THE ABDOMINAL MECHANISMS
OF A GRASSHOPPER

BY

R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine,
U. S. Department of Agriculture

THE ABDOMINAL MECHANISMS OF A GRASSHOPPER

By R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine, U. S. Department of Agriculture

CONTENTS

INTRODUCTION

This paper on the abdomen of Acridoidea is intended to follow sequentially an earlier paper in the same series entitled " The Thoracic Mechanism of a Grasshopper " (Smithsonian Misc. Coll., vol. 82, no. 2, 1929). Hence it will be observed that the numerical designation of the abdominal muscles continues from that of the thorax.

The primary object of the work here presented has been to arrive at an understanding of the mechanisms of copulation and oviposition in the Acrididae, which in this family present many peculiar features. Neither of these processes, the writer believes, has been fully understood or correctly described, though careful observations have been made on the processes of copulation and egg-laying among grasshoppers. With the closer studies on the behavior of insects now found necessary for economic purposes, it is becoming obvious that we must understand more fully the structure and mechanics of the anatomical mechanisms on which depends so much of the insect's activities. In addition to the functional phase of morphology, however, there is the no less important taxonomic aspect. Hence, in the following pages much attention is given to structures bearing on the relationships between the Acrididae, Tetrigidae, and Tridactylidae, and a brief comparative study of the anatomy of the external male genitalia is included, since these structures will undoubtedly be found to contain many characters of importance for the separation of species where other features are not sufficient for exact determinations.

The writer follows Blatchley (1920), Walker (1922), Brues and Melander (1932), and others in regarding the grouse locusts as constituting a family (Tetrigidae, or Acrydidae) distinct from that of the typical grasshoppers (Acrididae). Aside from superficial differences in such characters as the length of the pronotum, and in certain features of the tarsi, the grouse locusts are distinguished from the grasshoppers by the lack of the characteristic tympanal organs of the latter, and in the totally different nature of the external male genitalia, which in the grasshoppers have a unique and highly standardized type of structure that distinguishes the Acrididae from all other Orthoptera. The tetrigids, of course, in many ways, particularly in the general structure of the abdomen and in the structure and mechanism of the female ovipositor, show their relationship with the Acrididae, but this relationship is much more distant than is that of the several acridid subfamilies with one another. Some orthopterists, furthermore, would link the Tridactylidae with the Tetrigidae and Acrididae, but to the writer a close association of the tridactylids with the acridoid families seems doubtful, notwithstanding the close similarity of the ovipositor in these two groups.

I. GENERAL STRUCTURE OF THE ABDOMEN

The morphology of the adult insect abdomen is difficult to understand because of the complete suppression of the segmental appendages in the pregenital region, and the probable union of the appendage bases

with the primitive sterna in the definitive sternal plates. The lateral tergo-sternal muscles of the abdomen appear to have no counterparts in the thorax, unless it is to be assumed that they represent the leg muscles that have retained their ventral connections with the coxal elements of the definitive sterna, but a study of larval insects seems to indicate that the limb muscles have been lost with the suppression of the appendages. The abdomen of the imago is so completely adapted to its principal mechanical functions of respiration, copulation, and oviposition that the generalized structure in this region of the body is almost entirely obscured by secondary modifications. The acridid abdomen is a good subject for anatomical study, but it throws no light on the general morphology of the insect abdomen.

CHARACTERISTIC FEATURES OF THE ABDOMEN OF ACRIDOIDEA

The acridid abdomen consists of 11 distinct segments (fig. 1). The enlarged first segment is firmly attached to the thorax by its dorsal
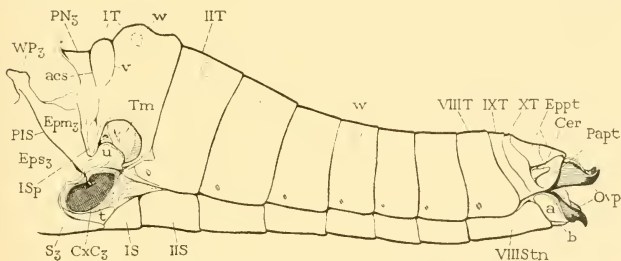
FIG. 1.—Abdomen and base of thorax of *Dissosteira carolina,* female.

and ventral plates (IT, IS), though these plates are widely separated from each other laterally by the hind coxal cavities (CxC_3). On the sides of the first tergum are situated the tympanal organs (Tm) characteristic of the Acrididae, and the first spiracles (ISp) are located in the anterior parts of the tympanal depressions. The following seven segmental annuli $(II\text{-}VIII)$ are simple secondary segments separated by ample conjunctivae that allow a considerable extension of the abdomen, as that of the female abdomen during oviposition. The tergal and sternal plates are united by inflected lateral membranes that permit the respiratory movements of vertical expansion and compression. The spiracles of these segments are located in the lower margins of the terga.

In the female the sternum of the eighth segment (fig. 1, $VIIIStn$) is the last of the series of ventral segmental plates. It is prolonged

beyond the tergum, and its posterior margin is reflected into the floor of the genital chamber beneath the base of the ovipositor. In the male (fig. 33 A) the abdomen terminates ventrally with the ninth sternum, which is much enlarged and subdivided into a proximal sternal plate (*IXS*) and a distal sternal lobe (*IXSL*). The terga of the ninth and tenth segments are narrow (figs. 1, 33 A) and are united with each other in both sexes. The tenth tergum of some species bears a pair of small median processes, known as the furculae, projecting backward from its posterior margin (figs. 38 A, B, 39, *f*). The ventral part of the ninth segment in the female is reduced to a narrow median space between the bases of the dorsal prongs of the ovipositor, and the venter of the tenth segment is a small membranous area above the base of the ovipositor. In the male the venter of the tenth segment is contained in the membranous dorsal wall of the genital chamber (fig. 24 A, *X.V*). The eleventh segment is the conical end piece of the body formed of a triangular dorsal plate, the epiproct (fig. 1, *Eppt*), and of two lateroventral plates, the paraprocts (*Papt*). Between the apices of these plates is the anus. The appendicular cerci (*Cer*) arise laterally on the base of the eleventh segment from membranous areas between the adjoining angles of the epiproct and paraprocts. The exposed part of the female ovipositor consists of four short, strongly sclerotized prongs (*Ovp*) projecting backward from the ventral parts of the eighth and ninth segments. The complex copulatory apparatus of the male (fig. 33 B) is ordinarily concealed within a genital chamber between the terminal lobes of the eleventh segment and the upturned lobe of the ninth sternum (fig. 24 A).

The abdomen of Tetrigidae is in general similar to that of the Acrididae, though it differs from the latter in several respects. The tergum of the first segment (fig. 2 C, *IT*) is solidly joined to the thorax, but the sternum (D, *IS*) has a flexible connection. Tympanal organs are absent. The first spiracles (C) are contained in the first tergum, but the other spiracles lie in membranous lateral areas of the dorsum beneath the lower edges of the terga, though the last two on each side (fig. 18 A) are contained in weakly developed laterotergal sclerites. Between the spiracles and the sterna of segments *II* to *VII* there is on each side a series of small laterosternal, or " pleural," sclerites (fig. 2 C, *lst*) best developed anteriorly, where there are two sclerites in segments *II* to *IV*. The terminal segments of the tetrigid abdomen, in both the female (fig. 18 A) and the male (fig. 27 A), are essentially the same as those of Acrididae, and the female ovipositor (fig. 18) has little to distinguish it from the acridid ovipositor. The phallic

organs of the male, however, are very simple in structure and in no
way resemble those of Acrididae (fig. 27 D).

The abdomen of Tridactylidae has certain features that are sug-
gestive of the tetrigid abdomen, but in many respects it is quite differ-
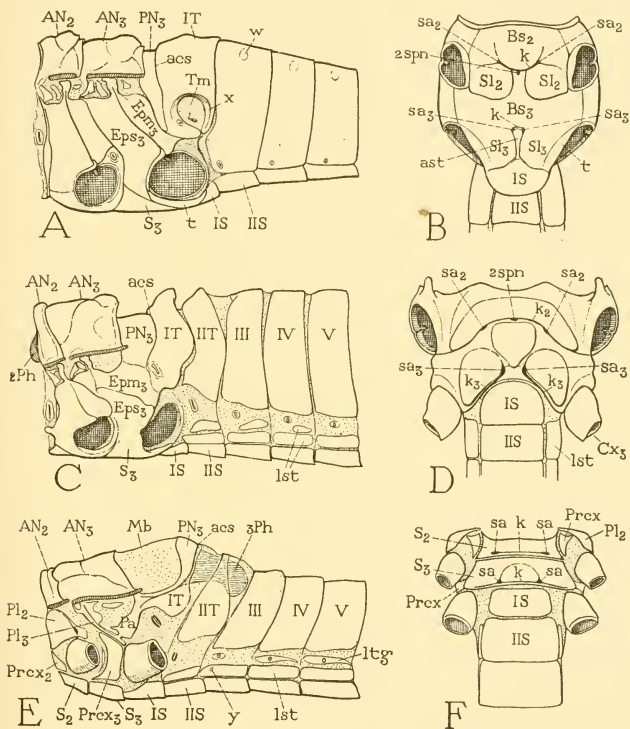
Fig. 2.—Relation of the abdomen to the thorax in Acrididae, Tetrigidae, and
Tridactylidae.

A, B, *Melanoplus mexicanus*. C, D, *Tettigidea lateralis*. E, F, *Rhipipteryx
biolleyi*.

ent from the abdomen of either the Tetrigidae or the Acrididae. The
base of the tridactylid abdomen (fig. 2 E, F) presents characters that are
peculiar to the family, and will be described later. The first seven
pairs of spiracles lie in the lateral membranous areas of the dorsum
beneath the edges of the terga, where some of them may be contained

in narrow laterotergal sclerites (E, *ltg*). The spiracles of the eighth segment lie in the lower parts of the tergum of this segment (fig. 19 A). The median sternal plates of segments *II* to *VI* or *VII* are flanked by narrow laterosternites (fig. 2 E, *lst*) and the sterna overlap the edges of the terga, the laterosternites being inflected. In *Tridactylus* and *Rhipipteryx* a small internal vesicle opens by an external pore (E, *y*) on the laterosternite of the third segment. According to Carpentier (personal communication) a similar anterior vesicle opens on the laterosternite of the second segment in *Rhipipteryx carbonaria*. The terminal segments of the tridactylid abdomen have many peculiar features, as will be shown in the description of the genital organs; but
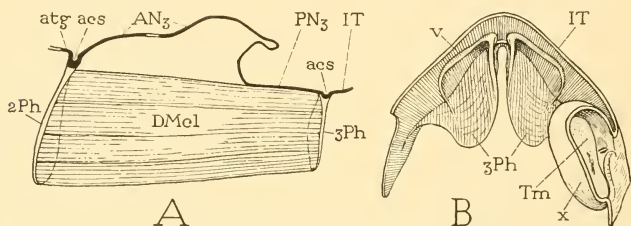
Fig. 3.—Relation of the phragmata to the segmental plates of the dorsum. *Dissosteira carolina.*

A, vertical section of dorsum of metathorax just to right of median plane, showing the antecostal sutures (*acs*) and phragmata (*2Ph, 3Ph*) marking the true intersegmental lines; the dorsum is occupied by a wing-bearing plate, the alinotum (*AN₃*), and a postalar postnotum (*PN₃*) equivalent to the acrotergite (*atg*) of the alinotum. B, posterior view of the first abdominal tergum, the lobes of the third phragma, and the right tympanal capsule.

the well-developed ovipositor of *Rhipipteryx* (fig. 19 A, *Ovp*) is surprisingly similar to the ovipositor of Tetrigidae and Acrididae. The male organs, on the other hand, have no resemblance whatever to those of Acrididae or to those of Tetrigidae.

The abdominal terga of the Acrididae, except the tergum of the first segment, are simple plates with no sutural divisions (fig. 1). The dorsal muscles arise on each tergum some distance behind the anterior margin (fig. 10 A), and the line of attachment here is marked, particularly in the male, by a short secondary tergal ridge (*tr*) on each side. True antecostae appear to be absent, since the muscles are inserted posteriorly on the weak anterior margins of the tergal plates. In the Tetrigidae, on the other hand, each tergum has a distinct marginal antecosta. Tergal apodemes are absent, except in the ninth segment, where, as in *Dissosteira* (fig. 14), there may be a pair of apodemal

lobes (*Ap*) projecting forward from the anterior margin of the tergum for muscle attachments.

The abdominal sterna of the Acrididae resemble the terga in that each is an undivided plate, but the sterna, as with pterygote insects generally, are presumably coxosternal plates in composition, though there are no styli on any of the abdominal segments. The first abdominal sternum (fig. 4, *IS*) is closely united with the metasternum of the thorax by an anterior extension (*ast*), which appears to be the acrosternite; otherwise it is a simple plate. The following sterna have each a pair of large apodemes on their anterior angles. The apodemes of the second and eighth sterna in the female (fig. 4), or of the second and ninth in the male (fig. 12), are simple anterior arms; but the intervening apodemes have lateral expansions that form distinct lateral apodemes in the more anterior segments of the female (fig. 4, *lAp*) and in all the segments of the male between the second segment and the ninth (fig. 12). The lateral apodemes give attachment to the dilator muscles of the abdomen (fig. 10 B, *ile*), which have their dorsal attachments ventrally on the lower edges of the terga. The intersegmental ventral muscles of the abdomen have their anterior attachments on the sterna some distance back of the anterior margins of the latter (figs. 8, 10 A), but they are attached posteriorly on the anterior margins of the sterna following. In the male the lines of origin of these muscles are strengthened in each segment by a well-developed transverse sternal ridge (fig. 12, *sr*); in the female the ridges are present only on the sterna of the more anterior segments (fig. 4). The musculature of the abdomen, and cuticular developments related to the muscles are in general weaker in the female than in the male.

In the Tetrigidae the median sternal plates of the abdomen appear to correspond with the sternal plates of Acrididae since they bear the sternal apodemes on their anterior angles. The small laterosternites (fig. 2 C, D, *lst*), therefore, are probably secondary developments in the membranes laterad of the sterna, and in a loose sense may be termed "pleurites," though there is nothing to suggest that they represent remnants of limb bases. According to Ford (1923) there are no muscles attached on the laterosternites of Tetrigidae, but there are groups of small lateral muscles attached dorsally in the membrane before and behind the spiracles and ventrally on the sterna. These muscles are evidently dorsosternal muscles, since the region of the spiracles is to be regarded as a part of the dorsum. The principal lateral muscles in Tetrigidae, as in Acrididae, are tergosternal muscles.

RELATION OF THE ABDOMEN TO THE THORAX

In both the Acrididae and the Tetrigidae the tergum of the first abdominal segment is firmly attached to the tergal and pleural sclerotization of the metathorax, and in Acrididae the first abdominal sternum is solidly joined to the metasternum. The movements of the abdomen as a whole take place between the first and second segments of the latter, and are produced by the longitudinal muscles of the first abdominal segment attached posteriorly on the second. In the female of *Dissosteira* there is one pair of very small oblique lateral muscles between the metathorax and the first abdominal segment (fig. 9, *140*).

The union of the first abdominal tergum with the metathorax in Acrididae and Tetrigidae is formed by the greatly expanded acrotergite of the first abdominal tergum, which becomes a large postnotum in the dorsum of the metathorax (fig. 2 A, C, PN_3). The postnotum is separated from the main part of the first abdominal tergum (*IT*) by a prominent transverse antecostal suture (*acs*), which extends across the back and downward on the sides. From this suture there depend internally the two lobes of the third phragma (fig. 3 A, B, *3Ph*). In *Dissosteira* the inner margin of each phragmatal lobe is braced posteriorly on a secondary ridge (B, *v*), which is marked externally by a short tergal suture on each side (fig. 1, *v*) behind the antecostal suture. The lobes of the third phragma give attachment to the posterior ends of the dorsal muscles of the metathorax (fig. 3 A), and thus attest that the antecostal suture (*acs*) through their bases is the true (primary) intersegmental line of the dorsum between the metathorax and the first abdominal segment.

Anteriorly the postnotum is continuous (fig. 3 A, PN_3) with the inflected scutellar margin of the alinotum of the metathorax (AN_3); its lateral extensions are united with the posterior (or dorsal) margins of the metathoracic epimera (figs. 1, 2 A, C, Epm_3). By these connections of the postnotum with the dorsal and pleural sclerotic parts of the metathorax, the lobes of the third phragma are securely braced against the pull of the dorsal muscles attached on them (fig. 3 A). The force of the muscles, therefore, is expended on the alinotum of the metathorax (AN_3), which responds by an upward curvature that depresses the wings on the pleural fulcra. In the usual intersegmental mechanism of secondary segmentation, in which the acrotergite is a mere flange on the anterior margin of the tergum following, and is separated by a conjunctival membrane from the preceding tergum, the contraction of the longitudinal muscles produces an approximation or overlapping of the consecutive segmental plates. The enlargement

of the acrotergite of the first abdominal tergum, accompanied by an obliteration of the conjunctiva behind the wing-bearing plate of the metathorax, is clearly, therefore, a device to suppress intertergal movement at this intersegmental junction.
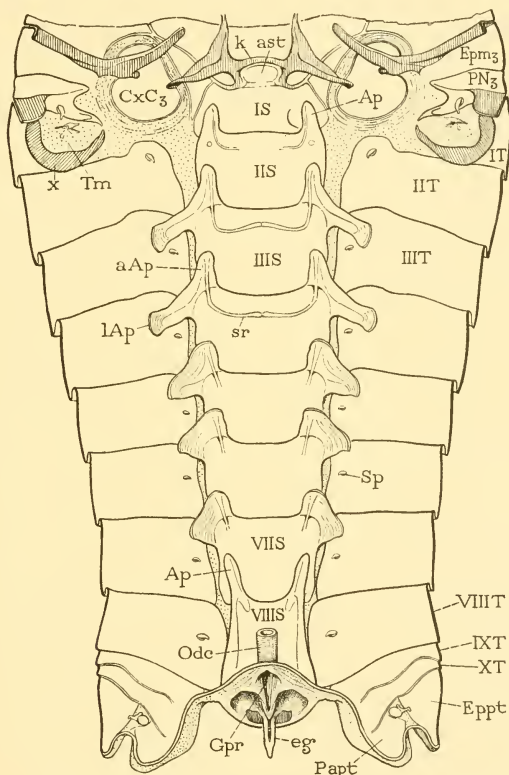
Fig. 4.—Dorsal view of the inner surface of the skeletal plates of the metathorax and abdomen of *Dissosteira carolina,* female; ovipositor removed exposing the floor of the genital chamber, the gonopore (*Gpr*), and egg guide (*eg*).

The ventral union of the abdomen with the thorax in Acrididae is even more complete than is the dorsal union. The sternum of the first abdominal segment (fig. 2 B, *IS*) forms virtually a part of the pterothoracic plastron. Its acrosternite is either a broad lobe (fig. 4, *ast*), or a narrow tongue (fig. 2 B, *ast*), but in either case it is solidly fused

with the metasternum in the notch between the sternellar lobes (Sl_3). There are no ventral muscles that extend from the thorax into the abdomen in Acrididae, and the first ventral muscles of the abdomen take their origin on a transverse ridge of the first abdominal sternum at the base of the acrosternite (fig. 8, $I43$). This ridge, therefore, is evidently the antecosta of the first sternum, and corresponds with the phragma of the first tergum, that is, it marks the true intersegmental line of the venter between the thorax and the abdomen. In the Tetrigidae the sternum of the first abdominal segment (fig. 2 D, IS) has a rounded anterior edge inserted into a wide emargination of the metasternum, but it is attached to the latter by a narrow, flexible membranous suture, and, therefore, does not give the abdomen a firm ventral connection with the thorax as in Acrididae. There is no evidence, therefore, that the small median area between the bases of the metasternal apophyses (sa_3) in the Tetrigidae represents the acrosternite of the first abdominal sternum; it appears rather to be the sternellum of the metathorax, which is suppressed medially in the Acrididae.

When we turn to the Tridactylidae by way of comparison it is to be seen that there is little similarity, either in the thoracic sclerotization or in the basal structure of the abdomen, between this family and the Acrididae or Tetrigidae. The pleural sclerites of the pterothorax in the tridactylids are reduced and widely separated by membranous areas (fig. 2 E). The sterna are simple segmental plates (F, S_2, S_3) entirely separated from each other. In the mesosternum the bases of the apophyses (sa) are far apart at opposite ends of a transverse sternacostal suture (k). The metathoracic apophyses are somewhat more approximated, and from each a suture extends forward in the basisternal region. These sutures in *Rhipipteryx* (fig. 2 F) are continuous anteriorly in a transverse arc, but in *Tridactylus* they remain separate, as shown by Ander (1934). The sternellum of each pterothoracic sternum is a narrow margined area behind the sternacostal suture (k), and is not produced into lateral lobes as in Acrididae. The first abdominal sternum (IS) is entirely distinct from the metasternum.

In the relations of the base of the abdomen to the thorax the tridactylids present some very unusual features. The tergum of the first abdominal segment is much reduced and does not contain the first spiracles (fig. 2 E, IT); the posterior dorsal and lateral parts of the segment are membranous. The acrotergite (PN_3) is a strongly developed though narrow sclerite on the anterior margin of the first abdominal tergum, but it is widely separated dorsally from the wing-bearing plate of the metathorax (AN_3) by a large membranous area

(Mb). Laterally, however, it is connected on each side with the posterior angle of the metanotum (AN_3), and by a strong postalar arm (Pa) with the lower end of the narrow metapleuron (Pl_3). The third phragma ($3Ph$) consists of a pair of long lobes projecting posteriorly from the antecostal suture of the first abdominal tergum through the first and second abdominal segments. The extraordinarily long dorsal muscles of the metathorax extending back to the third phragmatal lobes are plainly visible through the membrane separating the postnotum from the metathoracic alinotum.

THE ABDOMINAL SPIRACLES

The spiracles of insects, the writer assumes, belong to the dorsum. In a generalized arthropod the limb bases lie between the dorsum and the venter, and there is no evidence that the insect spiracles are developed on the bases of the limbs. The spiracles may be included in the tergal sclerotization of the dorsum, or they may lie free in a laterodorsal membrane, or again, they may be situated in small laterodorsal sclerites. The abdominal spiracles of Acrididae are all contained in the lower parts of the tergal plates (figs. 1, 2 A) ; in the Tetrigidae all but the first lie in the laterodorsal membranes below the terga (fig. 2 C) ; in the Tridactylidae the first two spiracles on each side are in the laterodorsal membranes of their segments (E), the others are contained in small laterotergites (ltg), except the last, which lies in the lateral part of the eighth tergum (fig. 19 A).

The abdominal spiracles of Acrididae are of the type of structure in which the closing apparatus is at the inner end of the atrium where the latter is joined by the spiracular trachea. They thus differ, as abdominal spiracles usually do, from the thoracic spiracles, which are closed by an approximation of the outer lips of the atrium.

The large first abdominal spiracles of *Dissosteira,* as already observed, lie in the anterior walls of the tympanal capsules (figs. 1, 6 A, 9 A, ISp). Each of these spiracles presents externally an oval aperture, the long axis of which is somewhat oblique. The walls of the atrium are direct inflections of the body wall. The dorsal atrial wall is immovable and is firmly supported by a dense sclerotization of the body wall above it ; the ventral atrial wall, on the other hand, is a freely movable plate, and a small area of the body wall below it is membranous. Viewed internally (fig. 5 A), it is seen that the movable ventral wall of the atrium (c) is produced posteriorly in a handle-like process, or manubrium (g), on which the spiracular muscles are inserted. The short occlusor muscle (148) takes its origin on the

margin of the tympanal capsule just above the spiracle; the long slender
dilator muscle (*147*), together with the tensor of the tympanum (*146*),
arises ventrally on an inflection of the membranous body wall (fig.
9 A) posterior and mesad of the hind coxa behind the small triangular
lateral sclerite of the metasternum (fig. 1, *t*). The occlusor muscle
closes the inner aperture of the atrium into the spiracular trachea by
bringing the inner margin of the movable plate of the ventral atrial
wall against the inner margin of the immovable dorsal wall. The
antagonistic dilator muscle counteracts against the occlusor and opens
the tracheal aperture.

The other abdominal spiracles have essentially the same structure
as the first spiracle, though they are successively smaller to the eighth,
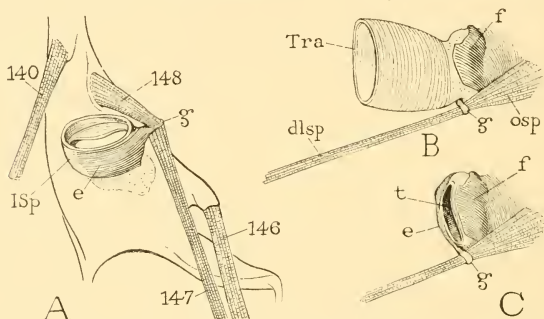
Fig. 5.—Structure of the abdominal spiracles. *Dissosteira carolina.*

A, right spiracle of first segment in rim of tympanum, inner view, showing
occlusor (*148*) and dilator (*147*) muscles. B, right spiracle of eighth segment
with end of trachea, inner view, showing occlusa (*osp*) and dilator (*dlsp*)
muscles. C, same, trachea removed, showing tracheal entrance (*t*) from atrium
and movable anterior valve (*e*) with manubrium (*g*) on which muscles are
attached.

which again is of larger size (fig. 1); also the obliquity of the aperture
is more pronounced in these spiracles (fig. 5 B, C), so that the movable
wall of the atrium (*e*) becomes anterior, with the manubrium (*g*)
directed downward, and the immovable wall (*f*) posterior. The short,
fan-shaped occlusor muscle of each spiracle (*osp*) arises on the tergal
wall behind the spiracle, and the long dilator muscle (*dlsp*) takes its
origin ventrally on the anterior part of the lateral margin of the cor-
responding segmental sternum.

THE TYMPANAL ORGANS

On the lower part of each lateral area of the first abdominal tergum
just behind the spiracle is located the large tympanal organ of Acridi-
dae (fig. 1, *Tm*). In *Melanoplus* the tympanum is contained in a

simple oval depression of the tergum (fig. 2 A), the margin of which
is interrupted ventrally, and the tympanum is thus continuous through
a narrow cleft in its frame with the membranous body wall below the
tergum. The same is true but less evident in *Dissosteira* (fig. 1). The
development of the organ in the nymph shows clearly that the tym-
panum is derived from a part of the laterodorsal membrane of the first
abdominal segment enclosed in a notch in the lower margin of the
tergum. In *Dissosteira* the tympanal depression is much deeper than
in *Melanoplus* and forms a large capsule-like cavity expanded within
the outer opening (fig. 6 A, *x*). The rear wall of the capsule is deeper
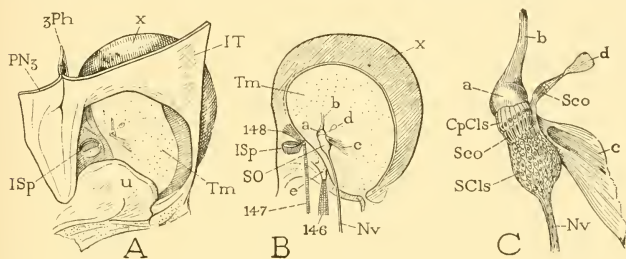
Fig. 6.—Tympanal organ of the first abdominal segment. *Dissosteira carolina*.

A, external view of left tympanal capsule and surrounding parts of body wall.
B, inner view of right tympanum and associated structures. C, tympanal sense
organ and its supports, inner view.

a, sclerotic tubercle of tympanum with arms (*b, c*) supporting the sense
organ; *CpCls*, cap cells of sense organ; *d*, pyriform sclerite of tympanum; *e*,
muscle process of tympanal capsule; *ISp*, first abdominal spiracle; *IT*, tergum
of first abdominal segment; *Nv*, nerve of sense organ; *3Ph*, lateral part of third
phragma; *PN₃*, lateral part of postnotum of metathorax; *SCls*, sense cells;
Sco, sense rods, scolopes; *SO*, scolopophorous sense organ; *Tm*, tympanum;
u, subtympanal lobe of metathorax; *x*, tympanal capsule; *146*, tensor muscle of
tympanum; *147*, dilator muscle of spiracle; *148*, occlusor muscle of spiracle.

than the front wall, and the plane of the tympanum is, therefore,
oblique, its outer surface being directed outward and posteriorly. The
first abdominal spiracle (*ISp*) is situated in the anterior wall of the
tympanal capsule, and a lobe (*u*) at the lower end of the metathoracic
epimeron (fig. 1) forms the lower lip of the outer opening of the cap-
sule. In the Acridinae the tympanal capsule is much narrower than
in Oedipodinae and Cyrtacanthacrinae.

The tympanum is a thin membrane stretched tightly between the
inner margins of the tympanal depression or capsule (fig. 6 B). A
small apodemal process (*e*) projects ventrally from the lower margin
of the latter and gives insertion to a muscle (*146*) arising ventrally
from a point in the membrane behind the base of the metacoxa laterad

of the first abdominal sternum (fig. 9 A). The dilator muscle of the spiracle (*147*) takes its origin at the same point. The muscle of the tympanal frame appears to be a tensor of the tympanum. In the anterior part of the tympanum are two small cuticular thickenings that support the sense organ on the inner surface (fig. 6 B, *SO*). The principal support is a wide-angled V-shaped sclerite with a narrow dorsal arm (B, C, *b*) and a broader ventral arm (*c*) diverging from an apical knob (*a*). The last is a pitlike invagination of the external surface of the tympanum, and the major part of the sense organ (B, C) is attached directly to its ventral surface. The other support is a much smaller pyriform sclerite (*d*) lying posterior to the angle of the V-shaped sclerite, to which is attached a small fusiform branch of the main sense organ (C).

The tympanal sense organ (fig. 6 B, *SO*) is a small oval body composed mostly of a mass of sense cells (C, *SCls*), but in its upper part is a stratum of elongate parallel cells containing sense rods, or scolopes (*Sco*), beyond which is a layer of large cap cells (*CpCls*) by which the organ is attached to the knob (*a*) at the angle of the V-shaped supporting sclerite. A slender posterior branch of the main organ contains a second smaller set of scolopes, and is attached by a fascicle of slender cap cells to the pyriform sclerite (*d*). From the ventral end of the organ the sensory nerve (*Nv*) proceeds to the large composite ganglion of the ventral nerve cord lying in the metathorax.

Between the tympana of the opposite sides of the body are two large air sacs given off from the lateral tracheal trunks in the base of the abdomen. The sacs completely occupy the cavity of the first abdominal segment above the alimentary canal, and their outer walls are pressed close against the tympana. The two sacs form such a large air-filled space in the base of the abdomen of *Dissosteira* that it is possible to look clear through the body of the insect, *i. e.*, into one " ear " and out of the other.

The tympanal organ of the Acrididae is usually regarded as a sound receptor, though little or no evidence of hearing on the part of the grasshoppers has yet been produced. Few species are capable of making sounds, and an auditory " sense " would not seem to be one of great importance to a grasshopper, but the elaborate mechanical and sensory structure of the tympanal organs suggest that the latter must subserve some function of importance in the life of the insect. Perhaps we are too prone to conceive of insect " senses " as sensory perception of stimuli. An insect merely reacts through its motor mechanism to certain stimuli. The reaction to stimuli from a tympanal receptor organ, therefore, may be something quite different from a general sensitivity to sound in the audible sense.

THE CERCI

The cerci of Acrididae vary in form and size from simple peglike organs (fig. 33 A, *Cer*) to broader lobes of irregular shape (fig. 35 A), sometimes provided with accessory processes (fig. 36). The cerci of *Dissosteira* are of the simple type; they are longer in the male (fig. 7 B) than in the female (A), but they have the same structure in both sexes. The appendages arise from membranous areas behind the posterior margin of the tenth abdominal tergum between the bases of the epiproct and the paraprocts (B, *Cer*). The base of each cercus has a large irregular lobe (*b*) extending mesally beneath the
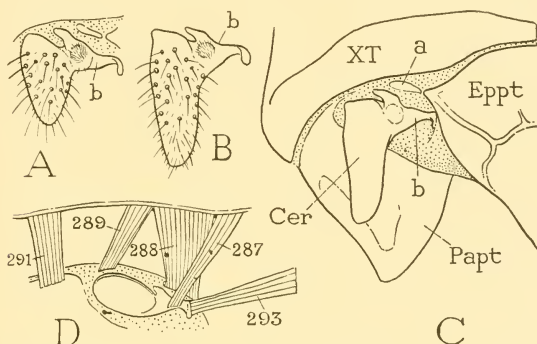
FIG. 7.—The cercus and its associated musculature. *Dissosteira carolina.*

A, left cercus of female, dorsal view. B, same of male. C, left half of terminal part of male abdomen, dorsal view. D, inner view of base of right cercus and its muscles.

edge of the epiproct, but it is not articulated to the surrounding scle-rites. The shaft of the organ is clothed with long and short setae, the short setae being more numerous on the apical part. Many of the larger hairs, especially on the proximal half of the cercus, arise from large, conspicuous, rosette-like alveoli with dark scalloped margins. Each cercus is penetrated by a large nerve, and its setae apparently are tactile organs.

Four muscles are intimately associated with each cercus, and are clearly concerned with its movements, though only two of them are inserted directly on the base of the cercus (fig. 7 D). The cerci of the male are erected during copulation and grasp the base of the sub-genital plate of the female. The elevation of each appendage is pro-duced by the two muscles, a broad median muscle (*288*) and a smaller

2

lateral muscle (*289*), both arising on the anterior margin of the tenth tergum. The median muscle is inserted on a small sclerite in the membrane behind the tenth tergum before the mesal lobe of the base of the cercus (C, *a*) ; the lateral muscle is inserted in the same membrane very close to the outer angle of the base of the cercus. A third muscle (D, *287*) arises anteriorly on the tenth tergum just mesad of *288*, and is inserted on the posterior margin of the basal lobe of the cercus. This muscle is evidently a depressor of the cercus. The fourth cercal muscle (D, *293*) is an adductor. It arises mesally on the anterior part of the epiproct (fig. 14) and is inserted on the extremity of the basal lobe of the cercus. Because of the oblique plane of the cercal base this muscle produces an adduction of the appendage. It is interesting to note that the cerci, which appear to be appendages of the eleventh segment, have only one pair of muscles (*293*) taking their origins in this segment, and that they have no muscular connections with the paraprocts.

II. THE ABDOMINAL MUSCULATURE

The body muscles are well developed in the abdomen of the grasshopper, particularly in the male, and individual muscles are easily identified. The several groups of muscles in the pregenital segments conform with the classification of the abdominal muscles into *dorsal muscles, ventral muscles, lateral muscles, transverse muscles,* and *spiracular muscles* as given by the writer in an earlier paper (Abdomen, Part I, Smithsonian Misc. Coll., vol. 85, no. 6, 1931). The plan of musculature in the pregenital segments, however, is lost in the genital and postgenital segments, and the muscles of these segments must be studied separately. The series of numerals designating the abdominal muscles follows that of the thorax of *Dissosteira* (Smithsonian Misc. Coll., vol. 82, no. 2, 1929). The transverse muscles are omitted from the descriptions of the segmental musculature and are treated as a separate topic.

MUSCLES OF THE FIRST SEGMENT

The musculature of the first abdominal segment is simpler than that of the following segments because of the elimination of some of the dorsal muscles and most of the lateral muscles.

140. Lateral oblique intersegmental muscle (figs. 5 A, 9 A).—A very slender muscle, observed only in the female, attached ventrally on the apex of the lateral arm of the metasternal apophysis, extending dorsally and posteriorly, mesad of the leg muscles, to the anterior

margin of the tympanal capsule of the first abdominal segment, to which it is attached dorsal to the spiracle. This is the only thoracico-abdominal muscle in the grasshopper.

141. Longitudinal dorsal muscles (fig. 8).—A broad sheet of muscles above the tympanal capsule, arising anteriorly on the first tergum somewhat behind the base of the phragma, inserted posteriorly on the anterior margin of the second tergum.

142a, 142b. Lateral oblique dorsal muscles (fig. 9 A).—Two small muscles arising laterally on the first tergum external to the longitudinals, extending ventrally and posteriorly, close to the tympanal capsule,
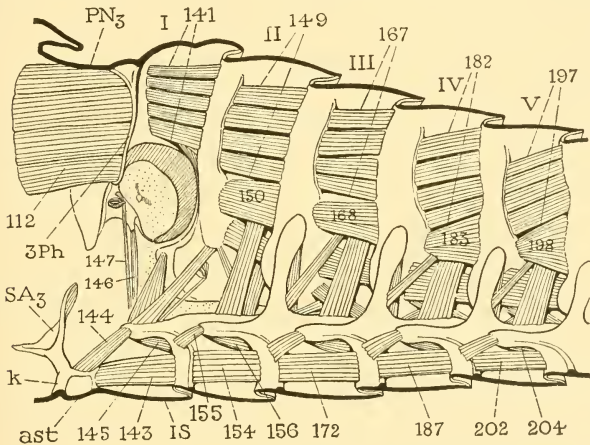
Fig. 8.—Muscles of the right side of the first five abdominal segments of *Dissosteira carolina*, male, together with the dorsal muscles (*112*) of the meta-thorax. (See fig. 10 A for identification of muscles.)

to their insertions behind the latter on the anterior margin of the second tergum.

143. Median internal ventral muscle (fig. 8).—A wide band of intersternal fibers over the lateral half of the sternal surface, arising anteriorly on the antecosta of the first sternum, inserted posteriorly on the anterior margin of the second sternum.

144. Lateral internal ventral muscle (fig. 8).—A cylindrical muscle arising laterally on the antecosta of the first sternum, inserted posteriorly on the anterior end of the apodeme of the second sternum.

145. External ventral muscle (figs. 8, 9).—This muscle is a sternal protractor. It takes its origin laterally on the posterior part of the

first sternum (fig. 9 B), and extends anteriorly and dorsally to its insertion on the under surface of the anterior apodeme of the second sternum. Its contraction separates the two sterna.

146. Tensor of the tympanum (figs. 8, 9 A).—This muscle is the only representative of the lateral muscles in the first abdominal segment of *Dissosteira*. It is a slender muscle arising laterad of the first sternum in the membrane behind the base of the hind coxal cavity, and extends dorsally to its insertion on the ventral process of the tympanal capsule. Its contraction evidently serves to stretch the tympanum.

147. Dilator muscle of the spiracle (figs. 5 A, 8, 9 A).—A very slender muscle arising with *146* in the membrane laterad of the first abdominal sternum, extending dorsally to its insertion on the manubrium of the ventral atrial plate of the first spiracle.

148. Occlusor muscle of the spiracle (figs. 5 A, 9 A).—A very short muscle arising on the anterior part of the tympanal capsule above the spiracle, inserted on the manubrium of the ventral atrial plate opposite the dilator.

MUSCLES OF THE SECOND SEGMENT

The musculature of the second abdominal segment conforms closely with that of the following segments except in the arrangement of the lateral muscles.

149. Median internal dorsal muscles (fig. 8).—A flat band of four more or less distinct groups of longitudinal fibers against the upper part of the tergum within the pericardial cavity. Origins anteriorly on the submarginal ridge of the second tergum, insertions posteriorly on the anterior margin of the third tergum.

150. Lateral internal dorsal muscle (figs. 8, 9 A).—A broad extrapericardial muscle on the lateral part of the tergum above the upper ends of the posterior lateral muscles, inserted in line with the intrapericardial dorsals on the anterior margin of the third tergum.

151. Paradorsal muscle (fig. 9).—This muscle lies against the side of the tergum below the extrapericardial dorsal muscle, external to the internal lateral muscle (*150*). It is inserted posteriorly on the anterior margin of the third tergum.

152, 153. External dorsal muscles.—Two small oblique or transverse muscles lying external to the internal dorsals in the posterior fold of the segment, where they arise on the posterior part of the second tergum. One extends dorsally, the other (fig. 9 B, *153*) ventrally to their insertions on the anterior margin of the third tergum.

These muscles in the second segment are similar to those of the third segment (fig. 10 A, *170, 171*). The external dorsals evidently produce a torsion of the adjoining tergal plates on each other.

154, 155, 156. Ventral muscles (fig. 8).—The ventral muscles of the second segment are the same as those of the first segment and of the segments following the second. They comprise median (*154*) and lateral (*155*) internal ventrals, which are sternal retractors, and an external muscle (*156*) on each side, which is a sternal protractor.

157-164. Lateral muscles (fig. 9).—The lateral muscles of the second segment differ in many respects from those of the segments following. They comprise an outer and an inner series of tergosternal
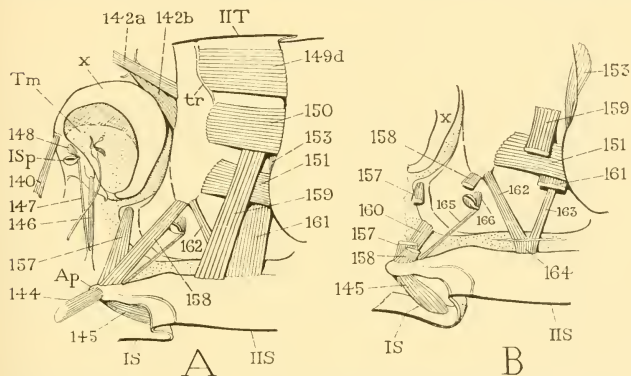
Fig. 9.—Lateral muscles of the first and second abdominal segments of *Dissosteira carolina*, right side, inner view, female.

A, all muscles in place. B, external lateral muscles of second segment (*160, 162, 163, 164*) exposed by cutting and partial removal of overlying muscles.

muscles, a pair of tergopleural muscles, and a sternopleural muscle. The inner series of tergosternals includes three muscles. The first (fig. 9 A, *157*) arises on the anterior lobe of the tergum and is inserted on the anterior apodeme (*Ap*) of the sternum; the second (*158*) arises on the tergum above the spiracle and has the same insertion as *157*. The third (*159*) is a much larger muscle arising on the tergum beneath the edge of the lateral dorsal muscle (*150*) and inserting on the lateral margin of the sternum. The outer series of tergosternals includes a short muscle (fig. 9 B, *160*) from the anterior ventral angle of the tergum to the anterior end of the sternal apodeme, and a broad posterior muscle (A, *161*) arising external to the paradorsal muscle (*151*) and inserted on the edge of the sternum behind

159. The two tergopleural muscles (B, *162, 163*) arise anteriorly and posteriorly on the lower part of the tergum external to *159* and *161*, and converge upon a narrow linear sclerite in the membrane between the tergum and the sternum. In all the other segments the external lateral muscles are attached directly on the sternum. The sternopleural muscle of the second segment is a group of very short fibers (B, *164*) connecting the pleural sclerite with the sternum.

165, 166. Muscles of the spiracle (fig. 9 B).—The dilator of the spiracle (*165*) is a long slender muscle arising on the apodeme of the sternum, the occlusor (*166*) a short muscle arising on the tergum; both are inserted on the manubrium of the movable valve of the spiracular atrium.

MUSCLES OF THE THIRD SEGMENT

The musculature of the third segment presents the typical abdominal musculature of the grasshopper, since its pattern is repeated in segments *III* to *VII* in both sexes, and its dorsal and ventral muscles are duplicated in the second segment.

167. Median internal dorsal muscles (fig. 10 A).—These muscles of the third segment, as those of the second, consist of four flat groups of fibers (*a, b, c, d*) lying within the pericardial chamber, extending from the anterior tergal ridge (*tr*) to the anterior edge of the following tergum. In the succeeding segments they become more oblique (figs. 8, 12, *182, 197, 227*) with their posterior ends dorsal to their anterior ends.

168. Lateral internal dorsal muscle (fig. 10 A).—The lateral dorsal muscle is separated from the median dorsals by the attachments of the transverse muscles of the dorsal diaphragm on the tergum (*td*), and is, therefore, extrapericardial. In the following segments this muscle becomes conspicuously fan-shaped (figs. 8, 12, *183, 198, 228, 243*).

169. Paradorsal muscle (fig. 10 A).—The paradorsal muscle is distinguished from the other lateral dorsal muscle (*167, 168*) by the fact that it lies external to the internal lateral muscles (*175, 176*). It has the same relations in some other insects, though it is a muscle not generally present. In *Dissosteira* it is repeated in the segments *II* to *VII* of both sexes, and in segment *VIII* of the male (fig. 12, *244*). The paradorsal muscle has been termed a " pleural " muscle, but it lies well within the area of the dorsum. Since it occurs in some larval insects lacking tergal plates, the writer here discards the former name of " paratergal " muscle. (Snodgrass, 1931.)

170, 171. External dorsal muscles (fig. 10 A).—External dorsal muscles occur in segments *II* to *VII* of both sexes, and also in segment *VIII* of the male. They take their origins on the posterior parts of the terga within the intersegmental folds, and are inserted on the overlapped anterior margin of the tergum following in each case. The median external dorsal of segment *III* (figs. 10 A, 11 B, *170*) arises

Fig. 10.—Muscles of the third abdominal segment of *Dissosteira carolina*.

A, muscles of the right side, inner view. *167*, median internal dorsals; *168*, lateral internal dorsal; *169*, paradorsal muscle; *170*, median external dorsal; *171*, lateral external dorsal; *172*, median internal ventral; *173*, lateral internal ventral; *174*, external ventral; *175, 176*, internal laterals; *177, 178, 179*, external laterals; *td*, attachment of dorsal transverse (diaphragm) muscles.

B, position of the muscles in cross-section of third segment, diagrammatic. *dil*, lateral internal dorsals; *dim*, median internal dorsals; *DS*, dorsal sinus; *DV*, dorsal blood vessel; *lAp*, lateral apodeme of sternum; *lle*, first external lateral muscle; *li*, internal lateral muscle; *p*, paradorsal muscle; *PvS*, perivisceral sinus; *td*, dorsal transverse muscles (of dorsal diaphragm); *tv*, ventral transverse muscles (of ventral diaphragm); *vil*, lateral internal ventral muscle; *vim*, median internal ventral muscle; *VNC*, ventral nerve cord; *VS*, ventral sinus.

dorsal to the lateral muscle (*171*); the first proceeds dorsally to its insertion, the second ventrally. In the posterior segments the corresponding muscles become much longer; the base of the median muscle has migrated ventrally, that of the lateral muscle dorsally, until the two muscles cross each other obliquely on the side of the tergum. The relations of the two muscles to each other and to the successive terga on which they are attached is best seen when the terga are pulled apart (fig. 11 C). The external dorsals in Acrididae, as already noted,

are evidently torsion muscles, their transverse positions enabling them to give a movement of partial rotation to the terga on each other.

In the generalized condition the external dorsal muscles are longitudinal in position and lie external to the internal dorsals, but they are commonly shorter than the latter; and have a tendency to become restricted to the posterior part of the segment. In many of the higher insects they become completely reversed in position, since they take their origins on the posterior part of the tergum and extend forward in the intersegmental fold to their insertions on the invaginated anterior margin of the following tergum. They thus become tergal protractors. The position of the external dorsals of the grasshopper is seen to be intermediate between the more primitive condition and that of complete reversal. The external ventral muscles, on the other hand, are reversed and hence function as sternal protractors.

172, 173, 174. The ventral muscles (fig. 10 A).—The ventral musculature of segment *III* is typical of that of all the pregenital segments (figs. 8, 12). The median internal ventrals (fig. 10 A, *172*) are the principal sternal retractors; the short lateral internal ventral on each side (*173*) arises at the base of the anterior apodeme (*aAp*) just before the angle of the sternal ridge (*sr*), and is inserted on the anterior end of the corresponding apodeme of the following sternum. The lateral external ventral on each side (*174*) is a sternal protractor, being completely reversed in position, with its origin on the posterior part of the sternum and its insertion anterior on the under face of the anterior apodeme of the following sternum.

The lateral musculature is alike in segments *III* to *VII,* there being in each of these segments representatives of the following five muscles of segment *III,* two of which are internal laterals, and three external laterals.

175. First internal lateral muscle (fig. 10 A).—A slender muscle arising dorsally beneath the edge of the lateral dorsal (*168*), extending ventrally and anteriorly to its insertion on the base of the lateral apodeme of the sternum.

176. Second internal lateral muscle (fig. 10 A).—A broad muscle arising on the side of the tergum just behind *175* and also beneath the edge of the lateral dorsal (*168*), extending ventrally to its insertion on the lateral margin of the sternum. The internal laterals are the principal expiratory muscles, since their contraction lifts the sternum and contracts the abdomen in a vertical direction.

177. First external lateral muscle (fig. 10 A).—This muscle arises ventrally on the anterior part of the ventral margin of the tergum,

and goes dorsally to its insertion on the outer face of the lateral apodeme of the sternum (fig. 10 B, *1le*). It is thus a dilator of the abdomen and an inspiratory muscle in respiration, since its contraction separates the sternum from the tergum (fig. 11 F, G).

178, 179. Second and third external lateral muscles (fig. 10 A).—These two muscles arise on the lateral part of the tergum below the
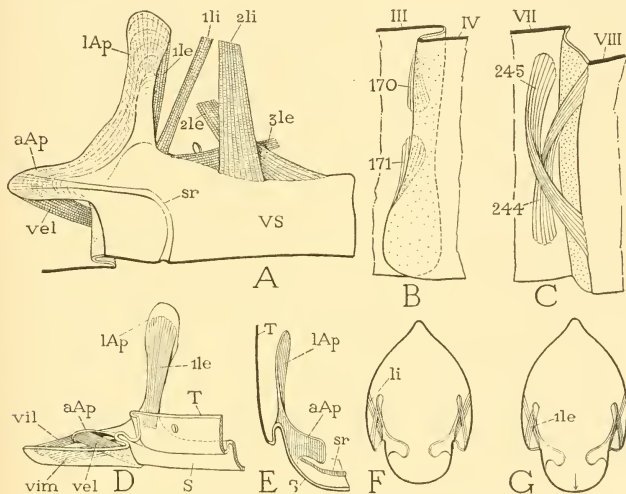

FIG. 11.—Abdominal mechanisms of Acrididae.

A, mechanism of tergosternal movements: tergum and sternum approximated by internal lateral muscles (*1li, 2li*), separated by first external lateral (*1le*), moved lengthwise on each other by oblique second and third external laterals (*2le, 3le*).

B, C, mechanism of torsion, or partial rotary movements of segments, by the transverse external dorsal muscles, best developed in posterior segments (C).

D, mechanism of tergosternal and intersternal movements: dorsoventral dilation produced by first external lateral muscle (*1le*); lengthwise sternal contraction by internal ventrals (*vim, vil*); protraction by external ventral (*vel*).

E, the sternal apodemes, right side, anterior view.

F, G, mechanism of respiration: expiratory movement (F) produced by internal lateral muscles (*li*, see A), inspiratory movement (G) by first external lateral (*1le*).

paradorsal muscle (*169*), and cross each other obliquely, the first going anteriorly, the second posteriorly, to their insertions on the opposite ends of the lateral margin of the sternum (fig. 11 A, *2le, 3le*). The muscles of this pair evidently serve to give forward and backward movements to the tergum and sternum on each other.

180, 181. Muscles of the spiracles.—The spiracular muscles are alike in segments *II* to *VIII,* and the description of those of the second spiracles (*165, 166*) will serve for each of the following spiracles.

MUSCLES OF THE EIGHTH SEGMENT

The muscles of the eighth segment are quite different in the male and the female. The musculature of this segment in the male (fig. 12) conforms with that of the preceding segments except for the reduction of the internal dorsals to a single broad band of fibers on each side (*242*), and in the absence of the first internal lateral. In the female most of the usual muscles are retained in modified form, but there are several muscles pertaining to the ovipositor and the oviducts that have no counterparts in the male. The muscles of the eighth segment of the female are as follows:

242, 243. Internal dorsal muscles (fig. 14).—A transverse series of six longitudinal groups of fibers on each side of the eighth tergum (*VIIIT*), inserted posteriorly on the apodeme and anterior margin of the ninth tergum (*IXT*). The lateral muscle on each side (*243*) is much larger than the others.

244. Paradorsal muscle.—Absent in the eighth segment of the female.

245. Median external dorsal muscle (fig. 14).—A broad muscle arising on the posterior margin of the eighth tergum, the fibers converging anteriorly and mesally to their insertions on the anterior apodeme (*Ap*) of the ninth tergum.

246. Lateral external dorsal muscle.—Absent in the female.

247. Median internal ventral muscle.—A slender muscle arising anterolaterally on the eighth sternum (fig. 13), inserted posteriorly on the median apodemal process of the anterior intervalvula of the ovipositor (fig. 17 D).

248. Lateral ventral muscle.—This muscle arises at the base of the apodeme of the eighth sternum (fig. 13) as in the preceding segments; but it is attached posteriorly in *Dissosteira* on the anterior basal sclerite of the first valvula of the ovipositor (fig. 17 A, B, E), and in *Melanoplus* (fig. 20 C) on the lateral pocket of the genital chamber.

249. External ventral muscle.—Absent in the female, unless represented by the depressor of the first valvula (fig. 17 A, B, *272*).

250. Internal lateral muscle (figs. 13, 14).—A very large triangular muscle arising laterally on the eighth tergum, its fibers spreading ventrally to their insertions along the entire lateral margin of the eighth sternum (fig. 13). This muscle evidently corresponds with the second

internal lateral of the preceding segments, the first being absent in the eighth segment both in the female and the male (fig. 12).

251. First external lateral muscle (figs. 13, 14).—A thick muscle arising in the lower anterior angle of the eighth tergum, inserted anteriorly on the outer face of the apodeme *(Ap)* of the eighth sternum.

252. Second external lateral muscle (figs. 13, 14).—A small muscle arising on the lower part of the eighth tergum below the spiracle, inserted on the base of the apodeme of the eighth sternum.

253. Third external lateral muscle.—Absent in the female.

254, 255. Muscles of the spiracle (figs. 13, 14).—Same as in the preceding segments.
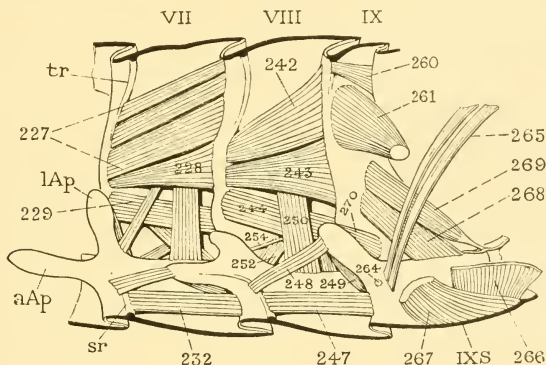

Fig. 12.—Muscles of the seventh, eighth, and ninth segments of the male abdomen of *Dissosteira carolina,* right side, inner view.

The following muscles of the eighth segment of the female have no representatives in the male.

256. Short protractor of the ovipositor.—A short muscle with a broad base arising on the side of the eighth tergum anterior to *250* (figs. 13, 14), inserted anteriorly on the anterior end of the apodeme of the ovipositor (fig. 17 A, C).

257. Anterior muscle of the median oviduct (fig. 13).—A slender muscle arising on the end of the apodeme of the eighth sternum, extending mesally to its insertion on the anterior end of the median oviduct. This muscle is absent in *Melanoplus.*

258. Posterior muscle of the median oviduct (fig. 13).—A long flat muscle arising on the end of the apodeme of the eighth sternum, extending mesally and posteriorly to the posterior end of the median oviduct.

259. The muscular sheath of the oviducts.—The walls of the median oviduct and of the proximal parts of the lateral ducts have a muscular sheath of internal circular fibers and external longitudinal fibers. The longitudinal fibers are continued upon the walls of the calyces, but the circular fibers appear to be absent in these parts of the lateral ducts, and no muscles are present on the anterior glandular parts.

MUSCLES OF THE NINTH SEGMENT

The musculature of the ninth segment differs so much between the male and the female that few muscles can be identified with each other in the two sexes, or homologized with muscles of the pregenital segments. Besides the segmental muscles there are in the female special muscles of the ovipositor, and in the male special muscles of the phallic organs.

In the male grasshopper the following nine muscles take their origins on the segmental plates of the ninth segment.

260. Internal dorsal muscle (fig. 12).—A small band of fibers arising near the mid-dorsal line on the anterior edge of the ninth tergum, the fibers spreading posteriorly and laterally to their insertions on the anterior margin of the tenth tergum. This small muscle is the only representative of the intertergal dorsals in the ninth segment of the male.

261. Retractor of the phallus.—A short, thick, conical muscle arising by a wide base dorsolaterally on the ninth tergum (fig. 12), inserted posteriorly and ventrally on a small oval sclerite in the wall of the genital chamber just laterad of the epiphallus (fig. 25 D).

262, 263. Muscles of the female not represented in the male.

264. Ventral dilator of the rectum.—A fan-shaped muscle arising on the ninth sternum at the base of the sternal apodeme (fig. 12 shows point of origin), the slender fibers spreading dorsally in a longitudinal plane to their insertions on the ventral wall of the rectum (fig. 16 A).

265. Ventral muscles (fig. 12).—A pair of straplike muscles on each side arising laterally on the ninth sternum at the base of the anterior apodeme, going posteriorly and dorsally to the membranous venter of the tenth segment just before the base of the paraproct.

266. Retractor of the aedeagus.—A broad, thin sheet of fibers arising from a median ridge of the ninth sternum (figs. 12, 25 A), attached dorsally to the wall of the genital chamber laterad of the base of the aedeagus (fig. 25 A).

267. Protractor of the aedeagus.—A large, triangular muscle arising by a long base on the median ridge of the ninth sternum, mesad

of *266* (figs. 12, 25 A), the fibers converging dorsally and anteriorly to their insertion on the lateral lobe of the epiphallus (fig. 25 A, D) ; its contraction probably elevates the distal part of the phallic apparatus.

268, 269. Internal lateral muscles (fig. 12).—Two large oblique muscles on each side in the position of the second internal lateral of the pregenital segments. The first is inserted ventrally on the lateral margin of the ninth sternum ; the second is inserted by a narrowed stalk at the edge of the ninth sternum between the basal and distal plates of the latter.

270. External lateral muscle (fig. 12).—This muscle clearly corresponds with the first external lateral of the pregenital segments. It arises on the anterior lateral area of the ninth tergum and is inserted on the outer face of the apodeme of the ninth sternum.

In the ninth segment of the female there are the following 10 paired muscles or sets of muscles, including the segmental muscles and the muscles of the ovipositor.

260. Internal dorsal muscles (fig. 14).—A transverse series of five small bands of longitudinal fibers on each side extending from the anterior margin of the ninth tergum to the anterior margin of the tenth tergum.

261. Not represented in the female.

262. Long protractor of the ovipositor.—Origin laterally on the posterior margin of the ninth tergum (figs. 14, 17 C), extends forward to its insertion on the anterior end of the apodeme of the ovipositor (fig. 17 C).

263. Retractor of the ovipositor.—Origin on the anterior margin of the ninth tergum (figs. 14, 17 C) ventrad of *262,* extends posteriorly to its insertion laterally in the base of the dorsal valvula of the ovipositor (fig. 17 C).

264. Ventral dilator of the rectum.—A fan-shaped group of slender fibers arising from the dorsal surface of the apodeme of the ovipositor (fig. 17 B), spreading to their insertions on the ventrolateral line of the rectum (fig. 16 A). If the ventral dilators of the rectum are identical in the male and female, their origins would seem to identify the apodemes of the ovipositor with the anterior apodemes of the ninth sternum in the male.

265-270.—These muscles of the ninth segment present in the male (fig. 12) cannot be identified with any certainty in the female, though it is possible some of them are included in the following musculature of the ovipositor.

271. Levator of the dorsal valvula (fig. 17 A, B, C).—A large thick muscle lying on the dorsal surface of the apodeme of the ovipositor,

attached anteriorly on the latter, and posteriorly on the dorsal margin of the base of the dorsal valvula.

272. Depressor of the ventral valvula (fig. 17 A, B).—A massive bundle of fibers arising on the ventral face of the apodeme of the ovipositor, inserted on the basal plates of the ventral valvula. This muscle possibly corresponds with the intersternal protractors, or external ventrals, of the pregenital segments.

273. Adductors of the ventral valvulae (fig. 17 C, D).—A pair of flat muscles arising anteriorly on the proximal parts of the inner margins of the apodemes of the ovipositor, the two converging posteriorly to the median apodeme of the ventral intervalvula (*f*). The retraction of the intervalvula causes an adduction of the valvulae.

Fig. 13.—Laterodorsal and ventral muscles of the seventh and eighth segments of the female abdomen of *Dissosteira carolina*, right side, inner view.

274. Adductors of the dorsal valvulae (fig. 17 A, B, C).—Origin on the proximal part of the dorsal surface of the ovipositor apodemes, insertion posteriorly on the posterior intervalvula (B, C, *piv*). The contraction of the convergent muscles of this pair approximates the valvulae of opposite sides.

275. Muscle of the second valvula (fig. 17 B, C).—A small muscle arising laterally on the dorsal surface of the anterior intervalvula, inserted posteriorly in the distal end of the small second valvula.

276. Dilator of the spermathecal aperture.—A very small muscle of a few delicate fibers arising on the lateral basal plate of the ventral valvula (fig. 17 E, *a*), inserted mesally on the side of the groove in the dorsal wall of the genital chamber containing the aperture of the spermathecal duct (fig. 20 D).

277. Muscles of the spermathecal duct.—The entire length of the spermathecal duct is covered by a muscular sheath consisting of outer longitudinal fibers and inner circular fibers.

The following muscles of the ninth segment of the male pertain entirely to the phallic organs and the ejaculatory duct. It is impossible to discover any identity between them and muscles of the female.

278. Epiphallic muscle of the aedeagus (fig. 25 B, C).—A long muscle lying dorsally in the basal fold of the phallus, attached anteriorly on the lateral lobe of the epiphallus (*h*), and posteriorly on the zygoma (*z*) of the aedeagal apodemes.

279. Lateral muscle of the aedeagus (fig. 25 B).—A short muscle arising lateroventrally in the base of the aedeagus, inserted dorsally on the lower edge of the lateral plate (*m*) of the aedeagus.

280. Muscle of the ventral lobe of the aedeagus (fig. 25 B).—A delicate muscle arising within the base of the aedeagus, inserted distally near the apex of the ventral lobe of the latter.

281. Lateral dilator of the endophallus (fig. 25 C, E).—A broad sheet of muscle arising dorsally on the aedeagal apodeme (*C, Apa*), the fibers extending ventrally and anteriorly to the endophallic apodeme (*C, E, w*).

282. Dorsal dilator of the endophallus (fig. 25 F).—A broad flat muscle on the dorsal surface of the endophallic bulb, arising laterally on the inner face of the aedeagal apodeme (*Apa*), inserted mesally on the dorsal edge (*x*) of the lateral plate of the endophallus.

283. Compressor of the endophallus (fig. 25, E, F. G).—An unpaired transverse muscle uniting the endophallic apodemes (*w*), the fibers covering the anterior and anteroventral walls of the endophallic bulb (G). This muscle approximates the endophallic plates and dilates the orifice of the ejaculatory sac.

284. Compressor of the ejaculatory sac (fig. 25 C, E).—A broad sheet of muscle arising internal to *281* (C) on the lateral plate of the endophallus, the fibers converging ventrally to their insertions on the lateral wall of the ejaculatory sac (E, *ejs*).

285. Muscles of the ejaculatory duct (fig. 25 E).—A thick sheath of circular fibers surrounds the ejaculatory duct from the entrance of the mucous glands to the beginning of the ejaculatory sac.

MUSCLES OF THE TENTH SEGMENT

The muscles of the tenth segment have no evident relation to the muscles of the preceding segments. They comprise muscles to the cerci, the epiproct and the paraprocts, dilators of the rectum, and in the female a transverse intrasegmental muscle.

286. Dorsal dilator of the rectum.—A group of slender fibers aris-
ing dorsally on the tenth tergum mesad of the other muscles (fig. 14),
spreading fanwise ventrally to their insertions laterodorsally on the
posterior part of the rectum (fig. 16 A).

287. Depressor of the cercus (figs. 7 D, 14).—A narrow muscle
arising anteriorly on the median part of the tenth tergum, inserted
posteriorly on the posterior margin of the median basal lobe of the
cercus.

288. Median levator of the cercus (figs. 7 D, 14).—A broad muscle
arising anteriorly on the tenth tergum laterad of *287*, inserted pos-
teriorly on the small sclerite between the tenth tergum and the basal
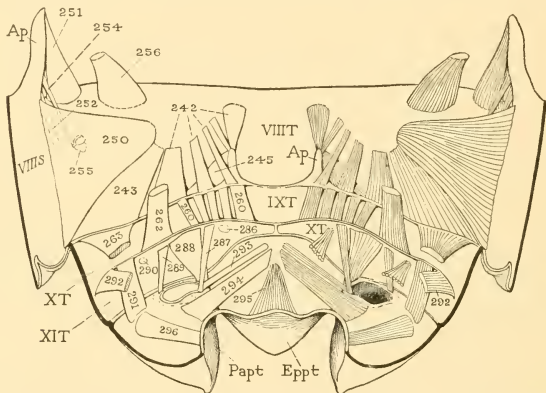
Fig. 14.—Dorsal muscles of eighth, ninth, tenth, and eleventh abdominal seg-
ments of female of *Dissosteira carolina,* ventral view.

lobe of the cercus, some of the mesal fibers in some cases inserted on
the basal angle of the epiproct.

289. Lateral levator of the cercus (figs. 7 D, 14).—A slender mus-
cle taking its origin on the tenth tergum immediately laterad of *288,*
inserted posteriorly in the membrane behind the tenth tergum close
to the outer angle of the base of the cercus.

290. Lateral dilator of the rectum.—A fan of fibers arising an-
teriorly on the lateral part of the tenth tergum (fig. 14, *290*), spread-
ing mesad in a horizontal plane to their insertions along the lateral
line of the posterior part of the rectum (fig. 16 A).

291. Ventral muscle of the paraproct (fig. 14).—A broad muscle
arising on the anterior margin of the lateral part of the tenth tergum,
inserted posteriorly on the base of the paraproct ventrally.

292. Transverse muscle (fig. 14).—An unpaired, straplike trans-
verse muscle, present only in the female, lying dorsal to the base of
the ovipositor and attached laterally on the ends of the tenth tergum.
(Only the ends of this muscle shown in the figure.)

MUSCLES OF THE ELEVENTH SEGMENT

The musculature of the eleventh segment includes muscles from the
epiproct to the cerci and paraprocts, and muscles from the epiproct and
paraprocts to the circumanal membrane.

293. Adductor of the cercus (figs. 7 D, 14).—A slender muscle
arising anteromedially on the epiproct, inserted on the inner extremity
of the basal lobe of the cercus.

294. Adductor of the paraproct (fig. 14).—A large muscle arising
medially on the epiproct just behind *293* in the female, extending
laterally and posteriorly to its insertion on the upper part of the para-
proct behind the base of the cercus. In the male this muscle arises
mesad of *293* and underlaps the base of the latter.

295. Dorsal dilator of the anus.—A median unpaired muscle arising
centrally on the epiproct (fig. 14), its fibers spreading distally to their
insertions on the dorsal part of the circumanal membrane (fig. 16 A).

296. Lateral dilator of the anus.—Origin on the paraproct near the
base of the outer wall of the latter (fig. 14) ; extends dorsally, mesally,
and posteriorly to its insertion ventrolaterally on the rectum just
within the anus (fig. 16 A).

THE TRANSVERSE MUSCLES

The transverse muscles of the abdomen comprise *dorsal transverse
muscles* (fig. 10 B, *td*) and *ventral transverse muscles* (*tv*). The
former are always the muscles of the dorsal diaphragm; the ventral
muscles may consist of segmentally individual bundles of transverse
fibers, but in the Acrididae they form a continuous muscular sheet, or
ventral diaphragm. The muscle uniting the opposite ends of the tenth
tergum in the female of *Dissosteira* (fig. 14, *292*) is literally a dorsal
transverse muscle, but it evidently does not belong to the series of
diaphragm muscles.

III. THE DIAPHRAGMS AND THE DORSAL BLOOD VESSEL

The so-called diaphragms of insects are transverse dorsal and ven-
tral partitions of the body cavity that separate from the axial pervis-
ceral sinus (fig. 10 B, *PvS*) a dorsal sinus, or pericardial cavity (*DS*),

3

and a ventral sinus, or perineural cavity (*VS*). Each of the dia-
phragms differs much in the degree of its development in different
insects. The dorsal diaphragm is almost always present in some form,
but the ventral diaphragm is frequently absent; the first is confined
principally to the abdomen, the second may extend into the thorax.
Probably each diaphragm consists of a double peritoneal membrane,
the layers of which are reflected from the walls of the body cavity; but
the membranes enclose between them the dorsal and ventral transverse
muscles, and the muscles become the more important elements of the
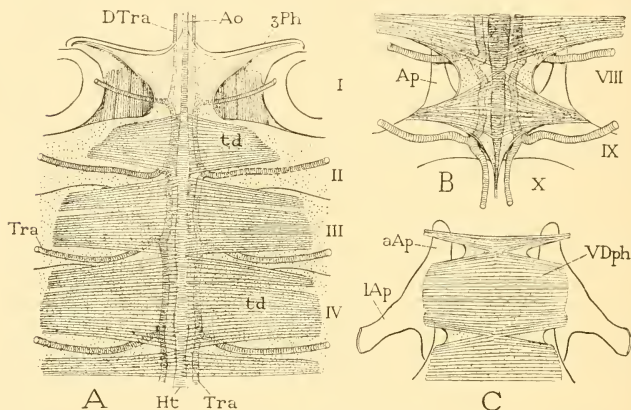
FIG. 15.—The dorsal blood vessel and diaphragms of *Dissosteira carolina.*

A, ventral view of anterior part of dorsal diaphragm extending to lobes of third
phragma (*3Ph*), showing segmental groups of transverse muscles (*td*), and
dorsal blood vessel along median line above the diaphragm. B, posterior part
of dorsal diaphragm and dorsal blood vessel in segments *VIII, IX,* and *X.* C,
dorsal view of part of ventral diaphragm, attached on lateral parts of sterna.

diaphragms, which by the vibratory contractions of the muscles serve
as important adjuncts to the heart in the circulation of the blood.

The dorsal diaphragm of Acrididae extends from the anterior end
of the first abdominal segment to the posterior part of the ninth seg-
ment, and is continued into the metathorax as a narrow membranous
fringe along each side of the aorta. In the first abdominal segment the
broad anterior margin of the diaphragm is attached to the posterior
faces of the lobes of the third phragma (fig. 15 A); the lateral edges
in this segment are free and deeply emarginate. In the following seg-
ments the limits of the dorsal diaphragm are difficult to define in a
ventral dissection, except by the muscle attachments, for the lower

diaphragm membrane appears to be everywhere continuous with a delicate peritoneal covering over the inner surfaces of the somatic muscles lying lateral of the pericardial cavity. The upper membrane of the diaphragm, however, being reflected upon the dorsal pericardial wall, more clearly marks the limits of the diaphragm itself. The two membranes of the diaphragm can be distinguished in whole preparations under the microscope by the two layers of nuclei, one dorsal to the muscle fibers, the other ventral. It is apparent that the two membranes, however, are simply continuations of a peritoneal lining of the perivisceral cavity and of a similar lining of the pericardial cavity, with the transverse muscles between them.

The muscles of the dorsal diaphragm in *Dissosteira* begin in the second segment of the abdomen (fig. 15 A) and end in the ninth segment (B). They consist of a double series of transverse fibers, separated into segmental groups, but for the most part approximately parallel. In all but the second and ninth segments the fibers are slightly divided into secondary anterior and posterior groups. This intrasegmental segregation of the fibers is more accentuated in *Melanoplus* than in *Dissosteira*. The fibers arise laterally on the tergal plates between the median and the lateral longitudinal dorsal muscles (figs. 8, 10). Their median ends branch toward the ventral wall of the heart, on which they break up into fine fibrils, and the fibrils from opposite sides appear to unite in an intricate plexus.

The dorsal blood vessel extends from beneath the brain into the tenth abdominal segment. Ostia and slight segmental enlargements of the tube are present in abdominal segments *II* to *IX* (fig. 15 A, B). Dorsal ampullar enlargements of the aorta occur in the mesothorax, metathorax, and first abdominal segment. Posteriorly the heart terminates in a narrow tapering tube extending into the tenth abdominal segment. For most of its length the dorsal vessel is accompanied by strands of nephrocytes, and the aortic ampullae are capped by dense masses of nephrocytic cells. The pericardial cavity contains also loosely scattered fat cells, and is penetrated by loops of the Malpighian tubules. The dorsal longitudinal tracheal trunks (fig. 15 A, B) lie along the sides of the blood vessel and are connected with the lateral trunks by transverse tracheae in the posterior part of each abdominal segment. It would appear that the blood has entrance into the pericardial cavity only above the free lateral margins of the diaphragm in the first abdominal segment, and at the posterior end of the diaphragm in the eighth and ninth segments.

The ventral diaphragm in *Dissosteira* extends from the head into the seventh (female) or eighth (male) abdominal segment. In the

anterior part of the thorax this diaphragm is merely a very delicate membrane attached laterally on the salivary glands and on masses of fat tissue. Between the widely spreading bases of the metasternal apophyses, however, there begins in the membrane a series of transverse muscle fibers, which continues to the posterior end as the principal tissue of the diaphragm. The fibers are attached in the metathorax to the metasternal apophyses, and in the abdomen on the lateral parts of the sternal plates (fig. 15 C). Most of the fibers go continuously across from one side to the other, but in each segment the anterior and posterior fibers spread somewhat forward and backward to bridge the spaces between the consecutive sternal plates. Posteriorly the ventral diaphragm ends abruptly in a free transverse margin, which in the female crosses the anterior part of the seventh abdominal segment, but in the male is in the anterior part of the eighth segment. In the female the last two ganglia of the ventral nerve cord lie beyond the diaphragm and are dorsal to the spermatheca, the anterior end of which may extend into the ventral sinus. In the male only the last ganglion is not covered by the diaphragm.

IV. THE PROCTODAEUM

The proctodaeum of the grasshopper is a tube of fairly uniform diameter composed of anterior and posterior sections separated by a narrower and usually bent middle section (fig. 16 A), but the relative size of the parts varies much in different specimens according to the distension, or according to the state of contraction of the muscles. The anterior end of the proctodaeum is marked externally by the origins of the Malpighian tubules (*Mal*), which are disposed in 12 groups of about 10 tubules each, arranged in a circle immediately behind the ventriculus (*Vent*). There is no clear anatomical division of the proctodaeum into an anterior intestine and posterior intestine, and there are no specifically developed internal valves, but four fairly well-marked proctodaeal regions may be distinguished by external and internal characters. The first is a short pylorus (*Py*) into which the Malpighian tubules open, the second is a long saclike ileum (*Il*), the third a narrower and usually bent colon (*Cln*), and the fourth is the large rectum (*Rect*) comprising a wide anterior rectal sac and a narrow terminal part extending to the anus.

The muscularis of the proctodaeum consists of external longitudinal fibers and internal circular fibers, the relation of the two sets of muscles on the proctodaeum being thus the same as that of the ventricular muscles (fig. 16 A), though the muscle fibers of these two parts of the alimentary canal are not continuous with each other.

The circular muscles of the proctodaeum begin just behind the bases of the Malpighian tubules, forming here a pyloric sphincter of large fibers (A, B, c), and continue (d) uninterruptedly over the entire length of the rest of the stomodaeal tube. They are particularly strong on the colon. The longitudinal muscles arise as distinct fibers on the anterior end of the proctodaeum in the neighborhood of the Malpighian tubules, but the fibers immediately converge over the pyloric sphincter into six equally spaced muscle bands (e) on the wall of the ileum,
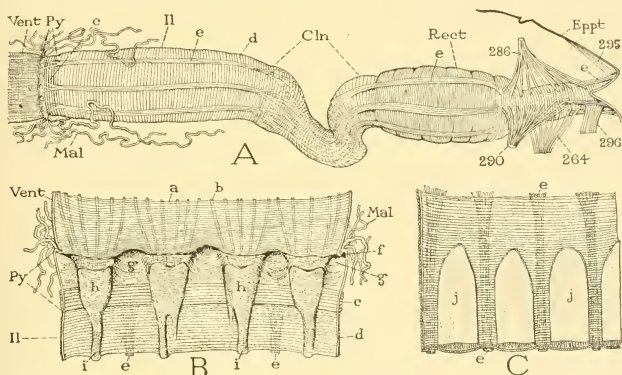
FIG. 16.—The proctodaeum of *Dissosteira carolina*.

A, general view of the proctodaeum, showing its subdivisions, its muscles, and groups of Malpighian tubules given off from anterior end. B, internal view of pyloric region between ventriculus and ileum, with pockets from which the Malpighian tubules arise. C, anterior ends of rectal " glands," inner view of rectal wall.

a, b, circular and longitudinal muscles of ventriculus; *c,* pyloric sphincter; *Cln,* colon; *d,* circular muscles of proctodaeum; *e,* bands of longitudinal proctodaeal muscles; *Eppt,* epiproct; *f,* fold marking terminus of ventricular wall; *g,* Malpighian pockets; *h, i,* internal folds of wall of ileum; *Il,* ileum; *j,* rectal pads; *Mal* Malpighian tubules; *Py,* pylorus; *Rect,* rectum; *Vent,* ventriculus; *264, 286, 290,* ventral, dorsal, and lateral dilator muscles of posterior part of rectum; *295, 296,* epiproctial and paraproctial dilators of the anus (see fig. 14).

and continue thus to the posterior end of the latter. Here each band breaks up into a group of fibers branching on the colon, some of which appear to go beneath the circular fibers to attach on the intima of the proctodaeal wall. On the posterior part of the colon the longitudinal fibers reassemble in six bands that traverse the outer wall of the rectal sac, and then again branch and appear to go beneath the circular muscles to be inserted on the wall of the terminal part of the rectum. Finally the longitudinal fibers appear once more as six short external bands on the terminal part of the rectum, and end with attachments on

the lips of the anus. The colon is the most strongly musculated part of the intestine, and, when in a state of contraction, it often appears as a very short connective between the distended ileal and rectal sacs.

The posterior part of the rectum is provided with fan-shaped dorsal, lateral, and ventral dilator muscles arising on the body wall and inserted on the proctodaeum in line with the longitudinal muscle bands of the latter (fig. 16 A). The dorsal dilators (*286*) arise medially on the tergum of the tenth abdominal segment (fig. 14), and their spreading fibers are inserted on the rectum along the lines of the laterodorsal longitudinal muscles. The lateral dilators (fig. 16 A, *290*) arise laterally on the tenth tergum (fig. 14), and are inserted in line with the lateral longitudinal muscles of the rectum. The ventral dilators (fig. 16 A, *264*) arise in the male at the bases of the anterior apodemes of the ninth abdominal sternum (fig. 12), in the female on the apodemes of the ovipositor (fig. 17 B), and are inserted in line with the lateroventral longitudinal muscles of the rectum.

The structure of the inner wall of the proctodaeum of *Dissosteira carolina* has been described and figured by Tietz (1923), who shows that the several parts of the intestinal tube present characteristic histological differences. Viewed internally, it is seen that the Malpighian tubules open into 12 pockets of the pyloric region (fig. 16 B, *g*), and that the pockets are somewhat overlapped anteriorly by a circular fold of the enteric wall (*f*). The proctodaeal intima lines the Malpighian pockets and is reflected to the edge of the overhanging fold. It is clear, therefore, that the crest of this fold (*f*) is the true line of separation between the mesenteron and the proctodaeum, and that the Malpighian tubules arise from the proctodaeum. Between the Malpighian pockets the wall of the proctodaeal pylorus forms 12 broad, padlike thickenings (*h*), which are crossed externally by the sphincter muscle (*c*), and which, therefore, may constitute collectively a pyloric closing apparatus between the stomach and the colon. Posteriorly the pyloric pads are narrowed and are either continued as well-marked folds on the wall of the ileum (*i*), or they are broken up into numerous small folds, according to the degree of tension in the ileal wall. The external longitudinal muscle bands of the ileum (*e*) lie between each alternate pair of internal folds. When the folds are accentuated by contraction of the proctodaeal muscles, they extend posteriorly through the colon to the rectum. According to Tietz (1923) the proctodaeal intima has a thickness of .008 mm in the ileum, and of .012 mm in the colon.

The inner wall of the rectal sac presents six long, flat, parallel thickenings lying between the external bands of longitudinal muscles, each

tapering or rounded at the ends, and having sharply defined margins formed by the covering cuticula (fig. 16 C, *j*). These structures are the so-called " rectal glands." In the grasshopper there is nothing to suggest that they have a secretory function, the surface cuticula being relatively thick, and the epithelium, as shown by Tietz (1923), consisting of simple columnar cells. For the same reasons, also, it does not seem probable that the rectal pads are organs for the absorption of water from the faeces (see Wigglesworth, 1932); in fact, any other part of the rectum would appear to be better adapted to an absorptive function. On the other hand, the hard flat surfaces of the pads, forming six plaques in strong relief on the inner wall of the rectum, suggest that, by contraction of the surrounding circular muscles, the structures may serve to compress the contents of the rectal sac and thus extract water from the faeces.

V. THE OVIPOSITOR AND ASSOCIATED STRUCTURES

The ovipositor of the Acrididae is primarily a digging organ that works by a forcible separation of the short recurved valvulae. It thus differs radically in its action from the usual egg-laying organ of other insects, in which the valvulae are interlocked and move lengthwise on one another. The acridid ovipositor, therefore, has quite a different mechanism from that of the sliding type of ovipositor. Though the prongs of the grasshopper's ovipositor, as shown by their development, are without doubt homologues of the valvulae of other insects, it is apparent that the usual supporting basal plates, or valvifers, are absent, and that the musculature of the acridid organ has little relation to that of an ovipositor in which the muscles of the valvifers are the principal motor elements. A second important function of the acridid ovipositor, however, is that of manipulating the eggs, as the latter issue from the oviducal opening, in such a manner that they may be placed appropriately in the egg cavity for the exit of the young grasshoppers.

STRUCTURE OF THE OVIPOSITOR

The exposed part of the grasshopper's ovipositor consists of a lower and an upper pair of strong, sclerotic, pronglike processes with curved tips turned ventrally and dorsally (fig. 1, *Ovp*). These processes are respectively the first and third valvulae (fig. 17 A, *1Vl, 3Vl*). The second valvulae (*2Vl*) are small, and are ordinarily concealed between the others, but they are not rudimentary in the sense of being functionless structures. The ovipositor projects posteriorly at the
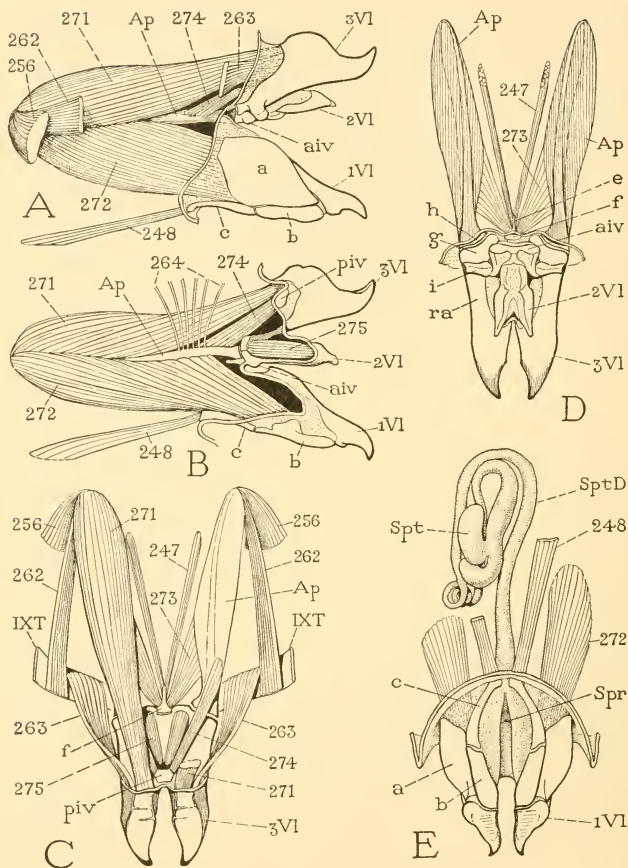
Fig. 17.—The ovipositor and its muscles. *Dissosteira carolina.*

A, ovipositor and muscles, left side. B, median section of ovipositor showing mesal view of right valvulae and muscles. C, dorsal view of ovipositor and muscles. D, ventral view of second and third valvulae, with apodemes, and muscles of anterior intervalvula. E, ventral view of ventral valvulae, dorsal wall of genital chamber with spermathecal aperture, and spermatheca.

a, lateral basivalvular sclerite; *aiv,* anterior intervalvula; *Ap,* apodeme of ovipositor; *b, c,* first and second ventral basivalvular sclerites; *e, f,* apodeme and apodemal sclerite of anterior intervalvula; *g,* base of third valvula; *h,* ventral lip of apodemal invagination; *i,* articular process on ramus of third valvula; *IXT,* lateral parts of ninth tergum; *piv,* posterior intervalvula; *ra,* ramus of third valvula; *Spr,* spermathecal aperture; *Spt,* spermatheca; *SptD,* spermathecal duct; *1Vl, 2Vl, 3Vl,* first, second, and third valvulae.

end of the abdomen (fig. 1) beyond the eighth sternum (*VIIIStn*) from beneath the lobes of the eleventh segment (*Eppt, Papt*), and thus might appear to belong to the ninth and tenth segments; the first valvulae, however, are developed in the nymph from the eighth segment, immediately behind the eighth sternum (fig. 22 A, C, *1Vl*), and the second and third valvulae from the ninth segment (A, C, D). In the adult several basivalvular sclerites are differentiated from the bases of the first valvulae (figs. 1, 17 A, *a, b, c*), which, though partially overlapped by the eighth sternum, are entirely separated from the latter by an inflection of the poststernal membrane that forms the female genital chamber. Between the bases of the dorsal valvulae are anterior and posterior intervalvular sclerites (fig. 17 B, *aiv, piv*) ; and a pair of large apodemes projects forward in the body cavity from the angles between the bases of the dorsal and ventral valvulae (A, B, D, *Ap*). An important accessory of the acridid ovipositor is the egg guide, a median process of the eighth sternum (fig. 20 A, *eg*).

The first, or ventral, valvulae of *Dissosteira carolina* (fig. 17 A, B, E, *1Vl*) are somewhat elongate lobes, flattened from side to side, ending each in a decurved point. Proximally they are united by the membranous integument between their bases, and their ventral walls are continued into the dorsal wall of the genital chamber (fig. 20 A). Each first valvula is differentiated into a strongly sclerotic terminal lobe (fig. 17 A, *1Vl*), and into a basal part containing a large lateral basivalvular sclerite (*a*) and two narrow ventral sclerites (*b, c*). The upper surface of the terminal lobe (B) is produced proximally as an elongate plate, or ramus, at the end of which is a wide transverse depression that fits closely upon a prominent abutment from the under surface of the basal ramus of the corresponding third valvula (D, *i*). Proximal to this articulation the dorsal wall of the ventral valvula is membranous and shortly ends at the ventral lip of the hollow base of the lateral apodeme (*Ap*). The lateral basivalvular sclerite of the first valvula (A, *a*) is a prominent plate exposed on the side of the abdomen behind the eighth sternum (fig. 1). The posterior ventral sclerite (fig. 17 A, B, *b*) is ordinarily partly exposed behind the eighth sternum, but the anterior ventral sclerite (*c*) is concealed in the dorsal wall of the genital chamber (fig. 20 A), where it flanks a median channel containing the spermathecal aperture (fig. 17 E).

The third, or dorsal, valvulae of *Dissosteira* (fig. 17 A, B, *3Vl*) resemble the ventral valvulae in general form, except that their points are turned upward, but they are larger and stronger than the ventral valvulae, and they have no basivalvular sclerites. Their dorsal surfaces proximal to the upcurved points are broad and flat. The under surface

of each dorsal valvula is prolonged anteriorly in a strong ventral ramus (D, ra), the expanded base of which (g) is firmly hinged to the dorsal lip of the exposed base (h) of the lateral apodeme of the same side. The apodemal bases, therefore, are the fulcral points for the movements of the dorsal valvulae. The ventral valvulae, on the other hand, have their fulcra of movement on the strongly protruding articular ridges (i) on the bases of the dorsal valvulae. The dorsal valvulae are united between their bases by a membranous integument containing the anterior intervalvula (D, aiv), the bases of the second valvulae ($2Vl$), and the posterior intervalvula (B, C, piv).

The second, or intermediate, valvulae (fig. 17 A, B, D, $2Vl$) are short lobes projecting from the membrane between the ventral rami of the dorsal valvulae. The two are adnate mesally for most of their length, but their sclerotic lateral and terminal parts form free lobes enclosing a trough-like depression between them (D). The united bases of the second valvulae are supported on a median process of the anterior intervalvula (aiv).

The intervalvulae are small sclerites lying between the bases of the dorsal valvulae, where, because of the position of the latter, they become dorsal and ventral relative to each other. The ventral anterior intervalvula (fig. 17 D, aiv) is a transverse sclerite bridging the space between the anterior ends of the ventral rami of the third valvulae, and giving support by a median process to the united bases of the second valvulae. Just before the transverse sclerite is a small, oval, median sclerite (f) bearing a short slender apodeme (e) on which are attached the muscles of the anterior intervalvula. The posterior intervalvula is a small hexagonal plate lying dorsally between the bases of the third valvulae (B, C, piv).

A characteristic feature of the acridid ovipositor is the presence of the pair of long, flat, lateral apodemes (fig. 17 D, Ap) extending forward from the angles between the bases of the dorsal and ventral valvulae. These apodemes are well developed also in Tetrigidae and Tridactylidae, but they have no apparent homologues in the ovipositor of other insects. They give attachment to the levator and depressor muscles of the valvulae, to the muscles of the posterior intervalvulae, and to the ventral dilators of the rectum, while the proctractor muscles of the ovipositor are inserted on their anterior ends.

The stalk of each apodeme is hollow, and its base appears as the strongly sclerotic lips of a transverse cleft in the angle between the bases of the dorsal and ventral valvulae, where, as already observed, the ventral ramus of the dorsal valvula is hinged to the dorsal lip of the apodemal invagination. It might be supposed, therefore, that the

apodemes of the acridid ovipositor represent anterior apodemal processes of the second valvifers in other insects, but it is quite impossible to reconcile the musculature of the acridid apodemes with that pertaining to the second valvifers in the usual type of ovipositor. According to Walker (1919) the ovipositor apodemes of *Melanoplus* are formed in the nymph as invaginations at the angles between the bases of the valvulae. It is perhaps possible that they are highly developed anterior apodemes of the ninth sternum (the latter being represented by the intervalvulae), since the space between the bases of the dorsal valvulae is bridged by the anterior intervalvula. It is significant that the ventral dilators of the rectum, which in the male arise anteriorly on the ninth sternum, take their origins in the female on the ovipositor apodemes (fig. 17 B, *264*).

The muscles of the acridid ovipositor function as protractors and retractors of the entire organ, as levators and depressors of the first and third valvulae, as abductors and adductors of the same valvulae, and as motors of the second valvulae; but it appears that some of them may act in more than one capacity. As above noted, it will be fruitless to attempt to trace any homologies between these muscles and the usual muscles of the ovipositor in other insects. It should be observed, however, that with the absence of valvifers in the acridid ovipositor there is correlated an absence of dorsal muscles corresponding with those ordinarily inserted on the valvifers.

The exsertion of the ovipositor evidently is brought about by two pairs of muscles inserted on the anterior ends of the lateral apodemes (fig. 17 A, C, *256*, *262*). Of these muscles those of the first pair are the short protractors (*256*) arising by wide bases on the anterior lateral parts of the eighth abdominal tergum (fig. 13). The others are the long protractors (fig. 17 C, *262*) arising laterally on the posterior margin of the ninth tergum (*IXT*). Retraction of the ovipositor is accomplished apparently by a pair of ventral muscles of the first valvulae, by lateral muscles of the third valvulae, and by muscles of the anterior intervalvula. The retractors of the first valvulae arise anteriorly on the eighth sternum (fig. 13, *248*) and in *Dissosteira* are inserted on the anterior ventral basivalvular sclerites (fig. 17 E, *248*). In *Melanoplus*, however, these muscles are inserted on anterior pockets of the genital chamber (fig. 20 C, *248*). The retractors of the third valvulae are lateral muscles arising anteriorly on the ninth tergum (fig. 17 C, *263*) and inserted posteriorly on the lateral margins of the bases of the third valvulae. These muscles would appear to act also as abductors of the valvulae. The retractors of the

anterior intervalvula (C, D, *247*) are a pair of slender muscles aris-
ing anteriorly on the eighth sternum (fig. 13) ; they probably assist
also in the adduction of the valvulae.

The muscles that open the valvulae dorsoventrally consist of the
four huge bundles of fibers arising on the lateral apodemes, one pair
dorsally (fig. 17 A, B, *271*), the other pair ventrally (*272*). The
dorsal muscles, which are the levators of the third valvulae, are in-
serted dorsally in the bases of these valvulae ; the ventral muscles, or
depressors of the first valvulae, are inserted within the bases of the
first valvulae on the lateral basivalvular sclerites and on the posterior
ventral sclerites (A, E, *a, b*). These four powerful muscles of the
ovipositor produce the movements of the valvulae by which the earth
is compressed peripherally in the digging of the egg chamber in the
ground.

The closing of the valvulae evidently is produced by muscles of
the anterior intervalvula, there being no muscles inserted on the
valvulae that directly oppose the opening muscles. The muscles of
the anterior intervalvula include the slender retractor muscles (fig.
17 C, D, *247*) arising anteriorly on the eighth sternum (fig. 13), and
a pair of short, broad muscles (fig. 17 C, D, *273*) arising on the ovi-
positor apodemes. Since the anterior intervalvula lies between the
bases of the dorsal and ventral valvulae, a pull on its muscles brings
the valvulae together. These same muscles also effect an adduction
of the valvulae of opposite sides.

Transverse movements of the valvulae, *i. e.,* movements of abduc-
tion and adduction, are not as pronounced as the dorsal and ventral
movements, but it can be shown experimentally on a dead specimen
that some of the muscles of the ovipositor separate or approximate the
valvulae of opposite sides. The only muscles that may serve as ab-
ductors of the valvulae are the retractor muscles inserted on the lateral
basal margins of the third valvulae (fig. 17 C, *263*), which arise
laterally on the ninth tergum. The adductors are muscles of the inter-
valvulae ; a forward pressure on these sclerites brings the valvulae of
opposite sides together. The anterior intervalvular muscles comprise
the median pair of slender muscles (fig. 17 C, D, *247*) arising an-
teriorly on the ninth sternum (fig. 13), and the lateral pair of wide
muscles (*273*) arising on the inner margins of the basal parts of the
lateral apodemes ; both pairs converge to their insertions on the small
median apodeme of the anterior intervalvula. The posterior inter-
valvular muscles consist of a single pair of muscles (B, C, *274*)
arising on the bases of the lateral apodemes, and converging pos-
teriorly to their insertions on the posterior intervalvula (*piv*). There

are no tergal muscles in Acrididae corresponding with those inserted on the intervalvulae in Gryllidae. (See Abdomen, Part II, Smithsonian Misc. Coll., vol. 89, no. 8, fig. 17 E, H, *5, 8.*)

The second valvulae are provided with a pair of short muscles arising anteriorly on the anterior intervalvula (fig. 17 B, C, *275*), and inserted distally in the free ends of the second valvulae. These small intermediate valvulae evidently are functional in guiding the eggs properly between the other valvulae in their passage through the ovipositor.

An important accessory of the acridid ovipositor is the *egg guide*. This organ is a small, tapering median process arising from the re-
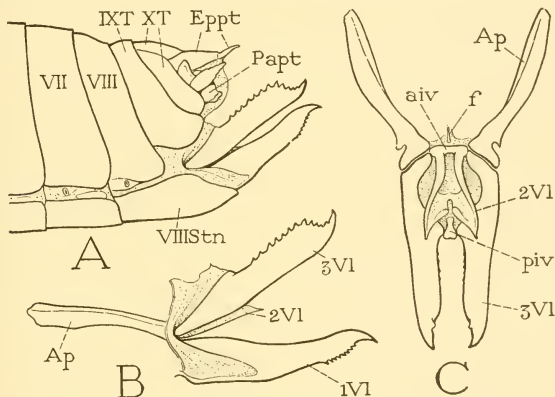
Fig. 18.—End of abdomen and ovipositor of *Tettigidea lateralis*.

A, terminal segments of abdomen, with ovipositor. B, left valvulae and apodeme of ovipositor. C, ventral view of second and third valvulae, intervalvulae, and apodemes of ovipositor.

flected distal end of the eighth sternum (figs. 4, 13, *eg*) directly in line with the opening of the oviduct (*Gpr*) in the floor of the genital chamber. The egg guide normally projects between the bases of the ventral valvulae, and serves to direct the eggs issuing from the gonopore upward and into the intervalvular space of the ovipositor. It is an immovable process developed in the nymph as a median outgrowth from the posterior margin of the eighth sternum.

The ovipositor of Tetrigidae, as illustrated by *Tettigidea lateralis* (fig. 18), is of the acridid type of structure in that it is composed of the first and third valvulae (B), and has a pair of lateral intervalvular apodemes (B, C, *Ap*) with muscles for opening the valvulae. The

second valvulae are small (C, $2Vl$) as in Acrididae and are supported by the anterior intervalvula (aiv). The first and third valvulae, however, are longer and slenderer than in the typical acridid ovipositor, and the apodemes are relatively short. Basivalvular sclerites are absent in *Tettigidea*, but Walker (1919) describes and figures basivalvular sclerites associated with the first valvulae in *Acrydium ornatum*, and Chopard (1920) shows a lateral sclerite (pileolus) at the base of the first valvula in *Paramastax laeta*. Walker describes also in *Acrydium* a sclerite interposed between the base of the third valvula and the lower edge of the ninth tergum, which he regards as a valvifer.

The ovipositor of the tridactylid genus *Rhipipteryx*, as Walker (1919) observes, " is remarkably similar to that of the Acridoidea." The female abdomen of *R. biolleyi* is elongate and slender. The last unmodified segment is the seventh (fig. 19 A, VII). The eighth segment, which is partly concealed within the seventh, has its tergum divided into two lateral plates by a median membranous area of the dorsum (A, B, $VIIIT$). The spiracles of this segment lie in the lower parts of the tergal plates. The tergum of the ninth segment (A, IXT) consists of two widely separated lateral plates (E, IXT), the anterior dorsal angles of which (C, E) are produced into a pair of slender arms invaginated beneath the dorsal membrane of the eighth segment. The tergum of the tenth segment (F, XT) is broken up into two large lateral tergites and a group of three small dorsal tergites. The lateral tergites extend forward between the arms of the ninth tergal plates, where they are united with each other anteriorly. The eleventh segment is represented by a shield-shaped epiproct (F, $Eppt$), and two large projecting paraprocts ($Papt$) bearing each a terminal lobe ($paptl$). The cerci (Cer) arise laterad of the epiproct at the bases of the paraprocts.

The exposed part of the ovipositor of *Rhipipteryx biolleyi* consists of four elongate conical processes (fig. 19 A, Ovp), which, as in Acrididae and Tetrigidae, are the first and third valvulae. Each ventral first valvula (C, $1Vl$) has an accessory tooth on its outer surface and a large lateral basivalvular sclerite (a) at its base. The latter appears on the side of the abdomen as a prominent plate behind the eighth sternum (A, a). The dorsal third valvulae (C, $3Vl$) are somewhat longer than the ventral valvulae, and each is supported on the distal margin of the lateral tergite of the ninth segment (IXT), to which it is articulated ventrally (E) by a condyle of the latter. Below and between the bases of the dorsal valvulae are two small intermediate second valvulae (E, $2Vl$), united at their bases by the anterior inter-

valvula (*aiv*). Both anterior and posterior intervalvulae (E, *aiv, piv*) are present in *Rhipipteryx* as in Acrididae and Tetrigidae, and a small median sclerite (*f*) before the anterior intervalvula gives attachment to a pair of convergent muscles (*5*).

The lateral apodemes of the ovipositor of *Rhipipteryx* are long spatulate plates arising between the bases of the valvulae, but each is more specifically connected with the corresponding ventral valvula (fig. 19 D, *Ap*), rather than with the dorsal valvula as in Acrididae. Walker describes the ovipositor apodemes of *R. forcipata* as shelflike extensions of the lower edges of the ninth tergum, having the same
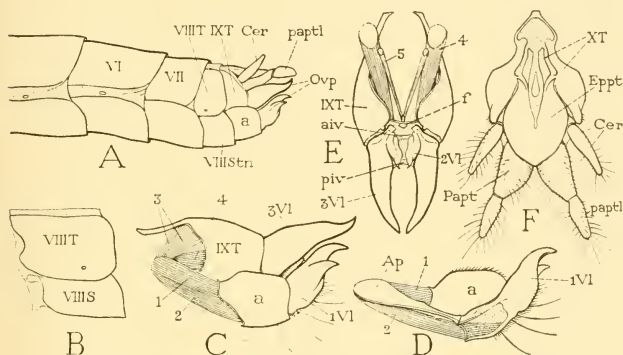
FIG. 19.—Abdomen and ovipositor of *Rhipipteryx biolleyi*.

A, terminal half of abdomen with ovipositor. B, lateral view of eighth segment removed from seventh. C, left view of ninth segment and ovipositor. D, mesal view of right ventral valvula, with right apodeme and muscles. E, ventral view of ninth tergum supporting second and third valvulae. F, dorsal view of tenth and eleventh segments, showing lobes (*paptl*) of paraprocts. (Lettering as on fig. 17.)

relation to the valvulae as the free apodemes of Acrididae. The writer, however, finds no tergal connections of the apodemes in *R. biolleyi*, in which the structures appear to be identical with the intervalvular apodemes of Acrididae. They give attachment to muscles very nearly the same as those of the Acrididae in their distribution to the basivalvulae (fig. 19 C, D, *1*), the ventral valvulae (*2*), the ninth tergum (C, *3*), and the dorsal valvulae (C, E, *4*).

THE FEMALE GENITAL CHAMBER AND THE SPERMATHECAL OPENING

The genital chamber, or copulatory pouch, of the female grasshopper is a flat horizontal invagination of the integument beneath the bases of the ventral valvulae and above the posterior margin of the

eighth abdominal sternum (fig. 20 A, *GC*). The anterior basivalvular sclerites of the first valvulae extend into its dorsal wall (figs. 17 E, 20 A, C, *c*), and in a depression between them is situated the aperture of the spermatheca (*Spr*). The opening of the median oviduct, or gonopore, lies anteriorly in the floor of the genital chamber (fig. 20 A, *Gpr*). A short distance before the spermathecal and oviducal apertures the genital chamber ends as a blind pouch. Here, in *Dissosteira,* a pair of muscles from the eighth sternum have their insertions on the ends of the anterior basivalvular sclerites (fig. 17 E, *248*). In *Melanoplus* the anterior end of the genital chamber is provided with two large lateral pockets (fig. 20 C, *l*), and the muscles (*248*), inserted on the basivalvular sclerites (*c*) in *Dissosteira,* are attached in *Melanoplus* on the walls of the lateral pockets. Similar pockets of the genital chamber in *Anacridium aegyptium* are described as " vésicules oviductaires " by Vardé (1929), who shows from a study of their histology that the pouches are glandular structures in this species.

The female genital chamber of insects generally is usually said to be an invagination between the eighth and ninth abdominal sterna. In the Acrididae, however, it is quite clearly an ingrowth between the eighth sternum and the bases of the first gonopods, which are located behind the sternum. This fact is noted by Nel (1929), who observes that the genital chamber in the female of *Colemania* and *Locustana* is " formed at the hind margin of the eighth sternum by the sternum overgrowing the bases of the anterior ovipositor lobes." The basal sclerites of the first valvulae thus come to lie in the dorsal wall of the genital chamber.

The female gonopore of adult Acrididae, as above noted, is situated on the floor of the genital chamber above the reflected posterior end of the eighth abdominal sternum. It is an elongate median aperture (figs. 4, 13, *Gpr*) between membranous folds that converge and unite posteriorly on the dorsal surface of the base of the egg guide. The oviductus communis (figs. 13, 20 A, *Odc*) extends forward to the seventh segment where it receives the lateral oviducts. The definitive position of the female gonopore in Acrididae, it is claimed by Nel (1929), is not the site of the primary invagination that gives rise to the median oviduct. In late embryos of *Locustana,* Nel says, the common oviduct first appears as an invagination of the conjunctival membrane between the seventh and eighth segments (fig. 20 B, *Odc'*), the aperture of which runs out as a groove on the venter of the eighth segment. In this respect, therefore, the acridid appears to recapitulate a more primitive condition permanently retained in Dermaptera. During the first nymphal stage of the grasshopper, as described by Nel,

the gonopore undergoes a posterior transposition that gives it its definite location behind the eighth sternum. In the early part of the first instar, Nel says, the oviduct opens on the extreme anterior part of the eighth sternum in the groove extending posteriorly from its aperture. During this instar the lips of the groove unite ventrally, the union proceeding from in front backward; the oviduct is thus extended pos-
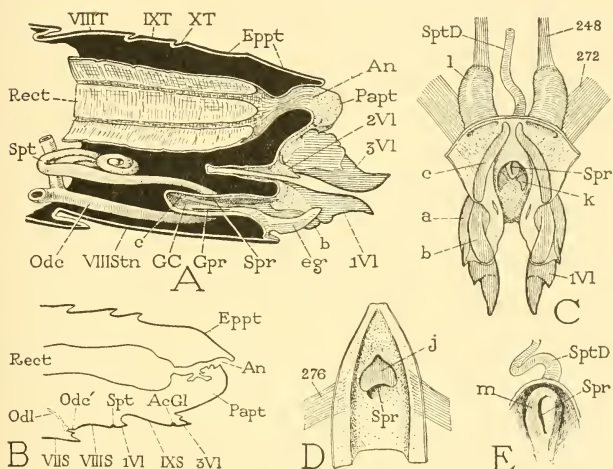

FIG. 20.—Structure and development of the female copulatory apparatus.

A, vertical section of end of abdomen of *Dissosteira carolina* just to left of median plane, showing genital chamber (*GC*) invaginated between bases of ventral valvulae and eighth sternum, with gonopore (*Gpr*) in its ventral wall and spermathecal aperture (*Spr*) in its dorsal wall, the eighth sternum terminating in the egg guide (*eg*). B, diagrammatic section of end of abdomen of first instar nymph of *Locustana* (from Nel, 1929), showing origin of median oviduct (*Odc'*) behind seventh sternum, and spermathecal invagination (*Spt*) at end of eighth sternum. C, ventral view of first valvulae and dorsal wall of genital chamber of *Melanoplus femur-rubrum*. D, spermathecal aperture of *Dissosteira carolina*. E, same of *Melanoplus mexicanus* (structure variable in this species).

teriorly, and its opening, the gonopore, migrates in the same direction, until finally, in the second instar, it takes its definitive position in the newly forming genital chamber behind the eighth sternum.

The typical acridid spermatheca is a long tubular organ extending forward in the ventral sinus of the body cavity beneath the ventral diaphragm (figs. 17 E, 20 A, *Spt*). The middle part is variously coiled, and the tube ends in an enlarged bifid terminal section. The spermatheca of the grasshopper is formed as a median invagination ·in a

groove of the body wall between the bases of the first valvulae (fig.
20 B, *Spt*), and, therefore, belongs to the eighth abdominal segment.
The usual bifid structure of the adult organ in insects suggests that
the spermatheca may have been paired in its origin, but one branch
is generally the sperm storage chamber, and the other a glandular
accessory.

The opening of the spermatheca in the dorsal wall of the genital
chamber in adult grasshoppers lies in a median channel of the mem-
branous space between the anterior basivalvular sclerites of the first
valvulae (figs. 17 E, 20 C, *Spr*). In *Dissosteira carolina* the aperture
is transverse above the posterior margin of a weakly sclerotic heart-
shaped sclerite (fig. 20 D, *j*). Structural details associated with the
spermathecal opening, however, may be quite different in different
acridid species. In *Melanoplus femur-rubrum,* for example, the
spermatheca opens through a crescentic longitudinal slit in an oval
area or sclerite contained in a median pocket of the genital chamber
wall (fig. 20 C, *Spr*). Behind it are two small triangular sclerites (*k*)
in the wall of the pocket. In *M. mexicanus* (E) the aperture is a cleft
between two lateral lips of a thick oval body (*m*) projecting from a
depression in the wall of the genital chamber. It is possible that struc-
tural differences in the female spermathecal opening may be found to
be correlated with differences in the male intromittent organ, since
coition is effected by way of the spermathecal duct.

Accessory genital glands of the ninth abdominal segment are usually
not developed in the Acrididae. According to Nel (1929), however, a
small median invagination is formed between the ovipositor lobes of
the ninth segment in young nymphs of *Locustana* and *Colemania*
(fig. 20 B, *AcGl*), which becomes a short tube, but remains vestigial
even in the adult. The function of the usual female accessory glands
is assumed in Acrididae by a long tubular diverticulum of each lateral
oviduct, or more strictly of the oviducal calyx, in which is secreted
the frothy material of which the egg pod is formed.

DEVELOPMENT OF THE OVIPOSITOR

It is commonly assumed that the ovipositor of pterygote insects is
formed from the limb appendages of the eighth and ninth abdominal
segments, that the valvulae are processes of the appendage bases, and
that the usual supporting plates, or valvifers, are derived from the limb
bases themselves. There is no doubt that the organ is formed from
ventral outgrowths and sclerites of the two genital segments, but it
is quite a different matter to prove that these parts represent true

segmental appendages. Even the fact that the first rudiments of the valvulae appear in some insects on the embryo in line with vestigial appendages on the pregenital segments is not necessarily evidence that they are homodynamous with the latter, since secondary structures arising in the same relative positions as the true limbs would be very likely to assume the same form in early stages of growth. The best evidence of the origin of the ovipositor from limb structures is furnished by the Thysanura, in which the valvulae are outgrowths of lateroventral plates of the genital segments that are clearly equivalent to the stylus-bearing plates present in some forms on the preceding segments, which plates, there seems little reason to doubt, represent the bases of true abdominal limbs. The ovipositor of Thysanura, therefore, appears to be formed of mesal processes (gonapophyses) of the coxopodites of the appendages of the eighth and ninth abdominal segments, and the fundamental similarity of the ovipositor in Thysanura and Pterygota leads us to conclude that the organ is an homologous structure in all insects in which it occurs.

The facts of the development of the ovipositor in Orthoptera are easy to ascertain and are in general well known. In a young nymph of the cricket *Nemobius* (fig. 21 A) two small conical processes (IVl) project from the membranous ventral part of the eighth segment behind the eighth sternum ($VIIIStn$), entirely free from the latter. These processes are the rudiments of the first valvulae. The valvulae of the ninth segment are not yet in evidence; the sternal region of this segment (IXS) shows no differentiation except two slight rounded swellings of its posterior margin. At a somewhat later stage (B, C), however, a pair of valvular processes is present on each genital segment. Those of the eighth segment (B, IVl) still arise from the membrane behind the reduced eighth sternum ($VIIIStn$). The processes of the ninth segment (C, $3Vl$), on the other hand, which become the third valvulae of the adult, arise directly from a median sclerotization of the ventral wall of the segment, at the sides of which is a pair of small but conspicuous oval lateral sclerites (x). There is thus no sternal plate in the ninth segment distinct from the bases of the valvulae.

The two primary pairs of valvular processes increase in length with successive instars (fig. 21 E), and the rudimentary second valvulae appear ventrally between the bases of the third valvulae (F, $2Vl$), but the relations of the valvulae to their respective segmental areas remain unaltered. Up to a late stage there is no evidence of the presence of valvifers, except for the small lateral sclerites (x) of the ninth segment, which increase in size and become more dorsal in position (F).

In the last nymphal stage of the cricket, as illustrated in *Gryllus* (fig. 21 G), the valvifers appear as weak sclerotizations in the areas previously membranous laterad of the bases of the valvulae. The
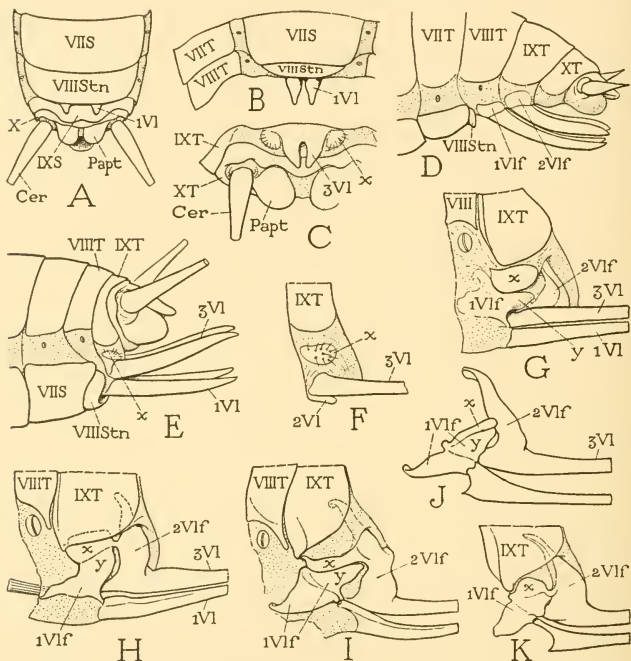

Fig. 21.—Development of the ovipositor of Gryllidae and Tettigoniidae.

A, ventral view of end of abdomen of very young nymph of *Nemobius*. B, seventh and eighth sterna of *Nemobius* at later stage. C, ninth and postgenital segments of same. D, end of abdomen and ovipositor of young nymph of *Neoconocephalus*. E, late instar nymph of *Nemobius*. F, same, lower part of ninth segment and valvulae. G, lower parts of genital segments with base of ovipositor of last nymphal instar of *Gryllus*, showing origin of first valvifer in podial area of eighth segment. H, base of ovipositor of adult *Gryllus assimilis*. I, same of *Orocharis saltator*. J, same of *Neoxabia bipunctata*. K, same of *Cyrtoxipha columbiana*.

first valvifer (*1Vlf*) lies in the ample membrane of the eighth segment behind the small eighth sternum. Ventrally it is connected with the base of the first valvula (*1Vl*), and posteriorly it is prolonged as a prominent lobe (*y*) inserted between the base of the third valvula and the lateral sclerite (*x*) of the ninth segment, which latter is now

closely associated with the lower margin of the ninth tergum. The second valvifer (*2Vlf*) is clearly differentiated in the ninth segment, and has essentially the adult form (H, *2Vlf*). Between the bases of the second and third valvulae of opposite sides are formed the small median sclerites that become the intervalvulae of the ninth segment in the adult.

Throughout the development of the gryllid ovipositor, it is to be observed, there is a significant difference in the position of the parts derived from the two genital segments. The first valvulae and the first valvifers are developed from the ventral membrane of the eighth segment entirely behind the eighth sternum. The sternal plate of the eighth segment, therefore, does not contain the limb bases of this segment. The valvifers and valvulae of the ninth segment, on the other hand, arise from the entire ventral region of this segment, except for a small median part from which are formed the intervalvulae. We may presume, therefore, that the apparent sternal region of the ninth segment has a coxosternal composition, as have the usual definitive sternal plates of the abdomen. The median sternal part forms the intervalvulae; the lateral coxal areas give rise to the valvulae and valvifers. In each genital segment the dorsal muscles of the respective valvifers arise on the tergum.

From the above it is evident that the facts of the development of the ovipositor need " interpretation " to make them fit with the theoretical origin of the ovipositor from segmental limbs, but, it should be observed, they are at least not inconsistent with this theory. It is important to note, furthermore, that the first valvulae are the gonapophyses of the first gonopods, while the first formed processes of the ninth segment are the third valvulae, which are elongations of the coxopodites; the second valvulae, or true gonapophyses of the ninth segment, are of later development. This same order of development of the ninth segment processes recurs in most insects with three valvular components in the ovipositor. In Gryllidae, as in Acrididae, the second valvulae remain rudimentary.

The primitive segmental relations of the valvifers in Gryllidae are somewhat confused in the final development of the basal mechanism of the ovipositor. Each first valvifer, as we have seen, in the last nymphal stage of *Gryllus* (fig. 21 G) has a posterior lobe (*y*) interposed between the base of the third valvula (*3Vl*) and the small lateral sclerite of the ninth segment (*x*), which latter has become closely associated with the lower edge of the ninth tergum (*IXT*). In the adult cricket (*H*) the sclerite *x* is solidly fused with the lobe *y* and thus becomes

virtually a part of the definitive first valvifer, by which the latter articulates with the ninth tergum; but the sclerite acquires also a flexible union with the second valvifer ($_2Vlf$), which gives the two valvifers on the same side a point of motion on each other. This same structure and mechanism occurs in other members of the same family (I, J, K). In the Gryllidae, therefore, the definitive first valvifer is a composite plate formed of the true first valvifer and of a small dorsal sclerite derived from the coxopodite region of the ninth segment, and thus acquires its secondary articulations with the ninth tergum and with the second valvifer. In the Tettigoniidae the valvifers have a simpler structure, and in the nymph (fig. 21 D) each is a small plate ($_1Vlf$, $_2Vlf$) in its respective segment; those of the first pair are entirely separated from the small eighth sternum ($VIIIStn$).

It will now be of interest to study the development of the ovipositor in a member of the Acrididae in order to discover if possible the nature of the disparity, so evident in the adult structure, between the acridid type of ovipositor and that characteristic of other insects. In a very young nymph of *Melanoplus* (fig. 22 A) the ventral plates of both genital segments are well developed and of approximately equal size. Rudiments of the first valvulae are evident as a pair of flattened lobes ($_1Vl$) slightly protruding from behind the sternum of the eighth segment; but the third valvulae ($_3Vl$) already have the form of small conical processes arising from the posterior part of the ninth sternum. Here, then, we encounter again the same differences in the relations of the valvulae to the sternal plates as was observed in Gryllidae and Tettigoniidae, namely, the origin of the first valvulae behind the sternum of their segment, and that of the third valvulae directly from the sternal plate. At a later stage in the growth of *Melanoplus* (B, C) the first valvulae have become conical processes, and the small second valvulae (C, $_2Vl$) have appeared between the bases of the third valvulae. From this stage to that of the adult but few external changes take place in the ovipositor. The intervalvular sclerites are developed medially before and behind the bases of the valvulae of the ninth segment, the ninth sternal region becomes otherwise reduced, while the eighth sternum increases its length and acquires a small median process on its posterior border, which is to be the egg guide. The valvulae take on the form characteristic of the adult, and those of the first and third pairs become densely sclerotic in the mature insect.

The acridid ovipositor is thus seen to be an organ formed entirely of the valvulae, there being no differentiation of valvifers in the coxopodite areas of either genital segment. In the eighth segment the coxopodite areas must lie in the membrane behind the eighth sternum

(fig. 22 A), but they are never apparent as specific structures. The coxopodites of the ninth segment, on the other hand, are evidently contained in the posterolateral parts of the apparent ninth sternum of the very young nymph (A, *IXS*); later they appear as distinct membranous lateral areas (C, *IXCxpd*) from which the third valvulae (*3Vl*) project as direct continuations, and from which the small second valvulae (*2Vl*) arise medially as endite lobes. The coxopodite areas remain membranous in the adult. The true sternal region of
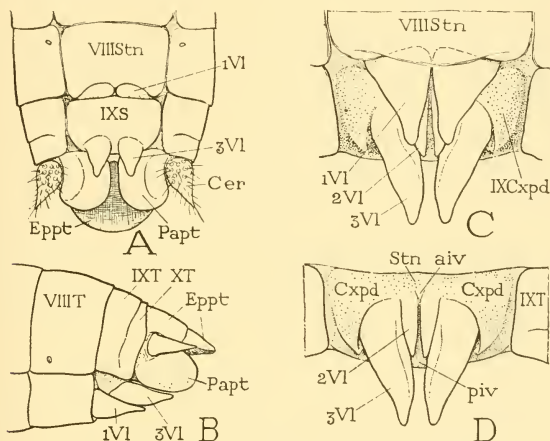

Fig. 22.—Development of the ovipositor of Acrididae.

A, ventral view of end of abdomen of first instar nymph of *Melanoplus*, showing first valvulae as small lobes arising between eighth and ninth sterna, and third valvulae as processes of ninth sternal plate. B, later stage of same, lateral view. C, same as last, ventral view, showing intermediate second valvulae. D, valvulae of ninth segment seen as processes of the coxopodite areas, in which valvifers are not formed in Acrididae.

the ninth segment becomes reduced to a narrow median band between the bases of the valvulae, which includes the areas (D, *aiv, piv*) in which finally will be formed the intervalvular sclerites.

From the above it seems clear that the peculiar feature of the acridid ovipositor is the lack of valvifer sclerites, a conclusion which might be deduced also from the absence of dorsal muscles corresponding with the tergovalvifer muscles of other insects. A different view of the matter, however, has been taken by Nel (1929), who contends that the manner and place of origin of the two first-formed pairs of ovipositor processes leave no doubt that the latter are serially ho-

mologous, while the absence of median lobes between the processes of the eighth segment shows that true gonapophyses are not developed on the gonopods of this segment. Nel concludes, therefore, that the first and third valvulae are developments of the gonocoxae, and that the second valvulae have no morphological equivalents on the eighth segment. As we have seen, however, the valvular processes of the eighth and ninth segments do not have a similar place of origin relative to the sternal regions or plates of their segments, and that a comparison of the development of the ovipositor of Acrididae with that of Gryllidae and Tettigoniidae shows clearly that the elements of the usual ovipositor that are absent in the acridid organ are the valvifers, which are the true representatives of the coxopodites. It may still be difficult to prove that the first valvulae are gonapophyses homodynamous with the second valvulae, and not coxal processes corresponding with the third valvulae; but the identical relations of the first and second valvulae to their respective valvifers in most insects, and the fact that these valvulae constitute the usual blades in the shaft of the ovipositor, to which the third valvulae are mere ensheathing lobes, leaves little basis for questioning the apparent and generally accepted homologies of the ovipositor components. There can be no doubt, at least, that the prongs of the acridid ovipositor correspond with the valvulae of the ovipositor of other insects.

OVIPOSITION

The females of Acrididae lay their eggs in holes made by the ovipositor; most species dig the egg cavity in the ground, a few bore into decayed wood or into the stems of living plants. The ovipositor, therefore, is both an excavating and an egg-laying instrument. In penetrating an even soil the abdomen usually extends downward in a slanting direction from the insect and then turns more or less parallel with the surface of the ground (fig. 23 F); the curvature of the extended abdomen is perhaps attributable to the fact that the protractor muscles of the abdominal sterna (fig. 8, *145-204*) have no dorsal opposition, since the external muscles of the back are transverse in position and give a lateral twist to the segments on one another. The shape of the burrow, however, is subject to much irregularity, especially where ovipositing insects are crowded on a small area, or where obstacles are encountered in the soil. When the abdomen is fully extended it may reach a length two or three times that of its usual retracted condition. The great extension of the abdomen is made possible by the size of the conjunctival membranes ordinarily inflected between the sclerotic parts of the segments (fig. 23 A, E).

The excavation of the egg cavity in the ground and the deposition of the eggs therein have frequently been described in a general way, but the process has been closely studied in the case of *Anacridium aegyptium* by Fedorov (1927), who confined females of this species in cages each having a narrow, glass-walled extension of the floor, 7 mm wide, filled with earth. The diameter of the female's abdomen being 7 mm, the procedure of digging and oviposition could be observed and photographed.

The female grasshopper, according to Fedorov's account, at the beginning of excavation arches her abdomen upward and directs the tip of the ovipositor downward against the soil. The valves of the ovipositor now begin opening and closing, making a hole in the earth, and the ovipositor gradually enters deeper and deeper, while the abdomen extends. The lengthening of the abdomen is accompanied by an unfolding of the conjunctival membranes principally between segments *IV* and *V, V* and *VI,* and *VI* and *VII,* and to a lesser degree of those between segments *III* and *IV,* and *VII* and *VIII.* The segments beyond the eighth do not extend, but are even more closely drawn together than usual. The entire extended abdomen may reach a length of 9 or 10 cm, its ordinary length being about $3\frac{1}{2}$ cm. While digging, the part of the abdomen beyond the sixth segment twists through an angle of 90°, now to one side, now to the other. The entire process of excavating the cavity in suitable earth without special obstacles takes from 1 to $1\frac{1}{2}$ hours. " The whole complex work of digging," Fedorov says, " may be analyzed as consisting of the following simple movements : (1) putting the valves of the ovipositor together, (2) a jerk downward, and (3) opening the valves ; apart from that the ovipositor is turned by muscles now to the left, now to the right."

Most observers of ovipositing grasshoppers have been much puzzled to understand the mechanism of the digging apparatus, or particularly the means by which the abdomen is extended to such a great length and apparently with sufficient force to penetrate the earth. Künckel d'Herculais (1894) noted that the fully extended abdomen of *Schistocerca peregrina* has a length of 8 cm, while the retracted abdomen, though filled with eggs, is only 5 cm long. On dissecting specimens with the abdomen protruded at maximum length he found the alimentary canal to contain air ; by letting out the air the abdomen could be restored to its ordinary size. Hence he concluded that the digging insects swallow air into the alimentary tract in order to give the abdomen the necessary extension, the surrounding blood serving to regulate the pressure. Contrary to the opinion of most writers,

Künckel d'Herculais says, the muscles play only a secondary rôle in the expansion of the abdomen. It has been suggested also that the abdomen is distended by blood pressure created by a contraction of the thorax, but Grasse (1922) observes that there is no external evidence of any such contraction. A contraction of the tergosternal abdominal muscles might be supposed to extend the abdomen lengthwise, but these muscles could not produce the extreme elongation
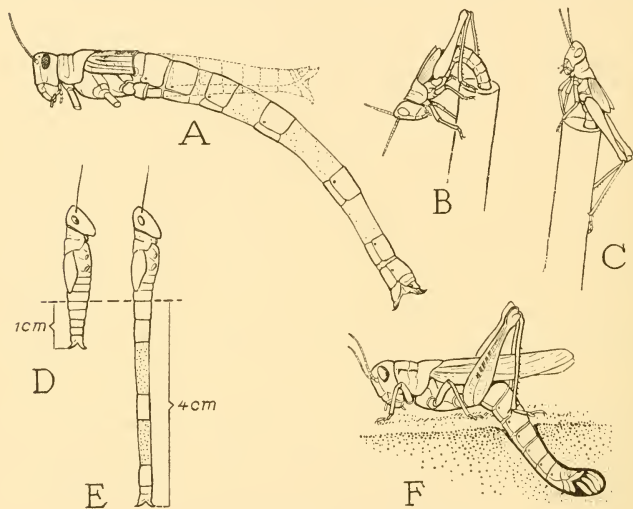

Fig. 23.—Oviposition of Acrididae.

A, *Schistocerca peregrina*, showing extent to which the female abdomen can be pulled out without tearing the conjunctival membranes (from Vosseler, 1905). B, C, two attitudes of *Chrysochraon dispar* ovipositing in cut ends of raspberry stems (from photographs by Ramme, 1927). D, E, diagrams showing relative lengths of retracted and extended abdomen of *Chrysochraon dispar* (from Ramme, 1927). F, grasshopper ovipositing in the ground, showing usual position of abdomen (from Walton, 1916).

attained during the digging process. Grasse maintained that the explanation of Künckel d'Herculais is correct, since he was able to demonstrate the extension of the abdomen by gently inflating the alimentary canal with a pipette inserted into the mouth of the insect and ligatured in the oesophagus through a hole at the back of the head. However, a different explanation of the abdominal extension has been proposed by Fedorov (1927), who says: " When the abdomen is fully extended it becomes obvious that the expansion is due to the air-sacs ;

one can see that the rhythmical movements of the abdomen, which apparently facilitate the work of the spiracles, result in the filling of the sacs with air, in their expansion and in the expansion of the abdomen." In his summary Fedorov definitely states : " Inflation of the air-sacs is the cause of the expansion of the abdomen."

Without having made more than casual observations on egg-laying female grasshoppers, the writer, after studying carefully the mechanism of the ovipositor, has no hesitation in saying that the above explanations of the extension of the abdomen during the digging process are not only highly improbable, but are quite unnecessary. It is true that the muscles of the abdomen are entirely inadequate to distend the telescopic abdominal tube to the length observed, and, as we have seen, the protractor muscles that are present are limited to the sternal region. Furthermore, the writer has frequently observed that females of *Dissosteira carolina* taken in late summer and fall have all the muscles of the visceral part of the abdomen in a very lax and apparently semidegenerate condition, contrary to what is found in the male. There is no reason to doubt the observations of Künckel d'Herculais that the alimentary canal contains air during the digging process, or that of Grasse that an inflation of the food tract will distend the abdomen ; nor is there any reason to question the statement of Fedorov that the air sacs become expanded as the abdomen lengthens. It is, however, quite too much to believe that the observed inflation of the alimentary canal or of the air sacs could be the means by which the abdomen is thrust out with sufficient pressure against the ovipositor to drive the latter into the ground. Insects can and do swallow air in sufficient amount to distend the body, as in moulting, but there is no demonstrated mechanism by which they can pump air into the air sacs and distend these delicate vesicles against any considerable opposing pressure.

An examination of the mechanism of the grasshopper's ovipositor shows that the latter is an organ fully competent to dig its own way into the ground ; it is a boring machine, which, once set in motion with its prongs against the soil, must automatically bury itself, and in so doing it will stretch the easily extended abdomen to its full capacity, so long as the insect maintains its hold on the surface of the ground. There is thus no question of the abdomen forcing the ovipositor into the earth ; the ovipositor digs the hole and pulls the abdomen in after it. The extension of the abdomen undoubtedly involves a distention of the air sacs, and is probably facilitated by an active swallowing of air on the part of the insect ; in fact, if the abdomen is actually increased in bulk by the drawing apart of its seg-

ments, it becomes a matter of necessity that there should be a compensation from some source, and the expansion of the air sac would take place automatically as in the inspiratory phase of breathing. The observed filling of the stomach and air sacs with air, therefore, is certainly not the active cause of the elongation of the abdomen; it seems much more probable that the inflation of these organs, followed by a closure of the mouth and spiracles, serves to maintain the extension of the abdomen when the valvulae of the ovipositor are closed, since the latter has then no means of holding its position in the earth.

If we consider the several digging movements of the ovipositor concisely enumerated by Fedorov, we can readily correlate them with muscles in the motor apparatus. The preliminary closing of the valvulae is effected by the muscles of the anterior intervalvula (fig. 17 D, C, *247, 273*); the downward thrust must be produced by the protractors inserted on the ends of the lateral apodemes (C, *256, 262*); the opening of the valvulae is the work of the powerful levators and depressors (A, B, *271, 272*); the twisting movements of the abdomen are accomplished by the transverse outer dorsal muscles between the successive tergal plates (fig. 11 B, C). In addition to these muscles there are the lateral retractors of the dorsal valvulae (fig. 17 C, *263*), evidently capable of pulling the ovipositor back into the genital segments. The muscular equipment of the ovipositor, therefore, is such that there is no need to invoke any other mechanism to account for the operation of the digging apparatus and the stretching of the abdomen than that of the ovipositor itself.

Species of Acrididae known to oviposit in dead wood or in the stems of plants include *Chloealtis conspersa* Harris of North America, and *Chrysochraon dispar* Germ. of Europe. Females of *Dissosteira carolina* are often to be seen along railroad tracks with the end of the abdomen inserted into a decayed part of a tie, though, so far as the writer knows, there is no record of their eggs being deposited in such places.

Chloealtis conspersa is said by Scudder (1874) to select for oviposition short sticks of decaying, charred, or pithy wood, but never to choose upright pieces of timber. " The holes," Scudder says, " are pierced at a slight angle to the perpendicular, away from the insect; they are straight for about a quarter of an inch, then turn abruptly and run horizontally along the grain for about an inch. The eggs (from 10 to 14 in number) are almost always laid in the horizontal portion of the nest." Blatchley (1920) also records observations on the wood-excavating habits of the same species. One female he discovered in

the act of boring a hole in the upper edge of the topmost board of a six-plank fence. " The abdomen," he says " was curved downward, and the toothed forcipate valves of the ovipositor used as pincers with which small pieces of wood were broken off." Within a distance of 30 feet on the top boards of the same fence, which were perfectly sound pine, he found 15 other holes, but none of them contained eggs, the wood apparently being too hard for the proper completion of the borings. Cavities made in stumps and logs, however, were found to have eggs in the horizontal part of each.

The oviposition habits of *Chrysochraon dispar* have been recorded by Ramme (1927), who says that all nests found in the neighborhood of Berlin except one were in stems of raspberry bushes, though other observers report finding them in rotten poplar stumps and in broken stems of *Angelica sylvestris*. Ramme studied the insects in cages, where they were supplied with short pieces of raspberry stems stuck into moist sand. A female about to oviposit, he says, crawls up a stem ; reaching the cut top she examines the pith with her antennae, and then climbs over the top and down the opposite side a short distance. As soon as the ovipositor touches the pith it begins digging into the latter, and soon forms a hole in which the end of the abdomen disappears (fig. 23 B) ; deeper and deeper it sinks until after a half hour or an hour the cavity is completed (C). Woody as well as fresh stems are accepted. When the boring is finished, the abdomen is buried to the fourth or at least to the middle of the fifth segment (E). The length of the abdomen beyond this point is ordinarily only 1 or $1\frac{1}{4}$ cm (D), but during the digging process it may be stretched to a length of 4 cm. In cages Ramme found that the insects were unable to penetrate the stems unless they had access to the cut tops of the latter, from which he concludes that in nature they must use injured or broken canes. In each nest 12 to 30 eggs are deposited, placed obliquely one above the other.

The action of the ovipositor in manipulating the eggs issuing from the oviduct has not received as much attention from students of acridian behavior as have the processes of digging and oviposition. Judging from the anatomical relation of the gonopore to the egg guide and the ovipositor (fig. 20 A), it is clear that an issuing egg must be conducted by the egg guide posteriorly and upward between the bases of the free parts of the ventral valvulae. The eggs are normally so oriented in the oviduct that the anterior pole (the head end of the future embryo) is anterior ; the protruding egg, therefore, has its posterior pole directed posteriorly and upward. Riley (1878) says the

newly emerging egg is received between the closed valvulae, and he figures it as being extruded upward and posteriorly from between the dorsal valvulae; at least, he assures us, this is what we should see "if we could manage to watch a female" during oviposition. If the female grasshopper habitually curves the end of her abdomen forward, as shown in Riley's familiar illustration, the eggs extruded in this way would naturally take the proper position in the nest with their anterior ends upward and sloped toward the exit. Most studies of the egg cavity, however, show that the burrow, when unobstructed, extends obliquely downward and backward from the insect. In this case the eggs must be tilted in a direction opposite that of their first position, namely, with the anterior pole upward and forward, if the young grasshopper is to have an easy escape from the nest.

Observations by Giardina (1901) on the extrusion of the eggs by females of *Pamphagus marmoratus,* which oviposited on the bottoms of cardboard boxes in which they were confined, seem to show that each egg is revolved through an angle of 45° as it leaves the ovipositor. Giardina observes that each egg issuing from the oviduct is conducted by the egg guide posteriorly and upward into the ovipositor, where it is at first received and held in this position between the ventral valvulae; but at this time the upper and lower valvulae are wide open, and the prongs of the lower valvulae are somewhat separated. Now, however, the valves suddenly close, and the egg is thrust between the dorsal valvulae, where it remains suspended until the arrival of the next egg, which causes the first to take a horizontal position with the posterior pole directed backward. Finally, with the advent of a third egg, the first, already liberated from the ovipositor, receives another push, which tilts it into a third position in which the anterior pole is directed upward and forward, *i. e.,* obliquely toward the upper wall and the exit of the nest (fig. 23 F).

The issuing eggs are always accompanied by a large amount of viscous frothy material, which soon hardens and forms the much-vacuolated mass enclosing the eggs, known as the "egg pod." The foamy nature of the egg covering is said to be imparted to the liquid fresh substance by movements of the valvulae. The female Acrididae lack the usual accessory glands of the genital apparatus that ordinarily form whatever adhesive or covering material is extruded with the eggs; the substance of the acridid egg pods is produced in long glandular diverticula of the anterior ends of the large calyces of the lateral oviducts, and is discharged with the eggs through the gonopore.

VI. THE EXTERNAL MALE GENITALIA

The external genital structures of the male are so different in the grasshoppers from these organs in other Orthoptera that little attempt will be made here to establish homologies between the acridid organs and the various types of genital structures found in the other orthopteroid families. Walker (1922) has presented a plausible though theoretical scheme for tracing the evolution of the male organs in the Orthoptera, and his ideas will be discussed in a future, more general paper. The acridid genitalia have been but little studied from a comparative standpoint, and only one writer (Hubbell, 1932) has attempted to make use of their characters for taxonomic purposes. The basic structure of the organs is surprisingly alike throughout the family, but there can be no doubt that distinctive specific variations are well marked in many cases.

GENERAL STRUCTURE OF THE MALE GENITALIA IN ACRIDOIDEA

The terminal part of the adult male abdomen in both Acrididae and Tetrigidae is characterized by a great enlargement of the ninth sternum, and by a partial or complete separation of the latter into a proximal part and a distal part that are more or less movable on each other (figs. 27 A, 33 A, 35 A, 36 B, 39 A, *IXS, IXSL*). The proximal sternal plate (*IXS*) may be designated the ninth sternum proper; the distal lobe (*IXSL*) is the male subgenital plate. Styli are absent in all Acridoidea, but if they were present on the ninth abdominal segment they undoubtedly would be carried by the genital lobe of the sternum, and for this reason the lobe is sometimes regarded as representing the united coxopodites of the ninth segment. Since, however, in the young male nymph there is no suggestion of the later division of the ninth sternum, it seems probable that the two sternal plates of the adult are the result of a secondary subdivision of the usual coxosternum of the ninth segment without reference to its more primitive composition.

The subgenital lobe of the ninth sternum is usually turned upward on the end of the proximal plate, and its dorsal margin may be tightly closed against the lobes of the eleventh segment (figs. 29 A, 30 A, 34 A). More generally, however, there is continued forward from the free margin of the subgenital plate a thick membrane, the pallium (fig. 33 A, *Pal*), which presents a rounded or hoodlike dorsal surface closing the space between the upper end of the genital plate and the eleventh segment. Behind the latter the pallium is always deeply inflected to form the posterior wall of the genital chamber (fig. 24 A,

Pal'). In the Tetrigidae the exposed dorsal part of the pallium forms
a long valvelike flap containing two elongate plates (fig. 27 A, B,
PlVlv). In *Tettigidea* the plates are separated by a median mem-
branous line (B), but in *Acrydium* and *Paratettix,* according to
Walker (1922), the pallial valve is armed between the plates with a
pair of bars terminating anteriorly in upcurved hooks.

The male genital chamber of the Acrididae (fig. 24 A, *GC*) has
the usual relations of the male genital pouch to the ninth and tenth

FIG. 24.—Diagrams showing the general structure of the male genitalia of
Acrididae.

A, vertical longitudinal section of end of male abdomen somewhat to left of
median plane, showing the organs contained in the genital chamber (*GC*), and
the endophallus (*Enph*) projecting into the body cavity. B, the aedeagus and
its basal apodemes. C, the aedeagus and endophallus.

Aed, aedeagus; *An,* anus; *Apa,* aedeagal apodeme; *bf,* basal fold; *Dej,* ductus
ejaculatorius; *dl,* dorsal lobe of aedeagus; *ejs,* ejaculatory sac; *Enph,* endophal-
lus; *Epph,* epiphallus; *Eppt,* epiproct; *GC,* genital chamber; *IXS,* sternum of
ninth abdominal segment; *IXSL,* genital lobe of ninth sternum; *Pal,* pallium;
Pal', inner fold of pallium; *Papt,* paraproct; *Phtr,* pallotreme (external opening
of endophallus); *Rect,* rectum; *sps,* spermatophore sac of endophallus; *vl,* ventral
lobe of aedeagus; *XT,* tergum of tenth abdominal segment, *X.V,* venter of tenth
segment. (For alphabetical lettering see fig. 25.)

abdominal segments—that is, it is an invagination cavity between
the end of the ninth sternum and the venter of the tenth segment.
Owing to the vertical position of the subgenital plate, however, and
the forward extension of the pallium from the latter, the opening of
the cavity is dorsal between the eleventh segment and the inflected
margin of the pallium. The anterior part of the genital chamber is
covered by the ventral walls of the tenth and eleventh segments, the
posterior part by the hood of the pallium. The floor of the chamber
usually slopes downward posteriorly from the venter of the tenth
segment (*X.V*) to the base of the inner pallial fold (*Pal'*).

The phallic organs of the Acrididae consist of a complex of structures arising from the floor of the genital chamber (fig. 24 A), and ordinarily they are entirely enclosed within the genital chamber. Posteriorly is the intromittent organ, or *aedeagus* (*Aed*), which has an upright position and is lodged in the pocket beneath the pallial hood. In front of the aedeagus is a broad sloping area of the genital chamber floor, often rounded and elevated, which rises posteriorly in a prominent transverse *basal fold* (*bf*) that more or less conceals the proximal part of the aedeagus. In the anterior pocket of the genital chamber, seated transversely on the floor of the latter beneath the venter of the tenth abdominal segment, is the *epiphallus* (*Epph*), a large irregular sclerite characteristic of the Acrididae.

The aedeagus (fig. 24 A, *Aed*) is a complex organ, somewhat variable in the relative size and shape of its parts in different genera, but having a constant basic structure that can be recognized in all cases without difficulty. It consists essentially of an irregular dorsal lobe (*dl*), and of a simple ventral lobe (*vl*). Because of the vertical position of the organ the dorsal lobe is anterior and the ventral lobe posterior. These two principal parts of the acridid aedeagus are apparently to be identified with corresponding lobes of the intromittent organ in Tettigoniidae; the ventral lobe is the most constant structural feature of the diverse copulatory apparatus of Blattidae, Mantidae, Tettigoniidae, and Gryllidae, since it always has the form of a soft or partly sclerotized flap projecting below the external genital opening. In the Acrididae the outer genital aperture, or *phallotreme,* is a vertical cleft in the entire length of the ventral (posterior) surface of the dorsal lobe of the aedeagus (figs. 24 C, 37 C, *Phtr*), but the ventral lobe (*vl*) projects beneath its proximal part, and thus has the same relation to the genital opening as has the corresponding lobe in the families above mentioned.

The dorsal lobe of the aedeagus is divided typically into a broad proximal part (fig. 24 B, *m*), and a smaller, usually cylindrical distal part (*r*), from the end of which there project two pairs of apical processes (*n, p*). In some forms, however, the distal part of the aedeagus is small or absent, and in such cases the apical processes are generally relatively large (fig. 31 C) and are carried directly by the proximal part (*m*). The distal part of the dorsal lobe is best developed in the Cyrtacanthacrinae (fig. 37 A). Both the distal and the proximal parts of the dorsal lobe are deeply cleft posteriorly by the phallotreme (figs. 24 C, 37 C, *Phtr*), which invades the extremity of the organ between the apical processes, and extends proximally to the base of the ventral lobe.

5

The lateral walls of the proximal part of the dorsal aedeagal lobe (fig. 24 B, *m*) are usually strongly sclerotized and are often produced dorsally in a pair of rounded lobes. The lateral sclerotizations are continued anteriorly into a pair of large aedeagal apodemes (*Apa*) invaginated in deep lateral pockets beneath the basal fold (A, B, *bf*) that arches over the base of the aedeagus. Within the dorsal part of this fold, in the wall of its ventral lamella, the bases of the apodemes are solidly united with each other by a strong, transverse sclerotic bridge, or *zygoma* (B, *z*). The aedeagal apodemes are the " endapophyses " of Walker (1922), and the zygoma the " arch of the endapophyses." The aedeagal apodemes give attachment to muscles inserted on the walls of the endophallus.

The ventral lobe of the aedeagus has the form of a broad trough-like fold (fig. 24 A, *vl*), usually membranous though sometimes more or less sclerotized, extending upward from the floor of the genital chamber at the base of the inner fold of the pallium (*Pal'*), and closely embracing the base of the dorsal lobe of the aedeagus. It thus conceals the lower part of the phallotreme. The ventral aedeagal lobe is termed the " subventral lobe " by Walker (1922).

The most highly developed and characteristic feature of the acridid phallic apparatus is a large endophallic structure deeply invaginated from the phallotreme into the ventral part of the ninth abdominal segment (fig. 24 A, C, *Enph*). The walls of the *endophallus* are covered by broad plaques of muscle fibers, which give the structure the appearance of a strong muscular bulb (fig. 25 C, E, F). It is necessary to remove these muscles in order to study the skeletal details of the endophallus as presented in the following descriptions.

The long, vertical, slitlike phallotreme opens directly into a laterally compressed cavity of the dorsal lobe of the aedeagus. At the base of the latter this open cleft passes into a short tubular meatus, which leads into a large inner chamber of the endophallus. In each lateral wall of the phallotreme cleft are two elongate parallel sclerites (fig. 24 C, *o, q*), from the outer ends of which project the external apical processes (*n, p*). The dorsal (anterior) sclerites (*o*) end proximally in the meatus, where they are connected with each other by a strong transverse arch (*t*) in the dorsal wall of the passage. The ventral (posterior) sclerites (*q*) extend proximally beyond the dorsal sclerites a short distance, where they become much narrowed, and then each makes an abrupt sigmoid flexure (*s*) dorsally in the lateral wall of the meatus, beyond which it expands anteriorly as a large plate (*u*) in the lateral wall of the endophallic chamber. The anterior end of each lateral endophallic plate is produced beyond the lumen of the
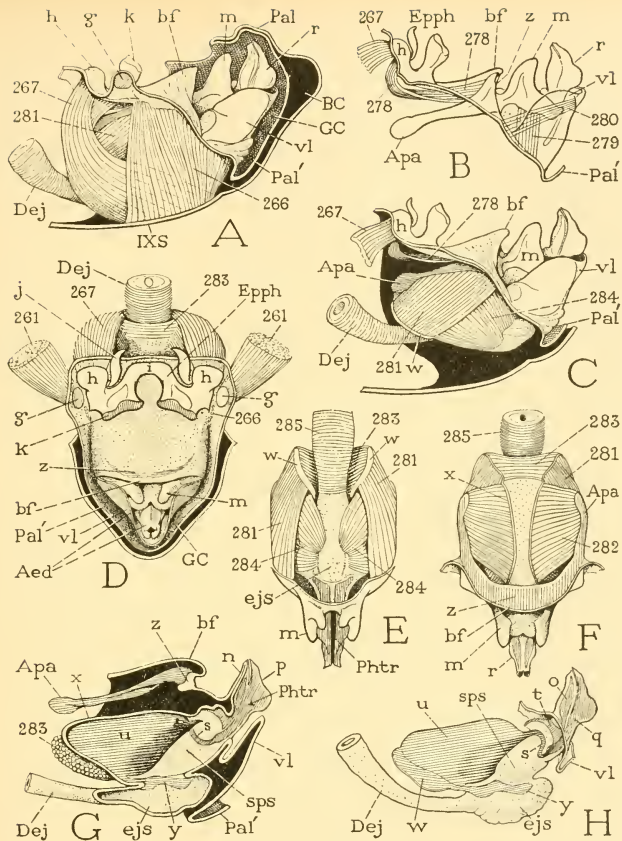
FIG. 25.—Male genitalia of *Dissosteira carolina*.

A, the phallic organs exposed by removal of tenth and eleventh segments and dorsal and lateral parts of ninth segment. B, lateral view of epiphallus and aedeagus with supporting floor of genital chamber. C, lateral view of phallic organs after removal of muscles *266* and *267* (A), showing muscles of endophallic bulb. D, dorsal view of phallic organs and floor of genital chamber. E, aedeagus and endophallic bulb, ventral view. F, same, dorsal view. G, median section of aedeagus and endophallus, with terminus of ejaculatory duct. H, lateral view of endophallus, distal part of aedeagus, and terminus of ejaculatory duct, muscles removed.

For abbreviations, see fig. 24. *g*, sclerites giving insertion to retractor muscles (*261*); *h*, lateral lobe of epiphallus; *i*, bridge of epiphallus; *j*, anterior process of epiphallus; *k*, posterior process of epiphallus; *m*, proximal part of dorsal lobe of aedeagus; *n*, anterior (dorsal) apical process of aedeagus; *o*, anterior (dorsal) lateral sclerite of phallotreme cleft; *p*, posterior (ventral) apical process of aedeagus; *q*, posterior (ventral) lateral sclerite of phallotreme cleft; *r*, distal part of dorsal lobe of aedeagus; *s*, arm of posterior phallotreme sclerite (*q*) continuous with endophallic plate (*u*); *t*, bridge of anterior phallotreme sclerites (*o*); *u*, lateral plate of endophallus; *w*, anterior apodeme of endophallic plate; *x*, dorsal edge of endophallic plate; *y*, gonopore process of endophallic plate; *z*, zygoma of aedeagal apodemes.

65

endophallus as a broad apodeme (w) for muscle attachments. The endophallic plates are the "endoparameres" of Walker (1922), who believes that they are representatives of external or variously invaginated plates or processes ("parameres") of other Orthoptera. By comparison with Tettigoniidae it does appear probable that the endophallus of Acrididae is produced as an invagination of the posterior surface of the dorsal lobe of the aedeagus.

The cavity of the endophallus is mostly a narrow vertical space between the lateral endophallic plates, but its posterior membranous part, somewhat expanded behind the oblique posterior margins of the lateral plates, forms a distinct section of the lumen, and may be designated the *spermatophore sac* (fig. 24 C, *sps*). The ejaculatory duct (Dej) opens into the ventral part of the spermatophore sac through a terminal *ejaculatory sac* (ejs). The aperture between the two sacs is the true *gonopore*. Dorsally the spermatophore sac communicates with the phallotreme cleft in the dorsal lobe of the aedeagus through the meatus at the base of the latter. From the lower anterior angle of each lateral endophallic plate a long process (y) projects backward in the membranous connecting wall between the spermatophore sac and the ejaculatory sac. The two processes thus closely embrace the gonopore (fig. 29 E, F, fig. 33 C), and, as will be shown later, by the action of the endophallic muscles they regulate the opening and closing of the gonopore. Lateral vesicles of the ejaculatory sac, such as are present in most other Orthoptera, are absent in the Acrididae.

The curious sclerite known as the epiphallus is a very prominent feature of the acridid genitalia. It is situated on the floor of the anterior pocket of the genital chamber beneath the venter of the tenth and eleventh segments (fig. 24 A, $Epph$), and is separated from the aedeagus by the sloping surface that culminates posteriorly in the hoodlike fold (bf) covering the base of the aedeagus. The morphological nature of the epiphallus is doubtful, since the sclerite cannot be satisfactorily identified with any part of the phallic structure in other insects. The plate is termed the "pseudosternite" by Walker (1922) and by Ford (1923). It has muscular connections both with the ninth sternum and with the zygoma of the aedeagal apodemes. In form the epiphallus is an irregular transverse sclerite (fig. 31 B) consisting of two expanded lateral lobes (h, h) connected by a narrow median bridge (i). Anteriorly the lateral lobes bear a pair of hooklike processes (j) directed forward, and posteriorly each is produced upward in a large thick irregular transverse process (k). Closely associated with the epiphallus laterally are two small oval

sclerites (*g*) in the floor of the genital chamber (figs. 25 D, 33 B, 35 B), on which are inserted strong muscles (*261*) from the lateral parts of the ninth abdominal tergum.

The aedeagus is ordinarily entirely concealed within the posterior part of the genital chamber beneath the hood of the pallium (fig. 24 A). In the protracted condition, however, the organ is exposed by a retraction of its coverings (fig. 33 B). The genital lobe of the ninth sternum (*IXSL*) is now depressed, and the pallium is turned inside-out, appearing in this condition as a large posterior fold (*Pal*) around the base of the aedeagus, while the basal fold of the genital chamber floor (*bf*) correspondingly embraces the aedeagus anteriorly; the epiphallus (*Epph*) has emerged from its pocket beneath the eleventh segment, and stands boldly exposed on the projected floor of the genital chamber anterior to the ensheathing folds of the aedeagus.

The exsertion of the phallic organs would appear to be accomplished by pressure resulting from a contraction of the pregenital part of the abdomen, since there are no muscles connected with the genital organs capable of producing the protracted condition of the latter (fig. 33 B). The aedeagus apparently is held in the position of retraction by a broad sheet of muscles on each side (fig. 25 A, *266*) arising medially on the ninth abdominal sternum and attached dorsally on the lateral margins of the genital chamber floor. To be exserted, the aedeagus must first be drawn forward from the pocket of the pallium; its release from the latter evidently is effected by the contraction of the strong muscles (D, *261*) inserted on the small sclerites (*g*) at the sides of the epiphallus, which take their origins on the lateral parts of the ninth tergum. The epiphallus itself is provided with a pair of large muscles (A, *267*) arising medially on the ninth sternum, which curve upward around the anterior end of the endophallic bulb and insert on the lateral lobes (*h*) of the epiphallus. It is probable that a contraction of these muscles brings about an elevation of the distal parts of the phallic apparatus, and that pressure from within the abdomen then protrudes the aedeagus. A second pair of epiphallic muscles (B, *278*) arises posteriorly on the zygoma of the aedeagal apodemes and extends anteriorly to the lateral lobes of the epiphallus. The action of these muscles is not clear, but the muscles undoubtedly play some part in the function of the epiphallus in copulation.

The following description of the musculature of the aedeagus and endophallus is based on a study of *Dissosteira carolina,* but a cursory examination of the other species suggests that the musculature and mechanism of the acridid male organs are the same throughout the family.

Two pairs of small muscles lie within the aedeagus, both arising within the base of the latter (fig. 25 B); those of one pair (*279*) extend dorsally to the lateral plate (*m*) in the proximal part of the dorsal lobe, those of the other pair (*280*) are attached distally on the ventral lobe. The other muscles of the aedeagus include the epiphallic muscles (*278*) already mentioned, which arise on the zygoma of the apodemes, and muscles that functionally pertain to the endophallus.

The endophallus is mostly ensheathed in broad muscle plaques, which make of the organ a strong muscular bulb, into which opens the ejaculatory duct. The endophallic musculature comprises dilator
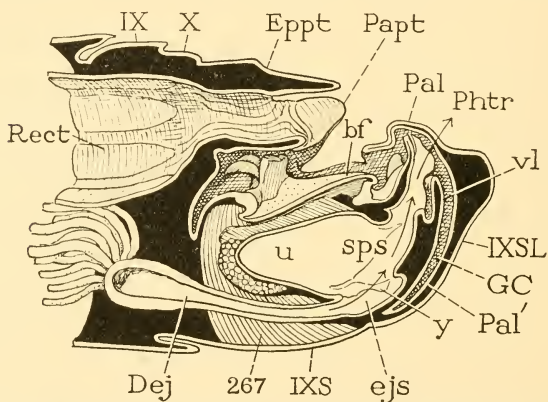
Fig. 26.—Median vertical section of the end of the male abdomen of *Dissosteira carolina* showing the retracted position of the phallic organs.

and compressor muscles of the endophallus, and compressors of the ejaculatory sac. The dilators of the endophallus include a pair of lateral muscles (fig. 25 C, E, *281*) and a pair of dorsal muscles (F, *282*). The lateral dilators are wide sheets of muscle fibers arising dorsally on the aedeagal apodemes (C, *Apa*), and extending ventrally and anteriorly to the outer surfaces of the anterior apodemes of the lateral endophallic plates (C, E, *w*). The dorsal dilators, which likewise are broad sheets of fibers (F, *282*), arise laterally on the inner margins of the aedeagal apodemes and are inserted mesally on the dorsal margins (*x*) of the endophallic plates. The single compressor muscle of the endophallus consists of a thick mass of fibers stretched transversely over the anterior end of the endophallic bulb (E, F, G, *283*)

between the inner faces of the anterior apodemes of the lateral plates. The compressors of the ejaculatory sac are broad plaques of fibers closely applied to the lateral walls of the endophallus (C, E, *284*); each arises on the entire outer wall of the lateral endophallic plate, and its fibers converge ventrally to their insertions on the lateral wall of the ejaculatory sac. In some cases a distinct branch of this muscle takes its origin on the endophallic apodeme (fig. 29 C, *284a*). The ejaculatory duct has a strong sheath of circular fibers (fig. 25 E, *285*) extending to the membranous terminal sac.

The function of the endophallic muscles is to regulate the gonopore, *i. e.*, the aperture of the ejaculatory sac into the spermatophore sac, and to drive the spermatophores through the gonopore, through the spermatophore sac of the endophallus, and through the phallotreme cleft of the aedeagus. If the endophallic cavity is opened from above by cutting its dorsal wall, and the lateral plates are spread apart (fig. 33 C), the slitlike gonopore (*Gpr*) is to be seen in the floor of the spermatophore sac between the posterior ends of the convergent gonopore processes (*y*) of the lateral plates. The gonopore processes are hinged to each other by points of contact just before the anterior end of the gonopore; as a consequence, an approximation of the endophallic plates, produced naturally by a contraction of the muscle between their anterior apodemes (fig. 25 E, F, *283*), results in an opening of the gonopore.

The endophallic mechanism is well illustrated in *Mermiria maculipennis* (fig. 29 E, F). When the lateral plates are separated, as in the ordinary state (E), the gonopore (*Gpr*) is closed to a narrow slit; but when the plates are brought together (F) the gonopore becomes a widely open aperture. Immediately beneath the gonopore is the membranous ejaculatory sac (fig. 25 G, H, *ejs*), which is a terminal enlargement of the ejaculatory duct. The compressor muscles inserted on the lateral walls of the ejaculatory sac (C, E, *284*) probably contract in unison with the compressor muscle of the endophallic plates, and force the spermatophore from the ejaculatory sac through the open gonopore into the spermatophore sac. The passage of the spermatophore through the spermatophore sac is not so easily explained, in the absence of direct observations on the action of the endophallic apparatus, and it seems probable that the endophallic muscles must produce movements of the endophallic walls other than those concerned with the opening and closing of the gonopore and the compression of the ejaculatory sac described above.

The male genitalia of the Tetrigidae, by comparison with the acridid organs, are not only very simple in structure, but, as observed

by Walker (1922), they " are surprisingly unlike those of the Acrididae." The phallus of *Tettigidea lateralis* (fig. 27 D) consists of a low ovate elevation on the floor of the genital chamber beneath the pallial valve (C). Sclerites in the lateral walls of the organ converge and unite anteriorly in a median process armed with small spines. Between the lateral plates is a large, widely open, membranous cavity, into the bottom of which the ejaculatory duct opens anteriorly (D, *Gpr*). The posterior wall of the cavity is directly continuous with the inner membranous fold of the pallium (*Pal'*). The ejaculatory
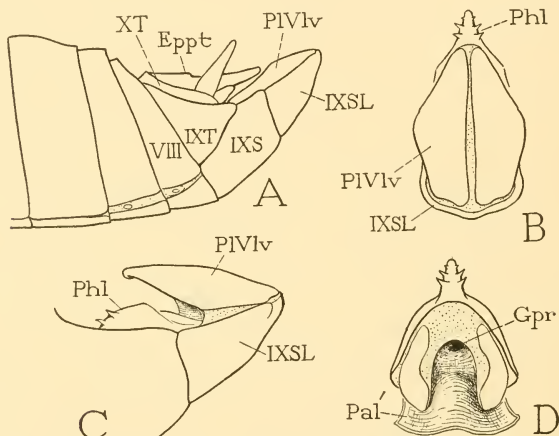
FIG. 27.—Abdomen and male genitalia of *Tettigidea lateralis* (Tetrigidae).

A, terminal part of abdomen. B, dorsal view of pallial valve (*PlVlv*) and anterior process of phallic organ. C, lateral view of ninth sternum and pallial valve, with phallic organ exposed beneath the latter. D, the phallic organ, dorsal view, with base of inner pallial fold.

duct has strongly muscular walls, and groups of muscle fibers arising on the phallic sclerites are inserted on its terminal part. Coition is probably effected by evagination of the endophallic sac. According to Walker the external phallic plates of the tetrigid organ represent the epiphallus (" pseudosternite ") of the Acrididae; but the attachment of the ejaculatory muscles upon them would make it seem more probable that they are external representatives of the invaginated endophallic plates of the Acrididae. These plates, Walker himself contends, are derived from external plates or processes (" parameres ") of other Orthoptera.

It is thus rather curious to find that, while the external parts of the male tetrigid abdomen (fig. 27 A) present the typical acridian characters, the structure of the phallic organs should have so little in common with these organs in the Acrididae. The male organs of Tridactylidae, furthermore, are entirely different from those either of the Tetrigidae or the Acrididae, which fact again is surprising considering the close resemblance of the female ovipositor in all three of these families. The lack of uniformity in the male organs, as compared with the female organs, suggests that the common basic structure of the phallus is something less fundamental than is that of the ovipositor.

COPULATION, AND INSEMINATION OF THE FEMALE

Preliminary to copulation the male grasshopper places himself well forward on the back of the female. With his fore legs he clasps the pronotum of the female, the claws holding at the notch in the anterior margin of the prothorax between the pronotum and the small exposed part of the episternum; the intermediate legs clasp the middle of the female's body; the hind legs are held in various positions and take little part in the copulatory act. The male then lowers his abdomen along the side of the female's abdomen (in pictures almost invariably on the left side, but Boldyrev says, sometimes on the left, sometimes on the right). The genital lobe of the ninth segment of the male is now depressed and the phallic organs protruded, the dorsal lobe of the aedeagus being turned upward and forward. In order to expose the spermathecal aperture of the female, which receives the end of the male organ in copulation, the male, as described by Boldyrev (1929) for *Locusta migratoria,* depresses the subgenital plate of the female with the anterior hooks of the epiphallus. The penis is then introduced into the genital chamber between and beneath the ventral valves of the ovipositor and is inserted into the spermathecal canal. In *Locusta migratoria,* according to Boldyrev, the separation of the lower valves of the ovipositor by the organ of the male stretches the dorsal wall of the genital chamber and pulls back the folds that ordinarily conceal the spermathecal opening; the latter is now " opened wide and the penis is plunged into it right up to its base." The penis, or dorsal lobe of the aedeagus, in *Locusta migratoria* is long, slender, and tapering (fig. 32 B) ; in forms in which the terminal part is short and thick, as in *Melanoplus* (figs. 37, 38, 40), it seems hardly possible that the entire organ can be inserted ; probably in such cases only the apical processes enter the spermathecal orifice. During copulation the cerci of the male are said to grasp the base of the subgenital

plate of the female, while the distal part of the plate is held down by the epiphallus.

Paired grasshoppers remain thus together for a number of hours, or for a day or more, in some cases for more than two days, the duration of copulation apparently being determined by the length of time necessary for the formation of the spermatophore, or spermatophores, and the transference of the latter to the female, or by the number of spermatophores produced. Individuals of each sex may have several successive matings.

It is now well established for the Acrididae that during copulation the spermatozoa are transferred from the male to the female in true spermatophores, which, as defined by Cholodkowsky (1910), are sperm-containing capsules *formed in the genital passage of the male*. In some cases only a single spermatophore is produced at each mating, which, with one end remaining in the genital passage of the male and the other inserted well into the spermathecal duct of the female, forms a conduit from one individual to the other through which the sperm are discharged by the action of the endophallic apparatus of the male; in other cases a number of small spermatophores are injected into the female. The spermatozoa, as in Tettigoniidae and Gryllidae, are united by their head ends in bundles, or spermatodesmata.

The spermatophores of *Locusta migratoria* and their formation have been studied by Iwanowa (1926), Sokolow (1926), and Boldyrev (1929). It appears that normally only one spermatophore is produced by this species at a single mating. Iwanowa reports finding sometimes three or four spermatophores in the receptaculum of the female, but Boldyrev gives evidence that insemination is accomplished properly with one spermatophore, and that if the male attempts to insert a second into the spermathecal orifice the process is not natural and cannot result in the discharge of the spermatozoa.

A spermatophore of *Locusta migratoria,* as described and figured by Boldyrev (fig. 32 D), is an elongate structure with transparent walls, consisting of a proximal sac constricted into two bladderlike compartments, and of a long slender distal tube. The length of the entire spermatophore is usually 25 to 27 mm, but it may reach 29 or 30 mm. The spermatophore thus greatly exceeds the length of the intromittent organ (fig. 32 B), since the latter measures not more than 5 or 6 mm from the gonopore at the bottom of the spermatophore sac of the endophallus (*sps*) to the tips of the apical processes of the aedeagus. Only the distal tubular part of the spermatophore is introduced into the spermathecal canal. The extrusion of the tube,

Boldyrev says, requires an hour or more, and the discharge of the sperm is not completed until $5\frac{1}{2}$ to 18 hours after copulation begins, the time apparently being dependent on the temperature. On opening the genital organs of males killed during copulation, Boldyrev found that the first bladder of the spermatophore is held in the ejaculatory sac (fig. 32 B, *ejs*), while the second lies in the membranous part of the endophallic cavity here termed the spermatophore sac (*sps*). The long spermatophore tube extends through the phallotreme cleft and protrudes forward from the distal end of the aedeagus between the bases of the anterior apical processes (C); in copulation it is deeply inserted into the spermathecal duct. During mating the two sexes are thus united by a tubular conduit through which the sperm are driven by the action of the endophallic apparatus from the male into the female. At the end of copulation the spermatophore tube is not drawn out of the female, but is broken off near its base. The detached tube is retained a long time in the spermathecal canal; the basal part of the spermatophore is soon rejected from the male.

With *Anacridium aegyptium,* as shown by Fedorov (1927), insemination of the female is accomplished by the introduction of from 6 to 30 spermatophores into the spermatheca, the usual number being from 12 to 18. In this species, however, the spermatophores are of relatively small size, about 1 mm in length. Each capsule is a hyaline body, broader at the anterior end, which bears a small appendage easily broken off. The spermatophores are formed in the beginning of the ejaculatory duct, but they do not attain their final shape until they reach the terminal part of the aedeagus. Fedorov believes that the spermatophores are all prepared during copulation, and that this accounts for the length of the copulatory period—$1\frac{1}{2}$ or 2 hours being necessary for the completion of one capsule and its transference to the female. He finds thus that 6 to 12 spermatophores correspond with 18 to 24 hours of copulation, 18 to 24 with 36 hours, and 30 with 60 hours. In about 4 to 6 hours after the beginning of copulation, Fedorov says, a milky-white jellylike mass containing the empty spermatophores that have been ejected from the spermatheca collects between the lower valves of the ovipositor where it becomes brittle and yellow as it dries, and after a few hours is lost, leaving no evidence of the insemination that has taken place.

EXAMPLES OF THE MALE GENITALIA OF ACRIDIDAE

The following descriptions of the male genitalia of representative species of the several acrid subfamilies will serve to illustrate the nature of specific variations in the form of the organs, and will show the fundamental unity of structure throughout the family.

Chorthippus bicolor Charp.—The Acridinae (Tryxalinae) have the typical acridid structure of the male genital organs, except that the distal part of the dorsal lobe of the aedeagus is suppressed, and the apical processes, which have the form of four long, closely appressed prongs, arise directly from the proximal part (figs. 28 E, 29 C).

The structure of the male genital organs of *Chorthippus bicolor* is shown in figure 28. The aedeagus (E, *Aed*) includes a dorsal lobe (*dl*) and a ventral lobe (*vl*), but the former consists principally of the usual proximal part of the dorsal lobe (*m*), which bears directly
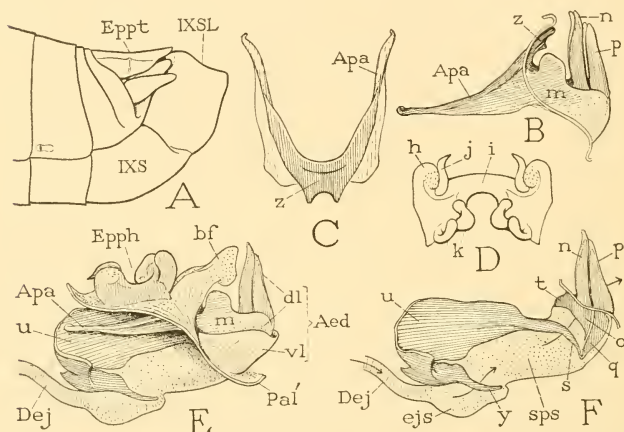
Fig. 28.—Male genitalia of *Chorthippus bicolor* (Acridinae).

A, end of abdomen. B, dorsal lobe of aedeagus and lateral apodeme, left side. C, aedeagal apodemes, dorsal view. D, epiphallus, dorsal view. E, phallic organs and floor of genital chamber, lateral view. F, endophallus and distal part of aedeagus.

the four large apical processes above noted (B, *n, p*). The aedeagal apodemes are well developed as long tapering arms extending forward from the base of the aedeagus (B, *Apa*) in deep invaginations beneath the basal fold (E); their proximal parts are united by a strong zygoma (C, *z*) in the under surface of the basal fold (B). From each of the apical processes of the aedeagus (F, *n, p*) a sclerite extends proximally in the inner wall of the endophallic meatus (*o, q*). Here the extremities of the dorsal pair of sclerites are united by a wide dorsal bridge (*t*), while the tapering ends of the ventral sclerites are sharply bent upward (*s*) and then gradually expanded anteriorly to

form the large lateral plates (*u*) of the endophalic walls. The ejaculatory sac (*ejs*) opens ventrally into the spermatophore sac of the endophallus (*sps*) between the gonopore processes (*y*) of the lateral plates, and the spermatophore sac discharges through the wide meatus and the phallotreme.

The epiphallus is a large sclerite of the usual type of structure (fig. 28 D) seated on the floor of the genital chamber (E, *Epph*) at the anterior end of the surface that forms the fold (*bf*) overlapping the base of the aedeagus.
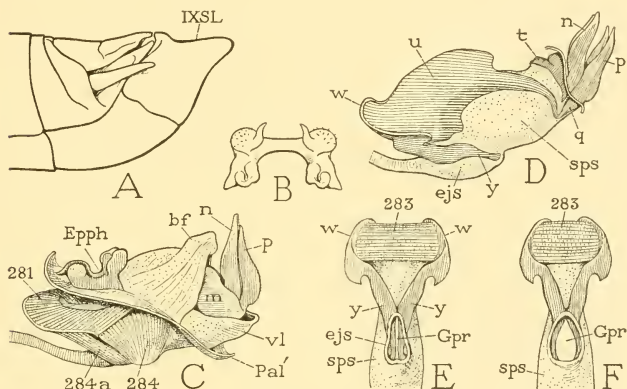
FIG. 29.—Male genitalia of *Mermiria maculipennis* (Acridinae).

A, end of abdomen. B, epiphallus. C, phallic organs with floor of genital chamber and muscles of endophallic bulb. D, endophallus and distal part of aedeagus. E, regulator mechanism of the gonopore, ventral view, closed. F, same, gonopore open.

Mermiria maculipennis Bruner.—The only differences in the male genitalia between this species and the last are in details of form and relative size of the parts (fig. 29). The epiphallus (B, C, *Epph*) has the usual shape; the basal fold (C, *bf*) forms a large hoodlike covering over the base of the aedeagus. The four large apical processes of the aedeagus, in the retracted condition, project dorsally from the supporting proximal part (*m*) of the dorsal lobe; the ventral lobe (*vl*) projects like a trough beneath the latter. The endophallus is large (D), but its lateral plates (*u*) with their apodemes (*w*) and gonopore processes (*y*) are of typical form. The closing and opening mechanism of the gonopore is easily studied in this species (E, F).

Camnula pellucida (Scudder).—There is little in the structure of the male genitalia to distinguish this oedipodine species (figs. 30, 31) from the acridine species just described, though there are many differences to be noted in details of form and relative sizes of the
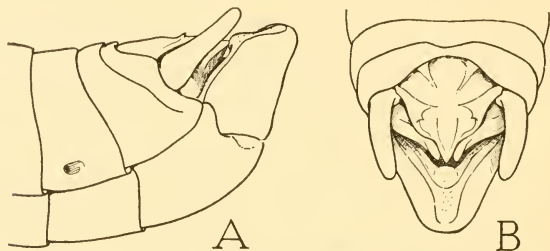

Fig. 30.—End of the male abdomen of *Camnula pellucida* (Oedipodinae). A, lateral view. B, dorsal view.
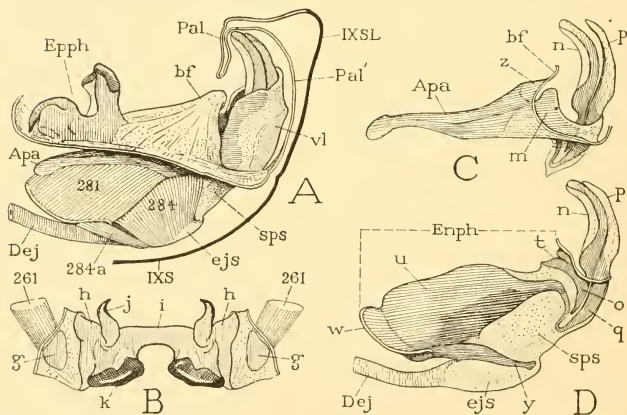

Fig. 31.—Male genitalia of *Camnula pellucida* (Oedipodinae).

A, the phallic organs situated on floor of genital chamber, and muscles of endophallic bulb. B, epiphallus, dorsal view, and associated retractor muscles. C, dorsal lobe of aedeagus and lateral apodeme, left side. D, endophallus and apical processes of aedeagus.

parts. The epiphallus is large and strongly developed (fig. 31 A, *Epph,* B). The basal fold (A, *bf*) covers the base of the aedeagus in the usual manner. The dorsal lobe of the aedeagus consists of a small proximal part (C, *m*) bearing two strong apodemal arms (*Apa*), and of four long curved apical processes (*n, p*). The ventral

lobe (A, *vl*) is unusually large and ensheaths much of the dorsal lobe. The endophallus has the typical form (D, *Enph*), with well-developed apodemes (*w*) and gonopore processes (*y*).

Locusta migratoria L.—The aedeagus of *Locusta migratoria* is quite different in shape from that of the other species here described, but its peculiarities may be seen as an exaggeration of the structure in *Camnula*. The ventral lobe is very large and, in the retracted position
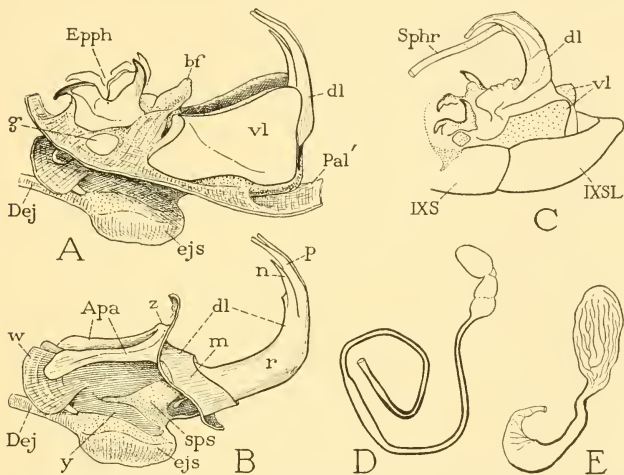
FIG. 32.—Male genitalia of *Locusta migratoria* (Oedipodinae), and acridid spermatophores.

A, phallic organs on floor of genital chamber, with endophallus and ejaculatory sac beneath the latter. B, dorsal lobe of aedeagus, with aedeagal apodemes and endophallus exposed by removal of floor of genital chamber and ventral lobe of aedeagus. C, aedeagus in protracted position, with protruding spermatophore (*Sphr*). D, spermatophore of *Locusta migratoria*. E, spermatophore of *Calliptamus italicus*. (C, D, E from Boldyrev, 1929.)

of the phallic organs (fig. 32 A), completely conceals all but the terminal parts of the dorsal lobe. Its upturned lateral walls contain each a large quadrate plate (*vl*) lying in a vertical plane at the side of the base of the dorsal lobe; ventrally the two plates are united by a median membranous area of the lobe. When the ventral lobe is removed (B) the dorsal lobe of the aedeagus (*dl*) is seen to have the form of a long, tapering tube, curved upward and ending in four slender apical processes. The organ, however, is not literally tubular, since the posterior wall is deeply cleft to its base: the opening is the

phallotreme, and in its inner walls are the usual phallotreme sclerites ending distally in the apical processes (*n, p*). The proximal part of the dorsal lobe (B, *m*) is small, but is quite distinct from the cylindrical distal part (*r*) and bears the two aedeagal apodemes (*Apa*). The phallotreme cleft leads through the meatus in the neck of the endophallus into the endophallic cavity. The spermatophore sac of the latter is small (*sps*), but the ejaculatory sac (*ejs*) is unusually large; the two communicate by the gonopore, which lies between the gonopore processes (*y*) of the lateral endophallic plates.
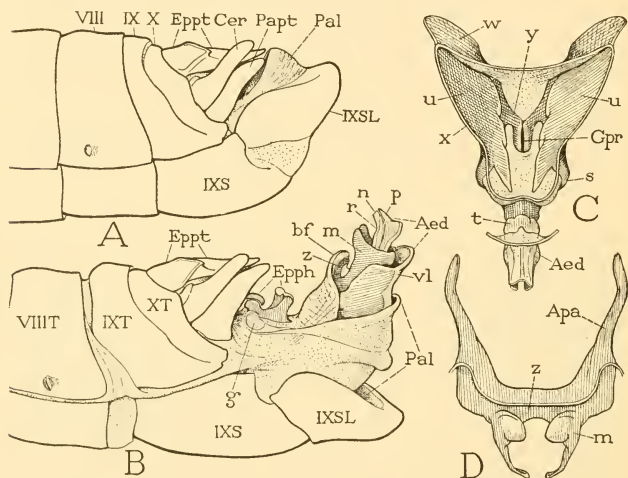
FIG. 33.—Male genitalia of *Dissosteira carolina* (Oedipodinae).

A, end of abdomen with phallic organs concealed in genital chamber. B, same, with phallic organs protracted. C, endophallic chamber opened from above, showing gonopore situated in its floor. D, proximal lobes of aedeagus (*m*) and aedeagal apodemes with basal zygoma, dorsal view.

In the position of protraction (fig. 32 C), as shown by Boldyrev (1929), the ventral lobe of the aedeagus is depressed and the dorsal lobe is projected upward with its apical processes turned forward. The spermatophore (*Sphr*) issues anteriorly from the upper end of the phallotreme cleft between the bases of the anterior processes.

Dissosteira carolina (Linn.).—The end of the male abdomen of *Dissosteira* is obtusely pointed (fig. 33 A) because of the conical form of the genital lobe of the ninth sternum (*IXSL*). The lobe is movable on the anterior sternal plate (*IXS*) by a wide membranous area separating the two. From its dorsal margin the pallium (*Pal*) is continued

forward as a hoodlike fold that meets the lobes of the eleventh segment, and is then reflected inward to form the posterior wall of the genital chamber (fig. 26). The genital chamber and the contained phallic organs are thus ordinarily entirely concealed beneath the tenth and eleventh segments in front, and the pallial hood behind. If the pallium is pulled back from the eleventh segment it is to be seen that the epiphallus occupies an anterior pocket of the genital chamber beneath the venter of the tenth segment, and that the aedeagus is contained in a posterior pouch lined by the inflected fold of the pallium (*Pal'*), which latter extends inward and ventrally to the base of the ventral lobe of the aedeagus (*vl*). The floor of the genital chamber laterally slopes downward from in front (fig. 25 A), where the epiphallus is seated upon it, to the base of the inner fold of the pallium, but medially, between the epiphallus and the aedeagus, it presents a broad, smooth, rounded surface (D), the posterior margin of which forms the basal fold (A, D, *bf*) overlapping the proximal part of the aedeagus. The epiphallus is a large irregular sclerite, consisting of two lateral lobes (D, *h, h*) connected by an arched bridge (*i*), and provided with the usual hooked anterior processes (*j*) and broad, strong posterior processes (*k*) having a vertical position. Just laterad of the epiphallus, in the wall of the genital chamber, are to be seen the small oval sclerites (*g*) that give insertion to the large retractor muscles (*261*) from the lateral parts of the ninth abdominal tergum.

The structure of the aedeagus is well shown in the protracted condition (fig. 33 B), in which the organ projects dorsally from a basal sheath formed of the everted pallium (*Pal*) and the basal fold (*bf*) of the genital chamber floor. The two parts of the dorsal lobe of the aedeagus (*r, m*) are quite distinct, the narrow distal part (*r*), ending in the small apical processes (*n, p*), being exserted from between the lobate lateral walls of the proximal part (*m*). The ventral aedeagal lobe (*vl*) embraces the dorsal lobe posteriorly, and between the two is a deep cavity into which opens the vertical slitlike phallotreme in the posterior wall of the dorsal lobe. The aedeagal apodemes (D, *Apa*) project downward and forward from the base of the dorsal lobe beneath the basal fold (B, *bf*), and their proximal parts are united by a wide zygoma (D, *z*) in the under side of the fold (B, *z*).

The phallotreme is a deep cleft in the dorsal lobe of the aedeagus; in its lateral walls are the usual two pairs of sclerites (fig. 25 H, *o, q*). The sclerites of the dorsal (anterior) pair end in the meatus, where they are united with each other by a transverse bridge (*t*) in the dorsal wall of the latter; the ventral (posterior) sclerites are continuous by narrow upcurved arms (*s*) with the lateral plates (*u*) of the en-

6

dophallic bulb. The posterior angle of each endophallic plate is armed internally by a free spinelike process (*G*), below which the margin of the plate extends obliquely downward and forward to the base of the gonopore process (*y*). Between the gonopore processes, as already shown, lies the gonopore, or true genital aperture (fig. 33 C, *Gpr*), by which the ejaculatory sac (fig. 25 G, H, *ejs*) communicates with the spermatophore sac (*sps*) of the endophallus.

Romalea microptera (Beauvois).—The distal lobe of the ninth sternum in this species shuts close against the epiproct and paraprocts, so that the pallium is not exposed and the end of the abdomen has a
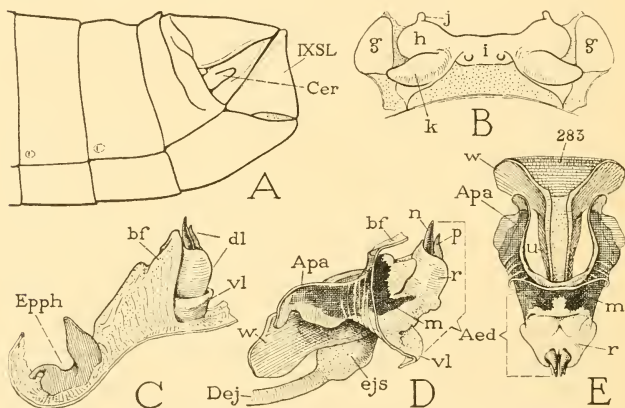
Fig. 34.—Male genitalia of *Romalea microptera* (Cyrtacanthacrinae).

A, end of abdomen. B, epiphallus, dorsal view. C, epiphallus and aedeagus on floor of genital chamber, lateral view. D, aedeagus and endophallus, lateral view. E, same, dorsal view.

truncate form (fig. 34 A). The epiphallus is deeply sunken in the anterior end of the genital chamber, and the basal fold rises steeply against the anterior surface of the aedeagus (C), concealing most of the basal parts of the latter. The dorsal lobe of the aedeagus has a well-developed cylindrical distal part (D, *r*) from which project two pairs of apical processes (*n, p*). The proximal part (*m*) bears a pair of short but very wide lateral apodemes (D, E, *Apa*). The endophallus is relatively small, but the anterior apodemes (*w*) of its lateral plates are large and widely divergent (E).

Schistocerca americana (Drury).—The elongate subgenital plate of the ninth abdominal sternum of this species has a broad, deeply emargi-

nate extension projecting far beyond the origin of the pallium from its dorsal lamella (fig. 35 A, B, *IXSL*). The exposed part of the pallium (*Pal*) forms a thick, transversely corrugated fold against the paraprocts. When the tenth and eleventh segments are removed (B) the genital chamber is exposed from above, and there are to be seen on its floor the phallic structures lying anterior to the aedeagus, the latter being still concealed beneath the pallial hood. The epiphallus consists of large lateral lobes (*h, h*) connected by a narrow median bridge; anterior processes are absent, but the posterior processes are present
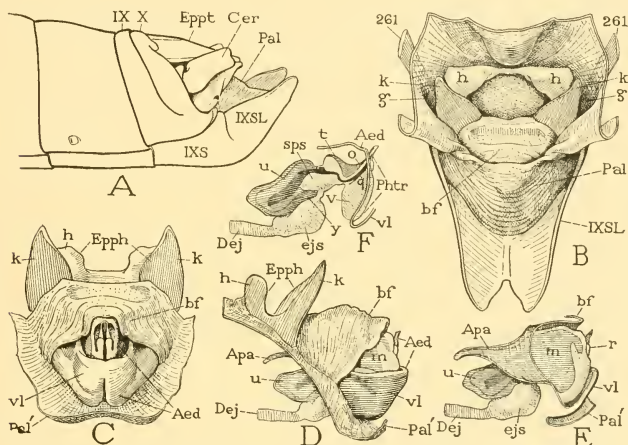
FIG. 35.—Male genitalia of *Schistocerca americana* (Cyrtacanthacrinae).

A, end of abdomen. B, dorsal view of genital lobe of ninth sternum, pallium, and anterior part of genital chamber, exposed by removal of tenth and eleventh segments. C, phallic organs, posterior view. D, same, lateral view. E, aedeagus with apodeme, endophallus, and ejaculatory sac. F, endophallus and apex of aedeagus.

in the form of large triangular plates (*k, k*). Between the bases of the latter the floor of the genital chamber presents a deep transverse groove, the part behind the groove terminating in the basal fold (*bf*). The aedeagus is small (C, D, *Aed*), but its ventral lobe (*vl*) is relatively large. The principal part of the dorsal lobe is formed of the usual proximal subdivision (D, E, *m*), the distal part (E, *r*) being much reduced and ending in a small spoutlike terminal lobe without apical processes. The aedeagal apodemes (E, *Apa*) are short but broad at their bases. The endophallus (F) has the usual structure, but has characteristic features. The phallotreme sclerites (*o, q*) are

very slender; those of the dorsal pair are united by an arched bridge
(*t*) in the dorsal wall of the meatus; each sclerite of the ventral pair
bears a large, thin, oval plate (*v*) in the lateral wall of the phallotreme
cleft. The ejaculatory sac (*ejs*) is relatively large and is separated
from the spermatophore sac (*sps*) by strong gonopore processes
(*y*) of the lateral endophalic plates.

Melanoplus differentialis (Thomas).—The ninth sternal lobe is
short in this species (fig. 36, *IXSL*), and from its dorsal margin the
exposed part of the pallium (B, *Pal*) rises like a dome behind the
eleventh segment. The phallic organs (fig. 37 A) are somewhat
crowded in the rather small genital chamber. The epiphallus (*Epph*)
is large but weakly sclerotized, and is deeply sunken into the folded
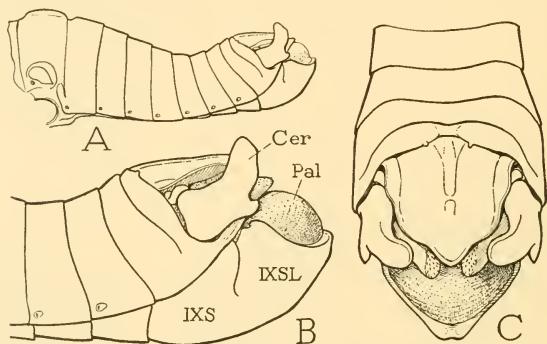
Fig. 36.—Male abdomen of *Melanoplus differentialis* (Cyrtacanthacrinae).
A, entire abdomen. B, end of abdomen, lateral view. C, same, dorsal view.

floor of the genital chamber. The basal fold (*bf*) is bilobed. The
dorsal lobe of the aedeagus is distinctly divided into a proximal part
(A, B, *m*) bearing the aedeagal apodemes (B, *Apa*), and a large cylin-
drical distal part (*r*). The ventral lobe (A, *vl*) is relatively small.
From the distal end of the aedeagus there projects only one pair of
apical processes (A, B, C, D, *n*), which are the usual anterior dorsal
processes continuous from the dorsal sclerites of the phallotreme cleft
(D, *o*). The ventral processes are present, but they are concealed
within the phallotreme cleft (C, *p*), since they arise deeply from the
walls of the latter and do not project from the apex of the aedeagus.
The endophallus (D) has the usual structure, though the sperma-
tophore sac (*sps*) is much reduced, and the ejaculatory sac (*ejs*) is
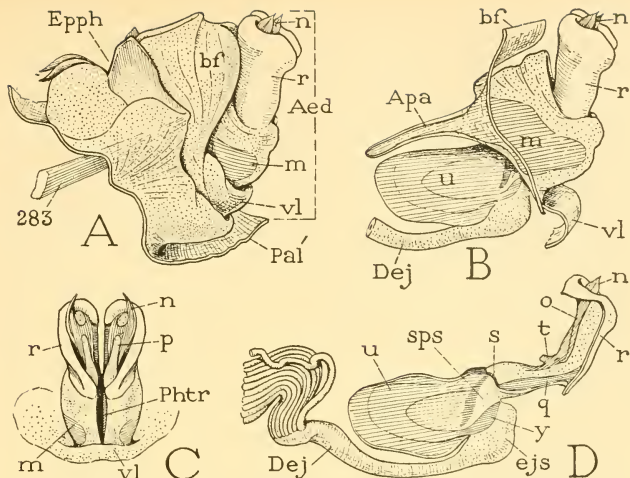turned upward against its posterior wall.

FIG. 37.—Male genitalia of *Melanoplus differentialis* (Cyrtacanthacrinae).

A, the external phallic organs on floor of genital chamber. B, aedeagus and endophallus. C, dorsal lobe of aedeagus, posterior view, showing phallotreme (*Phtr*) and apical processes (*n, p*). D, endophallus with apex of aedeagus, and ejaculatory duct.
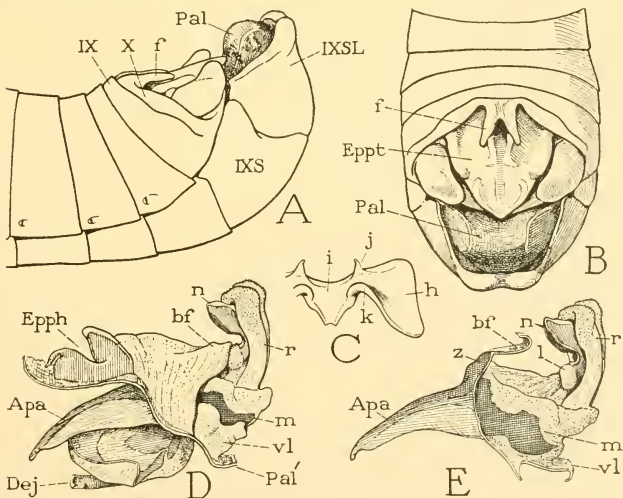

FIG. 38.—Male abdomen and genitalia of *Melanoplus mexicanus* (Cyrtacanthacrinae).

A, end of abdomen, lateral view. B, same, dorsal view. C, right half of epiphallus. D, external and internal phallic organs, with floor of genital chamber. E, aedeagus and apodeme, right side.

Melanoplus mexicanus (Sauss.).—The general features of this species are sufficiently shown in figure 38. The distal part of the dorsal lobe of the aedeagus is unusually long (D, E, *r*) and is produced into two terminal lobes laterad of the phallotreme cleft. The dorsal apical processes (*n*) thus come to project anteriorly below the summit of the terminal lobes. With the base of each of these processes there is connected a soft padlike lobe (E, *l*). The ventral apical processes are concealed within the phallotreme cleft as in the last species.

Melanoplus femur-rubrum (Degeer).—The exposed characters of the male abdomen of this species are shown in figure 39. The phallic organs are entirely concealed in the usual manner within the genital chamber (fig. 40 B). The epiphallus (A, B, *Epph*) is very large, especially as to its lateral lobes. Behind the epiphallus the genital
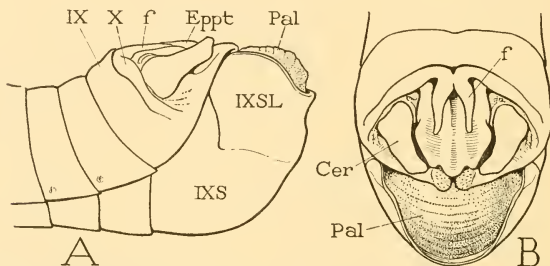

Fig. 39.—End of the male abdomen of *Melanoplus femur-rubrum* (Cyrtacanthacrinae).

A, lateral view. B, dorsal view.

chamber floor is elevated in a large cushionlike structure, the anterior part of which rests against the posterior epiphallic lobes, while the deeply cleft posterior part forms a thick bilobed basal fold (*bf*) covering the basal part of the aedeagus. The aedeagus (B, *Aed*) consists of an irregular dorsal lobe, and of a simple relatively small ventral lobe (*vl*). The dorsal lobe shows the usual subdivision into a proximal part (*m*) and a distal part (*r*), the latter bearing a single pair of large apical processes (*n*), which, as in other species of *Melanoplus,* are the usual anterior dorsal processes. Connected with the base of each of these processes is a soft, flat accessory lobe (C, *l*) lying on the dorsal surface of the base of the aedeagus. The ventral processes, as appears to be characteristic of *Melanoplus,* arise deeply within the phallotreme cleft (fig. 41 B, *p*) and only their tips appear externally before the bases of the dorsal processes (A, *p*). The phallo-
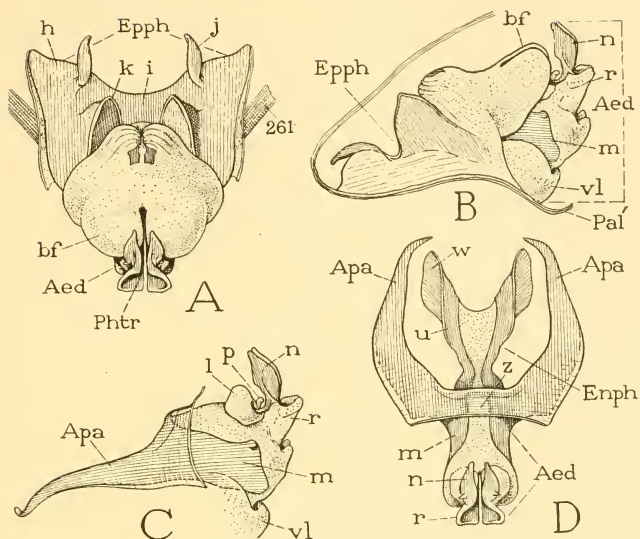
FIG. 40.—Male genitalia of *Melanoplus femur-rubrum* (Cyrtacanthacrinae).

A, the external phallic organs, dorsal view. B, same, lateral view, with part of genital chamber wall. C, aedeagus and apodeme, left side. D, aedeagus with apodemes, and endophallus, dorsal view.
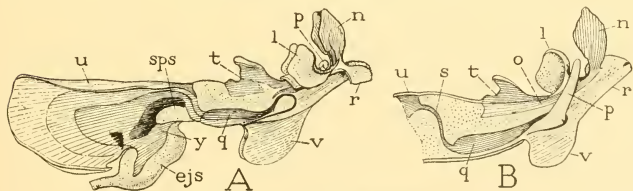

FIG. 41.—Male genitalia of *Melanoplus femur-rubrum* (Cyrtacanthacrinae).

A, endophallus and apical part of aedeagus. B, diagrammatic median section of distal part of aedeagus, exposing right inner wall of phallotreme cleft and meatus of endophallus, showing accessory lobe (*l*) of dorsal apical process (*n*), and internal origin of ventral apical process (*p*).

treme sclerites (B, *o, q*) extend forward in the walls of the phallo-
treme cleft from the bases of their respective processes (*n, p*).
Anterior to the phallotreme a tubular meatus (A) leads into the cavity
of the endophallus, and the ejaculatory sac (*ejs*) opens between large
gonopore processes (*y*) into the small spermatophore sac (*sps*). The
phallotreme cleft in the proximal part of the dorsal lobe of the aedeagus
has its lateral walls strengthened by a pair of thin oval plates (fig.
41 A, B, *v*).

The foregoing studies of three species of *Melanoplus* suggest that
the phallic structures will be found to be more variable and more spe-
cialized among the Melanopli than in the other acridid groups.

ABBREVIATIONS USED ON THE FIGURES

aAp, anterior sternal apodeme.
Aed, aedeagus.
AcGl, accessory genital gland.
acs, antecostal suture.
aiv, anterior intervalvula.
AN, alinotum.
An, anus.
Ap, apodeme.
Apa, apodeme of aedeagus.
ast, acrosternite (precostal lip of
    sternum).
atg, acrotergite (precostal lip of
    tergum).

bf, basal phallic fold.
Bs, basisternum.

Cer, cercus.
Cln, colon.
CpCls, cap cells of sense organ.
CxC, coxal cavity.
Cxpd, coxopodite (limb basis).
Dej, ductus ejaculatorius.
dil, lateral internal dorsal muscles.
dim, median internal dorsal muscles.
dl, dorsal lobe of aedeagus.
DMcl, longitudinal dorsal muscles.
DS, dorsal sinus.
DV, dorsal blood vessel.

eg, egg guide.
ejs, ejaculatory sac.
Enph, endophallus.
Epm, epimeron.

Epph, epiphallus.
Eppt, epiproct.
Eps, episternum.

GC, genital chamber.
Gpr, gonopore.

Il, ileum.
IXSL, genital lobe of ninth abdominal
    sternum.
lAp, lateral sternal apodeme.
lc, external lateral muscles.
li, internal lateral muscles.
lst, lalterosternite.
ltg, laterotergite.

Nv, nerve.

Odc, oviductus communis.
Odl, oviductus lateralis.
Ovp, ovipositor.
Pa, postalar arm of postnotum.
Pal, pallium.
Pal', inner fold of pallium.
Papt, paraproct.
paptl, lobe of paraproct.
Ph, phragma.
Phl, phallus.
Phtr, phallotreme.
piv, posterior intervalvula.
Pl, pleuron.
PlS, pleural suture.
PlVlv, pallial valve.
PN, postnotum.

Prcx, precoxal pleural sclerite.
PvS, perivisceral sinus.
Py, pylorus.

Rect, rectum.

S, definitive sternum.
sa, external pit of sternal apophysis.
SCls, sense cells.
Sco, scolops (sense rod).
Sl, sternellum.
SO, sense organ.
Sp, spiracle.
Sphr, spermatophore.
spn, external pit of sternal spina.
Spr, spermathecal aperture.
sps, spermatophore sac of endophallus.
Spt, spermatheca.
SptD, spermathecal duct.

sr, sternal ridge.
Stn, primitive sternum.

T, tergum.
td, dorsal transverse muscles.
Tm, tympanum.
tr, tergal ridge.
tv, ventral transverse muscles.

Vent, ventriculus.
vil, lateral internal ventral muscles.
vim, median internal ventral muscles.
Vl, valvula.
vl, ventral lobe of aedeagus.
Vlf, valvifer.
VNC, ventral nerve cord.
VS, ventral sinus.

WP, pleural wing process.

REFERENCES

ANDER, K.
  1934. Über die Gattung Cylindracheta und ihre systematische Stellung. Archiv Zool. K. Svenska Vetenskapsakad., vol. 26 A, no. 21, 16 pp., 13 pls.
BLATCHLEY, W. S.
  1920. Orthoptera of Northeastern America. Indianapolis.
BOLDYREV, B. T.
  1929. Spermatophore fertilization in the migratory locust (Locusta migratoria L.). Reports on Applied Entomology (Russian), vol. 4, pp. 189-218, 18 figs.
BRUES, C. T., and MELANDER, A. L.
  1932. Classification of insects. Bull. Mus. Comp. Zöol., vol. 73, 669 pp., 1121 figs.
CHOLODOWSKY, N.
  1910. Über die Spermatophoren, besonders bei den Insekten. Trav. Soc. Imp. Naturl. St. Pétersbourg, vol. 41, pp. 128, 129.
CHOPARD, L.
  1920. Recherches sur la conformation et le développement des derniers segments abdominaux chez les Orthoptères. Rennes.
FEDOROV, S. M.
  1927. Studies in the copulation and oviposition of Anacridium aegyptium L. Trans. Ent. Soc. London, vol. 75, pp. 53-61, pls. 5-8.
FORD, NORMA
  1923. A comparative study of the abdominal musculature of orthopteroid insects. Trans. Roy. Canadian Inst., vol. 14, pp. 207-319, pls. 7-23.
GIARDINA, A.
  1901. Funzionamento dell'armatura genitale femminile e considerazioni intorno alle ooteche degli Acridii. Giorn. Sci. Nat. Econ. Palermo, vol. 23, pp. 54-61, 8 figs.

GRASSE, P.
    1922. Étude biologique sur le criquet Égyptien, Orthacanthacris aegyptia
          (L.). Bull. Biol. France et Belgique, vol. 56, pp. 545-578.
HUBBELL, T. H.
    1932. A revision of the Puer group of the North American genus Melano-
          plus, with remarks on the taxonomic value of the concealed male
          genitalia in the Cyrtacanthacrinae. Univ. Michigan Mus. Zool.,
          Misc. Pubs., no. 23, 64 pp., 4 pls.
IWANOWA, S. A.
    1926. Zur Frage über die Spermatophorbefruchtung bei den Acridodea
          (Locusta migratoria L.). Zool. Anz., vol. 65, pp. 75-86, 10 figs.
KÜNCKEL D'HERCULAIS, J.
    1894. Mécanisme physiologique de la ponte chez les insectes orthop-
          tères de la famille des Acridides.—Rôle de l'air comme agent
          mécanique et fonctions multiples de l'armure génitale. C. R. Acad.
          Sci. Paris, vol. 119, pp. 244-247.
NEL, R. I.
    1929. Studies on the development of the genitalia and the genital ducts in
          insects. I. Female of Orthoptera and Dermaptera. Quart. Journ.
          Micr. Sci., vol. 73, pp. 25-85, pls. 2-4.
RAMME, W.
    1927. Die Eiablage von Chrysochraon dispar. Zeitschr. Morph. Ökol. Tiere,
          vol. 7, pp. 127-133, 8 figs.
RILEY, C. V.
    1878. The Rocky Mountain locust. First Ann. Rep. U. S. Ent. Comm.
          (Oviposition, pp. 223-225.)
SCUDDER, S. H.
    1874. The distribution of insects in New Hampshire. Geol. New Hampshire
          (Hitchcock Rep.), pt. I, pp. 331-384.
SNODGRASS, R. E.
    1929. The thoracic mechanism of a grasshopper. Smithsonian Misc. Coll.,
          vol. 82, no. 2, 111 pp., 54 figs.
    1931. Morphology of the insect abdomen. Part I. General structure of the
          abdomen and its appendages. Smithsonian Misc. Coll., vol. 85, no. 6,
          128 pp., 46 figs.
SOKOLOW, A. J.
    1926. Zur Frage der Spermatophorbefruchtung bei der Wanderheuschrecke
          (Locusta migratoria L.). Das Weibchen. Zeitschr. wiss. Zool.,
          vol. 127, pp. 608-618, 4 figs.
TIETZ, H. M.
    1923. The anatomy of the digestive system of the Carolina locust (Dis-
          sosteira carolina Linn.). Ann. Ent. Soc. Amer., vol. 16, pp. 256-
          268, pls. 17-21.
UVAROV, B. P.
    1928. Locusts and grasshoppers, a handbook for their study and control.
          Imp. Bur. Ent., London.
VARDÉ, V. P.
    1929. Contribution à l'étude morphologique et éthnologique des Orthop-
          tères Acrididae. I. Les vésicules oviductaires de Anacridium aegyp-
          tium L. Bull. Soc. Zool. France, vol. 54, pp. 477-483, 4 figs.

VOSSELER, J.

    1905. Die Wanderheuschrecken in Usambara im Jahre 1903/1904, zugleich ein Beitrag zu ihre Biologie. Ber. Ld.- u. Forstw. D.-Ostafrica, vol. 2, pp. 291-374, pls. 12, 13.

WALKER, E. M.

    1919. The terminal abdominal structures of orthopteroid insects. (Female.) Ann. Ent. Soc. Amer., vol. 12, pp. 267-316, pls. 20-28.

    1922. The terminal structures of orthopteroid insects. (Male.) Ann. Ent. Soc. Amer., vol. 15, pp. 1-76, pls. 1-11.

WALTON, W. R.

    1916. Grasshopper control in relation to cereal and forage crops. U. S. Dep. Agr. Farmers' Bull. no. 747.

WIGGLESWORTH, V. B.

    1932. On the function of the so-called " rectal glands " of insects. Quart. Journ. Micr. Sci., vol. 75, pp. 131-150, 2 figs.