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A CONTRIBUTION TOWARD AN ENCYCLOPEDIA OF INSECT ANATOMY

By
ROBERT E. SNODGRASS
Late Honorary Research Associate
Smithsonian Institution

(Publication 4544)

CITY OF WASHINGTON
PUBLISHED BY THE SMITHSONIAN INSTITUTION
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FOREWORD

At the time of his sudden death, on September 4, 1962, Robert E. Snodgrass was working on a book we might call "An Encyclopedia of Insect Anatomy." His notes and correspondence suggest several possible titles, but this one seems most appropriate for the material. To judge from the list of terms he had compiled for the letters A to D, I would estimate that the work was only somewhere between 10 and 20 percent completed. Most manuscripts would be unsalvageable when in such an early stage, but this one need not be thrown away. An encyclopedia may be considered as a dictionary in which definitions of maximum brevity are replaced by essays on the various terms. In this sense, each of the essays Dr. Snodgrass had written may be considered as complete—the work is incomplete only in the sense that he had progressed only a short way down the list of projected essays. Hence the title chosen for this publication.

In consultation with Mrs. Snodgrass and others it was decided not to attempt completing the work, because who besides Snodgrass could write Snodgrass's Encyclopedia? The essays are published almost word for word from the original manuscript. However, this was preliminary manuscript which did require some editorial emendations. No doubt, if he had lived, he would have done more revision—such was his habit—but I have kept changes to a minimum in order not to alter the author's meaning. Actually he had already done some rewriting, as shown by the fact that there were three versions of "Metamorphosis," two of "Pleuron," etc. In such cases the most extensive version is used here; in some cases additions to it are taken from the less extensive versions. No attempt was made to make the several essays stylistically consistent with one another; thus some begin with derivation of the word and/or a definition; others do not.

I presume that if this material had been completed it would have been assembled with the terms in alphabetical order. But, although Snodgrass had an aphabetical list from A to D, he was not writing simply by going down this list in 1, 2, 3 order. Rather he was writing on series of related topics. Accordingly, in view of the limited amount that had been finished, it seemed preferable to assemble the finished articles into a natural rather than an alphabetical order. Perhaps this decision has one disadvantage. A certain degree of repetitiousness is inherent in a presentation of this sort in contrast to the presentation in a textbook of anatomy or morphology. To remove the repetition would require so many cross references that the utility of the compilation would be seriously curtailed. Some of the repetition has been removed during editing this manuscript, but some of it has been left in for the same reason that the author put it there in the first place. With the subject-type of arrangement, instead of alphabetical, some of the repetitions are brought together in adjacent articles where they become obvious in a way they would not have been were the manuscript complete and alphabetically arranged.

Bibliographic references are limited to those he had written into the text.

It is one of the losses to entomology that this encyclopedia was not completed by the author. But even this group of essays is a contribution. Unfortunately, it is his last contribution to entomology.

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LIST OF SUBJECTS TREATED

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A CONTRIBUTION TOWARD AN ENCYCLOPEDIA OF INSECT ANATOMY

By Robert E. Snodgrass

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Insect, Entomology, Hexapoda: An insect, according to the composition of its Latin name (*in* + *sectum,* cut), is literally an "incut," as it is also by its Greek name, *entomon* (*en* + *tomos,* cut). The study of insects is *entomology* instead of insectology because the latter involves a combination from two languages. When arthropods came to be named according to the number of their legs, as decapods, myriapods, centipedes, etc., the 6-legged insects became hexapods and were classed as the Hexapoda (Gr. *hexa,* six, + *pous, podos,* leg). Hence we call them *insects,* classify them as *Hexapoda,* call their study *entomology,* and call ourselves *entomologists* (= students of incuts).

Anatomical names: The early zoologists who first studied the anatomy of invertebrate animals naturally carried over to what appeared to be functionally corresponding organs of the latter names that were long established in vertebrate anatomy. The anatomical names of insect parts, for example, except for a few applied on a basis of analogy, are almost wholly vertebrate names. It thus came about that the same names are applied to parts and organs in vertebrates and insects that can have no possible analogy. However, our whole anatomical terminology would be thrown into confusion if homology throughout the entire Animal Kingdom were made the basis of nomenclature. When organs are named on a functional basis, the same names are applicable to a worm, an arthropod, or a vertebrate.

A food tract extending through the body, for example, is literally an alimentary canal in any animal in which it occurs. A blood-pumping organ is properly a heart regardless of its structure. An appendage for walking is a leg. A head is a head whether on an insect, a snake, a man, or a snail. An organ of flight is a wing (*pteron* or *ala*) whether on an insect, a bird, a bat, an angel, the devil, or an airplane.

Of course, the early nomenclators made some mistakes in identifying organs of insects from comparison to vertebrates. For example, they called the cellular layer of the body wall below the cuticle the "hypoderm," whereas it really corresponds with the epidermis of the vertebrate. The preoral space between the mouthparts, which are modified legs, they regarded as the mouth cavity of the insect and called the food pocket over the hypopharynx, now known as the *cibarium,* the "pharynx," whereas a true pharynx is postoral and is an anterior part of the alimentary canal. Incidentally, they have left us the incongruous terms of epipharynx and hypopharynx for preoral structures which have no relation to the pharynx.

A notable misnomer in insects is the term "suture" commonly given to the grooves of the exoskeleton that form strengthening internal ridges. The word *suture* can mean only a seam (*sutura*) or line of union between adjoining parts, and undoubtedly it was suggested to the early entomologists by the sutures of the vertebrate skull. The word suture has a specific meaning that could be applied to any line of union, but cannot be made to mean anything else. It is a distortion of its meaning to apply it to a surface groove formed by inflection of the cuticle. Of course, it is only in a figurative sense that anything in anatomy may be called a suture. The only true anatomical sutures are those made by surgeons.

Another misnomer, now thoroughly established, is the application of the term *chorion* to the insect eggshell despite the fact that this shell is secreted by the ovarian follicle, whereas the vertebrate chorion is a cell layer proliferated by the embryo.

It seems better to live with these incongruities than to attempt to rectify all of them. After all, everyone has some concept of the meaning of terms such as mouth, heart, leg, etc., and the only persons likely to be concerned with the differences between, for instance, vertebrate and invertebrate hearts are those who know the differences. They will not be confused by using a term such as heart for several nonhomologous structures of different animal phyla.

Body segmentation: The primary body segments of an adult insect are the annular sections of the integument marked by the lines of attachment of the longitudinal muscles. A body segment literally should be a somite (*soma* + *ite*), but preliminary to body segmentation there are formed corresponding pairs of cavities, the coelomic sacs, in the mesoderm. Some embryologists, as Manton (1949), define the somites as the coelomic sacs and then contend that segmentation begins in the mesoderm. This usage is confusing because the true mechanical segmentation of the body results from muscle attachments to the body wall. The muscles themselves, however, are derived from the walls of the mesodermal coelomic sacs. Since the coelomic sacs are typically connected with the exterior by coelomic ducts, their primary function was probably the collection of waste products to be excreted through these ducts.

The primary segments of the body are established by the attachment of the longitudinal muscles to the cuticle. The lines of muscle attachment, as seen on the abdomen, are marked externally by transverse grooves which form internally submarginal ridges, the *antecostae,* near the anterior edges of the terga and sterna. In a soft-bodied worm or insect larva the musculature, attached at the true segmental lines, brings about a shortening of the body and allows squirming or flexing movements. In an animal with a fully sclerotized integument, however, such movements would be impossible. To give freedom of intersegmental movement, the posterior part of each segment remains membranous. The functional segments thus become the sclerotized annuli, and the connecting membranes are known as the intersegmental membranes. The definitive mechanism is thus a *secondary segmentation.*

Segments (L. *segmentum,* from *secare, sectum,* cut off): The term applies to body segments or *somites* and also to leg segments or *podites.*

The functional body segments are the sclerotized rings of the integument separated by flexible unsclerotized areas and movable on each other by intersegmental muscles.

The true body segments are limited by the lines of attachment of the longitudinal muscles, marked externally by grooves of the cuticle forming anterior submarginal ridges or *antecostae* of the segmental plates on which the muscles are attached. This is the *primary* body segmentation which corresponds with the musculature. The functional segments represent a *secondary* segmentation since the so-called intersegmental membranes are the posterior of the primary segments. This secondary segmentation allows the consecutive segments to be movable on each other because the connecting membranes can be infolded or extended according to the tension of the muscles. Where segments are united, as in the thorax, the membranes are either eliminated or themselves sclerotized as postnotal plates.

The leg segments are movable by muscles arising in the proximal segment, but the segmentation becomes confusing because the segments are often divided into non-musculated subsegments. A true leg segment is thus best defined as a section of the limb provided with muscles (see Legs). In the same way the apical segment, the flagellum, of an antenna is commonly divided into subsegments (see Antennae).

Segment areas and sclerotization: In an adult insect the cuticle of each segment is usually sclerotized in a definite pattern of plates, but the pattern may differ on different segments or on the same segment in different insects. There often results, therefore, some nomenclatorial confusion on the identification of the plates.

In an unsclerotized wormlike animal, such as *Peripatus,* having a series of legs along each side of the under surface, the only differentiation of the body wall is its division by the legs into a *dorsum* above the legs and a *venter* between them. If the segmental body wall, as in some crustaceans, is completely sclerotized, the dorsal plate is a *tergum* or *notum,* the ventral plate a *sternum.* In some of the diplopods and crustaceans and in the prothorax of some insects the upper part of the tergal arch is produced on each side into a *paranotal lobe.* The sclerotized lateral parts of the segment are then called the *pleura* (sing. *pleuron*), and the name tergum or notum is restricted to the dorsal sclerotization above the lobes. In the winged insects the paranotal lobes of the mesothorax and the metathorax are extended as the wings. The pleura of these segments have to serve as supports for the wings as well as supports of the legs and are modified accordingly. Each is strengthened by a strong internal ridge formed by an external groove or sulcus from the leg base up to the wing base. The groove differentiates the pleuron into an anterior area called the *episternum* and a posterior area called the *epimeron.* At the wing base various small sclerites are formed which control the movements of the wings. Other modifications of the pleura are often present (see Pleuron), and the pleural area in wingless insects may be largely unsclerotized. The prevalent theory that a large part of the thoracic pleuron has been derived from a primitive "subcoxal segment" of the leg seems quite unnecessary from a comparative study.

In the same way as the pleuron, the tergum and the sternum are usually differentiated into areas or distinct parts for mechanical reasons.

On the abdominal segments, the terga and sterna are connected by membranes that may be regarded as pleural. But the small sclerites sometimes found in the pleural membrane of the abdomen appear to be detached parts of tergites or sternites and hence to be laterotergites or laterosternites rather than true pleurites (see Abdomen).

Segmental plates: Sclerotization of the body wall cuticle is highly variable in different parts of the insect according to the functional requirements. On the abdomen typically the sclerotization forms a back plate or *tergum* and a ventral plate or *sternum* separated on the sides by membranous areas to allow for the movements of respiration. On the thorax the support of the wings above and the legs below necessitates the presence of a strong lateral or pleural sclerotization on each side. The head, though it includes at least four primary body segments, is continuously sclerotized above and on the sides to form a rigid cranium for the support of the antennae and the mouthparts.

Since the skeleton of each section of the insect's body is adapted to the functions of the particular part, it is difficult to deduce what the sclerotization of a primitive segment may have been. The centipedes with their undifferentiated bodies have on each segment a distinct dorsal and a ventral plate with the legs arising from flexible pleural areas between. This condition, however, is simply an adaptation to the centipede's way of locomotion and is not necessarily primitive. On the other hand, in the lower Crustacea, such as *Anaspides*, the back plates are continuous over the dorsum and down on the sides to the leg bases attached on the tergal margins. There are here no differentiated pleural plates. Among the Malacostraca, in the Mysidaceae the carapace covers only a part of the thorax, the segments behind it carry the legs on the lower margins of the terga, but where the carapace cuts through the back, the leg-carrying parts of the terga are cut off and are called pleural plates. The so-called pleural plates are here, therefore, only lateral parts of the tergal plates. Finally, in the diplopods the segments are continuous rings. It is clear, therefore, that there is no primitive basic pattern of segment sclerotization, nothing comparable to the evolution of the bony skeleton of vertebrates, among the arthropods. An original wormlike creature probably had a soft cuticle which has been variously sclerotized according to the needs in each group and according to the functional demands in each segment of the body.

The sclerotized cuticle also becomes variously reinforced by linear inflections that form strengthening ridges on the inner surface. On the external surface these appear as narrow grooves or sulci, long erroneously called "sutures" in entomological terminology. The sulci form characteristic lines on the head; on the thorax the pleuron is braced between the wings and the legs of the wing-bearing segments by a strong ridge-forming sulcus. Elsewhere, all over the body, similar reinforcing grooves may be present. They differentiate the cuticula into areas known as sclerites, and have given the impression that the insect skeleton is composed of plates united along "sutures."

Body regions and plates: In describing the surface regions of the body or those of a body segment, we have in general three areas to distinguish and in each segment three corresponding sclerotizations. To name these we have a choice of both Latin and Greek names for the body surface regions of an animal but no names for the segmental plates on the insects. Hence the available names have been used arbitrarily to fit the needs of insect anatomy without strict regard to the primary meaning of the words.

The entire back of the insect or the back of any segment may be called the *dorsum* (L. for back), and from this we have the term *dorsal.* The back plate of a segment may then be given the name *tergum,* another Latin word for back. In the thorax, however, the Greek name *notum* is preferable in order to combine properly with the Greek prefixes *pro-*, *meso-* and *meta-* which designate the segments.

For the sides of the animal we have no technical term in common use. Since, however, *lateral* refers to direction toward the side, it is to be assumed that the side itself is the Latin *latus.* Lateral sclerotizations of the segments, when not a part of the dorsal or ventral plates, are termed the *pleura* (Gr. *pleuron,* a rib), and the pleural sclerites are properly *pleurites.*

The whole underside of the animal is appropriately the *ventral surface* from the Latin word *venter.* The Latin word, however, meant specifically the belly (also the stomach or the abdominal cavity). A segmental sclerotization of the venter is a *sternum* (Gr. *sternon,* the breast or chest), whence sternutation or sneezing.

The segmental tergal and sternal plates are often called "tergites" and "sternites." The suffix *ite,* however, means "a part of" in anatomy, as in somite or podite. It is therefore incongruous to apply *ite* terms to whole plates, and, worse, it leaves us with no terms for parts of the terga and sterna when the latter are subdivided into true *tergites* and *sternites.* (It should be noted that tergite is properly pronounced in English as tĕr′-jīte.)

Tergum and notum: *Tergum* is Latin for the back of men or animals, but, since we have also the Latin word *dorsum* for the whole back (whence the adjective *dorsal*), it is useful to restrict the term tergum to a major plate of the dorsum. Many entomologists use "tergite" for a segmental back plate, but the suffix *ite* in biology means "a part of," as in somite and podite. Properly, therefore, a *tergite* should be a division of a tergum; if the word tergite is used for the entire segmental plate we are left without a word for the parts of a subdivided tergum.

Notum is the Latinized Greek equivalent of tergum (from Gr. *noton*). It is properly used for the back plates of the thorax in combination with the Greek prefixes *pro-*, *meso-*, and *meta-*.

Pleuron: The term is derived from the Greek *pleuron, pleura,* a rib. The pleura in general may be defined as the lateral sclerotizations of the body segments between the tergal and sternal plates. In insects such sclerotizations are present principally on the thoracic segments and are best developed in connection with the wings.

The insect pleuron seems to have no prototype in the other arthropods. In the primitive crustacean *Anaspides* the back plates of the thoracic segments are continuous over the dorsum and down the sides, and they support the legs on their lower margins. In the Malacostraca the carapace cuts out the back of the dorsal plates, leaving the lateral parts as plates supporting the legs. These plates might be called "pleurites," but they are simply remnants of the primitive terga. The diplopods likewise have no pleural plates separate from the terga. In the chilopods, plates in the pleural region above the coxae appear to be derivatives of the coxae.

Among the insects, the pleural sclerotization of the thoracic segments is never continuous with that of the dorsum. In the Protura and Thysanura, the terga and sterna are separated by wide membranous areas. The pleural sclerotization in each segment consists only of a pair of narrow sclerites concentrically arched over the base of the coxa; these are termed the *anapleurite* and the *catapleurite.* The same type of pleural sclerotization occurs in some larvae of the lower pterygotes and in adult termites. The presence of two supracoxal pleural arches in the thoracic segments may be regarded as a primitive condition in the insects having no relation to anything in the other arthropods.

In the pterygote insects the pleural sclerotization becomes more or less continuous over the sides of the thoracic segments but shows many modifications. Typically it is marked by a conspicuous groove, the *pleural sulcus,* extending upward from the leg base; this forms a strong ridge on the inner surface, on the lower end of which the coxa of the leg is articulated. This sulcus and its ridge differentiate the pleuron into an anterior *episternum* and a posterior *epimeron.* Usually a triangular plate below the episternum, termed the *trochantin,* forms by its lower angle an anterior articular point for the coxa. The episternum itself may be variously subdivided, and often peripheral parts of the pleural area remain membranous. In the wing-bearing segments the pleural sulcus extends up to the wing base, and its ridge forms the fulcral support of the wing. Before the wing fulcrum there is a small plate, the *basalare,* and behind it another, the *subalare,* that give attachment to the direct muscles of the wing. The pattern of the pleural sclerotization differs on the two alate segments according to the relative development of the wings and to the presence or absence of one of the pairs of wings.

It is clear that the thoracic pleura of the pterygote insects are adaptive developments, first for the support of the legs and then for the support of the wings as the latter were evolved from paranotal lobes. It has long been a popular theory that the pleura represent primitive subcoxal segments of the legs that have been incorporated into the thoracic wall. Yet a subcoxal segment is not present in any of the other arthropod groups; the coxa is always the functional base of the limb on which the principal motor muscles of the leg are attached. Differences in the leg segmentation among the arthropods are due principally to the presence of one or two segments in the trochanteral region of the leg. Most of the arthropods have a 7-segmented leg; the insect leg is 6-segmented by loss of the second trochanter (the crustacean basipodite).

Sternum: The word is derived from the Greek *sternon,* which means the human chest or breast region. In the Latin languages the name was taken as the basis for words meaning sneezing, as in Latin *sternuto* and *sternutatio,* in Italian *sternutare,* in Spanish *estornudar,* and in Latin-English *sternutation.* In vertebrate anatomy, however, the name sternum was given to the breast bone (*os pectoris* in Latin). In arthropod anatomy it has been extended to any one of the segmental ventral plates of the skeleton. It is thus a curious coincidence that the word sternum as used in entomology is cognate with words signifying sneezing.

External grooves of skeleton: Grooves on the surface of the integument, particularly those of the head and thorax, give the skeleton the appearance of being composed of sclerites united along these lines. The grooves, therefore, have long been called "sutures"

(L. *sutura,* a seam). This was probably first suggested by the sutures in the vertebrate skull, which are formed by the coming together of bones growing out from centers of ossification. The analogy has given rise to the false impression that the insect skeleton with its "sutures" is formed by the union of parts developing from separate centers of sclerotization.

Most of the grooves of the insect skeleton are actually lines of cuticular inflection forming internal ridges to strengthen the body wall in regions of mechanical stress. They are therefore not sutures in any literal sense, and for descriptive purposes are better termed *sulci* (L. *sulcus,* a groove or furrow). The Greek equivalent *aulax* has also been used.

In a few cases grooves of the insect skeleton are lines of secondary union between sclerites. These might figuratively be called sutures.

-Ite: A suffix used in biology to denote "a part of" some larger unit, as in *somite, podite, sclerite,* etc. Very commonly it is appended to *tergum* and *sternum* giving *tergite* and *sternite* for the major plates of the body segments. This usage, however, leaves us with no terms for subdivisions of the plates which properly would be the tergites and sternites.

We encounter also the term *gonocoxite* applied to what is evidently the coxa itself. The *ite* is here clearly unnecessary. The term *coxopodite,* however, is entirely correct since it means the coxal part of a leg.

Larva: The word is derived from Latin and means a spectre, a ghost, a hobgoblin, or a mask. If we take the last meaning, a mask, a young insect is best defined as a larva if it differs so much in appearance from its parents that it must be reared to determine its identity. When a young insect resembles its parents except for the full development of wings and reproductive capacity it is called a nymph or, in some aquatic orders, a naiad. [This distinction between and retention of the terms larva and nymph is not shared by many entomologists. Most embryologists and physiologists today do not make any distinction between the two; any immature insect is called a larva.—A. G. R.]

Larvae of different species differ so much in the degree of departure from the adult form that it is evident they have undergone various degrees of evolution diverging from the parental structure. Larvae therefore can in no sense be regarded as representing ancestral adult forms of their species, nor can they be attributed to "early hatching" of the embryo—once a popular theory. We must assume that at some time in the past history of the insects the young, as those of most other animal groups, resembled their parents except for immaturity, as does a modern young grasshopper or a young cockroach. The question then is: Why have the young of some groups departed from the parental form along their own lines of evolution? The question is not so difficult to answer as it might seem, since some larvae are very similar to the adults and others depart in varying degrees until they have lost all resemblance to the adults that produce them.

As long as the young insect can live and feed in the same environment as its parents, as the young grasshoppers and cockroaches do, there is no need of it having a special structure of its own. The adults of many insects, however, have taken advantage of their wings to explore other habitats for new sources of food, and in most cases they have been structurally modified for life on the wing and for feeding on some special kind of food. The flightless young, therefore, could not possibly keep up with their parents. So, to insure the survival of the young, nature has fitted them for a way of living and feeding of their own. The young cicada affords a very simple example of juvenile metamorphosis since it is adapted merely for burrowing in the earth. The young mayfly and stonefly are supplied with gills for an aquatic life. More extreme cases are seen in the young of Lepidoptera, Diptera, and Hymenoptera. Caterpillars are adapted for climbing and feeding on vegetation, whereas the adults fly around and usually suck nectar. The young mosquito would starve if it had to feed on blood as does its mother or on nectar as does its father. Hence it has become strictly adapted to an aquatic life and equipped with a special feeding apparatus of its own. Young muscoid flies could not live the life of their winged parents and have become transformed into maggots fitted for other ways of living. The grubs of many Hymenoptera are fitted for living in cells where they would be completely helpless if not fed by the adult.

In no case can the larva go over directly into the adult. It must at least discard its specialized larval structures, and the more it has departed from the parental form the more it has to discard. In extreme cases the larva is almost completely destroyed at the end of larval life. The modern adult represents the last stage of phylogenetic evolution of its species; the larva is a temporary specialized form of the young insect. In ontogeny the larva develops first, but it must at last give way to development of the adult. (See Pupa.)

Though the process of the destruction of the larval tissues and the resumption of imaginal development has commonly been called the "metamorphosis" of the insect, the true metamorphosis is the change of form the larva has undergone in its independent evolution. (See Metamorphosis.)

Pupa: The term is taken over from the Latin word for young girl, puppet, baby, or doll. While there is no question as to the applicability of the word, there has been much discussion as to the nature of the pupa. Does it represent the last nymphal instar of an insect without metamorphosis, or is it a preliminary form of the adult? Long arguments have been presented on each side of the question, but it seems that a few pertinent facts will give a sufficient answer.

Naturally, since the pupa is formed inside the larva, when the larval cuticle is shed the pupa has the elongate form of the larva. On the other hand, the pupa has the imaginal compound eyes and the imaginal mouthparts, legs, and wings in a halfway stage of development. Clearly, therefore, the young pupa is a preliminary developmental stage of the imago modeled in the larval cuticle. Within the larval cuticle it undergoes a stage of development and reconstruction until when it finally casts off the larval skin it has the typical form of a pupa. Thereafter it does not change in external shape.

The body of the mature pupa takes on the form of the imago. Thus it serves as a mold for the newly forming adult muscles and allows them to become attached properly on the imaginal cuticle. This alone has been proposed as a theory adequate to explain the pupa as a preliminary adult stage. On the other hand, it has been held that this theory of the pupa involves the unusual occurrence of a moult in the stage of holometabolous insects. But the mayflies moult once after attaining a fully winged condition, and the apterygote insects, as well as most other arthropods, moult successively throughout life. Still the pupal moult may be regarded as a secondary one necessitated by the immaturity of the pupa. Moulting is determined by hormones, and hormones are powerful controlling agents in development. Insect endocrinologists have shown that they can make various adult insects moult again by transplanting into them the appropriate endocrine glands.

The larval skin containing the young pupa has often been called the "prepupal stage of the larva," but with the moulting of the larval cuticle, not yet cast off, the larval life is ended. The young pupa ensheathed in the larval cuticle has been called the "prepupa," but it is simply a young pupa in a formative stage and still cloaked in the larval skin. It is not distinct from the mature pupa which is exposed at ecdysis when the larval skin is shed. The young pupa still enclosed in the larval cuticle has, therefore, been more properly named by Hinton (1958) the *pharate pupa* (from the Greek word for hidden or concealed). The same term would apply to any larval stage still cloaked in the skin of the preceding instar, and to the adult when it is still cloaked in the pupal skin. Among the muscoid flies, the larva completes its growth, changes to the pupa, and finally to the adult, all inside the cuticle of the third larval instar. The cuticle of the third larval instar becomes greatly modified during this time and it is termed the puparium after this modification; from the puparium the fully formed adult emerges.

Metamorphosis: The term is derived from the Greek words *meta,* a change, + *morphe,* form, + *osis,* a process of. Following its derivation the term metamorphosis means literally "a process of changing form," and it should be emphasized that the implied *change is one of form and not of substance.* Thus it is comparable to the change of water to ice, not to the replacement of ice crystals by salt crystals or something else. The term, however, is widely used in zoology for almost any conspicuous change of form that an animal makes during its development regardless of how this is done. The tadpole is said to metamorphose into a frog, but it does so by a continuous changing growth; and if this is metamorphosis then so is the embryonic development of any animal. The term probably originated with the early writers of fiction who were fond of inventing tales about human beings who, at the whim of some offended god or goddess, were transformed into other animals or trees. It is, of course, to be supposed that in such imaginary cases the flesh and bones of the human were directly transformed into those of the animal. The early naturalists took over the word metamorphosis and applied it to the seemingly similar transformations of insects such as that of a caterpillar into a butterfly at a time when it was perhaps not known that the caterpillar was simply a young butterfly. Once established, the word *metamorphosis* became a standard part of our entomological nomenclature well before the true nature of the change from larva to adult was known.

Modern studies on insect "metamorphosis" show that most of the larval tissues disintegrate and that the adult tissues and organs are newly built up in the pupa from cells that never formed an integral part of the larva. The adult cuticle is always a new secretion from the epidermal cells, which themselves may not change, though in some insects the larval epidermis itself is destroyed and replaced by an adult epidermis formed from islands of imaginal cells in the larval epidermis. The alimentary canal goes into dissolution, and the adult food tract is generated from replacement cells in the wall of the larval canal. The larval musculature may be completely destroyed and new muscles for the adult formed in the pupa. Some organs such as the tracheal and nervous systems may be simply remodeled to serve the needs of the adult. How much reuse versus remodeling versus replacement is involved for the cells within the nervous system has not yet been determined, but it is clear that the nervous system is not replaced in toto as some other systems are. Clearly, most of this process of change is not a metamorphosis of larval tissues into adult tissues but a replacement of larval organs by newly formed adult organs. The result is an entire transformation in the *appearance* of the insect between larva and adult. This is because the two stages are really two different animals—one stage is not transformed into the other. The egg simply has the potentiality of forming first the larva and then the adult, as was clearly expressed by Janet long ago (1909).

The term *metamorphosis* has become so firmly established in entomological nomenclature that undoubtedly it will persist even if its erroneous implications become generally recognized. Insects have become famous for their metamorphoses.

If the young insect in the form of a larva does not grow into the adult of its species, it may be of interest to speculate on its nature and how it came to differ from its parents. We must suppose that primitively the young of all insects resembled their parents except in matters of immaturity, as do the young of a modern cockroach or grasshopper. With most of the higher insects, however, the winged adults have become specialized for a life and ways of feeding that the flightless young could not follow. The young left behind were forced to adopt ways of living suitable to themselves and so have undergone a juvenile evolution quite independent of their elders; they have become specialized for their own various habitats and ways of feeding. Thus the larval stages have acquired many diverse forms in the several orders and have become as distinctive of their species as their parents (this is shown by the fact that taxonomists have been able to construct keys to larvae as well as to adults, and in some groups it is easier to identify larvae than the adults). Insect larvae, therefore, are not ancestral forms though many of them have taken on a wormlike shape. Structurally they remain insects. It must be clear that the evolution of young insects into their specialized modern larval forms is the *true metamorphosis* of the insects. When the larva has served its purpose in the life of its species, it is practically destroyed and the developmental process reverts to the adult, which alone can perpetuate the species. The larval destruction and the adult reconstruction take place simultaneously in the pupa which is itself a preliminary stage of the adult.

It is thus clear that the apparent change of the larval insect into the imago is not truly a metamorphosis. The term metamorphosis means literally "a change of form." The change from caterpillar to butterfly, however, is a change of form only in the eye of the beholder. Actually the change is a replacement of the larva by the butterfly. The writer has suggested the term *retromorphosis* for the reversion of morphogenesis to the adult line of development after the dissolution of the specialized larva (Snodgrass, 1961). The development of the adult and the destruction of the special larval tissues go on at the same time in the pupa, but the result is not a transformation of the larva into the adult.

Recapitulation: This term as applied to individual development implies that an animal in its ontogeny goes through stages of development that represent successive adult forms in its phylogenetic history. Garstang (1922) has severely criticized this theory in its general concept, contending that the ontogenetic form in one generation represents the ontogeny of preceding generations. This is particularly true of the larvae of holometabolous insects, which may be wholly adapted in their structure to their own way of living and feeding, and in no way represent adult ancestral forms of their species (see Larva, Metamorphosis).

The development of the insect embryo also is in many ways an adaptation to its life in an eggshell in which it cannot possibly follow the evolution of its free-living ancestors. In minor ways, however, the embryo is not necessarily prohibited from recapitulating the evolution of adult structures. It goes through a polypod stage, for example, when limb rudiments are present on all of the segments. At this stage it evidently represents a centipede-like ancestor. Moreover, the growth and development of all the appendages from simple undifferentiated lobes should repeat a similar origin of the limbs in some remote wormlike progenitor of the arthropods. Likewise, the development of wings from simple outgrowths of the integument, whether they remain on the surface or are temporarily sunken into pouches, would appear to repeat the evolutionary development of wings from paranotal lobes. In other words, ontogenetic recapitulation may take place in organs that are not affected by the living conditions imposed on the embryo or the larva.

Moulting: The physiological process of separating the body cuticle from a new cuticle being formed beneath it by the epidermis. How this separation is accomplished is uncertain but it is soon made more obvious by the secretion from the epidermis of a moulting fluid which digests a greater or lesser amount of the old cuticle while the new cuticle is being secreted. The terms *moulting* and *ecdysis* have often been confused, with, as one result, the naming of the moulting hormone as "ecdyson." Ecdysis, *q.v.*, is literally the coming out of the insect from its moulted cuticle, and is not dependent on any hormone.

The phonetic spelling "molting" which recently has become current in the U. S. A. is not justified by the derivation of the word from the Latin *mutare*. The "*u*" is clearly the essential vowel, and it is retained in other languages, as *mudare* in Italian and *mudar* in Spanish and Portuguese.

Ecdysis: The word is derived from the Greek word meaning "coming out." It is properly pronounced ĕk′-dĭ-sĭs but is commonly heard as ek-dy′-sis. The word has commonly been defined as synonymous with moulting, but the word can mean only the shedding or coming out of the moulted cuticle by the insect. Very commonly the newly moulted insect remains within the old cuticle for a variable length of time before emerging. With some insects, as the honey bee, the pupa goes through its preliminary change from the larval form within the last larval cuticle and comes out only when it has attained the final external form of the pupa. The most extreme case, however, is in the muscoid flies which form a puparium from the third larval cuticle, undergo the pupal stage within this, and then the adult emerges from it.

The insect within the moulted cuticle of the previous instar is the pharate (cloaked) period of the larva, pupa, or adult (Hinton, 1958).

Alimentary canal: The food tract of the mature insect always consists of three parts serially continuous but of different origins. The middle part, the *mesenteron*, represents the primitive endodermal stomach or archenteron of the gastrula; the anterior and posterior parts, the *stomodaeum* and *proctodaeum* respectively, are secondary ingrowths of the ectoderm. The origin and relations of the parts, however, are obscured in the development of the embryo by the various ways in which gastrulation takes place (see Gastrulation).

The two ends of the mesenteron must be interpreted as representing the two ends of the blastopore, though no distinct blastopore is formed in insect development. The anterior end of the mesenteron is, therefore, the primitive mouth, and the posterior end the primitive anus. With the ingrowth of the stomodaeum, however, the primary mouth is carried inward, and the anterior opening of the stomodaeum becomes secondarily the functional mouth of the adult. This mouth of the adult becomes surrounded during development by the outgrowing mouthparts and finally becomes enclosed by them in a space termed the *preoral food cavity* (often called the "mouth cavity" although, being outside the head, it is not truly a body cavity any more than is the space between the thoracic legs).

The stomodaeum has a strong muscular sheath consisting of an outer layer of circular fibers and an inner layer of longitudinal fibers. In the head there are also numerous dilator muscles from the head wall and from the tentorium. The stomodaeum is commonly differentiated into several parts. That just within the mouth may be called the *buccal cavity*, next is the *pharynx*, of different form in different groups, and then the tubular *oesophagus*. The oesophagus is usually enlarged posteriorly as a *crop*, though in some insects the crop is a diverticulum of the oesophagus. Following the crop is a short division, the *proventriculus*, which opens into the mesenteron through a funnel-like infolding of the stomach wall, known as the *stomodaeal valve*. The proventriculus is commonly armed internally with cuticular teeth or other structures that presumably give it the function of a gizzard to grind the food, but in other cases it may possibly serve as a strainer, or merely to regulate the passage of food into the stomach.

The mesenteron is usually a simple cylindrical sac, and it is the functional stomach or *ventriculus* of the insect. In some insects, however, it is divided into several parts (see Mesenteron). From the anterior end of the ventriculus there usually projects a circle of blind pouches, the *gastric caecae*, but tubular caecae may also be borne on other parts of the stomach in some species.

The proctodaeum is divided into two principal regions, an anterior tubular part, which may be termed the *anterior intestine*, and an enlarged posterior part commonly called the *rectum*. The end of the anterior intestine adjoining the stomach is termed the *pylorus* (gate keeper); it gives off the excretory *Malpighian tubules*. The part following the pylorus is often differentiated into an anterior *ileum* and a posterior *colon*. The rectum consists of a large anterior *rectal* *sac* and a posterior narrow part or *rectum* proper. The terminal opening is the functional *anus*.

Gastrula: The Greek word *gaster* really means the paunch or belly, but as used in anatomy the gaster is the stomach. Gastrulation, therefore, should mean stomach-formation regardless of the method of formation.

Borradaile and Potts (Invertebrata, p. 127) state: "Every triploblastic animal passes through a stage—the *gastrula*—in which it consists only of ectoderm and endoderm. Save in this essential feature, the gastrulae of different animals may be extraordinarily unlike, and, especially when the animal is developed from a very yolky egg, they are sometimes very difficult to recognize as such; but where the gastrula is well formed, as in the familiar development of *Amphioxus* or in that of a starfish, its two-layered wall may always be found to contain a cavity, the *archenteron*, which possesses a single opening, the *blastopore*."

The first development of a metazoic egg commonly leads to a hollow mass of cells known as the *blastula*. If the blastula represents a free-living ancestral form it probably obtained its food from the water through its surface cells. If it commonly lived on the bottom it would be natural that the cells of the underside would become specialized for ingestion and digestion of food material. Then it would be a further advantage if this surface should sink into the blastula. Thus the animal would become a two-layered sac, the cavity of which would be the primitive stomach or *archenteron*, the opening of which is the *blastopore*. The outer cell layer becomes the *ectoderm*, the lining of the stomach becomes the *endoderm*.

In a few of the metazoic animals the stomach is formed during embryonic development by introversion of the ventral wall of the blastula. In an elongate animal the blastopore becomes divided into a mouth and an anus. This stage in the ancestors of the arthropods has been thought to be well represented in the onychophoran embryo which presents a median ventral groove that closes between the two ends. However, Manton (1949) finds that this groove is not the elongated blastopore because its formation does not give rise to the endoderm; the endoderm is proliferated internally from a generative area behind the groove. It is this generative area which thus represents the true blastopore. The mouth-anus groove, therefore, is a secondary formation, but evidently it must be formed in some way from the blastopore.

The method of endoderm formation by introversion is commonly replaced by the internal proliferation of cells from the ventral surface of the blastoderm. It is bewildering to read the various conflicting accounts of gastrulation in the insects as reported by different writers and summarized by Johannsen and Butt (1941) and by DuPorte (1960), but much of the confusion results from not recognizing that introversion and proliferation may be just two superficially different ways of forming the endoderm.

Gastrulation: This is the process of formation of the stomach irrespective of the method by which it is accomplished. The word itself is derived from *gastrula,* the dimunitive form of the Greek word *gaster,* which is used in anatomy for the functional stomach of an animal.

The first development of the egg commonly leads to the formation of a hollow mass of cells known as the *blastula.* If the blastula represents a free-living ancestral form of the Metazoa, it probably obtained its food from the water through its surface cells. If it commonly lived on the bottom of a body of water, the cells of the undersurface may be supposed to have become specialized for the ingestion and digestion of food material. It would then be an advantage if these cells should sink into the blastula forming a cavity in which the food could be carried about and more leisurely digested. This food cavity is the primitive stomach or *archenteron,* the opening of which is the blastopore. The outer cell layer of the body is the *ectoderm,* the wall of the stomach is the *endoderm.*

In the embryogeny of a few of the lower Metazoa the stomach is formed by this method of introversion of the digestive cells of the blastoderm. However, when the egg, as in most insects, contains a large amount of yolk which becomes surrounded by the blastoderm, gastrulation by introversion becomes entirely impractical. Aside from the mechanical difficulties of invagination when the center of the blastula is filled with yolk, introversion would place the yolk (food) in the body cavity and outside the stomach. The insect embryo, therefore, cannot recapitulate the primitive method of stomach formation; it must adopt some other method.

The ways by which the endoderm is formed by the insect embryo, as reviewed by Johannsen and Butt (1941) and by DuPorte (1960), are seemingly so various that it becomes bewildering to attempt to interpret them all as derived from introversion or some modification thereof. However, the process of infolding one wall of the blastula may be replaced by the immigration of single cells. Such cells are usually called *yolk cells,* but, since they presumably act as *vitellophags* (yolk eaters), they probably serve for digestion of yolk during early stages of development; they should therefore be considered as endodermal. In some of the lower insects the yolk cells are said to form a stomach wall by investing the yolk. In such cases the yolk cells seem to demonstrate their endodermal nature.

With most of the higher insects a narrow ventral strip of the blastoderm becomes differentiated from the lateral plates, and either sinks into the yolk or is overgrown by the lateral plates. A ventral groove is thus formed along the ventral side of the blastoderm; this ventral groove has been regarded as a remnant of the elongated blastopore closed between the mouth anteriorly and the anus posteriorly. The enclosed ventral plate spreads out and divides into an inner endodermal layer and an outer mesodermal layer.

The early embryo of Onychophora presents a median ventral groove that eventually closes between the two ends which become the mouth and the anus. The onychophoran, therefore, has long been thought to give an example of the primitive blastopore of the arthropods. Manton (1949), however, has shown that this mouth-anus groove of the onychophoran is not the blastopore. The endoderm, she says, is proliferated from an area behind the anus, and cells from this area form the complete stomach epithelium. The mouth-anus groove is thus a secondary formation, though perhaps in some way derived from the blastopore.

Even in the insects it must be noted that the concavity of the ventral plate does not become the stomach lumen. The functional endoderm is proliferated from cell masses at the two ends of the endoderm, and in some cases also from the whole length of it. The growth of the definitive midgut epithelium from cell masses thus resembles the proliferation of endoderm in the Onychophora and of yolk cells in the lower insects. The business of endoderm is to surround the yolk in order to digest it. This is accomplished mostly by the anterior and posterior cell masses which send out ribbons or sheets of cells toward each other around the yolk; these eventually unite and form the stomach which thus comes to contain most or all of the remaining food (yolk) of the developing embryo.

Since in some cases the endoderm appears to be proliferated from the inner ends of the stomodaeum and proctodaeum, some embryologists have contended that the insect stomach is ectodermal. It is noted by Henson (1946), however, that the two ends of the stomach represent the extremities of the blastopore where naturally ectoderm should be generated externally and endoderm internally. It is evident, then, that while ancestral recapitulation plays no part in the formation of the insect's stomach, the embryo has adopted another method of gastrulation, namely cell proliferation, and thus does not violate the germ layer theory.

Mesenteron: As indicated by the origin of the word (Gr. *meso,* middle, + *enteron,* alimentary canal) this is the middle portion of the food tract. It extends from the ectodermal stomodaeum in front to the ectodermal proctodaeum behind, and it becomes the functional stomach of the insect, known as the *ventriculus.* It is probably always of endodermal origin though variously formed in the embyro (see Gastrulation; also Snodgrass, 1935, and DuPorte, 1960).

In form the mesenteron is typically an elongate cylindrical sac, but it may be a slender coiled tube, and in some insects it is differentiated by constrictions into several well-defined sections. The anterior part that surrounds the stomodaeal funnel is called the *cardia.* Blind tubular pouches, known as *gastric caecae* and varying in length and number, project from various parts of the stomach wall. Most commonly, however, they project from the anterior end of the stomach around the entrance of the stomodaeum.

The wall of the mesenteron is a thick epithelium of columnar cells separated from the hemocoel by a distinct basement membrane. Externally, beyond the basement membrane, there is a muscular sheath of longitudinally and circularly arranged fibers, but the arrangement differs from that around the stomodaeum and proctodaeum in that the longitudinal fibers are external to the circular ones. The inner ends of the epithelial cells are somewhat irregular and, as seen in sections, present what is known as a *striated border* due to the presence of alternating dark and clear lines that give a brushlike appearance. All the epithelial cells probably function for both secretion and absorption. Simple secretions are discharged through the striated border, but the cells also go through a disruptive process that has commonly been regarded as a form of holocrine secretion. Globules filled with granular material are extruded into the stomach lumen; these are then constricted and break off, followed by dissolution of their walls and the scattering of their contents. Whether this is a process of secretion discharge or simply a degeneration and dissolution of the cells, or both, it results in such a destruction of cells that they must be continuously replaced. Replacement is effected by groups of *regenerative cells* intercalated between the bases of the epithelial cells; by mitotic division these regenerative cells give rise to new cells that replace the worn out or discarded ones of the epithelium. In some cases the regenerative cells are contained in crypts projecting on the outer surface of the stomach. In some insects the epithelium is completely regenerated at each moult, and the larval epithelium is always replaced by an adult epithelium at the last moult of holometabolous insects, usually forming for the imago an entirely new type of stomach adapted to the special food of the adult.

Usually there is one or more very thin sheets of secreted material separating the food from the surface of the midgut cells. This is the *peritrophic membrane.* In some cases (e.g., Diptera) it is clearly produced by a ring of cells at the anterior end of the mesenteron; in other cases (e.g., honey bee) it is delaminated from the surface of the mesenteron. The peritrophic membrane is composed of chitin and protein, and obviously must be sufficiently permeable to permit the ready passage through it of digestive enzymes and of digested products from the food.

Stomodaeum and proctodaeum: The primary mouth (Gr. *stoma*) of the arthropods represents the enclosed anterior end of the blastopore, but it is carried inward by the tubular ingrowth of the ectoderm known as the stomodaeum. Thereby the primary mouth becomes the opening of the stomodaeum into the stomach, and the functional mouth of the insect is the external opening of the stomodaeum.

Likewise, the primary anus (G. *proktos*) represents the open posterior end of the blastopore, but it is carried inward by an ingrowth of the ectoderm that forms the proctodaeum. Thereby the primary anus becomes the opening from the mesenteron into the proctodaeum, and the functional anus of the insect is the external opening of the proctodaeum.

The words stomodaeum and proctodaeum mean literally "on the way to the mouth" and "on the way to the anus," respectively. And this is just what they are! The *-daeum* part of these words is taken from the Greek *hodaios* meaning "belonging to a way" (from *hodos,* a way or path). By eliding the *ho* and latinizing the rest of the word, *daeum* is obtained.

Head: The insect head is a continuously sclerotized cranium-like capsule. Its simpler or more generalized form and structure are best seen in the head of an insect such as a grasshopper or its relatives. In these the *face* is directed forward and the *mouthparts* hang downward. The *compound eyes* then have a lateral position, and the *antennae* arise from the upper part of the face. The mouthparts (mandibles, maxillae, and labium) are suspended from the lower cranial margins, as the legs are from the thorax. The hypognathous head, therefore, should be primitive since the mouthparts represent appendages serially homologous with the legs. The ventral wall of the head is completely concealed by the mouthparts; it contains the mouth opening into the alimentary canal, and supports below the mouth a large median tonguelike organ known as the *hypopharynx.* The back of the head is perforated by a large opening into the neck; it is analagous to the foramen magnum of the vertebrate skull but is called the *occipital foramen* in insects.

The cranial areas are given specific names. The top of the head is the *vertex;* the facial area between the antennae and compound eyes is the *frons;* below the frons is an area known as the *clypeus,* from which is suspended the broad, free anterior lip called the *labrum;* the sides of the head are the *genae;* and the back is the *occiput.* These head areas are merely topographical regions, though some may be separated by grooves or *sulci* of the cranial wall. Most commonly present is a prominent *frontoclypeal* or *epistomal sulcus* separating the clypeus from the frons and forming a strong internal ridge between the mandibles. Even this sulcus and ridge, however, may be absent, as in the cockroach in which the frontoclypeal region is continuous. In some insects a vertical groove below each compound eye separates the gena from the frons. A groove near the lower edge of the gena may set off a narrow *subgenal* area; internally it forms a ridge that strengthens the genal margin for the support of the mandible and the maxilla. The subgenal sulcus is usually continuous anteriorly with the epistomal sulcus. The occiput may be separated from the vertex and genae by an *occipital sulcus,* but this sulcus is not commonly present.

The head includes at least four primitive body segments united with an anterior protocephalic part bearing the eyes and antennae. The four known head segments are a premandibular segment bearing in some insects a pair of vestigial appendages, a mandibular segment, a maxillary segment, and a second maxillary segment the appendages of which unite to form the labium. None of the head grooves mentioned in the preceding paragraph represent lines of segment union; they are merely cuticular inflections forming internal ridges for the strengthening of the head wall along lines of mechanical stress. On the back of the head, however, there is a groove of a different nature. It closely surrounds the occipital foramen dorsally and laterally, setting off a narrow *postocciput* behind it and forming internally a deep ridge on which are attached muscles from the thorax that move the head. The fact that the basal angles of the labium are suspended from the postocciput indicates that the latter is a sclerotic remnant of the labial segment and that the *postoccipital sulcus* represents the intersegmental line between the first and second maxillary segments. This intersegmental line alone has been retained on the head to provide for muscle attachments from the thorax. Anterior to this line there are no somatic muscles in the head; there are only muscles connected with the appendages and with the proctodaeum. It is not to be concluded, however, that the narrow postoccipital flange of the head represents the entire labial segment; the segment may well include a part of the membranous neck too.

The mouth of the insect, as already mentioned, is in the concealed ventral wall of the head just above the base of the hypopharynx. Before the mouth, however, there is a large *preoral cavity* shut in by the mouthparts. Its anterior wall is the inner surface of the labrum and the clypeal region known as the *epipharynx.* Between the epipharynx and the base of the hypopharynx there is a food pocket, the *cibarium,* just before the mouth; the masticated food is deposited here before being taken into the mouth. The cibarium can be dilated by muscles from the clypeus, and contracted by transverse muscles in its anterior wall. In liquid-feeding insects, the cibarium becomes a sucking pump by the partial union of the edges of its epipharyngeal and hypopharyngeal walls. The duct of the thoracic salivary glands commonly opens into the preoral cavity above the base of the labium, but in some insects it enters the hypopharynx to open on it. In either case the saliva mixes with the food in the preoral cavity so that the food is all ready to be swallowed when taken into the mouth.

The cibarium was long regarded as the "pharynx" of the insect; hence we have the incongruous terms "epipharynx" and "hypopharynx" for parts outside the mouth and having no relation at all to the true *pharynx,* which is a part of the alimentary canal within the head. The misapplied terms are still in current usage because we have no appropriate substitutes for them. "Palatum" and "lingua" have been suggested, but both the palate and the tongue are properly intraoral.

The cranial walls are braced by an internal skeletal structure known as the *tentorium.* It consists essentially of two pairs of apodemal processes. A pair of posterior arms arises from pits at the lower ends of the postoccipital sulcus; these grow transversely and unite into a posterior *tentorial bridge* just within the occipital foramen. A pair of anterior arms arises from the subgenal sulci above the mandibles, or more frequently in the epistomal sulcus; these grow posteriorly and unite with the posterior bridge. Primarily the tentorium therefore comes to have the shape of the Greek letter π, but often the space between the arms is partly filled by a central sclerotization giving the structure a resemblance to a canopy suspended by four stays. It is probable that the structure got its name from the latter situation because *tentorium* is the Latin word for "tent." In some of the apterygote insects the anterior arms are not yet united with the posterior bridge, and there is evidence that these arms were primitively ventral head apodemes. On the other hand, in some of the higher insects modifications take place resulting in either enlargement or reduction of the anterior arms, and in some cases an obliteration of the middle part of the bridge. Such modifications, however, are clearly secondary.

In immature insects the frontal region of the head is commonly marked by an inverted Y-shaped line the stem of which continues back over the vertex to the postoccipital margin. This line has long been called the "epicranial suture," and supposed to be an important structural feature of the head. It is now known, however, to be a preformed line of weakness in the cuticle where the head wall will split at ecdysis (Snodgrass, 1947). The line on the vertex is continuous with the splitting line on the back of the thorax, and the arms diverge downward on the face at various angles from the compound eyes to the clypeus. Only rarely is a remnant of this *ecdysial cleavage line* preserved on the head of an adult insect.

This account of an orthopteroid head will give the student a picture of the fundamental structure of the head in a pterygote insect. Numerous modifications, however, will be found in other orders according to the position the head takes on the neck and its adaptations to different feeding habits on the part of the insects. The orthopteran is said to be *hypognathous* because the mouthparts hang downward from the lower margins of the cranium. In a *prognathous* beetle with forwardly directed mouth parts, the change in position of the head on the neck has involved various alterations in the head structure, particularly in its lower parts. A third type of head is *opisthognathous,* as in the Hemiptera, in which the sucking beak projects backward beneath the thorax and so causes adaptive changes in the head structure. These and other derived types of head structure cannot be fully described here; the student must refer to special papers on the subject or to more general texts for wider information. In the study of any insect head, however, an attempt must always be made to homologize the special features encountered with the fundamental head structure from which the specialized types presumably have been derived. To correlate structural evolution with changes in function is the essence of morphology.

To understand fully the nature of the insect head it would be necessary to know its phylogenetic evolution. This we cannot know, but we can infer something about it from embryonic development. The primary embryonic head in all the arthropod groups is a large lobe at the anterior end of the body on which the eyes and antennae are developed, and which contains the primitive brain ganglia. This *protocephalon* or first head, therefore, is entirely a sensory region. The mouth is formed by ingrowth of the stomodaeum at the base of its under surface. If the protocephalon truly represents the primitive head of arthropods it might well be termed the *archicephalon.* But as the head of the embryo, without any phylogenetic implications, it has been well named the *blastocephalon* by DuPorte (G. *blastos,* a bud or sprout, generally in embryology for the first recognizable beginnings of something, as in blastoderm, blastopore, ectoblast, etc.).

Behind the protocephalon of the early embryo is a region of four body segments in front of the thorax. The first of these segments in some insects bears a pair of minute, transient limb vestiges which correspond to the second antennae of Crustacea, the second is the segment bearing the mandibles, the third is the segment of the first maxillae, and the fourth is that of the second maxillae which unite with each other in insects to form the labium. These four segments are eventually consolidated with the protocephalon to form the definitive head. The ganglia of the first of these segments are drawn forward and unite with the protocephalic brain to become the tritocerebral lobes of the definitive brain. The ganglia of the other three segments combine to become the suboesophageal ganglion of the mature head. These are the visible facts of the embryonic development of the head. Theories on head segmentation are not so simple.

Inasmuch as the embryonic head lobe lies in front of the mouth, bears the antennae and the eyes, and contains the primitive brain, it has been interpreted as representing the *prostomium* of the annelid worms (Holmgren and Hanstrom). This idea gives a very simple concept of the relation of the arthropods to the annelids. More recent embryological studies on the arthropods have, however, revealed the presence of small, paired, temporary cavities in the mesoderm of the antennal region of the head, and another pair in the preantennal region. Some embryologists insist that any pair of coelomic sacs must represent a segment. They contend, therefore, that primitively the embryonic head lobe of insects contained both an antennal segment and a preantennal segment, thereby making six primary segments in the definitive head in addition to a small anterior prostomial region bearing the labrum. [The maximum number of segments in the insect head, based on these coelomic sacs, is nine according to Janet; four of these would be in front of the antennal segment, if the antenna does indeed respresent a segment.] The contention is logical if we accept the premises. Coelomic sacs are spaces in the mesoderm for the accumulation of waste products of metabolism, and most of them have ducts leading to the exterior. The outer walls of the sacs form the longitudinal muscles that determine the segmentation of the ectoderm. Where there is no ectodermal segmentation, as in the embryonic head of modern arthropod embryos may we not question that coelomic sacs are always accompanied by ectodermal segments? Those of the embryonic head may have purely a physiological function (and a transitory one since they are not carried over to later stages of the insect). The reported presence of coelomic sacs in the labrum is particularly difficult to account for since few morphologists regard the labrum as representing a segment. The actuality of an antennal segment and a preantennal segment in the primitive head of insects may, therefore, be doubted, but not outright denied.

A theory of head segmentation promulgated a few years ago caused much confusion by its sensational claim that the tritocerebral lobes of the brain are the ganglia of a "labral segment," because the labral nerves are connected with them (Ferris). This idea was based on observation that the endings of body nerves remain in the segment of their origin even after their central ganglion has been transposed to another segment, and that thus one may identify the segment of the ganglion. This generalization is true for *motor nerves* which arise from the ganglia and grow outwardly to the part which they will innervate. The labral nerves in question, however, are *sensory nerves* arising in the labral epidermis and growing in *to* the tritocerebral ganglia. The origins of sensory nerves do not identify the segment of the ganglion to which the nerves go, and nothing indicates that the labrum is a head segment. We have here an excellent example of how revolutionary ideas can be drawn from logical reasoning based on false premises.

Epicranial suture: See Ecdysial Cleavage Line of Head.

Ecdysial cleavage line of head: This is the familiar inverted Y-shaped line on the front of the head of young insects. The stem of this line on the top of the head is continuous with the ecdysial line on the back of the thorax. The arms of the cleavage line ordinarily diverge downward on the face at various angles, but in some hymenopterous larvae the stem is unbranched and continues straight down the face to the labrum. Though the cleavage line on the head has long been known as the "epicranial suture," and regarded as an important structural feature of the cranium, it is in no sense a "suture." It is merely a preestablished line of weakness where the head cuticle will split at ecdysis. A remnant of the line is rarely retained as a groove on the adult head (Snodgrass, 1947).

Antenna: The antennae are paired segmented appendages of the head of the trilobites and most of the mandibulate arthropods. They are absent only in the Protura, the chelicerates, *Limulus,* the arachnids, and some insect larvae. In the diplopods, chilopods, symphylans, and the entognathous hexapods, the antennae consist of a variable number of divisions each of which is provided with muscles inserted on its base and arising in the proximal division. Such antennae, therefore, are fully segmented, and probably represent the primitive antennal structure. In the Thysanura and the pterygote insects, however, the antenna consists of a basal stalk or *scape,* a small intermediate *pedicel,* and a distal *flagellum* which is usually subdivided into a variable number of *annuli.* The only muscles in an antenna of this type arise on the scape and are inserted on the base of the pedicel. The flagellar annuli have no muscles and vary in number from one to many; evidently the flagellum is a single subdivided segment. The pedicel contains a large sensory organ known as the Organ of Johnson. If the pedicel is a separate segment then it must have lost its muscles. The thysanuran-pterygote antenna consists of not more than three segments.

Each antenna is movable as a whole by muscles arising in the head and inserted on its base. These muscles usually arise on the anterior arms of the tentorium. The whole antenna is set into a membranous socket of the head wall, and is pivoted on a point on the lower rim of this socket. Thereby it is freely movable in all directions.

The antennae serve as delicate organs of touch and are the principal seat of the olfactory sense of insects. In addition, some insects, such as the male mosquito, hear at least the tone of the female's wing vibrations by means of sensory hairs on the antennae.

Whether the antennae are segmental appendages serially homologous with the mouthparts and the thoracic legs is a question bound up with that of the segmentation of the head (*q. v.*). When an antenna is amputated, the flagellum may be regenerated in a form resembling the distal part of a leg, but the significance of this phenomenon is uncertain.

Neck: The neck of the insect is a cylindrical membranous connection between the head and the prothorax. It varies somewhat in length in different insects. There are usually various plates, called *cervical sclerites,* in its walls; a lateral pair of these may form a support for the head by articulating on the postoccipital margin of the latter. The flexible neck allows for movement of the head in various directions by muscles arising in the prothorax and inserting on the postocciput or the postoccipital ridge.

The morphology of the neck is difficult to understand from its musculature. The principal longitudinal muscles are dorsal muscles from the intersegmental phragma between the pronotum and the mesonotum and extending to the postoccipital ridge of the head, and ventral muscles from the prosternal apodemes to the cross bar of the tentorium. The extent of the muscles, therefore, might suggest that the neck is a part of the prothorax. In this case the postoccipital ridge of the head would be the intersegmental line between the labial segment and the prothorax, but this ridge is evidently the line between the maxillary and labial segments. Otherwise we have to assume that the muscles are those of two primary segments, the labial and the prothoracic, that have become continuous with the obliteration of the intersegmental fold between labial and prothoracic segments. The embryo gives no clue to this problem because the labial segment before it is added to the head is followed directly by the prothoracic segment. Unfortunately, the development of the neck musculature has not yet been followed in the embryo. A larva has no appreciable neck.

The number of head-neck muscles is variable in different insects. In the locust head, muscles arise from the pronotum as well as from the following phragma. When lateral neck plates are present they usually support the head on anterior processes, but when neck plates are absent the head may be supported on anterior processes of the prothoracic epineura. When a pair of lateral neck sclerites on each side are angularly articulated end to end, attached muscles, by reducing the angle, serve to protract the head. The variable structure of the neck contrasts with the standardized structure of a thoracic segment, and suggests that the neck mechanism has been secondarily developed in the different insect orders.

Gula: The term is derived from the Latin word for gullet, windpipe, and neck, and in vertebrate anatomy it is used for the upper part of the ventral side of the neck next to the chin. In insect anatomy the gula refers to a ventral plate of the neck behind the base of the labium. It is commonly continuous with the postocciput of the cranium and may become united with the submentum of the labium behind the posterior tentorial pits. Since the anterior part of the neck is probably a membranous posterior part of the labial segment, both the postocciput and the gula appear to belong to the labial segment. The cervical sclerites lie behind the gula. A review of the literature is given by DuPorte (1962).

Thorax: The term is derived from the Greek word *thorax,* a breastplate of ancient Grecian armor; in anatomy it refers to the part of the human body covered by a breastplate. The thorax of insects is the locomotor section of the body between the head and the abdomen. It consists of three segments, the *prothorax, mesothorax,* and *metathorax,* as a result of the reduction of the number of walking legs to three pairs. Once established as the locomotor center, the thorax also became the site of wing development in the winged insects. Wings, however, are present only on the mesothorax and the metathorax, but either one of these pairs may be transformed into nonflight organs.

The thoracic wall of pterygote insects is necessarily well sclerotized and the presence of both legs and wings differentiates the circumference of the segments into tergal, pleural, and sternal. The tergal plates are termed *nota* (Greek) in order to combine properly with the Greek prefixes *pro-, meso-,* and *meta-*. The notum of the prothorax is relatively simple because of the absence of wings on this segment. In the winged segments, however, the notum becomes the essential lever for the wing movement since its lateral margins must vibrate up and down to give the vertical movement of the wings in flight. The notal movements result from an alternating longitudinal upward curvature and flattening of the notum produced by constriction of longitudinal and vertical muscles. In adaptation to its function, the wing-bearing notum must be properly flexible. It is typically divided by a V-shaped ridge-forming groove in the posterior part (the apex of the V is forward) ; this apparently controls the bending of the notum so that the principal lateral movements occur at the bases of the wings. Anteriorly it is commonly marked by a transverse groove, and the resulting three areas of the notum are termed the *prescutum, scutum,* and *scutellum.* Close to the anterior margin is another transverse groove that forms a deep internal ridge, the *prephragma,* for the attachment of the longitudinal dorsal muscles. These muscles, however, are intersegmental, their posterior attachment being on the phragma of the following segment. The two segments, therefore, must be solidly attached, and this is accomplished by a lengthening of the precostal part of the following segment as a *postnotal plate* firmly joined to the scutellar margin of the preceding notum. The contracting muscles thus give a strong upward curvature to the wing-bearing notum which effects the depression of the wings in flight. Flattening of the notum results from the contraction of vertical notosternal muscles, and produces the upward movement of the wings.

In the 4-winged insects, the two winged segments are essentially alike, the postnotal plate of the second being derived from the first abdominal segment, and the third phragma likewise. In the clistogastrous Hymenoptera, the first abdominal segment is so thoroughly incorporated into the thorax during early pupal development that it becomes virtually a part of the thorax in the adult stage. The abdominal pedicel is then formed from the second abdominal segment.

The pleuron of a winged segment is marked by a deep vertical or inclined groove from the leg base to the wing base. This forms a strong internal *pleural ridge* to strengthen the pleural wall in its double duty of supporting both the leg and the wing (see Pleuron). The ridge forms the coxal articular process at its lower end, and the wing fulcrum at its upper end. In the prothorax, the ridge supports the leg but usually does not extend on to the back. The pleural ridge also usually gives off a strong apodemal arm directed inwardly. The pleural sulcus divides the pleural surface into an anterior *episternum* and a posterior *epimeron,* but these parts may themselves be further differentiated into areas by sulci or by desclerotization.

The sternal region of the thorax is generally continuously sclerotized in each segment except for small membranous areas between the major plates. The latter is often differentiated by a transverse groove into an anterior *basisternum* and a posterior *sternellum.* Between the two parts at the ends of the groove arises a pair of sternal apodemes which are commonly united at their bases to form a Y-shaped process known as the *furca.* The arms of the furca turn outward and are closely associated with the inner ends of the *pleural process,* the two being usually connected by short muscle fibers. The pleural plates are then braced against the sternum. The small intersegmental sternites are known as the *spinasterna* because each usually supports a pair of internal processes for muscle attachments. There is, of course, much diversity in the relative size of the sternal parts in different insects, and a large part of the venter in each segment may be membranous. If the sternal sclerotization extends to the base of the leg on each side it forms a ventral articular process for the coxa.

While the above description applies to the thorax of most winged insects, there are structure and function variations in the different orders. In the honey bee, for example, a line of flexion in the mesonotum cuts across the posterior part of the scutum and scutellum between the bases of the wings. In two-winged insects the metathorax is generally much reduced in size but retains the fundamental thoracic structure, showing that the 4-winged condition is primitive for these groups.

Spiracle: The breathing apertures should be called spiracles from the Latin word *spiro,* to breathe, and *spiraculum,* a breathing hole. The term *stigmata* formerly given to them means "spots," and probably reflects the ignorance of the early entomologists regarding their function. A "stigma" was also a brand with which slaves were marked, and hence a blemish. The word should be discontinued as an entomological term.

A spiracle is more than simply a hole into a trachea; it is usually a depression of the cuticle into which the trachea opens, forming thus a spiracular atrium. Most spiracles have a special closing apparatus which may be the outer lips of the atrium but more commonly is a valvelike structure at the opening of the trachea operated by muscles.

Leg: The Latin word for leg is *crus, cruris,* but this word and its Greek equivalent *skelos* have not been adopted into anatomical terminology for the legs of an animal though we have the *crura cerebri* of the brain and *crural nerves* of the legs. On the other hand, the Latin *pes, pedis,* and the Greek *pous, podos,* each strictly meaning the foot, have become the basis of most leg names, as in biped, centipede, milliped, arthropod, diplopod, hexapod, etc.

In insect anatomy the word *leg* is used in a functional sense rather than a morphological one, since it is applied to the thoracic legs and to the abdominal prolegs of larvae though the two sets of organs have no homology. The thoracic legs represent the embryonic leg rudiments which reach their full development as organs of locomotion only on the thorax. The appendages of the head became feeding organs; those of the abdomen are represented by vestiges in the embryo which disappear unless some of the external genital organs are derived from them.

The thoracic legs of the insects are 6-segmented; those of most other arthropods usually have seven segments. The segments, beginning at the leg base, are named *coxa, trochanter, femur, tibia, tarsus,* and *pretarsus.* In a 7-segmented arthropod leg there are two segments in the trochanteral region, the *basipodite* and the *ischiopodite.* A *leg segment* is best defined as a section of the limb independently movable by muscles. The tarsus may be a single segment, but it is commonly divided into as many as five small parts which, though they are frequently called "tarsal segments" are really subsegments or *tarsomeres* since the only muscle of the tarsus are those of its base arising in the tibia. The pretarsus bears the terminal claws of the leg (often called tarsal claws). The pretarsus, however, is clearly an end segment of the leg corresponding with the crustacean dactylopodite. In some insects it is a simple clawlike segment; in others it becomes 3-clawed by the development of a pair of lateral claws, but generally the median claw is lost and the typical insect foot has only the pair of lateral claws.

The pretarsus has only a single ventral muscle of several branches arising in the more proximal segments of the leg; these attach on it by a long tendon traversing the tarsus. In this feature the insects resemble the centipedes (in the Crustacea there are both levators and depressors of the dactylopodite).

The *leg segments* are connected by short membranous areas that allow them movement on each other. These flexible areas are the true joints of the limbs (from the French word *joindre,* to join), and this term should not be used for the segments themselves. Movements of the segments are controlled by *articulations* between them which are sclerotic extensions through the joint membranes from the opposing ends of the segments. The movement of the distal segments at a joint depend on the nature of the articulation, some are dicondylic, others monocondylic.

The so-called *prolegs* of insect larvae are short, unsclerotized, cylindrical outgrowths of the body. They have no structural resemblance to the thoracic legs, and there is no proof that they originate from the abdominal leg vestiges usually present in the embryo. The best-known examples are those of the caterpillar, each of which end in a claw-bearing foot pad. Body muscles are attached on the base of the proleg, but the principal muscle is a long bundle of fibers arising on the lateral wall of the body and attached distally in the foot pad. The prolegs of the caterpillar serve principally for the support of the long and heavy abdomen and for grasping a stem or twig when climbing.

Wings: Of all the animals that fly, the insects alone have wings developed independently as organs of flight. The others have converted a pair of legs into wings. To be sure, the winged creatures of fiction imitate the insects in having wings specially created for flight, but it is doubtful that any of them could really fly if alive.

The insect wings grow out in immature stages of the nonmetabolous orders as small flat lobes from the edges of the back on the mesothorax and metathorax. Some fossil insects have similar lobes on the prothorax, suggesting that the ancestors of the winged insects had three pairs of *paranotal lobes.* Since at this stage they could not have served for flight, it is postulated that at first the lobes enabled the insects to glide through the air a longer distance than they could jump (in the manner of flying squirrels, etc.). If the second and third lobes then became lengthened and flexible at their bases, they might have been able to flap up and down, and thus sustain the insect in the air longer.

From some such early stage of wing development it seems to have required some evolutionary experimenting to produce an efficient mechanism of flight. The dragonflies have the simplest way of moving the wings. Each wing is pivoted on a process of the pleuron and is moved by antagonistic muscles inserted on the wing base at opposite sides of the fulcrum. Yet the dragonflies even today are among the most efficient of flying insects. The cockroaches, mantids, and termites are weak flyers compared with the dragonflies, and it is not well understood just how they move their wings. They have neither the dragonfly mechanism nor the typical thoracic musculature of the higher insects. The wings in these groups are supported on pleural fulcra, and muscles acting on the wing base before and behind the fulcrum probably effect a depression of the wings, while it is possible that the numerous leg muscles attached on the back sufficiently flatten the notum to raise the wings. Though the thoracic musculature of these insects is well known, no real study has been made of its action on the wings.

The typical insect wing mechanism is found in the mayflies and in all the higher orders. It provides for the up-and-down wing movements and for a partial rotation of each wing on its long axis, the latter being necessary for directed flight. Both sets of movements depend on a strong support of the wing on a pleural fulcrum.

The vertical wing movements result from an alternating upward curvature and flattening of the wing-bearing notum, the margins of which thus depress or elevate the attached wings on the fulcral supports. The notal movements are produced by the antagonistic contraction of the dorsal longitudinal muscles and the notosternal vertical muscles of the wing-bearing segments. But this action of the muscles involved some radical alterations in the thoracic structure. The dorsal muscles are intersegmental, and ordinarily serve to pull the two tergal plates together, accompanied by an infolding of the intersegmental membranes. To effect a dorsal curvature of the notum, therefore, the intersegmental membrane has to be replaced by a sclerotization that would solidly unite the consecutive notal plates. The sclerotized membrane forms the so-called *postnotum* of the back. The tension produced by the muscles must now effect an upward curvature of the notum, giving the downstroke of the wings. The upstroke then follows from the depression of the notum by the vertical notosternal muscles attached on it. With the development of the wings the dorsal muscles became enormously increased in size, and to accommodate them the notal ridges of their attachments have been expanded into large plates, the intersegmental *phragmata* of modern insects.

The wing being a flat fold of the body wall, its upper layer is continuous with the supporting notum, and its lower layer is reflected into the pleural wall. The basal region of the wing is largely membranous to allow for flexibility, but to maintain a hinge movement on the notum small sclerites are present in the membrane that articulate with specific wing processes of the notal margin. These sclerites, though on the upper surface of the wing, are known as the *axillaries.* A first axillary sclerite articulates with an anterior wing process of the notum, a third axillary with a posterior notal process. An intermediate second axillary loosely connects the other two and forms ventrally the pivotal point of the wing on the pleural wing fulcrum.

The mechanism that converts the flapping wing into an organ of flight pertains to the pleuron. The under surface of the wing is continued into the pleuron by wide membranous areas before and behind the pleural fulcrum. The wing, therefore, rocks freely on the fulcrum. In the membranes before and behind the latter are small sclerites, the *basalare* and *subalare* respectively, on each of which are attached vertical muscles. Since the sclerites are closely connected with the wing base, contraction of the basalar muscles turns the wing somewhat forward and deflects its margin during the downstroke. With the upstroke, the subalar muscles turn the wing posteriorly and deflect its posterior margin. The wing thus acts as a propeller, and with the downstroke it exerts a backward pressure on the air that drives the insect forward.

This account of the flight mechanism must be understood to give only its fundamentals and the action of the muscles that is the basis of the wing action with most insects. Other factors, however, may complicate the picture, and variations in the thoracic structure in the different insect orders involve modifications in the wing and its mechanism. A notable example is the conversion of the hind wings of Diptera into small knobbed oscillating stalks called *halteres,* so called because they were first regarded as balancers. It has now been shown that they have a gyroscopic action in some way stabilizing the insect's flight. The development of the halteres leaves no doubt that they are the reduced metathoracic wings. Another example is the modification of the forewings of beetles into elytra which seem to be good protective shields but are of no help in flying.

For a fuller discussion of the principles of flight mechanics and aerodynamics than can be given here the student is referred to the book "Insect Flight" by Pringle (1957).

Returning to the anatomy of the wings, the primitive wing lobes have been lengthened and properly shaped during their evolution into organs of flight. Necessarily, the wings must be as thin and light as possible, and at the same time stiff enough to withstand air pressure. This involved the development of lines of rigid, branching thickenings known as the *wing veins.* An old idea is that the veins were formed around tracheae, but this is not supported by recent critical studies (see Whitten, 1962). Another old idea is that the wings were first gills, but this idea has been superseded by the glider theory of wing origin. The venational pattern must have been established early in the evolution of wings since the wing veins seem to conform to a fundamental pattern which permits a generally uniform nomenclature.

In the holometabolous insects the *wing buds* of the embryo are sunken into pockets of the epidermis. These pockets become closed off externally, and remain thus concealed throughout larval life. The larva is thus not encumbered with externally growing wings, and none of the thoracic modifications related to the wings are developed until the pupal stage. Throughout the whole span of its life, then, the larva preserves the larval simplicity of its thoracic segments. The wing rudiments continue to grow in their pockets, and at the moult to the pupa they become evaginated as well developed lobes resembling the wing pads of hemimetabolous nymphs. Their final development, together with that of the adult thoracic structure is then developed within the pupa, so that the emerging adult is fully able to fly. In most cases the adult has to expand the wings and allow them to dry and harden, but in some aquatic groups (e.g., mayflies) the adults emerge and fly immediately.

It is clear that the evolution of the wings and of the thoracic modifications that enabled the glider lobes of the early insects to become organs of flight must have been a long and complex process. The winged insects, however, owe almost all that they are today to their wings. Note what simple creatures by comparison are the apterygotes, which probably have changed little since the time they first became hexapods. The wings of higher insects freed the adults from a ground existence, and many of them have taken advantage of their freedom to adopt new kinds of food and new ways of feeding, for which they have developed new types of mouthparts. The young in such cases could not lead the lives of their parents, and have become adapted to habitats and ways of living of their own. Thus it has come about that the young of these insects have been specialized to such an extent that they have lost all resemblance to their parents. The adult development is then delayed to the end of the larval life when the special larval tissues are destroyed in the pupa. This change from larva to adult is commonly known as metamorphosis, but really it is largely a replacement of the larva by the adult.

Abdomen: The name "abdomen" for the third section of the insect body does not clearly follow from its derivation; however, the insect abdomen does contain the principal viscera, and thus it may be likened to the vertebrate abdomen.

The primitive abdomen probably had 12 segments, this number being present in some embryos and in adults of the Protura. The terminal segment bearing the anus is probably a telson, since the last embryonic appendages in the embryo, which are retained as the cerci, pertain to the penultimate or eleventh segment. In most adult insects, however, there are only 10 abdominal segments, and the cerci are carried by the tenth segment and the anus is contained in an apical lobe.

The base of the abdomen may be broadly joined to the thorax or narrowed to a petiole. In the Hymenoptera the first abdominal segment is incorporated into the thorax as the propodium, and the second segment forms a petiole. The petiolate part of the abdomen is sometimes called the "gaster," but this is an inappropriate name for it, since the gaster is properly the stomach.

Male genitalia: The external genital equipment of male insects includes primarily organs for the insemination of the female and secondarily copulatory organs for holding her. To the taxonomist the male genitalia offer the best characters he has for the separation of species because of their highly diversified structure. This very fact, however, makes the study of the genital homologies difficult and has given rise to a great deal of confusion in current terminology. Recent studies on the development of the organs have given a better understanding of their basic structure and the homologies of the parts. Thus there has been made possible the adoption of a more uniform nomenclature. That confusion still persists is due largely to the fact that specialists in each order of insects insist on retaining their traditional ordinal nomenclature.

Since the inner organs of reproduction are duplicated on opposite sides of the body, and each has its own outlet duct, it is probable that primitively the ducts opened through paired external apertures, as they still do in some arthropods other than the insects. For efficient insemination of the female it became more practical to have the openings of the male ducts carried out to the ends of simple tubular outgrowths. Thus we find paired *penes* present in Crustacea and Diplopoda and, among the insects, in Ephemerida and Dermaptera. In most of the crustaceans and diplopods the penes arise on the bases of a pair of legs and are not themselves intromittent in function. The sperm is transferred from the male to the receptacle of the female by one or two pairs of modified legs (gonopods) of a following body segment. The insects have not adopted this indirect method of insemination, but they have developed a great variety of structures in the copulatory organs, associated with the organ of insemination, for grasping and holding the female.

The penes of Ephemeroptera arise from a small ventral plate or a pair of plates above the stylus-bearing plates of the ninth segment; these evidently belong to the much reduced tenth segment of the abdomen. The penes vary in form in different species, in some that are armed with subterminal prongs, and rarely they are united basally in a single organ, but the ducts are always separate.

In the Dermaptera the two penes are united basally on a long apodemal plate and are variously developed in their distal parts, so that they have little resemblance to the simple organs of the Ephemeroptera. Distally each organ splits into a median tube containing the exit duct and a strong outer lobe. In some species the two penes are united in a single organ with three terminal lobes, the median one giving exit to the two ducts, or to only a single duct if one duct is reduced and nonfunctional. The Dermaptera thus give an example of the modification potential of paired penes.

The division of each *penis* in the Dermaptera into a mesal lobe containing the duct and into a clasperlike lateral lobe is suggestive of the division of each primary phallic lobe of the higher insects into a mesomere and a paramere. In the latter, however, the ducts never enter the mesomeres but unite with a common duct formed between their bases.

The Thysanura in the adult stage have a single median penis arising between the bases of the ninth segment stylus-bearing plates; into the base of this the two genital ducts open by a common orifice. The penis, however, is developed from two small primary lobes that become concave on their opposed surfaces and unite to form the tubular organ of the adult. The penis lobes have no connection with the stylus-bearing plates of the ninth segment, and thus would appear to belong to the tenth segment. Heymons (1899) has noted that in fact the embryonic ducts of *Lepisma* end in the tenth abdominal segment.

In the Orthoptera and the higher insect orders, a new type of genital apparatus appears. It likewise begins as a pair of simple lobes, but the lobes do not give exit to the genital ducts. The paired ducts open into a single duct that grows inward between the lobes and becomes the unpaired ejaculatory duct of the adult. It is perhaps possible that the two lobes in this case are the paired penes of the lower insects from which the ducts have withdrawn, but there is no direct evidence for such. A common idea has been that the primary genital lobes are rudiments of appendages serially homologous with the embryonic limb vestiges of the pregenital abdominal segments and the thoracic legs. They arise, however, close together on the venter of the ninth segment in nymphal or late larval stages after the disappearance of the embryonic limb vestiges. Their position on the ninth segment is always behind the area of the sternal plate. Possibly, therefore, they belong to the tenth segment as do the penes of the lower insects, and have been moved forward into the "intersegmental" membrane of the ninth segment. In any case, the future history of these primary genital lobes has no counterpart in the lower insects.

Each primary lobe divides distally into two secondary lobes, a median *mesomere*, and a lateral *paramere*. Then in most cases the mesomeres unite by their edges to form a hollow median organ, the *aedeagus*, with the gonopore in its base; the lateral parameres become the claspers of the adult. The genital organs of the Orthoptera begin their development in this way as a pair of lobes that divide, but in their later growth they take on such a diversity of structure in the different families that the adult organs have little or no likeness to the genitalia of the other orders.

It is in the Hemiptera that we first encounter the genitalic structure typical of the higher orders. The mesomeres of the primary genital rudiments unite to form the median aedeagus, the parameres become the adult genital claspers. This same genitalic complex, though with many modifications, can be followed through to the most highly evolved orders. The parameres may be simple lobes, as in Hemiptera and Coleoptera, but in the other orders each is usually differentiated into a basal part and a muscularly movable distal part.

The known development of the genitalia leaves little doubt of the homologies of the major parts in the different orders. A great diversity in the genitalic nomenclature from one order to another, however, has grown up because most taxonomists are ordinal specialists and hence are interested in maintaining an established set of descriptive names handed down from their predecessors. This contrasts with their proclivity at changing the Latin names of the species and genera with which they deal. But a uniform nomenclature is desirable, as well as now being possible, and the lack of a uniform genital terminology is highly inconvenient to the nonspecialist and must be distressing to teachers and their students.

The common assumption that the primary genital lobes represent a pair of former legs has given the parameres the theoretical status of "gonopods." When divided, the basal part is identified as the "gonocoxite," the distal part as the "gonostylus." The aedeagus is then supposed to have been formed by the union of endite lobes of the "coxites." All this does very well as a basis for a practical nomenclature, but a leg origin of the genitalia has never been demonstrated or even supported by any concrete evidence. The postembryonic origin of the primary lobes and their median position behind the sternum of the ninth abdominal segment are in strong contrast to the true limb vestiges seen in the embryonic abdomen. There is no evidence that the mesomeres are endite lobes of the parameres. The primary genital lobes arise on the venter of the ninth abdominal segment, but always behind the region of the sternal plate. The adult organ, aedeagus and parameres, therefore, is supported on the posterior margin of the ninth sternum. When the parameres are separated from the aedeagus, they appear to be independent appendages of the ninth sternum, and have been regarded as such. The fact, however, that the parameres always originate as lateral branches of the genital rudiments shows that their lateral position results from a secondary displacement giving them a mechanical advantage as independently movable clasping organs. The subsequent division of the parameres into "coxites" and "styli" occurs secondarily and only in the higher orders. It seems desirable, therefore, to adopt a nomenclature free from unproven hypothetical assumptions of dubious validity.

The genital claspers need no other name than that of parameres (side parts), a name first given to them in the Coleoptera. The two segments have been called the "basimere" and the "telomere," which terms to be specific should be *basiparamere* and *teloparamere*. When the distal segments resemble grappling hooks they have appropriately been called *harpagones* (sing. *harpago*). The median organ that gives exit to the ejaculatory duct is best termed the aedeagus (*q. v.*) because the word means simply the principal genital part. By the dipterists it has been called the *mesosome,* by others the *phallus* or *phallosome,* or more generally the penis. Since the functional intromittent organ is usually the everted membranous inner wall of the aedeagus with the gonopore at its tip, this structure is more literally a penis.

The name phallus is not inappropriate for the medium genital organ alone, but the latter has for so long been known to entomologists as the aedeagus that this term has entomological priority, and the insect organ has no homologue even in other arthropods. The word "phallus" in ancient Greek was a vertebrate term and was specifically applied to an artifact, symbolical of generation, carried in certain processions.

Since we seem to lack a good general name for the genitalia of the insects, the writer (1941) has suggested that the term *phallus* might, consistent with its original meaning, be applied to the entire genital structure developed from the primary rudiments. The word combines euphoniously with prefixes and suffixes. The aedeagus and parameres are often not separated at their bases, in which case the three parts form a phallic unit with a common *phallobase.* The eversible inner tube of the aedeagus which serves as the functional penis of the insect may then be termed the *endophallus* (more euphonious than "endoaedeagus") in distinction to the outer genital parts as ectophallic structures. The primary genital lobes thus become the *phallic rudiments* and their branches *phallomeres.* The distal aperture of the aedeagus is the *phallotreme.*

This suggested nomenclature applies to only the major parts of the male genitalia which can be consistently named on a basis of homology. In all the insect orders, however, there are numerous secondary developments, and these structures must be given special names by workers in each order.

Aedeagus (variously written also aedaeagus, aedegus, aedoeagus, oedagus, edoegus, from Greek pl. *oidoia,* the genitalia + *agos,* chief or leader): The median organ of the male genitalia characteristic of pterygote insects from Hemiptera to Hymenoptera. The ejaculatory duct opens into it. The aedeagus is thus, as the name implies, the principal member of the genital complex. It is formed by the union of the two mesal branches (mesomeres) of the primary genital lobes at the sides of the gonopore. The gonopore, therefore, opens into the base of the aedeagal lumen, which latter is thus a secondarily added part of the genital exit passage, not a continuation of the ejaculatory duct, and its distal opening, the *phallotreme,* is not the gonopore.

The aedeagus is commonly known as the *penis* of the insect, but usually the whole organ does not serve for sperm intromission. The spermatazoa are discharged from the duct into the lumen of the aedeagus and then introduced into the female by eversion of the membranous inner wall of the aedeagus as a vesicle, or a long slender tube with the gonopore at its tip. This eversible tube, or *endophallus,* thus becomes the functional penis. In some insects the spermatozoa are incapsulated in a spermatophore, which during coition is attached to the opening of the spermathecal duct of the female. With others they are freely discharged either into the genital chamber of the female, from which they may make their way into the spermatheca, or they are introduced directly into the sperm receptacle. The endophallus may become a highly developed complex organ in itself, as in the honey bee, in which the outer part of the aedeagus is reduced to a pair of small plates guarding the phallotreme.

Though the aedeagus is fundamentally a tubular organ, it takes on various forms in different orders and families. In some Hymenoptera the lateral parts of the aedeagus become separated as a pair of free prongs (*sagittae*) from a median penis tube. Among the Diptera long rodlike processes (*paraphyses*) grow out from the aedeagal base.

When the aedeagus and the parameres are not separated at their bases, the three parts arise from a common *phallobase,* as among Coleoptera. In some cases the base of the aedeagus is connected with the parameres by a pair of small basal plates, or again the parameres may be entirely separated from the aedeagus.

Among the dipterists the aedeagus is known as the "mesosome," but this term (middle body) is not in itself specific for a genital organ. Others use the name phallus, which is from the Greek word for the male vertebrate organ with which the insect aedeagus has no possible homology (and in its ancient usage the "phallus" was particularly an artificial symbol of generation). *Aedeagus* is specifically an entomological term since the organ has no homologue even in other arthropods. Under the dissertation on Male Genitalia (*q. v.*) the writer has proposed that the term *phallus* is a convenient name for the whole genital complex developed from the primary genital rudiments.

Ovipositor: According to its derivation the word ovipositor should be applicable to any organ used for placing eggs. Among the insects, then, there are two types of ovipositors, one being the extensible abdomen itself, the other special pronglike outgrowths of the abdomen.

An ovipositor of the first type is present in the tubuliferous Thysanoptera, the Mecoptera, the Lepidoptera, the Coleoptera, and the Diptera. In these insects the distal part of the abdomen can be extended as a tapering, telescopic tube, near the end of which is the opening of the oviduct. Some of these insects deposit their eggs on exposed surfaces and protect them with a covering of glandular secretion. Others use the extended abdomen for inserting the eggs under the edges of loose bark, or into crevices, or for depositing them in rafts on the surface of water. In some of the fruit flies the greatly elongated abdomen has a sharp terminal point that enables the female to pierce the skin of fruit and insert their eggs into the flesh. A similar piercing tip is found in some primitive moths.

An ovipositor of the second type composed of movable sclerotic prongs is the organ usually referred to as the insect ovipositor. It is present in a very simple form in the Thysanura but is developed as a complex organ in some Odonata, in the Orthoptera, in the Hemiptera, and in the Hymenoptera. In these insects the ovipositor consists of two or three pairs of closely associated processes supported on two pairs of ventrolateral plates of the eighth and ninth abdominal segments.

An outgrowing genital process is in general a *gonapophysis,* a term applicable to the male as well as to the female. Specifically the prongs of the ovipositor are called the *valvulae* and the supporting plates the *valvifers* (valve carriers). The word *valva* in Latin was the name for one of a pair of folding doors; in modern mechanics a valve is a device for shutting off the flow of gas or water through a pipe, and in anatomy a valve is a fold in a blood vessel or the heart wall that regulates the flow of blood. Clearly, then, the use of the term *valves,* or the diminutive *valvulae,* for the prongs of the insect ovipositor has no justification from the original meaning of the word. The ovipositor is not a closing apparatus but a conducting organ. However, since we cannot well describe objects or anatomical parts without having names for them, the terms valvulae and valvifers will be used in the following description for the lack of appropriate substitutes.

In the typical pterygote ovipositor the free part of the organ is usually a tapering shaft composed of the first and second valvulae which enclose a narrow passageway for the eggs discharged from the opening of the oviduct between their bases. The ventral first valvulae slide back and forth on the second valvulae by interlocking ridges and grooves, and the second valvulae have a similar movement of their own alternating with that of the first valvulae. The movements of the valvulae are produced by muscles of the supporting valvifers, since the valvulae arise from the anterior ventral angles of their respective valvifers. The second valvifers are rocked on the lower edges, or sometimes on pivots, of the ninth tergum by strong antagonistic anterior and posterior muscles arising dorsally on the tergum. This imparts a back-and-forth movement to the second valvulae, which often united, giving a stronger support for the first valvulae. The first valvifers are small plates articulated on the anterior ends of the second valvifers, and each is provided with a muscle from the eighth tergum. The up-and-down movements of the first valvifers give a back-and-forth movement to the first valvulae on the second valvulae. The movements of the valvulae on each other carry the eggs through the channel of the ovipositor. The so-called third valvulae, when present, are usually either slender styluslike processes projecting from the rear ends of the second valvifers, or flat lobes that ensheath the distal end of the ovipositor shaft, but in some Orthoptera they are broad lateral plates of the shaft.

There are, of course, many variations in the size and shape of the ovipositor in the several orders of pterygote insects, but the general structure and mechanism of the organ are essentially the same in all. Insects that possess this type of ovipositor are able to deposit their eggs in the ground, to insert them into the stems and twigs of trees, or into the bodies of other insects. The ovipositor of some Odonata is a well-developed piercing organ by which the female inserts her eggs into the stems of underwater plants. In other Odonata the ovipositor has become greatly reduced and nonfunctional; such species merely drop their eggs on the water during flight. In the wasps and the bees the ovipositor has been remodeled into a stinging organ for the injection of poison from glands opening into its base. The eggs of these insects are discharged directly from the opening of the oviduct at the base of the sting.

Theoretically the ovipositor has been interpreted as a development from primitive legs of the eighth and ninth abdominal segments. The valvifers are supposed to be the coxae, the first and second valvulae to be coxal outgrowths, or gonapophyses, and the third valvulae perhaps coxal styli of the second valvifers. Superficially this interpretation looks plausible since the valvifers are moved by muscles arising on the terga of their respective segments, and a comparison with the simple ovipositor of Thysanura at first sight appears to bear out the suggested homologies. The two long slender gonapophyses of each genital segment of the Thysanura appear to arise from the anterior mesal angles of the stylus-bearing coxal plates. However, they are only closely attached to these plates, and their basal muscles arise on the sternal area or a sternal plate between them. The gonapophyses have no musculature from the coxal plates, as they should have if they are either telopodites of the limbs or gonapophyses of the coxae.

Matsuda (1957, 1958) has given a critical historical review of work on the structure of the insect ovipositor and of opinions that have been held on the homologies of its parts. Among the earlier writers, Heymons (1899 and earlier papers) was the foremost proponent of the concept that the gonapophyses (prongs of the ovipositor) are secondary ectodermal outgrowths of the eighth and ninth abdominal sterna in no way related to the transient embryonic limb vestiges on the other segments of pterygote insects, or to the stylus-bearing coxal plates of Thysanura. Tillyard (1917) notes that in the Odonata the rudiments of the ovipositor develop early in the larval life, "but have nothing to do with the primitive paired segmental appendages of the abdomen, which are lost during embryonic life." On the contrary, most subsequent writers down to the present time have held to the theory that the oviposior represents a pair of abdominal limbs of which the valvifers are the coxae. From a comparative study of the ovipositor muscles, however, Matsuda concludes that the musculature does not support the idea that the ovipositor has been derived from a pair of abdominal limbs. He concludes that the valvifers are sternal in origin, as claimed by Heymons. Certainly the ontogenetic origin of the ovipositor in the larva does not suggest that its rudiments represent legs. In the higher insects, as the writer (1933) has shown in the honey bee, the ovipositor is developed from two slender median processes on the venter of the eighth abdominal segment and two pairs on the ninth. These processes no more suggest a homology with legs than do the rudiments of the male genitalia.

Hence, if we do not wish to discard the idea of the leg origin of the ovipositor, the subject must remain doubtful until substantiated by better evidence than is at present available. The ovipositor is an organ peculiar to the insects that possess it. In no other arthropod is there any such structure, either anatomical or functional, associated with the opening of the oviduct.

Morphological generalizations are mental products of morphologists, but they are always intriguing in that they bring a lot of seemingly unrelated facts into a single concept. In this way they may be more convincing by the mental peace and satisfaction they give than by the evidence from the facts on which they are based. We must be cautious, then, not to accept a generalization on its mental appeal alone.

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