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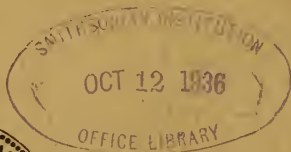
PART III. THE MALE GENITALIA
(INCLUDING ARTHROPODS OTHER THAN INSECTS)

BY

R. E. SNODGRASS

Bureau of Entomology and Plant Quarantine

U. S. Department of Agriculture



(PUBLICATION 3396)

CITY OF WASHINGTON
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I. INTRODUCTION

The series of papers entitled "Morphology of the Insect Abdomen" is concluded with the present contribution. Other papers on the male genitalia of insects, however, are designed to follow. The only excuse here offered for the obvious fact that Part III, on the one hand, greatly exceeds the scope of the general title, and, on the other, leaves much to be said about insect genitalia, is the writer's conviction that insects must be studied morphologically as arthropods—a practice at least not prevalent among entomologists. The literature of entomological morphology is replete with long discussions on the nature and

evolution of insect structures that unquestionably might be brought to more satisfactory conclusions if entomologists could get over the habit of thinking of insects purely as insects. Since insects are arthropods, a wider survey of the general field of arthropod anatomy will often lead to a better understanding of things about insect structure than can be derived from an intensive study of the insects themselves. For this reason the present paper, which has for its object an understanding of the fundamental nature of insect genitalia, includes a review of the genital organs in the major groups of the Arthropoda and, for good measure, also in the Onychophora.

The somatic adaptations of animals to the function of reproduction are in general of a superficial nature; they have not brought about the development of any fundamental organ or system of organs comparable with the structures that subserve most of the other important activities of the animal, such as locomotion, orientation, alimentation, or blood circulation. This condition evidently arises from the fact that the germ cells, in a physiological sense, are parasites of the soma; though they are given lodgment within the body, the accommodations for their growth and discharge have been built up by alterations of structures already present for some other purpose, or by the addition of rather haphazard accessories. In the annelid-onychophoran-arthropod series of animals the only common feature of the reproductive system is the inclusion of the primary germ cells in the mesoderm. The germ cells liberated from the mesoderm are never discharged directly to the exterior through the ectoderm, as in some of the Coelenterata; they are first given off internally, usually into the coelome or confined parts of the latter, where they undergo their development into ova or spermatozoa, and the gametes must then be extruded from the body cavity to the outside through openings in the body wall. The evolution of the reproductive organs in the Arthropoda has been largely a matter of developing special containers for the maturing germ cells and of establishing exit passages for the gametes. External accessories have been added in most groups to assure insemination of the female by the male or to aid the female in the deposition of the fertilized eggs.

ENUMERATION OF THE ARTHROPOD BODY SEGMENTS

Because of the great variation in the position of the genital openings in the Arthropoda, it becomes highly desirable, in a comparative study of the external genitalia, to be able to identify and briefly designate the corresponding body segments in the several arthropod groups.

To enumerate the segments consecutively would not be a difficult matter were it not for the uncertainty, or difference of opinion at least, concerning the number of somites that enter into the composition of the head. The discrepancy of opinion arises principally from a difference of interpretation concerning "segmentation" in the cephalic region anterior to the somite of the tritocerebral brain lobes. This somite carries the second antennae, or chelicerae, and is without question postoral in its origin, though its lateral parts may lap forward at the sides of the mouth and its appendages thus acquire a preoral position in the adult. The head region anterior to the tritocerebral somite, often called the *acron* in the embryo, has been supposed to include an antennal, a preantennal, and even a labral somite, the evidence adduced being the presence of corresponding coelomic sacs in the mesoderm associated with ganglionic centers of the ectoderm innervating the sensory and appendicular organs of the acronal region. The first antennae (antennules) are the procephalic appendages most commonly present in the arthropods, and the antennae of Onychophora would appear to be their homologues in this group of related animals; but the embryonic position of the antennae relative to the mouth is variable, in some cases the appendages are preoral, in others adoral, and in others again they are slightly postoral.

Segmentation in the articulate animals is closely associated at least with the formation of paired coelomic sacs in the mesoderm. In the embryology of the annelids, as is well known, the coelomic mesoderm usually takes its origin from a pair of teloblastomeres situated at first behind the blastopore. From these cells are proliferated forward in the ventrolateral parts of the body of the larva two bands of mesoderm, in which there may be formed several pairs of primary coelomic cavities. The secondary somites of the worm added during or after metamorphosis are generated from a zone of growth situated between the last larval somite and the small terminal region of the body containing the anus (periproct, pygidium, telson). The mesoderm of the postlarval somites is in most cases proliferated also from the primary mesodermal teloblastomeres, though in some it is said to have its source in the teloblastic ectoderm (Iwanoff, 1928). The forward growth of the mesoderm bands in the Annelida is arrested at the mouth of the larva, and the first pair of coelomic cavities lies just behind the mouth; as a consequence there remains anterior to the mouth an unsegmented region of the trunk, known as the prostomium (fig. 1 A, *Prst*). With later development, however, the interior of the prostomium may become completely occupied by extensions of the

coelomic cavities of the first postoral somite (*PMsd*), and the prostomial walls may thus be lined by a coelomic peritonium (see Meyer, 1901; Sokolow, 1911). The external organs of the prostomium in the Polychaeta include tentacles, palpi, eyes, and nuchal organs, but the cephalic coelome of the annelids is not known to be divided into corresponding sacs.

The coelomic mesoderm bands of the Onychophora also are teloblastic in their origin. Though they cannot be traced from a single

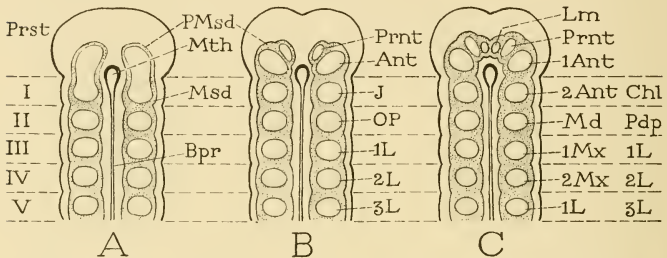


FIG. 1.—Diagrams showing the maximum observed development of the coelomic mesoderm in the anterior part of the trunk in Annelida, Onychophora, and Arthropoda, and the apparent homologies of the postoral somites.

A, Annelida: the coelomic sacs of mesoderm bands primarily all postoral, but the prostomium may be invaded by extensions of the coelomic sacs of first postoral segment. B, Onychophora: the coelomic mesoderm bands extend into the preoral region and here contain antennal and possible preantennal coelomic sacs (Evans, 1902). C, Arthropoda: the coelomic mesoderm bands may unite before the mouth and contain antennal, preantennal, and labral coelomic sacs (*Carausius*, Wiesmann, 1926).

Ant, coelomic sac of antenna; *1Ant*, same of first antenna (antennule); *2Ant* (*Chl*), same of second antenna or chelicera; *Bpr*, blastopore; *Chl* (*2Ant*), coelomic sac of chelicera or second antenna; *I-V*, coelomic sacs of first five somites; *J*, coelomic sac of onychophoran jaw somite; *L*, coelomic sacs of leg somites; *Lm*, coelomic sac of labral region; *Md* (*Pdp*), same of mandible or pedipalp; *Msd*, coelomic mesoderm; *Mth*, mouth; *1Mx*, *2Mx*, coelomic sacs of first and second maxillae, or of first and second legs of Chelicerata; *OP*, coelomic sac of oral papilla; *Pdp* (*Md*), same of pedipalp or mandible; *PMsd*, prostomial mesoderm; *Prst*, prostomium.

pair of teloblastomeres, they are generated from a multicellular germinal area of the blastoderm lying behind the blastopore. In their forward growth, however, the mesoderm bands of the Onychophora do not stop at the mouth; they extend into the head region anterior to the mouth (fig. 1 B) and are here excavated by a pair of large coelomic cavities (*Ant*) associated with the antennae, and possibly (Evans, 1902) by a pair of small transitory preantennal sacs (*Prnt*). Though the antennae and their nerve centers in the Onychophora lie well before the mouth, the antennal coelomic sacs are morphologically

adoral rather than preoral, since their posterior ends embrace the stomodaeum and give rise to the stomodaeal musculature (Kennel, 1888; Evans, 1902). The first truly postoral coelomic sacs of the Onychophora are those of the jaws (*J*); the next pertain to the oral papillae (*OP*).

Among the Arthropoda a teloblastic origin and growth of the coelomic mesoderm occurs in a sufficient number of cases (in certain Crustacea and Chilopoda) to suggest that it is the primitive method of mesoderm formation in this group as well as in the Annelida and Onychophora. The mesoderm bands extend into the procephalic lobes of the head as in adult Annelida and Onychophora, and may become here excavated not only by antennal (antennular) and preantennal coelomic sacs (fig. 1 C, *1Ant*, *Prnt*), but also, according to the observations of Wiesmann (1926) on *Carausius morosus*, by a pair of sacs in the labral region (*Lm*) lying immediately before the mouth. The preantennal and antennal sacs in this case, it should be observed, do not intervene between the labral sacs and the mouth, and are therefore not preoral; they lie at the sides of the mouth and are hence *adoral*. The labral sacs (or perhaps ocular sacs), on the other hand, are literally preoral, being adjacent to each other before the mouth. We may conclude, therefore, that in the Arthropoda, as in the Annelida, the coelomic mesoderm potentially surrounds the blastopore by the union of the mesoderm bands before the mouth, and that the antennal, preantennal, and labral coelomic sacs, when present, lie on adoral and preoral radii centering in the mouth (fig. 1 C). Whether these radial cavities of the mesoderm are to be called "somites" or not becomes largely a matter of definition. If the presence of a pair of cavities in the mesoderm associated with a pair of external organs and their ganglia is taken to define a segment, we may claim that the acron of the arthropods is potentially a segmented region. On the other hand, if a segment is conceived to be an independently movable section of the trunk, then there is no segmentation of the arthropod trunk anterior to the somite of the second antennae, shown either in the embryonic procephalon or in the corresponding part of the adult head capsule. According to Sollaud (1923), the first intersegmental groove in the embryo of Palaemoninae separates an anterior head region, or acron, from the first somite, which latter carries the second antennae. The crustacean acron, or preoral region of the embryonic head bearing the eyes and the first antennae, Sollaud believes, corresponds with the annelid prostomium. If this be true, it must be admitted that the prostomial region of an onychophoran (fig. 1 B)

or an arthropod (C) is invaded by the coelomic mesoderm, and may contain one, two, or three pairs of coelomic sacs.

According to this view, the preantennae and antennules of the Arthropoda are comparable with the prostomial tentacles and palpi of the Polychaeta, and the absence of individual coelomic sacs associated with the cephalic appendages of the latter may be attributed to the imperfect development or more primitive condition of the prostomial mesoderm in the annelids. The known facts of comparative embryology show clearly that the "segmentation" of the preoral mesoderm is highly variable, and it is perhaps significant that the most complete example of it has been found in an insect. In any case, the idea that the prostomium, or acron, of the articulate animals is a preoral trunk region inherently devoid of coelomic mesoderm is evidently a fallacious concept based on the condition in the specialized trochophore larva of polychaete annelids and other invertebrates. There would seem to be no morphological reason why the mesoderm bands should not encircle the blastopore, surrounding the mouth anteriorly as they do the anus posteriorly. On this theory it is easy to accept the claim of histoneurologists that the oculo-antennal part of the arthropod brain (protocerebrum and deutocerebrum) corresponds with the prostomial brain of the annelids, and that the second antennal brain lobes represent the ganglia of the first postoral somite.

Following the concept thus developed that the first antennal and preantennal coelomic sacs, when present in the Arthropoda, are primarily adoral in position and lie in a region of the head (the acron) corresponding with the prostomium of an annelid, the entirely practical plan is here adopted of designating numerically the truly postoral segments beginning with the tritocerebral somite as *Segment I* (fig. 1 C, I). The appendages of this segment are the second antennae of Crustacea, the chelicerae of Chelicerata (C, 2*Ant*, *Chl*), or the corresponding embryonic rudiments of these organs found in many Hexapoda. In any case, there is no doubt as to the identity of the tritocerebral somite, and there is no question that it is the *first postoral segment of the adult* in all the Arthropoda.

Some of the arthropods are *epimorphic*, the definitive number of body segments in such forms being established at the end of embryonic development; others are *anamorphic*, in which case either a fixed or an indefinite number of segments is added during postembryonic growth. The generation of new segments appears always to take place at one point, which is a zone of growth located between the last-formed somite and the terminal periproct, or telson. The occurrence of anamorphosis is well known in Crustacea, Diplopoda, Chilopoda.

and Protura; the process of segment formation has been followed in detail by Pflugfelder (1932) in a diplopod. If the generation of arthropod somites is invariably teloblastic, it would seem to follow that the numerical order of a segment in the body series of any arthropod would determine the homology of this segment with a segment of the same number in any other arthropod. This principle, however, does not apply to the anterior segments, since in the development of both the annelids and the arthropods there is a primary body region that becomes itself differentiated into a small number of somites. With the Polychaeta the first few body somites are formed directly in the hyposphere of the trochophore; the nauplius larva of Crustacea has a short body region containing two primary somites (second antennal and mandibular), the succession of secondary teloblastic somites beginning with the segment of the first maxillae. (See Iwanoff, 1928; Sollaud, 1923.)

ORIGIN OF THE GONADS AND THE GONODUCTS

The groups of primary germ cells that occur in the mesodermal tissues are known to students of the Annelida as the "gonads", and they are appropriately thus termed since the word means a "sprout" or "germinating bud". These germ cell groups of the annelids, however, correspond with the so-called "germaria" of the Arthropoda, and in arthropod anatomy the term "gonad" refers to the mesodermal sac that contains the germinal cells in its epithelial walls. This nomenclatural confusion is unfortunate, and it is difficult to remedy. For an arthropodist it is easier to use the term *germarium* in a general sense to include the annelid "gonads", and to retain the name *gonad* for the mesodermal sacs (ovaries or testes) that contain the germaria—a usage generally followed in zoology.

In the Annelida the primary germ cells are early localized in the coelomic epithelium, where, as they multiply, they form small cell masses, which may occur most anywhere in the coelomic walls or may be limited to definite areas of particular segments. The germ cells given off from the germarial centers undergo their development in the coelomic cavities or in coelomic pouches. In some forms the sex elements escape through temporary openings in the body wall, in others the posterior part of the body containing them is constricted off, but more generally they make their exit through special genital outlets, or through modified nephridia.

In the Onychophora the germarial centers of the embryo are located in the splanchnic walls of the mesoderm above the alimentary canal

in one or several somites near the posterior end of the body (fig. 2 A, *Grm*). The dorsal parts of the coelomic sacs of these segments (figs. 2 B, 3 A, *a*) become constricted from the lateral parts (*b*) forming a series of gonadial pockets containing the germ cells. At a cor-

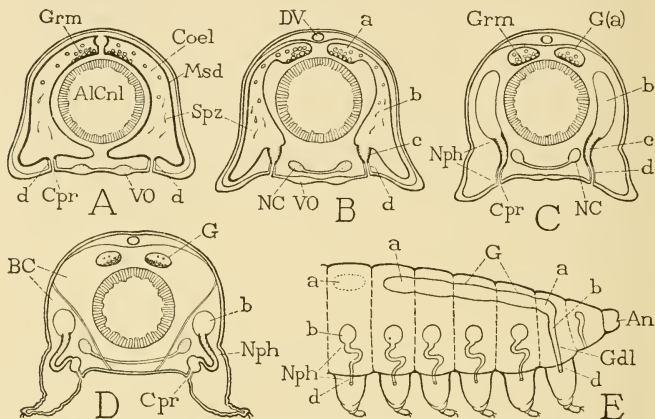


FIG. 2.—Diagrams showing the development of the gonads, gonoducts, and nephridia of Onychophora from coelomic sacs and coelomoducts (based on Kennel, 1888, Sedgwick, 1885, Evans, 1902).

A, cross-section of body segment at theoretical phylogenetic stage represented by embryo with complete coelomic sacs (*Coel*) and coelomoducts (*d*), germaria (*Grm*) dorsal in splanchnic walls of coelomic sacs, gametes (*Spz*) discharged through coelomoducts. B, later stage with gonadial pouches (*a*) constricted from lateral compartments (*b*) of coelomic sacs. C, still later stage, gonadial pouches (*B, a*) converted into gonadial sacs (*G*), lateral coelomic compartments (*b*) connected with coelomoducts, which have become nephridia (*Nph*). D, mature condition, gonads (*G*) a pair of dorsal tubes, lateral coelomic compartments (*b*) reduced to small end-sacs of nephridia. E, longitudinal section, showing gonad connected with lateral gonoduct (*Gdl*) formed of reduced coelomic sac of penultimate somite, which has maintained its continuity and has not been converted into a nephridium.

a, dorsal pouch of coelomic sac; *AlCnl*, alimentary canal; *An*, anus; *b*, lateral compartment of coelomic sac; *BC*, definitive body cavity; *c*, ventral diverticulum of coelomic sac; *Coel*, coelomic sac; *Cpr*, coelomopore; *d*, ectodermal part of coelomoduct; *DV*, dorsal blood vessel; *G*, gonad; *Gdl*, lateral gonoduct; *Grm*, germarium; *Msd*, mesoderm; *NC*, nerve cord; *Nph*, nephridium; *Spz*, spermatozoa; *VO*, ventral organ of ectoderm.

responding phylogenetic stage, it is to be presumed, the gametes (fig. 2 A, B, *Spz*) were liberated into the coelomic sacs and discharged through the open coelomoducts (*c, d*) of the latter. In the developing embryo, however, the gonadial pockets are soon shut off entirely from the rest of the coelome (C), and those of each side unite with

each other in a continuous tube (E, G). The two tubes thus formed become the definitive gonads. The germaria are now parts of the epithelial walls of the gonadial tubes; consequently the germ cells given off from the germaria are imprisoned in the gonads, and must be given some special means of escape to the exterior.

The genital exits of the Onychophora are formed in the last of the series of genital segments, which is the penultimate body somite. In this somite the coelomic sacs are retained entire (fig. 3 B); though they become much narrowed, they are not divided into dorsal and lateral compartments as in the preceding somites (fig. 2 C). Their dorsal ends unite with the posterior ends of the gonadial tubes (fig. 2 E), and there is thus established a pair of exit passages from the gonads opening externally through the primitive coelomoducts (*d*) of the segment. In other words, a relatively generalized condition is retained in the last genital segment, which allows the gametes to be discharged in the primitive manner through the coelomic sacs and their outlet ducts. The open passages take on a tubular form and become the definitive lateral gonoducts. Eventually the lateral ducts (fig. 3 C, *Gdl*) come together medially on the ventral surface of the last genital segment, and those of the male open into an ectodermal gonoductus communis (*Gdc*), or ejaculatory duct (fig. 6 C, D, *Dej*).

Among the Arthropoda a direct development of the gonads and gonoducts from coelomic sacs in a manner similar to the development of these organs in the Onychophora has been described by Heymons (1901) in *Scolopendra*. The dorsal parts of the coelomic sacs of the centipede embryo persist as a double series of closed chambers, which unite on each side, thus forming two long tubes with segmental compartments, in the epithelial walls of which are contained the germ cells. Later the dissepiments disappear, giving each gonadial tube a continuous lumen, and finally the two tubes combine to form the single definitive gonad. The gonoducts of *Scolopendra* are derived from the coelomic sacs of the greatly reduced last two somites. Each of these sacs gives off a small ventral diverticulum, or ampulla (fig. 3 D, *Amp*), into the corresponding rudimentary appendage of its segment (*2Gp*). The two sacs on each side then combine in a single vessel, and the sacs of the first pair join with each other above the alimentary canal and unite here with the posterior end of the gonadial tube. The ampullae of the second pair of sacs now withdraw from the appendages and migrate toward the median line on the ventral body surface, where finally they open into a median ectodermal invagination formed behind the sternum of the small last somite. The passages thus established from the gonadial tube to the exterior constitute the gono-

ducts. (In the male of *Scolopendra* only the right duct becomes the functional genital exit.) By comparison with Onychophora, it seems very probable that the ventral ampullae of the genital coelomic sacs of *Scolopendra* represent rudiments of coelomoducts that formerly opened on the bases of the segmental appendages.

The coelomic origin of the gonads and gonoducts is shown also in the embryonic development of various other arthropods, particularly in the Chelicerata. Hence, it is to be inferred that in cases where the gonads and their ducts appear first as solid cell masses, as with the insects, that this condition is a secondary modification, and that the lumen subsequently formed in the organs represents a part of the coelome. In certain insects it has been observed that the solid strands of cells that become the lateral genital ducts end with hollow ampullae. These ampullae lie in the appendage rudiments of the seventh abdominal segment in the female, or in those of the tenth segment in the male; in some cases the duct branches to each of these segments (see Heymons, 1892, 1895; Wheeler, 1893). When no appendage rudiments are present the ducts usually end in the same respective segments.

Inasmuch as the coelomic sacs of insects are seldom perfect and their cavities soon become confluent with the haemocoel, the evidence from embryology in this case does not show that the genital ducts are formed from entire coelomic sacs. The gonads and gonoducts appear first as solid strands of cells in the splanchnic walls of the mesoderm. It seems quite possible, therefore, that gonoducts may be formed by the closure of channels in the coelomic walls leading from the germinal areas to the coelomic outlets, just as the gonads are derived from a series of coelomic pockets containing the germ cells.

It is often said that the gonoducts are "modified nephridia". The assertion may be true with respect to some of the Annelida, but evidently when applied to Onychophora and Arthropoda it is not a correct statement of the facts. An onychophoran nephridium is a segmental coelomoduct connecting a remnant of the lateral coelomic compartment of the same segment with the exterior (fig. 2 D, *Nph*). The excretory head glands of Crustacea are organs of the same type of structure. An onychophoran or chilopod gonoduct, as shown by its development in *Peripatus* and *Scolopendra* (fig. 3 B, D), represents an entire coelomic sac together with its exit tube. Hence, if a nephridium of the onychophoran type is once formed in a segment, it cannot be converted into a genital duct. The onychophoran nephridia, on the other hand, might be regarded as remnants of segmental gonoducts, if it be assumed that each coelomic sac primitively contained a

germinal area in its wall, of which there is no specific evidence. The erroneous idea that arthropod gonoducts are modified nephridia is probably in part a result of the different significance of the term "gonad" as used by students of Annelida and Arthropoda, but it is largely based on a failure to recognize the essential difference between

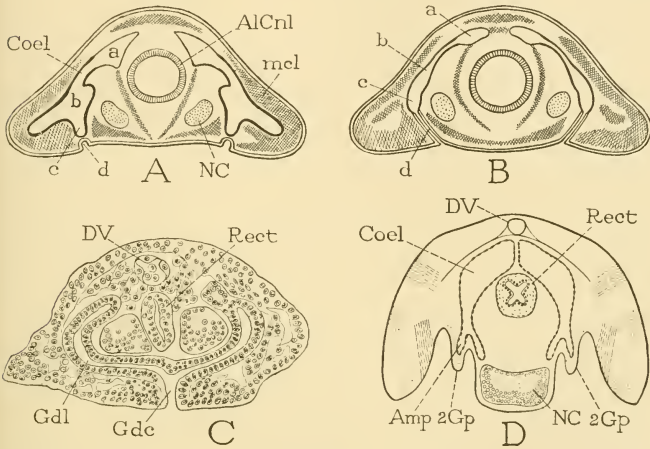


FIG. 3.—Development of the genital ducts in Onychophora and Chilopoda. (A, B from Kennel, 1888; C from Evans, 1902; D from Heymons, 1901.)

A, cross-section of a pregenital segment of *Peripatus*, diagrammatic, showing subdivision of the coelomic sacs and beginning of formation of coelomoducts (*c*, *d*). B, same through genital segment, showing formation of genital ducts from coelomic sacs and coelomoducts. C, section of genital segment of *Eoperipatus weldoni* with ectodermal gonoductus communis (*Gdc*) giving outlet to the lateral ducts. D, diagrammatic cross-section of genital segment of *Scolopendra* with coelomic sacs that will become genital ducts.

a, dorsal compartment of coelomic sac; *AlCnl*, alimentary canal; *Amp*, ampulla of coelomic sac in rudimentary gonopod; *b*, lateral compartment of coelomic sac; *c*, ventral diverticulum of coelomic sac; *Coel*, coelomic sac; *d*, ectodermal coelomoduct; *DV*, dorsal blood vessel; *Gdc*, gonoductus communis; *Gdl*, gonoductus lateralis; *Gp*, rudiment of gonopod; *mcl*, muscle; *NC*, nerve cord; *Rect*, rectum.

an annelid nephridium and the organs given the same name in Onychophora and Crustacea. As shown by Goodrich (1895, 1897-1900), the nephridia and gonoducts of Annelida are probably distinct and separate structures in their origin; in the Polychaeta the genital ducts in most cases are either united with the nephridia or are reduced to ciliated lobes of the coelomic walls, in which case the nephridia may serve as genital outlets. In the Onychophora and Arthropoda, on the

other hand, true nephridia are never developed; but coelomoducts (perhaps primitive genital outlets) may be formed in each segment of the Onychophora, and it is these structures, together with remnants of the coelomic sacs, that give rise to the segmental excretory organs of Onychophora and Crustacea commonly termed "nephridia", and which form the definitive genital ducts of the Onychophora and Arthropoda in particular somites.

When the germ cells multiply and are extruded from the germaria in a genital organ of the arthropod type, they are received at once into the lumen of the mesodermal gonadial sac. The gonadial sac, or gonad, furnishes the germ cells a protected space within the body in which they may complete their development. With the multiplication and growth of the germ cells the gonad increases in size by an extension of its cellular walls, and it also assumes the rôle of nutritive organ for the developing ova or spermatozoa within it. Any specific part of the sac that contains and nourishes the growth stages of the gametes, therefore, constitutes a *trophocyst*, or *vitellarium*, of the ovary or testis.

The mature gonad may retain the form of a simple sac, in the walls of which the germinal cells may be diffusely scattered or localized at some particular place, but with many of the arthropods the capacity and productivity of the gonad are augmented by a secondary lobulation of the walls or by the outgrowth of saclike or tubular diverticula (sperm tubes or egg tubes), each containing a germinal area, usually at its blind end. In some of the apterygote insects the gonadial diverticula have a segmental arrangement, but generally there is no relationship between the germinal pockets of the gonads and the body segments. Both the ovary and the testis are primarily single organs in the embryo; though primitively they may have been formed from the germarial pockets of several consecutive coelomic sacs, the coelomic components have nothing to do with the subsequent outgrowth of follicular or tubular diverticula. Any theory of metamerism in the reproductive organs of the arthropods, therefore, must go back to a very early phylogenetic stage when the germinal centers were segmentally arranged in the coelomic walls, and the gametes were discharged through open coelomoducts connecting the coelomic sacs with the exterior. The only case among the arthropods of multiple genital openings and genital ducts associated with gonadial sacs occurs in the Pycnogonida, but the great reduction of the body and the branching of the gonad into the legs gives reason for suspecting that the genital apertures on the second leg segments of these animals (fig. 7, *Gpr*) are secondary formations. The pycnogonid gonad is said to be a

single organ at an early stage of its development. It is most unfortunate that we know nothing of the genital openings of the trilobites.

The great variation in the position of the genital outlets in different groups of arthropods is only to be explained on the assumption that quite different pairs of coelomic sacs have been utilized as genital ducts. This assumption might seem to imply that the various arthropod groups were differentiated from common ancestors that still retained a full series of coelomic sacs with exit ducts; but the idea is entirely incompatible with the identity in structure of the gonads in closely related groups that differ in the segmental position of the gonoducts, as in Entomostraca, Chilopoda, and Hexapoda. Moreover, in the geophilomorphic chilopods the genital ducts may pertain to different segments in different individuals of the same species, according to variations in the total number of somites formed, the last somite being always the segment of the genital exit. The Chilopoda, the Protura, and the Collembola are alike in so far as the genital opening in each sex occurs on the last somite, but there is a great discrepancy in the number of somites between the genital segment and the mouth, there being 11 in Collembola, 17 in Protura, 21 to 30 in most Chilopoda, and as many as 175 in the Geophilomorpha. In these opisthogoneate groups new somites are not formed after the genital segment is established; in Hexapoda other than Protura and Collembola one post-genital somite may be added (during embryonic development) in the male, and four in the female. In the progoneate myriapods the seventh postoral somite becomes the genital segment, and an indefinite number of segments is generated in the postgenital region. The genital segment of Chelicerata is always the eighth postoral somite; in Malacostraca it is the tenth in the female and the twelfth in the male, but in both these groups there is a fixed number of postgenital segments.

The recent proposal made by Tillyard (1935) that the genital segment is an identical primitive somite in all the Arthropoda, and that its position in the definitive series of body segments is a matter of whether other somites have been added before or behind it, entirely disregards the evidence that somite formation in the arthropods proceeds always from a generative zone just before the telson. If teloblastic growth is a fundamental principle of development in the Arthropoda, the segment of the genital ducts cannot be an identical somite in all cases, and it is evident, therefore, that the genital outlet segment is not necessarily predetermined as such by morphological heredity.

EVOLUTION OF THE GENITAL EXIT APPARATUS

The free liberation of the gametes into the surrounding medium, where conjugation takes place as circumstances permit, is the usual mode of propagation with aquatic animals from coelenterates to fishes, though there are various exceptions to the rule. This method of propagation, however, becomes entirely impracticable for terrestrial animals. Hence, animals that live customarily on land either revert to the water at the breeding season, or they develop a genital apparatus for the direct transfer of the spermatozoa from the male into the body of the female. Propagation by sex mating, however, demands a fixed location of the genital orifices at definite points on the body wall in each sex, and the presence of an effective ejaculatory apparatus in the male. It is usually increased in efficiency by the development of a male intromittent organ, a female receptaculum seminis, and various devices for copulation.

All modern Arthropoda, except parthenogenetic and hermaphroditic forms, propagate by sex mating. This fact need not be construed to mean that the ancestors of the arthropods were terrestrial, but, if the mating habit was established by aquatic progenitors, it made the arthropods easily adaptable to life on land. Among aquatic forms, however, the sperm are not in all cases inserted into the genital ducts or a receptaculum of the female. With the Pycnogonida, the Xiphosurida, and many of the Crustacea, though copulation takes place, the eggs are inseminated outside the body of the female at the time of mating, and are then carried by one sex or the other, or deposited at the bottom of the water. In some of the Crustacea packets of sperm are attached to the under surface of the female's body, and fertilization of the eggs takes place later. With the majority of the arthropods, however, the spermatozoa or spermatophores are received into an ectodermal pocket of the female (thelecum, receptaculum seminis, spermatheca) situated near the openings of the oviducts, usually in close proximity to them. The eggs in most such cases are then fertilized as they issue from the ducts. The storage of the sperm in an ectodermal receptacle is thus only a modification of external insemination. In some arthropods, however, the sperm are introduced directly into the oviducts, and fertilization of the eggs may then take place in the ducts or in the ovaries. Finally, there is often present in the female an ectodermal pouch, the bursa genitalis, or genital chamber (bursa copulatrix), which receives the end of the male intromittent organ, and contains the spermathecal and oviducal apertures.

The primary exit ducts of the gonads must be principally mesodermal structures, considering their coelomic origin, but if they have

utilized the primitive coelomic outlets, each should have a small terminal part derived from the ectoderm. The primary gonoducts (fig. 4 A, *Gd*) are the *vasa deferentia* in the male, the *oviductus laterales* in the female. Their external openings are the primary gonopores (*Gprs*). The mesodermal ducts are usually provided with muscular sheaths for the expulsion of the gametes, but with most of the arthropods there has been added to the primary ducts, particularly in the male, a more effective *exit apparatus* formed of evaginations and invaginations of the body wall at the mouths of the ducts, usually accompanied by a special development of associated muscles. These ectodermal parts of the exit system are highly variable, but, on the other hand, they are often very similar in widely separated arthropod groups, in which the gonopores are situated on quite different body segments. Therefore, though it is convenient to employ a uniform system of nomenclature for these parts so far as possible, the use of the same terms in the description of the genital organs of different groups should not be taken to imply anything more than a structural or functional analogy in the parts named alike.

One of the first steps in the development of ectodermal genital accessories may consist merely of the formation of an external papilla bearing the opening of each duct (fig. 4 B, *Pen*). Such structures are usually termed *penes* in the male, whether they are functionally intromittent organs or not, but they may be present also in the female, as in *Xiphosura*. On the other hand, the mouth of each duct may be carried inward at the end of a tubular ectodermal ingrowth (*C*, *Dej*), which usually has a strong muscular sheath, and is termed a *ductus ejaculatorius* in the male, though the term would be quite as appropriate in the female. It is evident that the primary gonopores (*A*, *Gprs*) are now at the inner ends of the ejaculatory ducts (*C*), but to avoid a multiplicity of names the term *gonopore* is applied to the opening of any genital duct, whether primary or secondary. A combination of ejaculatory ducts with external penes is of common occurrence (*D*).

The primitive paired condition of the genital openings and associated structures is retained in some members of most of the arthropod groups, and is characteristic of Xiphosurida, Crustacea, and Diplopoda. In other groups, and in some of the crustaceans and diplopods, an unpaired condition of the terminal parts arises in various ways, and is subject to great modifications, which reach an extreme degree of development in the insects. In the first place, the penis may be a single median organ (fig. 4 E, *Pen*) with two separate openings for the ducts; but in general there is associated with a median penis a single ejaculatory duct (*F*, *Dej*), which receives the two vasa defer-

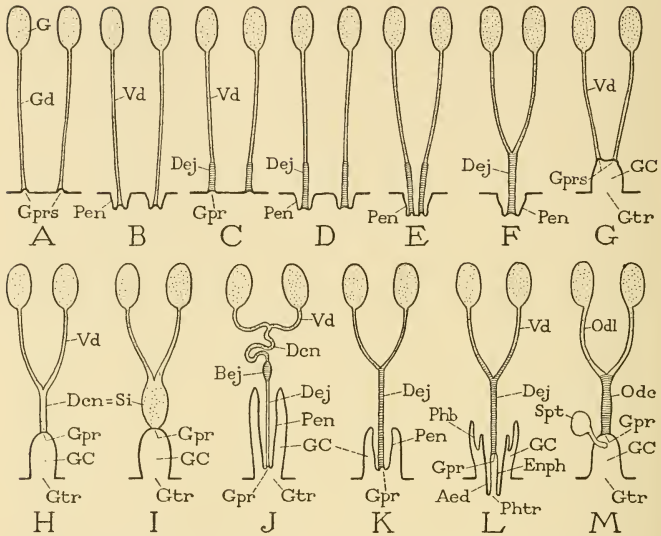


FIG. 4.—Diagrams showing some of the principal variations of the genital ducts and accessory structures.

A, simple condition with gonoducts opening separately through pores of body wall. B, vasa deferentia opening on a pair of penes. C, each vas deferens discharging through an ectodermal ductus ejaculatorius. D, the ejaculatory ducts opening on a pair of penes. E, the ejaculatory ducts opening separately on a single penis. F, a single ejaculatory duct and a single penis. G, the vasa deferentia discharging into a bursa genitilis, or genital chamber (GC). H, the vasa deferentia united distally in a ductus conjunctus (Dcn). I, the ductus conjunctus enlarged to form a saccus internus (Si), as in many Arachnida. J, a penis evaginated from the genital chamber, traversed by an ectodermal duct from an ejaculatory bulb (Bej), as in Phalangida. K, simple condition in insects, with ejaculatory duct, penis, and genital chamber. L, more complex condition in insects: penis subdivided into phallobase (Phb) and aedeagus (Aed), with ejaculatory duct discharging into an endophallic chamber (Enph); vasa deferentia may be partly replaced by arms of the ejaculatory duct. M, usual structure of genital exit passage of female insects: the common oviduct (Odc) opens into a genital chamber (GC), from which opens the spermatheca (Spt).

Aed, aedeagus; Dcn, ductus conjunctus; Dej, ductus ejaculatorius; Enph, endophallus; G, gonad; GC, genital chamber, or bursa genitilis; Gd, gonoduct; Gpr, gonopore (opening of a genital duct); Gtr, gonotreme (opening of the genital chamber); Odc, oviductus communis; OdL, oviductus lateralis; Pen, penis; Phb, phallobase; Phtr, phallotreme (opening of the endophallus); Si, saccus internus; Spt, spermatheca; Vd, vas deferens.

entia at its anterior end. The median penis of insects the writer (1935) has designated the *phallus*, but the insect phallus is an intromittent organ, whereas the median penis of most of the other arthropods is not. A median ejaculatory duct is probably in some cases a product of the union of paired ectodermal ducts (a *ductus conjunctus*), and in others an independently developed single invagination (*ductus communis*) at the approximated orifices of the primary ducts.

Another series of modifications in the development of unpaired external genital structures begins with the formation of a wide, open cavity of the ectoderm, into which the primary gonoducts discharge (fig. 4 G, *GC*). The external pouch in this case is the *bursa genitalis*, or *genital chamber*, and may be present in both the male and the female. Its usually large external opening is the *gonotreme* (*Gtr*). The mesodermal ducts (*Vd*) may open separately into the genital chamber (*Gprs*), or their proximal parts may combine to form a *ductus conjunctus* (*H, Dcn*) with a single gonopore (*Gpr*). This condition is common in the Arachnida, where the ductus conjunctus is often enlarged as an inner chamber, *saccus internus* (*I, Si*), of the exit apparatus. An unusual development among the Arachnida occurs in the Phalangida (*J*). The genital chamber (*GC*) here contains in each sex a large organ evaginated from its inner wall, which serves as a penis in the male (*Pen*) and as an ovipositor in the female. The organ is traversed by a slender ejaculatory duct (*Dej*) beginning with a *bulbus ejaculatorius* (*Bej*), into which opens the ductus conjunctus (*Dcn*) formed by the united vasa deferentia.

The bursa genitalis, or genital chamber, is of common occurrence also in both sexes of the Chilopoda and Hexapoda. In these two groups there is generally present in the male a single median penis, which in its simplest form is merely a conical or tubular outgrowth of the inner wall of the genital chamber (fig. 4 K, *Pen*) traversed by the ejaculatory duct (*Dej*) opening through the gonopore (*Gpr*) at its extremity. The median penis, or *phallus*, of the insects, however, may become a highly complex organ. It is often differentiated into a proximal part, or *phallobase* (*L, Phb*), and a distal *aedeagus* (*Aed*). The gonopore (*Gpr*) commonly becomes concealed within an end chamber, or *endophallus* (*Enph*), and the external opening is then the *phallotreme* (*Phtr*). In female insects the opening of the *oviductus communis* (*M, Odc*), which is the true gonopore (*Gpr*), is usually concealed in a large genital chamber (*GC*), the exposed external opening of which, or *vulva*, is the gonotreme (*Gtr*). The genital chamber contains also the aperture of the spermatheca (*Spt*), and is sometimes narrowed as a tubular *vagina* continuous with the median oviduct.

THE EXTERNAL GENITALIA

In a wide sense the external genitalia comprise all the secondary sexual characters or modified organs that are concerned with sex mating and egg laying, regardless of their position relative to the opening of the genital ducts. They include copulatory organs, the organ or organs of sperm discharge and intromission in the male, and in the female the seminal receptacle, often a copulatory pouch, and an ovipositor. Because of the variation in the position of the genital apertures, most of the external genital organs have no homology between the several major groups of arthropods, and very different structures may be similarly modified to subserve the same purposes.

The copulatory organs may be defined as structures that serve to hold the two mating individuals together during the insemination of the female or of the eggs. In some cases copulation is effected entirely by the intromittent organ of the male and the receiving pouch of the female; but more commonly the actual copulating, or holding of the female by the male, is performed by the legs or other appendages, which may be particularly modified for the purpose, and there may be developed also special processes of the body specifically adapted for clasping. In nearly all the arthropod groups some of the segmental appendages of the male are more or less altered in structure to serve as clasping organs. In the insects the legs may be used for holding the female and are sometimes modified to this end, but the most important copulatory structures of insects are the appendages of the male genital segment, which are often highly modified and intricately adapted to their function, though there may be present other appendicular, or non-appendicular, structures that have a similar or accessory function. If the female has any special organ of copulation it is usually the pouch that receives the male organ, which in most cases is a genital chamber (*bursa genitalis*) into which the oviduct opens; but the copulatory organ may be the seminal receptacle (*spermatheca*) itself, the orifice of which is sometimes specially adapted for the reception of the apical part of the male intromittent organ.

The intromittent organs of male arthropods include a great variety of structures. Only in rare cases do the paired penes serve for the actual introduction of the sperm into the female receptacles; a direct insertion of the two penes into the corresponding genital apertures of the female, however, is said to take place in certain entomostracan Crustacea, and it is possibly the mode of coition in the Ephemeroptera among the insects. In general, however, where paired penes occur, as

in Xiphosurida, Malacostraca, and Diplopoda, or where in these same groups there may be a single median penis, either the eggs are inseminated outside the body of the female, or the sperm are transferred to the female receptaculum by specially modified appendages (gonopods). In the Malacostraca the intromittent organs are the appendages of the first and second abdominal segments, so modified as to form organs for receiving the sperm or spermatophores from the penes or penis, and for inserting them into the oviducts or sperm receptacles of the female. Similarly in the proterandrious Diplopoda the eighth, or the eighth and ninth, pairs of legs are modified for intromittent purposes, the genital outlets being situated on a pair of penes, or a median penis, on the segment of the second pair of legs. Among the Arachnida the intromittent organs are the chelicerae in Solpugida, the pedipalps in Araneida. The males of opisthandrious Diplopoda are said to use the mandibles for transferring the sperm to the female. A nonappendicular intromittent organ not associated with the genital aperture occurs in the insect order Odonata. This organ is a large, median, penislike structure on the under surface of the second abdominal segment of the male, which receives the sperm from the genital opening on the ninth segment and is the agent of transfer to the female during copulation.

The median penis becomes the functional intromittent organ principally in the Chilopoda and the Hexapoda, though the mating habits of entomostracan Crustacea having a median penis are not well known, and a prominent exception among the arachnids occurs in the Phalangida, in which the sperm are transferred to the female through a large unpaired organ containing the genital exit duct. The penis of the chilopods is never highly developed, and appears to be merely a fold or conical outgrowth of the body wall around the genital aperture. The median penis (phallus) of the insects may be a small simple structure as in the chilopods, but more usually it has a tubular form, and may attain a great complexity of structure. Students of insect morphology have often regarded the insect penis as having some relation to the gonopods of the male genital segment (ninth abdominal), the organ being supposed to be formed by the union of branches or lobes from the bases of these appendages. The ontogenetic development of the insect penis, however, as will be shown in a later part of this paper, does not support this view, and considering that the analogous organs in other groups of arthropods are mere integumental outgrowths, there seems to be no reason for assuming the organ has any other morphological status in the insects.

II. ONYCHOPHORA

The Onychophora undoubtedly belong to the annelid-arthropod group of animals; their development is typically metameric and the embryonic mesoderm contains a complete series of segmental coelomic sacs. Certain features of their structure definitely separate the Onychophora from the Arthropoda, but, on the other hand, several important anatomical characters common to these two groups would appear to relate the onychophorans more closely to the proarthropods than to the annelids.

The structural disparity between the Onychophora and the Arthropoda is shown particularly in the nervous system and in the body musculature. The longitudinal nerve cords of the Onychophora not only do not form ganglia, but, instead of coming together as in the annelids and arthropods, they move farther apart during their development, and in the adult they lie laterad of a series of dorsoventral muscles on each side of the body that would prevent their median approximation. In the brain, the antennal nerve tracts run dorsal to the optic lobes instead of ventral to them as in the arthropod brain. The onychophoran body musculature consists of a continuous subepidermal muscle layer composed of distinct sets of circular, oblique, and longitudinal fibers, the arrangement of which in no way suggests a possible primitive pattern of arthropod musculature.

The relationship of the Onychophora to the Arthropoda is suggested by the leglike segmental appendages of the latter, though the onychophoran "legs" are little more than well-musculated pouches of the body wall bearing each a pair of claws. It is in the evolution of the mesodermal organs that are shown the most important features common to the Onychophora and Arthropoda. In each group the haemocoel is restored as the permanent body cavity as a result of the reduction or complete dissolution of the coelomic sacs. The nephridia of the Onychophora are coelomoducts, each with a remnant of the corresponding coelomic sac attached to its inner end. The head glands of Crustacea have the same structure as the onychophoran nephridia, suggesting that they have had a common origin with the latter, though they have lost the vibratile cilia still retained in the nephridial canals of the Onychophora. Finally, the reproductive system of the Onychophora is decidedly arthropodan in its structure, since the germaria (equivalent to the "gonads" of Annelida) are enclosed in gonadial sacs derived from the coelomic walls, and the gametes are discharged through gonoducts formed from a pair of coelomic sacs and their outlets. The structure of the nephridial and genital organs in the Onychophora and Arthropoda is, of course, a

necessary result of the general obliteration of the coelomic walls, and therefore might be supposed to be an independent development in each case.

The testes of Onychophora lie dorsally in the posterior part of the body; they are tubular in form (fig. 5 C, D, *Tes*) but vary in length in different species. Each discharges immediately into a saclike semi-

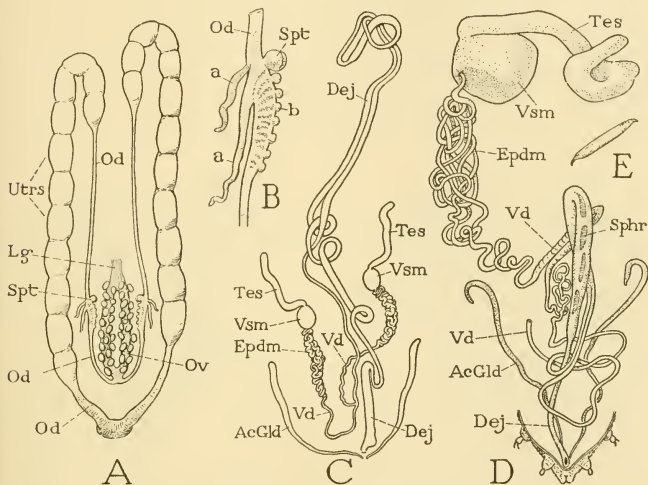


FIG. 5.—Onychophora: internal reproductive organs.

A, *Peripatoides novae-zealandiae*, female organs, dorsal view. B, same, ovarian end of oviduct with spermathecal and other diverticula. C, *Peripatus tholloni*, male organs (from Bouvier, 1905, with parts separated for clearness). D, *Peripatopsis blainvillei*, male organs (from Bouvier, 1902, with accessories omitted). E, same, spermatophore (from Bouvier, 1902).

a, b, diverticula of oviduct; *AcGld*, accessory genital gland; *Dej*, ductus ejaculatorius; *Epdm*, epididymis; *Lg*, ovarian ligament; *Od*, oviduct; *Ov*, ovary; *Sphr*, spermatophore; *Spt*, spermatheca; *Tes*, testis; *Utrs*, uterus; *Vd*, vas deferens; *Vsm*, vesicula seminalis.

nal vesicle (*Vsm*) with muscular walls, within which the spermatozoa are matured. The slender vasa deferentia (*Vd*) proceeding from the vesiculae are much convoluted and the upper part of each usually forms an epididymislike mass of closely entangled coils (*Epdm*). The ductus ejaculatorius (*Dej*) is a long, strongly muscled tube bent upon itself and often looped. The spermatozoa are enclosed in spermatophores formed within the upper part of the ejaculatory duct (D, *Sphr*). The spermatophores vary much in size and form in

different species from small podlike capsules (E) to long tubes or flask-shaped structures. Associated with the genital organs of the male is a pair of tubular accessory glands (C, D, *AcGld*).

The ovaries of the female are a pair of short tubes (fig. 5 A, *Ov*) lying above the alimentary canal near the posterior end of the body. The two organs are united at each end, and are suspended anteriorly by a broad ligament (*Lg*) from the dorsal diaphragm. The growing oocytes are contained individually in follicular diverticula of the ovarian walls, and the mature ova are fertilized within the ovaries or in the oviducts close to them. The oviducts are long tubes looped forward from the united rear ends of the ovaries and then backward to open into a common median invagination of the body wall at the

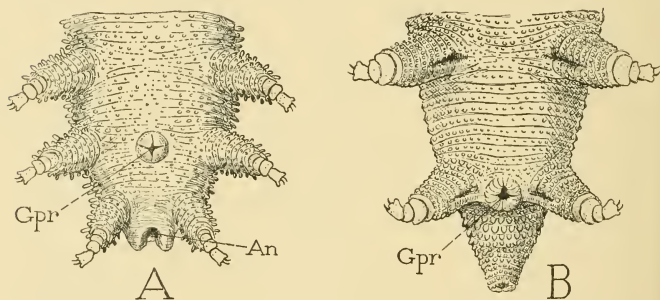


FIG. 6.—Onychophora: position of the genital openings.

A, *Peripatus*, gonopore (*Gpr*) between penultimate pair of legs. B, *Peripatoides novae-zealandiae*, gonopore between last pair of legs, but true terminal pair of legs probably here suppressed.

gonopore (*Od*). In most species each oviduct is provided with a small spermatheca (A, B, *Spt*) in the neighborhood of the ovary, and may have also other tubular or vesicular diverticula (B, *a, b*). The majority of the Onychophora are viviparous, and in such forms the embryos develop to maturity in uterine chambers of the oviducts (A, *Utrs*); with oviparous species the relatively large eggs are discharged from the body before development begins. Development is always direct, and the newly born or newly hatched young have the form of the adult.

Both male and female Onychophora have a single external genital opening (fig. 6, *Gpr*), which is located near the posterior end of the body, probably in all cases on the same body region, which is the venter of the penultimate somite before the terminal anal cone. When

all the somites have appendages, therefore, the gonopore lies between the penultimate pair of legs (A); but in some forms the legs of the last somite or of the last two somites are absent, and in such cases the gonopore is either between (B) or behind the last pair of legs present. The opening is usually situated on a small papilla, which may take the form of a short conical or tubular projection serving as a penis or as an ovipositor. Copulation in the Onychophora apparently has not been observed. Males in confinement have been recorded (Sedgwick, 1885) as depositing the spermatophores at random upon the outside of the female's body, but since the spermatozoa are found in the female within the oviducts and the spermathecae it would seem that normally the spermatophores must be transferred from the male directly into the genital opening of the female.

III. PYCNOGONIDA (PANTOPODA)

The body of a pycnogonid (fig. 7 A) consists principally of the appendage-bearing region composed of seven or eight segments, some of which are united; anteriorly, however, there is a large proboscis (*Prb*) with the mouth at its extremity, and posteriorly a rudimentary, unsegmented abdomen (*Ab*) bearing the anus. The first and second appendages (*Chl*, *Pdp*) evidently correspond with the chelicerae and pedipalps of other Chelicerata. The following appendages are leglike in form and have an ambulatory function, except the slender first pair (*IL*), which are used by the male for carrying the eggs, and which are much reduced or absent in the females of some species. The usual number of legs, including the "ovigerous legs", is five pairs, but in a few genera there are six pairs. The fifth legs are the seventh pair of postoral appendages, and thus correspond with the chilaria of *Xiphosura* (fig. 8 A, *Chi*). The sixth legs, therefore, when present, are represented in the Xiphosurida by the broad plate-like operculum of segment *VIII*, on the posterior surface of which are the genital apertures.

The genital openings of the pycnogonids in each sex are situated ventrally on the second segments of the legs (fig. 4 A, *Gprs*, B, C, *Gpr*). Typically there is a gonopore on each of the ambulatory legs, but the openings may be limited to the last two or three pairs, and in two genera they occur only on the terminal legs. During mating the male grasps the female, either dorsally or ventrally, and the eggs apparently are fertilized externally as they issue from the female. The fertilized egg masses are carried by the male attached to his ovigerous legs.

The segmental duplication of the gonopores in the Pycnogonida might seem to give support to the view that the primitive arthropods

had metamericly repeated gonads with individual segmental outlets. The ovaries and testes, however, which are formed during larval metamorphosis, are said to take first the form of a pair of simple tubes united with each other above the alimentary canal; later they acquire the characteristic branched adult structure by the extension of lateral diverticula into the leg bases above similar diverticula of the alimentary canal. The development of an outlet on each leg, therefore, may be merely the result of the great reduction of the body.

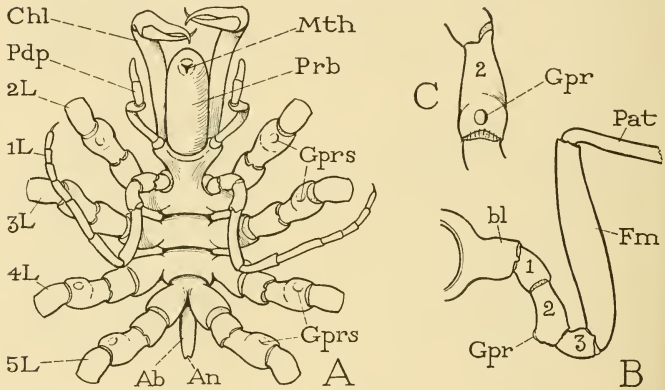


FIG. 7.—Pycnogonida: position of the genital openings.

A, *Chaetonymphon spinosum*, female, ventral view of body and bases of legs, with four pairs of gonopores (*Gprs*) on the second leg segments. B, same, base of leg, anterior view, showing position of gonopore. C, same, mesal view of gonopore.

bl, leg-bearing body lobe; *Chl*, chelicera; *Fm*, femur; *Gpr*, *Gprs*, gonopore, gonopores; *1L*, first leg; *2L-5L*, ambulatory legs; *Mth*, mouth; *Pat*, patella; *Pdp*, pedipalp; *Prb*, proboscis; 1, 2, 3, three small proximal leg segments.

The writer has been unable to find any information on the mode of origin of the genital ducts in the Pycnogonida, but since the segment of the genital openings is not fixed in the arthropods generally there is no reason why a condition of multiple openings might not be a secondary development. It should be observed, furthermore, that the position of the pycnogonid gonopores on the second segments of the legs does not conform with that of the genital apertures in other arthropods having the gonopores on the legs, since in the latter (Crustacea, Diplopoda) the apertures are on the bases of the first leg segments. In any case, the pycnogonids are in no sense primitive arthropods, since they are highly aberrant chelicerates, and have no similarity

to the trilobites. It is important to note, however, that in forms with six pairs of legs the body is divided into prosoma and opisthosoma between segments *VIII* and *IX* as in Xiphosurida, whereas in the other Chelicerata the division is between segments *VI* and *VII*.

IV. XIPHOSURIDA

The body of a horseshoe "crab" is distinctly divided into an anterior section and a posterior section, commonly called the *prosoma* and the *opisthosoma* (or cephalothorax and abdomen); but, as will presently be shown, the dividing line between the two parts does not correspond with that separating the two body regions termed prosoma and opisthosoma in the Arachnida, whereas, on the other hand, it is identical with that between the two body regions of Pycnogonida having eight pairs of appendages.

Each section of the xiphosurid body is covered by a broad carapace having the marginal parts widely inflected on the ventral surface of the animal. The opisthosoma is freely movable on the prosoma by a long transverse hinge between its carapace and the prosomal carapace. On the ventral surface (fig. 8 A) are 13 pairs of appendages, including the chelicerae (*Chl*), the pedipalps (*Pdp*), four pairs of legs (*IL-4L*), the chilaria (*Chi*), and 6 pairs of broad platelike structures overlapping each other posteriorly against the under surface of the opisthosoma. The first pair of these lamelliform appendages are united to form a large flat operculum (*Opl*), which mostly covers the following five appendages (*Apds IX-XIII*). On the posterior (dorsal) surface of the operculum are located a pair of small papillae containing the genital apertures in each sex (fig. 9 B, *Pen*). The other opisthosomal appendages bear each a group of lamelliform gills (*D, Brn*).

The dividing line between the two parts of the body in *Xiphosura* appears at first sight to lie between segments *VII* and *VIII*, since the chilaria clearly belong to the prosoma and the operculum is associated with the opisthosomal gill plates. A closer inspection, however, shows that the first appendages actually carried by the opisthosoma are the first pair of gill-bearing plates, and that the operculum hangs from a membranous area of the venter that is continuous laterally with the posterior angles of the prosomal carapace. Hence, as shown by Petrunkevitch (1922), the true division between prosoma and opisthosoma in *Xiphosura* lies between the somite of the operculum (segment *VIII*) and that of the first gill-bearing appendages (segment *IX*). The body division in the Xiphosurida, therefore, cor-

responds with that in species of Pycnogonida having eight pairs of appendages, but not with the division between prosoma and opisthosoma in Arachnida, where the two parts of the body are separated between segments *I* and *VII*. The genital openings, however, are on the same somite, which is segment *VIII*, in both Xiphosurida and Arachnida.

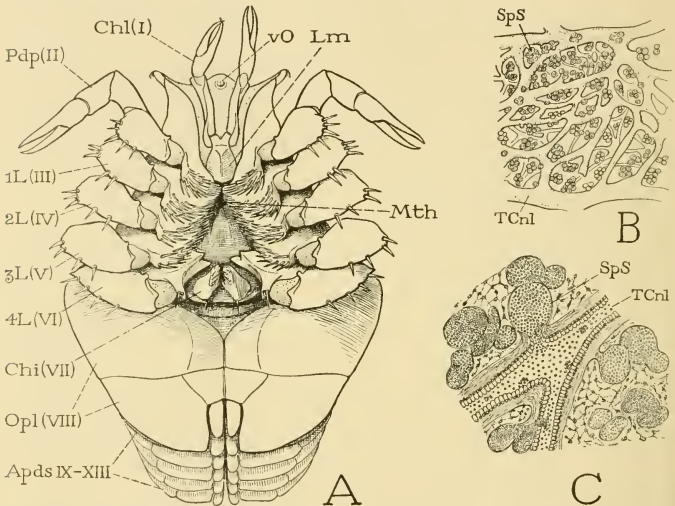


FIG. 8.—Xiphosurida: body appendages and structure of the testes of *Xiphosura polyphemus*.

A, ventral view of body and appendages of young female, with carapace and distal parts of legs removed. B, section of testis, showing testicular canals and sperm sacs (from Benham, 1883). C, part of last, more enlarged (from Benham).

Apds IX-XIII, gill-bearing appendages of opisthosoma; *Chi*, chilarium; *Chl*, chelicera; *I-XIII*, postoral somites corresponding with appendages; *1L-4L*, legs; *Lm*, labrum; *Mth*, mouth; *Opl*, operculum; *Pdp*, pedipalp; *SpS*, sperm sac; *TCnl*, testicular canal; *vO*, ventral ocellus.

The male gonads of *Xiphosura polyphemus*, as described by Benham (1883), consist of an intricate network of branching and reuniting testicular canals (fig. 8 B, C, *TCnl*) spread through the entire upper part of the body. The spermatocytes are developed in numerous small follicular diverticula, or sperm sacs (*SpS*), opening from the canals, and the mature spermatozoa are discharged through a pair of short vasa deferentia (fig. 9 B, *Vd*), which open separately on the genital papillae situated on the posterior (dorsal) surface of the base

of the operculum (*Pen*). The organs of the female are essentially like those of the male, and open on a pair of similar papillae.

The operculum (fig. 9 A, B) clearly includes in its composition a pair of appendages similar to the following gill-bearing appendages (C, D), but the median membranous area of its base (B, *V*), on

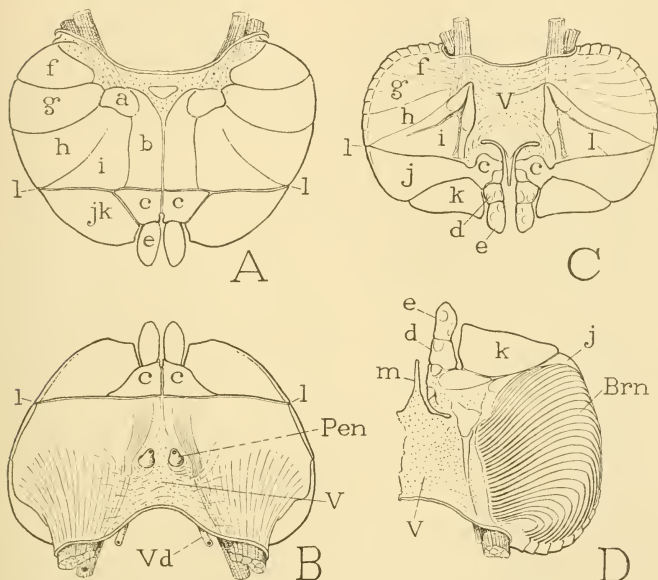


FIG. 9.—Xiphosurida: operculum and first gill-bearing appendages of *Xiphosura polyphemus*, male.

A, anterior (under) surface of operculum. B, posterior (upper) surface of operculum, with penes on median membranous area of base. C, first opisthosomal appendages, anterior (under) surface. D, posterior (upper) surface of right first opisthosomal appendage and median membrane.

a-l, subdivisions and sutures of appendages (see text); *Brn*, branchiac; *m*, median tongue of venter; *Pen*, penis; *V*, membranous venter of segment between bases of appendages; *l'd*, vas deferens.

which are situated the genital papillae, appears to be a fold of the venter of the opercular segment intercalated between the lateral appendicular elements. In the following segments the median membrane entirely separates the appendages (C, D, *V*) and ends with a free distal process (D, *m*) between them. The genital openings of the Xiphosurida, therefore, are situated, not on the bases of the appendages, but on the venter of the eighth segment, as in the Arachnida.

The xiphosurids copulate during the breeding season, but there is no intromission of the sperm. The eggs are fertilized outside the body of the female and are then usually deposited in sand at the bottom of the water, though the female of *Tachypleus gigas* (*Limulus moluccanus*) is said to carry them attached to the abdominal appendages.

V. EURYPTERIDA (GIGANTOSTRACA)

These extinct chelicerates are usually included with the Xiphosurida in the class Merostomata, but they have features characteristic of the Arachnida, and a general appearance that gives them a resemblance to the scorpions.

The body of an eurypterid contains 18 postoral somites (fig. 10 A), and ends with a telson (*Tel*) having the form of a large caudal spine or plate. The two major parts of the body, prosoma and opisthosoma, are separated between segments *VI* and *VII*, as in the Arachnida. The first opisthosomal segment is represented on the dorsal surface of the body by a small tergal plate (*C, VII*), but is not visible on the ventral surface (*A, B*). The first five ventral plates of the opisthosoma (*A, B, VIII-XII*) are said to bear gills on their upper surfaces, and hence probably represent the appendages of these segments united with the median sterna. The first ventral plate (*A, Opl*), since it belongs to segment *VIII*, represents the operculum of *Xiphosura*. It consists of two broad lateral parts separated by a median appendicular process (*oap*) of various forms. This opercular process, by comparison with the abdominal appendages of *Xiphosura* (fig. 9), would appear to be formed, as suggested by Störmer (1934), of the united telopodites of the opercular appendages. It has been supposed to be a genital organ, but this idea seems improbable except in the sense that the process may be a genital accessory of some kind. The genital openings have not been discovered, but it is to be supposed that they are concealed beneath the operculum.

In some of the eurypterids the opisthosoma is subdivided into a preabdomen and a postabdomen (fig. 10 B, C) by a difference in the width of the segments and their apparent mobility. Such forms have a resemblance to the scorpions (D), but it should be observed that the division between the two parts of the opisthosoma occurs between segments *XIV* and *XV* in the scorpions (D), while in the eurypterids (B, C) it is between segments *XIII* and *XIV*. In each group, however, there is the same number of segments in the "tail". Hence, it is possible that the eurypterids have lost one of the segments of the

preabdomen, since the extra segment of the scorpions appears to be in this region of the body. Moreover, the last gill plates of *Xiphosura* and the last lung books of the scorpion are on segment *XIII*, while the last gills of the eurypterids are said to be on

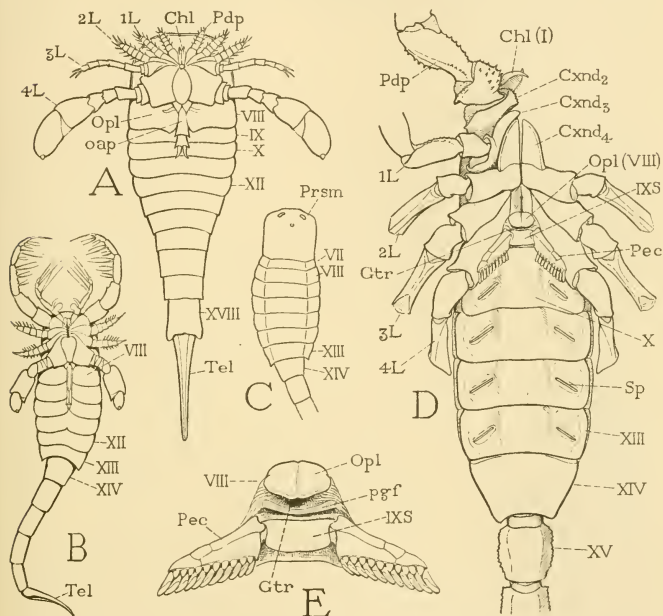


FIG. 10.—Eurypterida and Scorpionida: body segmentation and external genitalia.

A, diagram of an eurypterid, ventral view (from Clarke and Ruedemann, 1912). B, reconstruction of *Mixopterus kioeri* (outline from Störmer, 1934). C, same dorsal view of prosoma and preabdomen. D, body of a scorpion, ventral view. E, ventral parts of genital and postgenital segments of scorpion.

Chl, chelicera; *Cxnd*, coxal endite; *Gtr*, gonotreme (opening of genital chamber); *I-XVIII*, postoral somites; *1L-4L*, legs; *oap*, opercular appendage; *Opl*, operculum; *Pdp*, pedipalp; *Pec*, pecten; *pgf*, postgenital fold; *Prsm*, prosoma; *Sp*, respiratory orifice; *Tel*, telson.

segment *XVII*. The partial suppression of the first opisthosomal segment is a feature common to Eurypterida and Arachnida. Considering, therefore, the general structure of the eurypterids, so far as it is known, and in particular the arachnid type of their body division into prosoma and opisthosoma, it seems clear that the Eurypterida

are more closely related to the Arachnida than to the Xiphosurida. Aside from the adaptations to terrestrial life by the scorpions, such as the substitution of "lung books" for gills and the correlated suppression of the abdominal appendages or their incorporation in the sternal plates, the principal structural difference between the two groups might be reduced to the elimination of one gill-bearing segment in the eurypterids.

VI. ARACHNIDA

The number of postoral body segments present in adult or embryonic stages of Arachnida varies from a maximum of 19 in Scorpionida to a minimum of 13 in Araneida (not considering acarid forms in which the body segmentation is obscure). However, since the scorpions are said to have only 18 embryonic postoral neuromeres, it may be true as Petrunkevitch (1922) suggests, that two of the adult segments of the scorpion "tail" represent a single primitive somite, and that the maximum arachnid segmentation, therefore, may include only 18 postoral somites, as in Eurypterida, Malacostraca, and Hexapoda. On the other hand, as already noted, the fact that the last lung books of the scorpions and the last gills of *Xiphosura* are on segment *XIII*, though the last gills of Eurypterida are said to be on segment *XII*, is suggestive that the eurypterids have lost a segment in the gill-bearing region of the body. A terminal spine, poison claw, or flagellum, which is presumably the telson, is not counted in the above enumeration of segments.

The body division into prosoma and opisthosoma in Arachnida is between segments *VI* and *VII*, as in Eurypterida, but segment *VII* is always reduced and is often suppressed, so that the apparent division is usually between segments *VI* and *VIII*. A differentiation of the opisthosoma into a wider anterior preabdomen and a taillike postabdomen is conspicuous in Scorpionida (fig. 10 D), Palpigradida, and Pedipalpida (fig. 11 A). In the first two of these orders the division lies between segments *XIV* and *XV*, but in the third it is between segments *XV* and *XVI*. In no case does the arachnid subdivision of the opisthosoma correspond with the eurypterid division if the latter is actually between segments *XIII* and *XIV*, as it appears to be (fig. 10 B, C), but, as above noted, if it is assumed that the eurypterids have lost a segment in the preabdomen, the segmentation and body division of the eurypterids and scorpions becomes the same.

The Arachnida have a single median genital opening in each sex, which (except in some of the Acarina) always pertains to the second opisthosomal segment, or segment *VIII*, and thus has the same seg-

mental position as the paired gonopores of Xiphosurida; but the position of the opening is variable with respect to the ventral plate of the genital segment, since it is sometimes behind and sometimes before the genital sternum. The arachnid genital aperture is a *gonotreme* (fig. 4 G-J, *Gtr*), inasmuch as it is the immediate opening of an

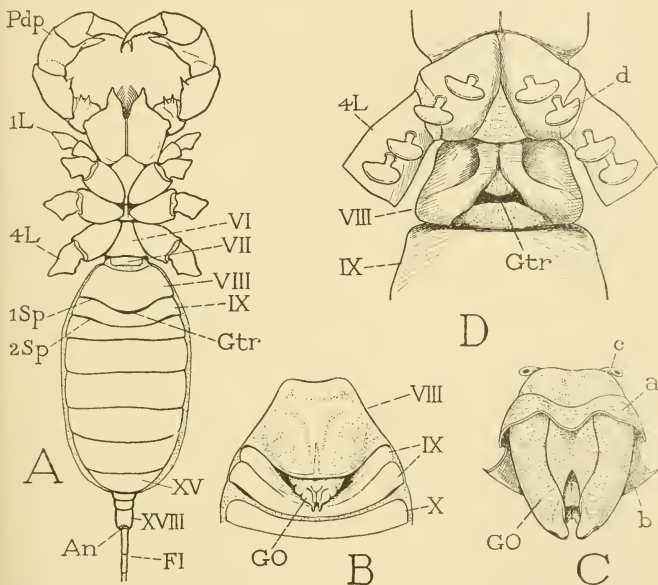


FIG. 11.—Pedipalpa and Solpugida: body segmentation and external genitalia.

A, *Mastigoproctus giganteus*, ventral view. B, *Tarantula palmata* (Amblypygi), base of abdomen of male, ventral surface, with end of genital organ projecting from genital chamber (from Börner, 1904). C, *Tarantula fuscimanus*, male genital organ, dorsal view, exposed by partial removal of walls of genital chamber (from Börner, 1904). D, a solpugid, last prosomal segment and base of opisthosoma with genital opening, ventral view (sex undetermined).

a, b, walls of genital chamber; An, anus; c, genital ducts; d, spatulate appendages of last legs; Fl, flagellum; GO, genital organ; Gtr, gonotreme; 1L-4L, legs; Pdp, pedipalp; Sp, respiratory apertures; VI-XVIII, postoral somites.

ectodermal genital chamber (*GC*) that contains the true gonopores or gonopore (*Gpr*).

The gonads of the Arachnida lie in the opisthosoma, in some cases above the alimentary canal, in others below it. Each organ in its fundamental structure is a mesodermal tube containing the germinal cells in its epithelial walls, and is continued anteriorly into a cor-

responding gonoduct. Both the gonad and the duct are ensheathed in a muscular coat. The tubular form of the gonad may be retained in the adult, but generally the primary tube becomes branched, producing either a pair of lengthwise tubes, or more commonly a number of lateral diverticula. In some cases the two gonads of opposite sides are united in a single tube or elongate sac, which is either simple or branched. In the Scorpionida mesal branches of the primary gonadial tubes are generally united with each other forming a series of loops, which may join with those from the opposite side, particularly in the female, to produce a composite gonad having the form of a wide-meshed net (see Pavlovsky, 1924, 1924a). The gonad of the net type in the scorpions resembles the reticulate gonad of *Xiphosura* (fig. 8 B) except that the latter has a much finer mesh, but the union of the gonadial branches appears to be independently evolved in the Scorpionida, and is thus no evidence of close relationship between the scorpions and the xiphosurids. In the arachnid ovaries the eggs are developed singly in numerous small follicular diverticula of the ovarian tubes, a feature which the arachnids have in common with Xiphosurida and Onychophora. The embryos of the viviparous scorpions develop either in swellings of the ovarian tubes between the egg follicles or in the follicles themselves.

The gonoducts, regardless of the form of the gonads, are always a single pair of tubes extending usually forward from the ovaries or testes. In both sexes of Scorpionida, in the males of Solpugida and Phalangida, and in the females of Chelonethida, the gonoducts open separately into the genital chamber (fig. 4 G), but in most other cases they unite in a common duct (H) or an inner sac (I) that discharges into the external genital chamber. Since neither the common duct nor the inner chamber is ever found to have a chitinous cuticular lining, the two appear to be structures of mesodermal origin probably formed by the union of the distal parts of the primary mesodermal ducts. The common duct in this case is not strictly equivalent to the usual ectodermal ductus ejaculatorius or the oviductus communis, and is hence here termed a *ductus conjunctus* (fig. 4 H, J, *Dcn*). The inner sac (I, *Si*), which is evidently an enlargement of the ductus conjunctus, is commonly called the "uterus internus" in arachnid anatomy, the name being applied alike in both the female and the male, but since the organ is not functionally a uterus even in the female, it is here termed the *saccus internus* (*Si*). The walls of the inner sac have a strong sheath of muscle fibers, and both the sac and the ducts may be provided with glandular and other kinds of diverticula, including the complex "paraxial organs" of male scorpions described by Pavlovsky (1924).

The external genital chamber, or bursa genitalis (fig. 4 G-J, *GC*), commonly known in arachnology as the "uterus externus", is undoubtedly an ectodermal pouch of the body wall since it always has a thick cuticular lining. Into its anterior end open either the paired gonoducts (*G*), or the median ductus conjunctus (*H*) or saccus internus (*I*). Diverticula of the bursal wall form accessory genital glands of various kinds, often of large size, and other structures of unknown function, which in some cases are eversible. In the female a pair of lateral pouches may serve as seminal receptacles. The external opening of the genital chamber, or gonotreme (*Gtr*), as already observed, is always associated with the venter of the second opisthosomal segment, which is segment VIII (figs. 10 D, E, 11 A, D, 13 A, *Gtr*). In the more generalized condition the gonotreme lies behind the sternal plate of the genital segment (figs. 10 E, 11 A, B), but when the genital region is displaced forward between the legs, as in the Phalangida (fig. 13 A), the genital sternum may become reduced or concealed by invagination within the bursa.

A comparison of the external genital structure of the more generalized Arachnida with that of *Xiphosura* shows that the lumen of the genital chamber in the former, into which the gonoducts open, must correspond with the external cavity behind the operculum of the latter, which contains the gonopores. The relation of the arachnid structure to the more primitive condition in *Xiphosura* is particularly evident in the scorpions, where the genital chamber opens behind a small opercular plate or pair of plates (fig. 10 D, E, *Opl*) on the venter of the eighth segment, and the gonoducts open separately into the anterior end of the enclosed cavity. The operculum of *Xiphosura*, as we have seen, clearly includes the appendages of the eighth postoral somite and a median fold of the venter of the same segment (fig. 9 B, *V*), on the posterior surface of which are located the genital papillae (*Pen*). In a truly primitive stage of the Chelicerata (except Pycnogonida), therefore, the paired gonoducts of each sex must have opened on the venter of the eighth postoral segment mesad of the bases of the appendages.

Most of the Arachnida do not have an organ for intromission of the sperm associated directly with the gonotreme. The mating habits of the arachnids are well known only in a few groups, but generally if the male personally inserts the spermatozoa or spermatophores into the sperm receptacle of the female, he uses for this purpose a pair of the body appendages, such as the chelicerae in the Solpugida, or the pedipalps in the Araneida. The female, however, may be inseminated in some indirect manner, as with the Chelonethida. At the time of

mating the male chelonethid attaches to the supporting surface beneath his body a filamentous spermatophore that carries a sperm-containing globule at its upper end; the globule is then taken into the genital opening of the female as the body of the latter passes over it during the mating performance (see Kew, 1912; Chamberlin, 1931). In some of the Pedipalpida and in the Phalangida, however, an exter-

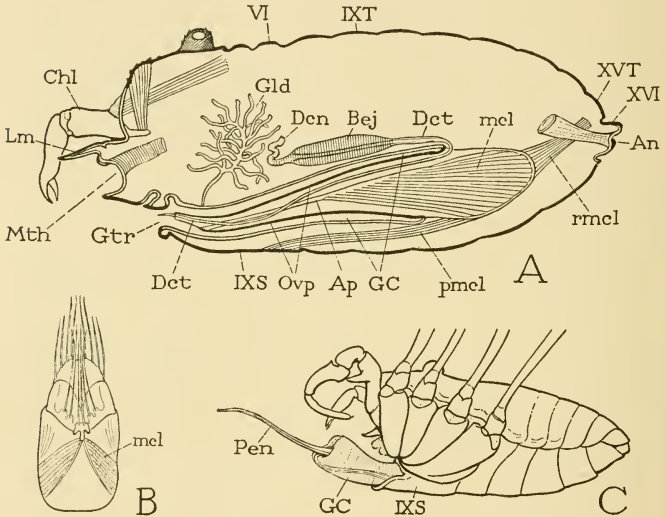


FIG. 12.—Phalangida: male and female genital organs.

A, *Liobunum*, female, diagrammatic longitudinal section of body showing position of retracted external genitalia. B, *Purcellia illustrans* (Cyphophthalmi), genital organ (from Hansen and Sørensen, 1904). C, *Liobunum*, male, genital organ protracted and genital chamber everted.

An, anus; Ap, apodeme; Bej, bulbus ejaculatorius; Chl, chelicera; Dcn, ductus conjunctus; Dct, exit duct of ovipositor; GC, genital chamber; Gld, gland; Gtr, gonotreme; IXS, IXT, sternum and tergum of ninth segment; Lm, labrum; mcl, muscle; Mth, mouth; Ovp, ovipositor; Pen, penis; pmcl, protractor muscle; rmcl, retractor muscle; VI-XVI, postoral somites.

nal genital organ is developed from the walls of the genital chamber, which in male phalangids, at least, undoubtedly serves to convey the sperm to the female. The males of some Acarina, also, have a genital tube which is said to be a true intromittent organ.

The external genital structures of the Pedipalpida are best developed in the genus *Tarantula*, the males of which have a large genital organ (fig. 11 C, GO) ordinarily mostly concealed within the

genital chamber (B). This organ is described by Börner (1902, 1904) as a complex of folds produced from the walls of the genital chamber ("uterus externus"), which enclose a ventral space into which opens the saccus internus ("uterus internus"). The organ is termed a "penis", though only its distal part is entirely free from the genital chamber wall, and its use has not been observed. Börner regards the lateral lobes of the organ as derivatives of the segmental appendages of the genital segment, but of this there appears to be no actual evidence, and, judging from *Xiphosura*, the genital appendages should be merged in the sternal plate of the eighth segment.

Among the Phalangida (Opilionida) the most generalized condition of the external genitalia is preserved in the Cyphophthalmi, where, as shown by Hansen and Sörensen (1904), there is a small sternal plate exposed before the genital opening, and a broad plate behind the latter. If we assume that the true first abdominal sternum is obliterated in the phalangids, as in most other Arachnida, then the pregenital plate must be sternum *VIII*, and the postgenital plate sternum *IX*. In the Phalangidae the anterior part of the venter of the opisthosoma is produced forward into the venter of the prosoma to such an extent that the genital opening comes to lie between the bases of the second pair of legs (fig. 13 A, *Gtr*), and the sternum of the postgenital segment forms a long quadrate plate (*IXS*) between the bases of the third and fourth pairs of legs. Lying before the gonotreme is a transverse fold which may be the sternum of the genital somite, but it appears to belong rather to the segment of the last pair of legs.

The gonotreme of the phalangid *Liobunum* (fig. 13 A) is a wide transverse cleft (*Gtr*) above the anterior margin of the postgenital sternum (*IXS*). It leads into a large sacklike genital chamber with membranous walls (fig. 12 A, *GC*), which in each sex extends far posteriorly in the ventral part of the body. The genital chamber contains a long, tapering, strongly sclerotized genital organ, which is an ovipositor (*Ovph*) in the female and a penis in the male. The organ is a tubular evagination of the posterior wall of the genital chamber, and is transversed by the outlet duct of the gonads (*Dct*). On its base are inserted two pairs of muscles, a long anterior pair (*pmcl*) arising on the posterior angles of the postgenital sternum (*IXS*), and a shorter posterior pair (*rmcl*) arising on the lateral areas of the tergum of the penultimate body segment (*XVT*). The genital organ has the same essential structure in each sex, though there are differences in its size and shape (fig. 13 B, D) to be noted presently. The lateral walls of the genital chamber are strengthened by two long,

thin, flexible sclerotic bands, best developed in the female (D, *b, b*). A pair of large branched glands open into the dorsal wall of the chamber a short distance behind the gonotreme (fig. 12 A, *Gld*).

The female genital organ, or ovipositor, of *Liobunum* is an elongate, continuously sclerotized, flask-shaped structure (fig. 13 D, *Ovp*), widest in its proximal half and tapering forward to its flattened distal end, which bears a small terminal spine (*a*). The expanded basal part of the organ is occupied by two masses of muscle fibers (figs. 12 A, 13 D, *mcl*) that converge distally from the lateral walls to their insertions on a long stalklike apodeme (*Ap*) arising from the ventral wall near the apex of the organ. The base of the ovipositor is deeply emarginate dorsally and ventrally. The dorsal emargination is entered from above by a slender duct (*Dct*) that proceeds from an elongate bulblike structure lying on the dorsal wall of the genital chamber (fig. 12 A, *Bej*), and is itself continuous anteriorly with the median ductus conjunctus (*Dcn*) from the ovaries. The bulb and the duct of the ovipositor are clearly ectodermal structures, since they have a strong cuticular lining. The bulb, *bulbus ejaculatorius* of Rössler (1882), is merely the upper end of the duct surrounded by a thick layer of circular muscle fibers; beyond the bulb the duct becomes an extremely fine cuticular canal without a muscle sheath, traversing the ovipositor to the base of the terminal spine, where it appears to open on the under surface of the latter. In some of the phalangids one or more pairs of small pouches diverge from the outlet duct just behind its opening; these pouches are said to be the sperm receptacles, but they were not observed in the species here described.

The genital organ of the male phalangid (fig. 13 B, *Pen*) has the same general structure as the ovipositor of the female, but in *Liobunum* it is much slenderer than the ovipositor, and in two species examined its distal part is decurved or hooked (figs. 12 C, 13 C, *Pen*). In the specimen shown at C of figure 12 the penis is exerted by a complete evagination of the walls of the genital chamber (*GC*). The initial act of protraction, it would seem, must be caused by a contraction of the long anterior muscles of the penis (fig. 13 B, *pmcl*), but in the fully exerted condition these muscles extend anteriorly to the base of the penis from their origins on the postgenital sternum. It is evident, therefore, that the final stage of protraction results from a general compression of the abdomen that everts the genital chamber. Retraction then must be brought about by the contraction of the reversed anterior muscles acting at first in cooperation with the greatly stretched posterior muscles (*pmcl*), which finally alone complete the process.

The morphology of the external genitalia of the phalangids has not been determined from embryological studies, but there can be no doubt that the cuticular parts, including the genital chamber, the genital organ, the duct of the latter and its bulb, are all derived from the ectodermal genital chamber ("uterus externus") of other arachnids

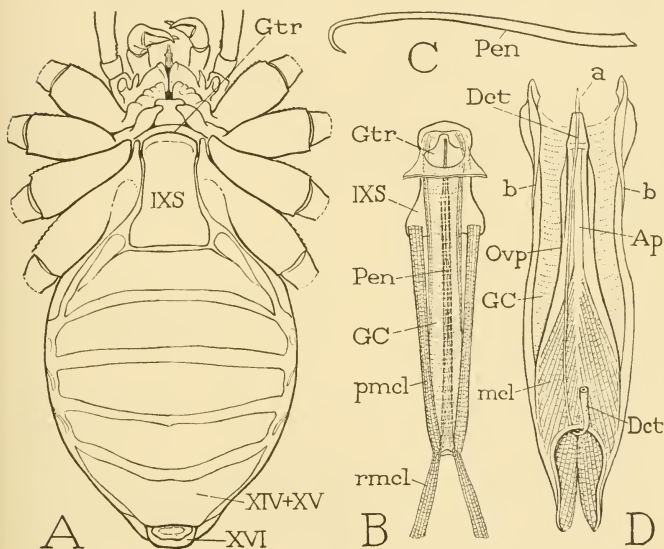


FIG. 13.—Phalangida: body segmentation and genital organs of *Liobunum*.

A, ventral surface of body and appendage bases of a male, showing anterior position of gonotreme (*Gtr*). B, genital organ of male (penis) retracted in genital chamber, dorsal view. C, penis, lateral view. D, genital organ of female (ovipositor) retracted in genital chamber, dorsal view.

a, apical point of ovipositor; *Ap*, apodeme; *b, b*, lateral sclerites in wall of genital chamber; *Dct*, exit duct of ovipositor; *GC*, genital chamber; *IXS*, sternum of ninth segment; *mcl*, muscle; *Ovp*, ovipositor; *pmcl*, protractor muscle of penis; *rmcl*, retractor muscle; *Pen*, penis; *XIV-XVI*, posterior somites.

(compare I and J of fig. 4). The inner duct (*Dcn*) opening into the bulb from the gonads is a mesodermal ductus conjunctus ("uterus internus"). The muscular bulb and the exit canal constitute an ejaculatory apparatus comparable with the male ductus ejaculatorius (K, *Dej*) or with the female oviductus communis (M, *Odc*) of other arthropods. In most of the Phalangida the genital organ (penis or ovipositor) has a closely ringed structure, and ends in two small

lobes; in some forms (fig. 12 B) it is much shorter than in the Phalangidae.

During mating of the phalangids, according to Henking (1888), the male and female stand face to face, and the male thrusts the penis into the genital opening of the female, its tip apparently entering the aperture of the ovipositor, since there is no other approach to the seminal receptacles. When the eggs are discharged they must traverse the excessively slender duct of the ovipositor; Henking records observations on *Liobunum hemisphaericum* in which he followed the transit of the eggs through the duct and saw their exit from its distal end. Since the duct has no muscular sheath, the eggs must be propelled through it, as noted by Rössler (1882), by the action of the bulbus ejaculatorius, which thus has a corresponding function in both the male and the female. The eggs of *Liobunum* are deposited in the ground.

VII. CRUSTACEA

The crustaceans, by comparison with the progoneate arachnids and diplopods or with the opisthgoneate chilopods and hexapods, might be said to be "mesogoneate", inasmuch as the genital openings are on the intermediate part of the body. However, if the numerical position of the segments is considered, the genital segment of some of the many-segmented branchiopods may be as far behind the mouth as that of the chilopods, and considerably to the rear of the genital segments of insects. The segmental position of the gonopores is highly variable in the Entomostraca, but in this group the apertures are always on corresponding segments in the two sexes; in the Malacostraca the genital openings are fixed with specific segments, but they are always on different segments in the male and the female.

To enumerate the postoral trunk segments of the Crustacea in conformity with the enumeration followed in the Chelicerata, we must begin with the somite of the second antennae, which morphologically corresponds with that of the chelicerae.

The gonoducts of the Entomostraca usually open separately to the exterior; in some cases the gonopores are on the limb-bearing thoracic region of the body, but more generally they occur on the abdomen. Intromittent organs are present in some groups, as in Branchiopoda and Ostracoda, the males of which may have a pair of penes, or a single penis through which both vasa deferentia discharge. Examples of the paired type of organ are shown here in two branchiopod species, *Branchipus serratus* (fig. 14 A, B) and *Polyartemia hazeni* (C). The two penes of the first species are short, thick papillae (A, *Pen*) projecting ventrally from the under surface of the second

abdominal segment (somite *XXVII*), but provided with muscles arising in both the second and the first segment. Each penis is armed distally with a hook (B) mesad of which is the gonopore. In *Polyartemia hazeni* the penes (C, *Pen*) are long tubular organs projecting posteriorly from the under surface of the first and second abdominal segments, which in this form are somites *XXI* and *XXII*. The branchiopods, except in cases of parthenogenesis, propagate by sex

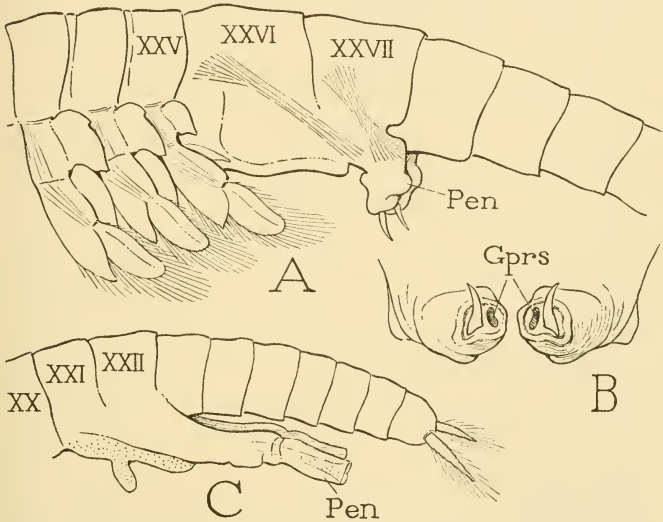


FIG. 14.—Crustacea—Branchiopoda—Anostraca: showing variable position of penes.

A, *Branchipus serratus*, with penes (*Pen*) arising on somite *XXVII*. B, same, end view of penes and gonopores (*Gprs*). C, *Polyartemia hazeni*, with penes on somite *XXII*.

mating, and the spermatozoa are said to be discharged by the male directly into the genital openings of the female; few observations, however, have been made on the exact manner of copulation and intromission.

The Malacostraca have a highly standardized body segmentation, there being, with few exceptions, 18 somites between the mouth and the telson. The trunk is consistently differentiated between segments *XII* and *XIII* into a cephalothoracic region and an abdomen; but the distinction between head and thorax is often somewhat con-

ventional, and when there is a well-marked anatomical separation the boundary is not the same in all cases. Carcinologists usually define the "thorax" as the body region composed of the eight segments between the second maxillary somite (*IV*) and the first abdominal somite (*XIII*), but in some cases the head includes the first of these segments. The abdomen contains six somites and the telson, except in one order, the Leptostraca, in which there are seven abdominal somites. The genital openings of the female are situated always on the sixth thoracic segment (somite *X*), those of the male on the eighth (somite *XII*). In some cases the gonoducts of the male have a single median opening. The female generally is provided with a sperm receptacle, which may be a median pouch of the ventral integument of the thorax, or paired sacs at the ends of the oviducts.

The gonads of the Malacostraca are tubular or sac-shaped organs, sometimes lobed or branched, lying in the dorsal part of the thorax and abdomen, or restricted to the thorax (figs. 15 G, 16 C, 17 C, 18 E). In the decapods the gonads of opposite sides are generally more or less united (figs. 17 C, 18 E). The germinal cells usually occupy one wall of the gonad, from which the oocytes or spermatocytes are proliferated into the lumen (fig. 15 E); the cells of the opposite wall (*NrCls*) may have a nutritive function. In *Anaspides*, as described by Smith (1909), the mesal walls of the ovaries are produced into long series of diverticula, in the apices of which are located the germinal cells, the organs thus resembling the ovaries of insects. The gonoducts are either straight or coiled, and generally open directly to the exterior, but in the Brachyura the oviducts end in large ectodermal sperm receptacles (fig. 18 H, *Spt*).

The gonopores of male Malacostraca are located typically on or close to the mesal surfaces of the coxopodites of the last pereopods (thoracic appendages), though they may lie on the sternal surface between the appendages (figs. 15 D, 16 A, *Gprs*). Usually each aperture is situated on the extremity of a small papilla or tubular outgrowth of the integument (figs. 16 B, 18 D, *Pen*), called a penis though it is not the actual intromittent organ. In some cases there is a single median penis arising from the venter of the eighth thoracic segment (fig. 16 D, *Pen*), which contains a common outlet duct receiving the two lateral gonoducts at its base. If direct internal insemination of the female from the penes, or penis, of the male takes place in any of the Malacostraca it is of rare occurrence, and has not been observed. With the majority of the Malacostraca the sperm (or spermatophores) are placed by the male in the oviducts or in a sperm receptaculum of the female, but the organs that accomplish the intro-

mission are usually modified parts of the first, or the first and the second, pleopods (abdominal appendages). In some cases, however, the spermatophores are merely attached to the under surface of the body of the female. Fertilization of the eggs takes place either within the oviducts, or in a brood pouch on the under surface of the female's body. A few examples of the external genitalia of the Malacostraca

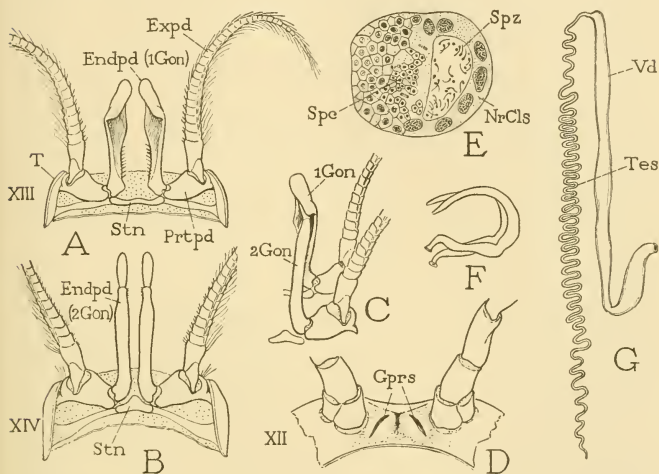


FIG. 15.—Crustacea—Malacostraca—Syncarida: male genitalia of *Anaspides tasmaniae*.

A, B, appendages of first and second abdominal segments, ventral view, showing mesal processes, or gonapophyses (probably the endopodites), that compose the intromittent organs. C, left gonopods, posterior (under) view, showing functional relation of gonapophyses. D, ventral surface of last thoracic segment, with gonopores. E, cross-section of testis. F, spermatophores. G, testis and vas deferens. (E, F, G from Smith, 1909.)

Endpd, endopodite; *Expd*, exopodite; *1Gon*, *2Gon*, first and second gonapophyses (probably endopodites); *Gprs*, gonopores; *NrCls*, nutritive cells of testis; *Prtpd*, protopodite; *Spz*, spermatocytes; *Spz*, spermatozoa; *Stn*, sternum; *T*, tergum; *Tes*, testis; *Vd*, vas deferens; *XII*, *XIII*, *XIV*, twelfth, thirteenth and fourteenth postoral somites.

will suffice to illustrate the general structure and variations of the organs in this group.

The typical structure of the external genital organs of male Malacostraca is well shown in the Anaspidacea. In *Anaspides tasmaniae* the male gonopores are two oblique slits on the venter of the eighth thoracic segment (fig. 15 D, *Gprs*) situated on oval elevations between the bases of the last pair of legs. The functional intromittent organs

are composed of two pairs of long processes arising from the inner ends of the basal segments of the first and second pleopods, which are, therefore, probably the endopodites of these appendages (A, B, *Endpd*). The genital processes, or gonapophyses, of the first pair (A) are expanded distally and hollowed on their inner surfaces; those of the second pair (B) are cylindrical, and their distal ends fit snugly into the concavities of the first pair (C). By means of these organs the male during mating inserts a pair of large, horseshoe-shaped spermatophores (F) into a two-branched receptacular pouch opening on the venter of the last thoracic segment of the female. The spermatophores are probably taken from the gonopores of the male into the cavities of the first gonapophyses, and forced from the latter by the second gonapophyses. Within the receptacular pouches of the female the spermatozoa are discharged from the spermatophores, and the latter are then rejected. Since there is evidence that fertilization of the eggs takes place in the oviducts, it is supposed that the spermatozoa are transferred into the openings of the latter on the sixth thoracic segment by means of setigerous lobes, present only in the female, on the inner surfaces of the coxopodites of the last three pairs of thoracic legs. The fertilized eggs are said by Smith (1909) to be deposited singly "under stones and among the roots of water plants" (his figure shows them on the branches of a liverwort).

The Isopoda generally have two separate genital exit ducts, which in the male open either by simple apertures (fig. 16 A, *Gprs*) or through a pair of small penes on the sternum of the last thoracic segment. In the Oniscoidea, however, which include the ordinary terrestrial isopods, there is present usually a single median penis (C, D, *Pen*), and the gonoducts unite at its base in a common exit tube. The median penis may be displaced posteriorly so that it arises from the membrane behind the last thoracic sternum, with its base between the appendages of the first abdominal segment (D, *Pen*). The intromittent organs of Isopoda, when present, are formed as in Anaspidacea of the inner arms, or endopodites, of the first and second pairs of abdominal appendages (D, E, *Endpd*). By means of these structures masses of spermatozoa that issue from the gonopores are inserted into the genital openings of the female. The terminal parts of the oviducts in some species of isopods are enlarged to serve as sperm receptacula, and the eggs are fertilized in the ducts. After mating, the female moults and in most species acquires a brood pouch (marsupium) on the under surface of the body, into which the fertilized eggs are discharged, and within which they are carried until the young hatch. The brood pouch is formed typically by broad

overlapping plates (oostegites) that grow over the thoracic venter from the bases of the legs, but in some species it is formed by anterior and posterior folds of the ventral integument, and in others by an invagination or a series of sacklike ingrowths of the membranous ventral wall of the thorax. In one genus, *Paragnathia*, the young are said to develop in the ovaries, which serve as uteri.

The Amphipoda are provided with a pair of small penes, but they have no organs of sperm intromission; the eggs are fertilized outside

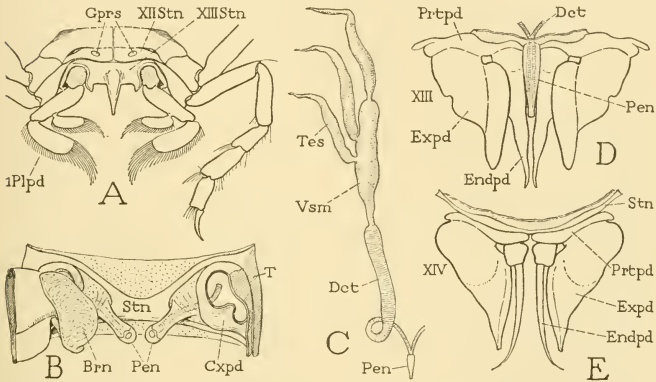


FIG. 16.—Crustacea—Malacostraca—Peracarida: male genitalia of Isopoda and Amphipoda.

A, *Scerolis* (isopod), ventral view of last thoracic and first abdominal segments, showing gonopores on sternum of somite XII. B, *Gammarus locusta* (amphipod), ventral view of last thoracic segment, showing penes arising at bases of coxopodites. C, *Porcellio laevis* (isopod), testis and exit duct of one side, and median penis. D, same, penis and first pleopods, ventral view. E, same, second pleopods.

Brn, branchia; *Cxpd*, coxopodite; *Dct*, genital exit duct; *Endpd*, endopodite; *Expd*, exopodite; *Gprs*, gonopores; *Pen*, penis; *Prtpd*, protopodite; *Stn*, sternum; *T*, tergum; *Tes*, testis; *Vsm*, vesicula seminalis; *XIIStn*, sternum of male genital segment; *XIIIStn*, sternum of first abdominal segment.

the body of the female. The penes, as illustrated in *Gammarus locusta* (fig. 16 B, *Pen*), are a pair of short cylindrical processes arising from membranous areas between the lateral arms of the last thoracic sternum and the bases of the coxopodites. During mating the male attaches himself to the back of the female and remains in this position until the female moults; then immediately the male curves his body under that of the female and attaches small masses of sperm to the body wall of the latter in the neighborhood of the oviducal apertures. The eggs, later extruded, are fertilized in the brood pouch beneath

the body. It is interesting to observe that in the Amphipoda and Isopoda insemination of the female precedes or follows a moult by the latter according as the spermatozoa are stored on or in a part of the body not involved by the moulting process, or in a part subject to removal at ecdysis. Insemination *before* the moult allows the development in the female of special ectodermal structures, such as the oostegites or brood pockets, necessary after the eggs are fertilized.

The Decapoda vary somewhat in their mating habits, but the spermatozoa are enclosed in spermatophores, which either are attached to the external integument of the female, or are inserted into an integumental pocket (*thelycum*, *annulus ventralis*) or into a pair of ectodermal spermathecae associated with the oviducal openings. Insemination of the female, therefore, takes place immediately *after* a moult to insure against premature loss of the sperm.

The external genitalia of male decapods include a pair of penes arising from the mesal surfaces of the coxopodites of the last pereopods, and the modified first and second pleopods, which are the active intromittent organs. The genital structures retain more of the generalized form in the Macrura than in the Brachyura. In *Cambarus virilis* the penes are small membranous lobes projecting mesally from the bases of the last pereopods (fig. 17 A, *Pen*), with the gonopores on their posterior surfaces. The sternum of the genital segment (*Stn*) presents a deep concavity between the coxopodites, which is continued forward on the next two segments, forming a ventral channel of the thorax in which are lodged the anterior ends of the gonopods. The first pair of gonopods are long, rigid appendages (B, D) projecting anteriorly in the thoracic channel as far as the bases of the second pereopods. The shaft of each of these appendages tapers to a slender distal process (*a*), but from its under surface there arises mesally a large lobe that splits into two proximal processes (D, *b*, *c*), the outer one of which (*b*) has a groove on its upper surface that leads into a deep cavity at the base of the lobe. The second gonopods (E) have more nearly the structure of the unmodified pleopods of the following segments. Each is a biramous appendage with the two arms (*Expd*, *Endpd*) supported on a two-segmented basal stalk (*Cxpd*, *ITr*). The larger endopodite bears a mesal lobe (*d*) at the end of its long first segment, which, when the appendage is turned forward beneath the corresponding first gonopod, clasps the latter at the base of its mesal lobe. The structure of the crayfish gonopods and the manner in which the appendages perform their function of sperm intromission during copulation are minutely described for *Cambarus affinis* by Andrews (1911). The spermatozoa are received from the

penes into the grooves of the mesal lobes and the pockets at their bases on the first gonopods, and are discharged into a receptacular pouch (annulus ventralis) on the venter of the female between the sterna

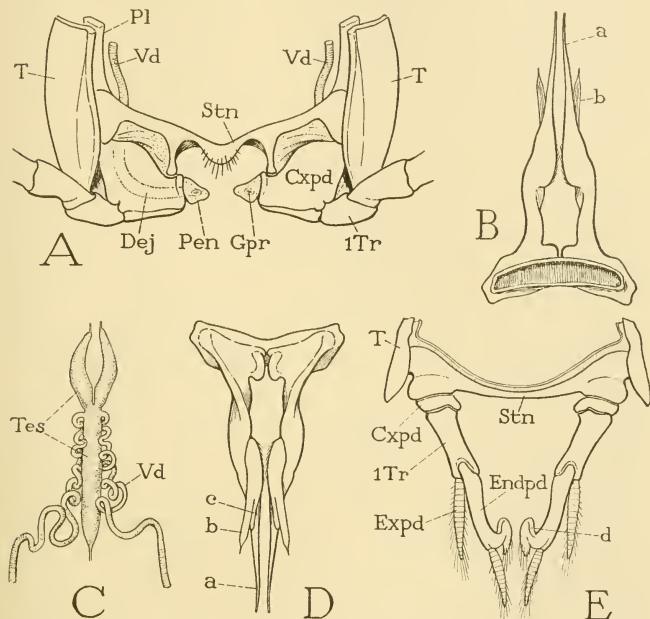


FIG. 17.—Crustacea—Malacostraca—Eucarida: male genitalia of a crayfish, *Cambarus virilis*.

A, posterior view of lower part of last thoracic segment, showing small penes projecting mesally from coxopodites. B, first gonopods projecting forward, anterior (upper) surface. C, testes and vasa deferentia, dorsal view. D, first gonopods (normally projecting forward in ventral channel of thorax), posterior (under) surface. E, second gonopods, posterior (under) surface.

a, distal shaft of first gonopod; b, c, outer and inner branches of ventral lobe of first gonopod; Cxp, coxopodite; d, distal lobe of second gonopod; Dej, ductus ejaculatorius; Endpd, endopodite; Expd, exopodite; Gpr, gonopore; Pen, penis; Pl, pleuron; Stn, sternum; T, tergum; Tes, testis; 1Tr, first trochanter (basipodite); Vd, vas deferens.

of the seventh and eighth thoracic segments. (See also Andrews, 1906.)

The crabs (Brachyura) differ from most of the other decapods in that the female has a pair of large pouchlike sperm receptacles

formed as invaginations of the body wall at the gonopores on the bases of the third pereopods, into which open the short oviducts (fig. 18 H, *Spt*). Inasmuch as the sperm containers are ectodermal structures, insemination takes place just *after* a moult of the female. The paired intromittent apparatus of the male crabs is a complex structure composed of the penes of the last thoracic segment, and the greatly modified first and second pleopods of the abdomen. Both sets of organs are ordinarily concealed in a deep median depression on the under surface of the thorax covered by the T-shaped abdomen when the latter is turned forward in its usual position.

In the blue crab, *Callinectes sapidus*, the principal member of each composite intromittent organ is the first pleopod (first gonopod). This appendage consists of a large flat coxopodite (fig. 18 B, *Cxpd*) projecting laterally from the small triangular sternum of its segment, and of a long tapering telopodite, or "flagellum", with an enlarged base. The thick base of the flagellum (*b*) turns mesally from the end of the coxopodite (*A, B*), and the slender, tapering distal part (*a*) extends anteriorly, overlapping its mate from the opposite side (*B*) in the ventral groove of the thorax above the flexed abdomen. The walls of the bulblike base of the flagellum are partly membranous (*B, D, mb*), and the posterior margin of the bulb is cleft by a deep groove that expands inwardly as a large internal cavity; the enlarged ends of the groove form a proximal foramen on the anterior surface of the bulb (*D, c*) and a distal foramen on the posterior surface (*B, d*). The groove, however, is continued from the lower lip of the distal foramen along the entire length of the slender distal part of the flagellum (*B, gr*), forming within the latter a tubular canal continuous with the cavity of the base and opening mesally near the tip. The second gonopod (*C*) resembles the first in general form, but it is much smaller, and has a small middle segment (*Bspd*) interpolated between the base of the flagellum and the coxopodite; the flagellum (*e*) is a short curved arm no longer than the bulbular base of the first flagellum. The penes of the crab arise from the mesal ends of the coxopodites of the last pereopods. Each is a long flexible tube (*D, Pen*) traversed by the gonoduct, which opens at its extremity.

The component elements of the genital complex of the crab are intimately associated with one another, and constitute an apparatus for conveying the spermatozoa from the male gonoducts into the seminal receptacles of the female. In the normal condition the penis of each composite organ lies mostly within the cavity of the bulbular base of first flagellum, which it enters by the anterior proximal foramen of the latter (fig. 18 A, *Pen*); the end of the second flagellum

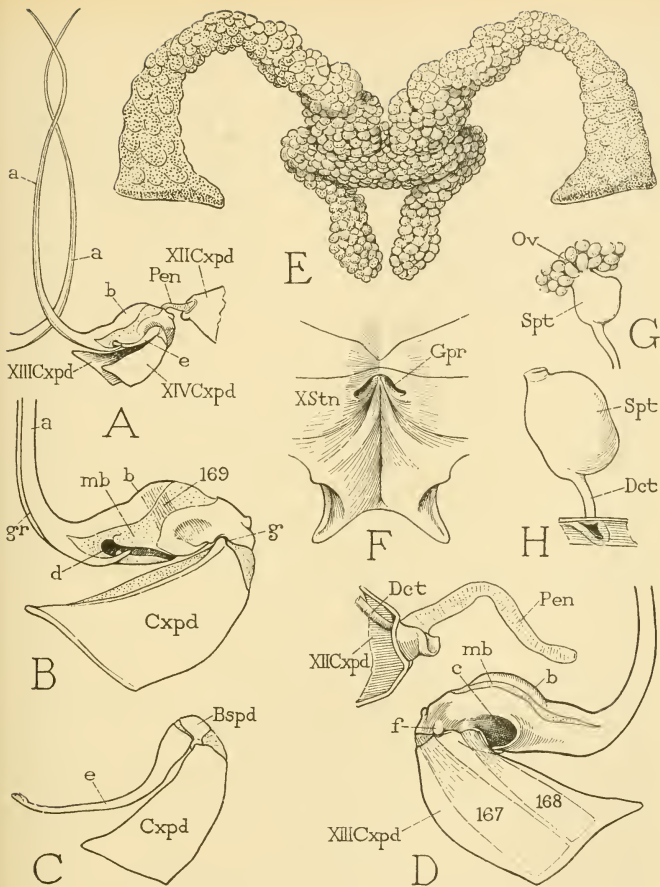


FIG. 18.—Crustacea—Malacostraca—Eucarida: male and female genitalia of a crab, *Callinectes sapidus*.

A, the intramittent apparatus, including on each side the penis and the modified first and second pleopods (gonopods), ventral view. B, base of left first gonopod, posterior (under) surface. C, left second gonopod, posterior (under) surface. D, left penis and base of left first gonopod, anterior (upper) surface. E, ovary, dorsal view. F, gonopores of female on tenth (third thoracic) sternum. G, spermatheca of a young hard-shell female. H, spermatheca of a soft-shell female probably ready for insemination.

a, distal shaft of first gonopod; *b*, bulblike base of telopodite of first gonopod; *Bspd*, basipodite; *c*, anterior proximal foramen of first gonopod; *Cxpd*, coxopodite; *d*, posterior distal foramen of first gonopod; *Det*, spermathecal duct; *e*, distal arm of second gonopod; *f*, *g*, anterior and posterior articulations of telopodite on coxopodite; *Gpr*, gonopore; *gr*, groove of first gonopod; *mb*, membrane; *Ov*, ovary; *Pen*, penis; *Spt*, spermatheca; *XStn*, sternum of genital segment of female; *XII Cxpd*, *XIII Cxpd*, *XIV Cxpd*, coxopodites of last pereopods and of first and second pleopods (gonopods); *167*, *168*, coxal muscles of telopodite; *169*, compressor muscle of bulb of first gonopod.

(*c*) similarly enters the posterior distal foramen of the bulb. The second flagellum thus would appear to act as a plunger for driving the sperm through the channel of the first. A strong transverse muscle (B, 169) crosses the middle of the bulb and evidently acts as a compressor of the latter.

The mating habits of the blue crab have been described by Hay (1905) and by Churchill (1921). During the breeding season the male crabs appear to be able to recognize females in a premoult condition. When a male encounters such a female he seizes her by the back with his second, third, and fourth pereopods, leaving the chelae free for feeding, and the last pereopods (swimming legs) free for swimming. In this position the two crabs swim about for a day or so; but as soon as the female is about to moult, the male releases her on the bottom of the water and stands guard until the shell is cast. The female then turns ventral side up and extends the abdomen, whereupon the male grasps her again, and insemination now takes place while the female is in the soft condition following the moult. The eggs are later fertilized as they are discharged through the seminal receptacles, and are carried in a mass attached to the pleopods of the female until they hatch the following spring.

VIII. MYRIAPODA PROGONEATA

The progoneate myriapods include the Symphyla, the Pauropoda, and the Diplopoda. These forms evidently constitute a natural arthropod group characterized by having the genital apertures in both sexes situated on the third postcephalic segment, which segment most probably is the seventh postoral somite. To enumerate the postoral somites in the progoneate myriapods, however, it is necessary to take a somewhat arbitrary view concerning the segmentation of the head and the anterior body region, since the literature on the subject is full of conflicting opinions and different interpretations of the observed facts.

If we start with the Symphyla as a basis for interpreting the progoneate segmentation, the matter is relatively simple, for here the gnathal region of the head supports a pair of mandibles and two distinct pairs of maxillary appendages, and the first postcephalic segment carries a pair of legs. Though postantennal appendages (second antennae) have not been discovered in any of the progoneate myriapods, Robinson (1907) reports the presence of a pair of "second antennal" ganglia in the embryo of a diplopod. It is entirely reasonable to assume, therefore, that the symphyliid head contains four postoral segments representing the second antennal, mandibular, and two maxillary somites of the Crustacea, or the corresponding somites

of Chilopoda and Hexapoda. There can be no question as to the identity of the first body segment in the Symphyla, since, though reduced, it bears a pair of legs. These first legs are small and lack one of the distal segments present in the other legs. Behind the bases of the third pair of legs is situated in each sex the median genital opening, which evidently belongs to the third body segment, though it may invade the venter of the following segment. If, therefore, we count the absent second antennal somite as segment *I*, the genital opening in Symphyla is on segment *VII*, which is the third body segment.

In the Pauropoda and Diplopoda a direct determination of the gnathal and postcephalic segmentation becomes impossible by reason of the facts that in the adult there is only one appendage in the maxillary region of the head, and the first apparent body segment is reduced and lacks appendages. As above pointed out, the evidence deduced from developmental studies is conflicting and inconclusive. By comparison with Symphyla, however, the genital segment of the pauropods and diplopods should be segment *VII*, since there is no evidence of variability in the position of the genital outlets in any of the progoneate myriapods. The male exit ducts of the Pauropoda open on a pair of small penes situated at the bases of the second pair of fully developed legs; the first legs, if present, are rudimentary and arise from an apparent neck region, which latter, therefore, must be regarded as the reduced first body segment. The single female outlet duct opens by a median aperture between the bases of the legs on the same segment as in the male. (See Silvestri, 1902; Attems, 1926.)

The Diplopoda have a distinct "neck segment" intervening between the head and the first leg-bearing segment of the body, which typically contains a large dorsal plate, the *collum*, and a small ventral plate, but apparently has no appendages. In the adult there is only one postmandibular appendage on the head, the *gnathochilarium*, which appears to have a composite structure. The first three body segments following the neck segment have each only one pair of legs, and the genital apertures are always on the segment of the second pair. In most of the diplopods (the Proterandria) the eighth or the eighth and ninth pairs of legs (those of the third "double segment") are modified in structure to serve as intromittent organs, and are termed the *gonopods*.

The dispute on the question of diplopod segmentation concerns the number of postoral somites in the head, the nature and composition of the gnathochilarium, and the relation of the plates of the neck segment to the cephalic capsule and the gnathochilarium on the one hand, and to the body on the other.

The gnathochilarium has been variously regarded as representing the first maxillae, the second maxillae, and both pairs of maxillae combined. Silvestri (1903) contends that the gnathochilarium is the united first maxillae. According to Robinson (1907), however, there are present in the embryo of *Archispirostreptus* separate rudiments of first and second maxillae, but the first disappear, and the second alone unite to form the gnathochilarium. In a more recent study on *Platyrrhacus amauros*, Pflugfelder (1932) asserts that, while two pairs of maxillary appendages are present, they are both combined in the gnathochilarium. The last two writers thus agree as to the number of primary head appendages that are present, but they differ with respect to the segmental connections of these appendages. Robinson assumes that the segment of the gnathochilarium is contained in the head capsule; the neck segment, she says, is represented in the embryonic nervous system by a pair of postmaxillary ganglia. Pflugfelder, on the other hand, claims that the second maxillary components of the gnathochilarium are the appendages of the neck segment, and that the first true body segment is that bearing the first pair of legs. Silvestri also regards the neck segment as the somite of the second maxillae of other arthropods, but he believes that these appendages are absent in the Diplopoda. If the gnathochilarium belongs to the neck segment, its muscles should arise in this segment, whereas, according to the description of the head and neck muscles of Diplopoda given by Silvestri (1903), the muscles of the gnathochilarium take their origin within the head capsule, and the posterior musculature of the head arising on the back plate of the neck segment is very similar to the prothoracic head musculature of insects. There seems to be little support for Silvestri's view that the second maxillae of the diplopods are absent.

Considering the general similarity of the diplopod head to the cranial capsule of other arthropods, and the evidence of fundamental unity in structure between the several groups of progoneate myriapods, the current view (see Attems, 1926) is here accepted that the diplopod head contains both the first and the second maxillary somites, and that the legless neck segment is the first body somite, homologous with the first leg-bearing segment of the Symphyla. The legs of this segment are small and reduced by the loss of one segment in Symphyla; in Pauropoda, if present at all, they are rudimentary; in Diplopoda they are absent. The genital apertures of the diplopods, we may therefore conclude, are on segment *VII* behind the mouth, as in the pauropods and symphyliids.

The genital openings in both sexes of the diplopods are more or less closely associated with the bases of the legs of the genital seg-

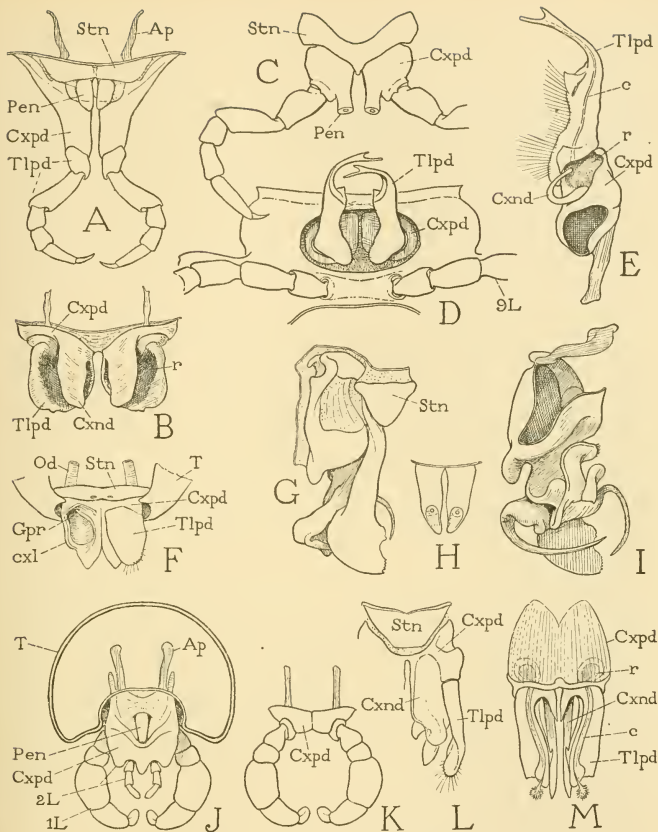


FIG. 19.—Diplopoda: external genitalia.

A, *Habrostreplus*, male, sternum, legs, and penes of third body segment, posterior view. B, same, gonopods of third body segment, anterior view. C, *Euryurus*, male, sternum, legs, and penes of third body segment, anterior view. D, same, seventh body segment, ventral view, showing position of gonopods and legs. E, same, right gonopod, anterior (upper) surface. F, *Parajulus impressus*, female, ventral part of third body segment and appendages, anterior view, telopodite of right appendage removed exposing gonopore on the coxopodite. G, *Thyropygus*, male, right gonopod, anterior (under) surface. H, same, penes, posterior surface. I, same, left gonopod, posterior (upper) surface. J, *Parajulus impressus*, male, third body segment and appendages of second segment, posterior view. K, same, appendages of second body segment, posterior surface. L, same, sternum and first gonopod of seventh body segment, anterior surface. M, same, second gonopods, posterior surface.

Ap, apodeme; c, sperm canal of gonopod; cxl, coxal lobe; Cxnd, coxal endite; Cxpd, coxopodite; Gpr, gonopore; 1L, first leg (on second body segment); 2L, second leg (on third body segment); 9L, ninth leg (second leg of seventh body segment); Od, oviduct; Pen, penis; r, sperm receptacle of gonopod; Stn, sternum; T, tergum; Tltpd, telopodite.

ment (fig. 19 C, F). The male ducts usually discharge separately on a pair of, small penes having the form of papillae or lobes arising either directly from the coxae of the second legs (C, *Pen*), or mesally behind the coxal bases (A), but in some forms the ducts open together on a median penis arising between or behind the legs (J, *Pen*). The legs of the genital segment in most cases have the typical leg form (A, C), but they may be reduced in size and otherwise modified, or united at their bases (J, *Cxpd*). In certain species the first legs also are modified in a manner suggestive that they take some part in copulation (J, *1L*, K).

The female genital ducts open either on the coxae of the legs of the genital segment, or on the sternal surface behind the leg bases. Usually the legs of the genital segment are not modified in the female, but there are exceptions, as shown in *Parajulus impressus* (fig. 19 F), in which the telopodites of the genital appendages are reduced to small lobes (*Tlpd*) and the oviducts open into large cavities on extensions of the united coxopodites (*Cxpd*). In forms in which the ducts open behind the legs, the apertures are usually contained in a complicated integumental structure (see Brölemann and Lichtenstein, 1919, and Seifert, 1932).

Intromission is accomplished in the ordinary diplopods (Proterandria) by the modified legs (gonopods) of the seventh body segment of the male, which transfer the sperm from the penes or penis of the third segment into the genital apertures of the female. In two of the diplopod groups, however, the relatively generalized Pselaphognatha and the Opisthandria, according to the classification of Attems (1926), none of the appendages is modified for the purpose of intromission, though in members of the first group the coxae of the eighth legs have external pouches, which Attems suggests may have some reproductive function. In the Opisthandria one or two pairs of legs at the posterior end of the body in the male are specially modified to serve as copulatory organs. With these legs the male is said to grasp the genital coxae of the female, while he inserts the spermatozoa into the female gonopores with his mandibles (Attems, 1926).

The gonopods of the seventh body segment of proterandrious male Diplopoda are analogous in their function to the gonopods of malacostracan Crustacea and the pedipalps of male spiders; in their structure even they are not dissimilar from these organs. The pair of appendages converted into gonopods is usually the first pair of legs of the seventh segment; the second legs of this segment are generally of usual form, but they may be absent, or modified also to form a second pair of gonopods. A typical diplopod gonopod (fig. 19 E)

consists of two segments, a basal coxopodite (*Cxpd*), and a distal telopodite (*Tlpd*). The essential feature of the organ is a *sperm receptacle* (*r*), which is an invagination cavity on the morphologically anterior surface of the coxopodite, and a *sperm canal* (*c*), which is usually a closed groove that traverses the telopodite from the sperm receptacle to the apex of the appendage. The coxopodite is generally provided with a movable endite lobe (*Cxnd*) of various shapes, which projects over the sperm receptacle, and when slender may be partly inserted into the proximal opening of the sperm canal. The bases of the appendages are often sunken into a deep cavity on the ventral surface of the body segment (D). The gonopods are subject to endless modifications in form, and their structural diversity in different genera and species furnishes valuable characters in diplopod taxonomy.

An example of gonopods having a highly diversified and complex structure is shown in the genus *Thyropygus* (fig. 19 G, I). A very much simplified structure, on the other hand, is found in *Habrostrepus* (B), in which the telopodite (*Tlpd*) of each gonopod has the form of a short broad lobe with a wide, basinlike sperm cavity (*r*) on its ventral anterior surface, which is partly covered by a flat endite lobe (*Cxl*) of the coxa. In some forms, as in *Parajulus* (L, M), both pairs of legs of the seventh body segment are transformed into gonopods, the second of which in this case contain the sperm receptacles (M, *r*) and canals (*c*). More extensive and detailed descriptions of the diplopod gonopods will be found in works by Vosges (1878), Verhoeff (1903), Silvestri (1916), Attems (1894, 1926), and Siefert (1932); the last writer gives also an account of the manner of copulation and insemination in *Polydesmus edentulus*.

IX. CHILOPODA (MYRIAPODA OPISTHOGONEATA)

The Chilopoda have a single median genital aperture, which in each sex is always behind the sternum of the last somite, that is, between the penultimate body segment and the anus-bearing end segment, or telson. The number of segments anterior to the genital segment, however, is so variable in the chilopods as a whole that no fixed numerical designation can be given to the genital segment itself. In the anamorphic forms (*Lithobius*, *Scutigera*), in which the adult segmentation does not vary, there are 19 definitive body segments, including the telson. Counting four postoral somites in the head, the genital segment in this group, therefore, is somite XXII. Among the Epimorpha, in which the definitive segmentation is in most forms complete at hatching, the number of segments is highly variable in the Geophilomorpha, even in the same species, and may be very large,

while in Scolopendromorpha there are either 26 or 28 body segments, but the number is constant for each species.

The gonads of the Chilopoda lie above the alimentary canal, as in Crustacea and Hexapoda, whereas in the progoneate myriapods they lie below the alimentary canal. The testes in Epimorpha consist of from 1 to 12 pairs of short spindle-shaped tubes each united at each end by a slender ductule with a common median gonoduct. Among the Anamorpha, *Lithobius* has a single median tubular testis, but *Scutigera* has two slender testicular tubes. The ovaries are in all forms united in a single median tubular gonad, in the walls of which the germ cells are arranged in a longitudinal band or a pair of lateral bands. The median gonoduct of each sex is apparently a ductus conjunctus; posteriorly it divides into two arms that embrace the rectum and unite again below it in a short exit or genital chamber, into which open one or two pairs of accessory glands, and in the female a pair of seminal receptacles. The left branch of the gonoduct in the Epimorpha becomes reduced or rudimentary, and only the right branch serves as the functional exit tube.

The external genital region of the chilopod body consists of two small legless segments intercalated between the last leg-bearing segment and the terminal anus-bearing telson. These segments, which in the Epimorpha are differentiated during embryonic development as two very small somites (fig. 20 A), are termed by Heymons (1901) the *pregenital segment* (*1gSeg*) and the *genital segment* (*2gSeg*). The two segments may bear each a pair of small or rudimentary appendages, which are the *first* and the *second gonopods* (*1Gp*, *2Gp*). The definitive genital opening is formed behind the sternum of the genital segment; the gonopore is usually concealed in a genital chamber, but in the male it is on a small protractile penis. In the Anamorpha, which add segments during postembryonic development from a generative zone before the telson, the genital segments are the last to be formed. The definitive segmentation of the chilopod body, therefore, depends on the number of somites generated before the establishment of the genital segments, after which there is no further somite propagation. The variable number of pregenital segments generated in the Chilopoda from a postgenital zone of growth, as already noted, must lead to the conclusion that the two segments in the definitive genital region are not homologous somites in all cases, notwithstanding their similarity of structure. However, the structure of these two segments is probably only that which any segments might take on if arrested in their growth at an early stage of development.

The most generalized condition of the genital region in the adult chilopod is found in the Geophilomorpha, in which both genital sterna

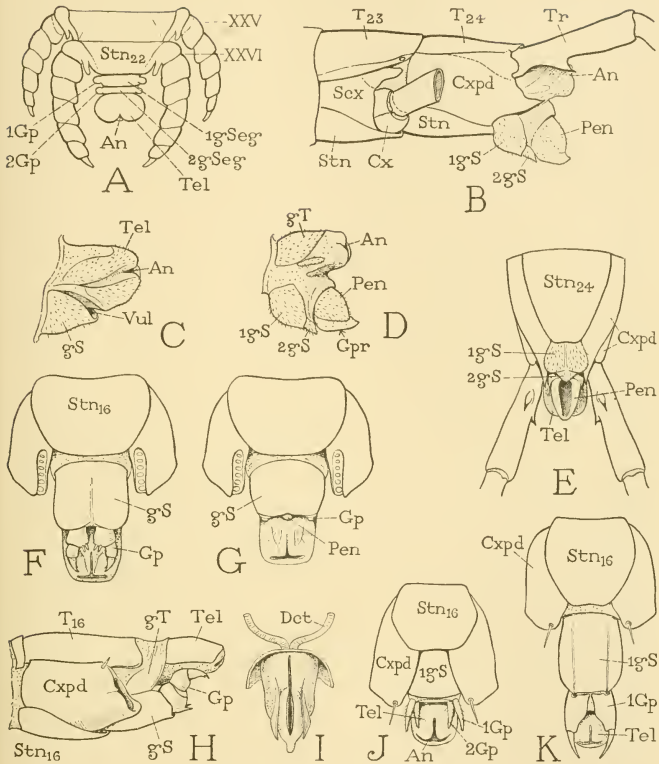


FIG. 20.—Chilopoda: external genitalia.

A, *Scolopendra*, posterior end of body of embryo, showing two small segments in genital region between last leg-bearing segment and telson (from Heymons, 1901). B, *Scolopocryptops*, male, terminal part of body with penis protracted. C, same, female, genital and anal segments. D, same, male, genital and anal segments, lateral view. E, same, male, posterior end of body, ventral view. F, *Lithobius*, female, posterior end of body, ventral view. G, same, corresponding segments of male. H, same, female, lateral view of posterior body segments. I, same, male, ventral view of penis and ducts. J, *Scutigera forceps*, male, posterior end of body, ventral view. K, same, corresponding segments of female, ventral view.

An, anus; Cx, coxa; Cxpd, coxopodite; Dct, genital duct; Gp, gonopod; 1Gp, 2Gp, first and second gonopods; gS, genital sternum; 1gS, 2gS, first and second genital sterna; 1gSeg, first genital, or pregenital, segment; 2gSeg, second genital, or genital, segment; gT, genital tergum; Pen, penis; Scx, sub-coxa; Sin, sternum; T, tergum; Tel, telson; Tr, trochanter.

are distinct, though only the second bears a pair of small, sometimes two-segmented gonopods, and the terga of the two segments are united in a single dorsal plate. In other forms the second sternum is either much reduced or obliterated, but the gonopods of the first segment or of both segments may be present. Both genital sterna appear to be retained in the male of *Scolopocryptops* (fig. 20 B, D, E), though the second ($2gS$) is very small and is absent in the female (C). A single tergal plate covers the back of the genital region of the male (D, gT). Neither pair of gonopods is represented, but a large median penis (B, D, E, *Pen*) is protractile from a bursa genitalis (genital chamber) invaginated above the genital sterna. In *Lithobius* there is a single large genital sternum in each sex, which presumably is that of the first genital, or pregenital, segment (F, G, gS). A pair of well-developed, three-segmented gonopods is present in the female of the species figured (F, H, Gp), but in the male (G) the appendages are rudimentary. The penis is a small conical organ opening ventrally by a median slit (I), and is ordinarily almost entirely concealed in the bursa genitalis (G). The male of *Scutigera forceps* (J) has two pairs of styluslike gonopods, the first borne by the pregenital sternum ($1gS$), the second by a small membranous fold possibly representing the venter of the second genital segment. In the female (K) only the anterior gonopods are present, but these appendages have the form of long two-segmented claspers borne by the large pregenital sternum ($1gS$). Copulation in the chilopods has not been observed, but the males of some species are known to produce spermatophores, and spermatozoa are found in the seminal receptacles of the female.

The chilopods resemble the hexapods in the possession of a median penis and in the modification of the appendages in the genital region to form accessory reproductive organs. The fact, however, that quite different somites may be involved in the development of the genital complex eliminates the question of homology between the parts, and the superficial likeness in the external genitalia of the Chilopoda and Hexapoda is thus no evidence of close relationship between these two groups.

X. HEXAPODA

The fundamental feature in the structural organization of the Hexapoda that distinguishes the six-legged arthropods from members of all other arthropod groups is the concentration of the locomotor mechanism in the three body segments immediately following the fourth postoral somite. The Hexapoda, therefore, include the Protura and Collembola as well as the ordinary insects. The number of seg-

ments behind the locomotor region, or thorax, is inconsequential, as is also the matter of whether the abdominal segmentation is completed before or after hatching.

The hexapods are always opisthogoneate in that the genital ducts extend posteriorly from the gonads and open near the end of the body, but there is considerable variation in the number of somites that precede the genital somite. In the Collembola the genital opening in each sex is at the posterior end of the fifth abdominal segment, which is segment *XII* from the mouth, and there is only one postgenital segment. The genital openings in Protura are likewise at the end of the penultimate segment, but this segment is somite *XVIII* (eleventh abdominal segment). In insects other than Collembola and Protura the primitive paired gonopores were probably in the female on somite *XIV* (seventh abdominal segment), and in the male on somite *XVII* (tenth abdominal). With most of the insects, however, the definitive genital outlet is the aperture of a secondary median duct, and is subject to migration in the female from the seventh abdominal segment to the eighth, ninth, or tenth, but in the male appears to be always between the ninth and tenth segments.

Considering the fact that somite formation is teloblastic in the arthropods, and that the generative zone lies just before the end-segment, or telson, it is evidently impossible that the genital segment can be the same somite in Collembola, Protura, and the other insects. With the establishment of the genital ducts in Collembola and Protura, somite formation has ceased, but the genital segment in the former is the fifth abdominal somite, and in the latter the eleventh. With the other insects, four embryonic somites may be generated in the female behind the segment of the primary genital ducts, and one in the male. The abdomen of all the hexapods except Collembola has thus become standardized with a maximum segmentation of eleven somites between the thorax and the telson; but the telson, except in Protura, is suppressed in the adult and the eleventh somite forms the usual proctiger, though it too is often reduced or united with the tenth. The reason for regarding the twelfth abdominal segment of the Hexapoda as the telson is that, when present in the embryo, it never has any of the appurtenances of a somite, such as appendages or nerve ganglia.

The lateral gonoducts of the male have separate openings to the exterior among the Hexapoda in Protura, Ephemeroptera, some Dermaptera, and perhaps secondarily in certain Diptera; but in general the lateral ducts discharge into a median ductus communis. Embryological evidence (see Heymons, 1895, 1897; Wheeler, 1893) gives reason for believing that the primary genital ducts of male

insects opened originally on segment *XVII*, which is the tenth abdominal segment (fig. 21 A, *Vd*), and that very probably the gonopores were located on the bases of the segmental appendages, as is the case in many other arthropods. The usual common exit duct, ductus ejaculatorius (B, *Dej*), is formed ontogenetically as a median invagination at the posterior margin of the venter of the ninth abdominal segment. Anatomically the point of origin of the ejaculatory duct

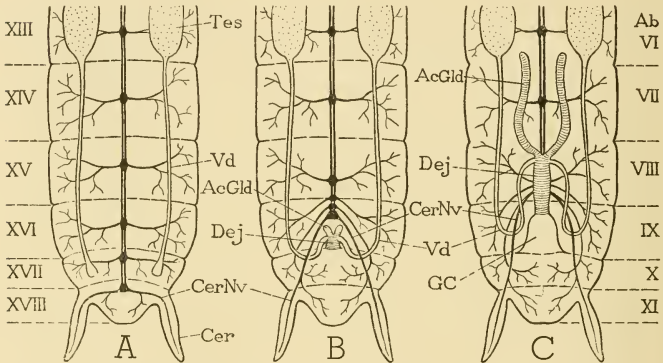


FIG. 21.—Diagrams showing the relation of the male genital ducts in Orthoptera to the nerves of the tenth and eleventh abdominal segments.

A, primitive stage: vasa deferentia (*Vd*) opening separately on tenth abdominal segment (postoral somite *XVII*) between the lateral nerves of tenth and eleventh segments. B, later stage: vasa deferentia opening medially into an ejaculatory duct (*Dej*) invaginated at posterior end of ninth abdominal segment; last three ganglia of nerve cord moved forward, drawing the cercal nerves (*CerNv*) over the genital ducts. C, definitive stage: the last four ganglia united in eighth abdominal segment; genital exit system extended forward by growth of ejaculatory duct and addition of genital chamber (*GC*), the vasa deferentia looped beneath the cercal nerves.

Ab, abdominal segments; *AcGld*, accessory genital gland; *Cer*, cercus; *CerNv*, cercal nerve; *Dej*, ductus ejaculatorius; *GC*, genital chamber; *Tes*, testis; *Vd*, vas deferens; *VI-XI* (on right), abdominal segments; *XIII-XVIII* (on left), postoral somites.

appears thus to be intersegmental between the ninth and tenth abdominal segments, but some incomplected observations made by the writer on the innervation of the genital organs in Orthoptera seem to indicate that the ductus ejaculatorius derives its innervation from nerve trunks that pertain to the tenth segment. It is possible, therefore, that the median genital duct of the male morphologically belongs to the tenth abdominal somite. Perhaps the median duct was primarily the outlet of the accessory genital glands (B, *AcGld*), but, whatever its

original nature may have been, since the vasa deferentia come to open into its anterior end at the bases of the glandular diverticula, the median duct of the male becomes the exit both for the secretion of the accessory glands and for the spermatozoa. The mouth of the common duct is the median gonopore of the male. The gonopore may be exposed on a small phallic papilla arising from the ventral membrane between the ninth and tenth abdominal segments, but generally this membrane is invaginated to form the male bursa genitalis, or genital chamber (*C*, *GC*), and the gonopore is then carried out upon a tubular evagination of the anterior wall of the chamber, which forms the usual phallic organ.

A study of the anatomical relations between the vasa deferentia and the posterior segmental nerve trunks of the abdomen in Orthoptera shows that the male genital ducts must originally have crossed over the lateral nerves of the tenth abdominal segment and attached to the ectoderm behind these nerves (fig. 21 *A*, *Vd*). The subsequent union of the vasa deferentia with the median ductus ejaculatorius (*B*), however, necessitated a median and forward migration of the posterior ends of the lateral ducts. The correlated forward retraction of the posterior part of the ventral nerve cord then drew the large nerves of the cerci (*CerNv*), given off from the terminal ganglion, over the incurved ends of the vasa deferentia (*Vd*). Hence, in the definitive condition (*C*), the vasa deferentia are always looped beneath the cercal nerves, but lie dorsal to the other lateral nerve trunks of the abdomen. This condition could follow only from one in which the primitive genital ducts turned downward to the body wall between the nerve trunks of the tenth and eleventh abdominal segments (*A*). Likewise, in female Orthoptera, the relation of the lateral oviducts to the nerve trunks shows that the primitive lateral ducts must have opened somewhere between the nerves of the seventh and eighth abdominal segments. Incidentally, the nerve-duct relation in the male demonstrates also that the cerci are appendages of the eleventh abdominal segment.

The paired penes of the Hexapoda are best shown as simple independent structures in some of the Ephemeroptera (fig. 25 *C*, *Pen*). They are supported on basal arms or a basal plate (*C*, *F*, *x*), which possibly may represent the sternum of the tenth abdominal segment. Since there are no true appendages on the tenth segment, there is no evidence as to what relation the penes may have had to the limb bases, but, judging from other arthropods, there is no reason to suppose that the primitive penes of the hexapods were structures other than papillae of the coxopodites containing the outlets of the genital ducts.

Among the mayflies as well as in the Protura and Dermaptera the penes show a tendency to combine into a single organ (penis conjunctus) as they do also in some Crustacea and Diplopoda.

The usual median intromittent organ, or phallus, of adult insects is evidently a *penis communis*, since neither in its structure nor its ontogeny is there any evidence that the organ has been produced by the union of a pair of rudiments containing the outlets or ends of the lateral genital ducts. It is formed as a tubular outgrowth of the body wall around the mouth of the ejaculatory duct, or by the union of phallic lobes that enclose the gonopore. The theory suggested by Crampton (1920), and formerly accepted by the writer (1931, p. 91), that the phallus has been evolved in part or entirely from mesal lobes of the appendages of the ninth abdominal segment, appears to be quite without anatomical or ontogenetic foundation. The genital appendages are variously and often highly developed, but they take no part in the formation of the phallus.

The phallic organ of insects is subject to endless variations in form, and it is not to be supposed that the numerous accessory structures encountered, or even the more general modifications are necessarily homologous developments in different groups of insects, for it must unquestionably be true that, with apparently unlimited variation, similar forms have been many times produced quite independently. Furthermore, as will later be shown, it is very probable that the median penis itself has been evolved in different ways in several insect groups. The musculature of the phallus, even among closely related insects, is so highly variable and so evidently adaptive in its nature, that it cannot be used for determining anatomical relationships or homologies in the phallic structures.

The intimate association of the phallus with the ninth abdominal segment has involved this segment so closely in the genital function that usually it is the segment of the genital region most affected by structural modifications adaptive to the mechanism of copulation and intromission. The ninth segment, in fact, may be designated *the genital segment* of male insects. The neighboring segments, however, are often variously modified also as parts of the genital complex, and in the higher Diptera all the segments beyond the fifth form a distinct genital section of the abdomen. A point that should be emphasized in the study of the male genitalia of insects, particularly in Orthoptera, is the fact that the structure of the phallic organ and of the genital segment is not necessarily, in its principal aspect, an adaptation to the functions of copulation and intromission, but may be very largely concerned with the formation of spermatophores and the transference of the latter to the female.

The male bursa genitilis, or genital chamber, which usually contains the phallic organ or organs, projects into the ninth abdominal segment (fig. 22 A, *GC*) since it is an invagination of the integument behind the ninth sternum, though its dorsal wall presumably belongs to the venter of the tenth segment. Appendages of the ninth segment (gonopods) may be entirely absent; in Orthoptera and some related insects they are small styluslike structures resembling the abdominal styli of Thysanura, though unlike the latter they are not provided

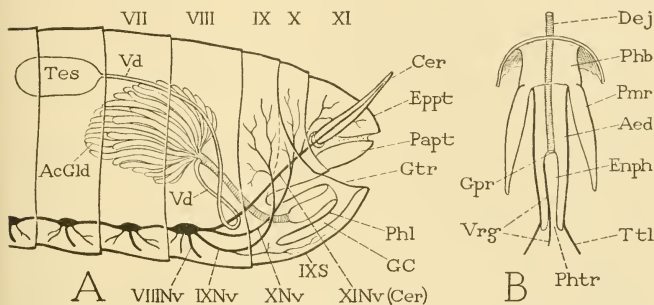


FIG. 22.—Diagrams of the position and structure of the external and internal genitalia of male insects.

A, general position and relation of the male reproductive organs of orthopteroid type. B, diagram of the median penis, or phallus, showing parts that commonly recur, but which are not necessarily or usually present in the same species.

AcGld, accessory genital gland; *Aed*, aedeagus; *Cer*, cercus; *Dej*, ductus ejaculatorius; *Enph*, endophallus; *Eppt*, epiproct; *GC*, genital chamber, or bursa genitilis; *Gpr*, gonopore (aperture of ejaculatory duct); *Gtr*, gonotreme (opening of genital chamber); *IXS*, sternum of ninth abdominal segment (male subgenital plate, hypandrium); *Papt*, paraproct; *Phb*, phallobase; *Phl*, phallus (median penis); *Phtr*, phallotreme (distal opening of endophallus); *Pmr*, paramere; *Tes*, testis; *Ttl*, titillator, *Vd*, vas deferens; *Vrg*, virga; *VII-XI*, seventh to eleventh abdominal segments; *VIII_{Nv}*, *IX_{Nv}*, *X_{Nv}*, *XI_{Nv}*, principal lateral nerves of eighth, ninth, tenth, and eleventh abdominal segments issuing from composite last ganglion of ventral nerve cord.

with muscles. In many of the higher insects, however, the appendages of the male genital segment take the form of large movable organs of various shapes usually adapted to grasping or holding the female. These genital claspers (valvae, harpes, harpagones) are always distinguishable from other similar but immovable or merely flexible lobes or processes borne on the ninth or other segments of the genital complex by the fact that they are independently movable by muscles inserted on or in their bases. Such appendages are most probably homologues of the thysanuran abdominal styli. In some cases the movable claspers are supported on distinct basal plates, but more commonly

the basal segments (coxopodites) of the gonopods of pterygote insects are incorporated in the wall of the segmental annulus. The movable claspers, together with the other genital processes that arise peripherally from the segments of the genital region, may be designated collectively the *periphallic organs*.

DEFINITIONS OF EXTERNAL GENITAL STRUCTURES OF THE MALE

The principal parts of the external genitalia and their commonly developed accessories in male insects and other arthropods may be named and defined as given in the following list of terms, but no general nomenclature can be devised to include names for all the minor modifications and special developments found in the various orders of insects.

Aedeagus (Aed).—The distal part of the phallus when the latter has a differentiated basal part; usually the principal part of the phallus, or the entire organ if the phallobase is suppressed; typically a sclerotic tube with the phallostreme at its extremity.

Bursa genitalis (GC).—The genital chamber of either the male or the female; in male insects a ventral invagination of the membranous integument behind the ninth abdominal sternum containing the phallus or phallic organs.

Copulatory organs.—Any structures used by either sex for grasping or holding the partner during mating, or particularly paired organs, usually segmental appendages, specially adapted or modified for copulatory purposes.

Ductus ejaculatorius (Dej).—The median exit duct of the male genital system; if formed by the union of a pair of primary ductus ejaculatorii it is a *ductus conjunctus*, if developed as a single median invagination of the integument serving as an outlet for both vasa deferentia it is a *ductus communis*.

Ectophallus.—The outer wall or exposed part of the phallus in distinction to the endophallus.

Endophallus (Enph).—An inner phallic chamber invaginated at the end of the ectophallus, and containing the true gonopore, or opening of the ejaculatory duct; typically an eversible sac or tube, often mistaken for the end of the ejaculatory duct, but sometimes a permanently internal phallic structure that may attain a complex development. (*Preputial sac*.)

Endotheca (Enth).—The inner wall of the phallosheath.

Epimerc.—A dorsal process of the phallobase.

Epiphallus (*Epph*).—A large, transverse sclerite developed in the dorsal wall of the base of the phallus, characteristic of Acrididae. (*Pseudosternite* of Walker.)

Genital chamber (*GC*).—See *bursa genitalis*.

Genital segment, or *gonosomite*.—Specifically the body segment bearing the openings of the primary genital ducts, or the segment with which the median gonopore is most closely associated, but also in a wider sense any one of the segments in a specially differentiated genital region of the body. In insects the genital segment is primarily the seventh abdominal somite in the female and the tenth in the male, but secondarily the female genital segment is usually the eighth or the ninth abdominal somite, and that of the male the ninth.

Gonapophysis (*Gon*).—Any part of a segmental appendage closely associated with the genital segment and having some function intimately related to intromission of the sperm by the male or the deposition of eggs by the female. In male Malacostraca the gonapophyses are the endopodites of the first and second abdominal appendages and serve as intromittent organs; in insects the gonapophyses are apparently endites of the appendages of the eighth and ninth abdominal segments, present in both sexes of some Thysanura, forming the usual ovipositor of female insects.

Gonopod (*Gp*).—An appendage of the genital segment or of an associated segment modified for some purpose in connection with copulation, intromission, or oviposition.

Gonopore (*Gpr*).—The external opening of a genital duct, whether exposed, or concealed in a secondary invagination of the integument, such as the genital chamber or an endophallic cavity.

Gonostyli.—The styli of the ninth abdominal segment of some male insects, presumably appendicular parts of the coxopodites of the gonopods, probably homologous with the movable claspers (*harpagones*) of many insects.

Gonotreme (*Gtr*).—The external opening of the *bursa genitalis*, or genital chamber, in either sex; the *vulva* of the female.

Harpagones (*Hrp*).—Movable periphallic appendicular organs of the ninth abdominal segment of the male, individually provided with muscles, probably derivatives of the gonostyli, sometimes supported on distinct coxopodite plates. (*Valvae*, *harpes*.)

Hypandrium (*IXS*).—The subgenital plate of the male, usually the sternum of the ninth abdominal segment.

Hypomere.—A ventral process of the phallobase.

Intromittent organs.—Any structure of the male serving for the introduction of the sperm or spermatophores into the female, in some

cases the paired penes, in insects usually the median penis, or phallus, but in many other arthropods modified appendages that assume the intromittent function, as in Araneida, Malacostraca, and Diplopoda.

Parameres (Pnr).—Lateral processes or lobes of the phallobase, probably secondary outgrowths having no relation to the gonopods.

Penis (Pen).—A general term applied to any integumental outgrowth containing the orifice of a male genital duct, whether intromittent in function or not, including the paired penes of many arthropods, or a median penis (phallus); but the term is often used also in a restricted functional sense for the part of the phallus or any other intromittent organ inserted into the female genital receptacle during mating. The primitive paired penes of most arthropods are on the bases of a particular pair of segmental appendages, or on the sternum mesad of the appendages. A median penis may be either a *penis conjunctus* or a *penis communis* according as it is formed by the union of a pair of penes, or by a secondary median outgrowth of the integument.

Periphallic organs.—Peripheral genital processes of the ninth segment or of other segments in the male genital complex of insects, including the movable claspers, or harpagones.

Phallic organs.—The median genital structures of male insects immediately concerned with the function of coition, or the introduction of the spermatozoa or spermatophores into the receptacular organ of the female; the phallic organs are highly variable, and are formed ontogenetically in various ways, but always independently of the periphallic organs.

Phallobase (Phb).—A differentiated basal part of the phallus, variable and often not distinct from the aedeagus. (*Tegmen* in Coleoptera.)

Phallocrypt (Crpt).—A pocket of the phallobase or of the genital chamber wall containing the base of the aedeagus or of the ectophallus.

Phallobases (Phn).—Phallic organs having the form of lobes produced from the genital chamber wall in the neighborhood of the gonopore; particularly developed in Blattidae and Mantidae, probably united in the median phallic organ of other Orthoptera, and perhaps represented by lobes that form the phallus in the ontogeny of some higher insects.

Phalotheca (Thc).—A fold sometimes extended from the phallobase around the base of the aedeagus, or produced as a tubular sheath enclosing the latter, in exceptional cases replacing the aedeagus.

Phallorema (Phtr).—The distal opening of the endophallus at the extremity of the ectophallus, the functional exit aperture of the genital tract when the true gonopore is contained in an endophallic chamber.

Phallus (Phl).—The usual median penis or single intromittent organ of male insects, variously formed and probably developed independently in several insect groups.

Preputial sac.—See *endophallus*.

Subgenital plate (IXS).—See *hypandrium*.

Titillators (Ttl).—Distal external processes of the aedeagus.

Virga (Vir).—A terminal phallic spine or slender rod usually arising from the wall of the endophallus and therefore protractile with the eversion of the latter.

COLLEMBOLA

The Collembola are hexapods with a differentiated thorax and abdomen, but having at most only six abdominal segments. Their embryology gives no evidence of a greater number of somites ever having been present, which fact is surprising considering that the immediate ancestors of all the other hexapods undoubtedly had a standardized abdomen of 12 segments. The single genital opening in each sex of the Collembola is on the extreme posterior part of the venter of the fifth abdominal segment; the gonopore thus has the same position relative to the terminal segment as has the genital opening in Chilopoda and Protura, but the disparity in the number of somites preceding the genital segment shows that the subterminal position of the gonopore in these three arthropod groups is not a matter of anatomical homology. The genital aperture of the Collembola is situated sometimes on a slight elevation of the integument, but there is no development of the external genital region sufficient to constitute an intromittent organ or an ovipositor.

The internal reproductive organs of Collembola have been studied by Sommer (1885), Fernald (1890), Willem (1900), Lécaillon (1901, 1902, 1902*a*, 1902*b*), Imms (1906), and De Winter (1913). The gonads lie ventro-laterally in the abdomen and the posterior part of the thorax (fig. 23 A), and in the mature condition they approximate each other *beneath* the alimentary canal (C, G). The testes are continuous posteriorly with short lateral ducts that join a common exit duct (A, B, *Dej*), the anterior end of which may be enlarged as a seminal vesicle (B, *Vsm*).

In the younger stages of all Collembola, according to Willem (1900), the gonads are simple fusiform sacs, each tapering anteriorly to a suspensory ligament; as development progresses, however, the organs in most cases lose their primitive form, become greatly enlarged, and variously modified in shape (fig. 23 F, G). The germinal area of each organ in some forms is situated in the dorsal or

lateral wall of the gonadial sac (B, D, G, *Grm*), and in this feature the gonads of certain Collembola preserve the generalized structure of the reproductive organs found in Onychophora, and in arthropods

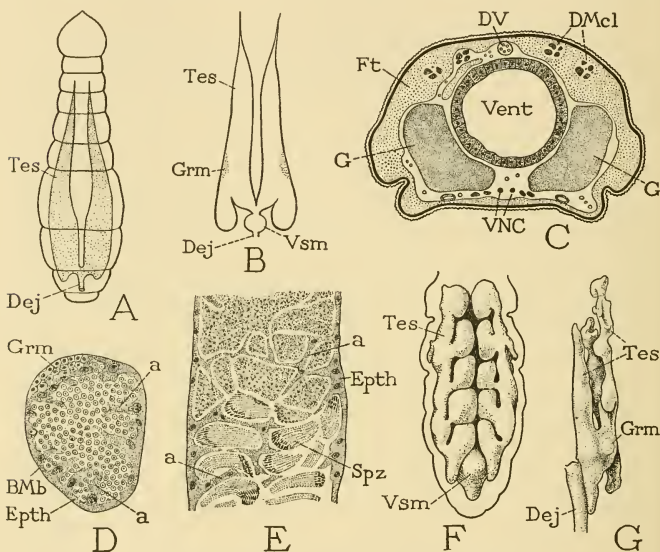


FIG. 23.—Hexapoda—Collembola: internal genitalia.

A, *Anurida maritima*, diagram of position of male gonads (from Imms, 1906). B, *Anurophorus laricis*, outline of testes showing position of germaria (from Lécaillon, 1902a). C, *Anurida maritima*, transverse section through fourth abdominal segment (from Imms, 1906). D, *Anurophorus laricis*, transverse section of testis, showing germarium in dorsal wall (from Lécaillon, 1902a). E, *Anurida maritima*, longitudinal section of posterior part of testis, showing bundles of spermatozoa separated by ingrowths of epithelial wall (from Imms, 1906). F, *Podura aquatica*, mature testis, dorsal view (from Willem, 1900). G, *Tomocerus vulgaris*, mature testis of right side, dorsal view (from Willem, 1900).
a, intratesticular ingrowths of testicular epithelium; *BMB*, basement membrane; *Dej*, ductus ejaculatorius; *DMcl*, dorsal longitudinal muscles; *DV*, dorsal blood vessel; *Epth*, testicular epithelium; *Ft*, fat tissue; *G*, gonad, *Grm*, germarium; *Spz*, spermatozoa; *Tes*, testis; *Vent*, ventriculus; *VNC*, ventral nerve cord; *Vsm*, vesicula seminalis.

other than insects in which the germinal cells have not become localized in the apex of the gonads or in the apices of lateral diverticula. Within the lumen of the testis the bundles of developing spermatozoa (E, *Spz*) are enclosed in compartments formed of intratesticular

prolongations (*a*) from the epithelial walls (*Epth*) of the gonad. The testicular cysts of other insects are said to be formed of cells descended from the spermatogonia.

The simple shape of the gonads is most fully carried over into the adult stage in *Anurida*, in which the ovaries and testes, though they may increase greatly in size from the immature stages, retain for the most part an undivided saclike form (fig. 23 A, B). The germinal area of *Anurida*, as described by Lécaillon (1902) and by Imms (1906), lies in the dorsal wall of the gonad (D, *Grm*). In the male, Imms says, "the germinal tissue is in the form of a mass or ridge, situated at about the middle of the length of the testis", in the female it forms in each ovary "a protruding ridge lying in the region of the third and fourth abdominal segments." In *Podura*, according to Willem (1900), the adult gonads are voluminous organs occupying the abdomen and the last two segments of the thorax. Each gonad is an irregular sac (F) with its mesal wall produced into five large pouches separated by deep incisions, but the germinal zone of the testis extends through the entire length of the dorsal wall of the organ, both on the undivided lateral part and on the mesal pouches.

In the Entomobryidae, as shown by Willem (1900), the immature gonads are simple fusiform sacs as in the young of Poduridae, but in each sex the germarium is localized in the apex of the organ, evidently a secondary condition, Willem contends. As development proceeds, however, each gonad grows anteriorly and posteriorly beyond the germinal zone in each direction, with the result that in the definitive organ, the germarium is a restricted area of the lateral wall of the gonad near the posterior end of the latter (fig. 23 G, *Grm*). In this family the gonad becomes two-branched by the development of a long mesal lobe opposite the germarium. The gonads of Neelidae and Sminthuridae are undivided tubes, but each tube is bent upon itself because of the limited space in the globular abdomen. According to Lécaillon (1902) the germinal zone in the male of these families is restricted to the apex of the testis; in the female of *Sminthurus*, Willem says, the germinal region of the ovary lies ventrally in the outer wall of the middle part of the tube, but much nearer the anterior end of the latter than in Poduridae and Entomobryidae.

From the above review of the structure and development of the collembolan gonads it is evident that the organs, beginning with a generalized condition, have followed a line of specialization confined to the Collembola. The primitive gonadial sac, as represented by the testis of Poduridae, probably had a germinal band in its dorsal wall. The localization of the germarium in the apex of the gonad in other

forms is, therefore, as Willem contends, a specialized condition; it results in the formation of a gonad resembling a single testicular or ovarial tube of Thysanura and Pterygota, but which cannot be a morphological counterpart of the latter, since the tubes of a compound gonad are developed as lateral outgrowths of the primitive sac.

The development of the eggs in the ovary of *Podura* is described by De Winter (1913), who shows that the oocytes are proliferated in rows extending peripherally from the germarium, and that they become enmeshed in a reticulum of cells that grow inward from the outer epithelium of the ovary. The distal oocytes, by reason of their closer contact with the blood, are the better nourished and develop into the functional ova, while the more central cells become degenerate, and some of them in contact with the outer cells are absorbed by the latter. The general structure of the ovary of *Podura*, with the peripheral development of the ova, and the close resemblance to the ovary of *Lithobius*, De Winter contends, shows that the poduran ovary is not derived by condensation or reduction from the compound type of insect gonad, but is a gonad of generalized structure, and represents the most primitive type of ovary found among the insects.

No verified observations have yet been made on the exact manner of insemination of the female by the male in Collembola. The curious mating habits of the Sminthuridae, however, have long been known and have recently been described in detail by Falkenhan (1932) and by Strebel (1932). The male approaches a female and with his antennae grasps the antennae of the female, the male antennae being specially adapted for clasping by a modification of the second and third segments. The male is then lifted by the female, who carries him around suspended before or above her body while she goes about the affairs of her ordinary life. The male remains inactive with his legs folded against the body, and is thus transported by the female for a time varying from a few hours to as long as a day and a half, but with intermissions the carrying of the male may be continued for four or five days. Only one writer, Lie-Pettersen (1899), claims to have observed the act of insemination; according to his account a male while suspended by the female was seen to emit a drop of spermatid fluid, which fell on the wall of the glass tube containing the insects, whereupon the male released himself, with his fore legs smeared the drop on his mouth parts, and then inserted the latter into the genital opening of the female. Neither Falkenhan nor Strebel, after prolonged observation, saw any act on the part of the mated sminthurids such as that described by Lie-Pettersen. Falkenhan postulates, however, that insemi-

nation may take place by the emission of a drop of spermatic fluid from the male, which, falling to the ground, is taken up directly by the female into her genital orifice. There seems to be little doubt that the mating performance of the Sminthuridae is accessory to insemination, since Falkenhan finds that the eggs of females that have not been allowed to mate are infertile. Egg laying takes place ordinarily about 14 to 18 days after mating, though the time varies according to temperature and the age of the female.

PROTURA

The Protura, in the fully matured stage, have 12 abdominal segments, and this character would appear to relate them more closely to insects other than Collembola, in which the maximum segmentation of the abdomen, as shown in the embryos of some forms, consists of eleven somites and a telson. The Protura differ from other hexapods in that the last two somites before the end segment, or telson, are formed during postembryonic growth, as in anamorphic Chilopoda. Whether segmentation is completed before or after hatching, however, cannot be a matter of great importance, since it is variable among the chilopods themselves. The genital openings of the Protura are on the penultimate body segment as in Collembola and Chilopoda, but, as already pointed out, the genital segment, though subterminal in position, is numerically quite a different somite in each of these three groups.

The gonads of Protura lie ventral to the alimentary canal, as in Collembola, but in their structure they resemble a single gonadial tube of an insect ovary or testis of the usual compound type, in which each tube has a germarial zone at its apex. The proturan ovary or testis, as described by Berlese (1910), is a large tubular sac with the tapering anterior end folded ventrally and posteriorly. In the deflexed apical region are contained the oogonia or spermatogonia, and the rest of the tube is occupied by the developing oocytes or spermatocytes. The oocytes are arranged in a single series ending with a mature ovum as in an ovariole of other insects, and the successive stages of the maturing spermatozoa form zones of growth as in an ordinary sperm tube. The proturan gonad thus does not have the primitive or generalized structure of a collembolan or chilopod gonad, and its simplicity of form, therefore, would appear to be the result of elimination of tubes from a compound organ, as is probably the case also in certain Diplura in which the gonad consists likewise of a single egg tube or sperm tube. The vasa deferentia of Protura discharge individually through terminal ejaculatory ducts, but the oviducts come together in a short median outlet tube.

The external genitalia of the Protura consist of a large bifid organ in each sex eversible from behind the sternum of the eleventh abdominal segment. In the female the common oviduct opens between the bases of the arms of the genital organ; in the male the lateral gonoducts traverse the arms and open separately near their apices (see Berlese, 1910; Prell, 1913; Tuxen, 1931). Nothing is known of the development of the proturan genital organ; its structure suggests an origin from a pair of organs. Crampton (1918) says its two arms are "doubtless homologous" with the paired penes of Dermaptera; but the different segmental relations of the organs in the two cases (with the eleventh abdominal segment in Protura, and the tenth or ninth in Dermaptera) would preclude any question of actual homology. The female has no seminal receptacle, and the mating habits of the proturans have not been recorded.

DIPLURA AND THYSANURA

The compound structure of the gonad first appears among the Hexapoda in the Diplura (Entotrophica) and the Thysanura (Ectotrophica). In *Campodea* the ovaries and the testes consist each of a single tube, as do the testes of *Japyx*, but in other members of both orders the gonads are compound, the number of tubules varying from two to seven on each side. In some cases, as in the female of *Japyx*, the gonadial tubes are segmentally arranged on the duct, suggesting that the compound structure of the gonad originated by the outgrowth of segmental diverticula from an elongate gonadial sac, each diverticulum carrying in its apex a part of the original germinal band. The gonoducts discharge through a single median aperture, which in the female is between the eighth and ninth abdominal segments, and in the male between the ninth and tenth. The male gonopore may be on a small integumental papilla in the Diplura; the Thysanura have a short tubular penis.

It is from the Thysanura that we derive the best evidence for the generally accepted view that the definitive sternal plates of the insect abdomen are in most cases composite structures formed in each segment by a continuous sclerotization of the areas of the true sternum and the flattened limb bases. In *Machilis* the venter of each abdominal segment anterior to the genital region is occupied by a small, anterior, median, triangular sclerite (fig. 24, A, *Stn*), and two large lateral plates (*Cxpd*) projecting posteriorly as free lobes and united with each other behind the median sclerite. The median sclerite is presumably the primary sternum of the segment. The lateral plates appear to be the bases (coxopodites) of the segmental appendages;

each may bear distally a stylus (*Sty*), and in some species, mesad of the latter, an eversible vesicle (*Vs*). The coxal plates are present also on the genital segments (F, G), but the sternal plate is absent on the ninth segment of the male (G) and on both genital segments of the female. Styli are characteristically present on the coxopodites

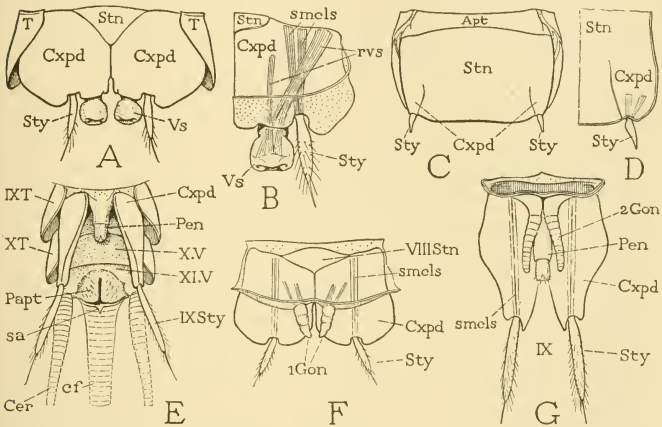


FIG. 24.—Hexapoda—Diplura and Thysanura: structure of the abdominal sterna and external genitalia.

A, *Nesomachilis maoricus*, ventral view of an abdominal segment, showing sternal surface formed of a small primary sternal plate (*Stn*) and two large coxopodite plates (*Cxpd*) bearing appendicular organs. B, same, dorsal view of right half of sternal plates, showing muscles of vesicula and stylus. C, *Heterojapyx gallardi*, ventral view of an abdominal segment, showing coxopodites incorporated into the sternum. D, same, dorsal surface of right half of sternum, showing muscles of stylus. E, *Nesomachilis maoricus*, posterior part of male abdomen, ventral view, showing penis arising between bases of coxopodites of ninth segment. F, *Machilis variabilis*, ventral plate of eighth abdominal segment of male, with pair of small first gonapophyses (*1Gon*), dorsal view. G, same, appendages and penis of ninth segment, with second gonapophyses (*2Gon*) arising from bases of coxopodites at sides of penis.

Apt, sternal apotome; *Cer*, cercus; *cf*, caudal filament; *Cxpd*, coxopodite; *1Gon*, first gonapophysis; *2Gon*, second gonapophysis; *Papt*, paraproct; *rvs*, retractor muscles of vesicula; *sa*, supra-anal lobe; *smcls*, stylus muscles; *Stn*, primary sternal plate; *Sty*, stylus; *T*, tergum; *V*, venter; *Vs*, vesicula; *VIII-XI*, abdominal segments.

of the genital segments of Thysanura, but they may be absent on the other segments; they never occur on the tenth segment, which also has no sclerotic plates in its venter (E, *X.V*). The abdominal styli of Thysanura are movable by muscles arising on the coxopodite plates (B, F, G, *smcls*), but the similar processes on the thoracic coxae of *Machilis* lack muscles, as do also the abdominal styli of Orthoptera.

Rudiments of appendages have been shown by Heymons (1897) to be present on each of the first 10 segments of the abdomen in the young embryo of *Lepisma saccharina*. With the dorsal growth of the embryonic walls, however, the appendage rudiments become gradually flattened, until finally they form the lateral parts of the definitive abdominal sterna. The styli of *Lepisma*, Heymons says, are not developed until a long time after hatching, but when they do appear they arise as outgrowths from the parts of the ventral body wall derived from the embryonic appendages.

In the Diplura the styli are small if present (fig. 24 C) and are borne by the sternal plates of the segments; but the stylus-bearing areas (*Cxpd*) of each sternum may be demarked from the true sternal area (*Stn*), and upon them arise the muscles of the styli (D). From this condition it is then only another step to that in which the ventral sclerotization of a segment becomes unified in a definitive sternal plate showing no evidence of its coxosternal origin, except for the possible retention of the styli.

On the genital segments of some species of Thysanura a slender process arises at or on the inner dorsal angle of the base of each coxal plate (fig. 24 F, G, *1Gon*, *2Gon*). These four processes may be termed *gonapophyses* because those of the female, which form an ovipositor in Thysanura, are without doubt homologous with the ovipositor blades so named in other female insects. The gonapophyses of the ninth segment in male Thysanura are closely associated with the penis (G, *2Gon*) and are often termed parameres because they are supposed to correspond with accessory genital structures called parameres in other male insects (see Heymons, 1897). The term "paramere", however, has been given to many different processes of the genital complex in pterygote insects, and it is not certain that any of them is a true gonapophysis. Heymons has shown that the genital processes of *Lepisma* are formed as outgrowths from the inner margins of the coxal plates of the eighth and ninth abdominal segments. "Gonapophyses" may be defined, therefore, as mesal processes of the bases of the gonopods; they would appear to be coxal endites specially developed on the appendages of the genital segments. In the Thysanura each gonapophysis is provided with small muscles arising on the supporting coxal plate (F).

The intromittent organ of male Thysanura consists of a median tubular penis, or phallus, arising from the venter of the ninth abdominal segment between the bases of the coxal plates of this segment (fig. 24, E, G, *Pen*), where it is closely embraced by the second gonapophyses if these processes are present (G). The organ appears

to be merely a tubular evagination of the body wall with the opening of the ejaculatory duct on its extremity. It may be differentiated by a circular fold into a proximal part (phallobase) and a distal part (aedeagus).

According to Heymons (1897) the embryonic gonoducts of *Lepisma saccharina* extend first to the tenth abdominal segment in the male, and to the seventh in the female. In each case the ducts end with ampullar enlargements. With the later reduction of the tenth segment during embryonic development the ampullae of the male are transposed to the ninth segment and become attached to the ectoderm at the posterior margin of this segment. Here an ectodermal ingrowth takes place between the ampullae, in which later is formed an invagination that, uniting with the ampullae, becomes the definitive ductus ejaculatorius. It is thus evident that male Thysanura must have had primarily paired genital openings on the tenth abdominal segment, and that these primitive gonopores secondarily migrated forward and approximated each other at the posterior edge of the venter of the ninth segment. Here they acquired a common outlet by the ingrowth of a median ectodermal tube. The definitive ejaculatory duct, therefore, is a ductus communis, and not the product of a union of the ends of the primary ducts. The common genital duct of the female, Heymons says, is similarly formed by a median ectodermal invagination on the eighth abdominal segment, that is, on the first somite behind the one on which the lateral ducts primarily opened.

EPHEMEROPTERA

The external male genitalia of the mayflies include a pair of movable appendicular clasping organs (fig. 25 A, *Sty*) carried by the ninth abdominal segment, and a pair of small penes (*Pen*) arising behind the sternal plate of this segment. The presence of two penes in the male might be supposed to be correlated functionally with the presence of two oviducal openings in the female, but there is no evidence that coition takes place during copulation, and spermatozoa have not been found in the oviducts of the female (a spermatheca being absent). It seems very probable, therefore, that the eggs are inseminated as they issue from the oviducts, since they are carried by the female until deposited in the water. The eggs are said to be easily fertilized artificially outside the body of the female (Wiebe, 1926). The ovaries and the testes are fully developed in the last larval stage, and it is then that the sex elements are brought to maturity. Prior to mating, the eggs are massed in the greatly distended saclike calyces of the oviducts, and the spermatozoa are stored in the seminal vesicles.

The insects are thus prepared to complete the reproductive function during the brief period of imaginal life. (See Needham, Traver, and Hsu, 1935.)

The genital claspers of male Ephemeroptera are movable appendicular organs structurally comparable with the abdominal appendages of Thysanura, and the same terminology may be used in each case with the understanding that the implied homologies may still be questioned for lack of positive evidence. Each clasper of the male mayfly appears to consist of two principal parts, a distal *stylus* (fig. 25 G, *Sty*), and a proximal *coxopodite* (*Cxpd*). The stylus is movable on the coxopodite by muscles arising in the latter, and hence its identity can be determined by finding the muscles inserted on its base. The identity of the coxopodite, on the other hand, is not so easily established, since, though the stylus muscles arise in the coxopodites, the latter may become united with each other or assume various relations with the supporting sternal plate of the ninth abdominal segment.

If the genital claspers of the mayflies are homologous with the thysanuran abdominal appendages, a generalized structure of the former should be something like that shown in *Blasturus nebulosus* (fig. 25 G), in which the coxopodites are borne on the posterior margin of the ninth abdominal sternum (*IXStn*) and are partially united with each other medially (cf. fig. 24 A). The stylus muscles here arise within the coxopodites, and the coxopodites themselves are movable by muscles (*cxmcl*) arising on the sternal plate. More generally, however, the stylus muscles take their origin from a broad plate continuous across the posterior margin of the sternum (fig. 25 A, H, L, M, *Cxpd*), consisting of a median area (*c*) and often a pair of lateral stylus-bearing lobes (H, *b*). It is suggestive, therefore, that the stylus-bearing plate, or *styliker*, is a product of the united coxopodites. If so, the lateral parts of the *styliker* may become secondarily completely separated from the median part (I, J, *c*), forming a pair of distinct stylus-bearing lobes (*b*) containing the stylus muscles. This last condition, well shown in *Ephoron leukon* (J), might therefore be taken as primitive, and the evidence would then seem to show that the *styliker* has been evolved by the union of a median part of the sternum with the coxopodites (J, I, H, G), and separated from the rest of the sternum as a stylus-bearing plate movable on the latter. The principal weakness of this second view is that it does not account for the original presence of the muscles that move the *styliker* (A, G, *cxmcl*), which according to the first view are assumed to be sterno-coxal muscles. The development of the claspers sheds no light on the morphology of the organs. As shown by Speith (1933) the

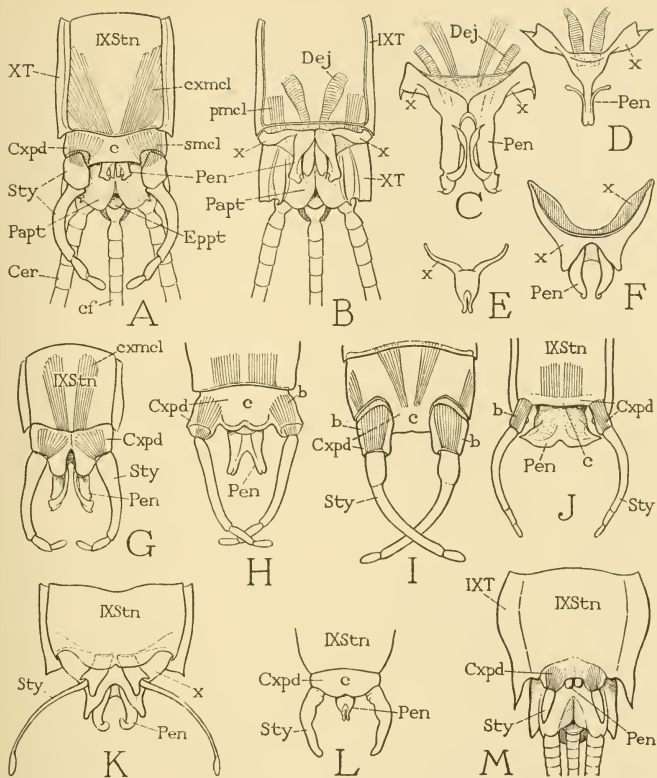


FIG. 25.—Hexapoda-Ephemeroptera: external male genitalia and associated structures.

A, *Ephemera simulans*, posterior part of abdomen, ventral view. B, same, styli and stylus-bearing plate removed, exposing bases of penes and supporting arms. C, *Blasturus nebulosus*, penes, ventral view. D, *Habrophlebiodes bettoni*, penis, ventral view. E, *Trichorythodes fallax*, penis, ventral view. F, *Campsurus decoloratus*, penes and basal plate, dorsal view. G, *Blasturus nebulosus*, ninth abdominal segment with styli and penes, ventral view. H, *Iron humeralis*, end of ninth abdominal sternum with styli and penes, ventral view. I, *Bactis vagans*, ninth abdominal sternum and styli, ventral view. J, *Ephoron leukon*, ninth abdominal sternum with styli and penis, ventral view. K, *Campsurus decoloratus*, ninth abdominal segment with styli and penes, ventral view. L, *Trichorythodes fallax*, ninth sternum with styli and penis, ventral view. M, *Onicigaster distans*, larva, posterior part of abdomen, ventral view.

b, stylus-bearing lobe of styliger (united coxopodites); c, median part of styliger; Cer, cercus; cf, caudal filament; cxmcl, muscles of coxopodite arising on ninth abdominal sternum; Cxpd, coxopodite; Dej, ductus ejaculatorius; Eppt, epiproct; IXStn, ninth abdominal sternum; Papt, paraproct; Pen, penis; pmcl, muscles of basal arms of penis arising on ninth sternum; smcl, muscles of stylus arising in coxopodite; Sty, stylus; x, basal arms or supporting plate of penes; XT, tenth abdominal tergum.

styliger plate is present in the larva (fig. 25 M), where, though it may differ in size and shape from that of the adult, it is already separate from the ninth sternum and gives origin to the stylus muscles.

The styli are slender appendages varying somewhat in relative length and thickness in different species. They are commonly jointed, i. e., subdivided into several parts called "segments", but the joints are often mere constrictions, and the intervening parts are not true segments since they are never muscled. Usually each stylus has three subsegments (fig. 25 G-J, L), but in some cases there are four (A), in others only two (K), and in the genus *Caenis* the styli are undivided. The larval styli may be simple unjointed processes (M, *Sty*), or they may be subdivided, but, according to Speith (1933), the number of parts is always less than that in the adult stylus of the same species. The basal part of the stylus in some cases might be confused with the coxopodite, or vice versa (A, I, J), and it is only by an examination of the musculature that the two parts of the appendage can be certainly identified: the stylus muscles always take their origin in the coxopodite, whether the muscle-containing part of the latter is a free lobe (I, J) or a part of the styliger plate (A, H).

The posterior position of the mayfly claspers on the ninth abdominal segment may be difficult to reconcile with the idea that the styli are serial homologues of the laterally placed gills of the more anterior segments in the larva (see Snodgrass, 1931), and yet the evidence is equally strong (or weak) in each case that the organ in question is a derivative of a segmental appendage. Perhaps the truth is that some of our ideas about insect morphology are not to be taken too seriously, but in their favor it may be said that, where inconsistencies are not too inconsistent, they establish a fundamental concept on which may be based a uniform terminology. The simple form of the genital appendages in certain larval Ephemeroptera (fig. 25 M) connects these organs with the styli of Thysanura and Orthoptera, and there can be little doubt that the ephemerid styli, on the other hand, represent the movable genital claspers of higher insects, though in the latter the organs seldom have a styluslike form. It is tempting to regard the abdominal stylus in any case as the telopodite of a simplified appendage—the only objection to so doing is the presence of a similar coxal stylus on the thoracic legs of *Machilis* in addition to the true telopodite.

The penes of the mayflies vary in shape and relative size in different species (fig. 25 B-H, J, K, *Pen*) and are often provided with accessory processes (C, D). They may be united with each other in varying degrees (D, E, H), but there are always two ejaculatory

ducts with separate orifices. The two penes are supported either on a pair of divergent basal arms (B, C, D, E, *x*), or on a common basal plate (F, K, *x*) with lateral prolongations. The ends of the basal arms are always intercalated between the adjacent lower angles of the tergal plates of the ninth and tenth abdominal segments (B, *x*, *x*), in some forms they are more closely attached to the ninth tergum, in others to the tenth. The supporting structure of the penes is usually concealed above the styli-ger plate, and is implanted on a mem-

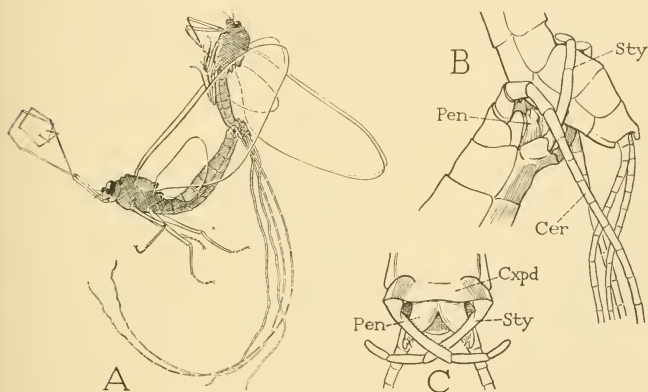


FIG. 26.—Ephemeroptera: copulation and external male genitalia of *Cinygmula mimus*.

A, male and female in copulation (drawn from a slide mount loaned by Dr. J. G. Needham). In life probably the body of the female is more nearly parallel with that of the male, and her thorax held in the loop of the long front tarsi of the male. B, the copulating parts of same, more enlarged, showing the use of the styli as claspers. C, end of male abdomen, ventral view.

Cer, cerci; *Cxp*, coxopodite plate, or styli-ger; *Pen*, penis; *Sty*, stylus.

branous area or fold between the ninth sternum in front and the paraprocts behind (B). There is thus no part of the venter of the male abdomen that can be referred to the tenth segment unless it is the basal plate or arms of the penes and the supporting membrane. Considering the evidence (see page 58) that the primary gonoducts of male insects opened on the tenth abdominal segment, it is consistent to suppose that the primitive paired penes were processes of the sternum or of the appendage bases of this segment. The paired penes of the Ephemeroptera, being evidently primitive organs, should therefore belong to the tenth abdominal segment, and the forward

extension of the paraprocts between the lower edges of the tenth tergum (B, *Papt*) suggests that the sternum of the tenth segment has been correspondingly displaced forward. The penes have the same position in larval mayflies (M, *Pen*) as in the adult, but the accessory structures are only weakly developed in the larva. Concerning the development of the penes in Ephemeroptera, Palmén (1884) says the larval vasa deferentia become attached to the body wall at the posterior border of the ninth segment, and at the points of attachment the penis rudiments grow out carrying with them the ends of the ducts.

The writer is indebted to Dr. Jay R. Traver, of Cornell University, for named specimens amply representing the principal variations in the male organs of Ephemeroptera, on which the preceding descriptions are based.

DERMAPTERA

Among the Dermaptera there appear to be retained the same two primitive features of the reproductive system found in the Ephemeroptera, namely, the location of the female genital opening immediately behind the seventh abdominal sternum, and the independence of the male exit ducts, which may open separately on a pair of penes. The lateral oviducts of female Dermaptera, however, come together in a short median oviductus communis, while in the male the independence of the gonoducts is never as complete as in the Ephemeroptera, and the paired penes are united upon a common basal plate that forms a large flat apodeme for muscle attachments. In many forms, moreover, the intromittent organ is a single penis with either a pair of outlet ducts, or a single complete duct. The external genitalia of Dermaptera have been described by Meinert (1868), Jordan (1909), Heymons (1912), Zacher (1911), Burr (1915, 1916), Crampton (1918), Walker (1922), Snodgrass (1935).

A dermapteran intromittent organ of the double type occurs only in the Labiduroidea. The two penes here present are concealed in a deep genital chamber above the long ninth abdominal sternum. Their bases arise close together (fig. 27 A) from the anterior wall of the genital chamber (*x-x*) where they are united upon a common apodemal plate (*Ap*) extending forward. Each penis (*Pen*) consists of a basal stalk bearing two distal lobes, and is traversed by a ductus ejaculatorius (*Dej*). The median lobe (*a*) is the true terminus of the penis and contains an eversible end-sac (preputial sac, *c*), into which the ejaculatory duct discharges; the lateral lobe (*b*) is an accessory process, or paramere, of the penis. A long slender rod, or virga, usually accompanies each ejaculatory duct, its apical part being pro-

tracted with the eversion of the end-sac. The ductus ejaculatorii, though independent for some distance before entering the penes, are united anteriorly in a ductus conjunctus (*Dejcn*), which takes its origin in a saclike seminal reservoir (*rs*) that receives the two vasa deferentia (*Vd*).

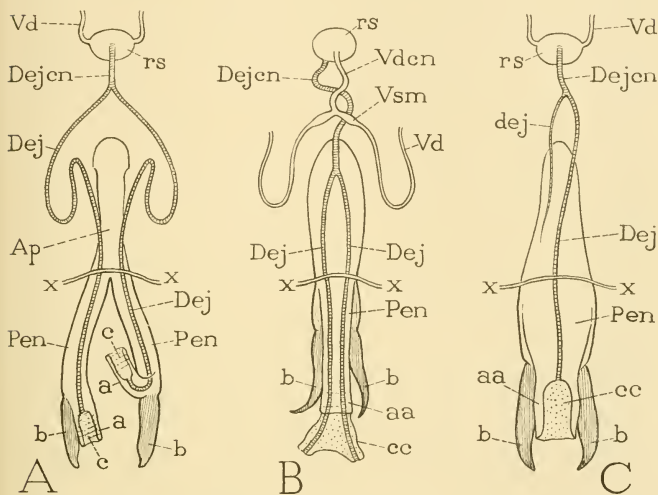


FIG. 27.—Hexapoda—Dermaptera: three types of structure in the male genital exit system and the intromittent organ. (Diagrams based on Meinert, 1864, 1868; Jordan, 1909; Heymons, 1912; Walker, 1922; Snodgrass, 1935.)

A, Labiduroidea, penes separate beyond common basal apodeme. B, *Hemimerus talpoides*, penes united, but both exit ducts retained. C, Forficuloidea, penes united, only one functional duct.

a, median lobe of penis; aa, median lobe of conjoined penes; Ap, basal apodemal plate of penes or penis; b, paramere lobe of penis; c, eversible end-sac of penis; cc, end-sac of conjoined penes; Dej, ductus ejaculatorii; dej, nonfunctional branch of ejaculatory duct; Dejcn, ductus ejaculatorii conjunctus; Pen, penis; rs, seminal reservoir; Vd, vas deferens; Vden, vas deferens conjunctum; Vsm, vesicula seminalis; x-x, anterior wall of genital chamber.

In *Hemimerus* and Forficuloidea the penis is a single structure (fig. 27 B, C), but, since it is armed with two paramere processes (*b, b*) arising at the sides of a median terminal lobe (*aa*) containing an eversible end-sac (*cc*), there can be no doubt that the organ has been produced by the union of two penes having the structure of the paired organs of Labiduroidea (A). Two ductus ejaculatorii traverse the penis of *Hemimerus talpoides* (B, *Dej*), but they fork in

the base of the penis from a ductus conjunctus (*Dejcn*) that proceeds from a seminal reservoir (*rs*), into which the vasa deferentia discharge by a common duct (*Vdcn*) after first enlarging as a pair of seminal vesicles (see Jordan, 1909, Heymons, 1912). The two exit ducts of *Hemimerus* open separately into the end-sac of the penis, which is shown everted in the diagram (B, *cc*). In *Forficula* (C), as described by Meinert (1864) and by Walker (1922), the vasa deferentia discharge separately into the seminal reservoir, and a single outlet duct (*Dejcn*) proceeds posteriorly from the latter but soon divides into two branches; one branch (*dej*), however, is rudimentary and has no distal connection, the other (*Dej*) traverses the penis as the functional duct and opens into the eversible end-sac (*cc*).

The presence of a rudimentary ejaculatory duct in the Forficuloidea leaves little doubt that the structure of the male organs in Labiduroidea (fig. 27 A) represents the more generalized condition in the Dermaptera, and that the imperfectly unified organs of the other groups (B, C) have been derived from completely paired structures. In *Hemimerus* the terminal parts of both exit ducts remain functional in association with a penis conjunctus; in Forficuloidea one duct is functionally suppressed. This manner of transition within the Dermaptera from paired penes with individual exit ducts to a single intromittent organ with one functional duct might be supposed to show the method by which the median penis (phallus) and single exit apparatus of other male insects has been evolved. There is, however, no specific evidence of the production of a median intromittent organ by the union of paired penes in any insects other than Dermaptera and Ephemeroptera, and in these two orders a union of the penes has taken place quite independently. Moreover, the ontogenetic development of the common ductus ejaculatorius of other insects shows that this duct, from its inception, is an independent median ingrowth of the ectoderm, and suggests that it probably originated phylogenetically as an invagination of the body wall at the approximated mouths of the lateral ducts, as it does in the ontogeny of Thysanura.

PLECOPTERA

The Plecoptera in some respects may present a fairly generalized condition of the specialized organization of the wing-flexing group of pterygote insects; but the male reproductive organs are in no way generalized, and they furnish no lead toward the evolution of the genitalia in higher insects. In fact, the structures that form the basis for most of the elaboration in the external genital mechanism of

other insects are either reduced or suppressed in both sexes of the stoneflies. In the female the gonotreme, or vulva, lies above the posterior margin of the eighth abdominal segment (fig. 29 C, *Gtr*), where it opens from a small genital chamber containing the oviducal and spermathecal apertures; but an ovipositor is entirely absent. The two small processes borne by the eighth sternum in females of *Pteronarcys* are clearly not true gonapophyses, since the latter always arise posterior to the sternal plate. In some forms the lateral oviducts appear to discharge separately into the genital chamber (vagina), in others they first unite with a very short oviductus communis (see Klapálek, 1896; Mertens, 1923; Wu, 1923). The genital segments of the male have no appendicular organs that can be referred to segmental limbs, comparable with the styli of apterygote insects, Ephemera, and Orthoptera, or with the movable claspers (harpagones) of other Pterygota. The functional intromittent organ is in most cases a phallic structure, though a median process of the epiproct has been described as a "sperm conveyor", and in the genus *Leuctra* it is possible that a pair of ventral processes of the tenth segment conduct the sperm to the female from the male genital opening situated at their bases. In the families Pteronarcidae and Perlidae the "penis" is principally a large, eversible endophallic sac, accompanied or not by an ectophallus; in the other families, Nemouridae and Capniidae, there may be present a short tubular ectophallus, which contains the opening of the genital exit passage, but the latter has not been shown to be eversible. The occurrence of "paired penes" has been claimed, but not demonstrated. Whatever accessory genital structures are present in the Plecoptera are secondary processes, usually of the tenth and eleventh abdominal segments, but also of the eighth and ninth. Information on the exact function of the phallic organs and accessory genital processes in the order is far from complete.

The internal reproductive organs of the Plecoptera are highly variable in the several families, particularly with respect to the grouping of the testicular tubules, and in the size and character of the median exit duct. The testes have no peritoneal investiture, the sperm tubes being free from one another, as are the egg tubes of the ovaries, and, so far as noted, the gonads have no suspensory ligaments in either sex. Only in the genus *Leuctra* (Nemouridae) have the vasa deferentia been described as being independent of each other (Klapálek, 1896; Mertens, 1923); in such cases the testes consist of groups of slender tubules arising from the anterior ends of the ducts (fig. 28 A, *Tes*). In other forms the vasa deferentia of opposite sides are united; in some cases they have coalesced for a considerable length

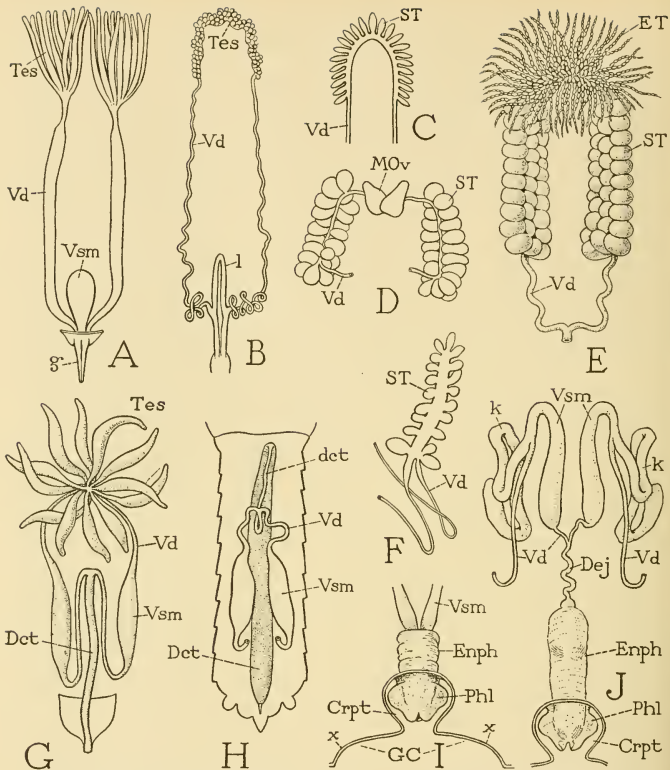


FIG. 28.—Hexapoda—Plecoptera: internal male reproductive organs. (A, B, C, and F from Klapálek, 1896; D from Junker, 1923; E from Schoenemund, 1912; G from Mertens, 1923; H from Wu, 1923.)

A, *Leuctra nigra*, testes in terminal groups at ends of vasa deferentia, median exit duct very short. B, *Perlodes (Dictyoptyeryx) microcephala*, vasa deferentia united anteriorly in arch bearing numerous sperm tubes, connected posteriorly by looped commissure (*l*). C, *Taenioptyeryx trifasciata*, sperm tubes in series on united anterior parts of vasa deferentia. D, *Perla marginata*, male larva 12 mm long, immature testes with "male ovaries" (*MOv*) and saclike sperm tubes (*ST*). E, same, older larva, with numerous egg tubes (*ET*) on anterior arch of vasa deferentia. F, *Capnia nigra*, single testis formed by lengthwise union of parts of vasa deferentia bearing sperm tubes. G, *Protonemoura praecox*, sperm tubes grouped at union of vasa deferentia, the latter discharge directly into long median exit duct. H, *Nemoura vallicularia*, vasa deferentia discharge into slender median exit duct (*dct*), which opens into large terminal exit duct (*Dct*). I, *Acroncuria arida*, median genital exit apparatus as seen in undisturbed dissection. J, same, parts of exit apparatus artificially extended.

Crpt, phallocrypt; *Dct*, large median exit duct; *dct*, small median exit duct; *Dej*, ductus ejaculatorius; *Enph*, endophallus; *ET*, egg tube; *g*, genital process of tenth sternum (see fig. 29, M); *GC*, genital chamber; *k*, diverticula of vasa deferentia; *l*, commissure between vasa deferentia; *MOv*, "male ovaries"; *ST*, sperm tube; *Tes*, testis; *Vd*, vas deferens; *Vsm*, vesicula seminalis; *x-x*, inner wall of genital chamber.

of their anterior parts (F), in others they are continuous end to end in an arch over the alimentary canal (B, C, D, E, G). The sperm tubes of the united ducts are either distributed along the lateral or anterior parts of the ducts (B, C, D, E), or they are clustered at the point of union (G). The various types of male organs found in the order are described and illustrated by Klapálek (1896) and Mertens (1923), and a more detailed account of their structure is given by Schoenemund (1912) for species of *Perla*, and by Wu (1923) for *Nemoura vallicularia*. In the male of *Perla marginata*, in which the united vasa deferentia form a large loop from one side to the other, the gonadial tubes of the anterior part of the arch, as shown by Schoenemund (fig. 28 E), during a late larval stage take on the form of small ovarioles (ET) and contain egglike cells, while those of the lateral parts form large oval testicular sacs (ST) in which the spermatozoa are developed. Each male ovariole, according to Schoenemund (1912) and Junker (1923), has the structure of a typical panoistic egg tube with a series of 12 to 18 oocytes enclosed individually in cellular follicles. At an earlier larval stage, Junker observed, the egg tubes are enclosed in a pair of ovarial sacs, or "male ovaries" (D, MOv), situated on the median part of the arch of the duct, but he says a few oocytes are to be found also in the saclike sperm tubes (ST). The "male eggs" of *Perla marginata*, however, were found by Junker to possess the diploid chromosomes of the spermatid cells; they never complete normal maturation, and the tubules containing them degenerate at the transformation to the adult.

The vasa deferentia are generally enlarged toward their posterior ends to form storage vesicles for the spermatozoa (fig. 28 A, G, H, J, Vsm). In some forms a tubular diverticulum (J, k) is given off from each duct. Klapálek describes a condition in species of several genera in which the two ducts are connected by a transverse vessel (B, l) looped forward between them, which he regards as a vesicula seminalis. In *Leuctra*, according to Klapálek and Mertens, a sperm vesicle in the form of a median pouch arises at the junction of the vasa deferentia with the ejaculatory duct (A, Vsm).

The median genital exit system of male Plecoptera varies considerably among different genera in the relative development of its parts, and the identities of the latter are difficult to follow in published descriptions of the genital organs. In a freshly dissected specimen of *Acroncuria* (fig. 28 I) the two tubular vesiculae seminales (Vsm) appear to discharge directly into a large sac (Enph) opening through the ectophallus (Phl); but if the parts are pulled out lengthwise (J) it is seen that there are short terminal sections of the vasa

deferentia beyond the vesiculae, which unite in a slender ductus ejaculatorius (*Dej*), and that the latter opens into the anterior end of the phallic sac (*Enph*). There can be no question in this species that the terminal sac of the exit system is an endophallic invagination from the mouth of the external penis, or ectophallus (*Phl*). The endophallus is everted during copulation (fig. 29 E, *Pen*), and in the protracted condition it forms the principal part of the intromittent organ. The everted "penis" of *Acroneuria pacifica* is figured by Needham and Claassen (1925), that of *Acroneuria evoluta* by Clark (1934). Other species shown to have an eversible phallic organ include *Pteronarcys nobilis* (Frison, 1935), *Perla hastata*, *Perlodes signatus*, and *Isoperla fusca* (Needham and Claassen, 1925). The wide exit tube of *Chloroperla grammatica* and of *Isopteryx tripunctata* described by Klapálek (1896) as the "ductus ejaculatorius" is very evidently an eversible structure. An eversible endophallus, therefore, is probably a characteristic feature of the families Pteronarcidae and Perlidae.

The walls of the endophallus are mostly membranous, but they may contain sclerotic areas or plates, and in some forms they are produced into folds or are armed with a pair of long rods or hooklike processes, all such structures taking an external position with the eversion of the sac. The exposed rods or hooks are called "titillators" by most writers, but a rodlike internal armature of the endophallus is generally termed a *virga* (fig. 22 B, *Vrg*), and the name *titillator* given to terminal processes of the ectophallus (*Ttl*).

The endophallus may be a direct invagination from the anterior wall of the genital chamber, as shown by Klapálek in *Chloroperla (Isopteryx) tripunctata*, in which the long tube, designated "ductus ejaculatorius" by Klapálek, opens simply by a wide mouth, from which project the tips of the endophallic rods, or virgae. In other Perlidae, however, an ectophallus may be present as a distinct "penis" projecting into the genital chamber and containing the mouth of the endophallus. An organ of this type is well shown by Walker (1922) in *Perla tristis* as a large globular structure concealed in the genital chamber above the ninth abdominal sternum. In *Acroneuria arida* (fig. 28 I, J) the ectophallus (*Phl*) is a thick, conical lobe somewhat constricted at its base, with an apical opening that leads into the wide endophallic sac (*Enph*). The phallus of this species, however, is not seen directly on opening the shallow genital chamber; it is concealed in a deep pocket (phallocrypt, *Crpt*) of the genital chamber wall, the aperture of which appears at the bottom of the external cavity. The

fully everted "penis" in this case includes the endophallus, the ectophallus, the phallocrypt, and probably also the shallow genital chamber.

In the families Nemouridae and Capniidae there appears to be no evidence that the functional intromittent organ is an everted structure. The median exit duct is in some cases short and in others long, and, in species studied, it terminates in an ectophallus, which, however, may be very small. The terminal exit duct of *Nemoura vallicularia*, as shown by Wu (1923), is a long median tube extending forward almost to the base of the abdomen (fig. 28 H, *Dct*); it is enclosed in a thick sheath of strong muscular fibers, and ends in a short, tapering sclerotic penis. Opening into the anterior end of this tube, however, is a much slenderer median duct (*dct*) that receives the two vasa deferentia, as in *Acroneuria* (J, *Dej*). We might suspect, therefore, that the large duct of *Nemoura* is a noneversible endophallus, and that the slender duct is the true ductus ejaculatorius. The internal genital structures of *Protonemoura praecox*, as described by Mertens (1923), are the same as those of *Nemoura vallicularia* except that here the vasa deferentia discharge directly into the large median tube, which latter Mertens says has extraordinarily strong muscular walls and evidently serves to expel the spermatic fluid. A similar, strongly muscular exit passage is present in *Taeniopteryx maura* and opens through a wide, bluntly conical ectophallus. The latter is protracted in one specimen observed, but there is no accompanying eversion of the duct. Wu (1923) describes the development of the exit duct in *Nemoura* from an invagination of the body wall between the ninth and tenth abdominal sterna, beginning with the ninth instar and increasing in length during subsequent instars. In the earlier stages the vasa deferentia open directly into the median tube, which thus appears in its inception to be the ductus ejaculatorius. A "diphallic" condition is said by Crampton (1918) to occur in *Nemoura completa*, but since the structures designated "penes" are not demonstrated to be such by dissection, we may suspect that they are merely phallic lobes, and that a single genital orifice will be found between them.

In the genus *Leuctra* the phallic apparatus is much reduced, and it appears that the intromittent function may be performed by a pair of processes arising from the sternum of the tenth abdominal segment. These structures are described by Klapálek in *L. nigra* and *cylindrica*, and by Mertens in *L. prima* and *hippopus* as a pair of sclerotic processes (Chitingräten, Titillatoren) arising at the sides of the genital orifice, and embraced by two prolongations of the plates of the tenth sternum. Each median process, according to these authors, is

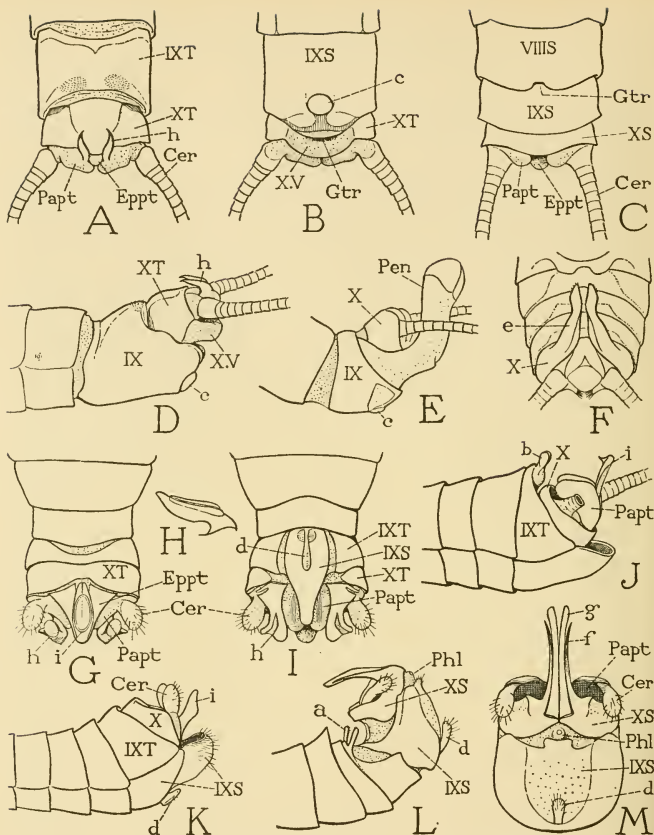


FIG. 29.—Hexapoda—Plecoptera: external genitalia.

A, *Acroneuria arida*, male, end of abdomen, dorsal view. B, same, ventral view. C, *Acroneuria arida*, female, end of abdomen, ventral view. D, *Acroneuria arida*, male, end of abdomen, lateral view. E, *Acroneuria evoluta*, end of abdomen with protracted penis (from Clark, 1934). F, *Neophasganophora capitata*, end of abdomen, dorsal view (from Frison, 1935). G, *Nemoura bifurcata*, end of abdomen, dorsal view. H, same, supra-anal process, lateral view. I, same, end of abdomen, ventral view. J, *Pteronarcys proteus*, end of abdomen, lateral view. K, *Taeniopteryx maura*, end of abdomen, lateral view. L, *Leuctra sibleyi*, end of abdomen, lateral view. M, same, ninth and tenth abdominal segments, ventral view.

a, tergal process of eighth abdominal segment; b, tergal process of ninth segment; c, percussion disc of ninth sternum; Cer, cercus; d, basal lobe of ninth sternum; e, lateral process of tenth segment; Eppt, epiproct; f, g, lateral and median ventral processes of tenth sternum; Gtr, gonotreme (opening of genital chamber); h, dorsal process of paraproct; i, median process of epiproct; IX, ninth abdominal segment; Papt, paraproct; Pen, penis (protracted phallic organs); Phl, ectophallus; S, sternum; T, tergum; X, tenth abdominal segment; X.V, membranous venter of tenth segment.

grooved on its inner surface, the two apposed processes thus forming a channel through which the spermatic fluid is conveyed from the ejaculatory duct. The four processes are well developed in *Leuctra sibleyi* (fig. 29 M, *f*, *g*), in which collectively they appear as a large arm projecting anteriorly above the end of the abdomen from the up-turned sternum of the tenth segment (L). The longer median processes (M, *g*) are flattened and slightly concave on their apposed faces, and are movably attached at their bases in notches of the tenth sternal plates (XS). The slenderer, tapering lateral processes (*f*) are direct continuations of the sternal plates, but, owing to a partial membranization of the latter, they can be turned outward by sternal muscles inserted laterad of their bases. The genital opening of *L. sibleyi* appears to be on a small phallic papilla (L, M, *Phl*) in the membranous area between the ninth and tenth abdominal sterna at a point where the discharged sperm might enter the channel between the sternal processes of the tenth segment. The median exit duct is shown by Klapálek and by Mertens to be very short in species of *Leuctra* (fig. 28 A), with a median stalked "vesicula seminalis" arising from it at the junction with the vasa deferentia.

The external genital armature of male Plecoptera consists of secondary outgrowths or lobes of the posterior abdominal segments. Though some of these structures are movable by a special adaptation of the segmental muscles, it is clear that none of them represents the styli of the apterygote insects and Orthoptera, or the stylus derivatives in the form of independently muscled claspers, or harpagones, of the Ephemera and higher insects, which so commonly are the most important features of the periphallial genitalia. In the evolution of the Plecoptera, therefore, the usual accessory genital structures, including the ovipositor of the female, have been discarded, and in the male there has been developed a profusion of secondary structures.

The principal accessory genital developments of male stoneflies pertain to the tenth and eleventh abdominal segments, but lesser structures occur frequently on the ninth segment, and sometimes on the eighth. Among the species here illustrated, examples of tergal processes on the eighth and ninth segments are seen in *Leuctra sibleyi* (fig. 29 L, *a*) and in *Pteronarcys proteus* (J, *b*). In *Acroneuria* the ninth sternum bears a smooth round or oval elevation near its posterior margin (B, D, E, *c*) known as the percussion disc, or hammer, with which the male is said to make a drumming sound by tapping on the surface beneath him (see Macnamara, 1926). Most of the Nemouridae have a small elongate ventral lobe flexibly attached to the base of the ninth sternum (I, K, L, M, *d*). The posterior margin

of the ninth sternum may form but a rounded lip beneath the genital opening, or gonotreme, above it (B), or it may be produced into a subgenital lobe of varying length (I, K, M), which in some forms is differentiated from the rest of the sternum by a weaker sclerotization (K).

The tenth segment is always a distinct annulus, though it varies in form and size and in the relative development of its sclerotized areas. In some species the tergum of the tenth segment is a large plate covering the back and sides (fig. 29, A, D, G, XT), whereas the venter is unsclerotized (B, D, I) and may appear as a membranous fold behind the gonotreme (B, XV). In others the reverse occurs, a large sternal plate being the principal sclerite of the tenth segment (L, M, XS); or again, both the tergum and the sternum may be confluent in a continuously sclerotized ring (J, K, X). The armature of the tenth segment consists most commonly of lateral lobes or hooklike processes produced upward from the posterior margins (F, e); but in *Luctra*, as already described, the sternum of the segment bears a group of processes arising just behind the genital orifice (M, f, g). By the upward curvature of the end of the abdomen the tenth segment may be inverted (L, XS), and the sternal processes then project dorsally and anteriorly. In some forms a short process arises from the posterior margin of the tenth sternum.

The eleventh segment consists of the usual epiproct and paraprocts (fig. 29 A, *Eppt*, *Papt*), with the cerci (*Cer*) arising at the bases of the latter. The cerci are typically long, slender, multiarticulate appendages, but in the Nemouridae they are reduced, those of the male in most cases consisting of a single "segment" (G, I, K, L, M, *Cer*). The armature of the eleventh segment includes a pair of processes borne by the paraprocts, and a median process of the epiproct, though either or both may be absent. The paraproctial processes arise from the upper surfaces of the paraprocts and project dorsally. They commonly have the form of a pair of hooks (A, D, h), but they may take on more complex shapes (G, I, h). They are said to be used by the male for depressing the subgenital plate of the female. In the mating position the male rests upon the back of the female, and, in the manner of a grasshopper, lowers his abdomen on one side of that of the female and turns the end upward beneath the genital region of the female (see description by Hagen, 1877, figure by Wu, 1923). The everted or protracted phallus projects upward and forward, its end presumably being inserted into the female genital chamber.

The median process of the epiproct is variously developed, often attaining a large size and complex structure (fig. 29 G, J, K, i). It

has been fully described in *Pteronarcys* by Hagen (1877) and by Smith (1917). The organ usually projects dorsally or forward from the end of the epiproct, and may be grooved lengthwise on its posterior surface. It was first described by Hagen as a "penis" in the sense of being an organ for conducting the sperm from the genital aperture of the male to that of the female, a function which Hagen claimed to have proved by observation, and the organ has since been known generally as the "sperm conveyor." In *Nemoura vallicularia*, however, Wu (1923) observes that the supra-anal process serves merely to support the ninth segment of the female during mating, and Needham and Claassen (1925) describe the organ of *Perlodes signatus* as a guide for "the large soft penis that issues from the apex of the ninth segment beneath." Hagen and Smith apparently did not observe the eversible penis in *Pteronarcys*, which has been shown by Frison (1935) to be present and protractile in this genus.

For a more extensive comparative study of the external genital structures of male Plecoptera the student should consult the works of Klapálek (1896), Smith (1917), Crampton (1918), Walker (1922), Needham and Claassen (1925), and Frison (1935).

ORTHOPTERA

As this paper was originally planned, the Orthoptera were to occupy a prominent place in it, because it was supposed that, considering the antiquity of the Orthoptera in hexapod chronology, the structure and development of the external genital organs of the male would give evidence of the nature of the primitive phallic organs of insects in general. More familiarity with the subject, however, now suggests that the complex phallic structures of the various orthopteroid families have been evolved within the order; there is no evidence that in their origin these structures have been developed from paired penes, and in their evolution certainly they have not produced an organ comparable with the phallus of other insects.

The male genitalia of Blattidae consist essentially of three phallic lobes arising from the anterior wall of the genital chamber close to the opening of the ejaculatory duct. Two of these lobes, or phallobes, are right and left with respect to the gonopore, the third is ventral. In young nymphs the phallobes are simple lobes of small size, but with each ecdysis the lateral lobes increase in size and present an altered or more complex structure. In the adults of some forms (*Blatta*, *Periplaneta*) the right and left phallobes (parameres of Walker, 1922) become large organs subdivided into many parts

and provided with an elaborate musculature, while the ventral phallosome takes the shape of a broad lobe with the gonopore on its base. In others (*Blattella*, *Ectobia*) the lateral phallosomes retain a relatively simple form, and become retracted into pouches of the genital chamber laterad of the gonopore, while the ventral lobe forms the mouth of a large endophallic sac receiving the ductus ejaculatorius into its anterior end, and having a long rod, or virga, in its dorsal wall. The exact use of the phallic organs of Blattidae during mating has not been observed, and apparently it is not known in what manner the spermatozoa are transferred to the female seminal receptacle. In *Blatta orientalis* the spermatozoa occur within the receptacle attached externally to long tubular spermatophores.

In Tettigoniidae and Gryllidae a phallic organ is variously developed, including ectophallic and endophallic parts, but there is no close resemblance in any case to the genital structures of Blattidae, and there is little in the ontogeny of the organ to indicate that the adult structures have been evolved from any type of primitive structure common to the Orthoptera. The principal modifications of the phallus in the Tettigoniidae and Gryllidae are adaptations to the formation of spermatophores and the introduction of the latter into the genital chamber or the spermathecal orifice of the female; the phallic mechanism is fairly well understood in most cases. The complex phallic organ of Acrididae is perhaps an extreme development of the tettigoniid type of structure, in which a large endophallic cavity becomes an important part of the phallic apparatus.

The Male Genitalia of Orthoptera will be the subject of a separate paper designed to follow, in which will be discussed the structure and function of the male organs in orthopteroid families other than Acrididae.

REFERENCES

ANDREWS, E. A.

1906. The annulus ventralis. Proc. Boston Soc. Nat. Hist., vol. 32, pp. 427-479, pls. 43-48.

1911. Male organs for sperm-transfer in the cray-fish, *Cambarus affinis*: their structure and use. Journ. Morph., vol. 22, pp. 239-291, 31 text figs., 4 pls.

ATTEMS, C. G.

1894. Die Copulationsfüsse der Polydesmiden. Sitzungsber. Kaiserl. Akad. Wiss., Math.-Natur. Cl., vol. 103, Abt. 1, pp. 39-54, 4 pls.

1926. Diplopoda. Kükenthal and Krumbach's Handbuch der Zoologie, vol. 4, 1st half, pp. 29-238, figs. 29-273.

BENHAM, W. B. S.

1883. On the testis of *Limulus*. Trans. Linn. Soc. London, 2d ser., Zool., vol. 2, pp. 363-366, pl. 38.

BERLESE, A.

1910. Monografia dei Myrientomata. Redia, vol. 6, pp. 1-182, pls. 1-17.

BÖRNER, C.

1902. Arachnologische Studien. II, III. Zool. Anz., vol. 25, pp. 433-466, 14 figs.
1904. Beiträge zur Morphologie der Arthropoden. I. Beitrag zur Kenntnis der Pedipalpen. Zoologica. Orig.-Abh. Gesamtg. Zool., vol. 42, 174 pp., 114 text figs., 7 pls.

BOUVIER, E. L.

1902. Sur l'organisation, le développement et les affinités du Peripatopsis Blainvillei Gay-Gervais. Zool. Jahrb., Suppl. 5 (Fauna Chilensis, 2), pp. 675-730, pls. 20-22.
1905, 1907. Monographie des Onychophores. Ann. Sci. Nat., Zool., sér. 9, vol. 2, pp. 1-383, pls. 1-13; vol. 5, pp. 61-318, 191 figs.

BRÖLEMANN, H. W., and LICHTENSTEIN, J. L.

1919. Les vulves des Diplopodes. Archives Zool. Exp. Gén., vol. 58, pp. 173-218, 31 figs.

BURR, M.

- 1915, 1916. On the male genital armature of Dermaptera. Journ. Roy. Micr. Soc., London, 1915, pp. 413-447, 521-546, pls. 5-9; 1916, pp. 1-18, pls. 1-4.

CHAMBERLIN, J. C.

1931. The arachnid order Chelonethida. Stanford Univ. Publ., Biol. Sci., vol. 7, no. 1, 284 pp., 71 figs.

CHURCHILL, E. P.

1921. Life history of the blue crab. Bull. U. S. Bur. Fisheries, no. 36 (1917-1918), pp. 91-128, pls. 47-55.

CLARK, R. L.

1934. The external morphology of *Acroneuria evoluta* Klapálek (Perlidae, Plecoptera). Ohio Journ. Sci., vol. 34, pp. 121-125, 4 pls.

CLARKE, J. M., and RUEDEMANN, R.

1912. The Eurypterida of New York. New York State Mus. 65th Ann. Rep., Mem. 14, vol. 1, text, 439 pp.; vol. 2, pls.

CRAMPTON, G. C.

1918. A phylogenetic study of the terminal abdominal structures and genitalia of male Apterygota, ephemerids, Odonata, Plecoptera, Neuroptera, Orthoptera, and their allies. Bull. Brooklyn Ent. Soc., vol. 13, pp. 49-68, pls. 2-7.
1920. Remarks on the basic plan of the terminal abdominal structures of the males of winged insects. Canadian Ent., vol. 52, pp. 178-183, pl. 6.

DE WINTER, L.

1913. Études sur l'ovogenèse chez les Podures. Archives Biol., vol. 28, pp. 197-227, pls. 7-10.

EVANS, R.

1902. On the Malayan species of Onychophora. Part II.—The development of *Eoperipatus weldoni*. Quart. Journ. Micr. Sci., vol. 45, pp. 41-88, pls. 5-9.

FALKENHAN, H.-H.

1932. Biologische Beobachtungen an *Sminthurides aquaticus* (Collembola).
Zeitschr. wiss. Zool., vol. 141, pp. 525-580, 18 figs.

FERNALD, H. T.

1890. The relationships of arthropods. Studies from Biol. Lab., Johns Hopkins Univ., vol. 4, pp. 431-513, pls. 43-50.

FRISON, T. H.

1935. The stoneflies, or Plecoptera, of Illinois. Illinois Nat. Hist. Surv. Bull. 20, no. 4, pp. 281-471, 344 figs.

GOODRICH, E. S.

1895. On the coelom, genital ducts, and nephridia. Quart. Journ. Micr. Sci., vol. 37, pp. 477-510, pls. 44, 45.

- 1897-1900. On the nephridia of the Polychaeta. Parts 1-111. Quart. Journ. Micr. Sci., vol. 40, pp. 185-195, pls. 6-9; vol. 41, pp. 439-457, pls. 32-35; vol. 43, pp. 699-748, pls. 37-42.

HAGEN, H.

1877. Beiträge zur Kenntnis von *Pteronarcys*. Entom. Zeitung Stettin, vol. 38, pp. 477-489.

HANSEN, H. J., and SÖRENSEN, W.

1904. On two orders of Arachnida: Opiliones and Ricinulei. 182 pp., 9 pls. Published by Roy. Soc. London. Cambridge.

HAY, W. P.

1905. The life history of the blue crab (*Callinectes sapidus*). Rep. U. S. Bur. Fisheries for 1904, pp. 397-413, 4 pls.

HENKING, H.

1888. Biologische Beobachtungen an Phalangiden. Zool. Jahrb. (Abt. Syst.), vol. 3, pp. 319-335, 1 fig.

HEYMONS, R.

1892. Die Entwicklung der weiblichen Geschlechtsorgane von *Phyllodromia* (*Blatta*) *germanica* L. Zeitschr. wiss. Zool., vol. 53, pp. 434-536, pls. 18-20.

1895. Die Embryonalentwicklung von Dermapteren und Orthopteren, 136 pp., 12 pls. Jena.

1897. Entwicklungsgeschichtliche Untersuchungen an *Lepisma saccharina* L. Zeitschr. wiss. Zool., vol. 62, pp. 583-631, pls. 29, 30.

1901. Die Entwicklungsgeschichte der Scolopender. Zoologica. Orig.-Abhandl. Gesamtmg. Zool., vol. 33, 244 pp., 42 text figs., 8 pls.

1912. Über den Genitalapparat und die Entwicklung von *Hemimerus talpoides* Walk. Zool. Jahrb., Suppl. vol. 15 (2), pp. 141-184, pls. 7-11.

IMMS, A. D.

1906. Anurida. Liverpool Marine Biol. Committee, Memoirs, vol. 13, 99 pp., 7 pls.

IWANOFF, C. P.

1928. Die Entwicklung der Larvalsegmente bei den Anneliden. Zeitschr. Morph. Ökol. Tiere, vol. 10, pp. 62-161, 40 text figs., pls. 1-7.

JORDAN, K.

1909. Notes on the anatomy of *Hemimerus talpoides*. Novitates Zool., vol. 16, pp. 327-330, pl. 18.

JUNKER, H.

1923. Cytologische Untersuchungen an den Geschlechtsorganen der halb-zwitterigen Steinfliege *Perla marginata* (Panzer). Arch. Zellf., vol. 17, pp. 185-359, pls. 9-12.

KENNEL, J.

- 1884, 1888. Entwicklungsgeschichte von *Peripatus Edwardsii* Blanch. und *Peripatus torquatus* n. sp. Arbeiten Zool.-Zootom. Inst. Würzburg, vol. 7, pp. 95-229, pls. 5-11; vol. 8, pp. 1-93, pls. 1-6.

KEW, H. W.

1912. On the pairing of Pseudoscorpiones. Proc. Zool. Soc. London, 1912, pp. 376-390, 4 figs.

KLAPÁLEK, F.

1896. Über die Geschlechtsteile der Plecopteren, mit besonderer Rücksicht auf die Morphologie der Genitalanhänge. Sitzungsber. Kaiserl. Akad. Wiss. Wien., Math.-Natur., vol. 105, Abt. 1, pp. 683-738, 5 pls.

LÉCAILLON, A.

1901. Recherches sur l'ovaire des Collembes. Archives d'Anat. Micr., vol. 4, pp. 471-610, pls. 13-16.
1902. Sur le testicule d'*Anurida maritima* Laboulb. Bull. Soc. Entom. France, 1902, pp. 64-67, 1 fig.
- 1902a. Sur le testicule d'*Anurophorus laricis* Nic. Bull. Soc. Philomath. Paris, vol. 4, pp. 46-52, 2 figs.
- 1902b. Sur la disposition, la structure et le fonctionnement de l'appareil reproducteur mâle des Collembes. Bull. Soc. Philomath. Paris, vol. 4, pp. 99-103.

LIE-PETERSEN, O. J.

1899. Biologisches über norwegische Collembolen. Bergens Mus. Aarbog, 1899, no. 7, 12 pp.

MACNAMARA, C.

1926. The "drumming" of stoneflies (Plecoptera). Canadian Ent., vol. 58, pp. 53, 54.

MEINERT, F.

1864. De Danske arter af Forficula. Naturhist. Tidsskr., 3 R, vol. 2, pp. 427-482, pl. 19.
1868. Om dobbelte Saidgange hos Insekter. Fortsatte Bidrag til Forficulernes Anatomi. Naturhist. Tidsskr., 3 R, vol. 5, pp. 278-294, pl. 12.

MERTENS, H.

1923. Biologische und morphologische Untersuchungen an Plekopteren. Arch. Naturg., vol. 89, Abt. A, Heft 2, pp. 1-38, 18 figs.

MEYER, E.

1901. Studien über den Körperbau der Anneliden. V. Mitt. Zool. Sta. Neapel, vol. 14, pp. 247-585, pls. 12-17.

NEEDHAM, J. G., and CLAASSEN, P. W.

1925. A monograph of the Plecoptera or stoneflies of America north of Mexico. 397 pp., 50 pls. Lafayette, Ind.

NEEDHAM, J. G., TRAYER, J. R., and HSU, YIN-CHI.

1935. The biology of mayflies. 759 pp., 40 pls., 168 text figs. Ithaca, N. Y.

- PALMÉN, J. A.
1884. Über paarige Ausführungsgänge der Geschlechtsorgane bei Insekten. 107 pp., 5 pls. Helsingfors.
- PAVLOWSKY, E. N.
1924. On the morphology of the male genital apparatus in scorpions. (Russian with Eng. résumé). Trav. Soc. Nat. Leningrad, Zool. Physiol., vol. 53, pp. 17-86, pls. 1-3.
1924a. Skorpiotomische Mitteilungen. IV. Zur Morphologie der weiblichen Genitalorgane der Skorpione. Zool. Jahrb. (Anat.), vol. 46, pp. 493-508, 6 text figs., pl. 17.
- PETRUNKEVITCH, A.
1922. The circulatory system and segmentation in Arachnida. Journ. Morph., vol. 36, pp. 157-188, pls. 1, 2.
- PFLUGFELDER, O.
1932. Über den Mechanismus der Segmentbildung bei der Embryonalentwicklung und Anamorphose von *Platyrhacus amauros* Attems. Zeitschr. wiss. Zool., vol. 140, pp. 650-723, 40 figs.
- PRELL, H.
1913. Das Chitinskelett von Eosentomon. Zoologica. Orig.-Abh. Gesamtg. Zool., vol. 25, 58 pp., 6 pls.
- RIMSKY-KORSAKOW, M.
1911. Über die systematische Stellung der Protura Silvestri. Zool. Anz., vol. 37, pp. 164-168, 1 fig.
- ROBINSON, MARGARET.
1907. On the segmentation of the head of Diplopoda. Quart. Journ. Micr. Sci., vol. 51, pp. 607-624, pl. 37.
- RÖSSLER, R.
1882. Beiträge zur Anatomie der Phalangiden. Zeitschr. wiss. Zool., vol. 36, pp. 671-702, pls. 41, 42.
- SCHOENEMUND, E.
1912. Zur Biologie und Morphologie einiger Perla-arten. Zool. Jahrb. (Anat.), vol. 34, pp. 1-56, pls. 1-2.
- SEDGWICK, A.
1885. The development of *Peripatus capensis*. Quart. Journ. Micr. Sci., vol. 25, pp. 449-468, pls. 31, 32.
- SEIFERT, B.
1932. Anatomie und Biologie des Diplopoden *Strongylosoma pallipes* Oliv. Zeitschr. Morph. Ökol. Tiere, vol. 25, pp. 362-507, 86 text figs.
- SILVESTRI, F.
1902. Ordo Pauropoda, 85 pp., 56 figs. Acari Myriopoda et Scorpiones hucusque in Italia reperta. Portici.
1903. Classis Diplopoda. Vol. 1, Anatome, 272 pp., 346 text figs., 4 pls. Acari Myriopoda et Scorpiones hucusque in Italia reperta. Portici.
1916. Contribuzione alla conoscenza degli Stemmiuloidea (Dilopoda). Boll. Lab. Zool. Gen. e Agr. R. Scuola Sup. d'Agric. Portici, vol. 10, pp. 287-347, 49 figs.
- SMITH, G.
1909. On the Anaspidacea, living and fossil. Quart. Journ. Micr. Sci., vol. 53, pp. 489-578, 62 text figs., pls. 11, 12.

SMITH, LUCY W.

1917. Studies on North American Plecoptera (Pteronarcinae and Perlodini). Trans. Amer. Ent. Soc., vol. 43, pp. 433-489, pls. 29-34.

SNODGRASS, R. E.

1931. Morphology of the insect abdomen. Part I. General structure of the abdomen and its appendages. Smithsonian Misc. Coll., vol. 85, no. 6, 128 pp., 46 figs.

1935. Principles of insect morphology. New York.

SOKOLOV, I.

1911. Über eine neue Ctenodrilusart und ihre Vermehrung. Zeitschr. wiss. Zool., vol. 97, pp. 547-603, pls. 27-29.

SOLLAUD, E.

1923. Recherches sur l'embryogénie des Crustacés décapodes de la sous-famille des "Palemoninae." Bull. Biol. France et Belgique, Suppl., vol. 5, 234 pp., 5 pls.

SOMMER, A.

1885. Über *Macrotoma plumbea*. Beiträge zur Anatomie der Poduriden. Zeitschr. wiss. Zool., vol. 41, pp. 683-718, pls. 34, 35.

SPEITH, H. T.

1933. The phylogeny of some mayfly genera. Journ. New York Ent. Soc., vol. 41, pp. 55-86, 327-363, pls. 16-29.

STÖRMER, L.

1934. Merostomata from the Downtonian sandstone of Ringerike Norway. Skr. Vid.-Akad. Oslo. I. Mat.-Natur. Cl. 1933, no. 10, 125 pp., 12 pls.

STREBEL, O.

1932. Beiträge zur Biologie, Ökologie und Physiologie einheimischer Collembolen. Zeitschr. Morph. Ökol. Tiere, vol. 25, pp. 31-153, 9 text figs.

TILLYARD, R. J.

1935. Evolution of progoneate and opisthgoneate types in the Myriapod-hexapod group of terrestrial Arthropoda. Amer. Journ. Sci., vol. 30, pp. 438-449.

TUXEN, S. L.

1931. Monographie der Proturen. I. Morphologie. Zeitschr. Morph. Ökol. Tiere, vol. 22, pp. 671-720, 20 figs.

VERHOEFF, K. W.

1903. Über Diplopoden. 3. Zur vergleichenden Morphologie der Juliden-Gonopoden. Arch. Naturg., vol. 69, Bd. 1, pp. 183-196, pls. 8, 9.

VOSGES, E.

1878. Beiträge zur Kenntnis der Iuliden. Zeitschr. wiss. Zool., vol. 31, pp. 127-194, pls. 11-13.

WALKER, E. M.

1922. The terminal structures of orthopteroid insects: a phylogenetic study. Ann. Ent. Soc. Amer., vol. 15, pp. 1-76, pls. 1-11.

WHEELER, W. M.

1889. The embryology of *Blatta germanica* and *Doryphora decimlineata*. Journ. Morph., vol. 3, pp. 291-386, pls. 15-21.

1893. A contribution to insect embryology. Journ. Morph., vol. 8, pp. 1-160, pls. 1-6.

WIEBE, A. H.

1926. The first three larval stages of *Hexagenia bilineata* Say. Ohio Journ. Sci., vol. 26, pp. 267-274, pl. 1.

WIESMANN, R.

1926. Zur Kenntniss der Anatomie und Entwicklungsgeschichte von *Carausius morosus* Br. III. Entwicklung und Organogenese der Cöloblasen, pp. 123-328, 86 figs. Zool.-vergl. anat. Inst. Univ. Zurich.

WILLEM, V.

1900. Recherches sur les Collemboles et les Thysanures. Mém. Cour. et Mém. Sav. Étrang., Acad. Roy. Belgique, vol. 58, 144 pp., 17 pls.

WU, C. F.

1923. Morphology, anatomy and ethology of *Nemoura*. Bull. Lloyd. Libr., no. 23, Ent. Series no. 3, 80 pp., 16 pls.

ZACHER, F.

1911. Studien über das System der Protodermapteren. Zool. Jahrb. Syst., vol. 30, pp. 303-400, 80 figs.