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A REVISED INTERPRETATION OF THE
EXTERNAL REPRODUCTIVE ORGANS
OF MALE INSECTS

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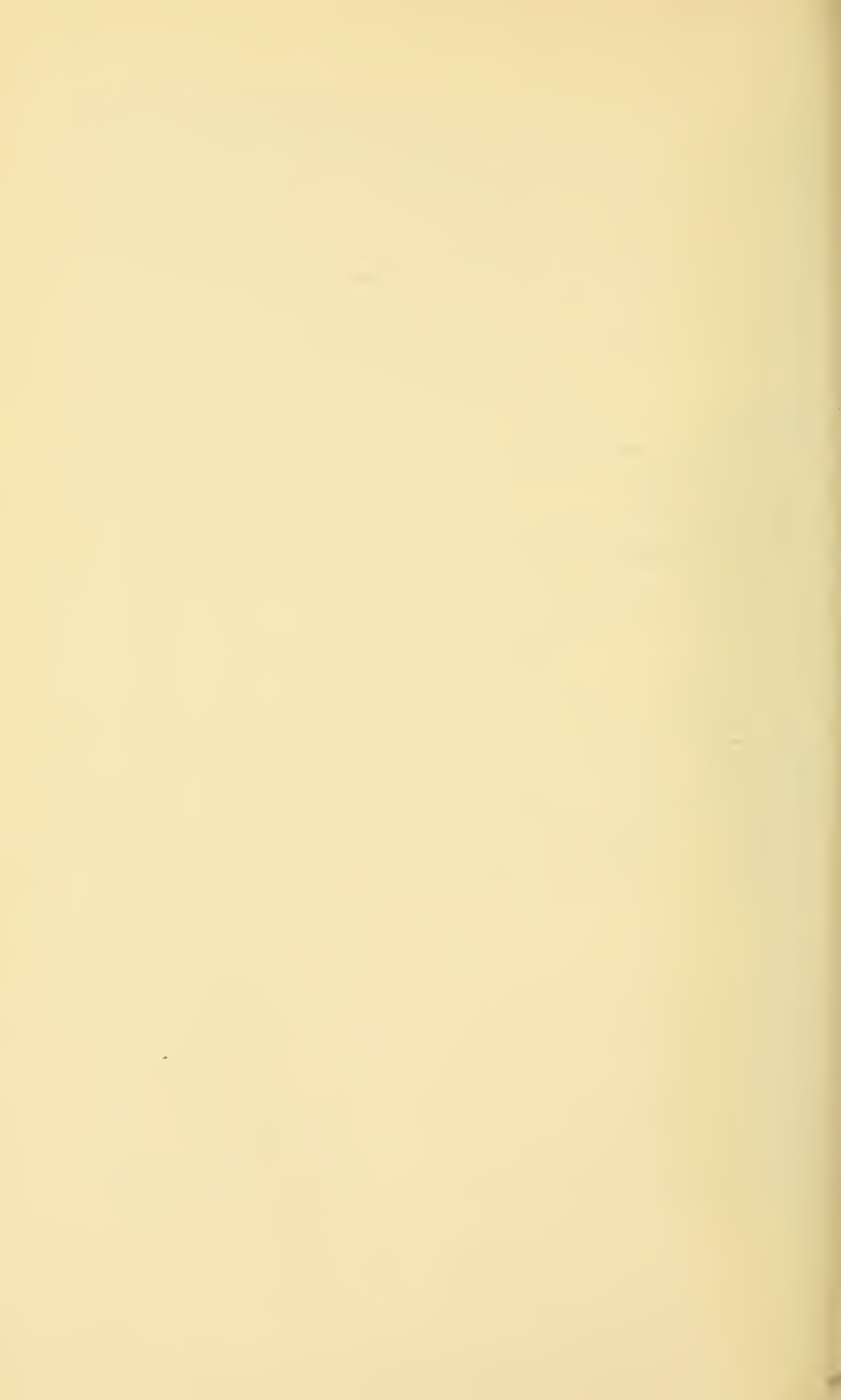
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INTRODUCTION

There is nothing in taxonomic biology so hard to eradicate as a dead idea embalmed in a traditional nomenclature. This observation applies particularly to the study of the external genital organs of male insects. The great diversity in structural detail of the genitalia gives these organs a value for the identification of insect species almost equal to that of fingerprints for the identification of human individuals. On the other hand, the very structural diversity of the organs makes it difficult to understand their fundamental nature and the homologies of their parts. Consequently in taxonomic descriptions of the genitalia there is such a lack of uniformity in concepts of homology and in the adopted terminology that one specialist hardly knows what the other is talking about. Those who are interested in current nomenclatural systems used by taxonomic specialists are referred to the "Taxonomist's Glossary of Genitalia in Insects," edited by S. L. Tuxen (1956).

When homologies cannot be determined by comparative anatomy alone we must have recourse to ontogeny. Fortunately something of the development of the genitalia is now known in most of the major orders of insects. On the basis of this scattered information the writer has attempted in the following discussions to analyze the subject anew in the hope of arriving at a better understanding of the fundamental structure and the homologies of the genitalia, from which a uniform terminology might be devised.

The development of the external genital organs has been described in Thysanura by Lindsay (1939), and Qadri (1949); in Orthoptera by Else (1934), Roonwal (1937), and Qadri (1940); in Hemiptera by Christophers and Cragg (1922), Pruthi (1925a), George (1928), Metcalfe (1932b), Rawat (1939), and Qadri (1949); in Coleoptera by Kerschner (1913), Pruthi (1924), Metcalfe (1932a), and Srivastava (1953); in Siphonaptera by Sharif (1937); in Trichoptera by

Zander (1901); in Lepidoptera by Zander (1903), Mehta (1933), and Rakshpal (1944); in Diptera by Christophers (1922), Christophers and Barraud (1926), and Abul-Nsar (1950); in Hymenoptera by Michaëlis (1900), Zander (1900), Tiegs (1922), Snodgrass (1941), and D'Rosario (1942).

In all these insect orders the definitive genital structure, whether simple or complex, is derived from a pair of small ectodermal outgrowths (fig. 1 A, *PhL*), which appear on the nymph or larva, and may be termed the *primary phallic lobes* (*phallos*, emblem of generation). The terminal ampullae (*Amp*) of the vasa deferentia (*Vd*) are commonly observed to lie partly within the lobes. In the Ephemeroptera (B) the primary lobes become a pair of penes (*Pen*); in Thysanura they unite to form a simple median penis. In the higher orders, from Orthoptera to Hymenoptera, each primary lobe divides into two secondary lobes (C), or *phallomeres*, which may be designated *mesomeres* (*Mmr*) and *parameres* (*Pmr*). Between the bases of the mesomeres an ectodermal ingrowth forms the *ductus ejaculatorius* (*Dej*), the opening of which is the *gonopore* (*Gpr*). The ampullae unite with the inner end of the duct and are carried inward with its further growth. In the Orthoptera the four phallomeres develop into organs of various types. In the higher orders the mesomeres become hollowed on their opposed surfaces and unite with each other to form the tubular median organ known as the *aedeagus* (D, *Aed*). The lumen of the aedeagus is thus not a continuation of that of the ejaculatory duct, but a newly formed extension of the genital passage, which may be distinguished as the *endophallus* (*Enph*); its opening at the end of the aedeagus is the *phallostreme* (*Phtr*). The endophallus with the gonopore at its inner end (F, *Gpr*) is usually eversible from the aedeagus (I), bringing the gonopore to its tip.

The parameres elongate and usually become the principal genital claspers of the adult. If they are not completely separated from the aedeagus (E) the three parts are supported on a common *phallobase* (*Phb*). Usually, however, the parameres retain only a narrow basal connection with the aedeagus (F), and they may be so far displaced laterally (G, H) as to appear to be independent appendages of the ninth segment.

Inasmuch as the name "paramere" has been given to so many different parts of the adult genital structure, some writers contend that the term is thereby rendered meaningless and should be discarded. This verdict, however, is equivalent to denying a true claimant his rights because of impostors. The term *paramere* was coined by Verhoeff (1893), and by him was specifically given to the lateral genital

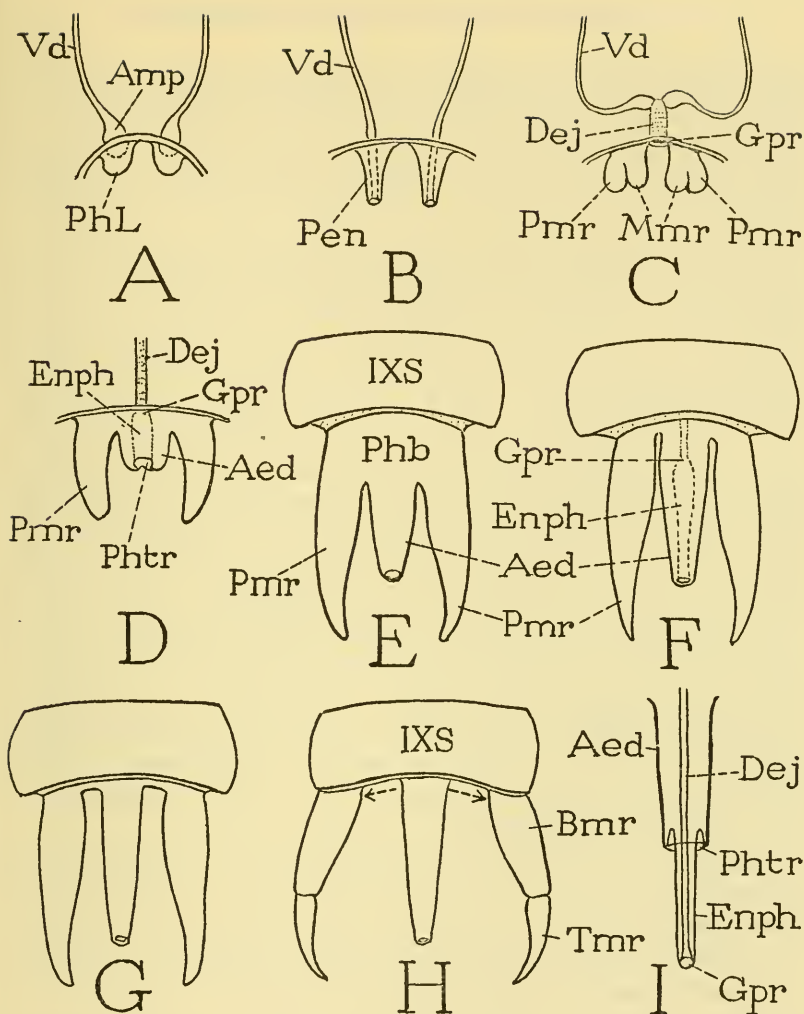


FIG. 1.—Diagrams illustrating the common origin and various types of development of the phallic organs.

A, the primary phallic lobes (*PhL*) invaded by the ampullae (*Amp*) of the vasa deferentia (*Vd*). B, penes of Ephemeroptera, giving exit to the genital ducts. C, the usual division of the phallic lobes into mesomeres (*Mmr*) and parameres (*Pmr*); ejaculatory duct (*Dej*) developed between the mesomeres, opening through the gonopore (*Gpr*). D, mesomeres united to form the aedeagus (*Aed*); aedeagal lumen, or endophallus (*Enph*), opening through the phallosome (*Phtr*). E, aedeagus and parameres not completely separated from common phallobase (*Phb*). F, aedeagus and parameres with only narrow basal connections. G, parameres removed from aedeagus. H, parameres more widely displaced from aedeagus on margin of ninth abdominal sternum (*IXS*), divided into basimeres (*Bmr*) and telomeres (*Tmr*). I, aedeagus with endophallus everted, bringing the gonopore to its tip.

lobes of Coleoptera. These lobes have been shown to be derived from the lateral branches of the primary phallic rudiments. Structures of other insects having the same origin, therefore, are legitimately parameres (side parts) regardless of what they may be called by taxonomists.

Because of their community of origin, the parameres and the aedeagus are primarily closely associated at their bases, and this condition where it occurs in the adult (fig. 1 E, F) should be a relatively primitive one. Generally the phallic organs lie close behind the ninth abdominal sternum (E, *IXS*), or before the margin of its anteriorly reflected posterior part. To better serve their clasping function, however, the parameres tend to move away from the aedeagus along the sternal margin (G), and in many of the higher insects they have come to have a lateral position on the ninth segment (H), where they are commonly mistaken for ninth-segment appendages. Gustafson (1950) says, "There is a strong tendency for the gonapophyses (parameres) of the male to fuse with the phallus." Considering the common origin of the parameres and the "phallus" (aedeagus), however, the facts should be stated in the reverse—the parameres have a tendency to separate from the aedeagus. Finally, in the higher orders, the parameres may become two-segmented by a secondary constriction dividing each clasper into a proximal *basimere* (H, *Bmr*) and a distal *telomere* (*Tmr*). The telomeres have been called also *harpagones* (sing. *harpágo*, a grappling hook).

Inasmuch as the parameres and the aedeagus are developed from a single pair of primary genital lobes, the three parts together are here termed the *phallus*, or *phallic organs*, though the name "phallus" is sometimes given to the aedeagus alone. The phallic organs serve the dual function of *copulation* and *intromission*.

Specific examples of the development and the adult structure of the phallic organs will be given in subsequent parts of this paper. While the aedeagus and parameres are almost constant parts of the adult genital apparatus, either or both may be absent, and many secondary accessory parts appear that have little relation in the different orders. These secondary structures must be given specific names in taxonomy. Finally, there may be processes and lobes of various kinds developed on the eighth, ninth, and tenth abdominal segments that appear to serve some function in copulation, in which even the cerci of the eleventh segment may be involved. All these structures together with the true genitalia are often termed collectively the *terminalia*.

In the Thysanura the penis lies between a pair of stylus-bearing plates which probably are correctly regarded as the coxae of former ninth-segment limbs. In some species of Machilidae endite processes arise from the inner basal angles of the coxal plates and embrace the penis (fig. 2 G, *Endt*). In the Ephemeroptera the coxae are united in a plate behind the ninth sternum (fig. 3 A, *Cx*) and the styli (*Sty*) are usually developed into long clasping organs. Distinct coxal plates and styli are again found in the orthopteroid *Grylloblata* (fig. 5 A), but where styli are present in other insects the coxae are united with the sternum. The occurrence of coxal plates and styli in these three groups of insects has furnished a basis for most theories on the homologies of the genital structures in the other insects.

The stylus-bearing plates are commonly called "coxites" by students of the genitalia, but, if the plates are supposed to be the coxae of former limbs, why the addition of *ite*, a biological suffix meaning "a part of"? "Coxopodite," on the other hand, is a perfectly good compound, meaning the "coxal part of a leg," but it is unnecessary. The fact, already noted, that the parameres of the adult insect very commonly have a lateral position on the ninth sternum has led quite naturally, from a study of adult anatomy, to the current interpretation of the parameres as being the coxal plates of the ninth segment, termed "gonocoxites." That they are often two-segmented strengthens this concept because the distal segments then are "gonostyli." However, this interpretation entirely ignores the development of the parameres from lateral branches of the primary phallic lobes, and the fact that they thus have a common origin with the aedeagus. In spite of this, the theory of the coxal nature of the parameres survives by hypothetical manipulation of certain facts concerning the aedeagus.

The aedeagus of the adult insect may be either wholly membranous or entirely sclerotic, but in some cases the sclerotization takes the form of lateral plates or rods in the aedeagal wall, which are called "penis valves," though nothing about them suggests a valvular nature. According to the theory that the parameres are the coxal plates of the ninth segment, the aedeagus must have a connection with these plates. The "penis valves," therefore, are supposed to be derived from endite processes of the coxal plates, such as are present in some species of *Machilis* (fig. 2 G, *Endt*). As this theory is elaborated and diagrammed by Michener (1944), the endites are assumed to unite with a primitive median penis to form the aedeagus, and thus become the "penis valves" of this organ. But here theory assumes priority over facts. The coxal endites of Machilidae are not united with the penis, they are not present in other male thysanurans, nor are there cor-

responding structures in other male insects. The so-called "penis valves" are well developed in Hymenoptera (fig. 15, *r*), but they are clearly seen to be only lateral sclerotizations of the otherwise membranous aedeagus. The penis of Thysanura is formed by the union of two rudiments entirely comparable to the phallic lobes of other insects that give rise to both the aedeagus and the parameres. The same rudiments in the mayflies develop directly into a pair of penes having no connection with the coxal plate of the ninth segment. There is no convincing anatomical evidence, therefore, that the parameres are ninth-segment coxae, or that the aedeagus has any relation to the latter.

The next question that comes up is: do the phallic organs belong to the ninth or the tenth segment of the abdomen? Most writers refer them to the ninth, but there is sufficient evidence in the lower insects to warrant the belief that primarily the phallic rudiments are developed on the tenth segment. Their origin at least in part on the tenth segment has been observed by Roonwal (1937) in *Locusta*, by Qadri (1940, 1949) in Orthoptera and Hemiptera, by Sharif (1937) in Siphonaptera, and by Tiegs (1922) in the chalcid *Nasonia*. Else (1934) claimed to have traced the phallic rudiments from the appendage buds of the tenth abdominal segment in the embryo of *Melanoplus*. In nymphal insects the rudiments are described as formed in the genital chamber just behind, or above, the ninth abdominal sternum, but in holometabolous larvae they may appear to be actually on the venter of the ninth segment, in which a sternal plate has not yet been formed. Embryological studies on Thysanura and Orthoptera have shown that the vasa deferentia first extend into the tenth segment, on which presumably were the primitive male genital openings. The forward looping of the vasa deferentia in adult Orthoptera from beneath the long cercal nerves of the eleventh segment, as they are carried forward by the ejaculatory duct, is highly suggestive, as the writer (1937) has shown, that the vasa deferentia primarily ended in the tenth segment. The fact that the phallic organs get their musculature from the ninth segment might be taken as evidence that they belong to this segment. Since, however, the tenth sternum is commonly much reduced, it is possible that the phallic musculature is derived from the original intersegmental muscles between the ninth and tenth sterna.

Writers who have taken it for granted that the phallic organs represent a pair of segmental limbs point out that they cannot be appendages of the tenth abdominal segment, because in lepidopterous and tenthredinid larvae the limbs of this segment are present as prolegs,

and two pairs of appendages cannot be developed on one segment. However, numerous reasons have been given by Hinton (1955) for believing that the prolegs are secondary organs adapting the long-bodied larvae for crawling and climbing. He shows that neither in their structure nor in their musculature do the prolegs have any likeness to thoracic legs, and concludes that they are new locomotor organs developed on the site of the disappeared embryonic leg vestiges. Now we must consider the question as to whether or not the phallic organs themselves represent a pair of legs.

A proper interpretation of the nature of the adult genital organs could be deduced only from a knowledge of what the organs were in the primitive ancestors of the insects, but this we do not know. In the minds of most entomologists, or at least in their writings on the insect male genitalia, there seems to be little question that the phallic organs are specially modified segmental appendages of the ninth or the tenth abdominal segment. Some go so far even as to see in the dual branching of the primary lobes a retention of a supposedly biramous limb structure. Among the arthropods, however, the biramous limb is a crustacean specialty, and it is too much to believe that it should occur among the insects only in the male genital appendages. This theory would have to assume that the endopodites unite to form the aedeagus, and it does not account for the undivided penes of the mayflies. Generalization can be stretched to the breaking point.

Only one writer, Else (1934) in his study of *Melanoplus*, has claimed to have observed the derivation of the phallic rudiments from abdominal appendage buds of the embryo, specifically those of the tenth segment. Wheeler (1893), on the other hand, said the tenth-segment limb buds on the embryo of *Xiphidium* gradually become smaller and finally disappear. Most observations on the origin of the phallic rudiments show that the buds usually appear first on the nymph or the larva, and often in the later instars. The post-embryonic appearance of the phallic rudiments, therefore, suggests that they are not equivalent to the transient limb vestiges on the abdomen of the embryo.

Michener (1944) has reasonably said: "That the copulatory organs are new structures seems far less probable than that they are derived from pre-existing structures." His further contention, however, that the pre-existing structures were segmental limbs would assume that there is no alternative. Are we to imagine that before these limbs were modified into genital organs the male insects used a pair of legs for the discharge of the sperm? If so, where were the gonopores in relation to these legs? Among other modern arthropods, as in *Limulus*,

the pycnogonids, and many of the crustaceans and diplopods, the gonopores are on the limb bases, and usually open through a pair of penes. In some of the crustaceans and diplopods the penes are on the sternum between the legs, and the two may be united in a single median penis. In the insects typical paired penes are present in the Ephemeroptera. Hence it would seem quite probable that the primitive male insects should have had a pair of penes on the genital segment, and that the oviducts of the female opened separately, as they still do in the Ephemeroptera. A logical deduction, therefore, is that the paired phallic rudiments of modern insects represent a pair of primitive penes. A penis origin of the phallic lobes is further suggested by the fact that the terminal ampullae of the vasa deferentia usually lie partly within these lobes (fig. 1 A). Though in the higher insects the genital ducts do not open through the phallic lobes, in the Ephemeroptera and those Dermaptera that have paired penes the ducts discharge individually through the latter, and therefore primarily must have opened through the primitive penis lobes. In insects that have a median ejaculatory duct developed between the phallic lobes, the mesodermal ampullae withdraw from the lobes and open into this secondary ectodermal outlet (fig. 1 C).

Admittedly it is difficult to imagine that from a pair of simple penes could have been evolved the large and complex genital organs of the higher insects. Yet, whatever the primary phallic rudiments may be, they do develop into all the variety and complexity of the mature genitalia.

It is true that in some arthropods in which the female has a sperm receptacle the actual intromission of the sperm by the male is accomplished by a pair of legs, but these legs are not those of the segment bearing the genital openings or penes. In most of the malacostracan crustaceans, for example, the male genital outlets are on the last thoracic segment, but the sperm is received by the modified first two abdominal appendages (pleopods) and by them introduced into the receptacle of the female. Likewise in the diplopods the penes are on the third body segment, and the intromittent appendages are usually one or both pairs of modified legs on the seventh segment. In these cases the male practices what amounts to artificial insemination, as does the male spider with his pedipalps. This method of insemination has no counterpart among the insects.

The concept of a penis origin of the phallic lobes leads to a much broader generalization than does the idea that they represent a pair of segmental limbs. We may then correlate the organs of sperm emission in all the arthropods, whether they are penes on the leg bases,

paired or single penes on the venter of the genital segment, or the variously developed phallic organs of most insects. To this may be added the fact that the phallic organs in their early development never have the structure of a leg, and it is only in their higher evolution that they suggest anything of a leg nature. On the contrary, the mouth parts of insects, which unquestionably are remodeled legs, always show in their structure or development their leg origin, and the leg structure is most evident in the lower orders.

The frequent occurrence of the genital apertures on the coxae of a pair of legs among the arthropods may perhaps be traced back to the Onychophora, in which the nephridia open at the mesal sides of the leg bases. The genital ducts are merely a particular pair of nephridial ducts (coelomoducts) that have come to serve as gonoducts. Where penes occur, they are secondary ectodermal outgrowths around the mouths of the ducts. It is quite reasonable, therefore, to suppose that in the early arthropod ancestors of the insects the penes were on the bases of a pair of legs. That these legs are represented by the parameres, however, seems very improbable, since each phallic rudiment becomes a penis in the mayflies, and parameres are lateral branches of the primary lobes developed principally in the higher insects. In their simplest functional form the phallic lobes are penes not associated with appendages, each of which is penetrated by an ectodermal duct that connects with the terminal ampulla of a vas deferens.

Many of the lower invertebrates that are permanently aquatic discharge the reproductive elements freely into the water, where union between the ova and spermatozoa takes place. This method of propagation would not be practicable with land animals, and most of the arthropods have improved on it by the development of sperm receptacles in the female and intromittent organs in the male. By this device the inseminated female can fertilize the eggs whenever the eggs are mature, a method particularly favorable for life on land. Since, however, most Crustacea have sperm receptacles and intromittent organs, it is probable that the ancestors of the terrestrial arthropods were thus equipped before they left the water, but the great diversity in the segmental position of the genital openings and the spermatheca in different arthropod groups would indicate that the organs have been separately developed and not derived from a common ancestor. In *Limulus* and the arachnids the genital ducts in both sexes open consistently on the eighth body segment, from which fact it might be inferred that the same was true of the trilobites. By contrast, the gonopores of the mandibulate arthropods are on different segments in the several classes and even within a single class, so we

have no evidence as to what may have been the primitive position of the genital outlets in these arthropods.

The manner by which the diversity in position of the genital outlets came about in the evolution of the early arthropods is difficult to understand. Gustafson (1950) has proposed as an explanation that "it seems most probable that the primitive ancestors of the Arthropoda possessed paired gonads, gonoducts and gonopores in nearly every segment of the body," and that differences in the position of the outlets resulted from "segmental localization" of the gonads. This idea is a rather extravagant assumption, and embryogeny gives no support to any such theory. Multiple segmental gonads with separate nephridial outlets might have been present in some remote worm progenitor of the arthropods, but among modern forms multiple gonopores occur only in some of the aberrant pycnogonids, and even the Onychophora have a single genital opening. It is hardly to be supposed, therefore, that the early arthropods themselves had more than one pair of genital outlets. Still it is difficult to account for the later differentiation in the segmental position of the gonopores.

From the work of Tiegs (1940, 1947) on the progoneate Symphyla and Pauropoda it appears that functional genital ducts may be secondary ectodermal ingrowths that connect with the gonads, while the primary, posterior mesodermal ducts degenerate. Yet we cannot invoke secondary duct-formation of this kind as a general explanation of the differing positions of the gonopores, because the ectodermal ducts are usually connected with mesodermal ducts. It is possible, however, that during the anamorphic development of the early arthropods, by mutations and selection, different coelomic ducts were utilized as genital outlets. In this connection it is significant that in the chilopods the genital opening is always on the last body segment regardless of the number of segments in the adult centipede, showing that the genital segment is not *numerically* determined as such in development. Among the geophilid centipedes the number of body segments differs in different species, and even between individuals of the same species.

As the several modern groups of arthropods became differentiated, a single fixed position of the genital outlets would not be convenient for all types of body structure. For a crustacean swimming with its abdomen the gonopores are best situated on the thorax, while with the arachnids the genital outlet is quite appropriate on the anterior part of the abdomen, and with the centipedes and insects the posterior part of the body serves best for copulatory purposes. The progoneate modern myriapods, however, seem to have found the opisthgoneate condition of their ancestors unsatisfactory and developed new, ecto-

dermal genital outlets on the anterior part of the body. Even here, the segment of the gonopores in Symphyla is not the same as in Pauropoda and Diplopoda.

External fertilization of the eggs is still prevalent even among those arthropods in which the females have sperm receptacles. The female crayfish, for example, discharges her eggs on the venter of the thorax while she lies on her back, and the eggs are inseminated as they flow backward over the orifice of the spermatheca. In the insects the spermatheca and the oviduct open into a genital chamber, but this chamber is merely an outside space partly enclosed by the sternal plate beneath it. The eggs discharged from the oviduct are here fertilized from the spermatheca. The "uterus" of most viviparous insects is an enlargement of the genital chamber and is thus anatomically equivalent to the incubation pouch of a marsupial. In only a few insects are the eggs inseminated in the ovaries or in the haemocoel. The discharge of spermatozoa into a genital chamber or directly into a spermatheca involves possession by the male of efficient organs of copulation and intromission, and with such organs the insects are more amply provided than are any of the other arthropods.

The great structural diversity in the male genitalia of insects is the delight of taxonomists, the despair of morphologists. In the following sections of this paper, however, an attempt will be made to show that the parts of the male genital apparatus in all the principal orders of insects can be uniformly interpreted and named as here proposed, if the known facts of their development are given priority over theoretical generalizations.

I. PROTURA, COLLEMBOLA, DIPLURA

The genital equipment of these entognathous hexapods offers nothing that contributes to an understanding of the genitalia in Thysanura and Pterygota. The complex male genital organ of Protura arises between the eleventh and twelfth abdominal segments and clearly can have no homologue in the other hexapods. In the Collembola the genital opening is on the posterior part of the fifth abdominal segment, but external genitalia are absent. In the male dipluran *Heterojapyx* there is a genital pouch behind the eighth sternum, which contains in its dorsal wall a small plate, apparently the ninth sternum, bearing a pair of styluslike processes. Immediately behind this plate is the simple genital opening. Though the Collembola are the oldest hexapods known in the geological record, having been found in the middle Devonian, they are certainly not ancestral to the other orders.

They are an early offshoot from the hexapod line, which proved to be so successful that the Collembola have continued to the present time with few evolutionary changes.

II. THYSANURA

Inasmuch as the thysanurans are more closely related to the winged insects than are any of the other apterygote hexapods, it is reasonable to suppose that they should give us a reliable picture of the basic structure of the insect male genitalia, and most theories on the nature of the genital organs take their start from the Thysanura. However, it is well known that appearances are sometimes deceptive, and that apparent likeness is not always evidence of homology.

In most thysanuran species there is a pair of large, triangular stylus-bearing plates on the under side of the ninth abdominal segment (fig. 2 F, *IXCx*). These plates presumably are coxal remnants of former appendages, as are similar plates on the preceding segments, in which there may be a small sternal plate at their bases. Between the bases of the ninth-segment coxal plates arises a small median genital outlet tube, commonly called the penis, though functionally it is not an intromittent organ.

Sweetman (1938) has described the elaborate courting maneuvers of the sexes of *Thermobia domestica*, after which the male deposits a spermatophore on the surface in front of the female. Then, after being touched as a signal by the male, the female walks over the spermatophore until her genital region comes in contact with it. The spermatophore adheres to the female, but soon she turns around and bites it, and finally eats it. The fate of the contained spermatozoa is not recorded. Most remarkable is the mating behavior of *Machilis*, as described by Sturm (1952). The participants first meet head to head. Then the male attaches nearby a thread extruded from the penis, and with the female turns through a half circle until the female is parallel to the thread with her ovipositor directed toward the attachment point. Now the male discharges several droplets of sperm on the thread, which the female attempts to take into her ovipositor with the assistance of the male, who reaches back with one of his antennae, loads it with sperm from the thread, and delivers it to the ovipositor of the female. After insemination is thus accomplished, the female departs. The whole performance lasts about five minutes.

In some species of Machilidae the penis is closely flanked by a pair of endite processes (fig. 2 G, *Endt*) from the mesal basal angles of the coxal plates. From this simple structure in the Thysanura has

been evolved the theory that the coxal plates become the lateral genital claspers (parameres) of the higher insects, and that the aedeagus has been formed by the union of the coxal endites with a primitive median penis. Unfortunately, the known facts of the development of the genital organs do not substantiate this interpretation.

The thysanuran penis is double in its origin, being formed in nymphal instars by the union of two primary lobes entirely comparable with the phallic rudiments of other insects. In *Machilis*, as described

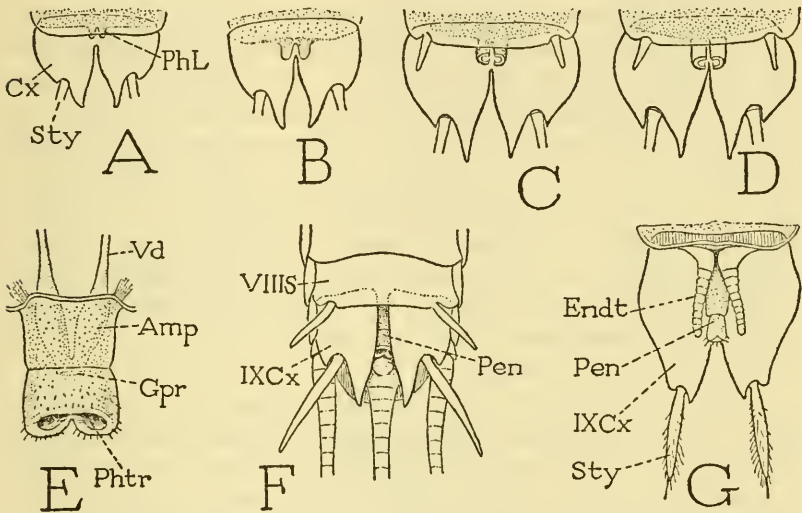


FIG. 2.—Thysanura.

A-D, *Ctenolepisma longicaudata* Esch., developmental stages of the penis (from Lindsay, 1939). E, *Ctenolepisma urbana* Slabaugh, mature penis. F, same, end of abdomen, ventral. G, *Machilis variabilis* Say, ninth-segment coxal plates and penis, dorsal.

by Qadri (1940), the penis rudiments are present in the genital cavity of very young nymphs and develop independently of the ninth-segment appendages. In *Ctenolepisma*, according to Lindsay (1939), the penis rudiments appear first on the eighth instar as a pair of small lobes on the intersegmental membrane at the base of the cleft between the coxal plates of the ninth abdominal segment (fig. 2 A, PhL). In the tenth instar (B) the rudiments have increased in size, in the eleventh and twelfth instars (C, D) their opposed surfaces are concave, and finally the two lobes unite to form the tubular organ of the adult (E). The mature penis appears to be divided into a proximal and a distal section, but since the ampullae (*Amp*) of the vasa defer-

entia (*Vd*) open into the base of the distal section (*Gpr*), the latter alone is the true penis, the proximal part being a secondary outgrowth of the genital chamber wall. The very short undivided terminal part of the exit passage is said by Qadri (1953) to be formed as a shallow depression between the bases of the primary penis lobes, and therefore represents the ejaculatory duct. In an immature instar the ampullae end blindly, and just behind each is a penis bud. This relation of the ducts to the penis rudiments suggests that the latter were primitively a pair of penes.

In its ontogenetic development the thysanuran penis has no relation to the ninth-segment coxal plates, and the endites of the latter are not united with it. The independence of the penis in its origin from ninth-segment structures, Qadri notes, obviously assigns the penis lobes to the tenth segment, and this conclusion is supported by the observation of Heymons (1897) that the embryonic male genital ducts in *Lepisma* end in the tenth abdominal segment, where presumably they opened to the exterior through a pair of primitive penes. The penis rudiments of Thysanura do not divide to form parameres as do the phallic lobes in most of the higher insects, but the double origin of the penis clearly identifies the thysanuran organ with the aedeagus of the other insects.

The coxal plates and styli of the ninth segment are not known to have any genital function. The abdominal styli, unlike the coxal styli of the thorax, are muscled and perhaps may be remnants of telopodites; they serve to support the abdomen and are active in locomotion. The coxal endites of the ninth segment of *Machilis* are male homologues of the second gonopophyses, or valvae, of the female ovipositor. In some species the first gonopophyses are represented in the male by a pair of small endites on the eighth segment.

III. EPHEMEROPTERA

The mayflies characteristically have a pair of long clasping styli (fig. 3 A, *Sty*) arising ventrally from a transverse plate (*Cx*) behind the ninth abdominal sternum. The styli are movable by muscles (*smcl*) from the supporting plate, which fact identifies the plate as the fused coxae of the ninth segment. An enlarged basal joint of the stylus, therefore, cannot be mistaken for the coxal plate. In some forms (C) evidence of the dual nature of the plate is retained. The styli are usually long, curved, jointed arms by which the male securely grasps the abdomen of the female during mating, but they may be relatively simple (G), and in some species they are typically styliform (E).

Also characteristic of the mayflies is the presence of a pair of penes (fig. 3 A, B, C, F, *Pen*) giving exit individually to paired genital ducts. The penes arise from two small, transverse plates (B, *XS*) or a single plate (D) in the membrane between the ninth sternum and

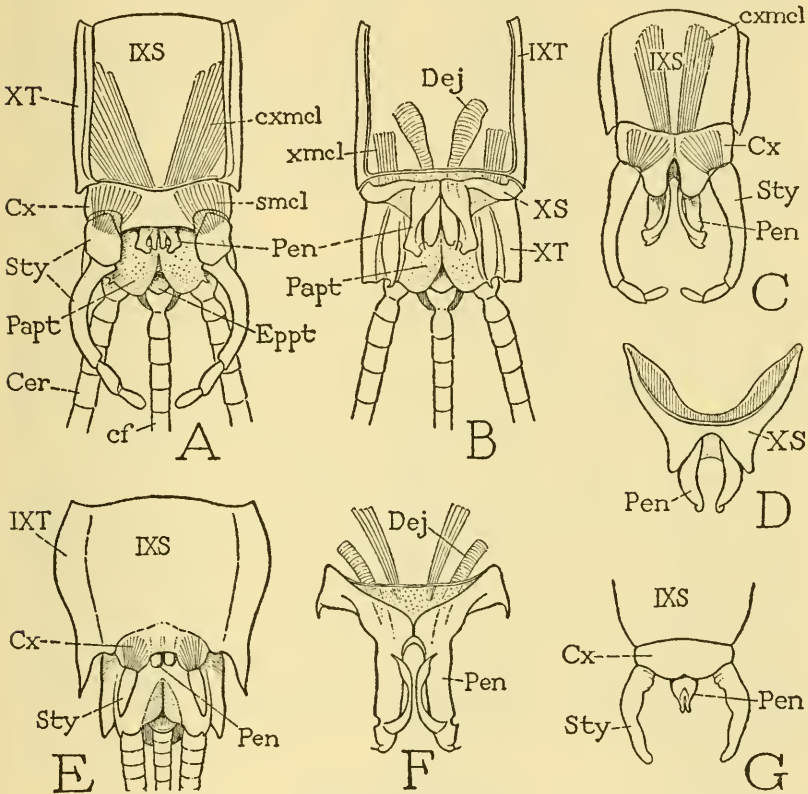


FIG. 3.—Ephemeroptera.

A, *Ephemera simulans* Walker, end of abdomen, ventral. B, same, coxal plates removed, exposing tenth sternal plates bearing penes. C, *Blasturus nebulosus* Walker, end of abdomen, ventral. D, *Habrophlebiodes betteni* (Needham), tenth sternum and penes. E, *Oniscigaster distans* Eaton, larva, end of abdomen, ventral. F, *Campsurus decoloratus* (Hagen), tenth sternum and penes. G, *Trichorythodes fallax* Traver, end of abdomen and single penis, ventral.

the paraprocts, as may be seen by removal of the underlying coxal plate (B). These plates evidently represent the tenth abdominal sternum, since muscles from the ninth sternum are attached on them (B, *xmcl*). The complete independence of the penis plates and the penes from the coxal plate of the ninth segment is quite out of har-

mony with the idea expressed by some writers that the penes are "endopodites" or "gonapophyses" of the ninth-segment appendages; or, more briefly said, the theory is not in harmony with the facts.

In some species the penes are armed with processes of various shapes (fig. 3 F), and the usual two penes may be united at their bases or combined in a single organ (G), but the ducts remain separate. The structure and musculature of the mayfly penes in seven genera have been described by Levy (1948), who says that the penes of *Siphonurus* have muscles arising on the ninth sternum; in four other genera there are only muscles that lie entirely within the penes, which probably flex them mesally, while in *Ephemera* and *Blasturus* there are no penis muscles.

The larval penes are merely a pair of short simple lobes projecting from above the coxal plate of the ninth segment (fig. 3 E, *pen*). According to Qadri (1940) the penes are developed in the young larva from a pair of outgrowths in the genital chamber behind the ninth sternum. The rudiments do not divide during their growth, and the various processes or hooks that may be developed on them have no likeness to the parameres of higher insects. The ephemerid penes are the most primitive male genital organs of the insects, and since it is hardly to be questioned that they are homologues of the primary phallic lobes of other insects, the inference is clear that the latter were originally a pair of penes. The Ephemeroptera in no way suggest that the insect male genitalia took their origin from a pair of legs. The penes are ectodermal outgrowths on the venter of the tenth abdominal segment containing the ends of the genital ducts. As such, they have exact counterparts in various other arthropods as shown in the Introduction.

IV. DERMAPTERA

The Dermaptera have no styli or appendages of any kind on the ninth abdominal segment. The genital equipment of the male is either a pair of penes with individual ducts, or a single organ containing both ducts or only one duct. The presence of paired penes would appear to be the more primitive condition within the order, but the females of all species have only a single genital opening.

Paired penes are characteristic of the Labiduroidea. In *Anisolabis maritima* (fig. 4 E) each organ consists of a long basal stalk bearing two apical lobes. The mesal lobe (*Mmr*) is a hollow continuation of the stalk giving exit to the contained duct. The lateral lobe (*Pmr*) appears as a sclerotized appendage of the stalk. The two penes are

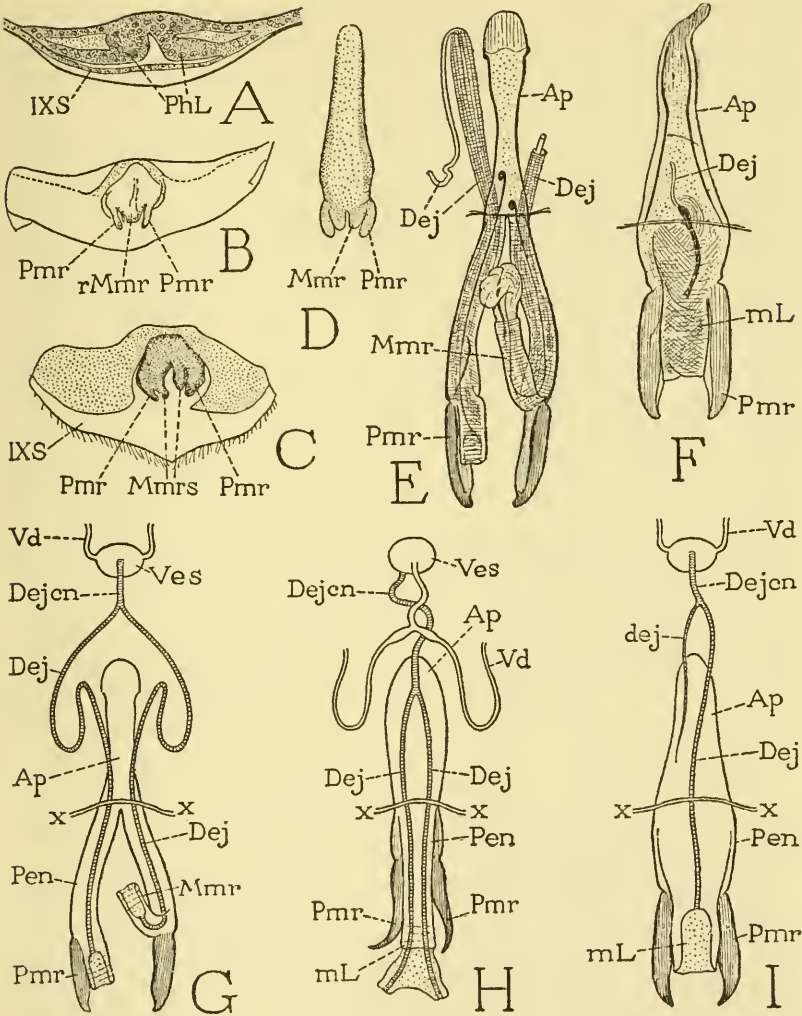


FIG. 4.—Dermaptera.

A, *Forficula auricularia* L., transverse section through primary phallic lobes of first-instar nymph (from Qadri, 1940). B, same, genitalia of full-grown nymph (from Qadri, 1940). C, *Hemimerus hanseni* Sharp, genitalia of nymph (from Qadri, 1940). D, *Anisolabis maritima* (Gené), genital organ of last-instar nymph. E, same, genital organ of adult. F, *Forficula auricularia* L., genital organ of adult. G, *Anisolabis maritima* (Gené), diagram of double penes and ducts. H, *Hemimerus hanseni* Sharp, diagram of single genital organ with two ducts. I, *Forficula auricularia* L., diagram of single genital organ with one functional duct.

united at their bases in a large, internal apodemal plate (*Ap*) on which the phallic muscles are attached. The long ejaculatory ducts of the penes (*G*, *Dej*) unite in a short common duct (*Dejcn*), which joins a vesicle (*Ves*) that receives the two vasa deferentia (*Vd*). Neither the intromittent organ nor the exit system of the adult, therefore, is strictly double as in Ephemeroptera. In the last nymphal stage of *Anisolabis* the genital organ is an elongate structure (*D*) divided only at its distal end into median and lateral lobes. These lobes, however, are entirely comparable to the mesomeres and parameres of higher insects, so that there can be little question that the mesal lobes of the adult organ (*E*, *G*, *Mmr*) are the persisting mesomeres and the lateral lobes (*Pmr*) the parameres. In *Forficula* Qadri (1940) has shown that the single phallic organ of the adult (*I*) arises from a pair of typical phallic rudiments in the first-instar nymph (*A*, *PhL*), which later (*B*) unite at their bases and divide distally into mesomeres and parameres. The adult male organ of Dermaptera, therefore, is double in its origin, and its rudiments are comparable to the penes of Ephemeroptera. Phallic parameres make their first appearance in the Dermaptera.

Hemimerus talpoides has a single genital organ (fig. 4 H) with two parameres, but the mesomeres are united in a common median lobe (*mL*) comparable to the aedeagus of the higher insects, except in that it gives exit to the two primary ducts. In the nymphal organ of *Hemimerus* (*C*), as shown by Qadri (1940), the phallic lobes are broadly fused at their bases and divided distally into mesomeres and parameres. Clearly the median lobe of the mature organ of *Hemimerus* is formed by the union of the mesomeres.

The phallic organ of *Forficula* (fig. 4 F) resembles that of *Hemimerus* (*H*) in that it has a single median lobe, but one duct (*I*, *dej*) is abortive, the other (*Dej*) alone remaining as the functional genital outlet. According to Qadri the median phallic lobe of *Forficula* is formed mainly from the right mesomere of the nymph (*B*), the left one being reduced and practically obliterated. In both *Hemimerus* (*H*) and *Forficula* (*I*), as in *Anisolabis* (*E*, *G*), the base of the external part of the genital organ is produced into a large apodemal plate (*Ap*). The adult organ of *Forficula* (*F*, *I*) has a close resemblance to the nymphal organ of *Anisolabis* (*D*), and it is apparent that the apodeme of the adult organ is merely an extension of the undivided base of the nymphal organ (*B*, *C*).

If the separate openings of the ejaculatory ducts on the phallic mesomeres in Dermaptera has any phylogenetic significance, it must mean that primitively the ducts opened through the primary phallic

lobes themselves, and that these lobes represent a pair of primitive penes such as those of the Ephemeroptera. On the other hand, the development of parameres at lateral branches of the phallic rudiments appears to relate the penis rudiments of the Dermaptera to the primary phallic lobes of the higher insects.

The evolution of a single phallic organ from a pair of primary rudiments in the Dermaptera, however, does not parallel the phallic development in the higher insects from a pair of similar rudiments. The mesomeres of the Dermaptera are penetrated individually by ectodermal exit ducts, which Qadri (1940) says are formed in *Forficula* during the second nymphal instar. The two ducts unite in a short common duct that joins the vesicle of the earlier-formed vasa deferentia. Where the two mesomeres are united, the median lobe thus formed contains the ends of both ducts, or only one functional duct if the other is reduced. In the development of the higher insects, on the other hand, the phallic lobes are never penetrated by ducts; the common ejaculatory duct is formed as an ectodermal ingrowth between the bases of the lobes, and, when the latter unite to form an aedeagus, the duct discharges through the aedeagal lumen. It is only in their earliest stage of development, therefore, that the phallic organs give evidence of their common origin from a pair of genital lobes, which in the mayflies still function as individual penes.

V. ISOPTERA, EMBIOPTERA, ZORAPTERA, PLECOPTERA, PSOCOPTERA

The members of these orders offer little of interest in a general study of the male genitalia. Ninth-segment styli are present in most of the Isoptera, but if the termites ever had phallic organs they have been greatly reduced or entirely suppressed. In a few species of Isoptera and Embioptera the ejaculatory duct opens on a small penis, but in neither order are parameres present. The Zoraptera have a small tripartite genital organ, with the genital opening on the base of the median prong. The Embioptera are characterized by the division of the ninth abdominal tergum into asymmetrical plates of various forms, and the presence of mesal lobes on the bases of the cerci.

The Plecoptera have no styli or appendages of any kind on the ninth abdominal sternum. The ejaculatory duct discharges through a long, probably eversible endophallic sac, which opens either directly to the exterior or on a small penis. In *Chloroperla*, according to Qadri (1940), the penis is formed from a pair of small outgrowths in the anterior end of the genital chamber between the ninth and tenth

abdominal sterna, and each rudiment divides into a dorsal and a ventral lobe as in Orthoptera.

In the Psocoptera there is a variously developed median genital organ, or aedeagus, and a pair of lateral arms on each side, generally termed the outer and inner parameres (see Badonnel, 1956, and Klier, 1956). The inner parameres are probably branches of the outer parameres, but since, so far as the writer knows, the development of the organs has not been studied, we cannot be sure of their homologies. Badonnel (1934), however, observes that since the parameres and the aedeagus are branches of the same trunk, they may be considered as lobes having a common origin. A full account of the internal and external genital organs of male Psocoptera, mating of the sexes, and insemination of the female by a spermatophore is given by Klier (1956).

VI. ORTHOPTERA

Among the orthopteroid insects ninth-segment styli occur in the males of Grylloblattidae, Blattidae, Mantidae, and Tettigoniidae. In the last three families the styli arise directly from the margin of the sternal plate, which presumably is a coxosternum. In *Grylloblatta* (fig. 5 A), however, the styli (*Sty*) are carried on large, asymmetrical coxal plates (*Cx*) movably articulated on the ninth sternum. According to Walker (1943) the coxal plates are strongly muscled, but the styli have no muscles. There can be no question here that the coxal plates and styli are ninth-segment appendages corresponding with the coxal plates and styli of the ninth abdominal segment in Thysanura; they have no anatomical relation to the phallic organs.

The genital equipment of *Grylloblatta* consists of two soft lobes at the sides of the gonopore (fig. 5 B). The short right lobe, or right phallomere (*rPhm*), has several irregular plates in its dorsal wall; the left lobe (*lPhm*) is a long, twisted, saclike structure. The rudiments of these organs in the nymph are shown by Walker (1922) to be a pair of low, rounded lobes (*C, PhL*) behind the ninth sternum. Since the adult organs are developed directly from these primary lobes, which evidently represent the phallic rudiments of other insects, the adult lobes are not equivalent to parameres, and are here termed simply *phallomeres* (phallic parts).

The phallic organs of the Orthoptera in general present a great diversity of structure characteristic of the different families. From the studies of Qadri (1940) on the development of the genitalia in Blattidae, Tettigoniidae, and Acrididae, and the observations of other

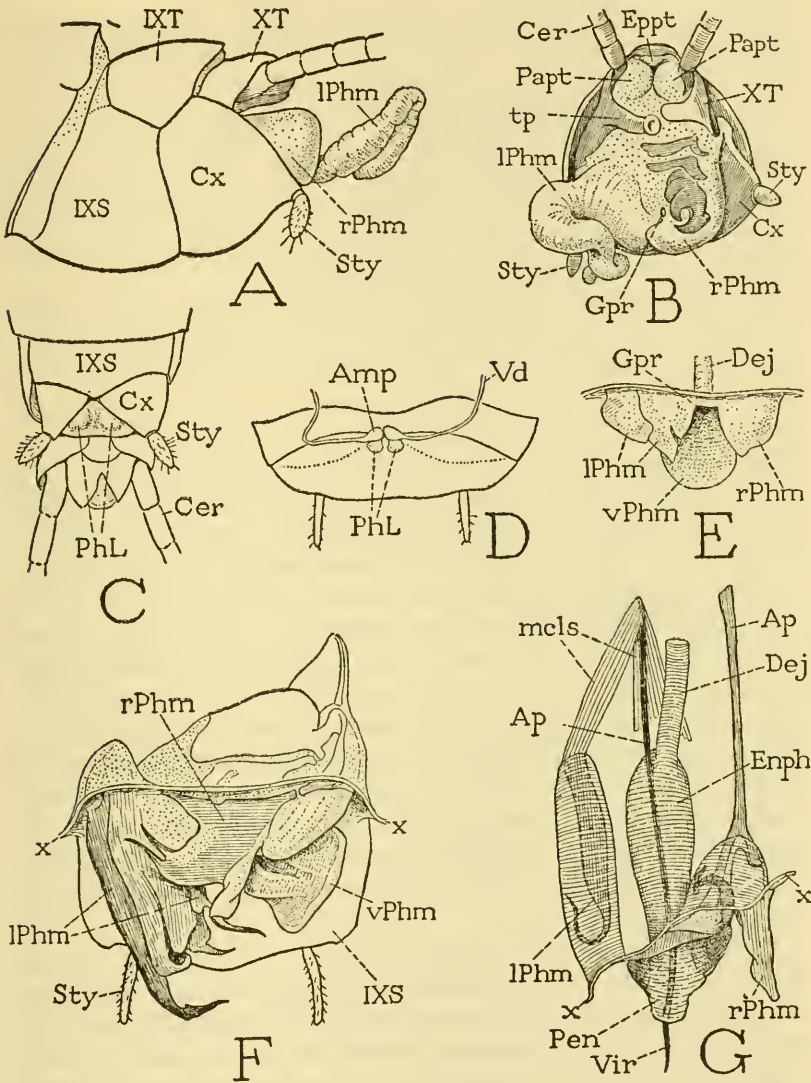


FIG. 5.—Orthoptera.

A, *Grylloblatta campodeiformis* Walker, end of abdomen, left (from Walker, 1922). B, same, end of abdomen with mature genital structures, posterior (from sketch by Walker). C, same, end of abdomen of half-grown male nymph (from Walker, 1922). D, *Periplaneta americana* (L.), primary phallic lobes of second-instar male nymph (from Qadri, 1940). E, same, genitalia of later nymphal instar. F, *Blattella germanica* L., male genitalia of adult, dorsal. G, *Blattella germanica* (L.), male genitalia of adult, dorsal.

writers, it is probable that in all the orthopteroid insects the external genital organs arise from a single pair of primary rudiments. The primitive phallic lobes as generally seen in the nymph lie behind the ninth abdominal sternum and thus appear to belong to the tenth segment. Though Else (1934) claimed to have traced them from the appendage buds on the tenth segment of the embryo in *Melanoplus*, his observation has not been verified. In a former paper on the structure of the adult organs of Orthoptera, the writer (1937) failed to observe their origins in the earliest instars.

The two primary phallic lobes, according to Qadri in the families studied by him, split horizontally into four secondary lobes, two dorsal and two ventral. These four phallomeres either remain as lobes surrounding the gonopore, or they become variously combined and elaborated into complex genital structures. A relatively simple condition is retained in the Mantidae and among the Blattidae in *Blatta* and *Periplaneta*. In *Periplaneta* Qadri says the primary genital rudiments (fig. 5 D, *PhL*) are present in the base of the genital chamber in the newly hatched nymph. Later the primary lobes divide horizontally into four parts, which are at first dorsal and ventral, but the two lobes on the left unite (E), and finally in the adult of both *Periplaneta* and *Blatta* (F) they form a highly complex composite left phallomere (*lPhm*). The right dorsal phallomere (*rPhm*), armed with a hook and spines, overlaps the left phallomere, and with its base are associated a complex of plates in the wall of the genital chamber. These phallomeres serve as copulatory organs. The right ventral phallomere (*vPhm*) remains as a simple lobe beneath the gonopore, and probably manipulates the spermatophore. This type of genital apparatus undergoes many modifications in other blattid genera.

A quite different type of genital structure is found in the genera *Blattella*, *Supella*, *Ectobius*, and *Leucophaea*. Here there are present only two, asymmetrical phallomeres (fig. 5 G) sunken into pouches at the sides of a short, membranous median penis (*Pen*), through which opens an endophallic sac (*Enph*). In *Leucophaea maderae*, van Wyk (1952) says the left phallomere is first formed in the fourth-instar nymph as a lobelike outgrowth of the genital chamber wall above the ninth sternum; the rudiment of the right phallomere appears in the sixth instar. The membranous median penis is formed "by an evagination of the genital chamber wall around the mouth of the ductus ejaculatorius," and "could not be identified in the nymphal stages." It is interesting to note that in this group of blattids the genitalia resemble those of *Grylloblatta* in that there is only one pair of phal-

lomeres, apparently developed directly from phallic lobes of the nymph.

The development of the genital organs in the Orthoptera from a single pair of rudiments leaves no doubt that in their origin the genitalia of Orthoptera are homologous with those of other insects. In their later growth, however, they follow special lines of development, giving rise to adult structures having no counterparts in other orders. The primary phallic lobes may develop directly into a pair of phal-lomeres, and though more commonly each divides into two parts, the resulting four phal-lomeres never form a typical aedeagus and parameres. The Orthoptera are genitalic individualists.

VII. HEMIPTERA (RHYNCHOTA)

It is difficult to give an intelligible general account of the male genitalia in this order because of their apparent differences in different groups. The genital parts have consequently been variously interpreted and named by taxonomists according to what particular theory of homology is accepted. That the structural differences in the organs are more apparent than real, however, can be deduced from comparative studies of selected forms and from what is known of the development of the organs.

In most of the Homoptera a pair of parameres is more or less closely associated with the aedeagus, and the three parts are developed from a pair of typical phallic rudiments. The primary phallic lobes are said by Qadri (1949) to be visible from the very onset of post-embryonic development. They arise behind the ninth abdominal sternum, are innervated from the tenth-segment ganglion, and therefore must belong to the tenth segment. Other writers have commonly referred the phallic organs of the Homoptera to the ninth segment of the abdomen, and some regard them as derivations of ninth-segment appendages; but these writers have given no evidence in support of theories that are not in accord with the facts of development.

The ninth abdominal sternum of some Homoptera bears a pair of lobes of various length, called "subgenital plates." Pruthi (1925a), after showing that the aedeagus and the parameres develop from one pair of primary lobes and the subgenital plates from an entirely distinct pair, says: "The subgenital plates seem to be the coxites of the ninth sternum; and both the aedeagus and the parameres, derived from a primitive single pair of appendages, correspond to the endopodites." To discredit any such idea as this, we have only to refer

back to the Thysanura to see that the phallic rudiments have no connection with the ninth-segment coxal plates, which latter are supposed to be represented in the homopteron by the subgenital plates. There is little evidence that the subgenital plates are other than mere lobes of the ninth sternum, though they may be flexibly attached on the latter. If they are ninth-segment appendages, then the common interpretation that the parameres are "coxites" becomes untenable.

A relatively simple condition of the homopterous genitalia, in which the parameres are closely associated with the base of the aedeagus, is seen in the Indian cicadellid *Idiocerus atkinsoni*, described by Pruthi (1925b). The aedeagus (fig. 6 B, *Aed*) is a long slender organ, for most of its length adnate on the dorsal wall of the genital chamber; proximally it is supported on a median basal plate (*BP*). The two long, divergent parameres (*Pmr*) are articulated on the basal plate of the aedeagus, which appears to serve as a fulcrum for their movement by muscles attached on basal apodemal arms (*Ap*). In addition to these phallic organs there is a pair of long narrow subgenital lobes (*A*, *sgl*) flexibly attached on the ventral arc of the ninth sternum (*IXS*).

The development of the genitalia of *Idiocerus* has been shown by Pruthi (1925b) to proceed in the usual manner from a pair of primary phallic rudiments ("paramere" lobes) that divide and eventually form the aedeagus and parameres. The subgenital plates are outgrowths from the ninth abdominal sternum. Metcalfe (1932b) likewise describes the origin of the aedeagus and parameres in the cercopid *Philaenus spumarius* from a pair of ectodermal outgrowths that appear in an early nymphal stage at the sides of the gonopore (fig. 6 J, *PhL*). At a later stage (K) each primary lobe divides into two secondary lobes, mesomeres (*Mmr*) and parameres (*Pmr*), and still later the mesomeres unite to form the aedeagus. Both Pruthi and Metcalfe contend that the phallic lobes and the subgenital plates pertain to the ninth segment, and conclude that they represent respectively the "telopodites" and "coxites" of this segment. Qadri (1949), on the other hand, regards the phallic lobes of Hemiptera as belonging to the tenth segment, and as having thus no relation to the subgenital plates of the ninth segment. Since there is no concrete evidence of any anatomical relation of the phallic rudiments with the subgenital plates or other appendages of the ninth segment, we may accept the developmental facts as described by these writers, and pass over their theoretical interpretations.

Since the aedeagus and parameres are developed from common rudiments, a close association of the three parts, as in *Idiocerus* (fig.

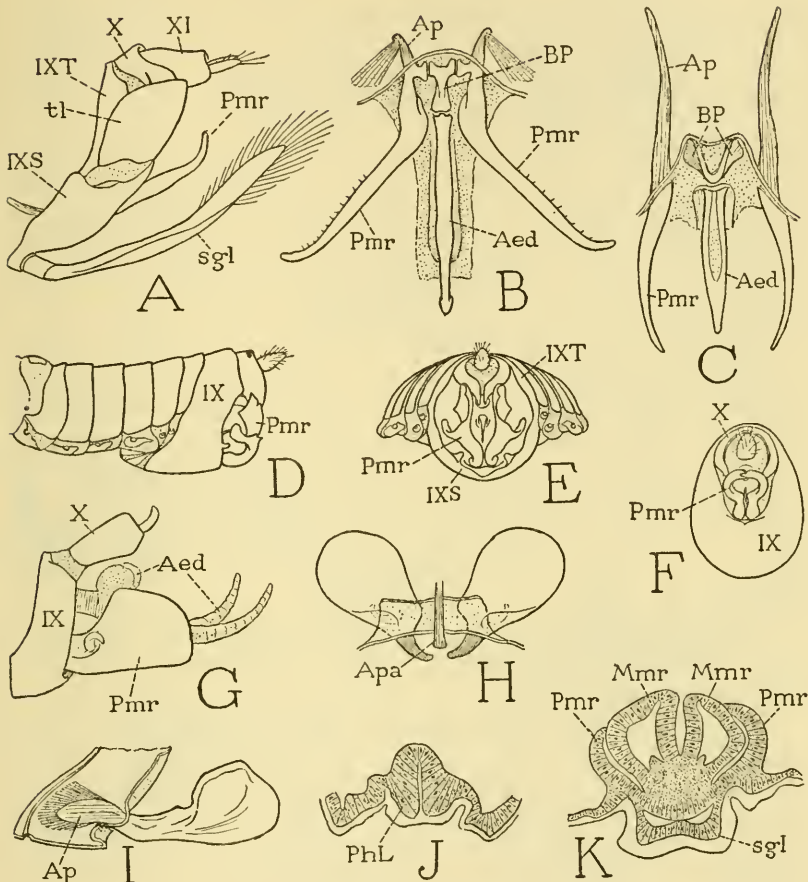


FIG. 6.—Homoptera.

A, *Idiocerus atkinsoni* Leth. (Cicadellidae), ninth and tenth abdominal segments, lateral, with subgenital lobe of left side. B, same, aedeagus and parameres, ventral. C, *Stictocephala bubalus* (Fab.) (Membracidae), aedeagus and parameres, ventral. D, *Megameles* sp. (Delphacidae), abdomen. E, same, end of abdomen, posterior. F, *Perigrinus maidis* (Ashm.) (Delphacidae), end of abdomen, posterior. G, *Poblizia fuliginosa* (Oliv.) (Fulgoridae), end of abdomen, left. H, same, showing parameral apodemes convergent to end of aedeagal apodeme, anterior. I, *Laternaria* sp. (Fulgoridae), right paramere and muscles, mesal. J, *Philaenus spumarius* L. (Cercopidae), section through primary phallic lobes of young nymph (from Metcalfe, 1932b). K, same, later stage, primary lobes divided into mesomeres and parameres (from Metcalfe, 1932b).

6B), must represent the retention of a relatively primitive condition in the adult. In some other Homoptera, however, the parameres become displaced laterally from the aedeagus (C) and lose their connection with the basal plate of the latter. In still others the parameres become movably seated on the margin of the ninth sternum, as in the Delphacidae (D, E, F), in which they are articulated close together (E, F, *Pmr*) on the ventral rim of the ninth segment. From this position the parameres may be supposed capable of moving outward to the lateral parts of the segment. Thus we find in the Fulgoridae (G) a pair of large clasper lobes (*Pmr*) arising from the sides of the ninth segment. In this position the parameres are readily mistaken for ninth-segment appendages ("coxites"). Qadri (1949) asserts that the fulgorid claspers, in fact, are not derived from the phallic rudiments, but are formed at a later stage of development, and are therefore ninth-segment appendages. However, the fulgorid claspers (I) have the structure and musculature of the parameres in other families, and the evidence of lateral displacement of the parameres is too evident to be discounted. The apodemes of the fulgorid claspers, moreover, converge to the end of the median aedeagal apodeme (H, *Apa*).

The aedeagus of the Homoptera presents numerous modifications and complexities of structure in different families and genera, but with its features we need not be concerned in the present discussion.

In the Heteroptera there is present in most families a pair of small movable appendages borne on the ninth abdominal segment well separated from the aedeagus. Typical examples are shown on figure 7 at G, H, K, L (*Pmr*). According to Qadri (1949) these appendages are developed in the last nymphal stage quite independent of the phallic lobes, and are therefore styli of the ninth segment. Dupuis (1955), however, questions the accuracy of Qadri's observations, and he interprets the heteropterous claspers as displaced phallic parameres. A comparative study of the genital organs in different families will bear out Dupuis's conclusions, and it seems hardly probable that claspers should be developed from two different sources in the same order.

A simple condition of the genital organs among the Heteroptera is seen in the nymph of Cimicidae (fig. 7D). Here there is a simple median aedeagus (*Aed*) flanked by a pair of small parameres (*Pmr*). The three parts are shown by Christophers and Cragg (1922) to be developed from a pair of primitive phallic lobes (A, *PhL*) that first appear on a young nymph between the ninth and tenth abdominal segments. With further development each lobe divides into a meso-

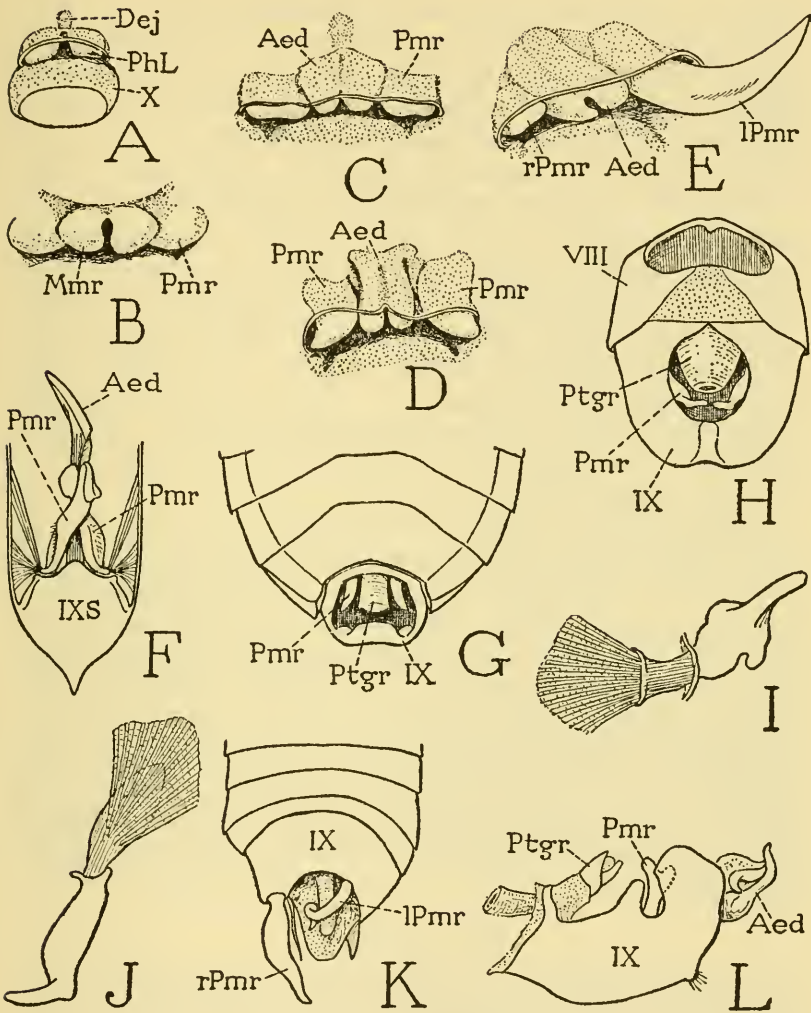


FIG. 7.—Heteroptera.

A-E, *Cimex lectularius* L., development of the phallic organs (from Christophers and Cragg, 1922). A, nymph at end of penultimate instar, ventral; B, nymph at later stage; C, last instar; D, later stage of same; E, near end of last instar, ventral. F, *Naucoris cimicoides* (L.), aedeagus, parameres, and dorsally reflected end of ninth sternum, dorsal. G, *Euschistus servis* (Say), end of abdomen, dorsal. H, *Anasa tristis* (DeG.), end of abdomen, dorsal. I, *Euschistus variolarius* (P. de B.), paramere. J, *Anasa tristis* (DeG.), paramere. K, *Hesperolabops picta* (H., M., and P.), end of abdomen, dorsal. L, *Notonecta variabilis* (Fieb.), ninth abdominal segment and proctiger, left.

mere and a paramere (B); later the mesomeres unite to form the aedeagus (C, D). Finally the left paramere (E, *lPmr*) becomes long and sharp-pointed, serving the adult male as an instrument (formerly called the "penis") for piercing the integument of the female to allow the injection of sperm from the aedeagus. There is no question that the parameres of the bedbug are phallic derivations.

In *Naucoris cimicoides* (fig. 7 F) the slender aedeagus (*Aed*) is closely embraced by a pair of arms (*Pmr*) that unquestionably appear to be parameres. They are so interpreted by Rawat (1939), who says they arise in the same way as the parameres of Homoptera, and that one of the basal muscles of each organ is attached on a ridge connecting the paramere with the base of the aedeagus. There is thus no doubt that the claspers of *Naucoris* are true parameres. In the adult, however, they are displaced from the aedeagus and are articulated on the margin of the dorsally reflected posterior part of the ninth sternum (F, *IXS*).

The secondary articulation of the parameres on the edge of the ninth sternum, which occurs in many insects, gives these appendages a fulcrum for more effective movement, and, once established, there is nothing to prevent their migration to a more lateral position. Thus among the Heteroptera we find the parameres in various degrees separated from the aedeagus (fig. 7 G, H) until they come to have the appearance of being appendages of the ninth sternum (K, L). Regardless of their position, however, the parameres have the same structure (F, I, J), each being produced basally into a muscle-bearing apodeme. We may conclude, therefore, that in all the Hemiptera the claspers, whatever their position may be in the adult, are phallic parameres.

VIII. COLEOPTERA

The male genital organ of the beetles is characteristically a tripartite structure composed of the aedeagus and parameres supported on a proximal plate, or phallobase. The shape and relative size of the parts are highly variable in different species. The terms here used are not those commonly found in the nomenclature of coleopterists, in which the phallobase is the "basal piece," the phallobase and the parameres together the "tegmen," the parameres the "lateral lobes," and the aedeagus the "median lobe" or "penis." According to a current theory of genital homologies, however, as reflected in a paper by Wood (1952) on Coleoptera, the phallobase is the "gonocoxite" and the parameres are "gonostyli." This nomenclature presupposes a

relation of the parts so named to the ninth-segment appendages of Thysanura, which is not borne out by the known development of the genital organs in Coleoptera, as in other insects, from a single pair of primary phallic rudiments. It may be noted here again that the term *paramere* was first given by Verhoeff (1893) to the lateral phallic lobes of Coleoptera, and thus has unquestioned priority for these structures, though it has been applied to various other parts of the genitalia.

The phallobase in what is probably its generalized form is an elongate ventral plate (fig. 8 B, *Phb*) with its margins folded dorsally (A), and sometimes fused in a complete arch over the base of the aedeagus (F, I). However, it may be reduced to a small basal collar (C). In other cases the phallobase becomes a narrow U-shaped band (F) curved over the base of the aedeagus (*Aed*) with long arms carrying the parameres (*Pmr*). As a modification of this form it may take that of a V (G) enlarged around the aedeagus (H). In some species the phallobase is provided with a large apodeme (I, J, *Apb*) giving attachment to strong muscles (I, *mcl*) of the parameres.

The parameres are of various sizes and shapes; in some species they are movably articulated on the phallobase (fig. 8 A, B, C, F, *Pmr*), in others they are continuous with it (G, H, I). In a few species parameres are absent. The aedeagus is usually a sclerotic tube lying between the parameres (A, B, C, *Aed*), or between the arms of the phallobase (F, H). It may be provided with a pair of long aedeagal apodemes (A, H, *Apa*). In *Phyllophaga* (I) there is a single aedeagal apodeme covered by the apodeme of the phallobase (*Apb*). The aedeagus contains an eversible endophallus, which when everted appears as a simple sac, or vesica, or as a long tube that becomes the functional intromittent organ, or penis, with the gonopore at its apex.

The development of the male genitalia of Coleoptera from a single pair of primary phallic rudiments has been described by Kerschner (1913) and by Pruthi (1924) in *Tenebrio molitor* L., by Metcalfe (1932a) in *Sitodrepa panicea* L., by Pradhan (1949) in *Anthrenus fasciatus* Herbst, and by Srivastava (1953) in *Tribolium castaneum* Herbst.

In the larva of *Tenebrio molitor*, according to Pruthi, there appears just behind the ninth abdominal sternum a small pocket in the body wall with a minute external opening. The lateral walls of the pocket become thickened, and when the larva is almost fully grown the thickenings project into the lumen of the pocket as a pair of conspicuous budlike lobes. On the approach of pupation each bud

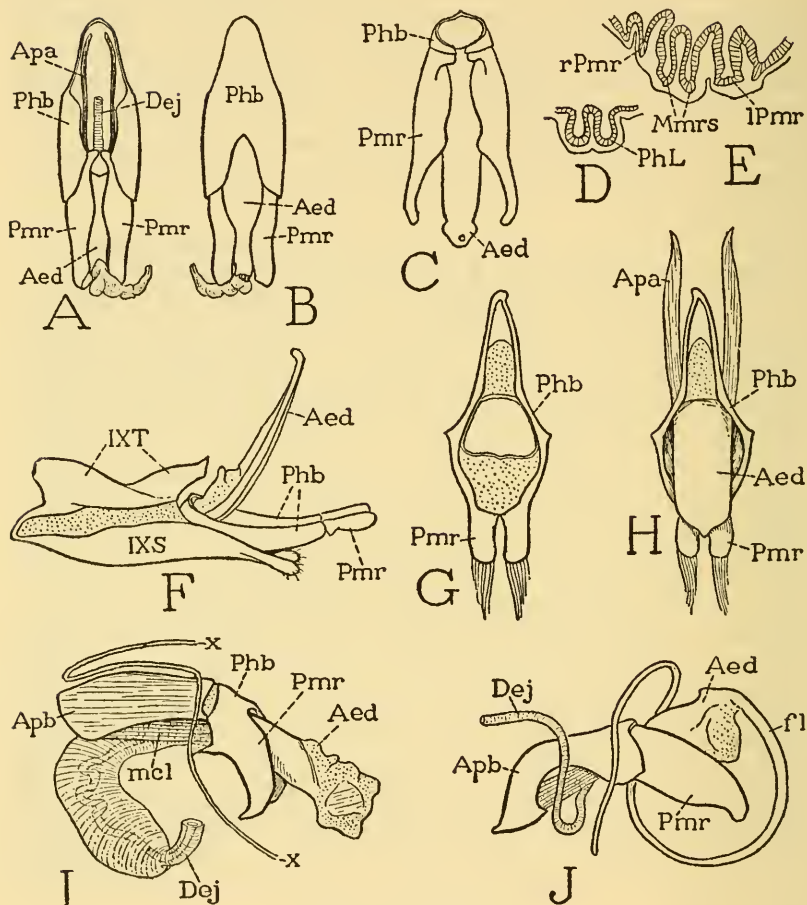


FIG. 8.—Coleoptera.

A, *Ceruchus striatus* Lec. (Lucanidae), phallus, dorsal. B, same, ventral. C, *Cratognathus niger* Westw. (Lucanidae), phallus, dorsal. D, *Stegobium (Sitodrepa) paniceum* (L.) (Anobiidae), horizontal section of phallic lobes of prepupa (from Metcalfe, 1932a). E, same at later stage, phallic lobes divided into mesomeres and parameres (from Metcalfe, 1932a). F, *Stenotrachelus aeneus* Payk. (Serropalpidae), ninth abdominal segment and protruding phallic organs, left. G, *Cerambycid* sp.?, phallobase and parameres, dorsal. H, same, with aedeagus, ventral. I, *Phyllophaga chiriquina* (Bates) (Scarabiidae), phallic organs, left. J, *Pseudolecamus capriolus* (L.) (Lucanidae), phallic organs in functional position, left.

splits into two lobes, forming thus two pairs of processes which are the rudiments of the aedeagus and the parameres of the mature organ. During pupation the genital pocket enlarges and its inner end everts, carrying with it the four genital lobes, which thus come to be borne on an undivided basal stalk (the future phallobase). The median lobes, which are grooved on their opposed surfaces, now come together and unite, first along their dorsal margins and then ventrally, producing in this manner a tubular organ, which is the aedeagus. The lateral lobes develop directly into the parameres.

The development of the genital organs of the anobiid *Sitodrepa panicea* as described by Metcalfe is very similar to that of *Tenebrio*. In the larval stage a depression of the body wall is formed behind the ninth abdominal sternum, from which, in the pupal stage, a median ingrowth becomes the ejaculatory duct. Then there arises at the sides of the mouth of the duct a pair of ectodermal outgrowths (fig. 8 D, *PhL*), which are the primary genital rudiments. Each rudiment soon divides by a vertical cleft into a pair of secondary lobes (E). Then the lobes of the inner pair (*Mmrs*) fuse along their dorsal and ventral margins to form the aedeagus, the lateral lobes become the parameres (*Pmr*). In beetles that have no parameres, such as *Gasteriodesa polygona* L. and *Anthonomus pomorum* L., Metcalfe says the primary genital lobes fuse to form the aedeagus without any preliminary division.

Though neither Pruthi nor Metcalfe appear to have any doubt that the genital organs of Coleoptera belong to the ninth abdominal segment, it is to be noted that they both describe the rudiments as arising in a pocket *behind* the ninth sternum. It might be suspected, therefore, that the organs really pertain to the venter of the reduced tenth segment. Ninth-segment styli are not present in any adult Coleoptera, but Pruthi describes a pair of small styluslike papillae on the posterior margin of the ninth sternum in the larva of *Tenebrio*, which are lost at pupation. He regards these structures as "coxites" of the ninth segment, but he states significantly that they have no connection with the genital rudiments.

IX. MEGALOPTERA

In this group we first encounter a two-segmented structure of the genital claspers, which is characteristic also of the Trichoptera, Mecoptera, orthorrhaphous Diptera, and some Hymenoptera. Developmental studies of the genital organs in Trichoptera, Diptera, and Hymenoptera have shown that the claspers in these orders are formed

from lateral branches of the primary phallic lobes, and that the segmentation results from a secondary constriction in the primarily undivided clasper. The claspers in these orders are therefore phallic parameres, though they have generally been called "coxites" and "styli" on the theory that they represent the ninth-segment appendages of Thysanura. A theory, however, cannot take precedence over the known facts of development. The two segments of the holometabolous parameres were termed by Crampton (1942) *basimeres* and *distimeres*, but linguistically *telomere* should be preferable to the hybrid "distimere."

Since apparently no studies have been made on the development of the genital organ in the Megaloptera or other Neuroptera, we must depend on comparative anatomy for an interpretation of homologies. The close association of the claspers with the aedeagus in some adult Megaloptera, however, leaves little doubt that the three parts are derived from common rudiments as in other insects.

In the species of *Agulla* illustrated at C of figure 9 the male genital complex consists of a pair of large, two-segmented parameres and a thick, bottle-shaped aedeagus. The long basimeres (*Bmr*) embrace the aedeagus (*Aed*) and are closely connected with its base, but laterally they are attached to the margins of the ninth segment (*A*). The movable telomeres (*C*, *Tmr*) are each articulated on the end of an internal ridge of the basimere (*B*, *ri*) and equipped with abductor and adductor muscles. Ventrally from the bases of the parameres two narrow sclerotic ridges converge into the under wall of the aedeagus (*C*) and follow the edges of a median groove of the latter to its distal end. The lateral walls of the aedeagus are formed by two long plates. The phallotreme is a transverse aperture at the apex of the aedeagus, and opens from a large, probably eversible, endophallic sac.

The genital organ of *Agulla adnixa* (fig. 9 D) is similar to that of the species just described, but the parameres and the aedeagus are broadly continuous at their bases. Where they separate there is attached ventrally on each side a hooked triangular plate (*a*). In *Agulla arizonica* (*E*, *F*) each plate has a thick posterior arm. These plates are termed "fragmenta of the coxopodites" by Ferris and Pennebaker (1939), but in *A. arizonica* (*G*) they arise distinctly from the base of the aedeagus. Michener (1944) likens the plates to the claspettes of Diptera and the volsellae of Hymenoptera, but they are not comparable to either of these structures, both of which are associated with the parameres.

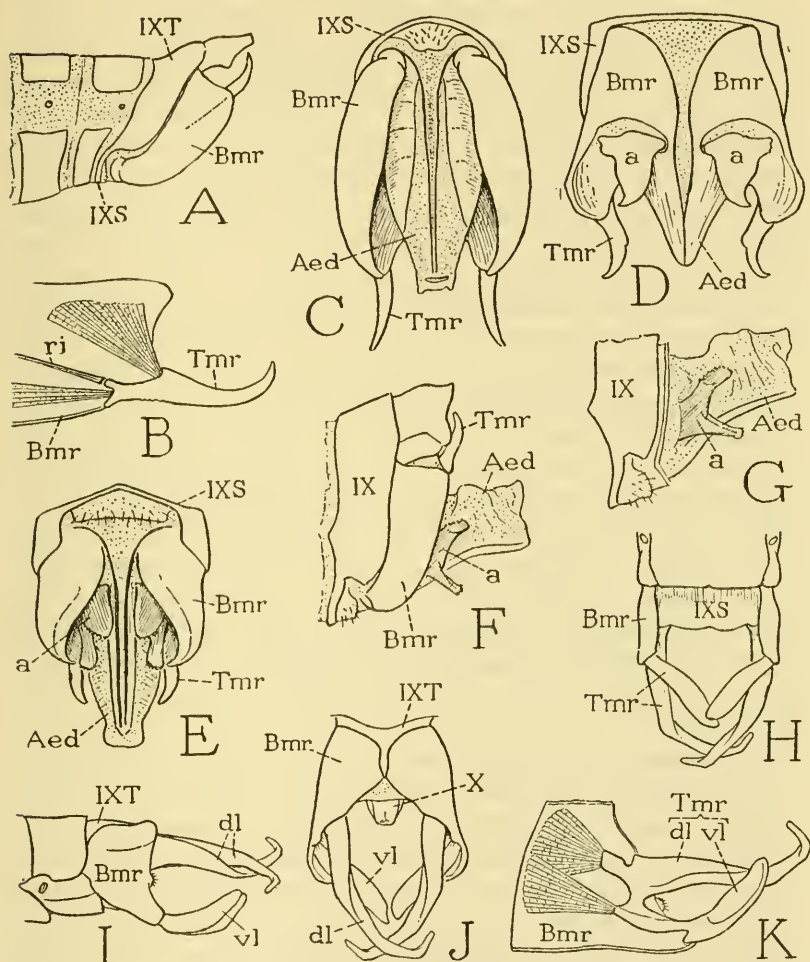


FIG. 9.—Megaloptera.

A, *Agulla* sp., end of abdomen, left. B, right telomere and muscles from basimere, mesal. C, same, phallic organs, ventral. D, *Agulla adnixa* (Hagen), phallic organs, ventral. E, *Agulla arizonica* Banks, phallic organs, ventral. F, same, end of abdomen, left. G, same, ninth abdominal tergum and aedeagus, left, parameres removed. H, *Corydalis cornutus* (L.), end of abdomen, ventral. I, same, end of abdomen, lateral. J, same, ninth abdominal tergum and parameres, dorsal. K, same, right telomere and muscles from basimere, mesal.

a, a, accessory phallic plates.

In *Corydalus cornutus* the parameres are highly developed, but the aedeagus is greatly reduced and is scarcely perceptible as a distinct organ. The basimere of each paramere is a large lateral plate (fig. 9 I, *Bmr*) attached to the narrow ninth segment, which is mostly concealed within the eighth segment. Dorsally (J) the basimeres are separated only by a median tongue of the ninth tergum (*IXT*), but ventrally (H) a wide sternal plate intervenes between their lower margin. The basimeres each bear two pairs of arms (I, J), a long, forcipate dorsal pair (*dl*) and a shorter ventral pair (*vl*). The two arms on each side, however, are branches of a single telomere as shown by the fact that they arise from a common base (K) inflected into the end of the basimere, on which two large muscles are attached.

The genital structure of *Agulla* is cited by Michener (1944) as showing that "the gonocoxites, gonostyli, and the penis are clearly homologous with those of *Machilis*." The likeness between the two, however, must be visible only to one whose vision is clarified in the light of a theory. The "gonocoxites" and the penis of *Machilis* have quite separate origins, and even in the adult there is no actual connection of the coxal plates with the penis. The demonstrated origin of the parameres and the aedeagus in other holometabolous insects from a common pair of rudiments is good reason for believing that the closely associated claspers and aedeagus of the adult *Agulla* had a like origin, and that the megalopterous claspers are phallic parameres.

The genitalia of the Planipennia do not resemble those of the Megaloptera, and are difficult to understand. The principal clasping organs in some families are a pair of large, variously armed lobes articulated on the dorsal part of the ninth abdominal segment. Ferris (1940) refers these lobes to the tenth segment, and Carpenter (1940) calls them "anal plates." The small aedeagus is supported on a transverse plate in the floor of the genital chamber, which Carpenter calls the tenth sternum, and it may be such. A similar plate arched over the base of the aedeagus in the mantispid *Climaceiella* is the "coxo-podite" of Ferris (1940). In reference to the same species Michener says "a sclerotic arch extends between the bases of the gonocoxites over the aedeagus," which "appears to be a fusion product of the bases of the gonocoxites." The union of the bases of a pair of legs behind the sternum of their segment would be a rare anatomical event, but, as we shall see, the parameres of the higher insects are frequently connected by an interparameral bridge.

X. TRICHOPTERA

The trichopterous genitalia include a median aedeagus and a pair of lateral parameres. The parameres are articulated on the posterior margin of the ninth abdominal segment (fig. 10 A, E) and are muscled from the sternum (C, E). In some families the parameres are undivided lobes (E, *Pmr*), in others they are distinctly two-segmented (A) and the telomere is provided with antagonistic muscles arising in the basimere (C). Because of the apparent relation of the parameres to the ninth abdominal segment, as seen from the side, the parameres are commonly regarded as gonopods of this segment, and their parts are called "gonocoxites" and "gonostyli." This interpretation, however, ignores the ontogenetic evidence of the origin of the claspers in common with the aedeagus from a pair of primary phallic rudiments, and their subsequent lateral migration to the sides of the ninth segment.

The development of the trichopterous male genitalia has been fully described for species of *Limnophila* by Zander (1901). The first rudiments of the organs appear toward the end of the larval period, when there is to be seen in sections just behind the ventral margin of the ninth abdominal segment a small, flask-shaped pouch. From the inner wall of the pouch there grows out a pair of small lobes. Then, on the median dorsal wall of each lobe a vertical cleft is formed, by which the primary lobe is partly divided into two secondary lobes (fig. 10 F, *Pmr*, *Mmr*). The cleft deepens until each primary lobe is completely divided (G), while the pouch becomes wider. The two median lobes quickly unite to form the aedeagus (*Aed*); the lateral lobes, or parameres (*Pmr*), however, move slowly toward the side walls of the pouch and become broad, flat appendages ("valvae" of Zander) projecting outside the pouch. When the larva begins to change to the pupa, the genital pouch flattens out, bringing the parameres and the aedeagus to the outer surface of the body. The base of the aedeagus, however, becomes surrounded by a circular ingrowth of the body wall, which is the aedeagal pocket of the adult. This account by Zander shows clearly that the trichopterous claspers are parameres derived with the aedeagus from a pair of primary phallic lobes, and that their lateral position in the adult is secondary.

Further evidence of the phallic nature of the trichopterous claspers may be seen in the fact that the two basimeres are often connected in the adult by a broad sclerotic bridge (fig. 10 B, *pmB*) in the ventral wall of the genital chamber below the base of the aedeagus. Close behind the bridge is a dorsally inflected posterior part of the ninth

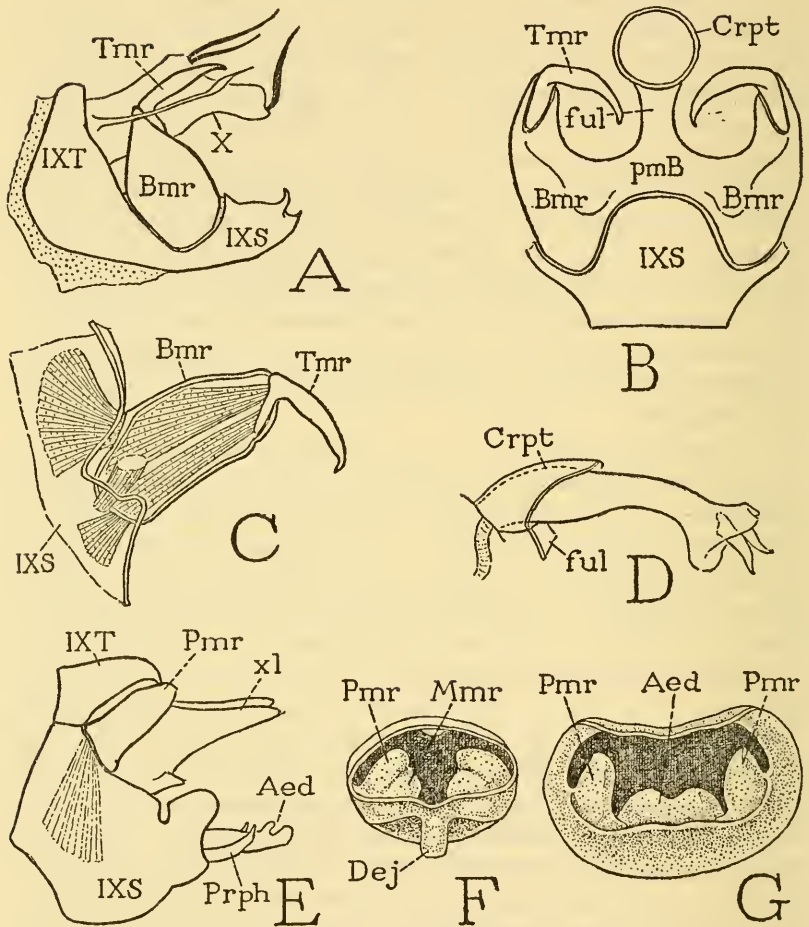


FIG. 10.—Trichoptera.

A, *Neuronia semifasciata* (Say), end of abdomen, left. B, same, end of abdomen, posterior. C, same, right paramere and muscles, mesal. D, aedeagus and crypt, left. E, *Platycentropus maculipennis* Rambur, end of abdomen, left. F, *Limmophilus bipunctatus*, genital pocket with primary phallic lobes dividing into mesomeres and parameres (from Zander, 1901). G, same, later stage, phallic lobes completely divided, mesomeres united to form aedeagus (from Zander, 1901).

sternum (*IXS*). It is evident, therefore, that in such species the parameres have simply expanded their united bases along the margin of the sternum until their free parts have attained a lateral position on the ninth segment. In both their development and in their adult structure the trichopterous claspers attest that they are not primarily ninth-segment appendages. The position of the parameral bridge immediately adjoining the reflected posterior margin of the ninth abdominal sternum (*B, IXS*) is suggestive that the bridge is derived from the tenth sternum. From the middle of the bridge a lobe (*ful*) extends upward and supports the lower rim of the aedeagal pouch (*Crpt*). This lobe is the "juxta" of lepidopterists; it appears to serve as a fulcrum for the movement of the aedeagus.

The aedeagus of the Trichoptera is a large sclerotic organ (fig. 10 D) arising from a pouch, or aedeagal crypt (*Crpt*), of the genital chamber wall above the parameral bridge (*B, pmB*). The aedeagus of *Neuronia* (D) in the nonfunctional position is ensheathed in a groove on the ventral side of the tenth segment (*A, X*). In some species long processes arise from the base of the aedeagus, which may be dorsal, ventral, or lateral (*E, Prph*). These aedeagal processes have been called "titillators" and "parameres," but, as suggested in the Introduction, such structures might be termed paraphyses.

The tenth segment often has a pair of appendicular processes of various forms and sizes arising from its base. In *Neuronia* (fig. 10 A) these processes are long, slender lateral arms, suggesting by their position the so-called "socii" of Lepidoptera, but it seems improbable that they are cerci.

XI. LEPIDOPTERA

The genitalia of Lepidoptera have many features in common with those of Trichoptera, particularly in the presence of large lateral parameres ("harpes," "valvae") articulated on the ninth abdominal segment, and in the partial ensheathment of the aedeagus in a pouch of the genital chamber wall. Furthermore, the bases of the parameres may be confluent in an interparameral bridge behind the margin of the ninth sternum.

In some Lepidoptera, as in *Carþocapsa* (fig. 11 A), though the parameres (*Pmr*) are attached laterally on the ninth abdominal sternum, their bases converge medially behind the sternum (*B*) and are here articulated on a small median plate (*BP*) in the floor of the genital chamber. From this plate an arm (*ful*) extends upward and forks around the mouth of the aedeagal pouch. The base of the

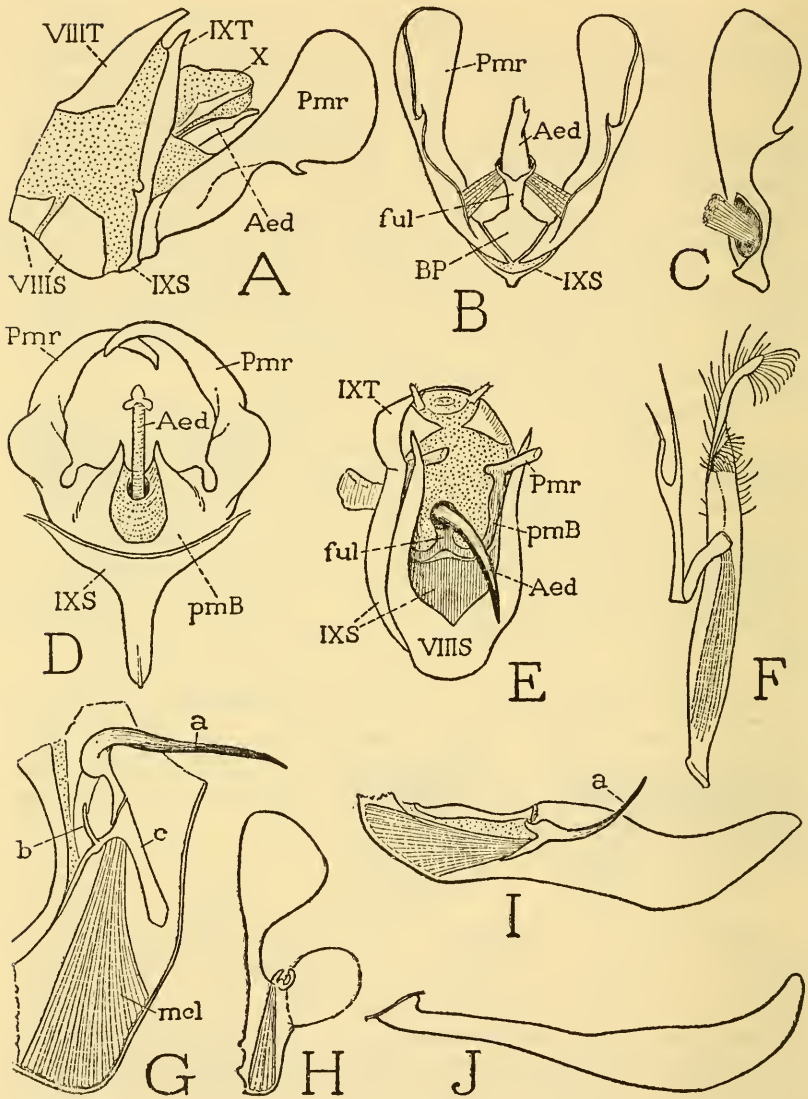


FIG. 11.—Lepidoptera.

A, *Carpocapsa pomonella* (L.), terminal abdominal segments and genital structures, left. B, same, genitalia, ventral. C, same, right paramere, mesal. D, *Bombyx mori* (L.), genitalia and ninth abdominal sternum, ventral. E, *Malacosoma americanum* (F.), end of abdomen, posterior. F, *Promalactis holozona* Meyrick, left paramere, mesal. G, *Sepsis artica* (Freyer), basal part of right paramere, mesal. H, *Pseudoletia unipuncta* (Haw.), left paramere, mesal. I, *Feltia herilis* (Grote), right paramere, mesal. J, *Heliothis phloxiphaga* Grt. and Rob., left paramere, mesal.

a, b, prongs of mesal armature of paramere; c, plate in mesal wall of paramere.

aedeagus is thus dissociated from the interparameral plate only by being sunken into a pouch above it. Otherwise the plate supporting the aedeagal pouch is quite comparable to the basal plate of the aedeagus in those Homoptera in which the parameres are articulated on it (fig. 6 B). The articulation of the parameres on the basal plate that supports the aedeagus in *Carpocapsa* suggests that the parameres and the aedeagus have a common origin as in other insects. The flexor muscles of the lepidopterous parameres are shown by Forbes (1939) to arise on the inner face of the supporting plate of the aedeagus; in *Carpocapsa* these muscles (fig. 11 B) arise on the branches of the arm that embrace the aedeagal pouch.

The arm of the basal plate that supports the aedeagal pouch (fig. 11 B, *ful*) is the *juxta* of lepidopterists, but the word "juxta" is an adverb and not a noun in Latin. The arm apparently serves as a prop for the movement of the aedeagus, and is here termed the aedeagal *fulcrum*.

In some other lepidopterous families, as seen in *Bombyx* (fig. 11 D), the bases of the parameres are united in an interparameral bridge (*pmB*) lying close to the margin of the ninth sternum, as in the trichopteron *Neuronia* (fig. 10 B). In *Bombyx*, however, there is no fulcral arm from the bridge to the aedeagal pouch.

An interesting condition is seen in *Malacosoma* (fig. 11 E), showing the extent to which modification may be carried without disrupting the fundamental plan of structure. The parameral bridge (*pmB*) with the aedeagal fulcrum (*ful*) has the shape of a W, the lateral arms of which extend far above the level of the aedeagal pouch, where they support a pair of short, rodlike parameres (*Pmr*). The ventral part of the ninth sternum (*IXS*) is a large plate beneath the bridge with its posterior end reflected forming a pocket like the toe of a slipper. The eighth sternum (*VIIIS*) projects ventrally beyond the ninth and is produced upward in a pair of long, tapering lateral arms behind the ninth segment.

Studies on the developmental origin of the lepidopterous claspers are not all in harmony. Mehta (1932, 1933) claimed that the phallic rudiments in *Pieris* and other species, which appear in the fourth larval instar, unite to form only the aedeagus. The rudiments of the claspers (valvae) he says are formed later than the aedeagal lobes toward the end of the larval period as thickenings of the lateral walls of the genital chamber. Mehta contends, therefore, that the claspers are appendages of the ninth abdominal segment.

On the other hand, Zander (1903), and Rakshpal (1944) say that both the claspers and the aedeagus of species they studied are de-

veloped from a single pair of phallic rudiments as in other insects. According to Zander, in *Paraponyx stratiolarius* a pair of genital rudiments first appears in a small flask-shaped pouch on the ventral region of the ninth abdominal segment toward the end of the larval period. The lobes divide in the usual manner into four secondary lobes; those of the median pair unite to form the aedeagus. The lateral lobes move posteriorly on the walls of the pouch, and when the latter opens out, as the larva enters the pupal stage, these lobes are carried to the exterior, where they grow quickly into strong appendages, which are the parameres (valvae) of the adult. Likewise Rakshpal finds that in *Galleria* and *Acroia* both the aedeagus and the parameres are formed by the splitting of a pair of primary phallic rudiments. The parameral lobes (valvae) he says become separated from the aedeagus shortly before pupation. It seems fair to conclude that Mehta failed to observe the lateral displacement of the clasper rudiments, and that the lepidopterous valvae are truly phallic derivatives, and are therefore parameres as in Trichoptera. The close association of the parameral bases with the aedeagus in the adult supports this conclusion.

The parameres of Lepidoptera are highly variable in shape and relative size, but there is no division into a basimere and a muscularly movable telomere as in many of the Trichoptera (fig. 10 C). On the mesal surface of each paramere in many lepidopterous families, however, is an armature consisting of one or two variously developed processes, with which is associated a long muscle arising in the base of the paramere (fig. 11 F, G, H, I, *a*, *b*).

A typical example of the parameral armature is seen in *Sepsis arctica* (fig. 11 G). Here there is a long, strong, tapering distal process (*a*) turned ventrally from a thickened base with a proximal extension apparently articulated on the end of an elongate plate (*c*) in the mesal wall of the paramere. A slender dorsal recurved arm of the plate bears a small second free process (*b*). In the notch between the plate and its arm is attached a large muscle (*mcl*) from the extreme base of the paramere. In the genus *Pseudoletia* (H) there are two very small processes arising side by side, with the muscle attached on one of them. In *Feltia herilis* (I) the single, hooked process has a basal arm on which the muscle is attached, but it is little movable on the paramere. An unusual structure is seen in *Promalactis holozona* (F) in which the parameral armature consists of a single, long, sharply elbowed arm ending in two tapering prongs. This appendage is articulated on the paramere, and evidently is movable by the muscle attached on its base.

The parameral armature was termed the "stylus" by Warren (1926), who illustrated it in numerous species of HesperIIDae. Most lepidopterists call the major process the "clasper," and the smaller one the "ampulla" because it is sometimes enlarged at the end. The presence of a muscle associated with these structures, sometimes attached directly on the base of the major process, might suggest that the latter is the telomere of a two-segmented paramere displaced proximally on the mesal surface. However, in most cases the prongs seem to be firmly fixed on the parameral surface, and to have only an indirect connection with the muscle. Yet it is difficult to account for the presence of a muscle within the paramere if it has no homologue in other orders. Forbes (1939) says the muscle of the clasper is "found in every member examined of the Lepidoptera which has a functional valve." The writer, however, has failed to see the muscle in such forms as *Carpocapsa* (fig. 11 C) and *Heliothis* (J), which have no parameral armature.

XII. MECOPTERA

The mecopterous genitalia resemble those of Trichoptera that have large, two-segmented claspers borne on the ninth abdominal segment. In *Panorpa* (fig. 12 A) the oval basal segments (*Bmr*) of the claspers are set into deep emarginations of the ninth-segment annulus; the hooklike distal segments (*Tmr*) are articulated on the basal segments and are provided with abductor and adductor muscles (C). The tergum of the ninth segment is produced into a pair of short arms; the sternal region bears two long subgenital lobes (*sgl*) projecting posteriorly. The aedeagus is a complex structure (G) between the bases of the claspers.

Most students of the mecopterous genitalia, including Ferris and Rees (1939), Grell (1942), and Tjeder (1956), have regarded the panorpid claspers as gonopods of the ninth abdominal segment composed of "gonocoxites" and "gonostyli." In this they conform with the terminology formerly used by the writer (1935), which is here discarded as no longer tenable. Apparently no studies have been made on the development of the mecopterous genitalia, but when we turn from *Panorpa* to *Merope* a condition is found strongly suggestive that the claspers are phallic parameres. In *Merope tuber* the claspers are long, slender, two-segmented arms (fig. 12 D); their bases converge above the ninth sternum and are united above and below the aedeagus (E, *Aed*), which is mostly invaginated between them. Crampton (1931) noted that the claspers of *Nannochorista* appear to be solidly

united, and Michener (1944) says the claspers of *Apterobittacus*, *Bittacus*, and *Panorpa* "are fused both above and below the base of the aedeagus, encircling a genital foramen," but he appears to attach no significance to this fact. Yet it is evident that there is here an inti-

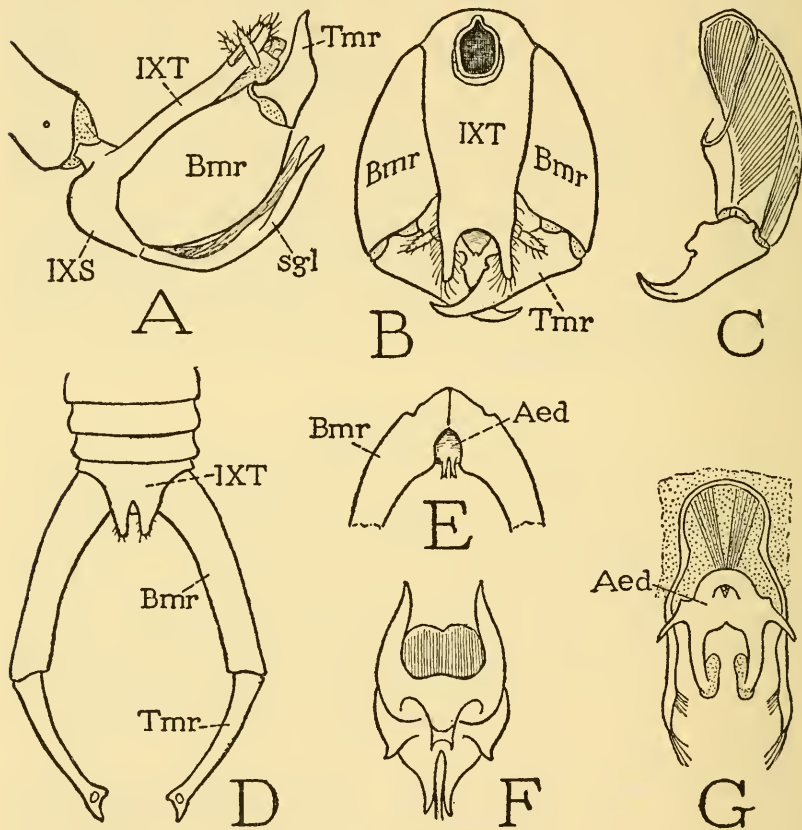


FIG. 12.—Mecoptera.

A, *Panorpa* sp., end of male abdomen, left. B, same, ninth abdominal segment and parameres, dorsal. C, same, paramere with muscles of telomere. D, *Merope tuber* Newm., end of abdomen, and parameres, dorsal. E, same, united bases of parameres and end of aedeagus. F, same, aedeagus, dorsal. G, *Panorpa* sp., aedeagus.

mate association of the claspers with the aedeagus characteristic of insects in which the claspers are known to be developed from lateral lobes of the phallic rudiments. From anatomical evidence, therefore, we can hardly avoid the conclusion that the claspers of Mecoptera are phallic parameres, which, as in Trichoptera, may be more or less dis-

placed laterally on the margin of the ninth segment. Though Crampton (1931) regarded the mecopterous claspers as "gonocoxites," he later (1942) asserted that they must be parameres as in related holometabolous insects.

The aedeagus of *Merope tuber* (fig. 12 F) is an oval, capsulelike structure with a pair of long, dorsal basal arms, pointed lateral lobes, and two tapering, spine-bearing distal processes. It is mostly enclosed by the united bases of the parameral basimeres (E, *Aed*). In *Panorpa* the aedeagus is highly variable in different species. In the species shown at G of the figure it is a flattened structure with tapering lateral processes and a pair of posterior arms. Surrounding the base is a narrow U-shaped sclerotization in the supporting membrane, the arms of which are produced into a pair of free processes at the sides of the aedeagus. These processes have been called "parameres," but since no strictly comparable structures have been observed in other insects, they would appear to be special developments in the Mecoptera.

XIII. DIPTERA

In this order the male genitalia attain a varied and complex structure. While many of their unusual features are simply modifications of the basic structure of the genital organs, others are secondary additions to it. The problem of determining whether secondary parts in different families are homologous or not and of devising names for them is the business of the taxonomists. The major problem for the morphologist concerns the nature of the clasping organs of the Orthorrhapha, and the question of their possible homologues in the Cyclorrhapha, but some attention must be given also to the nature of the secondary organs.

In the Nematocera the claspers are two-segmented appendages closely resembling the parameres of Trichoptera and Mecoptera. They are usually articulated on the ninth segment, but are often interpolated between the tergum and the sternum of this segment, and may even be partly or entirely fused with the sternum. Consequently the claspers of the Diptera have commonly been regarded as "gonopods" of the ninth segment. Arising from the mesal surfaces of the basal segments of the claspers there may be variously developed structures that form a pair of "inner claspers"; and long or short processes are sometimes closely associated with the base of the aedeagus. All these structures have been differently interpreted and named by different students of the dipterous genitalia, leading to a great confusion of terminology and ideas of homology, which has been amply reviewed

by Crampton (1942), who fortunately has left us a sound morphological basis for a uniform nomenclature.

A relatively simple structure of the genital organs is seen in the Culicidae. It must first be observed that the eighth abdominal segment and the ninth segment with its appurtenances in the mosquitoes have been inverted (fig. 13 A), so that the claspers (*Pmr*) are dorsal in position and the proctiger (*Ptgr*) ventral. According to Christophers (1922) the inversion is completed in *Culex fatigans* 24 to 48 hours after emergence of the adult. The ninth segment is greatly reduced (A) and is normally concealed within the eighth. The irregular tergum is produced into a pair of processes beneath the bases of the claspers (B); the small sternum (C) somewhat overlaps the upper surfaces of the claspers. In the following descriptions "dorsal" and "ventral" will be used in a morphological sense.

The typical structure of the culicid genitalia is well shown in *Anopheles* (fig. 13 D). The large, two-segmented claspers are membranously attached to the annulus of the ninth segment. Between their bases is a short, slender aedeagus (*Aed*) connected with the proximal angles of the claspers by a pair of small *basal plates* (*bp*). Arising proximally from the mesal surface of each clasper is a broad, mostly membranous, spine-bearing lobe (*clsp*), known as a *claspette* or *claspette lobe*. In *Anopheles* the two lobes are confluent ventral to the aedeagus, but in other species the claspettes may be entirely separate and take on various forms. In *Aedes pullatus* (E), for example, they are sclerotic hook-shaped processes (*clsp*). Claspettes of this type have usually been termed "parameres" by dipterists without checking on their credentials. The anatomical unity of the genital parts in the mosquito, together with their development from a single pair of rudiments, leaves no doubt that the true parameres are the large outer claspers.

Christophers (1922) has shown that the whole genital complex of *Anopheles* is developed from a single pair of primary phallic lobes, which he called the "proandropodites." The primary rudiments (fig. 14 A, *PhL*) are formed behind the ninth abdominal sternum as the larva enters its last instar. The lobes at first sink into pockets of the epidermis, but in the pupa they are everted and become relatively large (B). With further development a secondary lobe (C, *Mmr*) is budded off mesally from the dorsal side of the base of each primary lobe. A fissure now surrounds these mesal lobes and cuts them off from the principal lobes (D). The mesal lobes elongate (E) and then unite (F, G) to form the aedeagus (*Aed*), or "phallosome" of Christophers. The main lobes become the parameres (C, *Pmr*), or "an-

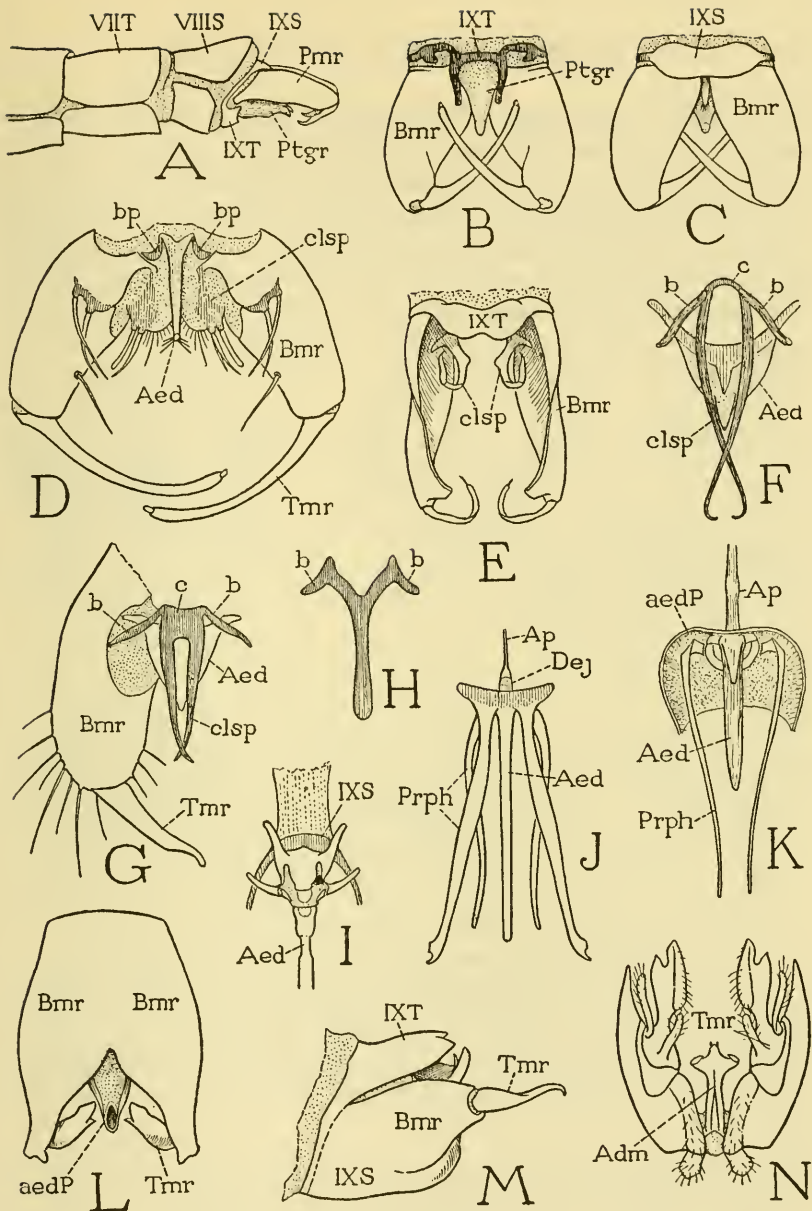


FIG. 13.—Diptera.

A, *Aedes aegypti* (L.) (Culicidae), end of abdomen with segments VIII and IX. B, *Anopheles quadrimaculatus* Say (Culicidae), ninth tergum and parameres. C, same, ninth sternum and parameres. D, same, aedeagus and claspets. E, *Aedes pullatus* (Coq.) (Culicidae), ninth tergum, parameres, and claspets. F, *Forcipomyia cilipes* (Coq.) (Heleidae), claspets and aedeagus, ventral. G, *Forcipomyia specularis* (Coq.) (Heleidae), right paramere, claspets, and aedeagus, ventral. H, *Palpomyia* sp. (Heleidae), claspets united in a median lobe. I, *Lucilia scricata* Meigen (Calliphoridae), base of aedeagus and associated processes. J, *Blepharocera tenuipes* Walker (Blepharoceridae), aedeagus and paraphyses. K, *Tabanus sulcifrons* (Macq.) (Tabanidae), aedeagus and paraphyses in base of aedeagal pouch. L, same, parameres and outer end of aedeagal pouch. M, *Bibio longipes* Lw. (Bibionidae), ninth abdominal segment and left paramere. N, *Tipula triplax* Walker (Tipulidae), parameres and adminiculum, posterior.

b, b, basal arms of claspets; c, basal union of claspets.

dropodites," each of which is finally divided into a large basal segment and a slender distal segment. At the base of each paramere appears a fold (G, *bf*), apparently the rudiment of the claspette lobe.

Likewise, though under different names, the parts of the genital apparatus of *Phlebotomus* are shown by Christophers and Barraud (1926) to be derived from a single pair of primary genital lobes (here termed "precoxites") that appear in the last larval instar at the bases

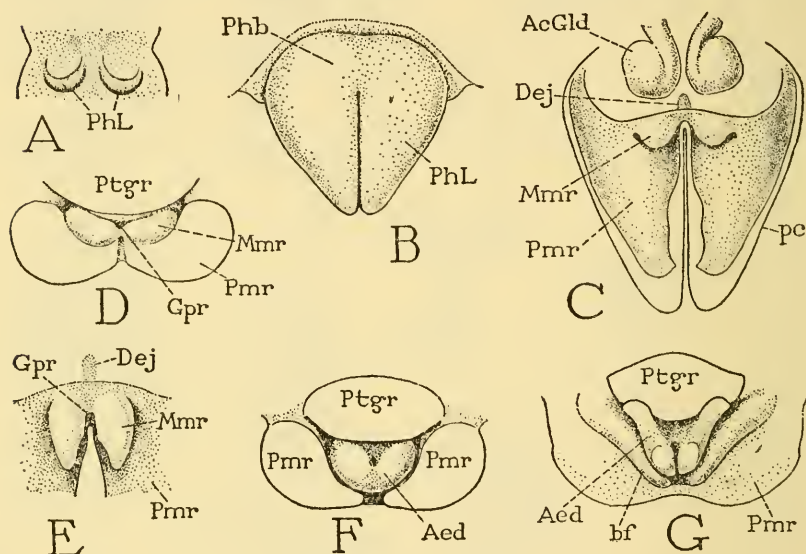


FIG. 14.—Diptera, development of the phallic organs of Culicidae.

(From Christophers, 1922, with names used in this paper.)

A, primary phallic lobes behind ninth abdominal sternum of last larval instar. B, same, later stage. C, differentiation of primary lobes into mesomeres and parameres within pupal cuticle. D, mesomeres uniting around the gonopore. E, later stage, mesomeres enlarged. F, mesomeres united to form the aedeagus. G, folds (*bf*) developed on bases of parameres, probably rudiments of claspette lobes.

of the anal lobes. In the pupa a pair of median lobes is cut off from the bases of the primary lobes and form the intermediate parts of the genital complex. The aedeagus of *Phlebotomus* is quite different from that of the mosquito; it is sunken into an ensheathing pouch and has two long apical processes that project from the mouth of the pouch. The lateral lobes become secondarily constricted into basal parts ("coxites") and distal parts ("styles"). There are no claspettes or other secondary structures developed from the parameres of *Phlebotomus*.

These accounts of the development of the phallic organs in two species of Diptera show that the claspers are lateral branches of the primary phallic rudiments, and are therefore parameres as in other insects. Crampton (1942, p. 85) has strongly contended that "if comparative morphology has any meaning at all, the segmented genital forceps flanking the aedeagus in male Mecoptera, Trichoptera, Diptera, etc., must be homologous with the genital forceps, or parameres, flanking the aedeagus in male Hymenoptera, Coleoptera, etc., instead of representing the coxites and styli of lower insects, as maintained by other investigators."

Van Emden and Hennig (1956) object to Crampton's use of the term paramere for the lateral claspers. They say that the developmental studies of Abul-Nasr (1950) on dipterous genitalia "seem to have proved that the structures under discussion are genuine gonopods." Actually, what Abul-Nasr has shown is that the entire genital complex of Diptera is derived from a pair of primary lobes as in other insects. The primary lobes divide each into two secondary lobes, one lateral, the other mesal. The lateral lobes become the claspers; the mesal lobes form the aedeagus and whatever structures may be intermediate between the aedeagus and the claspers. In the case of "*Chironomus*" (*Tendipes*), however, in which there is no aedeagus, mesal lobes developed on the basal segments of the claspers evidently become the endoparameral processes of the adult called "parameres." These processes are solid outgrowths from the distal parts of the basimeres, and clearly are secondary structures not equivalent to the claspettes of other species. An identity of the lateral claspers with gonopods of the ninth segment is apparently taken for granted in Abul-Nasr's discussion; by his own evidence the claspers are phallic parameres.

The adult structure of the genitalia in many nematocerous families is similar to that of the Culicidae, but the parts themselves are highly variable in form. Parameral claspers are present in most of the Orthorrhapha; they may become displaced laterally from the aedeagus and attached laterally on the annulus of the ninth segment. In *Tabanus* (fig. 13 L) the basimeres are united ventrally with each other; in various nematocerous and brachycerous species the basimeres may be partly or entirely fused with the ninth sternum (M). Among the Tipulidae the basimeres are often so deeply interpolated between the tergum and the sternum of the ninth segment that the writer formerly (1904) interpreted them as the "pleura" of this segment. The telomeres likewise are variable and may be complicated by the development of accessory lobes (N).

The claspettes of the Nematocera are of interest because of the

various forms they assume. They are always connected with the inner faces of the parameres, and thus appear to be secondary outgrowths of the latter. As already noted, in the Culicidae they may be membranous lobes confluent beneath the aedeagus (fig. 13 D) or entirely independent sclerotic arms (E). In the Heleidae the claspettes may be broad platelike appendages of the parameres, but in species of *Forcipomyia* (F, G) they are long, slender processes connected with the parameres by only a pair of basal arms (*b, b*). In *F. cilipes* (F) the two claspettes are joined by a narrow median basal bridge (*c*), which in *F. specularis* (G) becomes a wide plate solidly supporting the claspette processes. Finally the claspettes in some species are themselves united in a single median process (H), which may take the form of a broad spatulate lobe. In the last case "claspette" becomes a doubtfully appropriate term; but nomenclature often is not sufficiently elastic to keep pace with the anatomical versatility of insect structures.

Another set of structures occurring in various unrelated species are outgrowths arising at the base of the aedeagus, which are quite distinct from the parameral claspettes. In *Blepharocera tenuipes* (fig. 13 J) four long arms (*Prph*) arise from a small basal plate that supports also the rodlike median aedeagus (*Aed*). In *Tabanus sulcifrons* (K) the aedeagus and a pair of long slender accessory processes connected with its base arise from the inner end of a deep pouch that opens by a narrow aperture between the parameres (*L, aedP*). These basal processes of the aedeagus, which occur also in some other insects, seem to have been given no special names; they are here termed in general *paraphyses* (lateral outgrowths). Structures perhaps of a similar nature are the short processes arising from a basal plate of the aedeagus in the muscoid flies (I). These processes are commonly called "gonapophyses," but Crampton (1942) suggests the name *gonites* for them, since the term gonapophyses commonly refers to the valves of the female ovipositor. Some recent writers, however, call the processes "parameres" in the belief that they represent the phallic parameres of other Diptera. That they cannot be parameres is pointed out by Crampton, since they are present in some brachycerous families that have true lateral parameres.

In the Cyclorrhapha parameral claspers appear to be suppressed. Some writers suggest that a pair of lobes or arms on the lower posterior angles of the ninth tergum are "gonopods" representing the parameres, but we have no account of the development of the genitalia in the cyclorrhaphous flies. The lobes in question may be solid outgrowths of the tergum, flexible at their bases, or freely movable by

muscles, and they probably serve as claspers, but it is incongruous that either gonopods or parameres should be borne on the tergal plate of a segment. Crampton called these lobes "surstyli." Paired lobes or processes of various shapes and sizes are of common occurrence on the ninth abdominal tergum throughout the insects, and, as already noted, are conspicuous in some Culicidae (fig. 13 B).

XIV. HYMENOPTERA

The genital organ typical of male Hymenoptera (fig. 15 A) differs in several respects from that of other insects. The parameres are never entirely separated from the aedeagus, the three parts being united proximally in a common base. Between the parameres and the aedeagus on each side is a pincerlike organ known as the *volsella* (*Vol.*). These several elements are differentiated at an early stage of development (D) from the primary phallic rudiments (C). Finally, the whole phallic structure of the adult is supported on a sclerotic *basal ring* (A, *BR*)

The basal ring is typically an annular sclerite; it may be much reduced or incomplete, but rarely is it absent. According to Zander (1900) the ring is formed relatively late in development from the epidermis at the base of the primary phallus. Yet it becomes an essential part of the adult organ, since the extrinsic phallic muscles from the ninth abdominal segment are inserted on it.

The hymenopterous parameres are usually elongate, undivided lobes of various shapes united proximally with the aedeagus (fig. 15 G, *Pmr*). In most of the Chalastogastra, however, the parameres are distinctly segmented into basimeres and telomeres (L), and the telomeres are movable by muscles from the basimeres. In some of the Clistogastra the distal part of the paramere may be flexible or even articulated on the basal part (N), but in only a few such cases is the telomere provided with muscles. The writer (1941) limited the term "paramere" to the free terminal part of the clasper, or to the movable telomere, and called the basal part the "parameral plate" because it is so intimately united with the base of the aedeagus; but clearly the whole structure is the paramere.

The free part of the aedeagus projects from between the bases of the parameres (fig. 15 A, G, L, *Aed*) and assumes various forms. Characteristically it contains a pair of rods (A, *r*) in its lateral walls, the apices of which usually project as free points. These aedeagal rods are called "parameres" by Beck (1933), who says they "are the gonapophyses of the ninth sternite." Other writers more commonly

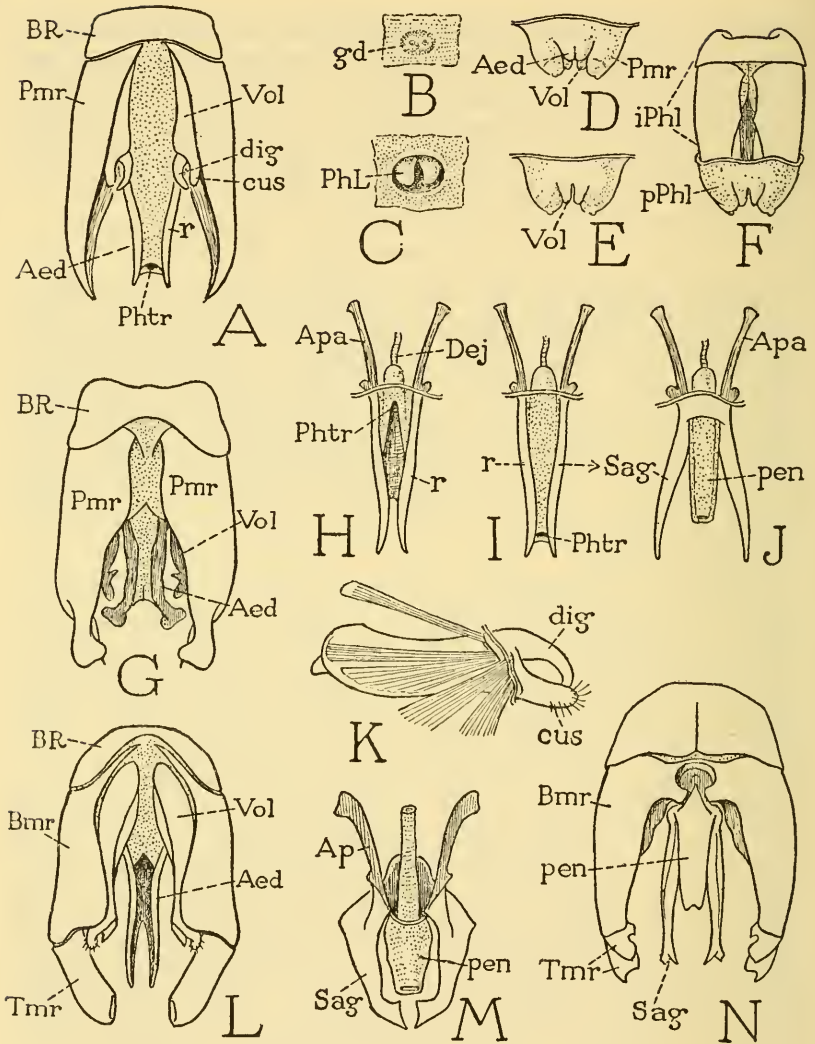


FIG. 15.—Hymenoptera.

A, diagram of general structure of hymenopterous phallic organ, ventral. B, *Vespula maculata* (L.), genital disc on venter of ninth abdominal segment of penultimate larval instar. C, same, phallic lobes in pocket of integument of next larval instar. D, same, phallic organ of pupa, dorsal. E, same, ventral. F, same, phallic organ of adult growing from within pupal organ. G, same, adult phallus. H, diagram of primitive hymenopterous aedeagus, ventral. I, aedeagal groove closed, bringing phallosome to apex. J, typical phallic structure of Apoidea. K, *Megaryssa lunator* (F.), volsella and muscles. L, *Xiphydria maculata* (Say), phallus, ventral. M, *Anthophora abrupta* Say, penis and sagittae, ventral. N, *Bombus lapidarius* (L.), phallus, dorsal.

term them the "penis valves," which Michener (1944) defines as "mesal basal processes of the gonocoxopodites," and homologizes them with the ninth-segment coxal endites of *Machilis* (fig. 2 G, *Endt*). However, the aedeagal rods of the Hymenoptera have no connection with the parameres, which are supposed to be the "gonocoxites" of the ninth segment. Their bases are prolonged into free apodemes (fig. 15, H, I, J, *Apa*), on which the aedeagal muscles are attached. Deprived of any theoretical status, the rods are simply lateral sclerotizations of the aedeagus supporting the aedeagal apodemes.

In most of the bees the aedeagal rods have become almost entirely separated from the median membranous part of the aedeagus (fig. 15 J, M, N), giving the apoid aedeagus a tripartite structure. The free lateral rods are then known as the *sagittae* (J, *Sag*), but their identity with the rods in other forms is shown by the fact that they still carry the aedeagal apodemes (J, M). The median remnant of the aedeagus may be termed the *penis* (*pen*). The *sagittae* of *Bombus* are said by Zander (1900) to be developed directly from the aedeagal lobes of the primary phallic rudiments, the penis being a secondary outgrowth between them. This observation shows at least that the aedeagal rods belong to the aedeagus and not to the parameres or "coxites." In some of the Hymenoptera, particularly among the Chalastogastra and Ichneumonidae, the aedeagus appears to retain a primitive structure in that it is widely open below (H, L) with the phallotreme (H, *Phtr*) at the base of the ventral channel. In most cases, however, the aedeagus is closed below, bringing the phallotreme to the apex (I, J, M, N).

An endophallic sac traverses the aedeagus from the phallotreme and may project beyond the aedeagal base, where it receives the ductus ejaculatorius (fig. 15 H, *Dej*). The honey bee has no aedeagus, since the primary median lobes of the phallic rudiments do not unite. Both the mesomeres and the parameres remain undeveloped and in the adult form only a pair of small lobes guarding the phallotreme. The endophallus, on the other hand, is enormously developed, and when partly or fully everted becomes the functional intromittent organ.

The volsellae appear to be phallic elements peculiar to the Hymenoptera. In most families they are well developed, but in the bees they are much reduced or absent. Typically each volsella consists of an elongate plate on the ventral surface of the phallus lying close to the inner margin of the corresponding paramere (fig. 15 A, L, *Vol*). At its free distal end the volsellar plate bears two small processes that form a pincer, one being an immovable projection or *cuspis* (A, K, *cus*) of the plate, the other a curved or hooked *digitus* (*dig*) movably

opposed to the cuspis. Both cuspis and digitus are strongly muscled (K), and a large protractor muscle of the entire volsella arising in the neighboring paramere is attached on the inner end of the plate. Retractor muscles arise proximally in the paramere and on the aedeagal apodeme. A full description of the phallic musculature and mechanism of a braconid is given by Alam (1952). The elaborate musculature of the volsellae seems to show that in the insects special muscles can be developed wherever they are needed. The volsellae evidently are important elements of the genital mechanism in Hymenoptera. According to observations of Peck (1937) on ichneumonids taken during mating, the volsellar pincers grasp the membrane near the female gonopore, keeping the membrane taut while the aedeagus is inserted. In the braconid *Stenobracon* Alam says the two digiti enter the gonopore. The volsellae are developed from a pair of small ventral lobes of the pupal phallus (D, E, *Vol*) and are thus independent primary elements of the hymenopterous genital complex.

The development of the hymenopterous phallus has been described by Seurat (1899) in the braconid *Dorcytes*; by Michaëlis (1900) in *Apis*; by Zander (1900) in *Vespa*, *Bombus*, and *Apis*; by Boulangé (1924) in *Sirex*; and by Snodgrass (1941) in *Vespula* and *Apis*. In *Vespula* the genital rudiments are first visible as a pair of minute thickenings in a small disc (fig. 15 B, *gd*) on the posterior part of the venter of the ninth abdominal segment of a late-instar larva. Beneath the disc in a pocket of the integument of the enclosed instar are two small primary phallic lobes (C, *PhL*). In the pupa (D) the primary lobes have divided into six secondary lobes united on a common base. The median dorsal lobes (*Aed*) will form the aedeagus, the lateral lobes (*Pmr*) the parameres, and the ventral lobes (D, E, *Vol*) the volsellae. The greatly larger phallus of the adult (F, *iPhl*) will then develop from within the pupal organ (*pPhl*), and finally take on the mature structure (G). The whole genital complex of the adult thus takes its origin from a single pair of minute phallic rudiments.

SUMMARY

1. The organs associated with the genital outlet in the male insect, in all orders in which their ontogenetic origin has been observed, are developed from a pair of primary phallic lobes that appear on the nymph or larva.
2. In the lower insects there is evidence that the phallic rudiments pertain to the tenth abdominal segment. In the higher insects they usually rise on the apparent posterior part of the ninth segment of the

larva, but in the adult they are situated *behind* the sternal plate of this segment.

3. The terminal ampullae of the vasa deferentia usually lie at least partly within the phallic lobes, suggestive that originally they may have opened through the lobes, and that the latter, therefore, were a pair of penes. This suspicion appears to be confirmed in the Ephemeroptera, if the rudiments of the two penes in this order are homologues of the phallic lobes in other insects, as they appear to be. The ephemeropterid penes are penetrated by ectodermal exit ducts that unite with the vasa deferentia.

4. In insects other than the Ephemeroptera a secondary median ectodermal ejaculatory duct grows inward between the bases of the phallic lobes. The ampullae of the vasa deferentia then withdraw from the lobes to unite with the inner end of this duct, which becomes the definitive genital outlet.

5. In the Thysanura the primary phallic lobes unite to form a simple median penis giving exit through a very short ejaculatory duct to both vasa deferentia.

6. The primary phallic lobes of insects that have lateral copulatory claspers associated with a median intromittent aedeagus divide each into two secondary lobes. The secondary lobes of the median pair, or *mesomeres*, unite with each other to form the aedeagus, the lateral lobes, or *parameres*, become the claspers. Secondarily in their development the parameres may become two-segmented.

7. Stylus-bearing plates of the ninth abdominal segment, which are commonly regarded as the coxae of former limbs of this segment, are present in Thysanura, Ephemeroptera, and Grylloblattidae. The current idea that the parameral claspers are "coxites" equivalent to these stylus-bearing plates ignores the fact that the parameres are derived along with the aedeagus from the phallic lobes, and that the single penis of the Thysanura is also formed from two primary phallic lobes that have no actual connection with the coxal plates. The idea expressed by some writers that the phallic lobes are the telopodites of ninth-segment appendages would imply that the telopodites of a primitive pair of legs have united to form an intromittent organ, the aedeagus, an interpretation hardly to be taken seriously. Likewise, the theory that endites of the ninth-segment coxae, such as are present in some species of Machilidae, have united with a primitive median penis to form the aedeagus is untenable since it is not supported by observed facts. The coxal endites of Machilidae are not united with the penis, which, moreover, is itself formed from two primary lobes. The so-called "penis valves" of the aedeagus of some insects, inter-

puted as "coxal endites," are merely lateral sclerotizations of the aedeagal wall.

8. In some Orthoptera styli are borne on the ninth sternal plate of the male abdomen, in which case it is evident that the corresponding coxae have been incorporated into the definitive sternum. Yet the phallic lobes in this order divide as usual each into two secondary lobes. Therefore, if these secondary phallic lobes in Orthoptera are equivalent to the mesomeres and parameres of other insects, the parameres are not coxal plates, or "coxites." However, in the Orthoptera the phallic lobes do not form typical parameres and an aedeagus.

9. The commonly held idea that the phallic lobes represent a pair of appendages of the ninth or tenth abdominal segment must assume that the male genital organs were once a pair of legs. It is not explained, however, in what manner these legs became modified into an intromittent organ containing the genital outlet and into a pair of lateral claspers. If the phallic lobes of modern insects ever had any relation to appendages, it seems more probable, by comparison with other arthropods, that they were originally penes on the coxae of a pair of legs. If so, the supposed appendages themselves have been suppressed, and the isolated penes then developed into the aedeagus and parameres of modern insects. If the parameres represent the coxae of the vanished legs, they must be theoretically regenerated from the penes they once bore. Considering the known facts concerning the ontogenetic development of the phallic organs, it needs a strong imagination to visualize their evolution from a pair of legs. Though Else (1934) claimed to have traced the phallic rudiments of *Melanoplus* from tenth-segment limb buds on the embryo, it is perhaps possible he confused the limb buds with the genital rudiments. Other writers describe the phallic lobes as making their first appearance on the nymph or larva, after the abdominal limb buds of the embryo have disappeared.

10. Since biological theories of origins and evolution cannot be subjected to experimental tests, as can theories in physics, and since we cannot go backward in time to observe the facts, no biological theory is really capable of demonstration. For practical purposes, therefore, in the study of the insect male genitalia, if we care to disregard questions of the nature of the primitive phallic organs, and theories on the homologies of the adult organs, we still have the known facts of their ontogenetic development. It has been demonstrated that the aedeagus and claspers are derived from a pair of primary rudiments, and this fact gives us a basis for homologizing these major parts of

the genitalic complex throughout the insect orders. On this assured information a simple, uniform terminology can be based.

II. Most taxonomists seem to regard the preservation of a traditional anatomical nomenclature as something to be desired above all else; but the result is confusion, since each taxonomist has his own traditional nomenclature. The plan here offered, therefore, would relieve this confusion, and is one that *can* be consistently followed if nomenclatural uniformity is desired. In addition to the major phallic organs, however, numerous secondary structures have been developed independently in nearly all the insect orders. Such structures necessarily must be given special names for taxonomic purposes.

ABBREVIATIONS ON THE FIGURES

- | | |
|---|---|
| <i>AcGld</i> , accessory gland. | <i>gd</i> , genital disc. |
| <i>Adm</i> , adminiculum. | <i>Gpr</i> , gonopore. |
| <i>Aed</i> , aedeagus. | <i>iPhl</i> , imaginal phallus. |
| <i>aedP</i> , aedeagal pouch. | <i>lPmr</i> , left paramere. |
| <i>Amp</i> , ampulla. | <i>mcl</i> , <i>mcls</i> , muscle, muscles. |
| <i>Ap</i> , apodeme. | <i>mL</i> , median lobe. |
| <i>Apa</i> , aedeagal apodeme. | <i>Mmr</i> , <i>Mmrs</i> , mesomere, mesomeres. |
| <i>Apb</i> , apodeme of phallobase. | <i>Papt</i> , paraproct. |
| <i>bf</i> , basal fold. | <i>pc</i> , pupal cuticle. |
| <i>Bmr</i> , basimere. | <i>pen</i> , median lobe of aedeagus. |
| <i>bp</i> , basal plate. | <i>Pen</i> , penis. |
| <i>BP</i> , basal plate. | <i>Phb</i> , phallobase. |
| <i>BR</i> , basal ring. | <i>PhL</i> , primary phallic lobe. |
| <i>Cer</i> , cercus. | <i>Phm</i> , phallomere. |
| <i>cf</i> , caudal filament. | <i>Phtr</i> , phallotreme. |
| <i>clsp</i> , claspette. | <i>pmB</i> , interparameral bridge. |
| <i>Crpt</i> , aedeagal crypt. | <i>Pmr</i> , paramere. |
| <i>cus</i> , cuspis. | <i>pPhl</i> , pupal phallus. |
| <i>Cx</i> , coxa. | <i>Prph</i> , paraphysis. |
| <i>cxmcl</i> , coxal muscle. | <i>Ptgr</i> , proctiger. |
| <i>dej</i> , nonfunctional duct. | <i>ri</i> , ridge. |
| <i>Dej</i> , ductus ejaculatorius. | <i>rMmr</i> , right mesomere. |
| <i>Dejcn</i> , ductus ejaculatorius conjunctus. | <i>rPhm</i> , right phallomere. |
| <i>dig</i> , digitus. | <i>rPmr</i> , right paramere. |
| <i>dl</i> , dorsal lobe of telomere. | <i>S</i> , sternum. |
| <i>Endt</i> , coxal endite. | <i>Sag</i> , sagitta. |
| <i>Enph</i> , endophallus. | <i>sgl</i> , subgenital lobe. |
| <i>Eppt</i> , epiproct. | <i>smcl</i> , stylus muscle. |
| <i>fl</i> , flagellum. | <i>Sty</i> , stylus. |
| <i>ful</i> , fulcrum (juxta). | |

<i>T</i> , tergum.	<i>Vir</i> , virga.
<i>tl</i> , tergal lobe.	<i>vl</i> , ventral lobe of telomere.
<i>Tmr</i> , telomere.	<i>Vol</i> , volsella.
<i>tp</i> , tergal process.	
	<i>xl</i> , lobe of tenth segment.
<i>Vd</i> , vas deferens.	<i>x-x</i> , cut edge of genital chamber.
<i>Ves</i> , vesicle.	

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