip of the ovipositor is inserted into the bark of a tree. The broad, strongly serrate extremities of these valvulae (fig. 31 C) indicate that they play an important part in cutting out the egg chamber, and furthermore, the ends of the outer valvulae are often found in freshly killed specimens to be in different positions on the apex of the median shaft formed of the united inner valvulae, indicating that the outer valvulae are protracted alternately on the ridges of the median shaft (D).

The great size of the muscles of the second valvifers (fig. 34, *6*, *7*), particularly of the posterior muscles (*7*), leaves little doubt that the median shaft of the ovipositor, formed of the solidly united second valvulae, with its strong, sharp spearheadlike tip (fig. 31 C, *2Vl*), is an important piercing implement of the egg-laying apparatus. Because of the union of the second valvulae, the corresponding muscles of the second valvifers on opposite sides probably work in unison.

The mechanism of the ovipositor of any insect could not accomplish the results it does if the parts of the organ were rigid. The valvulae slide lengthwise upon one another by the movement of the valvifers because they are pliable, and because of the flexibility of their basal connections. A wooden model of the cicada's ovipositor, for example, could not be made to do anything more than to move the shaft up and down at its base. The writer has elsewhere (1921) described the method by which the female 17-year cicada excavates the egg cavities in the twigs of trees in which she deposits her eggs.

Since the Hemiptera are in some respects one of the most highly specialized and individualized orders of insects, it is somewhat surprising that the ovipositor should be more generalized in its structure than in either the Orthoptera or the Hymenoptera. The only orders of insects that seem to approach the Hemiptera in the structure of the head and mouth parts are the Corrodentia and the Thysanoptera. Most of the Corrodentia have a small, simple ovipositor, but in some forms the organ is reduced or absent. Chapman (1930) says, " In *Psocus; Peripsocus,* and certain other genera, a distinct if not long and strongly chitinized ovipositor is present. It is composed of three pairs of gonapophyses, one pair arising from the eighth segment and two pairs from the ninth." In *Ectopsocus parvulus,* as described by Weber (1931), there are three pairs of small, soft processes surrounding the female gonopore, which appear to represent the three pairs of valvulae, since one pair arises on the eighth segment and the others on the ninth. The genital processes hold the eggs as the latter issue from the ovipositor, but there is present no mechanism for their movement.

An ovipositor is well developed in one suborder (Terebrantia) of the Thysanoptera, but it is so minute in the ordinary species that the writer has not been able to make a detailed study of its structure. It consists of a large single dorsal piece presumably the united second valvulae, and of two strongly serrate ventral blades. The first valvifers appear to be a pair of triangular plates on the sides of the eighth segment immediately below the lateral edges of the eighth tergum. A third pair of valvulae was not observed in the species examined.

VII. THE OVIPOSITOR OF HYMENOPTERA

The ovipositor of the Hymenoptera, regardless of the shape, length, or function assumed by the shaft of the organ, has the same basic structure throughout the order. In its general form and in the composition of the shaft the hymenopterous ovipositor resembles the ovipositor of the Hemiptera more closely than that of the Orthoptera, but it has one particular feature, namely, the articulation of the second valvifers on the first valvifers, instead of on the ninth tergum, which is a characteristic feature of the ovipositor of Gryllidae, though the mechanism is not exactly the same in the two cases. The salient points in the structure of the hymenopterous ovipositor may be summarized as follows:

1. The subgenital plate of the female is the seventh sternum, and the base of the ovipositor is contained in a vestibular cavity.

2. The eighth tergum in lower families is a dorsal plate of the usual form exposed externally; in the bees it is entirely concealed within the seventh segment, its median part is reduced to a membranous fold over the back, and the lateral parts form a pair of small sclerites bearing the eighth spiracles.

3. The eighth sternum is completely suppressed in all Hymenoptera, though the venter of the eighth segment may be represented by a fold of membrane beneath the gonopore.

4. The first valvifers are entirely dissociated from the other parts of the eighth segment and form an intimate part of the basal mechanism of the ovipositor or sting. Their muscles, however, take their origin on the eighth tergum. Each is a small triangular plate bearing the ramus of the first valvula on its anterior end, and articulating posteriorly by its dorsal angle with the ninth tergum, and by its ventral angle with the second valvifer.

5. The ninth tergum is complete in lower families, its widened lateral parts being continuous dorsally at least in a narrow sclerotic bridge, with which the proctiger may be united; in the bees the ninth tergum consists of two large lateral sclerites, known as the " quadrate plates ", but the median part of the ninth dorsum is membranous and not distinct from the proctiger.

6. The second valvifers are oblong plates bearing anteriorly the rami of the second valvulae, and posteriorly the third valvulae. Each is articulated by its dorsal margin with the ventral posterior angle of the first valvifer (not with the ninth tergum), and is provided with the usual anterior and posterior muscles arising on the ninth tergum.

7. The venter of the ninth segment is always membranous, there being no intervalvular sclerites.

8. The shaft of the ovipositor or sting is composed of the first and second valvulae, the first being ventral, the second dorsal. The second valvulae are united with each other beyond their convergent rami, either solidly or by membrane, and two pairs of muscles are inserted on their bases, one pair arising on the proximal parts of the rami, the other on the inner faces of the second valvifers. These muscles of the second valvulae are characteristic features in the mechanism of the ovipositor or sting of the Hymenoptera, but they appear to have no homologues in other insects.

9. The third valvulae are free lobes ensheathing the distal part of the shaft of the ovipositor; they vary greatly in length according to the length of the ovipositor.

10. The proctiger is always present. In lower families it consists of a dorsal and a ventral plate, and bears a pair of small appendicular processes; in the higher families it becomes reduced to a simple membranous tube or cone.

Four examples, selected from the Tenthredinidae, Braconidae, Ichneumonidae, and Apidae, will serve to illustrate the characteristic structure and some of the principal modifications of the ovipositor as the organ is developed in the Hymenoptera.

PTERONIDEA RIBESII (SCOPOLI)

The relatively large abdomen of the female currant sawfly contains the usual 10 abdominal segments present in the Hymenoptera. The eight pairs of spiracles are located in the lower parts of the tergal plates. The first segment is broadly joined to the thorax; its tergum is divided dorsally by a median membranous area, and the precostal region forms a narrow postnotal plate of the metathorax; the venter of the first segment is reduced and contains no sternal sclerite.

The seventh segment forms the last completely exposed annulus of the abdomen. Its tergum (fig. 35 A, *VIIT*) resembles the terga of the preceding segments, but the sternum (*VIIS*) is extended as a subgenital plate beneath the base of the ovipositor, and ends in two small lobes embracing the ventral valvulae. Above the seventh sternum is a vestibular cavity, in the anterior wall of which is the gonopore. The eighth tergum (*VIIIT*) has the same shape as the seventh, but its lower ends are overlapped by the posterior lateral angles of the seventh sternum. The venter of the eighth segment is represented only by the membranous integument forming the anterior wall of the vestibulum containing the genital aperture. The ninth tergum (*IXT*) is narrowed dorsally, but is expanded on the sides of the ninth segment, where its lower margins overlap the second valvifers (*2Vlf*). Between the valvifers the membranous venter of the ninth segment forms a deep concavity in which is lodged the shaft of the ovipositor. The abdomen terminates with a conical proctiger (*Ptgr*) bearing ventrolaterally a pair of slender processes (*Soc*). Beneath the proctiger the third valvulae (*3Vl*) project as a pair of short, broad, dark-colored lobes, normally embracing the tip of the ovipositor (*Ovp*).

The ovipositor of *Pteronidea ribesii* is rather weak, since the eggs of the currant sawfly are deposited on the surface of the leaves of the food plant, but it has the characteristic form of the sawfly ovipositor. The shaft of the organ is composed of the broad, laterally compressed first and second valvulae (fig. 35 B, *1Vl, 2Vl*), which are respectively ventral and dorsal to each other. The dorsal blades are united for their entire length by a narrow median membrane (E). The outer surface of the distal part of each valvula is crossed by a series of strong, oblique ridges (C, D); the membranous proximal part is traversed by a narrow flexible ramus (*C, r1vl, E, r2vl*) which curves upward to the basal attachment of each valvula with the corresponding valvifer.

The first valvifer is a small triangular sclerite lying anterior to the lower end of the ninth tergum (fig. 35 B, *1Vlf*), where it is mostly concealed beneath the lower part of the eighth tergum (A). It is definitely articulated by its dorsal posterior angle (B, C, *a*) to the ventral anterior angle of the ninth tergum, and by its ventral angle (*b*) to the dorsal edge of the second valvifer. The ramus of the first valvula is continuous with the first valvifer at the anterior angle of the latter (*c*).

The second valvifer is a large elongate plate (fig. 35 B, E, *2Vlf*) lying beneath the eighth and ninth terga (A). It is connected by membrane with the ninth tergum, but has no articulation with the latter, its fulcrum of movement being the articulation with the lower angle of the first valvifer (B, *b*). The wide membranous proximal part of the second valvula is broadly united with the ventral margin of the anterior part of the second valvifer (E), but its ramus (*r2vl*) is attached to the anterior angle of the valvifer. Posteriorly the second valvifer bears the short, broad third valvula (A, B, E, *3Vl*).

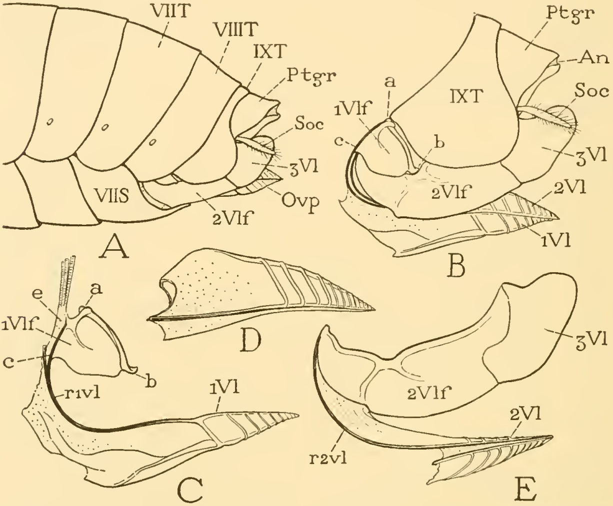

FIG. 35.—Abdomen and ovipositor of *Pteronidea ribesii* (Tenthredinidae).

A, end of abdomen with ovipositor in natural position.
B, ninth segment, with proctiger and ovipositor.
C, left first valvifer and first valvula.
D, distal part of second valvula.
E, left second valvifer and second and third valvulae, with united ends of second *valvulae* turned outward showing long ramus (*r2vl*) united with second valvifer.

a, articulation of first valvifer with ninth tergum; *b*, articulation of first valvifer with second valvifer; *c*, attachment of ramus of first valvula to first valvifer; *e*, attachment of muscle from eighth tergum on first valvifer.

The basal mechanism of the tenthredinid ovipositor brings about an opposite movement of the dorsal and ventral valvulae by the interaction of the two valvifers on each other, and of the first valvifer on the ninth tergum. A dorsal rotation of the anterior end of the second valvifer on the lower point of the first valvifer causes a rotation of the first valvifer on the ninth tergum, and vice versa, with the result that the first and second valvulae are simultaneously moved in opposite directions.

The proctiger of the lower Hymenoptera is of particular interest because of the pair of appendicular processes arising from it. In *Pteronidea* the proctiger consists of a bonnetlike dorsal plate (fig. 35 B, *Ptgr*) and of a broad, flat, membranous ventral flap, which enclose the anus (*An*) between their distal ends. The appendicular processes (*Soc*) are attached to the margin of the lower ends of the dorsal plate of the proctiger. The writer has been unable to find any trace of muscles connected with these appendages, though a large muscle extends into the proctiger from the ninth segment dorsal to the base of each process.

The proctiger of the Hymenoptera is probably a compound segment containing the tenth and eleventh abdominal somites, though there is little evidence even in the larvae of the presence of the eleventh somite. It has been shown by Nelson (1918), however, that in the embryo and young larva of the honey bee there is evidence of 11 abdominal ganglia. The newly hatched larva has nine distinct ganglionic masses in the nerve cord of the abdomen, the last of which lies in the caudal region behind the eighth segment, and contains three pairs of nerve centers, making thus a total of 11 pairs of ganglionic centers in the abdomen, which is indicative of the presence of the same number of somites. In the mature larva the composite end ganglion has united with the ganglion of the eighth somite to form the definitive terminal ganglion of the adult.

The appendages of the proctiger have usually been regarded as the cerci. If, however, we accept the embryological evidence that cerci are the appendages of the eleventh abdominal segment, it is difficult to see how these appendicular processes of the proctiger in adult Hymenoptera can be cerci, since in larval stages of the same insects the eleventh segment is absent, or represented only by the circumanal lobes of the terminal segment. The postpedes, or terminal appendages, of sawfly larvae clearly belong to the tenth abdominal segment, as do those of lepidopterous larvae, and it is claimed by Middleton (1921) that these larval appendages of *Pteronidea ribesii* give rise to protuberances of the tenth segment in the pupa within which the processes of the proctiger of the adult are developed. Though Middleton calls the adult processes " cerci " his own evidence suggests that they are identical in origin with the appendages of the tenth segment of the larva and are, therefore, not true cerci. The same argument applies to the appendicular processes of the proctiger present in adult males of some Lepidoptera, termed the *socii* by lepidopterists. The socii evidently are not cerci, since the eleventh abdominal segment is suppressed in the caterpillars and the last appendages in both the larva and the embryo are those of the tenth segment. Hence, it seems probable that the proctiger of adult Lepidoptera and Hymenoptera is mostly the tenth segment of the abdomen, and that its appendicular processes, if they represent segmental appendages at all, are the appendages of the tenth segment. Likewise the processes of the proctiger in adult male Trichoptera appear to be homologues of the socii of Lepidoptera, and here again the terminal appendages of the larva belong to the tenth abdominal segment. The writer, therefore, tentatively designates the appendages of the proctiger in Trichoptera, Lepidoptera, and Hymenoptera the *socii,* since clearly it is more probable that they represent the pygopods, or appendages of the tenth segment, present in the larvae, than that they are the cerci, or appendages of the eleventh segment, which segment is suppressed in the larvae of all these insects.

On the other hand, the terminal appendicular processes of the abdomen of adult Mecoptera and Diptera may be true cerci. In *Panorpa* they arise from a small but distinct end piece of the abdomen beyond the tenth segment, which bears the anus on its ventral surface, and is therefore the eleventh segment. The morphology of the terminal appendages of Mecoptera and Diptera is discussed in a recent paper by Gerry (1932), who regards the structures as cerci.

ATANYCOLUS RUGOSIVENTRIS (ASHMEAD)

The ovipositor of this member of the Braconidae will illustrate the structure of the slender, elongate type of ovipositor characteristic of many of the parasitic Hymenoptera. The functional abdomen of a braconid, as that of all the higher families of the order, contains only nine segments, since the first abdominal segment forms the propodeum of the thorax, and there is but one postgenital segment, which is the proctiger.

The abdomen of *Atanycolus rugosiventris* (fig. 36 A) is elongate oval, rather broad, and of a pale orange color contrasting with the blackish thorax, head, and legs, and the dusky wings. The terga and sterna of the visceral region are separated by wide lateral membranous areas, and the tergal plates of segments III and IV are fused. The slender shaft of the ovipositor (*Ovp*) is nearly as long as the abdomen and thorax, and the third valvulae (*3Vl*) are correspondingly lengthened and narrow. In life the third valvulae probably ensheath the ovipositor between their hollowed inner surfaces. The seventh, eighth, and ninth tergal plates of the abdomen are narrowed above (B) and separated by wide intersegmental membranes. The seventh sternum (*VIIS*) projects posteriorly beneath the base of the ovipositor as a large subgenital plate. There is no eighth sternum, and the venter of the eighth segment is represented only by the membrane of the anterior wall of the vestibulum beneath the gonopore. The proctiger (*Ptgr*) contains a dorsal and a ventral plate, and bears laterally a pair of small appendicular processes (socii).

The shaft of the ovipositor and the third valvulae project from above the seventh sternum (fig. 36 B). The dorsal second valvulae are solidly united with each other in the free part of the ovipositor (D, *2Vl*), and the tip of the resulting median dorsal piece of the shaft is somewhat enlarged and slightly decurved (C). The first valvulae slide freely on the ventral margins of the second valvulae, and their distal ends (C) are strongly serrate on their lower edges. The basal ramus of each first valvula (E, *r1vl*) curves upward and posteriorly to its attachment (*c*) with the dorsal margin of the corres-

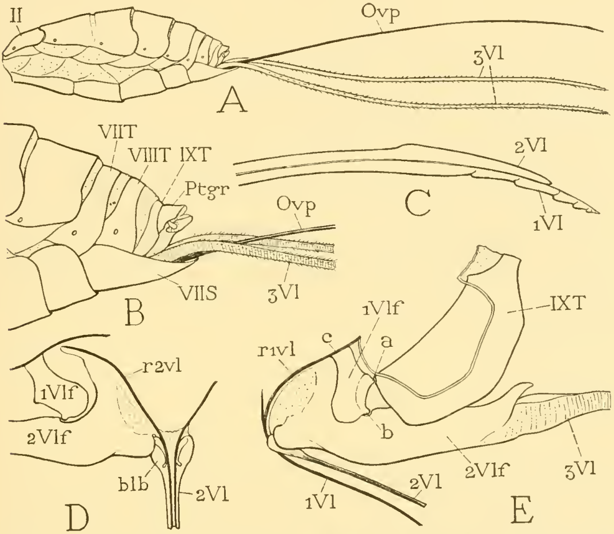

FIG. 36.—Abdomen and ovipositor of *Atanycolus rugosiventris* (Braconidae).

A, abdomen, with ovipositor separated from the ensheathing third valvulae.
B, end of abdomen and base of ovipositor.
C, distal part of shaft of ovipositor.
D, ventral view of base of united second valvulae, with ramus of right side showing union with second valvifer.
E, base of ovipositor and ninth tergum, showing articulation of first valvifer at *a* with ninth tergum, and at *b* with second valvula.

ponding first valvifer (*1Vlf*). The proximal ends of the united second valvulae (D, E, *2Vl*) present two lateral swellings which abut against the anterior ends of the second valvifers, but from each a narrow ramus (D, *r2vl*) curves upward and posteriorly against the inner face of the ramus of the first valvula of the same side, and is broadly attached to a proximal dorsal lobe of the second valvifer (*2Vlf*).

The first valvifer is a small plate (fig. 36 E, *1Vlf*) articulating between the anterior ventral angle of the ninth tergum (*a*) and the dorsal margin of the second valvifer (*b*); it gives attachment to the ramus of the first valvula (*r1vl*) by its upper margin (*c*). The lateral part of the ninth tergum (*IXT*) has the form of a sclerotic fold, the outer wall of which is deeply emarginate where the wide intersegmental membrane behind the eighth tergum is attached to it.

The second valvifer is a large, elongate plate (fig. 36 E, *2Vlf*), overlapped by the lower angle of the ninth tergum, but, as in *Pteronidea* and other Hymenoptera, having no articulation or specific point of movement on the latter; it rocks on the ventral pivot (*b*) of the first valvifer. The anterior end of the second valvifer is expanded in a dorsal lobe (D) to which the ramus of the second valvula (*r2vl*) is attached. Posteriorly the second valvifer bears the long, slender third valvula (E, *3Vl*).

The mechanism of the braconid ovipositor is the same as that of *Pteronidea.*

MEGARHYSSA ATRATA (FABRICIUS)

The species of the ichneumonid genus *Megarhyssa* are remarkable for the great length of the bristlelike ovipositor, which they insert into dead wood of trees in order to deposit their eggs in the burrows of wood-boring larvae on which their own larvae are parasitic.

The end of the abdomen of *Megarhyssa* is greatly enlarged and curiously modified (fig. 37 A). The modification involves the seventh, eighth, and ninth segments. The seventh segment is abruptly expanded from the end of the sixth; its sternum (*VIIS*) is turned forward and projects downward beneath the anterior end of the seventh tergum (*VIIT*). The eighth tergum (*VIIIT*) lies behind the seventh tergum, but its narrowed elongate, ventral ends are inflected within the lower parts of the seventh segment; the eighth sternum, as in other Hymenoptera, is completely obliterated. The ninth tergum is concealed dorsally within the overlapping eighth tergum, but its lateral parts are exposed ventrally (*IXT*) below the eighth and seventh segments. When the ninth tergum is removed from the other segments, however, it is seen to consist of a long oval lobe on each side (B, *IXT*) having the usual relations with the valvifers of the ovipositor (*1Vlf, 2Vlf*); its dorsal part forms a narrow median bridge between the lateral lobes, with which is ankylosed the dorsal plate of the proctiger (*Ptgr*).

The ovipositor of *Megarhyssa* is in no way different structurally from that of a braconid. The first valvifer (fig. 37 B, C, D, *1Vlf*) is a small oval plate articulating dorsally with the ninth tergum (B, *a*), and ventrally with the second valvifer (C, *b*). The first valvula arises from its dorsal end (D, *c*) and curves downward and posteriorly around the lower end of the second valvifer. Each first valvula has a slender but conspicuous basal branch (B, D, *v*). The second valvifer is an elongate plate (C, E, *2Vlf*) with its anterior end produced upward in a hook-shaped lobe, to which the first valvula (*1Vl*) is attached; distally it bears the long, slender

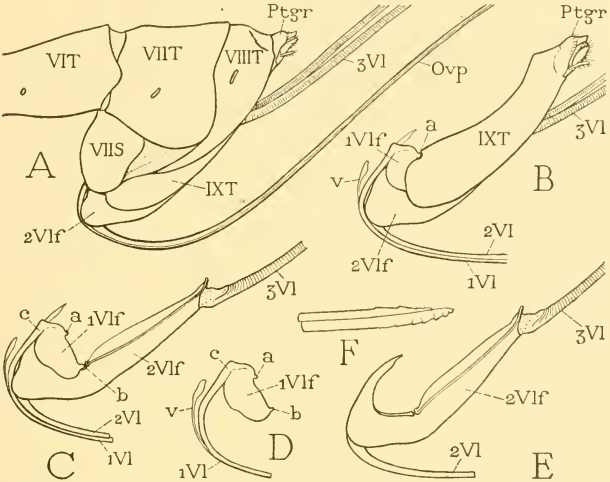

FIG. 37.—End of abdomen and structure of ovipositor of *Megarhyssa atrata* (Ichneumonidae).

A, end of abdomen and basal parts of ovipositor.
B, ninth segment and proctiger with basal parts of ovipositor.
C, base of ovipositor, left side.
D, first valvifer and proximal end of first valvula.
E, second valvifer, with proximal parts of second and third valvulae attached.
F, distal end of shaft of ovipositor.

third valvula (*3Vl*). The second valvifer rocks on the pivot of the lower articular point of the first valvifer (C, *b*). The curved basal rami of the two valvulae of each side are closely associated with each other, that of the second valvula lying against the inner face of the ramus of the first valvula. The two ventral first valvulae slide freely on the lower edges of the completely united dorsal second valvulae. The tip of the ovipositor (F) presents no unusual features.

APIS MELLIFICA LINNAEUS

The sting of the bee has been the subject of many anatomical studies, and the structural details of its skeletal parts are well known; the mechanism of the stinging apparatus, however, has not been fully understood, and none of the various attempts to explain how the bee stings is based on a correct dissection of the musculature. The sting of the bee is morphologically the ovipositor, but by both the worker and the queen it is used exclusively for purposes of stinging. Though structurally the organ has been but little modified to adapt it to its secondary use, it is effectively disqualified for egg-laying purposes through the obstruction of the channel of the shaft by a pair of valvular lobes arising from the first valvulae that serve for driving the poison liquid through it.

The principal feature that endows the bees and other stinging Hymenoptera with their stinging properties is the conversion of one of the accessory glands of the female genital system into a poison-secreting organ. The duct of this gland, which appears to be the right gland of a pair of accessory glands, opens into a large sac (fig. 41, *PsnSc*) that discharges directly into the proximal end of the channel of the sting. The other, much smaller, tubular gland (*BGl*), generally known as the "alkaline gland", lies to the left of the poison sac. The experiments of Carlet (1890), which seemed to show that it is only the mixture of the secretions from both glands that has maximum toxic qualities, are not generally accepted as conclusive, and Trojan (1930) has recently shown that in the honey bee the two glands do not open together, nor even at points where their products could readily mix. The alkaline gland opens ventrally in the membrane between the rami of the valvulae just before the base of the shaft of the sting, and entirely outside the channel of the latter. Nothing definite is known concerning the function of the alkaline gland, but it has been supposed that its secretion in the bee serves to lubricate the sliding parts of the sting, or to neutralize the acid secretion of the other gland when the bee has failed in an attempt to inflict a wound. In many other Hymenoptera, however, the alkaline gland is much larger than in the honey bee, and in general it appears that this gland is best developed in the solitary bees.

General structure of the abdomen.—In order to understand the stinging mechanism of the bee it will be necessary to know something of the structure and musculature of the entire abdomen, since the movements of the abdomen as a whole are important in the act of stinging. The abdomen is divided at the petiole between the first and second segments (fig. 38 D). The first segment is the *propodeum;* the rest of the abdomen is called the *postabdomen.* The propodeum, however, is virtually a part of the thorax, and it is often convenient to refer to the body section beyond it as the " abdomen ", though the segments should be enumerated beginning with the propodeum. In the act of stinging, the bee not only moves the postabdomen as a whole on the propodeum, but it bends the distal segments of the former abruptly downward and protrudes the sting often in an approximately vertical direction. The general abdominal musculature of the bee has been described by Betts (1923) and by Morison (1927).

The petiolate structure of the abdomen, which brings the point of flexibility at the base between the first and second segments, gives a much freer movement to the abdomen than is possible in the more usual condition in which the play is between the metathorax and the first abdominal segment, because it allows the muscles between the first and second segments to be the effectors. With insects having the second pair of wings well developed, the dorsal muscles of the metathorax are a part of the wing mechanism; but in the higher Hymenoptera the hind wings and the metathorax are both greatly reduced, and the metathoracic muscles are in consequence so small and so cramped for space that they could have little effectiveness in giving movement to the abdomen. In the bees, the second phragma of the thorax extends backward through the metathorax into the posterior part of the propodeum (fig. 38 A, *2Ph*). A pair of muscles (d_3) arise in lateral concavities on the posterior surface of the phragma and converge posteriorly and medially to a small median apodemal process of the dorsal wall of the propodeum just above the petiole (fig. 39, d_3). These muscles are evidently the longitudinal dorsals of the metathorax, the posterior ends of which have migrated far backward on the tergum of the propodeum.

The propodeum of the honey bee (fig. 38 D, *I*) consists mostly of a large, strongly convex tergal plate (*T*) solidly incorporated into the thorax by a complete fusion with the upper edges of the

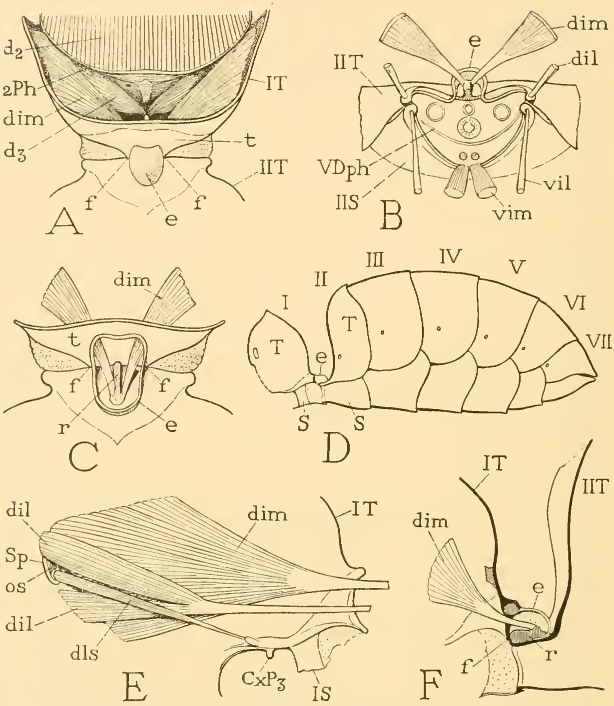

FIG. 38.—Structure of the abdominal petiole of *Apis mellifica,* worker (Apidae).

A, propodeum and petiole, dorsal view, with upper wall of propodeum removed to show muscles.

B, anterior end of petiole, showing muscle attachments on second segment.

C, dorsal view of petiole and end of propodeum, with dorsal wall of membranous pouch (*e*) removed to show insertion of levator muscles (*dim*).

D, abdomen, including propodeum.

E, dorsal muscles in right side of propodeum, mesal view.

F, levator mechanism of the petiole.

d_2, dorsal muscles of mesothorax; d_3, dorsal muscles of metathorax; *dil,* lateral dorsal muscle of propodeum; *dim,* median dorsal muscle of propodeum; *dls,* dilator muscle of spiracle; *e,* membranous dorsal wall of dorsal pouch of petiole; *f, f,* fulcra of postabdomen on propodeum; *os,* occlusor muscle of spiracle; *r,* median ridge on floor of pouch of petiole; *t,* posterior triangular area of tergum of propodeum; *vil,* lateral ventral muscle of propodeum; *vim,* median ventral muscle of propodeum.

posterior parts of the oblique metathoracic pleura. The propodial sternum is reduced to a narrow, weakly sclerotic band (*S*) in the membrane between the hind coxae and the second abdominal sternum. The short petiole of the postabdomen is formed mostly of the constricted anterior part of the second abdominal segment, and involves both the tergum and the sternum of this segment. The large first abdominal spiracles are located laterally on the anterior part of the propodeum.

The posterior declivous surface of the dorsal plate of the propodeum terminates in a small triangular area above the petiole (fig. 38 A, *t*). The median apical part of the triangle is deeply excavated by a horseshoe-shaped notch, the lateral extremities of which form a pair of points (*f, f*), which articulate with the anterior margin of the second tergum, and constitute the fulcra on which the postabdomen moves on the propodeum. The intersegmental membrane between the fulcra is arched upward in a small dome (*e*), which extends from the propodial notch backward on the dorsal surface of the petiole. There is thus formed upon the anterior part of the petiole beneath the membrane, a small pocket communicating with the cavity of the propodeum through the notch in the dorsal wall of the latter (C). The floor of the pocket is strongly sclerotized and presents a small, median, dorsal ridge (C, *r*). On the posterior end of this ridge, within the pocket, are inserted the tendons of a pair of large muscles (*dim*) which take their origins on the lateral walls of the propodeum (A). These several correlated structures and the pair of propodeal muscles constitute the levator apparatus of the postabdomen (F). The insertion of the muscles on the posterior end of the petiole ridge (*r*) gives the muscles a short leverage on the abdomen distal to the fulcra (*f*). The mechanism is thus, as noted by Betts (1923), a lever of the third order, and, considering the weight of the postabdomen, it is surprisingly effective.

The levator muscles of the postabdomen are evidently the median internal dorsals of the propodeal segment (fig. 39, *dim*). They converge from the sides of the propodeum into the dorsal pocket of the petiole (fig. 38 A, B, C). Each is a broad, fan-shaped muscle (E, *dim*) with a flat, tapering tendon. A second pair of muscles from the propodeum is inserted on the second abdominal tergum at the lateral extremities of the anterior margin of the petiole (B, *dil*), and would appear to be the lateral internal dorsals of the first segment (fig. 39, *I, dil*). Each is distinctly two-branched (fig. 38 E, *dil*), one branch arising above the propodeal spiracle (*Sp*), the other below it, the fibers of the two branches converging upon the end of a long slender tendon. The tendons of these muscles support the lateral margins of the ventral diaphragm, which latter extends into the propodeum and is attached anteriorly on the endosternum of the pterothorax. The long slender dilator muscle of the spiracle (*dls*) lies between the two branches of the lateral dorsal muscle, and is attached posteriorly on a small process of the lower margin of the propodeum close to the pleural articular process of the metacoxa (CxP_3). The ventral muscles of the petiole comprise two pairs of muscles arising anteriorly on the endosternum of the pterothorax (fig. 39, *I, vim, vil*). Those of the larger median pair are attached close together on the sternal margin of the aperture of the petiole (fig. 38 B, *vim*) ; the smaller muscles of the lateral pair (*vil*) are inserted by slender tendons on the lateral extremities of the sternal margin. The median ventrals are antagonistic to the median dorsals, but both the lateral dorsals and the lateral ventrals serve to move the postabdomen from side to side.

The postabdomen consists of six exposed segments (fig. 38 D), of which the last, or segment *VII,* has a conical shape, with a cleft on each side between the tergum and the sternum. Within the seventh segment is a large vestibular chamber in which are concealed the genital segments, the proctiger, and the sting (fig. 40).

The musculature of the postabdomen is rather simple; it is clearly adapted to produce the movements of respiration and the motions of the segments that accompany the use of the sting. The pattern of the muscle arrangement is repeated in each of the first five segments, with a few modifications in the first segment. We may, therefore, examine the musculature of the third segment of the postabdomen, which has been concisely described by Morison (1927), as an example of the musculature of segments *III* to *VI*. The names here applied to the individual muscles are those proposed by the writer (1931, p. 34) as generally applicable to the muscles of the pregenital region of the insect abdomen. They have a locational significance, and are therefore somewhat briefer than functional terms, and can be used for corresponding muscles where the action is different. The muscles found in each side of the third segment of the postabdomen (fig. 39, *IV*), omitting the diaphragm muscles, are as follows:

Musculus dorsalis internus medialis (*dim*).—A broad band of oblique fibers on median part of dorsum extending from the antecosta (*Ac*) of tergum *IV* posteriorly and medially to antecosta of tergum *V*.

M. dorsalis internus lateralis (*dil*).—A narrower band of fibers on lateral area of dorsum, attached anteriorly on tergum *IV* just behind marginal apodeme (*a*), extending posteriorly and ventrally to antecosta of tergum *V*.

M. dorsalis externus (*de*).—A short protractor muscle. Origin on posterior margin of tergum *IV;* insertion anteriorly on marginal tergal apodeme of segment *V*. The corresponding muscles of segments *II* and *III* are more oblique or almost transverse in position. The innervation of the protractors, which according to Morison is from the ganglion of the more anterior segment in each case, shows that these muscles belong to the segments giving attachment to their posterior (morphologically anterior) ends.

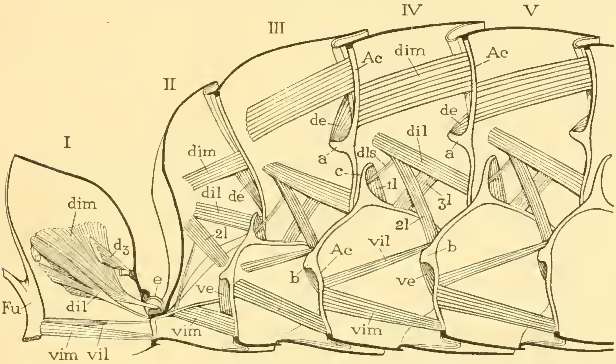

FIG. 39.—Muscles in right half of first five abdominal segments of *Apis mellifica,* worker, with muscles of dorsal and ventral diaphragms omitted.

a, anterior tergal apodeme; *b,* anterior sternal apodeme; *c,* lateral sternal apodeme; d_3, dorsal muscles of metathorax attached on propodeum; *de,* external dorsal muscles; *dil,* lateral internal dorsal muscles; *dim,* median internal dorsal muscles; *dls,* dilator muscle of spiracle; *e,* dorsal wall of pouch of petiole; *1l, 2l, 3l,* first, second, and third lateral muscles; *ve,* external ventral muscle; *vil,* lateral internal ventral muscles; *vim,* median internal ventral muscles.

M. ventralis internus medialis (*vim*).—A strong oblique muscle extending from antecosta of sternum *IV* posteriorly and medially to antecosta of sternum *V*.

M. ventralis internus lateralis (*vil*).—A narrow lateral oblique muscle from anterior part of sternum *IV,* close to or beneath origin of *vim,* to anterior apodeme (*b*) of sternum *V*.

M. ventralis externus (*ve*).—A short sternal protractor arising on posterior part of sternum *IV;* insertion anteriorly on anterior apodeme of sternum *V*.

M. lateralis primus (*1l*).—A tergosternal dilator of the abdomen. Origin on ventral margin of tergum *IV;* insertion dorsally on lateral apodeme (*c*) of sternum *IV*.

M. lateralis secundus (*2l*).—Origin dorsally on anterior lateral part of tergum *IV* external to *dil;* extends posteriorly and ventrally to insertion on posterior lateral part of sternum *IV*.

M. lateralis tertius (*3l*).—Origin dorsally on lateral part of tergum *IV* external to *dil;* extends ventrally and anteriorly, external to *2l,* to lateral margin of sternum *IV*. The second and third laterals are tergosternal compressors of the abdomen.

M. occlusor spiraculi.—A very small muscle between the ends of the closing valve of the spiracle. (Spiracle lies external to lateral muscles.)

M. dilator spiraculi (*dls*).—Origin on lateral arm of sternum; insertion on lower end of closing valve of spiracle.

The musculature of the first postabdominal segment (fig. 39, *II*) is somewhat reduced. The internal dorsals (*dim, dil*) are both present, though they are shorter than segmental length. The external dorsal (*de*) arises dorsally on the posterior part of tergum *II* and is inserted ventrally on the antecosta of tergum *III*. Of the sternal muscles the lateral internal ventral is absent; and there is but one lateral muscle present (*2l*), which corresponds with the second of the other segments.

The last exposed segment of the postabdomen, or segment *VII,* is conical in shape. Its basal part is largely retracted within the sixth segment; its apex forms the tip of the abdomen. The tergum and sternum are separated posteriorly on each side by a deep cleft (fig. 43 B), and the narrow posterior end of the sternum (A) is cut by a median notch through which the sting glides when it is protruded. The tergum (B, *VIIT*) is a large bonnet-shaped plate with a prominent apodeme (*a*) projecting anteriorly from each side of the dorsal part of its anterior margin, on which is inserted a strong protractor muscle from the posterior margin of the sixth tergum. The seventh sternum (A, *VIIS*) is a broad heart-shaped plate with its expanded basal lobes concealed above the sixth sternum. The body cavity in the seventh segment is greatly reduced by the invagination cavity containing the genital segments, the sting, and the proctiger (fig. 40). This cavity, formed by inflection of the integumental membrane (*bw*) from the posterior margins of the tergum and sternum of the seventh segment, is rather more than an ordinary vestibular invagination, and is generally called the *sting* *chamber.* Its anterior wall is formed of the venter of the eighth segment, and contains the genital opening (fig. 44 A, *c*).

The eighth segment is much reduced and is mostly membranous, but in the queen it forms a distinct oval annulus (fig. 44 A, *VIIIT, VIIIV*) at the anterior end of the sting chamber surrounding the basal parts of the sting and the proctiger. The dorsum of the eighth segment is a weakly sclerotized fold across the back (fig. 40, *VIIIT*), but on each side it contains a large tergal sclerite, the *lamina spiracularis* (figs. 40, 44 A, *Lsp*), in which is situated the eighth spiracle. From each spiracular plate a membranous fold (fig. 44 A, *VIIIV*) extends downward on the anterior wall of the sting chamber, and these folds, which are continuous ventrally beneath the genital opening, represent all that is left of the eighth venter.

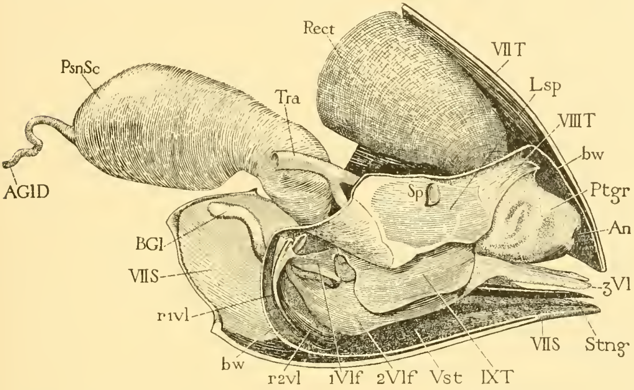

FIG. 40.—End of abdomen of *Apis mellifica*, worker, with left side removed, exposing the sting chamber containing the external parts of the stinging apparatus and the proctiger, and showing also the poison sac and a part of the rectum. (From Snodgrass, 1910.)

The genital structures contained in the seventh segment, as well as the eighth segmental annulus itself, are much better developed in the queen than in the worker. By depressing the seventh sternum of the queen there is to be seen on the anterior wall of the sting chamber, immediately before the base of the sting, a triangular depression (fig. 44 A, *a*) between the folds of the eighth venter (*VIIIV*). Within this depression is a large, transverse median genital aperture (*c*) and, at the sides of and below the latter, two other openings (*d, d*). The median orifice leads into a large median genital pouch (*B, b*), and the lateral openings into a pair of lateral pouches (*e, e*). The median pouch receives anteriorly the short oviductus communis (*Odc*), and dorsally at its anterior end the duct of the spermatheca (*SptD*).

The structure of the female genital apparatus in the bee has been described by Zander (1916) and by Bishop (1920). Both these writers apply the term "vagina" (or Scheide) to the entire passage that leads posteriorly from the confluent lateral oviducts, and appear to imply that it corresponds with the median oviduct of other insects. It is clear, however, since the spermatheca opens into the anterior end of the median pouch, that this part of the exit apparatus is derived from the genital chamber of the eighth segment, and that only the short, narrower tube anterior to the spermathecal opening is the true oviductus communis (cf. fig. 44 B with fig. 8 C). The shallow external triangular cavity containing the openings of the three genital pouches is called the "bursa copulatrix" by Bishop; but inasmuch as the common entrance cavity, the median pouch, and the lateral pouches are all parts of the genital chamber and have a copulatory function, the term "bursa copulatrix" should be applied to these parts collectively, since they are but differentiations of a single primitive invagination of the eighth segment, the genital chamber. The median pouch receives the median eversible part of the male organ during copulation and the lateral pouches the lateral lobes (pneumophyses). Bishop distinguishes two regions in the median pouch, the anterior of which contains the opening of the spermathecal duct, but in the gross anatomy of the organ this differentiation is not evident externally. Two pairs of muscles from the spiracular plates of the eighth tergum are inserted on the dorsal wall of the median pouch (fig. 44 B, *15, 16*), and a large muscle (*9*) from the antecosta of the seventh sternum (*VIIS*) is inserted on the anterior wall of each lateral pouch.

In the worker the genital organs are greatly reduced; lateral pouches of the genital chamber are scarcely perceptible, but the common oviduct opens into a median pouch, from the dorsal wall of which arises the duct of the rudimentary spermatheca.

The lateral oviducts of the bee, according to Zander (1916), are mostly of ectodermal origin, the primitive mesodermal strands of the embryo being replaced as far as the calyces during postembryonic development by lateral branches of the ectodermal oviductus communis.

The valvifers of the eighth segment (fig. 40, *1Vlf*) are entirely dissociated from the rest of the segment, since they form essential elements in the basal mechanism of the sting, but their true segmental relations are attested by the muscles that connect them with the spiracular plates of the eighth tergum (fig. 46 D, E, *14*).

The ninth segment has lost all resemblance to a segmental annulus. The median part of its dorsum is indistinguishable from the membranous wall of the proctiger (fig. 40, *Ptgr*) ; the lateral parts, however, form a pair of large quadrate plates (*IXT*), which are important elements of the sting mechanism. Each is overlapped dorsally by the spiracular plate of the eighth dorsum. The pleural parts of the ninth segment are represented by the oblong second valvifers (*2Vlf*), which are largely overlapped by the quadrate tergal plates. The ventral region of the segment, lying between the valvifers, is membranous and is ordinarily arched upward (fig. 45 A, *IXV*), forming beneath it a deep concavity thickly clothed with slender spinelike hairs, in which is lodged the bulbous basal part of the sting.

The proctiger, when fully protruded (fig. 40, *Ptgr*), is a membranous cone with the anal opening (*An*) at its distal end. The ventral wall of the proctiger contains a weakly sclerotized area.

Structure of the sting.—The stinging apparatus of the bee involves nearly all the parts that are invaginated within the seventh abdominal segment (fig. 40). These parts include the spiracle-bearing plates of the eighth tergum (*Lsp*), the lateral plates of the ninth tergum (*IXT*), the first and second valvifers (*1Vlf, 2Vlf*), and the valvulae, which form the rami and shaft of the sting (*Stng*). The proctiger (*Ptgr*), because of its natural connections, is intimately associated with the stinging mechanism. The structure of the sting of the honey bee has been described by Sollmann (1863), Kraepelin (1873), Cheshire (1886), Snodgrass (1910, 1925, 1933), Zander (1911), Betts (1923), Leuenberger (1928, 1929), and various other writers. The well-known facts are repeated here in order to show the homologies between the parts of the sting and those of the ovipositor of other insects, and also that their description may serve as as basis for a closer study of the musculature and a better understanding of the mechanism of the sting.

Students of bee anatomy have adopted special names for the parts of the sting apparatus, which are convenient to use for descriptive purposes. The lateral sclerites of the eighth tergum bearing the spiracles are known as the *spiracular plates* (*laminae spiraculares*) ; the lateral sclerites of the ninth tergum are the *quadrate plates,* the first valvifers are the *triangular plates* (*Winkel* of German writers), and the second valvifers the *oblong plates.* The first valvulae are the *darts,* or *lancets* (*Stechborsten*). The structure formed by the united second valvulae (fig. 41, *2Vl*) is sometimes called the sheath of the sting (Cheshire, 1886, Snodgrass 1910, 1925), or the *shaft* (Betts, 1923); but, since this part is hollowed beneath to form a channel giving passage to the poison, European writers generally term it the sting trough, or gutter (*Stachelrinne, fourrou-guttière*). The enlarged basal part of this organ is the *bulb* (*blb*); the slender tapering distal part we may term the *stylet* (*stl*). The third valvulae (figs. 40, 41, *3Vl*) are sometimes called the " palpi " of the sting, but since their chief function is, as in other Hymenoptera, to ensheath the distal part of the sting or ovipositor shaft, they are better termed the *sheath lobes* (*Stachelscheiden*),

The general structure of the bee's sting differs but little from that of the ovipositor of other Hymenoptera, and it is only in certain details that the sting is specialized for its specific function of ejecting the poison liquid from the reservoir of the poison gland.

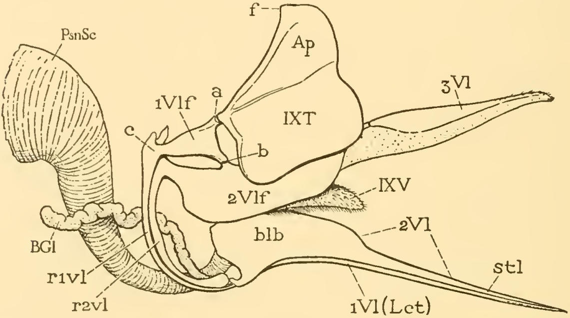

Fig. 41.—The sting and associated parts of *Apis mellifica,* worker. (From Snodgrass, 1910, but relettered in accord with the general nomenclature of the ovipositor adopted in this paper.)

The spiracular plates of the eighth tergum overlap externally the upper ends of the lateral plates of the ninth tergum (fig. 40). The spiracular plates of the worker are triangular in shape (fig. 43 B, *Lsp*), with the lower anterior angle of each produced into a process for muscle attachment. In the queen the plates are relatively larger and of irregular form (fig. 44 C). Though the spiracular plates are connected entirely by membrane with the surrounding parts, they have an elaborate musculature, which will be fully described later, but it should be noted particularly that they are anchored in position by dorsal muscles from the seventh tergum and ventral muscles from the seventh sternum (fig. 43 B). On the other hand, each spiracular plate is connected with the ninth tergal plate of the same side by two muscles (*10, 11*) from its upper end, and with the first valvifer by a single muscle (*14*) from its lower margin.

The quadrate plates, or lateral tergal sclerites of the ninth dorsum (fig. 41, *IXT*), are the suspensory plates of the sting mechanism. Because of their membranous dorsal connections they are freely movable on their upper angles (*f*) within the overlapping spiracular plates. Each quadrate plate is a large four-sided sclerite, articulated anteriorly with the dorsal posterior angle (*a*) of the first valvifer (*1Vlf*). Its dorsal part projects into the body cavity as a flat apodemal extension (*Ap*) on which important muscles of the sting mechanism are attached; its lower edge overlaps the second valvifer (*2Vlf*), with which it is connected by a membranous fold of the integument.

The triangular plate, or first valvifer (fig. 41, *1Vlf*), is a relatively small sclerite lying anterior to the quadrate plate. Its anterior angle (*c*) is continuous with the upper end of the ramus of the lancet, or first valvula (*r1vl*), and its posterior angles (*a, b*) articulate respectively with the anterior angle of the quadrate plate (*IXT*) and the dorsal margin of the second valvifer, or oblong plate (*2Vlf*). The single muscle of the first valvifer, which arises on the lower margin of the spiracular plate (fig. 43 B, *14*), is inserted on the upper edge of the valvifer very near the posterior dorsal angle (fig. 42 A, *14*). In the usual position the muscle is horizontal.

The oblong plate, or second valvifer (fig. 41, *2Vlf*), lies beneath the first valvifer and the quadrate plate. Its articulation with the lower posterior angle of the first valvifer (*b*) is somewhat before the middle of its dorsal margin. Its anterior end is narrowed and continuous with the ramus of the second valvula (*2rvl*); posteriorly it supports the third valvula (*3Vl*), which in the bee is a short, soft, mostly membranous appendage.

The oblong plates of opposite sides are connected medially by an ample membrane thickly clothed with hairs, which represents the venter of the ninth segment. The membrane is ordinarily arched upward above the base of the sting (fig. 45 A, *IXV*), forming below it a deep cavity in which the bulb of the sting is ensheathed, but, when the sting is depressed, the membrane is partly everted and appears as a hairy pad over the bulb (fig. 41, *IXV*).

The shaft of the sting is composed of the united second valvulae (fig. 41, *2Vl*), and of the slender first valvulae, or lancets (*1Vl*). The single dorsal piece, formed of the second valvulae, is enlarged basally as the bulb of the sting (*blb*); its distal tapering part is the stylet (*stl*). The lancets slide freely on the lateral ventral margins of the bulb and stylet (fig. 42 E); their lower edges are in contact, and between the three parts of the shaft is the poison canal of the sting (*r*). In the bulb the canal expands to a large chamber, in which lie a pair of pouchlike valves borne on the upper edges of the lancets (A, *Vlv*) that serve to drive the poison liquid through the canal, from which it makes its exit near the tip of the sting from a ventral cleft between the lancets. The stings of the worker and the queen differ principally in the size and form of the shaft. The shaft of the queen is relatively larger and is strongly bent downward in the region of the bulb; when exserted, therefore, it curves ventrally or anteriorly according to the position of the abdomen. The poison sac opens directly into the base of the bulb (fig. 42 C, *PsnSc*). The distal end of the stylet is narrow but rounded, and in the worker it has three pairs of very small lateral barbs on its dorsal surface. The tips of the lancets are acute, and the terminal part of each lancet of the worker is strongly serrate ventrally on its outer surface by a series of 10 retrorse barbs.

The shaft of the sting is supported at its base on the rami of the valvulae (fig. 41, *r1vl, r2vl*). The two pairs of rami are widely divergent as they curve upward to their connections with the valvifers (*1Vlf, 2Vlf*). A membrane stretches between the rami of the second valvulae. The two rami of each side are united by a groove-and-ridge connection continuous with that on the shaft (fig. 42 E), but since the ramus of the first valvula lies against the outer surface of the ramus of the second valvula (fig. 41), the groove of the first valvula, which follows the dorsal edge of the lancet (fig. 42 A, *d*), goes over to the inner face of the ramus (*d'*).

In order to understand an important point in the mechanism of the sting it will be necessary to give close attention to certain details of structure at the base of the bulb. Each second valvular ramus is rather broad (fig. 42 B, *r2vl*) and presents a rounded lobe (*w*) near its lower end. The direct union of the ramus with the bulb is a narrow sclerotic bar (*x*), but laterad of it a hooked process (*y*) from the base of the bulb makes a very fine connection (*z*) with the lobe (*w*) of the ramus. The muscle of the ramus (*20*) is inserted on this process.

The basal surface of the bulb is inclined forward considerably in advance of its connections with the rami (fig. 42 C), and a membranous fold projects from it dorsally into the body cavity. In this fold there lies a Y-shaped rod, the *furcula* (C, *Frc,* D), the arms of which are connected with the base of the bulb, while the median stem curves upward and posteriorly above the latter, and above the membranous ninth venter (*IXV*). Upon the furcula are inserted a pair of large muscles from the second valvifers (fig. 45 A, *19*). These muscles serve to deflect the distal end of the shaft of the sting, since their pull is on points at the base of the bulb anterior to the articulations of the latter (fig. 42 B, C, *z*) with the lobes of the rami. The rôle of the furcular muscles in the mechanism of the sting has not generally been understood. Zander (1911) and subsequent writers have regarded them as protractors of the sting shaft; but, as will later be shown, the outward thrust of the sting is brought about by other means, while simultaneously the shaft is depressed by the muscles inserted on the furcula.

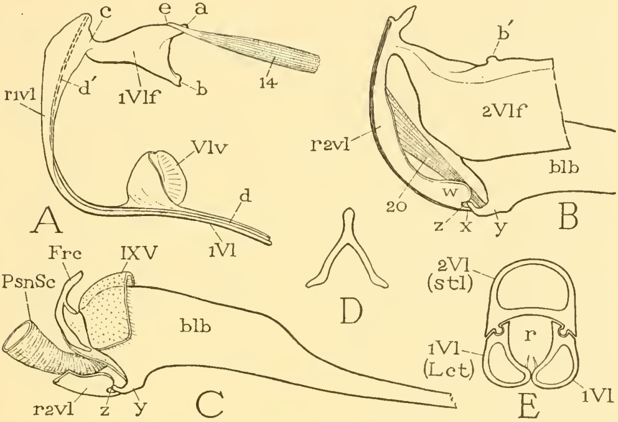

FIG. 42.—Structural details of the various parts of the sting of *Apis mellifica*, worker.

A, left first valvifer and proximal half of first valvula.

B, anterior part of left second valvifer with ramus of corresponding second valvula and basal part of bulb, showing articulation of the latter on the ramus, and the ramus muscle.

C, basal mechanism of shaft of sting and attachment of furcula.

D, furcula.

E, cross section of distal part of shaft of sting.

a, articulation of first valvifer with ninth tergum; *b*, articulation of first valvifer with second valvifer; *b′*, corresponding articular point of second valvifer; *c*, attachment of first valvula to first valvifer; *d*, *d′*, groove of first valvula; *e*, insertion on first valvifer of muscle (*14*) from spiracular plate of eighth tergum; *r*, poison canal of sting; *w*, distal lobe of ramus of second valvula; *x*, connection between ramus and bulb of second valvula; *y*, articular process of base of bulb; *z*, point of articulation between ramus and bulb of second valvula.

The morphological nature of the furcula has been somewhat puzzling to students of bee anatomy, but it is evident that the furcula is merely a movable apodeme contained in a membranous fold at the base of the bulb. The homologues of the muscles inserted upon it in the bee are attached in the braconid (fig. 45 B, *19*) directly to a bulbous enlargement of the base of the ovipositor, while in the ichneumonid (C) they are inserted on a ligamentous stalk containing a small U-shaped sclerotization. The depressor mechanism of the shaft of the sting in the bee, therefore, is clearly a development from a much simpler mechanism of the ovipositor in the lower Hymenoptera, but it appears to have no counterpart in other orders of insects.

Muscles of the seventh segment and the sting.—Since the muscles of the seventh and genital segments cannot all be certainly identified with specific muscles of the preceding segments, they will be given descriptive names by which they may be recognized; they are designated on the figures with arabic numerals. The numbered series of muscles applies in full to the queen only, certain muscles being absent in the worker. The list of muscles here recorded for the terminal segments of the bee, 22 in all, is somewhat greater than that given by Betts (1923) and Morison (1927). Certain other discrepancies in the accounts will be noted at the appropriate points, as will also a few additions and corrections that must be made in the description of the muscles of the sting as given by Sollmann (1863), Kraepelin (1873), and Zander (1911).

The following nine muscles belong to the seventh segment:

1. First internal dorsal muscle.—A rather wide muscle in the worker arising anteriorly on seventh tergum (fig. 43 B); extending posteriorly and ventrally to dorsal lobe of spiracular plate. Smaller in the queen (fig. 44 C), where its insertion on spiracular plate is on dorsal margin of anterior lobe.

2. Second internal dorsal muscle.—Found only in the queen. A slender muscle arising dorsally on lateral part of seventh tergum; insertion ventrally on dorsal margin of spiracular plate above the spiracle (fig. 44 C). Not described by Betts or Morison.

3. External dorsal muscle (not shown in the figures).—A wide muscle against outer face of spiracular plate, present in both worker and queen. Origin ventrally near lower lateral margin of seventh tergum; insertion dorsally on upper margin of dorsal lobe of spiracular plate, as indicated in the figures (figs. 43 B, 44 C, *3*). This muscle is a protractor between the tergal plates of segments *VII* and *VIII*.

4. First lateral tergosternal muscle.—Origin posteriorly on lateral part of seventh tergum external to spiracular plate (fig. 43 B); insertion anteriorly on lateral apodeme of seventh sternum (A, B).

5. *Second lateral tergosternal muscle.*—Origin dorsally above *4* on lateral part of seventh tergum (fig. 43 B); insertion ventrally on lateral margin of seventh sternum (A). In the queen there are two branches to this muscle, a short outer group of fibers arising on the seventh tergum below the spiracles being inserted on the sternum along with the fiber of the inner group.

6. *Occlusor of the spiracle.*—A small muscle between ends of closing valve of seventh spiracle (fig. 43 B).

7. *Dilator of the spiracle.*—A long slender muscle arising on margin of seventh sternum just before lateral apodeme; inserted on lower end of closing valve of seventh spiracle (fig. 43 B).

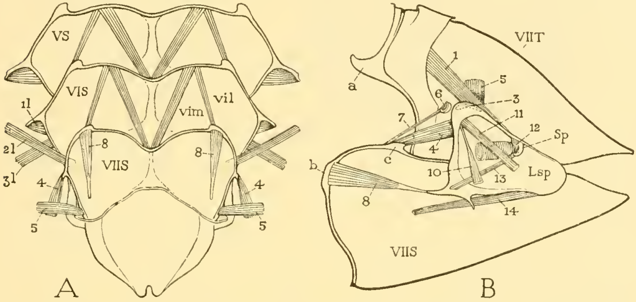

FIG. 43.—Musculature of posterior abdominal segments of *Apis mellifica*, worker.

A, muscles of fifth, sixth, and seventh sterna.

B, muscles of right half of seventh segment and of right spiracular plate of eighth segment, mesal view.

8. *Intersegmental sternotergal muscle.*—Origin on anterior apodeme of seventh sternum (fig. 43 A, B); fibers in the worker convergent posteriorly to insertion on a tendon attached to end of ventral anterior point of spiracular plate of eighth tergum (B), but in the queen (fig. 44 C) attached directly to anterior lobe of spiracular plate. This muscle cannot be homologized with any muscles of the preceding segments, since no muscle in the latter segments has corresponding connections.

9. *Median internal ventral muscle.*—Present only in the queen (fig. 44 B). A short, thick, conical muscle arising anteriorly on antecosta of seventh sternum (*VIIS*) in position of the usual median ventrals (fig. 43 A, *vim*); fibers divergent posteriorly to insertion on anterior wall of corresponding lateral pouch of genital chamber (fig. 44 B, *e*). Not mentioned by other writers.

The following muscles of segment *VIII*, here enumerated as muscles *10* to *16*, are all attached on the spiracular plate of the eighth tergum:

10. First dorsal muscle.—A very slender muscle in the worker (fig. 43 B), a large muscle in the queen (fig. 44 C), arising dorsally on upper part of inner face of spiracular plate; inserted ventrally on outer surface of ninth tergal (quadrate) plate anteriorly at base of dorsal apodeme of the latter.

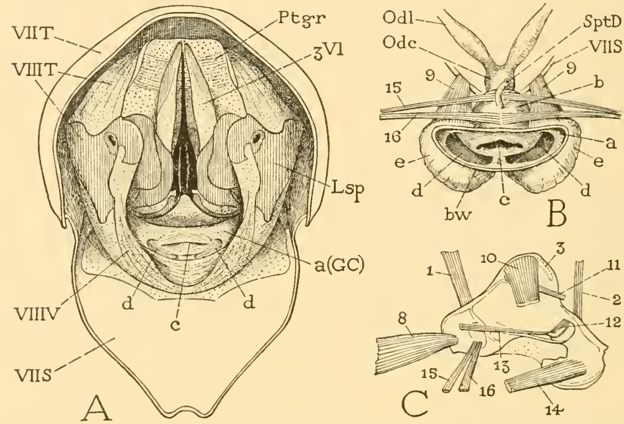

Fig. 44.—External genital apparatus, and muscles of the spiracular plate of eighth segment of *Apis mellifica*, queen.

A, the sting chamber opened from behind by separation of tergal and sternal plates of seventh segment, showing the complete annulus of eighth segment (*VIIIT, VIIIV*), with outer depression (*a*) of genital chamber at base of ovipositor between folds of eighth venter (*VIIIV*).

B, the genital pouches and the oviducts, posterodorsal view, with wall of outer cavity of genital chamber (*a*) cut away along line *bw*, and apertures of pouches (*c, d*) distended.

C, right spiracular plate of eighth segment and its muscles, mesal view.

a, shallow external cavity of genital chamber; *b*, median pouch of genital chamber; *c*, aperture of median pouch; *d, d*, apertures of lateral pouches; *e, e*, lateral pouches of genital chamber.

11. Second dorsal muscle.—Origin on inner face of dorsal lobe of spiracular plate (figs. 43 B, 44 C); insertion posteriorly and ventrally on posterior dorsal angle of quadrate plate of ninth tergum (fig. 45 A). In the worker this muscle arises just behind *10* (fig. 43 B); in the queen (fig. 44 C) it arises external and ventral to origin of *10*.

12. Occlusor of the spiracle.—A short, relatively broad muscle in the worker arising dorsally on marginal ridge of spiracular plate, with fibers convergent ventrally to insertion on lower end of closing valve of eighth spiracle (fig. 43 B) ; in the queen this muscle attached as usual to both ends of spiracular valve (fig. 44 C).

13. Dilator of the spiracle.—A slender muscle arising on anterior ventral part of spiracular plate, crossing the plate obliquely to insertion on lower end of closing valve of spiracle (figs. 43 B, 44 C).

14. Tergovalvifer muscle.—A long muscle, horizontal in the usual position. Origin posteriorly on ventral margin of spiracular plate in the worker (fig. 43 B), on inner face of posterior lobe of plate in the queen (fig. 44 C) ; insertion anteriorly on posterior end of first valvifer (figs. 42 A, 45 A). This muscle is the only representative in the bee of the usual tergal muscles of the first valvifer.

15. First tergoventral muscle.—A slender muscle, present only in the queen, arising on anterior lobe of spiracular plate (fig. 44 C) ; extends mesally and anteriorly to dorsal wall of median pouch of genital chamber anterior to duct of spermatheca (B).

16. Second tergoventral muscle.—Similar to the last and present only in the queen. Origin just behind *15* on spiracular plate (fig. 44 C) ; insertion on dorsal wall of median pouch of genital chamber posterior to spermathecal duct (B).

It will be observed that there are 11 muscles, including the spiracular muscles, attached on each of the spiracular plates of the eighth tergum in the queen (fig. 44 C), and eight in the worker (fig. 43 B). Morison (1927) says there are nine in the worker, but he describes a small muscle from the antero-ventral margin of the plate to the side of the quadrate plate, which was not observed by Betts (1923), and which the writer has been unable to find. It is evident that the spiracular plates are important parts of the general sting mechanism, but since the muscles from them to the parts of the eighth and ninth segments that compose the sting apparatus are all small, it is probable that they do not produce any of the major activities of the latter.

The muscles of the ninth segment include the principal muscles of the stinging mechanism, and the muscles of the proctiger. Their distribution and functions have been discussed particularly by Sollmann (1863), Kraepelin (1873), Zander (1911), and Snodgrass (1933). These muscles are as follows, on each side:

17. Anterior tergal muscle of the second valvifer (fig. 45 A).—A large tergopleural muscle composed of two distinct bundles of fibers, one dorsal (*17a*), the other ventral (*17b*). Fibers of dorsal group arise on posterior dorsal angle of quadrate plate of ninth tergum, and cover both surfaces of dorsal apodemal part of the plate; insertion anteriorly on upper extremity of ramus of second valvifer (*r2vl*). Fibers of ventral group (*17b*) arise posteriorly on inner face of quadrate plate, and lie parallel to those of dorsal group; insertion anteriorly on anterior arm of second valvifer (oblong plate).

Much confusion has existed as to the insertion points of these muscles. Sollmann (1863) correctly gave the insertion of the upper muscle on the extremity of the ramus of the second valvula, but the lower muscle he wrongly described as attached on the first valvifer (Winkel); Kraepelin (1873), on the other hand, erroneously ascribed the dorsal muscle to the first valvifer, but correctly described the attachment of the lower one on the second valvifer. Kraepelin's error has been followed by Zander (1911), Betts (1923), and Morison (1927). The two groups of fibers in the bee very clearly correspond with the usually single anterior tergal muscle of the second valvifer (figs. 29, 34, *6*). In some Hymenoptera, as in *Megarhyssa* (fig. 45 C), they form two quite distinct muscles (*17a, 17b*). These muscles are the *protractors* of the lancets.

18. Posterior tergal muscle of the second valvifer.—A broad, flat, tergopleural muscle covering most of the inner face of quadrate plate of ninth tergum, on which it arises dorsally and anteriorly (fig. 45 A); insertion ventrally on posterior part of dorsal ridge of second valvifer (*2Vlf*). This muscle is the *retractor* of the lancet.

In the queen a slender muscle arises dorsally on the posterior dorsal angle of the quadrate plate, and is inserted ventrally on the second valvula mesad of *18*. This muscle is described by Morison (1927) as a distinct muscle, but it is here regarded as a branch of *18*, since the two have the same insertion, and together would represent the usual posterior tergal muscle of the second valvifer (figs. 29, 34, *7*).

19. Muscle of the furcula.—A highly developed muscle in the bee (fig. 45 A), consisting of a wide layer of strong fibers arising ventrally on most of length of inner surface of second valvifer (oblong plate); fibers curve anteriorly, dorsally, and mesally over ninth ventral membrane (*IXV*) to insertion on stem and upper part of arm of furcula (*Frc*). This muscle is much smaller in lower Hymenoptera; in the braconid *Atanycolus* it is inserted directly on a small basal swelling of the united second valvulae (B, *19*); in the ichneumonid *Megarhyssa* (C, *19*) it is attached on a short ligamentous process arising from a hooked dorsal extension of the base of the united second valvulae; in the tenthredinid *Pteronidea,* a corresponding muscle arising on the second valvifer is inserted on a long basal process of the second valvula. A representative of this muscle has not been found in other orders of insects.

The muscles of the furcula are usually regarded as the protractors (Vorstossmuskeln) of the sting. It was correctly observed by Kraepelin (1873), however, that they can act only in the capacity of deflecting the distal end of the shaft since they pull upward on the base of the bulb.

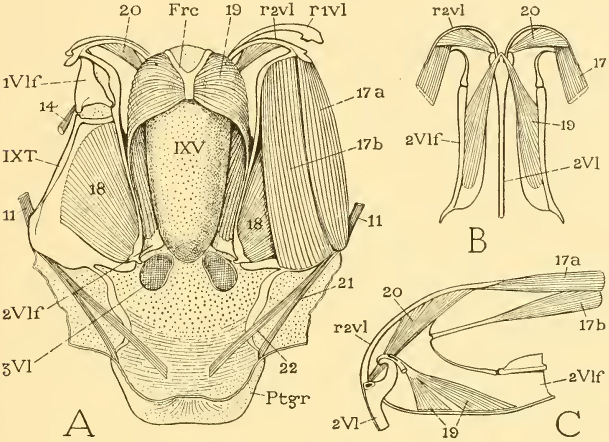

Fig. 45.—Musculature of the hymenopterous ovipositor or sting.

A, sting of *Apis mellifica,* worker, with venter of ninth segment and proctiger, dorsal view, showing muscles of the stinging apparatus.

B, second valvifers and base of shaft of ovipositor of *Atanycolus rugosiventris,* with muscles inserted on the latter, dorsal view.

C, anterior end of right second valvifer, mesal view, with right ramus and base of shaft of ovipositor of *Megarhyssa atrata,* showing anterior muscles (*17*) of valvifer, and muscles of the shaft (*19, 20*).

20. Ramus muscle of the second valvula.—A rather small muscle in the worker bee attached dorsally on upper part of ramus of second valvula (figs. 42 B, 45 A), and ventrally on lateral process (*y*) of base of bulb (fig. 42 B). In *Atanycolus* (fig. 45 B) and in *Megarhyssa* (C) this muscle is relatively larger and stretches like a bowstring between the two extremities of the strongly arched ramus. The ramus muscle appears to have no homologue in insects other than Hymenoptera.

21, 22. Muscles of the proctiger.—Two slender muscles arising from posterior dorsal angle of quadrate plate (fig. 45 A); extending posteriorly and ventrally to ventral wall of proctiger, where one (*21*) is inserted laterally, the other (*22*) medially.

The mechanism of the sting.—When a worker bee is held securely by the thorax, preferably in a pair of forceps, her ineffectual attempts to use the sting are accompanied by a strong deflection of the end of the abdomen. The shaft of the sting is thrust out from the cleft between the tergal and sternal plates of the seventh segment, and slides back and forth in the terminal notch of the sternum. The exposure of the shaft is usually greatest as the direction of the thrust approaches a perpendicular to the axis of the body; the seventh sternum is depressed and the bulb of the sting appears in the opening above it. The third valvulae, or so-called " palpi " of the sting, are not in evidence while the shaft is probing for an object to strike, and the writer has never observed any use made of these organs by the bee to suggest that they have a tactile function, or that by means of them the bee determines where a vulnerable spot is presented for her attack, as she has been supposed and even said to do. The third valvulae do not issue from the sting chamber. The highly mobile abdomen swings around in all directions on the petiole, and the decurved tip strikes at random until an object is encountered, which, if nothing else presents, may be the body, head, or mouth of the bee herself.

The deflection of the terminal part of the abdomen is brought about by the contraction of the oblique lateral intertergal dorsal muscles (fig. 39, *dil*) and the median intersternal ventral muscles (*vim*) of the segments concerned. The accompanying movements of the abdomen as a whole depend upon the mechanism of the petiole and are produced by the muscles of the propodeum inserted upon the second segment.

The entire act of stinging involves three separate movements, or sets of movements, in the sting apparatus. The first accomplishes the outward thrust of the shaft, the second the depression of the shaft, and the third the movements of the lancets on the stylet. The first two movements are simultaneous, but each has its own mechanism, while the movement of the lancets depends on a third mechanism quite distinct from the other two.

When the bee persists in her attempts to sting an inaccessible or nonexistent object, the shaft, as we have seen, glides rapidly back and forth in the notch of the seventh sternum, and with each outward thrust is exposed for nearly its entire length. If now, while the bee is held under the microscope, the plates of the apical segment are separated with a needle or a pair of slender forceps, it is to be seen that the movements of the shaft are produced by corresponding movements of the entire basal part of the sting apparatus. The latter, however, does not move back and forth horizontally in the position of repose (fig. 46 A) ; on the contrary, the whole structure, including the valvifers and the quadrate plates of the ninth segment, swings downward and posteriorly on the upper angles of the quadrate plates, and the shaft, which at the same time is unsheathed and depressed, is driven out from the sting chamber at the tip of the abdomen (B, C). By a reverse set of movements in the basal apparatus the sting is retracted and elevated to its initial horizontal position and ensheathed between the second valvifers and their distal lobes. Conversely, it can be demonstrated on a freshly killed specimen that back-and-forth movements of the shaft involve these same swinging movements of the basal apparatus. The free movement of the basal parts is made possible by the membranous connections of the latter with the sur-

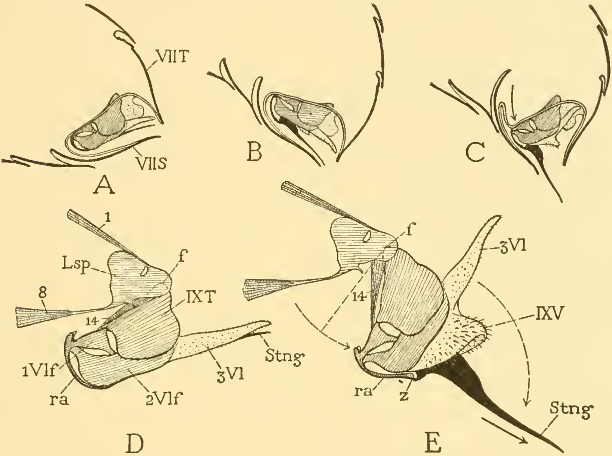

Fig. 46.—Relative positions of the parts of the sting of a worker bee, *Apis mellifica,* in repose and action.

A, sting in usual position within the sting chamber.

B, end of abdomen bent down, shaft of sting unsheathed and partly depressed ready for extrusion.

C, basal part of sting apparatus swung posteriorly as indicated by arrow, sting fully depressed and extruded.

D, usual position of basal parts of sting, ninth tergal plates, and spiracular plates of eighth segment within the sting chamber during repose.

E, position of same parts when shaft of sting is fully protruded.

rounding parts, and particularly by the ample length of the membranous floor of the sting chamber reflected from the seventh sternum.

The relative changes in position of the various parts of the sting apparatus before and after the protrusion of the shaft are shown at D and E of figure 46. The axis of revolution in the basal parts passes through the upper ends (*f*) of the quadrate plates (*IXT*), which are overlapped by the spiracular plates (*Lsp*) of the eighth segment. The spiracular plates themselves are but little affected by the movements of the sting, since they are held in place by their dorsal and ventral muscles (*1, 8*). In the position of protraction (E) the sting base is almost at right angles to the lower margins of the spiracular plates, and the sheath lobes, or third valvulae (*3Vl*), are pointed upward. The shaft of the sting, on the other hand, has retained its position in the direction of the thrust by a movement of depression. The depression of the shaft somewhat flattens the curve of the rami (*ra*), and is accompanied by an eversion of the membranous ninth venter, which now appears as a large hairy lobe (*IXV*) over the bulb of the sting.

The mechanism of the stinging apparatus of the bee was first studied by Sollmann (1863), who observed that the outward thrust of the shaft is produced by a backward swing of the supporting basal parts. His explanation of the movements of the latter, however, is mostly fanciful, since he attributes them to muscles that either do not exist or do not have the attachments he ascribed to them. It was later shown by Kraepelin (1873) that there are no muscles immediately connected with the sting or its basal support that can give the movements of protraction and retraction to the shaft. Accepting this fact, Kraepelin says: "Ich nehme daher keinen Anstand, als treibendes Princip für die Bewegung des Stachels im engeren Sinne die Blutflüssigkeit zu bezeichnen, welche ja auch bekanntermassen bei den Hervorstülpen des Penis und ähnlicher Körperanahänge eine so wichtige Rolle spielt. Bei jeder stechenden Biene kann man eine seitliche Annäherung der Abdominalwandungen mit Lichtigkeit beobachten, bei frisch getödeten aber genügt ein geringer Druck auf die vordern Hinterleibssegmente, um den Stachel in normaler Weise hervortreten zu lassen."

A careful examination of the bee confirms the truth of Kraepelin's statement concerning the lack of any special muscles for the protrusion and retraction of the sting, and makes it clear that the shaft is driven out of the sting chamber by pressure exerted against the membranous walls of the latter from within the body cavity of the abdomen. The rotund anterior part of the postabdomen, by a bulblike action of compression and expansion, thus swings the basal support of the sting back and forth on its points of suspension at the dorsal angles of the quadrate plates, and the shaft is correspondingly protruded and withdrawn. It is possible that the strong contraction of the seventh abdominal segment, which elevates the broad anterior lobes of the sternum, may cause the latter to press directly on the base of the sting, but if this is partly accountable for the sting protraction it is only a minor factor. Kraepelin's account of the mechanism of protraction and retraction of the sting seems to have made little impression on other students of the bee, for all subsequent writers appear to assume that the outward thrust of the shaft is caused by the muscles of the furcula arising on the second valvifers.

While, then, we can explain the protraction and retraction of the sting only as the result of a bulblike action of the abdomen, it is not true that any compression of the abdomen, either in a living bee or a freshly killed specimen, will exsert the sting. The movement of protraction in the basal apparatus must be accompanied by a depression of the distal part of the shaft; otherwise the latter will be simply tilted upward with the sheath.

The depression of the shaft during the outward thrust and its elevation with the reverse movement are brought about by a special mechanism of the basal apparatus, which includes the furcula, the furcular muscles, the rami, the ramus muscles, and the articular points between the base of the bulb and the distal lobes of the rami. It is curious that all students of the mechanism of the bee's sting, since Kraepelin (1873), have regarded the furcular muscles as the protractors (Vorstossmuskeln) of the shaft. An examination of the sting structure shows at once that the shaft of the organ can have no horizontal movement between the second valvifers (oblong plates), on which the furcular muscles are attached, except what little motion might result from the flattening of the rami. Furthermore, a backward pull on the furcula in the direction of its muscles (fig. 47 B, *19*) has an immediate response in the depression of the distal end of the shaft (C). The fulcra of the vertical movements of the shaft are the points of articulation between the basal processes of the bulb and the distal lobes of the second rami (fig. 42 B, C, 47 B, *z*). When the shaft is turned down (fig. 47 C) the curves of the rami are flattened, and the ramus muscles (*20*), which are attached on the basal processes of the bulb distal to the fulcra (*z*), are stretched. The ramus muscles, therefore, are the antagonists of the furcular muscles (*19*) and serve to elevate the shaft and to restore it to its position of repose between the second valvifers and their distal lobes.

The third set of movements in the sting apparatus, namely, the movements of the lancets on the stylet, has to do with the penetration

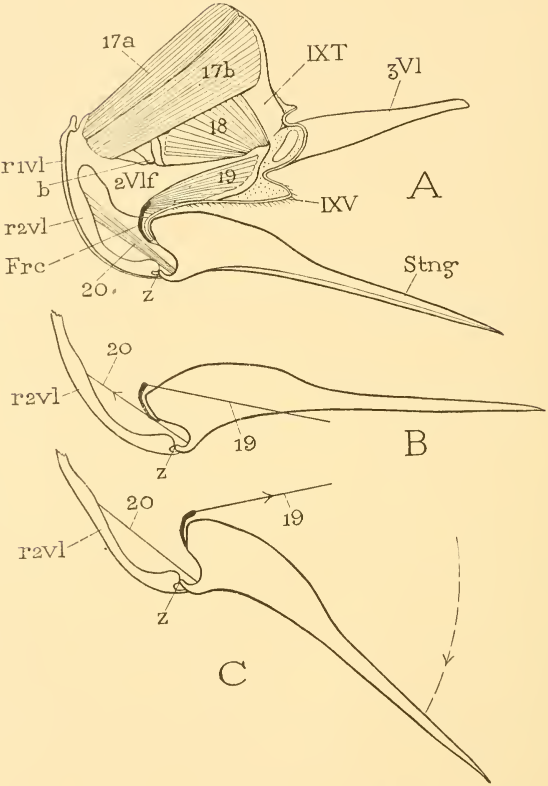

FIG. 47.—Mechanism of the sting of *Apis mellifica,* worker.

A, mesal view of right half of sting apparatus with shaft partly depressed, showing anterior and posterior muscles (*17, 18*) of second valvifer, muscles of furcula (*19*), and ramus muscle (*20*).

B, the shaft in usual position, with ramus muscle (*20*) contracted.

C, the shaft depressed by contraction of furcula muscle (*19*).

b, ventral articulation of first valvifer on second valvifer; *Frc,* furcula; *IXT,* tergal plate of ninth segment (quadrate plate); *IXV,* venter of ninth segment; *r1vl,* ramus of first valvula; *r2vl,* ramus of second valvula; *Stng,* shaft of sting; *3Vl,* third valvula; *2Vlf,* second valvifer (oblong plate); *z,* basal articulation of shaft on ramus of second valvula.

of the wound by the shaft after the tip of the latter has once been inserted; and incidentally these movements accomplish also the injection of the poison by motion of the valves of the lancets in the poison chamber of the bulb. The skeletal parts in the basal apparatus concerned with the movement of the lancets are the first and second valvifers and the quadrate plates; the motor elements are the anterior and posterior muscles of the second valvifers.

It will be unnecessary to review the opinions of other writers on the working of the mechanism that moves the stylets, since all investigators except Sollmann (1863) have wrongly attributed the attachment of the dorsal group of fibers of the anterior second valvifer muscles (fig. 47 A, *17a*) to the first valvifers, while Sollmann on his part, besides committing various other inaccuracies, believed the ventral group of fibers (*17b*) to be attached on the first valvifer. Hence, all descriptions of the sting mechanism contain the error of attempting to explain the movements of the lancets as caused by muscles inserted on the first valvifers. Notwithstanding this mistake, Kraepelin (1873) is not far wrong in his account of the working of the sting, inasmuch as he deduces the correct movements of the lancets from his concept of the mechanism.

The only muscle inserted on the first valvifer (triangular plate) in the bee, as already shown, is the slender muscle from the lower margin of the spiracular plate of the eighth segment (fig. 46 D, E, *14*); but this muscle is attached on the valvifer so close to the posterior end of the latter, and has such a weak support on the spiracular plate, that it seems probable its chief function is to maintain a proper relation between those two sclerites. The principal muscles that accomplish the movements of the lancets in the bee are undoubtedly the large anterior and posterior muscles of the second valvifers (oblong plates) that have their origins on the quadrate plates of the ninth tergum (fig. 47 A, *17*, *18*). The homologues of these muscles are readily identified in all pterygote insects; in the Hymenoptera the fibers of the first muscle are separated into two distinct groups (*17a*, *17b*), but they are all inserted on the anterior arm of the second valvifer or on the upper extremity of the ramus of the second valvula. The posterior muscle (*18*) arises anteriorly and dorsally on the inner face of the quadrate plate, and its fibers converge posteriorly and ventrally to their insertion on the posterior end of the elongate second valvifer. These two sets of muscles are antagonistic to each other because the fulcrum of the second valvifer on the first valvifer (*b*) lies between their attachments on the former plate.

In most other insects the second valvifer is articulated directly to the ninth tergum, and has a simple rocking movement on the latter produced by the alternate contraction of its anterior and posterior muscles, because the tergum forms ordinarily a complete dorsal arch over its segment and is relatively immovable. In the Hymenoptera, however, the second valvifer articulates with the first valvifer, which in turn articulates with the ninth tergum, and this interpolation of the first valvifer between the tergum and the second valvifer considerably changes the mechanism; but in the bees a further modification results from the reduction of the ninth tergum to the pair of lateral quadrate plates which are themselves freely movable because of their membranous connections with the surrounding parts. Observations on the freshly extracted sting of a living bee show that the principal activity in the basal apparatus that accompanies the protraction and retraction of the lancets consists of a back-and-forth vibration of the quadrate plates and a quick elevation and depression of the anterior ends of the first valvifers (triangular plates). The second valvifers (oblong plates) remain relatively stationary, but there is sometimes a quivering of the third valvular lobes.

The working of the mechanism that moves the lancets will be readily understood if a cardboard model is cut out representing the skeletal parts of one-half of the sting apparatus (fig. 48). The first valvifer of the model should be attached by pins to the quadrate plate and to the oblong plate, and the lancet must be twisted so that it will slide against the lower edge of the stylet when the two are held together by a wire loop. We have observed on the living bee that the muscles between the quadrate tergal plate (fig. 47 A, *IXT*) and the oblong plate (*2Vlf*) move the quadrate plate and not the oblong plate. This is just the reverse of the usual interaction of the corresponding plates in other insects. If, therefore, the quadrate plate of the model (fig. 48 A, *IXT*) is moved alternately in the direction of its two antagonistic muscles (*17, 18*), while the oblong plate (*2Vlf*) is held stationary, the effect is a simple back-and-forth movement of the lancet on the lower edge of the stylet. Hence, when the posterior muscle (*18*) contracts, as shown at A, it moves the quadrate plate rearward, and the latter pulls on the dorsal angle (*a*) of the first valvifer (*1Vlf*), with the result that the valvifer is rotated upward on its ventral angle (*b*) and retracts the lancet (*Lct*). On the other hand, when the anterior muscle (*17*) contracts, as at B, the quadrate plate is pulled forward and rotates the valvifer downward, which movement protracts the lancet. It is possible that the slender muscle (A, *14*) from the spiracular plate to the posterior end of the first valvifer may be an accessory retractor of the lancet, as supposed by Kraepelin.

Because of the double articulation of the first valvifer on the quadrate plate and the oblong plate (fig. 48 A), and of the difference in length between the two axes (*ab* and *ac*) of the valvifer, a very small movement of the quadrate plate (B, *d*) produces a relatively large movement of the lancet. In the living bee the motion of the quadrate plate appears as a quivering or rapid back-and-forth vibration, its actual displacement being scarcely perceptible. When the sting is extracted, however, with the shaft in the wound, the motion of the quadrate plates is greatly increased.

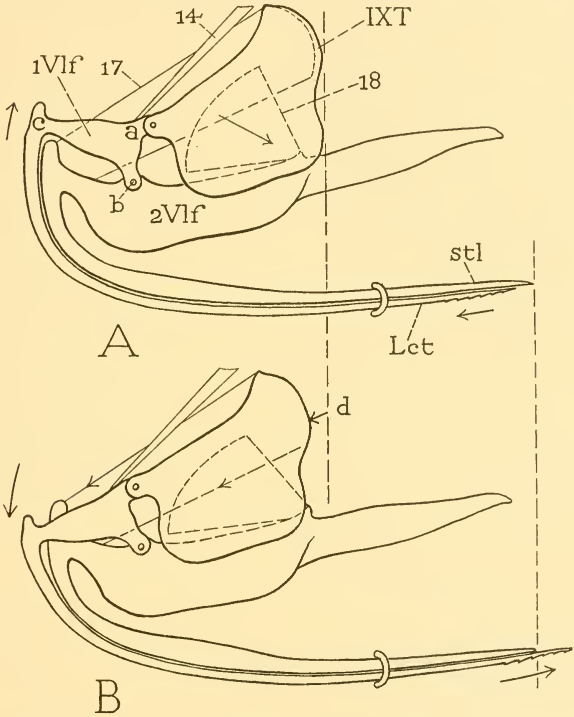

FIG. 48.—Diagrams of a model of the sting of the honey bee to show the mechanism of retraction and protraction of the lancets.

A, the lancet retracted by contraction of ventral muscle (*18*) of quadrate plate (*IXT*) attached posteriorly on oblong plate (*2Vlf*).

B, the lancet protracted by contraction of dorsal muscle (*17*) of quadrate plate attached anteriorly on oblong plate.

If the oblong plate of the model (fig. 48 A, *2Vlf*) is moved simultaneously with the quadrate plate, but in the opposite direction, the effect is to protract and retract the stylet in the same direction as the lancet, but with each stroke the lancet moves faster and farther than the stylet. Observations on the living bee, however, do not show that this movement ordinarily takes place, though it seems entirely possible.

When the tip of the sting of a living bee is examined under the microscope, and is not allowed to touch an object it can penetrate, only one lancet (the left, in the experience of the writer) is seen to move back and forth on the stylet and to be protracted beyond the latter. Hence, it seems probable that as soon as the tip of the shaft is inserted into the skin of the victim by the backward swing of the basal apparatus, the left lancet must be thrust out in advance of the stylet, where it holds its position in the wound by means of its barbs, and that then the right lancet is forced in beyond the left. Successive alternating thrusts of the lancets would then bury the entire sting shaft deeper and deeper in the flesh in the manner commonly observed. The force of the backward pull of the retractor muscles is now expended, not on the retraction of the lancets, but in stretching the protractor muscles, which, when thus restored to a condition of activity, give, each in turn, another thrust to the lancets. The motion of the lancets operates the valves attached to the dorsal margins of the lancets within the cavity of the bulb of the shaft, and the valves drive the poison liquid through the channel of the sting, from which it issues by way of the ventral cleft between the distal ends of the lancets.

ABBREVIATIONS USED ON THE FIGURES

a-a, dorso-pleural line.
Ac, antecosta.
AcGl, accessory gland.
AcGlD, duct of accessory gland.
AcGlO, opening of accessory gland.
aiv, anterior intervalvula.
Am, amnion.
An, anus.
Ap, apodeme.
Apd, appendage

b-b, pleuro-ventral line.
bcpx, bursa copulatrix.
BGl, "alkaline" gland of bee.
blb, bulbous basal part of united second valvulae.
Bs, basisternum.
bv, basivalvula.
bw, cut edge of body wall.

Cd, cardo.
Cdbl, cardioblast.
Ccr, cercus.
cf, caudal filament.
Cocl, coelomic sac.
Cx, coxa.
CxC, coxal cavity.
CxP, pleural coxal process.

D, dorsum.
d_2, dorsal muscles of mesothorax.
d_3, dorsal muscles of metathorax.
dil, lateral internal dorsal muscle.
dim, median internal dorsal muscle.
dls, dilator muscle of spiracle.

Ecd, ectoderm.
EMsd, somatopleure of mesoderm.
Epm, epimeron.
Eppt, epiproct, eleventh abdominal tergum.
Eps, episternum.
ET, egg tube of ovary.

Frc, furcula.
Fu, furca, endosternum.

GC, genital chamber (bursa copulatrix).
GCls, germ cells.
Gd, gonad.
gmcl, muscle of gonapophysis.
Gon, gonapophysis.
Gpr, gonopore, ostium oviductus.
Gpr′, primary median gonopore of female.
Grm, germarium of ovary.

Ht, heart.

I-XI, abdominal segments.
IMsd, splanchnopleure of mesoderm.
IS-XS, abdominal sterna.
IT-XIT, abdominal terga.
IXV, venter of ninth abdominal segment.

LB, limb basis.
Lct, lancet (first valvula).
ld, laterodorsal area.
le, external lateral muscle.
li, internal lateral muscle.
Lsp, lamina spiracularis of eighth tergum.

Mb, intersegmental membrane.
Mcls, muscles.
Msd, mesoderm.

NlR, neural ridge.

Od, oviduct.
Odc, definitive oviductus communis.
Odc′, primary rudiment of median oviduct.
Odl, oviductus lateralis.
Opr, oviporus.
os, occlusor muscle of spiracle.
Ovl, ovariole.
Ovp, shaft of ovipositor.

P, pleural, or podial, region of body.
Papt, paraproct.
Pcx, postcoxale.
Pdcl, ovariole pedicel.
piv, posterior intervalvula.
Ph, phragma.
pl, pleurite.
Plstn, pleurosternal plate.
PN, postnotum.
pnvl, pons valvularum.
Proc, proctodaeum.
PsnSc, poison sac.
pt, paratergite.
Ptgr, proctiger.

ra, ramus of valvula.
r1vl, ramus of first valvula.
r1vli, inner ramus of first valvula.
r1vlo, outer ramus of first valvula.
r2vl, ramus of second valvula.
Rect, rectum.

S, definitive sternum.
Scx, subcoxa.
smcl, muscles of stylus.
Sp, spiracle.
Spr, spermathecal pore.
Spt, spermatheca.
SptD, spermathecal duct.
St, stipes.
stl, stylet (slender distal part of united second valvulae).
Stn, primitive sternum.
Stng, sting.
Sty, stylus.

T, tergum.
td, dorsal transverse muscle.
TF, terminal filament of ovariole.
Tlpd, telopodite.
Tm, tympanum.
tv, ventral transverse muscle.

V, venter.
Vag, vagina.
VDph, ventral diaphragm.
ve, external ventral muscle.
vi, internal ventral muscle.
VIIIStn, sternum of eighth abdominal segment (not including the first valvifers).
VIIIV, venter of eighth abdominal segment.
vil, lateral internal ventral muscle.
vim, median internal ventral muscle.
Vl, valvula (*1Vl,* first valvula; *2Vl,* second valvula; *3Vl,* third valvula).
Vlf, valvifer (*1Vlf,* first valvifer; *2Vlf,* second valvifer).
VNC, ventral nerve cord.
Vs, vesicle.
Vst, vestibulum.
Vul, vulva, ostium vaginae.

W, wing.

Y, yolk.

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