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BY
R. E. SNODGRASS
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INTRODUCTION

It is regrettable that we must arrive at an understanding of things by way of the human mind. Lacking organs of visual retrospection, for example, we can only hold opinions or build theories as to the course of events that have preceded us upon the earth. Knowledge advances by what biologists call the method of trial and error, but the mind can not rest without conclusions. Most conclusions, therefore, are premature and consequently either wrong or partly wrong, and, once in every generation, or sometimes twice, reason back tracks and takes a new start at a different angle, which eventually leads to a new error. By a zigzag course, however, progress is slowly achieved. Error, then, is a byproduct of mental growth. It is not a misdemeanor in scientific research unless the erring one clings to his position when he should see its weakness. It is better to write beneath our most positive contentions that we reserve the right to change of opinion without notice. The reader, therefore, should not take it amiss if he finds certain conclusions drawn in this paper that do not fit with former statements by the writer, for no apology will be offered.

I. EVOLUTION OF THE ARTHROPOD HEAD

The head, as a differentiated region of an animal, is a more ancient structure than is any other specialized part of the body, and a proper understanding of the head structure involves an examination of the evidence of cephalic evolution from the very earliest period when evidence of head development can be found. Most of the Arthropoda have well developed heads, and that the arthropod head is a specialized body region, just as is the thorax or the abdomen in forms where these body regions are differentiated, is shown by the fact that in the embryo it consists of a series of body segments. In most cases, and particularly in insects, however, the head differs from the other body regions in that its component segments become so thoroughly consolidated in the adult as to leave little evidence of the primitive elements in the head structure. Even in the ontogenetic record the true history of the head development is so obscure in many respects, and so much deleted in the early passages, that, though all the facts of embryology were known, it is probable that the assembled information would still give but an incomplete account of the phylogenetic evolution of the head. It is only by a comparative study of the head structure and its development in the various arthropod groups, and by an effort to correlate the known facts of arthropod organization with what is known in other animals successively lower in the scale of evolution, that we may arrive at a satisfactory conclusion as to the steps by which the complex head of an insect has been evolved—and even then we must allow much for errors of judgment.

CEPHALIZATION

It has been but little questioned that the numerous groups of metazoic animals are derived from a creature resembling the blastula of embryonic development (fig. 1 A). The embryonic blastula is exemplified, among living animals, in the early stage of the free-swimming larval planula of the Coelenterata (fig. 2 A). The planula develops directly from the coelenterate egg, and has the form of a hollow mass of cells, the outer surface of which is covered with vibratile cilia. The uniform motion of the cilia propels the animal through the water in the direction of one axis of the body (fig. 3), and thereby one end is distinguished as *anterior* and the opposite as *posterior*. The creature thus becomes uniaxial and bipolar, though as yet there may be no differentiation of body structure. The functional differences at the two poles of the body, however, determine the course of the subsequent development of physical characters. Structural differentiation of the end of the body that is forward in usual progression is called *cephalization,* a term meaning the process of evolving a head.

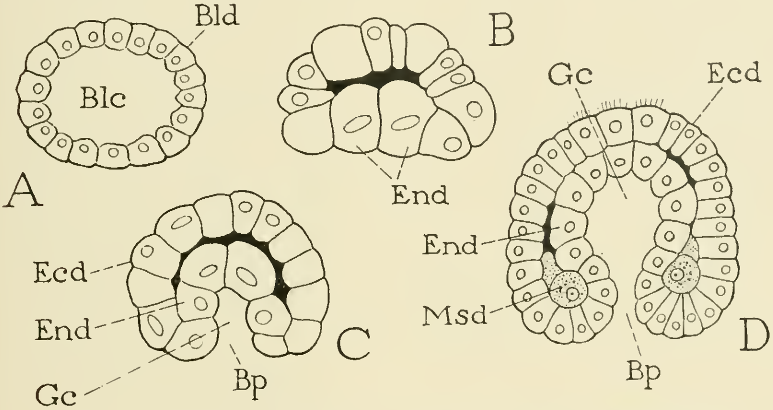

Fig. 1.—Typical early stages in general embryonic development.

A, blastula stage, diagrammatic, consisting of a blastoderm (*Bld*) surrounding a blastocoele cavity (*Blc*). B, C, D, stages in development of a chiton (from Kowalevsky, 1883): B, differentiation of cells in blastula; C, gastrulation, forming gastrocoele cavity (*Gc*), lined with endoderm (*End*), and opening through blastopore (*Bp*); D, later stage, showing origin of mesoderm layers (*Msd*) just within lips of blastopore.

The body of the planula is usually larger at the anterior end (figs. 2, 3), and only in this does the planula attain cephalization in the strict sense. Its principal structural differentiation occurs at the posterior pole, where there takes place an ingrowth of cells (fig. 2 B-D) that soon fills the hollow of the body, and finally, by the appearance of a cavity within its mass, becomes the wall of the stomach of the mature animal. The process of forming a primitive stomach, or *archenteron*, as it takes place in the planula, is typified by that of gastrulation in ordinary embryonic development (fig. 1 A-D). The planula, of course, is a specialized larval form, and its manner of endoderm formation can not be taken as showing how the archenteron was evolved, but the free-swimming planula does show that the primitive mouth, or *blastopore* (fig. 1 C, D, *Bp*), was formed at the *posterior* pole of the body, and not at the anterior pole. It is interesting to note, therefore, that the position of the mouth opening was not necessarily a primary determining factor of cephalization; the practical site for a mouth in a free-swimming, ciliate animal was determined by the direction of the animal's movement. Korschelt and Heider (1895) have stated, if a monaxial, heteropolar planula is allowed to swim through water containing particles of carmine, it can be seen that the particles are repulsed at the anterior and lateral parts of the body, but that they accumulate at the posterior pole. "Here accordingly," say Korschelt and Heider, "was a favorable place for the reception of particles of food, and by a flattening or shallow invagination of the posterior pole these favorable conditions were increased. The archenteron, therefore, in its earliest beginnings was a pit in which to catch particles of food."

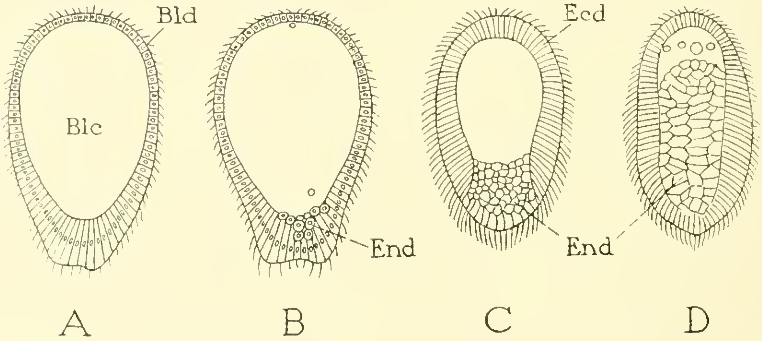

FIG. 2.—Formation of the endoderm in a coelenterate planula larva by proliferation of cells from posterior pole. (From Hatschek, 1888, after Claus.)

Blc, blastocoele; *Bld*, blastoderm; *Ecd*, ectoderm; *End*, endoderm.

This is a satisfactory explanation of the origin of the gastrula if not questioned too closely; but Bidder (1927) rather disturbs the idea with his statement that "the laws of viscous matter make it clear that the free-swimming gastrulae we observe as larvae could never earn their own living, since the stream-lines would carry every particle of food outside the cone of dead water which is dragged behind the gastrula mouth." On the other hand, Bidder admits, "creeping planulae or gastrulae might pick things up." A creeping animal, however, would never in the first place develop a mouth at the rear end of the body. What we want is an explanation of the original posterior position of the blastopore, and if none offered will suffice, we must be content with the fact.

The further history of the coelenterate larva has no bearing on the evolution of insects, for the creature soon becomes attached by its head end, and, probably as a result of the sedentary, plant-like habits of its immediate ancestors, develops into a polype or jellyfish having a radiate, flower-like type of structure. Some writers have suggested that the worms and the arthropods may have been evolved from an elongate medusa, but it seems more probable that the Coelenterata, the Annelida, and the Arthropoda are all to be traced back to a free-swimming gastrula ancestor. The mature planula is a specialized gastrula, but it is of general interest in that it gives us a passing glimpse of a free-living animal in the blastula and gastrula stages at a time when cephalization was first established in the Metazoa.

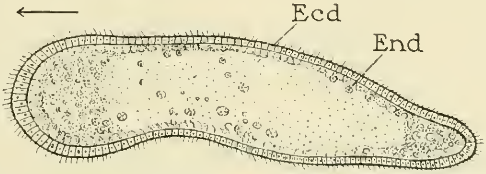

FIG. 3.—Free-swimming planula larva of a coelenterate, *Sympodium corralloides*, with ciliated ectoderm, and completely-formed endoderm. (From Kowalevsky and Marion, 1883.)

The structure and development of the arthropods suggest that these creatures were developed from forms adapted to a creeping rather than a swimming mode of progression. Some planula larvae lack cilia and have creeping habits, and such forms, though they have nothing to do with the arthropod ancestors, show that a free-living creature in the blastula or gastrula stage may change its mode of progression. The creeping habit as an habitual mode of progression entails some fundamental structural adaptations. An animal that crawls must keep one surface against the support, and thus it establishes a functional distinction between its upper surface and its lower surface, which has led to the structural differentiation of *dorsiventrality;* and from this, in combination with movement in one direction, finally, bilateral symmetry of organization necessarily follows.

Progression by crawling instead of by swimming alters the whole status of the relation between the animal and the environment. A mouth at the posterior end of the body now becomes quite impracticable, and embryonic history shows that crawling animals proceeded to rectify the defect, supposedly inherited from their free-swimming ciliate ancestors, by lengthening the mouth, or blastopore, in a forward direction on the under side of the body. In the young *Peripatus* embryo, for example (fig. 4 A, B), the blastopore is a long slit on the ventral surface of the blastoderm. Later, the edges of the slit come together (C) and unite except at the two ends, where openings remain into the archenteron that become the mouth and anus of the mature animal. In insects and other arthropods, the process of gastrulation in the embryo (fig. 5 A) is clearly a modification of that in *Peripatus,* by which many of the details have been omitted and the whole procedure greatly altered. In most insects (fig. 5 B), gastrulation resembles that of the planula (fig. 2) in so far as it takes place by an internal proliferation of cells from the blastoderm, but most of the gastrulation area gives rise to mesoderm, the true endoderm being formed only at the two extremities of the inner layer (fig. 5 C, *AMR*).

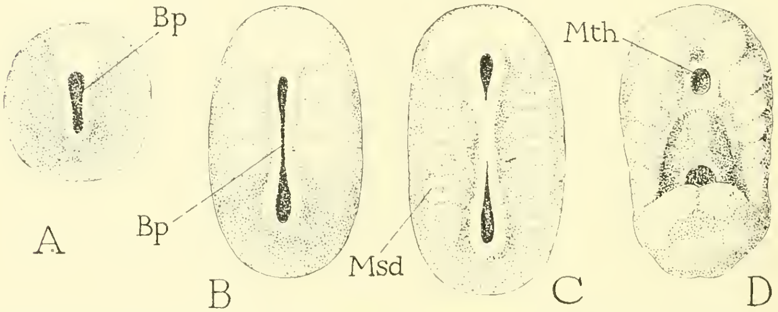

FIG. 4.—Early stages in the development of *Peripatus capensis.* (From Balfour, 1883.)

The blastopore (*Bp*) elongates on ventral surface of embryo, and then closes except at the two ends (C) where open extremities become mouth and anus. Segmentation appears as series of coelomic sacs in mesoderm (see fig. 6, *Msd*).

The mesoderm, and the associated mesenchyme, play an important part in the organization of all the higher Metazoa, since they form the internal organs that lie between the ectodermal covering of the body and the endodermal epithelium of the alimentary canal. The mesoderm is of particular importance in segmental animals because it is in this layer that metamerism originates. Mesoblastic tissue is produced in a gastrulated embryo in two ways: First, in the form of scattered cells proliferated from the inner surface of the invaginated endoderm; and second, in the form of cell layers. The scattered cells form a loosely coherent mesenchyme; the cell layers constitute the true mesoderm. The primitive mesoderm cells are given off from the endoderm near where the latter joins the ectoderm, that is, just within the lips of the blastopore (figs. 1 D, 6, *Msd*). In the young annelid larva, the mesoderm cells first form two lateral bands of tissue at the posterior end of the body (fig. 7 D, *Msd*). Later, the extended mesoderm tracts become excavated by a series of cavities, the coelomic sacs, which mark the beginning of segmentation. In *Peripatus* (fig. 4), likewise, two rows of coelomic sacs (*Msd*) are formed as paired cavities in the mesoderm, which extends laterally between the ectoderm and the endoderm along the line of junction between these two

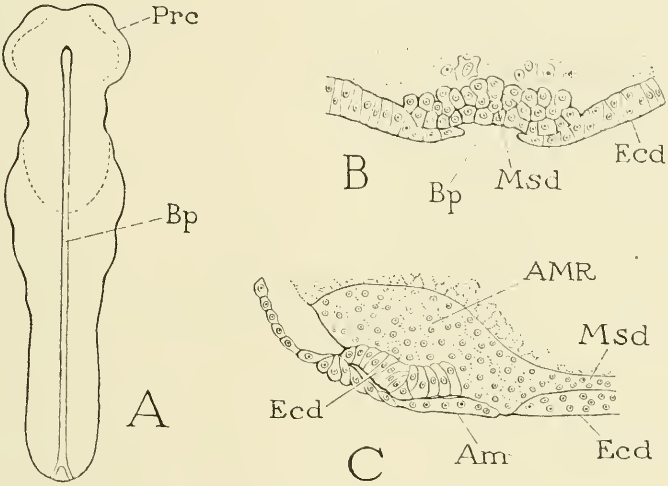

FIG. 5.—Gastrulation in insects.

A, embryo of *Leptinotarsa decimlineata* with long gastrulation groove, or blastopore (*Bp*), on ventral surface. (From Wheeler, 1889.)

B, cross section through blastopore of embryo of *Forficula*, showing mesoderm (*Msd*) formed by invagination of middle plate. (From Heymons, 1895.)

C, anterior mesenteron, or endodermic, rudiment (*AMR*) formed at anterior end of mesoderm (*Msd*) in embryo of honeybee. (From Nelson, 1915.)

layers (fig. 6, *Msd*). In the annelids, the coelomic sacs form the entire segmented body cavity; in *Peripatus* and most of the arthropods, the greater part of the definitive body cavity is derived from a space between the ectoderm and the endoderm lined with mesenchymatic cells.

It is most important to bear in mind the intimate relation that exists between the mesoderm and the endoderm. In the arthropods, especially in insects, the process of gastrulation, as above noted, is greatly modified, and mesoderm tissue alone is proliferated along the greater part of the length of the blastopore area, which in only a few generalized forms appears as a true opening. At each end of the mesoderm, however, endodermal tissue is formed (fig. 5 C, *AMR*), and the two endoderm rudiments mark the anterior and the posterior limits of the mesoderm—consequently, they define the area of segmentation.

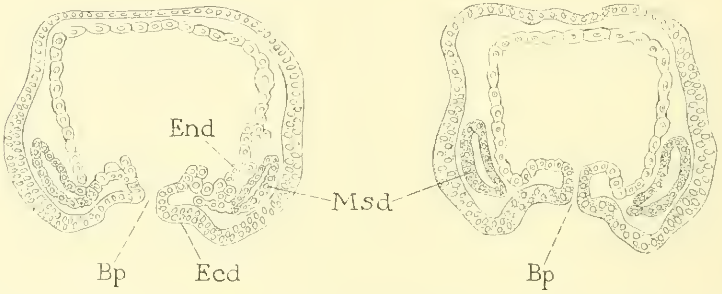

FIG. 6.—Formation of mesoderm in *Peripatus capensis*. (From Balfour, 1883.)

Cross sections of embryos through blastopore, showing formation of mesodermic coelomic sacs (*Msd*) from endoderm (*End*) just within lips of blastopore (*Bp*).

It is unnecessary to speculate as to the phylogenetic steps that may have led from the early creeping gastrula form of animal to the wormlike ancestor of the arthropods, but we must note the important advance in cephalization, and the possibilities of further head development that came with the establishment of a mouth at the anterior end of the body. Food, whether living or inert, had now to be recognized and seized on contact. Consequently, it became highly important to the animal to be able to determine its course according to favorable or unfavorable conditions of the surroundings. The ectoderm of the anterior end of the body developed a special sensitiveness to environmental changes, and, probably by means of ectodermal processes extending into the body, communicated the stimuli received from without to the internal tissues. Certain groups of the sensitive cells then were withdrawn into the body where they became the rudiments of a central nervous system. Other sensory cells, remaining at the surface but sending processes inward to the buried cells, formed the peripheral sensory system. This anterior differentiation of sensory and conductive tissues opened still other possibilities of cephalization, which have led to the development of the brain and all the complex sense organs located on the head in higher animals.

It is difficult to establish, by concrete example, the contention that the change in the position of the mouth resulted from a change in the manner of locomotion, but it is indisputable that the ancestors of the worms and the arthropods must have assumed the crawling habit at some stage in their evolution. The chaetopod annelids, in their embryonic development, arrive at a first larval stage known as a *trochophore* (fig. 7 D), which is a free-swimming creature with well differentiated anterior and posterior poles, and a dorsal and a ventral surface, with the mouth situated anteriorly in the latter. If dorsiventrality is to be attributed to a creeping mode of locomotion, then there must be some stage omitted between that represented by the free-swimming planula, and that of the free-swimming trochophore, because there is no evident reason, otherwise, why two forms having the same mode of life should have an organization so different. The trochophore is without doubt a specialized larval form modified secondarily for a swimming habit. It can not, therefore, be taken to represent an ancestral form of the worms; but it is the only free-living creature that shows us the beginning of the worm organization, and its structure can certainly be traced into that of the arthropods.

The annelid trochophore is typically ovate in shape with the larger end forward (fig. 7 D), or rather, upward, since the creature floats upright in the water, but the side in which the mouth (*Mth*) is located is called the ventral surface because it becomes the under surface of the mature worm. The mouth lies a little below the middle of the body, and the anus (*An*) is situated at the posterior pole. The body is surrounded by several bands of vibratile cilia. The principal band (*b*), comprising usually two rows of cilia, is situated on the widest part of the body and just before the mouth. It divides the animal into a preoral, or *prostomial*, region (*Pst*), and into a postoral, or *metastomial*, region (*Mst*). A second band of cilia (*c*) is generally present a short distance behind the mouth, and sometimes there is a third, preanal band (G, *d*) near the posterior end, which sets off a terminal circumanal region, or *periproct* (*Ppt*). At the anterior end of the body there is a central tuft of tactile hairs (G, *a*), a pair of small lateral tentacles (*Tl*), and one or more simple eye spots (*O*).

The mouth of the trochophore (fig. 7 D, *Mth*) opens into an ectodermal *stomodeum* (*Stom*), which leads into a large endodermal stomach, or *mesenteron* (*Ment*), of two parts, the second of which communicates with the exterior through a short ectodermal *proctodeum* (*Proc*). In development, the endoderm is formed by invagination at the posterior end of the body (fig. 7 A, B, *End*), but the blastopore (*Bp*) soon shifts to the ventral surface (C) and elongates forward. The posterior part of the blastopore is then closed; the

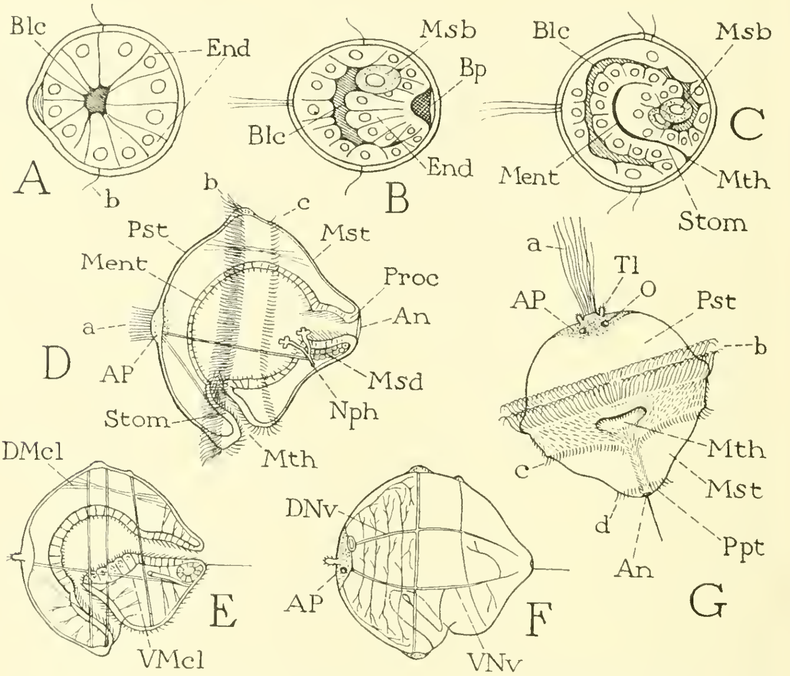

FIG. 7.—Structure and development of an annelid trochophore larva. (From Hatschek, 1888-91, but figures A to F turned in position of adult worm with mouth downward.)

A, blastula stage with endoderm cells (*End*) differentiated at posterior pole. B, gastrulation, showing a primitive mesoblast cell (*Msb*) of one side. C, gastrulation completed, mesenteron (*Ment*) detached from ectoderm at posterior end, its anterior end opening through stomodeum (*Stom*) and mouth. D, full-grown trochophore larva of *Polygordius*. E, diagrammatic view of the muscle system. F, the nervous system. G, ventral surface of a trochophore.

a, apical tuft of cilia; *An*, anus; *AP*, apical plate; *b*, preoral band of cilia; *Blc*, blastocoele; *Bp*, blastopore; *c*, postoral band of cilia; *d*, circumanal band of cilia; *DMcl*, dorsal muscle; *DNv*, dorsal nerve; *End*, endoderm; *Ment*, mesenteron; *Msb*, primary mesoblast cells; *Msd*, mesoderm; *Mst*, metastomium; *Mth*, mouth; *Nph*, nephridium; *O*, eye spot; *Ppt*, periproct; *Proc*, proctodeum; *Pst*, prostomium; *Stom*, stomodeum; *Tl*, tentacle; *VMcl*, ventral muscle; *VNv*, ventral nerve.

anterior open extremity is carried inward by an ectodermal invagination which becomes the *stomodeum* (C, *Stom*), the external opening of which is the definitive mouth (*Mth*). The proctodeum and the anus are formed later by a posterior invagination of the ectoderm, and the proctodeum secondarily opens into the posterior end of the stomach. At the anterior end of the preoral region of the body, or prostomium, the ectoderm is thickened to form a sensory *apical plate* (D, G, *AP*) beneath the sensory organs here located, and from it ectodermal nerve tracts extend posteriorly in the body wall (F). Typically, there is a pair of dorso-lateral longitudinal nerves (*DNv*), and a pair of ventro-lateral nerves (*VNv*). The simple musculature of the trochophore (E) is developed from mesenchyme tissue; the epithelial mesoderm forms only the pair of mesoderm bands (D, *Msd*) and a pair of nephridia (*Nph*) in the posterior part of the body. This description of the trochophore is based mostly on that of Hatschek (1888-1891), from whose work the illustrations of figure 7 are taken.

The trochophore develops into the worm form of its parents by a metamorphosis involving an elongation of its posterior end (fig. 9), accompanied by a reduction of the cephalic swelling, until finally, in the adult, the only differentiation in the head region is an anterior, median prostomial lobe overhanging the mouth (fig. 10, *Pst*). The prostomium usually bears the principal sensory areas or organs of the worm, and a ganglionic nerve mass is differentiated from the inner surface of its ectoderm, which becomes the supraoesophageal ganglion, or *brain,* of the annelid. In the Polychaeta, the prostomium may bear one or more pairs of eyes, and several pairs of sensory tentacles (fig. 10). As the body of the young worm elongates, it becomes transversely segmented, the somites increasing in number posteriorly as the segmented area lengthens.

The young arthropod embryo, in its first definite form (fig. 8 A), consists of a large head region, the so-called cephalic lobes (*Prc*), and of a slender body (*Bdy*). The mouth (B, *Stom*) is situated on the ventral surface of the cephalic enlargement. The proctodeal invagination and the anus are formed, usually in a later stage, at the posterior end of the body.

The large-headed stage of the young arthropod embryo has a certain resemblance to the trochophore stage of the annelid larva; but it is probable that the similarity between the two forms has no genetic significance, and that the size of the cephalic lobes in the arthropod embryo is to be explained as an acceleration of development. Yet, it is evident that the cephalic region of the arthropod embryo corresponds with the prostomial and metastomial regions of the trochophore, and includes also the next following somite, for the first antennae, which are the appendages of the second somite of the arthropods, are developed on the cephalic lobes of the embryo (fig. 8 B, C, D, *Ant*). In the insect embryo, furthermore, the region of the rudimentary second antennal appendages, or the tritocerebral segment (fig. 8 C, *III*), is often incorporated into the cephalic lobes. It is probable, therefore, that the very early insect embryo represents a higher stage of cephalic evolution than does the annelid trochophore larva, in as much as it has already progressed to a point where the head includes two or three of the body segments.

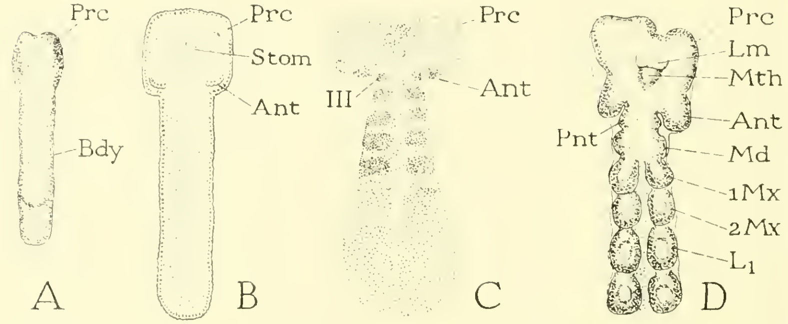

FIG. 8.—Young stages of insect embryos, showing cephalic lobes, beginning of segmentation, and formation of appendages.

A, germ band of *Blatella germanica* on seventh day, with cephalic lobes (*Prc*) indicated. (From Riley, 1904.)

B, embryo of same, about nine days old, with cephalic lobes developed into a distinct protocephalon (*Prc*), antennae (*Ant*) appearing, stomodeum (*Stom*) indicated as thickening of ectoderm. (From Riley, 1904.)

C, young embryo of *Lepisma*, with well-developed protocephalon (*Prc*), bearing stomodeum and rudiments of antennae, with tritocerebral segment (*III*) closely associated with its base. (From Heymons, 1897.)

D, embryo of *Blatella* late in tenth day, with labrum (*Lm*), mouth (*Mth*), and antennae (*Ant*) on protocephalon (*Prc*), followed by rudiments of postantennal appendages (*Pnt*), mandibles (*Md*), first maxillæ (*1Mx*), second maxillæ (*2Mx*), and legs (L_1). (From Riley, 1904.)

The definitive head of the arthropod may contain as many as six or seven of the body segments. Before going farther in the study of progressive cephalization, then, it will be necessary to understand something of the development and general organization of the body in segmented animals.

DEVELOPMENT OF THE BODY IN SEGMENTED ANIMALS

In the Annelida, the worm form is developed from that of the trochophore by an elongation of the posterior part of the larval body (fig. 9), and by a decrease in the relative size of the cephalic enlargement. The young worm is a cylindrical creature with only a comparatively small prostomial lobe projecting before the mouth. With the elongation of the body, the alimentary canal and the mesoderm bands are correspondingly lengthened, and the trochophore muscles and nerves are continued into the new region. The external surface of the body of the trochophore is marked off into several areas by circular bands of cilia; the worm body, on the other hand, is constricted by transverse grooves into a series of segments, or somites. The segmentation of the adult worm *originates in the mesoderm bands* by the development in the latter of a series of paired coelomic sacs. Secondarily, the mesodermic divisions become impressed upon the body wall, and the segmentation expressed externally by a series of transverse, circular grooves on the intersegmental lines. In the worms, the segments increase in number from before backward by the differentiation of new segments between the last one formed and the periproct. The latter remains as an undifferentiated terminal piece of the body bearing the anus. The prostomial region of the trochophore becomes the prostomium of the adult worm; the metastomial region in the Archiannelida constitutes the first body segment, or that immediately behind the mouth; but in the Polychaeta and Oligochaeta the metastomium is said to unite with the next somite to form a compound peristomial segment.

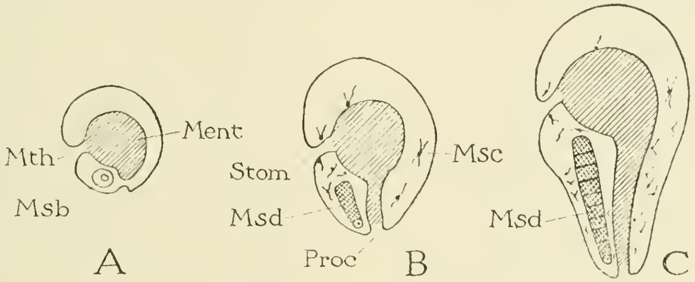

Fig. 9.—Diagrams of the development of an annelid trochophore larva, and early stage in its metamorphosis into a segmented worm. (From Hatschek, 1888-'91.)

A, early larval stage, showing a primary mesoblast cell (*Msb*) of one side. B, later stage in which the mesoblast has formed scattered mesenchyme cells (*Msc*), and a ventro-lateral band of mesoderm (*Msd*) in each side of the body. C, early stage of metamorphosis in which each mesoderm band has divided into a number of primary segments.

In the adult annelid (fig. 10), the body, as distinguished from the head, is all that part of the worm that lies posterior to the mouth (A, *Mth*), and the only differentiated head region is the prostomium

(*Pst*), though the peristomium (*Prst*) is sometimes called a part of the "head". The prostomium varies in size from a small lobe overhanging the mouth, to a large area extended posteriorly into the dorsal region of the peristomium (B). It bears the principal sensory organs, eyes and tentacles (*O*, *Tl*), of the anterior part of the worm. The alimentary canal extends entirely through the body from the mouth at the anterior ventral edge of the peristomium to the anus at the end of the periproct.

The nervous system of the adult annelid consists of a brain located before or above the oesophagus, derived from the ectodermal apical plate of the prostomium of the trochophore (fig. 7 F, *AP*), and of a ventral nerve cord of segmental ganglia and intervening connectives, formed from two nerve strands developed from the ectoderm of the ventral body wall and prolonged from the ventro-lateral nerve strands of the trochophore. The ventral cord, therefore, is connected with the brain by a pair of connective nerve cords passing to the sides of the oesophagus. Usually, the two ventral nerve strands are united along the midline in adult worms, but in certain polychaete forms (Serpulidae) the two cords are said to remain separate, though connected by transverse, interganglionic commissures in each segment.

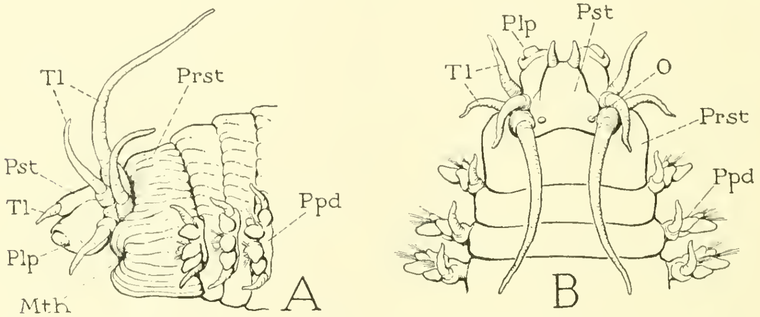

FIG. 10.—Anterior end of an adult polychaete annelid worm, *Nereis virens*. A, lateral view. B, dorsal view.

Mth, mouth; *O*, ocellus; *Plp*, prostomial palpus; *Ppd*, parapodium; *Prst*, peristomium; *Pst*, prostomium; *Tl*, prostomial tentacles.

In the Arthropoda, body segmentation begins during an early embryonic stage, and the somites are added, in general, as in the annelids, from before backward by the differentiation of new segments behind the last one formed. In some of the arthropod groups, segmentation is completed in a postembryonic stage; in insects (except Protura), however, the somites are all defined before the creature leaves the egg, and the typical sequence of segmentation is not always followed.

The component segments of the cephalic lobes, or head of the arthropod embryo, are never distinct, but the subsequent development of the anterior nerve centers shows that the lobes comprise two segments at least, in addition to a prostomial region, and that usually a third segment is more or less included in their posterior part.

The way in which metamerism arose in the phylogenetic history of segmented animals is not known, and it is not necessary to believe that the method of segment formation in either the annelid larva or the arthropod embryo gives a picture of primitive segmentation in the course of evolution. The development of the trochophore into the worm is clearly a process of metamorphosis, that is, it is the return of a specialized, aberrant larva to the ancestral form represented more nearly in that of the adult; and it is well known that embryos do not keep closely to the phylogenetic path in the details of their development. Since so many other essential features in the body structure of animals are connected with the mode of locomotion, the writer holds as most probable the idea that segmentation also had its beginning as an adaptation to a specific kind of movement. The creeping, worm-like ancestors of the annelids and arthropods certainly at an early period must have developed a contractile tissue in their mesoderm bands—that they did so is attested by the early development of a central nervous system consisting of motor neurons, following the lines of the later established ventral longitudinal muscle bands. It is, then, clear that a breaking up of the contractile tissue into short lengths would give a greater efficiency of movement, with the possibility of more variety of action, and that, with the differentiation of true muscle fibers, the attachment of the ends of the fibers to the ectoderm would carry the metamerism into the body wall. The fact that embryonic segmentation begins anteriorly and progresses backward, in itself suggests that metamerism originated in a creeping animal; in a free-swimming form, the progress of segmentation should be the reverse, for the motile region of the animal would be the tail end. Organs developed at the time of metamerism or subsequent to it, such as nephridia, tracheae, and external appendages, are repeated in each segment, those antedating segmentation either remain unsegmented, as the alimentary canal, or take on a secondary segmentation, as do the body wall and the nervous system.

There are other theories of metamerism: Hatschek (1888-1891) enumerates five views that have been proposed to explain the origin of body segmentation, but none of them is based on the simple fact that in embryonic development, metamerism begins in the mesoderm and secondarily spreads to other tissues. The older locomotion theory was defective in that it attributed the formation of segments to the mechanical stress of movement.

At the completion of metamerism, a segmented animal has attained a generalized structural stage in which it consists of a segmented body part coëxtensive with the length of the alimentary canal (fig. 11), and of a prostomial region (*Pst*) anterior to the mouth (*Mth*). Since the mouth in annelids and arthropods marks the site of the original anterior extremity of the blastopore on the ventral surface of the body (figs. 4 B, 5 A, *Bp*), it is evident that *mesodermal segments can not be formed morphologically anterior to the mouth*, and therefore, that *the preoral region is never truly segmented*. The common idea, then, that the arthropod mouth lies behind the first head segment, or, as proposed by some writers, behind the second or even the third segment, disregards the fundamental relation between the endodermal and mesodermal layers. Segmentation can not exceed the extent of the mesoderm, and the primitive extent of this layer in the annelids and arthropods is defined by the positions of the mouth and the anus. The blastopore never extends quite to the true cephalic extremity. The stomodeal invagination, which gives rise to the definitive mouth, is thus preceded by an unsegmented prostomium. The closed posterior end of the blastopore, however, is at the posterior extremity of the body, where the blastopore and endoderm originated, and the later formed proctodeum, therefore, opens terminally in the periproct. In some arthropods a median lobe, or suranal plate, grows out over the anus from the periproct, and simulates the prostomial lobe at the anterior end of the body. Likewise, there may be lateral and subanal lobes of the periproct.

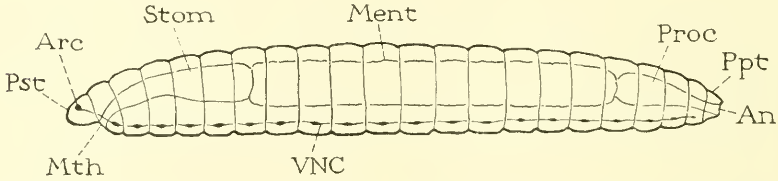

FIG. 11.—Diagram of the structure of a theoretically generalized segmented animal.

An, anus; *Arc*, archicerebrum; *Ment*, mesenteron; *Mth*, mouth; *Ppt*, periproct; *Proc*, proctodeum; *Pst*, prostomium; *Stom*, stomodeum; *VNC*, ventral nerve cord.

In as much as the most important evidence of the segmentation of the arthropod head is derived from a study of the cephalic nerve masses, it will be necessary to understand next the essential features in the evolution of the central nervous system in segmented animals.

The annelids, as already noted, have a ganglionic nerve mass lying in the anterior part of the body, before or above the stomodeum, which takes its origin from the ectodermal apical plate of the prostomium (fig. 7 F, *Ap*). This, the most primitive brain of the annelid-arthropod series (fig. 12 A, *Arc*), has been named by Lankester (1881) the *archicerebrum* (a happy, though mismated union of linguistic elements). In the trochophore, a pair of dorsal and a pair of ventral nerves (fig. 7 F, *DNv, VNv*) extend backward from the apical plate, but in the adult worm and in arthropods only the nerves of the ventral pair are retained. In the more primitive condition, the two ventral nerve strands have a latero-ventral position (fig. 12 A,

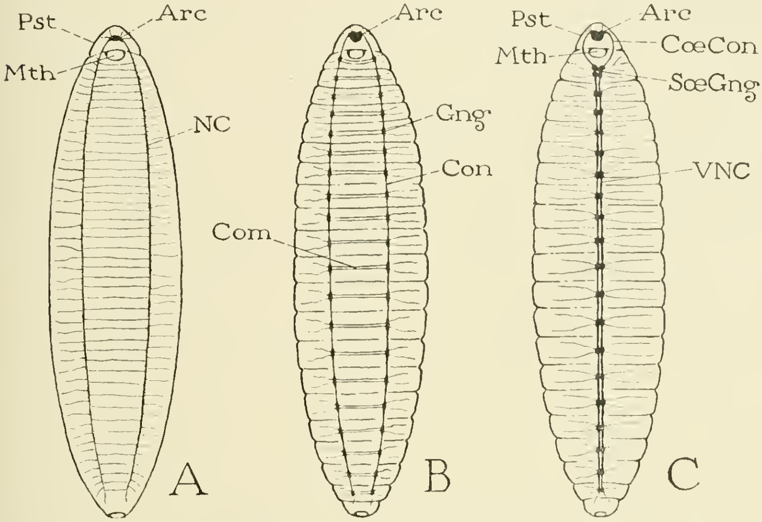

FIG. 12.—Diagrams suggesting the evolution of a central nervous system of annelid-arthropod type of structure.

A, theoretical structure of nervous system in an unsegmented pre-annelid form, consisting of a prostomial archicerebrum (*Arc*), and of two ventro-lateral nerve cords (*NC*), connected medially by transverse nerves, and giving off nerves laterally to body wall and internal organs. Nerve cells diffused along the cords.

B, simple nervous system of the ladder type in a segmented animal. The nerve cells aggregated into segmental groups, or ganglia (*Gng*), along the cords; the intervening parts of cords converted into connectives (*Con*), and the transverse ventral nerves forming commissures (*Com*) between the ganglia.

C, the segmental pairs of ganglia united into compound ganglia of a median ventral nerve cord (*VNC*), in which the first, or suboesophageal, ganglion (*SoeGng*) is postoral, and connected with archicerebrum of prostomium (*Arc*) by connectives (*CoeCon*) encircling the mouth (*Mth*).

NC), and it seems reasonable to attribute the special development of these nerves in a creeping animal to the special development of sensitivity in the ectoderm along the edges of the body in contact with the supporting surface.

That the nerve strands were primarily unsegmented is shown by the fact that they are not ganglionated in the Archiannelida, and by their condition in *Peripatus* where the nerve cells are still distributed along the length of the cords, and segmental grouping of the cells is but slight. A concentration of the nerve cells of the cords in each segment is, then, only a simple adaptation to efficiency where metamerism becomes the established body structure. After the segregation of the nerve cells into pairs of segmental ganglia, the intervening fibrous tracts of the cords remain as connectives between the successive ganglia in each chain, while transverse ventral nerves, originally going from one cord to the other, become commissures uniting the ganglia of each segmental pair. In this way, apparently, a simple nervous system, formed primarily as two parallel strands of nerve tissue, became a segmented system of the ladder type (fig. 12 B). In the further course of evolution, the ganglia of each segment come together medially and combine into a single ganglionic mass, or segmental ganglion (C), which, in some arthropod groups, acquires an addition from a secondary median cord of nerve tissue developed from the ventral ectoderm along the midline of the body. The transverse commissures are now internal fibrous tracts of each double ganglion, but the lengthwise cords persist usually as paired interganglionic connectives. Each definite body ganglion, or pair of ganglia, innervates, in general, only the parts and organs of its own segment, but all the ganglia show a tendency to migrate along the cords, especially in a cephalic direction, and to unite with other ganglia to form composite ganglionic masses. Whatever may be the final position of any pair of ganglia, however, its nerves in most cases still go to the segment in which the ganglia originated. The nervous system, thus, often gives a key to the body segmentation where the latter is obscure or obliterated.

The next important stage of development is that, characteristic of the arthropods, in which are formed the external *segmental appendages*. The organs designated " appendages " in the limited sense are hollow, ventro-lateral outgrowths of the body wall (figs. 13, 14, 22), which become movable by muscles inserted on their bases, and flexible by a series of joints in their walls, also provided with muscles. Here again, we connect structural evolution with movement, for undoubtedly the segmental appendages in the first place were all organs of locomotion, giving a new power of movement supplanting the wriggling and creeping of earlier ancestral forms. The question of whether the appendages were first used for propulsion through the water, or for progression on a solid support will not be discussed here, but, in the course of their evolution, the appendages have become specialized to serve a great variety of functions. Moreover, by the functional grouping of the appendages, the corresponding body segments have themselves become differentiated into groups forming often quite distinct body regions (fig. 13 B), of which the head of an insect is one of the most highly evolved.

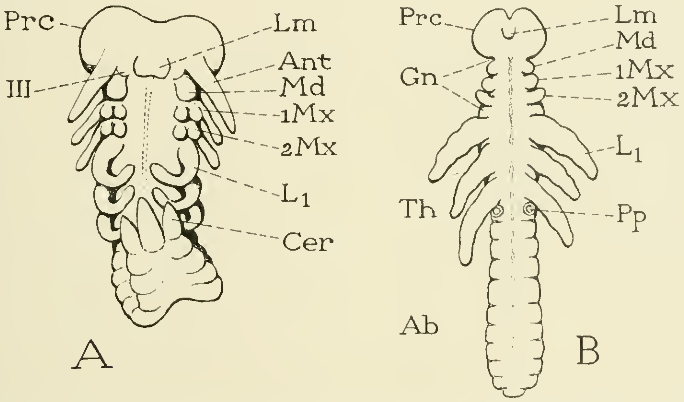

FIG. 13.—Young insect embryos at a stage when the thorax is already differentiated, but in which the gnathal segments are not yet added to the protocephalon to form the definitive head.

A, embryo of *Lepisma saccharina* (from Heymons, 1897). B, embryo of *Ranatra fusca* (from Hussey, 1926).

Ab, abdomen; *Cer*, cercus; *Gn*, gnathal segments; *III*, tritocerebral segment; *L₁*, first leg; *Lm*, labrum; *Md*, mandible; *1Mx*, first maxilla; *2Mx*, second maxilla; *Pp*, "pleuropodium"; *Prc*, protocephalon; *Th*, thorax.

THE PROTOCEPHALON

The arthropods differ from the annelids in the possession of a composite head, or *syncephalon*, formed by the union of several of the anterior segments with the prostomium.

In the embryonic development of most Arthropoda the head is first differentiated as a swelling of the anterior end of the body, forming the so-called cephalic lobes (fig. 8 A, B, *Prc*). On this region are developed the labrum (D, *Lm*), the eyes, the stomodeal invagination (B, *Stom*), or mouth (D, *Mth*), the antennae (*Ant*), and in some cases the postantennal appendages, when the last are present (fig. 22 A, *2Ant*). The cephalic lobes soon become a very definite embryonic head (fig. 13 A, B, *Prc*), which either remains as the entire adult head (certain crustaceans), or constitutes the basic structure to which other body segments are added later to form the definitive head. It is impossible, therefore, to escape the conclusion that the primary embryonic head represents an early phylogenetic stage of cephalization, which was characteristic of the ancestors of all the arthropods. This first arthropod head may be termed the *protocephalon* (procephalon, Patten, 1912) to distinguish it from the prostomial head of the annelids, which might fittingly be designated an *archicephalon,* though Crampton (1928a) has proposed this term to denote a later formed cephalic region composed of the protocephalon and the mandibular segment.

There has been some uncertainty as to the number of segments involved in the protocephalon, for the segmentation of the cephalic lobes is never clearly marked in the embryo, and the existence of primary head segments is usually indicated rather by the presence of the head appendages, and by the divisions of the cephalic nerve mass, than by the appearance of metamerism in the head itself. It appears most probable, however, for reasons to be given presently, that the protocephalon comprises a prostomial region and two or three primitive somatic segments. The adult arthropod brain is a syncerebrum, consisting always of two parts, the protocerebral and deutocerebral lobes, to which in most cases are added the ganglia of a following segment, which constitute then the tritocerebral brain lobes. The protocerebral lobes are the most complex part of the brain, and they are probably formed of elements derived from a primitive prostomial region and from the ganglia of a preantennal segment. The deutocerebral lobes are simple developments of the ganglia of the antennal segment. The postantennal ganglia do not always enter into the composition of the definitive brain, and their segment is often not a part of the protocephalic head of the embryo, as indicated by the position of its appendages (fig. 8 D, *Pnt*, fig. 22 B, C, *Ch*; D, *Pnt*).

The segmental position of the mouth has been the subject of much difference of opinion. Most writers hold that the stomodeal invagination is situated in or before the first true head segment; others claim that it lies behind the second, or even the third segment (Comstock and Kochi, 1902; Holmgren, 1909, 1916; Henriksen, 1926). It was long ago pointed out by Lankester (1881) and by Goodrich (1898), however, that only on the assumption that *all* the true head segments of arthropods are *postoral* in position can the arthropod head segmentation be homologized with the anterior body segmentation of the annelids. Whatever part of the head is truly preoral, according to this view, belongs to the prostomium. Moreover, Lankester argued, the arthropod brain must contain a median anterior rudiment derived from the prostomial ganglionic mass, or archicerebrum, in addition to the ganglia of the component segments. " In the Chaetopoda," Lankester says, " the prae-oesophageal ganglion appears always to remain a pure archicerebrum. But in the Crustacea (and possibly all other Arthropoda * * *) the prae-oesophageal ganglion is a syn-cerebrum consisting of the archicerebrum and of the ganglion masses appropriate to the first and second pair of appendages which were originally postoral, but which have assumed a praeoral position whilst carrying their ganglionic masses up to the archicerebrum to fuse with it."

According to Lankester's view, then, the arthropod head should comprise a prostomial region and several postoral segments, and the brain correspondingly should include the prostomial archicerebrum and the paired postoral ganglia of the first two segments, with the ganglia of the third segment added in most cases. This idea, expressed theoretically by Lankester and by Goodrich, has been given substantial support by Heymons in his study of the development of *Scolopendra*, and more recently by Wiesmann from a study of the embryo of *Carausius*.

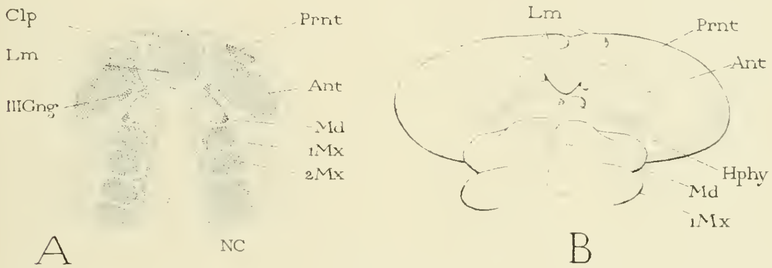

Fig. 14.—Young embryos of a chilopod and an insect showing rudiments of preantennal appendages.

A, anterior end of embryo of *Scolopendra* (from Heymons, 1901). B, same of a phasmid, *Carausius morosus* (from Wiesmann, 1926).

Ant, antenna; *Clp,* clypeus; *Hphy,* hypopharynx; *IIIGng,* tritocerebral ganglion; *Lm,* labrum; *Md,* mandible; *1Mx,* first maxilla; *2Mx,* second maxilla; *Prnt,* preantenna.

The head of *Scolopendra*, Heymons (1901) says, is formed during embryonic development by the union of an unsegmented preoral region and six postoral segments. The preoral part Heymons calls the " acron," taking this term from Janet (1899) in a slightly altered sense; it is the primary " Kopfstück," which clearly is the prostomium. The first true metamere, or postoral segment, is marked by a pair of small coelomic sacs in the mesoderm, and bears a pair of evanescent preantennal appendages (fig. 14, *Prnt*), which at an early stage lie on a line posterior to the mouth. Later, this segment loses its identity, and it can not be traced in the composition of the adult head. The second metamere is the antennal segment, bearing the antennae of chilopods (fig. 14 A, *Ant*) and insects (fig. 13 A, *Ant*), or the corresponding first antennae (antennules) of Crustacea (fig. 22 A, *1Ant*). The third metamere is the so-called intercalary segment, marked by a pair of coelomic sacs and corresponding ganglia in *Scolopendra* (fig. 14 A, *IIIGng*), bearing the highly developed second antennae of Crustacea (fig. 22 A, *2Ant*), the chelicerae of Arachnida (fig. 22, B, C, *Ch*), or the rudimentary post-antennal appendages of insects (fig. 22 D, *Pnt*). The fourth, fifth, and sixth metameres of the definitive chilopod head are the segments of the gnathal appendages (fig. 14 A, *Md, 1Mx, 2Mx*), which have united with the protocephalon.

The adult brain of *Scolopendra,* Heymons finds, is a composite of preoral and postoral ganglionic elements. The preoral parts are derived from the ectoderm of the prostomial region, the postoral parts are the paired ganglia of the first three head metameres. The prostomial elements include a median archicerebral rudiment that becomes the anterior part of the supraoesophageal commissure, and paired lateral rudiments, which form the dorsal cortical plate, the frontal lobes, and the optic lobes of the definitive brain. The ganglia of the first metamere, or preantennal segment, are a pair of small nerve masses which unite with the prostomial rudiments to form the protocerebral lobes of the adult brain. The ganglia of the antennal segment constitute the deutocerebrum; those of the postantennal segment become the tritocerebral lobes. The definitive location of the preantennal and antennal ganglia anterior to the mouth is a secondary one, and their union before or above the stomodeum, Heymons explains, comes about ontogenetically through the late development of the transverse commissures, which are not formed until the respective ganglia have acquired a preoral position. Wheeler (1893) had suggested that "the arthropod protocerebrum probably represents the annelid supraoesophageal ganglion, while the deuto- and tritocerebral segments, originally postoral, have moved forward to join the primitive brain." This essentially is also Heymon's earlier view (1895), but the existence of a separate pair of preantennal segmental ganglia was not suspected at that time.

For many years Heymons' observations on the development of the head of *Scolopendra* have remained unverified. It is, therefore, of particular interest to find essentially the same structure now described for an insect. Wiesmann (1926), studying the development of a phasmid, *Carausius morosus,* reports that the head is composed of a prostomial region and of six postoral metameres with paired coelomic sacs, of which the first metamere bears a pair of small, evanescent preantennal appendages (fig. 14 B, *Prnt*). Wiesmann, however, claims that the prostomium is a segment, because he finds in its mesoblastic tissue a pair of small cavities at the base of the paired rudiments of the labrum. The prostomial region of the adult arthropod contains a part of the body lumen, but from this it does not necessarily follow that its primitive mesoblastic cavities are homologous with the coelomic sacs of the true mesoderm, the extent of which should be limited by the length of the blastopore (see page 16). More likely, the mesoblast of the prostomium is a mesenchyme. In any case, however, it is only a matter of definition as to what we shall call a "segment."

The assumption of the presence of one or more preoral segments in addition to the prostomium disregards the fundamental relation between the embryonic germ layers. As already pointed out, the position of the mouth, or of the stomodeal invagination, marks the anterior end of the blastopore; the extent of the endoderm, except as it expands within the body, is determined by the length of the blastopore; the mesoderm is derived from the endoderm, and in the mesoderm metamerism originates. Therefore, in a bilateral animal, it seems clear, *true segments can not lie morphologically anterior to the mouth.* In the insect embryo, the anterior mesenteron rudiment actually defines the anterior limit of the mesoderm. Later formed segmental regions or appendages that appear to be preoral must, then, have acquired this position secondarily. In the figure of a *Peripatus* embryo (fig. 4 D) it is clearly seen how the anterior coelomic sacs may extend laterally before the mouth, and how corresponding appendages might come to have a preoral location topographically, though being morphologically postoral.

In the insect brain, there has never been noted a distinction between ganglionic rudiments of a preantennal segment and prostomial elements in the composition of the definitive protocerebral lobes, and the optic lobes are commonly referred to the first segment, though their independent origin is recognized. In the Crustacea, however, preantennal ganglia have been recorded, and Daiber (1921) says, "since ontogeny appears to give support to the view that the optic lobes are secondary structures, we must suppose that the segmental ganglia of the preantennal segment have been mostly suppressed, and that remains of them are represented in the ganglion cells of the roots of the oculomotor nerves. The ganglion pair found in the embryo of *Astacus* and *Iaera* between the ganglionic fundaments of the optic lobes and those of the antennal ganglia, and which later fuse with the brain ganglia, are probably to be explained as the true segmental ganglia of the preantennal appendages."

It may be questioned if there is ever a true segmental separation between the ocular and antennal region of the insect head, since whatever division does occur between the two parts appears relatively late in development, and is, therefore, probably of a secondary nature. Holmgren (1916), from a comparative study of the histology of the brain of annelids and arthropods, concluded that the protocerebral and deutocerebral parts of the definitive arthropod brain are secondary subdivisions of one primitive nerve mass, which, moreover, Holmgren would identify with the archicerebrum of the annelids. This conclusion is scarcely tenable, because, interpreted literally in terms of annelid structure, it would assign the antennae to the prostomium, and because it disregards the evidence of the postoral position of both the preantennal and antennal rudiments in the embryo.

It is usually assumed that the compound eyes of crustaceans and insects belong to the preantennal segment, which, on this assumption, is designated the "ocular" segment. Heymons (1921), however, claims that in *Scolopendra* the eyes and the optic lobes are derived from the ectoderm of the prostomial region. It is perhaps not necessary to believe that the grouped ocelli of the Chilopoda, even the composite "pseudo-compound" eyes of *Scutigera*, are related to the true compound eyes of crustaceans and insects, since the details of structure in the two cases are quite different; but it would seem less probable that the optic lobes of the brain should have a separate origin in the different arthropod groups. In many of the Crustacea, the compound eyes are pedunculate, being situated on segmented stalks having an ample musculature innervated from the protocerebrum, and this fact gives strong support to the idea that the eyestalks are appendages of the preantennal segment. Experiments have shown that if an eye-stalk is amputated, an antenna-like organ is often regenerated from the stump, on which an eye is not developed. These results recall the experiments of Schmitt-Jensen (1913, 1915) who cut off the antennae of a phasmid (*Carausius morosus*) and found that the appendages were regenerated in a form closely resembling the tarsi of the thoracic legs, each, in some cases, with a pair of terminal claws and a pulvillus.

It is difficult to evaluate these regeneration phenomena, for it seems highly improbable that the insect antenna ever had the specialized structure of the thoracic appendages of modern adult insects. Many writers hold that the crustacean eye-stalks are secondary outgrowths; and, as for their innervation from the protocerebral lobes, it might be claimed that the roots of the oculo-motor nerves come from a part of the protocerebrum derived from the prostomial archicerebrum. A definite opinion on these matters must await the results of further research. Since, however, in the Annelida, the prostomium is the seat of primary sensory development, and of the principal sense organs (fig. 10), it is at least in harmony with the assumed annelid ancestry of the Arthropoda to suppose that the arthropod eyes had their origin on the prostomial region of the head, and that their definitive posterior, dorsal location has resulted from the backward revolution of the anterior part of the head, a transformation that actually takes place in the growth of the embryo.

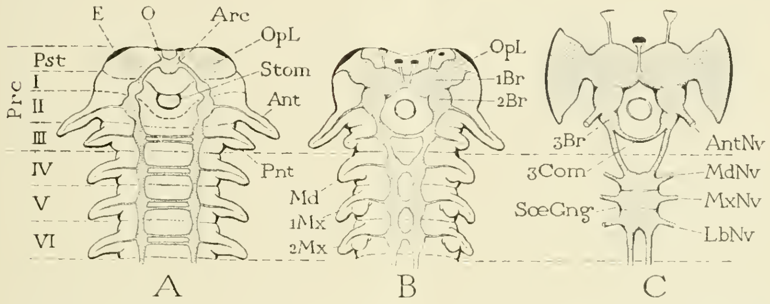

Fig. 15.—Evolution of the insect brain as it must be conceived *if* it includes an archicerebral rudiment, and *if* the compound eyes and the optic lobes are derived from the prostomial region, as claimed by Heymons.

A, theoretical generalized condition in which the ganglia of the prostomium (*Pst*), preantennal segment (*I*), antennal segment (*II*), and postantennal segment (*III*) are yet distinct, and in which the prostomial archicerebrum (*Arc*) is the brain.

B, the prostomium and the first three postoral segments united into a protocephalon; the brain composed of protocerebral lobes (*1Br*) formed of the archicerebrum (*Arc*) and ganglia of preantennal segment (*I*), and of deutocerebral lobes (*2Br*) representing ganglia of antennal segment (*II*); ganglia of postantennal segment (*III*) distinct and connected by postoral commissure. This condition retained in some lower crustaceans.

C, the definitive condition in all insects: the ganglia of postantennal segment (*III*) are added to the brain to form the tritocerebral lobes (*3Br*) of the latter; the ganglia of the gnathal segments (*IV, V, VI*) united in a compound suboesophageal ganglion (*SoeGng*).

Ant, antenna; *AntNv,* antennal nerve; *Arc,* archicerebrum; *1Br,* protocerebrum; *2Br,* deutocerebrum; *3Br,* tritocerebrum; *3Com,* tritocerebral commissure; *E,* compound eye; *LbNv,* labial nerve; *Md,* mandible; *MdNv,* mandibular nerve; *1Mx,* first maxilla; *2Mx,* second maxilla; *MxNv,* maxillary nerve; *O,* ocellus, *OpL,* optic lobe; *Pnt,* postantennal appendage; *Prc,* protocephalon; *Pst,* prostomium; *SoeGng,* suboesophageal ganglion; *Stom,* stomodeum.

We may conclude, without going farther into matters of controversy, that the immediate ancestors of the arthropods possessed a long, segmented body, at the anterior end of which was a specialized cephalic region, differing from the annelid head in that it comprised both the prostomium and the first two or three primitive body segments. In this early arthropod head, or protocephalon, the prostomium was still an important element; it perhaps carried the ocular organs, though tentacles were probably lacking, and it was extended dorsally on the facial aspect of the head between the bases of the antennae; on its ventral part, just before the mouth, there was a median lobe, the labrum. The first true head segment was much reduced, and its appendages were vestigial, or absent, unless they are represented in the eye-stalks of modern crustacea. The second head segment bore the antennae, simple, jointed appendages, which acquired a preoral position on the sides or front of the head by a secondary forward migration of their bases. These two segments and the prostomium became intimately fused, and in the ontogenetic development of present-day arthropods they appear as a unified, bilobed cephalic enlargement of the young embryo (figs. 8, 13, 16 A, B, C, 22 C, D, *Prc*). The brain at this stage was a syncerebrum, consisting of the archicerebrum and optic lobes fused with the ganglia of the preantennal and antennal segments, the two lateral nerve masses being united above the stomodeum (fig. 15 B). The third postoral segment was probably more or less closely associated with the second, but, judging from embryonic evidence (fig. 8 D), it did not at first form an integral part of the protocephalon. Its ganglia (later the tritocerebral lobes of the brain) at this stage constituted the first ganglia of the ventral nerve cord.

There can be no question that the arthropods are to be divided into two principal groups, one represented by the modern mandibulate forms, the other by those in which the appendages of the fourth segment retained the more generalized structure of the pedipalps of modern arachnids and xiphosurans. The separation of the two groups must have taken place in the protocephalon stage, for, as will later be shown, the unity of structure in the mandibles of all the mandibulate forms is such as to leave no doubt that the mandible is a common inheritance from a primitive mandibulate ancestor. But, before the definitive gnathal segments were added to the head, it would seem that the postantennal, or tritocerebral, appendages must have assumed the principal gnathal function by means of basal endites that served as masticatory lobes. In the xiphosurans and arachnids, these appendages have become the chelicerae, if modern embryology is rightly interpreted; in the crustaceans they lost their gnathal function and were developed into the second antennae; in the land-inhabiting myriapods and insects they have become reduced to rudiments, or to embryonic vestiges.

Insects were thoroughly modern in the later part of the Carboniferous period, when their remains are first known from the geological records. They must have been in the course of evolution during all the preceding extent of the Paleozoic era. Scorpions are found in the Silurian rocks, eurypterids in the Ordovician. Crustaceans, as represented by trilobites and other forms, were well developed in the Cambrian. The common arthropod ancestors in the protocephalic stage, long antedating the divergence of the several modern groups, must have existed, therefore, in remote ages of Pre-Cambrian time.

THE DEFINITIVE ARTHROPOD HEAD

In all modern arthropods, at least one pair, and usually several pairs of the segmental appendages following the protocephalon are modified to form organs of feeding, and they are crowded forward toward the mouth, those of the first pair coming to lie at the sides of the mouth opening. These appendages become the "mouth parts" of insects, and in general they may be termed the *gnathal appendages*. As a consequence of the forward transposition of the gnathal appendages, the postoral, sternal parts of the protocephalic segments are reduced and in most cases practically obliterated, their places being taken by the sterna of the gnathal segments. Early in the course of evolution, therefore, the gnathal segments themselves must have had a tendency to fuse with the protocephalon to form an enlarged head region; and nearly all the arthropods show in some degree the results of this tendency toward a more extensive cephalization of the anterior segments in the formation of a composite definitive head.

The condensation of the anterior segments has resulted in the formation of a definite cephalic structure in many of the arthropod groups. Among the Crustacea, however, there is much variation in the composition of the head. In the decapods, the protocephalon alone forms a distinct though immovable head piece—it is that part attached within the anterior end of the carapace, overhung by the rostrum, that bears the eyes, the antennules, the antennae, and the labrum, and which may be easily detached from the region covered by the carapace (fig. 17 B). The segments of the mandibles, the maxillae, the maxillipeds, and the legs are united dorsally in the wall of the carapace. The jaws of the decapods, therefore, are not attached to the primitive head, and though the protocephalon and carapace may be said to constitute a "cephalothorax," there appears to be no reason for regarding the region of the carapace formed of the gnathal segments as a part of the head, since there is no evidence that the decapod head ever included more than the protocephalon.

The generalized malacostracan crustacean, *Anaspides,* also retains the protocephalon as an independent head piece attached within the projecting anterior rim of the mandibular segment. The large mandibular segment is likewise free from the following maxillary segment, but the two maxillary segments and the first maxilliped segment are fused into a composite region bearing the maxillae and the first maxillipeds.

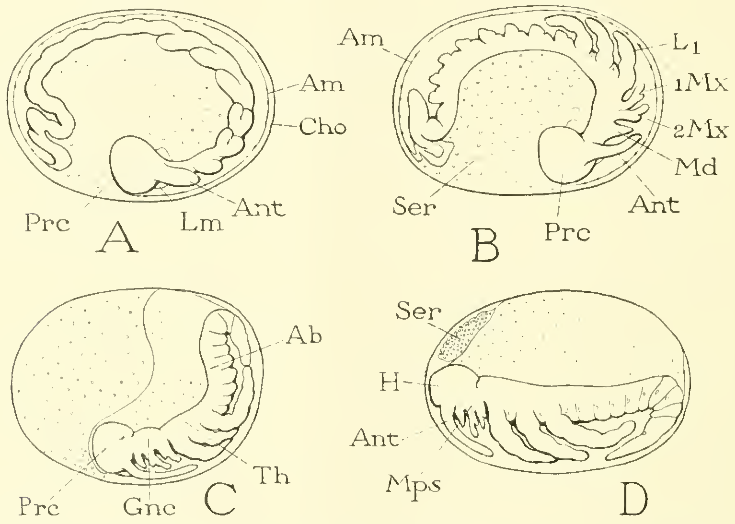

Fig. 16.—Four stages in the development of *Forficula.* (From Heymons, 1895.)

A, embryo differentiated into a protocephalic head, and a body. B, appendages of gnathal segments (*Md, 1Mx, 2Mx*) well developed. C, the gnathocephalic region (*Gnc*) compact, but still distinct from protocephalic region. D, protocephalic and gnathocephalic regions united in the definitive head (*H*).

Ab, abdomen; *Am,* amnion; *Ant,* antenna; *Cho,* chorion; *Gnc,* gnathocephalon; *H,* definitive head; L_1, first leg; *Lm,* labrum; *Md,* mandible; *1Mx,* first maxilla; *2Mx,* second maxilla; *Prc,* protocephalon; *Ser,* serosa; *Th,* thorax.

In most of the other Crustacea, the head either is a unified cephalic structure consisting of the protocephalon and the three gnathal segments, in some forms with one or two of the maxilliped segments added, or it exhibits varying stages in the condensation of the gnathal and maxilliped segments with the protocephalon. A relatively primitive condition is shown by *Eubranchipus* (Anostraca), in which the protocephalon itself is a distinct and well-developed head capsule (fig. 17 A, *Prc*) carrying the first and second antennae (*1Ant, 2Ant*), the eyes (*E*), and the labrum (*Lm*); but to it is attached the tergum of the mandibular segment (IV) bearing the large, jaw-like mandibles (*Md*). Following the mandibular segment, comes the region of the two maxillary segments (*V* + *VI*) with the rudimentary first and second maxillae on its under surface. *Eubranchipus* thus represents a stage in the evolution of the head almost equivalent to that in the embryonic development of insects shown in figure 16 C where the gnathal segments (*Gnc*), in process of being united with the protocephalon (*Prc*), still constitute a distinct body region. In *Limnadia* (Choncostraca), the structure of the head is essentially as in *Eubranchipus,* but the gnathal segments are more intimately united with the protocephalon, and the second antennae are typical biramous appendages.

In *Apus* (Notostraca) the head is more highly evolved (fig. 17 D, E), and its lateral and posterior margins are produced into a large cephalic carapace (*Cp*). The protocephalon and the gnathal segments are united, but their respective areas are well defined dorsally (D). The protocephalon (*Prc*) is set off from the mandibular tergum (*IV*) by a sinuous transverse groove (*x*); on its upper surface it bears the group of head sense organs, including the compound eyes (*E*), and, on its lower surface (E), the antennae (*Ant*) and the labrum (*Lm*). The tergal region of the mandibular segment (D, *IV*) is distinctly limited posteriorly by a second suture (*y*) on the dorsal surface of the carapace, behind which is a narrow area representing the dorsal wall of the two maxillary segments (*V* + *VI*), from the posterior edge of which is reflected the median part of the carapace. Back of the head, and partly covered by the carapace, is the long, flexible body of forty or more segments. Here is a condition quite different, therefore, from that of the decapods (fig. 17 B, C), in which latter the protocephalon has retained its individuality, while the gnathal segments have united with those of the maxillipeds and the ambulatory limbs to form the region of the carapace (C, *Cp*).

In the Amphipoda and the Isopoda, the head consists of the protocephalon, the three gnathal segments, and one or two of the maxilliped segments. In these groups, however, the head segments are fused into a cranium-like capsule (figs. 17 F, H, 28 A), in which little or no trace of the original head segmentation is to be discovered. In form and general appearance, the amphipod head (fig. 17 H) often curiously suggests the head of an insect, but both the amphipod and the isopod cranium appears to contain at least one more segment than is known to be included in either the insect or the myriapod head.

The head in the Chilopoda (fig. 17 G), Diplopoda (K), and Hexapoda (I), is a highly evolved cranial capsule composed of the protocephalon and the gnathal segments, but so thoroughly fused are all the cephalic elements that the segmental composition of the head is no longer discernible in the head wall. The insect head is a well-standardized structure, which, though varying greatly with regard to form, is the same in fundamental construction throughout all the insect orders. The myriapod head, likewise, exhibits no modifications in its basic structure, and, from a study of the head alone, it is impossible to judge whether the cephalic structures of the myriapods and of the insects has had a common origin, or whether in each group the head has been evolved along a separate line of development. Considering the differences in the head appendages, and especially in the mandibles, as will be shown later, it appears probable, however, that the myriapods and insects are not as closely related as the form of the head might otherwise suggest. The insect head resembles also the head of the amphipods and isopods, as already pointed out, but it can be shown that the evolution of the head appendages has run parallel in the insects and the crustaceans, and here again, therefore, we must conclude that the similarities in the head structure are only equal results of the primary tendency toward a condensation of the gnathal segments with the protocephalon, in consequence of the drafting of the appendages of these segments into the service of the mouth.

Considering all the evidence, especially that which will be adduced from a study of the mandibles, it seems most probable that the several principal arthropod groups represent independent lines of descent from ancestors differentiated at an early stage in the evolution of the composite head structure. The early development of the thorax in the insect embryo, before the gnathal segments are added to the head (fig. 13), is evidence that the insects formed a distinct arthropod group long before the completion of the definitive head, unless the differentiation of the thorax in the young insect embryo is to be regarded as a precocious embryonic development, comparable with the early development of the head in the vertebrate embryo. It is scarcely necessary, however, to postulate, as suggested by Walton (1927), a separate origin of the insects from annelids.

In the Arachnida, the protocephalon constitutes a distinct head at an early embryonic period, but, as shown in Balfour's illustration (fig. 22 C, *Prc*), it does not include at this stage the tritocerebral segment (*III*) in its composition. At a later stage, however, the tritocerebral segment and the five following segments are usually added to the protocephalon to form a cephalothorax (fig. 17 J, *Cth*). The appendages of the cephalothorax of an adult arachnid are the chelicerae

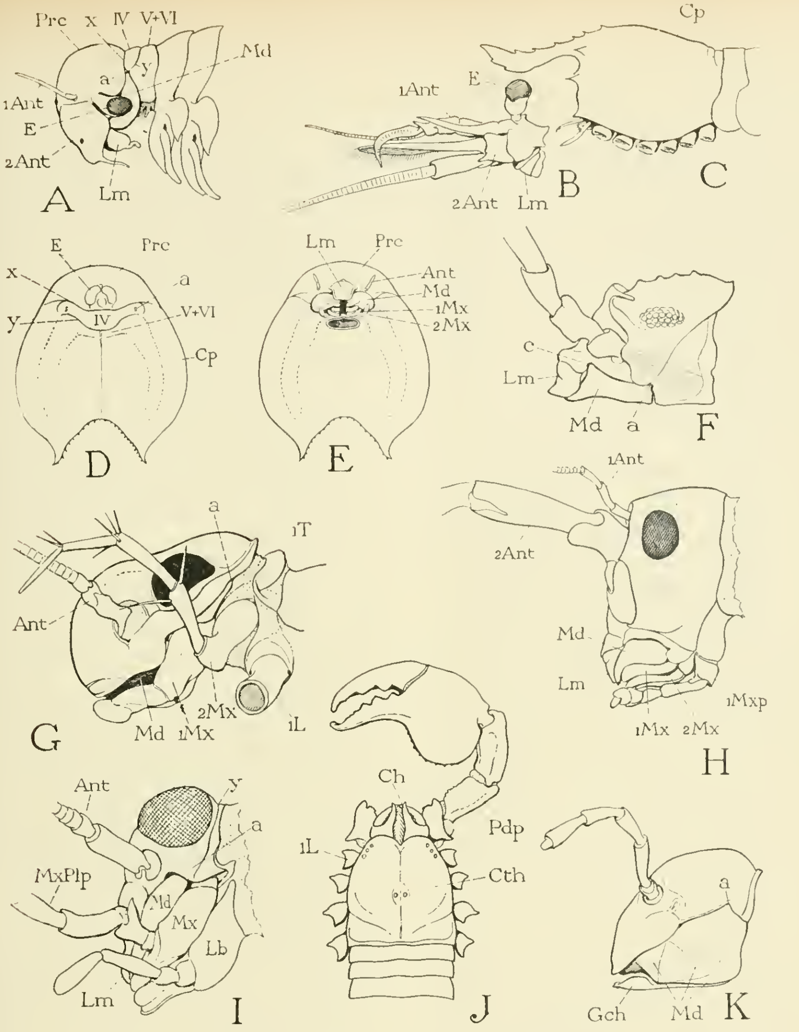

FIG. 17.—Head or head region of various arthropods.

A, head and anterior body region of *Eubranchipus vernalis* (Phyllopoda, Anostraca), with gnathal segments (*IV, V, VI*) distinct from protocephalon. B, protocephalic head piece of *Spirontocaris polaris* (Decapoda) separated from the carapace. C, carapace of *Spirontocaris polaris* from which the protocephalon (B) has been detached. D, head and head carapace of *Apus longicaudata* (Phyllopoda, Concostraca), dorsal view, showing segments *IV, V, VI* added to protocephalon (*Prc*) and forming carapace. E, ventral view of same. F, head of *Porcellio* (Isopoda) with maxillae removed. G, head of *Scutigera forceps* (Chilopoda). H, head of *Orchestoidea californica* (Amphipoda). I, head of *Machilis* (apterygote insect). J, cephalothorax and anterior abdominal segments of a scorpion (Arachnida). K, head of *Euryurus erythropygus* (Diplopoda).

a, dorsal (or posterior) articulation of mandible; *Ant*, antenna; *1Ant*, first antenna; *2Ant*, second antenna; *c*, anterior articulation of mandible; *Ch*, chelicera; *Cp*, carapace; *Cth*, cephalothorax; *E*, compound eye; *Gch*, gnathochilarium; *IV*, mandibular segment; *1L*, first leg; *Lm*, labrum; *Md*, mandible; *1Mx*, first maxilla; *2Mx*, second maxilla; *1Mxp*, first maxilliped; *MxPlp*, maxillary palpus; *Pdp*, pedipalp; *Prc*, protocephalon; *1T*, first tergum; *V*, first maxillary segment; *VI*, second maxillary segment; *x*, suture between protocephalon and mandibular segment; *y*, suture between mandibular and first maxillary segments.

(*Ch*), or tritocerebral appendages, the pedipalps (*Pdp*), which are the mandibular appendages of other groups, and four pairs of legs (*L*), which are represented by the two maxillae and the first two pairs of maxillipeds in the Crustacea. Antennae are lacking in all adult arachnids, but some writers (Croneberg, 1880, Jaworowski, 1891) have reported the presence of antennal rudiments in the embryos of certain species (fig. 22 B, *Ant*). The comparative lack of specialization in the arachnid limbs suggests that the Arachnida are an ancient group of arthropods having little direct relationship to other forms, except to the Xiphosura and possibly to the extinct eurypterids. In the Solpugida, the cephalothoracic region is divided into an anterior cephalic part carrying the eyes, the mouth, the chelicerae, the pedipalps, and the first pair of legs, and into a posterior thoracic part carrying the second, third, and fourth pairs of legs. The division between these two body parts, as compared with insects, falls between the first and second maxillary segments, and the parts, therefore, are in no way comparable with the insect head and thorax. In the ticks (Ixodoidea), the head-like structure known as the capitulum is said to bear only the chelicerae and the pedipalps. In its composition it is thus equivalent to the protocephalon with only the first gnathal segment added.

Cephalization in the Arthropoda, then, apparently has progressed from the prostomial stage (archicephalon) to the formation of a protocephalon, from a protocephalon to the usual definitive head, or telocephalon, and finally to the union of head and body regions in a cephalothorax. The archicephalic stage is to be inferred from the evident derivation of the arthropods from an annelid-like ancestor having the prostomium as the only defined head. The protocephalic stage is shown in the development of all arthropod embryos, and is retained in the decapods and related crustaceans, where the carapace is a gnatho-thoracic structure. The telocephalic stage exhibits a progressive evolution in phyllopods, amphipods, and isopods by the addition of one, two and three, four or five segments to the protocephalon; in insects and myriapods it has reached a standardized condition in which the head is composed of six segments and the prostomium. The cephalothoracic stage is characteristic of the Xiphosura and Arachnida, in which the segments of all the fully developed appendages are united, and combined with the prostomium.

A study of the head alone does not furnish a sufficient basis for a discussion of the inter-relationships of the various arthropod groups, but it must be recognized that the facts here given, and others to be described in this paper have an important bearing on the subject, and that their significance has not been fully taken into account by those who have formulated theories of arthropod relationships and descent.

II. GENERAL STRUCTURE OF THE INSECT HEAD

The almost complete suppression of the primitive intersegmental lines in the insect head makes a study of the head segmentation in insects a difficult matter, and investigators differ widely in their views as to the parts of the adult head that have been derived from the several head segments. Since the prostomial region and the three segments of the protocephalon are never distinct, even in the earliest embryonic stages, it seems fruitless to speculate as to what areas of the adult cranium are to be attributed to them individually, but the general protocephalic region must be at least the region of the clypeus and frons, the compound eyes, and the antennae. In as much as the muscles of the three pairs of gnathal appendages have their origins in the posterior parts of the head, it is reasonable to assume that the areas upon which these muscles arise represent the walls of the gnathal segments that have been added to the protocephalon.

According to Heymons (1895), who bases his conclusions on a study of the embryonic development of the head in *Periplaneta* and *Anisolabis*, the entire cranium except the frons and the region of the compound eyes and the antennae is formed from the walls of the mandibular, maxillary, and labial segments. Janet (1899), taking the attachments of the muscles of the appendages on the head walls as criteria of the respective segmental limits, maps the cranium into areas that closely correspond with the segmental regions claimed by Heymons. From Riley (1904), on the other hand, we get a quite different conception of the definitive head structure. According to Riley's account of the development of the head of *Blatta*, the great cephalic lobes of the embryo form most of the adult head capsule. The dorsal and lateral walls of the gnathal segments, Riley says, are so reduced by the posterior growth of the cephalic lobes that little remains of them in the adult head—only the extreme posterior and postero-lateral parts of the cranial walls, and the postoral ventral region being referable to them. This view must assume that the muscles of the gnathal segments have moved forward to the protocephalic region as their own segments became reduced, and it would nullify the evidence of head segmentation based on muscle attachments. The writer is inclined to agree with Heymons and Janet that the muscle attachments on the lateral and dorsal walls of the cranium should be pretty closely indicative of the limits of the gnathal terga in the composition of the head, but it must be admitted that muscle bases can undergo rather extensive migrations. That the gnathal segments contribute a considerable part to the cranial walls of the definitive insect head is clearly suggested by Heymons' figures of the development of Forficula (fig. 16), and, as already shown, there can be no doubt that these segments enter bodily into the head composition of Crustacea that have a well-defined composite head. With insects, it is a question of the degree of reduction that the gnathal segments have suffered after their union with the protocephalon.

By whatever phylogenetic course the cephalic region of the insect body has arrived at its definitive state, it acquired long ago a cranium-like form, and a definite structure that has since been modified only in superficial characters, adaptive to different modes of living and to different ways of feeding in the various groups of modern insects.

THE HEAD CAPSULE

The chitinous walls of the definitive head capsule constitute the *epicranium*. In an adult insect head preserving the typical embryonic position, with the facial aspect directed forward (fig. 18 B), the mouth parts are suspended from the ventro-lateral edges of the epicranium. A pair of *compound eyes* (*E*) typically have a lateral or dorso-lateral position, and three ocelli (*O*) occur between them on the dorsal or facial area of the head (A). The antennae (*Ant*) vary in their location from positions just above the bases of the mandibles (fig. 50 A, *Ant*) to a more median site on the dorsal part of the face (fig. 18 A, B). The top of the head, or *vertex* (fig. 18 A, B, *Vx*), is marked by a median *coronal suture* (A, *cs*) that turns downward on the face and divides into the *frontal sutures* (*fs*), which diverge ventrally to the anterior articulations of the mandibles (*c*). The coronal suture and the frontal sutures together constitute the *epicranial suture*. The lines of these sutures are marked internally by ridges, and the coronal ridge is sometimes developed into a plate supporting muscle attachments. The median facial region between and below the frontal sutures is the *frons* (*Fr*), ventral to which is the *clypeus* (*Clp*), with the *labrum* (*Lm*) suspended from the lower margin of the latter.

The posterior surface of the epicranium (fig. 18 C) is occupied by the opening (*For*) from the head cavity into the neck, usually a large aperture, properly termed the *foramen magnum* by analogy with vertebrate anatomy, but commonly called the " occipital foramen " by entomologists. The surface of the head surrounding the foramen dorsally and laterally is the occipital area. Its anterior limit is defined in orthopteroid insects by the occipital suture (*ocs*). The occipital area is subdivided by a suture lying close to its posterior margin, here named the *postoccipital suture* (fig. 18 B, C, *pos*), which sets off a narrow marginal rim of the cranium, or *postocciput* (*Poc*), to which the neck membrane is directly attached. The postoccipital suture, though sometimes inconspicuous by reason of the reduction of the

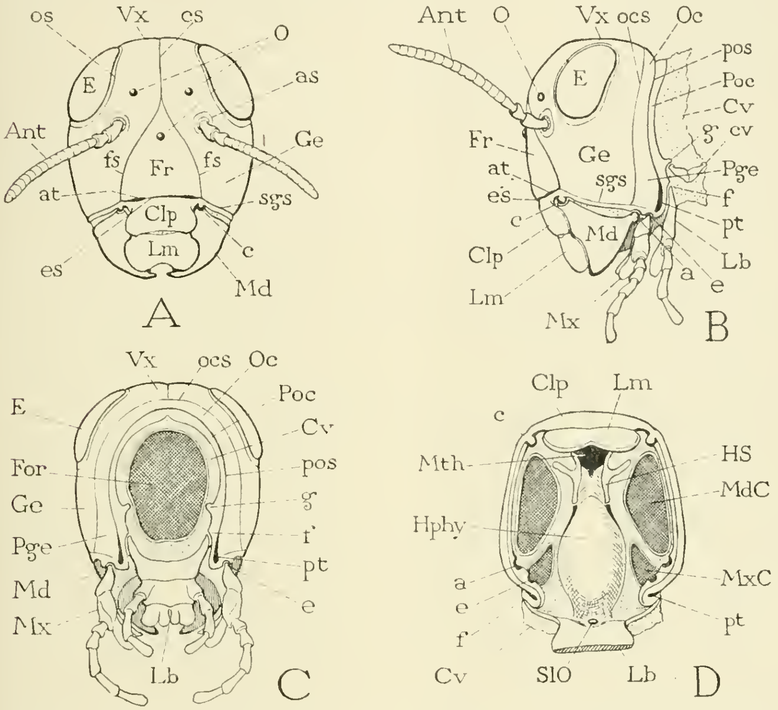

FIG. 18.—Generalized structure of the head of an adult pterygote insect, diagrammatic.

A, anterior view. B, lateral. C, posterior. D, ventral.

a, posterior articulation of mandible; *Ant,* antenna; *as,* antennal suture; *at,* anterior tentorial pit; *c,* anterior articulation of mandible with cranium; *Clp,* clypeus; *cs,* coronal suture; *Cv,* neck (cervix); *cv,* cervical sclerite; *E,* compound eye; *e,* articulation of maxilla with postgenal margin of cranium; *f,* articulation of labium with postoccipital rim (*Poc*) of epicranium; *For,* foramen magnum; *Fr,* frons; *fs,* frontal suture; *g,* postoccipital condyle for articulation of first cervical sclerite with head; *Ge,* gena; *Hphy,* hypopharynx; *HS,* suspensorium of hypopharynx; *Lb,* labium; *Lm,* labrum; *Md,* mandible; *MdC,* opening in head wall where mandible removed; *Mth,* mouth; *Mx,* maxilla; *MxC,* opening in head wall where maxilla removed; *O,* ocelli; *Oc,* occiput; *os,* ocular suture; *ocs,* occipital suture; *Pge,* postgena; *Poc,* postocciput; *pos,* postoccipital suture; *pt,* posterior tentorial pit; *sgs,* subgenal suture; *SlO,* orifice of salivary duct; *Vx,* vertex.

postoccipital rim, is the most constant suture of the cranium. The dorsal part of the occipital area before it is termed the *occiput* (*Oc*), and the lateral ventral parts the *postgenae* (*Pge*). Rarely the occiput and the postgenae are separated, as in *Melanoplus*, by a short suture on each side.

The lateral areas of the cranium, between the occipital suture and the frontal sutures, and separated dorsally by the coronal suture, have been appropriately termed by Crampton (1921) the *parietals*. The parietal area behind and below the compound eye is the *gena* (fig. 18 B, *Ge*), that between the eyes is the vertex. The lower marginal area of each lateral wall of the head is commonly marked by a submarginal suture (fig. 18 A, B, *sgs*), which forms an internal ridge strengthening the ventral lateral edge of the cranium (fig. 39 A, *SgR*). The suture has been termed the "mando-genal" suture (Yuasa, 1920, MacGillivray, 1923), but, for grammatical reasons, the writer would substitute the term *subgenal suture*, and call the corresponding ridge the *subgenal ridge*. The ridge is sometimes known as the "pleurostoma." When an epistomal ridge separates the clypeus from the frons, it unites the anterior ends of the subgenal ridges.

The true ventral wall of the head is the region between the bases of the mouth parts (fig. 18 D), the median area of which is produced into the variously modified lobe known as the *hypopharynx* (*Hphy*). Anterior to the base of the hypopharynx, and immediately behind the posterior, or epipharyngeal, surface of the labrum and clypeus is the *mouth* (*Mth*). The space inclosed by the labrum and the mouth parts is often called the "mouth cavity," but, since it lies entirely outside the body, it is more properly a *preoral cavity*.

The frons, clypeus, and labrum belong to the prostomial region of the head. The frons and clypeus are not always distinct, but when they are separated, the dividing fronto-clypeal groove, or *epistomal suture* (fig. 18 A, B, *es*), extends typically between the bases of the mandibles. That the more primitive division of the prostomium, however, is that between the labrum and the clypeal area is evidenced by the fact that the labral retractor muscles always extend from the base of the labrum to the frontal area (fig. 19, *2*, *3*). The clypeus, on the other hand, can not be regarded as a mere articular region between the labrum and the frons, secondarily developed into a chitinous plate, as some writers have suggested, because the most anterior of the dilator muscles of the stomodeum have their origins upon its inner surface (fig. 41, *33*, *34*). The external suture separating the clypeus from the frons appears to be incidental to the development of an internal *epistomal ridge* (fig. 39 A, B, C, *ER*) forming a brace between the anterior articulations of the mandibles. The typical position of the fronto-clypeal suture is on a line between the mandibular bases passing through the roots of the anterior arms of the tentorium; but the suture and its ridge are often arched upward, as in the Hymenoptera, Psocidae, and Homoptera (fig. 46 E, F, G, H), or bent dorsally in an acute angle, as in the caterpillars (fig. 50 A). The fronto-clypeal suture is to be identified by the origin of the anterior arms of the tentorium from its internal ridge; the frontal region above it is marked by the attachments of the labral retractor muscles, and the clypeal region below is distinguished by the origins of the first anterior stomodeal muscles on its inner surface. The value of these characters will be illustrated in succeeding parts of this paper. The clypeus may be secondarily divided into an *anteclypeus* and a *postclypeus,* the latter sometimes attaining a special development, as in Homoptera.

If the prostomial region of the adult head embraces only the labrum, clypeus, and frons, the frontal sutures must separate the prostomial area from the area derived from the segmental elements of the head, as maintained by Riley (1904); but, if the compound eyes and the optic lobes of the brain had also a prostomial origin, as claimed by Heymons (1895, 1901), then an area between and including the compound eyes must be regarded as a part of the general prostomial region. Following Heymons' interpretation, Berlese (1909) recognizes a "postfrons" embracing the ocular region, and a "prefrons," which is the ordinary frontal sclerite. Whatever the facts of the case may be, it will be most convenient to retain the name "frons" for the latter sclerite. In general, the frontal sutures mark the lines of cleavage in the facial cuticula at the time of a molt, but there are exceptions to this rule, for the cuticular splits, when extended from the end of the coronal suture, may diverge to the sides of the frons, and may even extend laterad of the bases of the antennae, as in Odonata (fig. 46 I).

The frontal sutures are often obscured or are lacking, and the frons then becomes confluent with the lateral epicranial walls. The anterior median ocellus, when present, is located upon the frons, or on the frontal region; the paired ocelli usually lie above or posterior to the upper ends of the frontal sutures, though in some cases they appear to be in the sutures. The antennae are usually situated on the facial aspect of the head, but they never truly arise upon the frons. In post-embryonic stages, the antennae occupy positions varying from points just above the mandibles, as in caterpillars, to points laterad of the upper end of the frons; they sometimes lie against the frontal sutures, and by an approximation of their bases, they may constrict the frons between them. The reversed relative position of the antennae and the compound eyes, as between embryonic and adult stages, comes about through the posterior revolution of the ocular region and the forward migration of the antennae. The antennal socket is generally strengthened by an internal circular ridge on the cranial wall surrounding it (fig. 39 A, *AR*), and the compound eye is likewise encircled by an inflection of the cuticula close to its base (*OR*). These ridges and their external sutures set off the so-called ocular and antennal sclerites (fig. 18 A, B).

The posterior, or occipital, surface of the epicranium (fig. 18 C) is usually but a narrow area surrounding the foramen magnum (*For*) dorsally and laterally, the foramen being normally completed ventrally by the base of the labium (*Lb*), or by the neck membrane in which the labium is suspended. When the foramen is small, however, the occipital area often becomes a wide transverse surface on the back of the head, and its ventral, or postgenal, parts may form median processes that sometimes unite into a bridge beneath the foramen, in which case the latter becomes entirely surrounded by chitinous walls (fig. 48 B, C). The occipital suture (fig. 18 B, C, *ocs*), when present, is generally located about where the dorsal and lateral areas of the head wall are reflected upon the posterior surface. It does not seem probable that the occipital suture is a primitive intersegmental line of the head, for, though it lies approximately between the mandibular and maxillary regions, it does not consistently separate the bases of the mandibular and maxillary muscles, and the posterior articulation of the mandible is with the postgena *posterior* to the lower end of the suture (fig. 18 B, *a*). As is the case with most of the skeletal grooves, it is probable that the occipital suture has no significance in itself, and that it is merely incidental to its corresponding internal ridge, which strengthens the posterior part of the cranium along the line where the dorsal and lateral areas are reflected into the posterior surface.

In the Machilidae the posterior part of the epicranium is crossed by a prominent suture lying close behind the eyes dorsally (fig. 17 I, *y*) and extending downward on each side of the head to a point on the lateral margin of the cranium between the base of the mandible (*Md*) and the base of the maxilla (*Mx*). This suture, therefore, appears to separate the region of the mandibular segment from that of the maxillary segment in the cranial wall, and if it does so, it may be the homologue of the mandibulo-maxillary suture in the phyllopod crustaceans (fig. 17 A, D, *y*), and of the corresponding suture in the more generalized malacostracan forms, such as *Anaspides*. Crampton

(1928a) has called the mandibulo-maxillary suture the "archicephalic" suture, since he calls the region before it the "archicephalon," but the term thus applied denotes too much antiquity for a stage that is clearly subsequent to several others in the head evolution. A similarly-placed suture is present in the head of *Japyx* (fig. 30 B, *PcR*), but the relation of the suture here to the bases of the head appendages can not be determined. The occipital suture of the pterygote insect head, ending laterally *before* the posterior mandibular articulations, therefore, is probably not the mandibulo-maxillary suture of the simpler crustaceans, or the homologue of the posterior suture in the head of *Machilis*.

The postoccipital suture (fig. 18 B, C, *pos*) is a most important landmark of the head because it is invariably present, and because of its constant anatomical relations to other parts. The posterior tentorial pits (*pt*) are always located in its lower ends, and if the pits migrate in position, as in some of the Coleoptera and other insects, the lower ends of the suture are correspondingly lengthened (fig. 49 C, *pt, pt*). Frequently the suture is inconspicuous by reason of its closeness to the margin of the cranium, and for this reason, probably, it has not been given sufficient attention by entomologists. Comstock and Kochi (1902) believed that the suture is the groove between the pleurites of the maxillary segment; but Riley (1904) claimed, from a study of the developing head of *Blatta,* that the suture is the intersegmental groove between the maxillary and the labial segments, and that the postoccipital sclerite is a remnant of the wall of the labial segment, which segment is otherwise obliterated or represented in the anterior part of the neck membrane. This view is at least in harmony with certain anatomical relations in the adult head, and is tentatively adopted in this paper.

Internally, the postoccipital suture forms a postoccipital ridge (fig. 39 A, *PoR*) just within the foramen magnum, and upon this ridge are attached the anterior ends of the dorsal muscles of the prothorax (figs. 45 A, 57 A, B, C). The ridge, therefore, must be a primary intersegmental fold corresponding with the ridges or phragmata supporting the longitudinal muscles in the thorax and abdomen. If it does not represent the fold between the maxillary and labial segments, it should be that between the labial segment and the prothorax. If the first possibility is true, as claimed by Riley, there is an intersegmental line lost somewhere in the neck, and the muscles going from the first phragma of the thorax to the postoccipital ridge of the head must be regarded as extending through the region of two primary segments. If, on the other hand, the posterior ridge of the head is the intersegmental fold between the labial and the prothoracic segments, the muscles in the neck are all muscles of the prothorax, and the neck itself is prothoracic. It is evident that much morphological significance hinges on this problem. The neck sclerites, for example, in the first case, might belong either to the labial segment or to the prothorax, or to both; in the second case, they could pertain only to the prothorax. The relation of the posterior arms of the tentorium to the postoccipital suture and ridge will be noted under the special description of the tentorium (page 50).

The labrum, the appendages of the gnathal segments, and the hypopharynx constitute the *mouth parts* of insects. The gnathal appendages are the mandibles, the first maxillae, and the second maxillae, which last are united in insects to form a labium. The morphology of these appendages will be discussed in a later section (pages 79-90), but it is important here to understand their relations to the cranial wall. The mandible in biting pterygote insects is typically suspended from the lower edge of the gena and postgena, and swings outward and inward on a longitudinal axis between anterior and posterior articulations with the head wall. The anterior articulation is with a condyle at the contingent angles of the gena and clypeus (fig. 18 A, B, D, *c*), the posterior with a shallow facet on the lower margin of the postgena (B, D, *a*).

The maxilla hangs from the lower edge of the postgena, upon which it is freely movable by a single articular point just before the lower end of the postoccipital suture (fig. 18 B, D, *e*). The labium, in generalized insects, is suspended from the neck membrane, but each lateral angle of its transverse base is closely attached to the postoccipital rim of the head (B, C, D, *f*). The positions of the maxillary and labial articulations relative to the postoccipital suture (*pos*) are in harmony with the idea that this suture is the intersegmental groove between the maxillary and the labial segments. In some insects, the labium is shifted forward between the ventral edges of the postgenae, and thus becomes removed from its primitive position. In such cases, as in caterpillars (fig. 53 A) and adult Hymenoptera (fig. 48 B, C), the ventral angles of the postgenae may approach each other medially, or even unite into a ventral bridge (hypostoma) behind the labium. In other insects, in which the posterior part of the head is lengthened, the base of the labium is elongated between the postgenae, forming the plate known as the *gula*. These modifications, however, will be discussed more fully in section VI of this paper.

The head is attached to the thorax by a cylindrical, membranous neck, or *cervix* (fig. 18 B, *Cv*). In each lateral wall of the neck there is typically a pair of lateral neck plates, or cervical sclerites, hinged to each other. The first is articulated anteriorly to a small process, the *odontoidea* (Yuasa, 1920), or the *occipital condyle* (Crampton, 1921), on the rear margin of the postoccipital rim of the head (B, C, *g*) just above the base of the labium. The posterior neck plate articulates with the anterior margin of the prothoracic episternum. Other cervical sclerites of less constant form are sometimes present in the ventral wall of the neck, and occasionally there are chitinizations also in the dorsal wall. The lateral neck sclerites are important elements in the mechanism for moving the head on the thorax. Upon them are inserted muscles from the postoccipital ridge of the head, and from the inner surface of the prothoracic tergum (fig. 45 A, B).

The uncertainty of the morphology of the insect neck, and consequently of the neck skeleton, furnishes a problem still to be solved. As already pointed out, the status of the neck and of its sclerites will depend upon that of the postoccipital rim of the head: if the latter is an anterior remnant of the labial segment, the neck sclerites may belong to the labial segment, or also to the prothorax; if, however, the postoccipital ridge of the head, upon which the anterior ends of the dorsal prothoracic muscles are attached, is the infolding between the head and the prothorax, then the neck can only be a part of the prothorax. The second assumption looks improbable in view of the position of the labial articulations in generalized insects (fig. 18 B *f*).

THE LABRUM AND EPIPHARYNX

The labrum is a characteristic feature of the arthropod head, and probably corresponds with the tip of the annelid prostomium. In the embryo (figs. 8 D, 13, 22 A, D, *Lm*), it appears at an early stage as a median ventral lobe of the prostomial region, lying just before the point where the stomodeal invagination will be formed. In the mature head the mouth opening (figs. 18 D, 19, *Mth*) is immediately behind the base of the labrum (*Lm*), and the posterior, or epipharyngeal, surface of the latter is continued directly into the dorsal wall of the pharynx (fig. 19, *Phy*). The adult labrum takes on various forms in different insects, but it is typically a broad flap freely suspended from the lower edge of the clypeus (fig. 18 A, *Lm*). When movable, the labrum is provided with muscles inserted on its base, having their origin on the inner surface of the frons. Typically, there are two pairs of these muscles, one pair (fig. 19, *2*) inserted anteriorly on the labral base, the other (*3*) posteriorly on the chitinous bars of the inner face of the labrum known as the tormae (figs. 37 B, 42 A).

The points of origin of the labral muscles serve to identify the frontal sclerite, or the true frontal region when the frontal sutures are lacking. Frequently there is only one pair of labral muscles (fig. 50 E, G), and when the labrum is immovable on the clypeus, both pairs are lacking. The labro-frontal muscles are to be regarded as median muscles of the prostomium. On the posterior surface of the labrum there is often a median lobe, the *epipharynx* (fig. 19 *Ephy*), that fits between the bases of the closed mandibles, and obstructs the entrance to the mouth (*Mth*) when the labrum is closed upon the hypopharynx.

THE STOMODEUM

In the embryonic development of arthropods, the endodermal part of the alimentary canal, which becomes the true stomach, is formed within the body and has at first no opening to the exterior. The anterior and the posterior ectodermal parts, or *stomodeum* and *proctodeum,* of the definitive alimentary tube are ingrowths of the ectoderm at the two extremities of the blastopore. Their inner ends abut against the ends of the endodermal sac, and their final union with the latter takes place by an absorption of the adjacent walls. In some insects the proctodeum does not open into the ventriculus until the end of the larval stage.

If the ontogenetic development of the alimentary canal is to be translated literally into phylogenetic evolution, we should have to believe that the arthropod stomach was once a closed sac, and that the stomodeum and proctodeum are secondary means of communication with it. But, if insects have had a continuous line of free-living ancestors, this seems unlikely, and it is more probable that, in their actual history, the stomodeum and the proctodeum have been formed as open invagination of the primitive circumoral and circumanal regions, and that the discontinuous development of the three parts of the alimentary canal in ontogeny is an adaptation to embryonic or larval conditions.

It has been proposed by Janet (1899, 1911) that the stomodeum consists of the walls of three primitive segments that once formed the true anterior end of the body, but which have been inverted, as the primitive mouth, now the orifice from the stomodeum into the stomach, was retracted. This theory would give a plausible explanation of the presence of the stomodeal ganglia, but it must assume that these ganglia have been formed from paired ventral rudiments which have migrated dorsally and fused on the upper surface of the stomodeum. The known origin of these ganglia from the epithelium of the dorsal wall of the stomodeum, however, is direct evidence that they do not belong to the system of the ventral nerve cord.

The stomodeum (fig. 19) is usually differentiated into several parts in the mature insect, which may include a *buccal cavity* (*BuC*), a *pharynx* (*Phy*), an *oesophagus* (*OE*), a *crop* (*Cr*), and a *proventriculus* (*Pvent*). The entire length of the tube, except the extreme anterior end, is surrounded by circular and longitudinal muscles. In general the circular muscles form an external layer, the longitudinals an internal layer, but the arrangement and relative development of the two layers varies much in different insects, as will be illustrated in the grasshopper and the caterpillar (pages 115 and 145). The buccal cavity, the pharynx, the oesophagus, and the crop are provided with dilator, or "suspensory" muscles arising on the walls of the head, on the tentorium, and on the walls of the thorax (figs. 41, 44, 55).

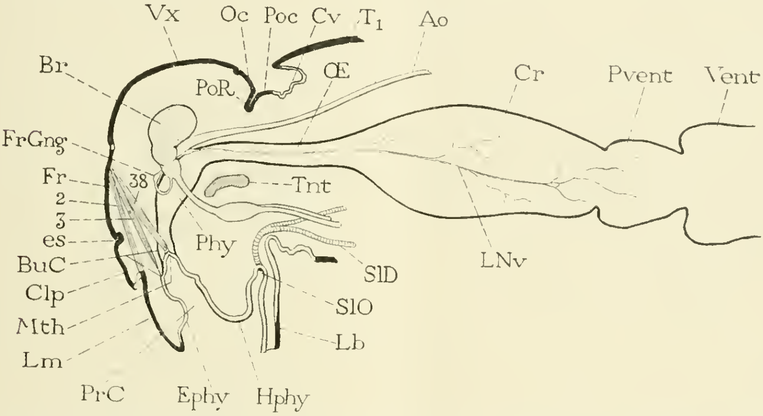

FIG. 19.—The stomodeum of an insect, and its relation to associated organs in the head, diagrammatic.

Ao, aorta; *Br*, brain; *BuC*, buccal cavity; *Clp*, clypeus; *Cr*, crop; *Ephy*, epipharynx; *es*, epistomal suture; *Fr*, frons; *FrGng*, frontal ganglion; *Hphy*, hypopharynx; *Lb*, labium; *Lm*, labrum; *LNv*, lateral stomodeal nerve; *Mth*, mouth; *Oc*, occiput; *Œ*, oesophagus; *Phy*, pharynx; *Poc*, Postocciput; *PoR*, postoccipital ridge; *PrC*, preoral cavity; *Pvent*, proventriculus; *SlD*, salivary duct; *SlO*, orifice of salivary duct; T_1, tergum of prothorax; *Tent*, body of tentorium; *Vent*, ventriculus; *Vx*, vertex; *2*, anterior labral muscle; *3*, posterior labral muscle; *38*, retractor muscle of the mouth angle.

The parts of the stomodeum can not be concisely defined, because they are functional adaptations of structure varying in different insects, rather than strictly morphological regions of the stomodeal tube. The buccal cavity is the anterior, or ventral, end of the stomodeum, including the region of the mouth opening (fig. 19, *BuC*). The dilator muscles of the stomodeum that have their insertion on the dorsal wall of the buccal cavity arise upon the clypeus, and this relation between the region of the buccal cavity and the clypeus appears to be a constant one. In the cicada, the sucking pump is a mouth structure quite distinct from the true pharynx, and the origin of its dilator muscles upon the large striated facial sclerite of the head wall helps to identify this plate as the clypeus (fig. 46 H, *Clp*). In many insects, however, there is no structural distinction between the region of the buccal cavity and that of the pharynx. The retractor muscles of the mouth angles (fig. 19, *38*) have their origin on the inner surface of the frons, and their points of attachment give another character, in addition to that furnished by the labral muscles, for the determination of the frons when the limits of this sclerite are obscured, or the identity of the plate otherwise doubtful. The mouth retractors are inserted upon chitinous processes that extend into the stomodeal walls at the mouth angles from the suspensorial rods of the hypopharynx (fig. 42 B, *y*). Usually these processes are short and inconspicuous, but in the bees they form long arms united at their bases in a chitinous plate in the floor of the buccal cavity.

The region of the pharynx is usually marked by a dilation of the stomodeum, and sometimes it forms an abrupt enlargement of the tube. The frontal ganglion is situated on its dorsal wall (fig. 19, *FrGng*), and the circumoesophageal connectives lie at its sides. The dorsal dilator muscles of the pharynx have their origin on the frons, on the parietals, on the dorsal arms of the tentorium, and rarely one or two pairs may encroach on the area of the clypeus (caterpillars). The pharynx of the Orthoptera is divided into an " anterior pharynx " and a " posterior pharynx " (Eidmann, 1925), but the part called the posterior pharynx, the dorsal dilator muscles of which arise on the posterior dorsal walls of the head, appears to correspond with the oesophageal region in some other insects.

The oesophagus, when there is a distinct oesophageal region, is a narrow tubular part of the stomodeum following the pharynx (fig. 19, *OE*), and varies much in length in different insects. Its posterior end enlarges into the crop (*Cr*), or the crop is sometimes a lateral diverticulum. The terminal part of the stomodeum in biting insects is usually a well-defined proventriculus (*Pvent*). The chitinous intima of all parts of the stomodeum may be provided with short hairs, spicules, or chitinous nodules, but the inner cuticular structures are best developed in the proventriculus, where they generally have the form of longitudinal ridges or plates, with deep grooves between them.

According to the views of the earlier students of the digestive organs of insects, the proventriculus constituted a gizzard; its inner chitinous fold, and its sheath of strong muscle fibers, it was pointed out, must serve to break up the larger or harder pieces of the food material not sufficiently crushed by the jaws. Experimental evidence of this function, however, is lacking, and Plateau (1874, 1876) argued that the proventriculus is merely an apparatus for passing the food from the crop into the stomach. More recently, Ramme (1913) has shown that the proventriculus, in Orthoptera and Coleoptera at least, has another important function in that the furrows between its chitinous ridges serve to conduct the digestive secretions of the ventriculus into the crop, where they attack the food material in advance of its entrance into the stomach. The channels between the proventricular folds, then, rather than the folds themselves, are to be regarded as having the primary functional importance. Otherwise, the proventriculus serves to conduct the food mass into the ventriculus. In *Dytiscus,* according to Ramme, the armature of the proventriculus retains the indigestible parts of the food, which are later ejected from the mouth; but in Orthoptera all the food matter passes through the alimentary canal.

THE HYPOPHARYNX

When the gnathal segments are added to the protocephalon during embryonic growth, their sternal parts lose their identities in the general postoral ventral wall of the definitive head. On this region there is developed a median lobe between the bases of the mouth parts known as the *hypopharynx* (fig. 18 D, *Hphy*). The name is poorly chosen, because the organ in question lies on an exterior surface of the head entirely outside the pharynx, but it is a heritage of earlier days in entomology and is now well established in entomological terminology.

There is a difference of opinion among embryologists as to how many of the gnathal sterna contribute to the formation of the hypopharynx. According to Heymons (1901), the hypopharynx is formed in insects on the sternal region of the mandibular and first maxillary segments, but in the chilopods it arises on the mandibular segment alone. The fusion of the bases of the second maxillae in insects, and the similar union of both pairs of maxillary appendages in the chilopods gives reasons for this view, but, as will be shown presently, the primitive adductor muscles of all the gnathal appendages have their origin on the hypopharyngeal region in the chilopods and in the apterygote insects—a condition which indicates that at least some part of each gnathal sternum enters into the hypopharyngeal region. Riley (1904) describes the hypopharynx of *Blatella germanica* as formed in the embryo from the sterna of the mandibular, first maxillary, and second maxillary segments.

In the more generalized pterygote insects, the hypopharynx hangs like a tongue in the preoral cavity (fig. 19, *Hphy*) behind the mouth (*Mth*), shut in anteriorly by the labrum, laterally by the mandibles and maxillae, and posteriorly by the labium. Its base generally extends posteriorly to the labium (figs. 18 D, 19), and in the groove between the two organs is situated the orifice of the salivary duct (*SLO*). In general, therefore, the salivary orifice serves as a landmark for separating the hypopharynx from the labium, or for determining the hypopharyngeal region when a specific hypopharyngeal lobe is lacking, as in the honeybee; but the opening of the salivary duct may be at the apex of the hypopharynx, as in Homoptera, or, when the hypopharynx and labium are united, as in many insect larvae (fig. 54 A, D), it may lie at the tip of the combined labio-hypopharyngeal structure.

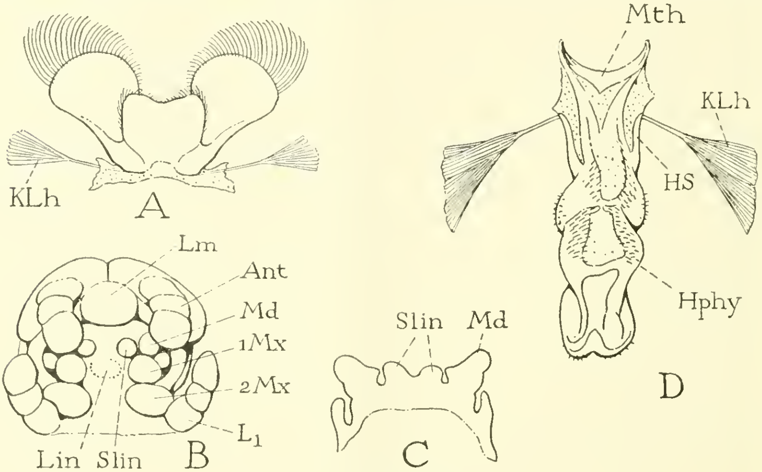

FIG. 20.—The hypopharynx.

A, three-lobed hypopharynx of an ephemerid nymph, with ventral adductor muscles of mandibles (*KLh*) attached to its base. B, head of embryo of *Anurida maritima* (from Folsom, 1900), ventral view, showing median lingua (*Lin*) and paired superlinguae (*Slin*) that combine to form hypopharynx of adult. C, transverse section through mandibles of embryo of *Tomocerus plumbeus* (from Hoffman, 1911), showing origin of superlinguae (*Slin*) from inner angles of mandibles. D, hypopharynx of *Microcentrum rhombifolium*, ventral, with rudiments of suspensorial arms (*HS*) on which ventral mandibular adductors (*KLh*) are attached.

In some insects the hypopharynx consists of a median part and of two lateral lobes. In such cases it usually projects forward like a lower lip beneath the mouth opening. The lateral lobes are best developed in the more generalized insects, both apterygote (fig. 21 D, *Hphy*) and pterygote (fig. 20 A), and in coleopteran larvae, but possible traces of them are to be found in many of the higher orders. The occurrence of the hypopharyngeal lobes has been well reviewed by Crampton (1921a) and by Evans (1921), and those of lepidopteran larvae have been described by de Gryse (1915). The median lobe of the hypopharynx is best distinguished as the *lingua,* though some writers call it the "glossa"; the lateral lobes have been termed "paraglossae" and "maxillulae," but Folsom (1900) has given them the more distinctive name of *superlinguae,* because the lateral lobes of the labium are commonly known as the paraglossae.

The nature of the superlingual lobes of the hypopharynx has been much discussed. Hansen (1893) proposed that they represent the first maxillae, or maxillulae, of Crustacea, and Folsom (1900) believed that their identity as such was established in the discovery of what he regarded as a corresponding pair of ganglia in the embryonic head of *Anurida.* Crampton (1921a), on the other hand, argued that the superlinguae of insects must be the homologues of the paragnatha of Crustacea, and it will be shown later in this paper that the identity in the relations of each of these organs to other structures of the head can leave little doubt of the truth of Crampton's contention. The superlinguae, then, are not the first maxillae of Crustacea; but if the superlinguae represent a segment in the insect head, the paragnatha have a like significance in the crustacean head. It now appears probable, however, that neither of these organs has a segmental value, since Folsom's claim of the presence of a pair of superlingual ganglia has not been verified by subsequent research, and Hoffmann (1911) appears to have demonstrated that in the collembolan, *Tomocerus plumbeus,* the superlinguae are derived during embryonic development from the inner basal angles of the mandibles (fig. 20 C, *Slin*).

In the Chilopoda and Diplopoda there is a single median hypopharyngeal lobe forming a projecting lip below the mouth opening (fig. 21 A, B, C, *Hphy*). In the Crustacea, the paragnaths usually lie to each side of the median line, and are associated with the first maxillae, but in some forms, as in *Gammarus,* they are united on a common median base, forming a bilobed structure very similar to the hypopharynx of the apterygote insect *Japyx* (fig. 21 D).

The base of the hypopharynx is supported anteriorly, in generalized insects, by a pair of chitinous plates or bars that extend laterally at each side of the mouth, and form a suspensorial apparatus for the hypopharynx (fig. 18 D, *HS*). The plates appear to be chitinous remnants of the mandibular sternum. They are best developed in the myriapods. In *Lithobius* (fig. 21 A), *Scolopendra* (B), and *Scutigera* (C), each plate is a large, irregular sclerite (*HS*) attached laterally to the lower margin of the head wall at a point (*d*) before the base of the mandible, and ending mesally in the side of the hypopharynx. In some chilopods a process on the anterior free part of the mandible articulates against the hypopharyngeal plate of the same side.

Attems (1926) describes the suspensorial plates of the hypopharynx in the chilopods as a mandibular support (" kommandibular Gerüst "), but the homologous sclerites and their apodemal processes in the diplopods he calls the " tentorium." The writer has not observed corresponding structures in the Crustacea. In insects the hypopharyngeal supports are variously developed, but are usually reduced, and often rudimentary. In *Machilis* (fig. 21 E, *HS*) their outer ends are broadly fused with the basal angles of the clypeus (*Clp*); in *Japyx* (D) the plates are reduced and united in a W-shaped sclerite in the base of the hypopharynx; in *Dissosteira* (fig. 42 B, C, *HS*) they are slender bars extending outward to the bases of the adductor apodemes of the mandibles; in *Microcentrum* (fig. 20 D, *HS*) they are rudimentary prongs diverging from the base of the hypopharynx. In many cases a process extends from each hypopharyngeal bar into the lateral walls of the mouth, where it supports the insertion of the retractor muscle of the mouth angle (figs. 42 B, 44, *38*), and may give rise to an extensive pharyngeal skeleton. In the bees these processes form the long rods bearing the protractor muscles of the pharynx, though the hypopharyngeal bars themselves are lacking.

In the chilopods and in the apterygote insects, an apodemal process arises from the inner end of each suspensorial plate of the hypopharynx, and extends posteriorly below the sides of the pharynx (fig. 21 A, C, D, *HA*). Upon these apodemes arise the retractor muscles of the hypopharynx, the ventral dilators of the pharynx, and ventral adductors of the mandibles, the first maxillae, and the second maxillae. These muscles are all properly *sternal* muscles, and their origin in the Chilopoda and Apterygota on the hypopharyngeal apodemes, which are sternal apophyses of the head, attests a primitive relation in these groups between the muscles of the gnathal appendages and the sternal parts of their segments. In some of the Crustacea, the corresponding muscles have their origins on a central endoskeletal structure that arises on the sternal region of the gnathal segments behind the mouth In many Crustacea, however, and in the Diplopoda, the ventral muscles of the gnathal appendages, especially those of the mandibles, show a highly specialized condition in that they are mostly separated from their sternal connections and united upon a common transverse ligament. In the pterygote insects the hypopharyngeal muscles, the ventral dilators of the pharynx, and most of the fibers of the ventral adductors of the mouth part appendages arise on the endoskeletal structure of the head known as the *tentorium*. Evidently, then, the

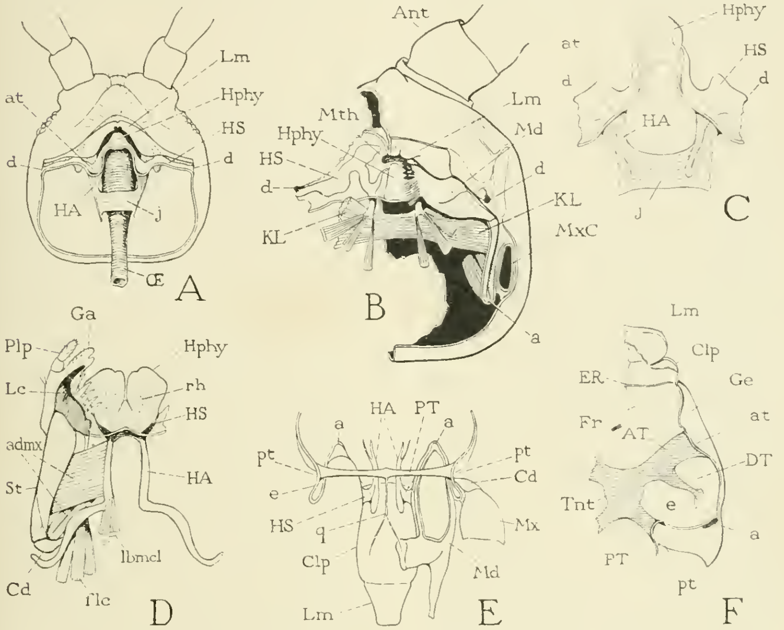

FIG. 21.—The hypopharyngeal apophyses and the tentorium.

A, under surface of head of *Lithobius*, mandibles and maxillae removed, showing suspensorial plates (*HS*) of hypopharynx suspended from points (*d*) on margins of head, and hypopharyngeal apophyses (*HA*) invaginated from their inner ends and connected by ligamentous bridge (*j*) beneath pharynx.

B, Head of *Scolopendra*, ventral, maxillae and right half of cranium removed, showing attachment of mandibular adductors (*KL*, *KL*) on ligament uniting the hypopharyngeal apodemes.

C, *Scutigera forceps*, ventral view of hypopharynx (*Hphy*), suspensorial plates (*HS*), their apodemes (*HA*) and uniting ligament (*j*).

D, *Heterojapyx gallardi*, ventral view of right maxilla, hypopharynx (*Hphy*), and hypopharyngeal apodemes (*HA*) upon which arise muscles of the maxilla (*admx*), the labium (*lbmcl*), and the mandibles (not shown).

E, *Nesomachilis maoricus*, posterior view of unconnected anterior and posterior arms of tentorium (*HA*, *PT*), part of the head wall with clypeus (*Clp*) and labrum (*Lm*), base of maxilla (*Mx*), and mandible (*Md*).

F, Ephemerid nymph, ventral view of tentorium and part of left side of head, showing anterior tentorial arms (*AT*) arising from ventral margin of gena (*Ge*).

tentorium must have some relationship with the hypopharyngeal apophyses of the Apterygota and the Chilopoda, and with the sternal apodemes of the gnathal segments in the Crustacea. The nature of this relationship will be shown following the anatomical description of the tentorium.

THE TENTORIUM

The tentorium of orthopteroid insects is a horizontal, X-shaped brace between the lower edges of the cranial walls (fig. 39 B, *Tnt*). It consists of a central *body* with a pair of divergent *anterior arms* (*AT*) and a pair of divergent *posterior arms* (*PT*). The arms are hollow invaginations of the head wall. The roots of the anterior arms appear as external pits, in most insects lying just before the anterior articulations of the mandibles (fig. 18 A, B, *at*) in the epistomal suture, when the latter is present; the roots of the posterior arms form depressions in the lower ends of the postoccipital suture (B, C, *pt*). Usually there is a pair of internal processes, or *dorsal arms* of the tentorium (fig. 39 A, C, *DT*), arising centrally at the junction of the anterior arms with the body, and extending dorsally and anteriorly to the facial wall of the head near the bases of the antennae. Sometimes these arms are fused with the cuticula of the cranial wall, but generally they are attached only to the hypodermis, and often their outer ends are weak and tendinous. Riley (1904) says that the dorsal arms of the tentorium of *Blatta* arise in the embryo as processes from the inner ends of the anterior arms. The tentorium undergoes many modifications of form in different insects, according as certain parts become more highly developed and others reduced, but its typical structure is seldom obscured.

In its typical form, the tentorium is a simple " tent," as its name implies, composed of the central plate, or body, suspended by the four stays, or arms, from the four ventral angles of the head. Yet, morphologists have always been suspicious of accepting the tentorial structure at its apparent face value. Some writers would homologize the arms with the apophyses of the thoracic pleura, others with the apophyses of the thoracic sterna. Either disposition suggests, then, that there should be a pair of such processes for each of the head segments. Wheeler (1889) thought that he found in the embryo of *Leptinotarsa* (*Doryphora*) five pairs of tentorial invaginations, representing each head segment but the last. Other investigators have not verified this, and most students of the development of the insect head report the presence of only the two pairs of invaginations that form the anterior and the posterior arms of the definitive structure.

Besides bracing the walls of the cranium, the tentorium gives attachment to muscles of the hypopharynx, of the mandibles (in some insects), of the maxillae, of the labium, of the pharynx, and, when dorsal arms are present, to muscles of the antennae. Such a comprehensive relation to the musculature of the head appendages, therefore, furnishes ample ground for the suspicion that the tentorium includes in its composition more than is evident in its adult structure. Janet (1899), after making a careful analysis of the muscles arising upon the tentorium in the head of an ant, concluded that the tentorium must be composed at least of three pairs of processes corresponding with the antennal, the maxillary, and the labial segments. The antennal processes, according to Janet's homology, are the anterior arms, the labial processes are the posterior arms; the maxillary processes are assumed to have lost their connection with the head wall, after their inner ends had united with those of the other processes in the formation of the central tentorial body. Janet's scheme, however, is not complete without the assumption of mandibular elements in the tentorium, for, in some of the lower insects, certain muscles of the mandibles are attached upon the tentorium. Since these muscles were not then known, Janet suggested that the homotypes of the mandibular tentorial processes are represented on the mandibular segment by the points where the corpora allata have their origin in the hypodermis. All the tentorial processes, both real and hypothetical, Janet regarded as homologous with the *furcal invaginations* of the thoracic sterna, because the tentorium of the adult insect supports the *adductor* muscles of the head appendages. This is sound reasoning, and the conclusion probably comes as close to the truth in the matter as the truth may be approached by induction from the facts presented by the higher insects; but a study of the Apterygota, the Myriapoda, and the Crustacea throws an entirely new light on the origin and evolution of the tentorium, and dispels the obscurity which has led to so many theories concerning the nature of this head structure.

The morphology of the tentorium, briefly summarized from facts later to be described, is as follows: The anterior arms and the part of the body of the tentorium on which the ventral adductor muscles of the mandibles, the maxillae, and the labium have their origin are identical with the hypopharyngeal apophyses of the Myriapoda and Apterygota, and have their prototypes in the ventral apodemes of the gnathal segments in Crustacea. From their positions just laterad of the hypopharynx, the bases of the apophyses have moved outward in the ventral wall of the head before the bases of the mandibles to the lateral ventral edges of the cranium, where they come to lie in the subgenal sutures.

Then, proceeding forward, they have migrated to the fronto-clypeal suture on the facial aspect of the head. The primitive condition is found in Chilopoda, Diplopoda, and Apterygota; intermediate conditions occur in the Ephemerida and Odonata; the final condition is characteristic of all Pterygota, except the Ephemerida and Odonata. The posterior tentorial arms are invaginations in the lower ends of the postoccipital suture of the cranium, which is probably the intersegmental groove between the first and second maxillary segments. These arms are absent in the Myriapoda and most Apterygota; they are present in *Machilis* and in some Crustacea, where their inner ends are united to form a transverse bar through the back of the head; they are present in all Pterygota, where the anterior arms are united with them to form the typical four-branched tentorium. The dorsal tentorial arms are processes of the anterior arms and may secondarily become attached to the dorsal or facial wall of the cranium.

The muscles of the tentorium, with the exception of the antennal muscles usually arising on the dorsal arms in pterygote insects, are all muscles that primitively have their origin on the *sterna of the gnathal segments.* They include two sets of median longitudinal ventral muscles, one set going anteriorly to the hypopharynx, and the other posteriorly to the sternum or sternal processes of the prothorax; they include also the transverse ventral adductors of the mandibles, the first maxillae, and the second maxillae, and the ventral dilators of the pharynx. In the Chilopoda and Apterygota, all these muscles arise from the hypopharyngeal apodemes, except some of the mandibular muscles which may become detached from the apophyses, or retain a direct connection with the base of the hypopharynx. The hypopharyngeal apodemes are, therefore, paired apophyses of the region of the gnathal sterna. There is no evidence that they are composite structures; each appears to be a single process invaginated from a chitinous remnant of the mandibular sternum (the suspensorial plate of the hypopharynx), but since it bears the sternal muscles of the three gnathal appendages, either the bases of these muscles have migrated forward, or each apophysis is a process of the three united sterna. When the two apophyses move to the positions on the front wall of the head characteristic of the orthopteroid branch of the Pterygota, they retain the muscle attachments, and when they unite with the posterior arms to form the typical tentorium, the head presents the aspect of having none of the ordinary sternal muscles of the appendages attached on its sternal region, except for the small mandibular adductors present in some of the lower Pterygota that have retained their origin directly on the base of the hypopharynx.

The antennal muscles that take their origin on the dorsal arms of the tentorium in most adult pterygote insects have evidently migrated secondarily to this position after the attachment of these arms to the dorsal wall of the cranium. In the crustaceans, myriapods, and many insect larvae, the antennal muscles have the primitive attachment on the walls of the head capsule (figs. 23 B, 50 B, C, E, F, *3*).

Evidence fully supporting the above statements is easily adduced from a comparative study of the head structure and the gnathal musculature in the Myriapoda, Apterygota, Ephemerida, Odonata, and orthopteroid Pterygota. Many of the facts have been described by other writers, but their significance appears to have been unrecognized.

In the Chilopoda, the hypopharyngeal apodemes are large chitinous processes (fig. 21 A, B, *HA*) that arise from the inner ends of the suspensorial plates of the hypopharynx (*HS*) close to the base of the hypopharynx (*Hphy*). Each projects posteriorly at the side of the pharynx, and the two are bridged below the pharynx by a sheet of ligamentous tissue (A, C, *j*). Upon the arms, or on processes of the arms, and on the uniting ligament arise the ventral adductor muscles of the mandibles (B, *KL*), and of the first and second maxillae. The relations here are the same as in the thorax of an insect where the ventral leg muscles arise from a pair of sternal apophyses. In the Diplopoda, a highly specialized condition has arisen through the separation of the inner ends of the muscles from the apodemes and their union across the median line by a tough transverse ligament (fig. 26 A, *k*). The large mandibular adductors (*KL, KL*) here pull against each other from the two ends of the ligament. The ligamentous bridge suggests, in a way, the body of a tentorium, but as will be seen it has no relation to the insect tentorium. A similar condition of the mandibular adductors exists in many of the Crustacea (fig. 27 A, B, *KL*), and in some of the fibers of these muscles in the apterygote insects (C, D, *KLk*), as will be described later in connection with the mandibles (page 62).

In the Apterygota, the hypopharyngeal apodemes are well developed and extend far back in the head. Those of *Japyx* (fig. 21 D, *HA*) are slender rods running parallel beneath the sides of the pharynx and then diverging outward and posteriorly to the head wall behind the cardines of the maxillae (*Cd*), but their ends appear to be free and not attached to the cuticula of the cranium. Upon these arms arise the hypopharyngeal retractor muscles, a set of mandibular adductors (fig. 27 C, *KLt*), the adductors of the maxillary stipes and cardo (fig. 21 D, *admx*), and muscles of the labium (*lbmcl*). The hypopharyngeal skeleton of *Japyx* was described first by Meinert (1867), and later by von Stummer-Traunfels (1891). The latter writer called it the " Stützegerüst," or supporting framework of the hypopharynx; he figured it in *Tetrodontophora gigas* and in *Campodea staphylinus,* and he says it has essentially the same structure in *Japyx, Campodea,* and Collembola. Folsom (1899) described the hypopharyngeal skeleton of the collembolan, *Orchesella cincta,* as consisting of a thin median plate with paired anterior, dorsal, and posterior arms. The anterior arms, he says, are united with the lateral lobes of the hypopharynx, the others are attached to the cranial walls by fibrous strands. This structure of the collembolan head, upon which arise muscles of the pharynx, the mandibles, and the maxillae, Folsom points out is the true tentorium, homologous with that of the Orthoptera and other mandibulate insects. The failure to recognize this fact, he says, " has led students to assign an altogether undue importance to the ' Stützapparat ' of the ligula (hypopharynx), which has erroneously been regarded as a sort of substitute for a tentorium." " Partly as a result of this error," he adds, " systematists have acquired an exaggerated opinion of the differences which separate Collembola and Thysanura from insects of other orders."

The tentorium of the Protura has been described by Berlese (1910) and by Prell (1913). The anterior arms of the structure are united in a median bar, but each arm itself is forked anteriorly, and the two forks are said by Prell to make connections with the base of the hypopharynx and with the fronto-clypeal ridge of the head. Both Berlese and Prell call this endoskeletal structure of the proturan head the " tentorium," but Prell observes that it has a close resemblance to the " Zungenapparat " of the Collembola and suggests a homology with this structure. It is now to be seen that the two structures are, indeed, identical, and that the hypopharyngeal apophyses of the Apterygota are the primary elements of the pterygote tentorium.

In *Machilis* (figs. 21 E, 27 D), the hypopharyngeal apodemes (*HA*) arise from suspensorial plates (fig. 21 E, *HS*) connected laterally with the cranial walls as in the chilopods, but their points of origin from these plates are at the basal angles of the clypeus (*Clp*). There is in *Machilis* also a well-developed posterior tentorial bar (*PT*) extending transversely through the back of the head from pits (*pt*) in the lower ends of the postoccipital suture. The maxillary cardines (*Cd*) are attached to the margin of the cranium just anterior to these posterior tentorial depressions. The inner ends of the hypopharyngeal apodemes (*HA*), or anterior tentorial arms, of *Machilis* become weak and fibrous, and in specimens cleaned in caustic they do not connect with the posterior tentorial bar. The tentorium of *Machilis,* therefore, appears to be in an intermediate stage of development in which the anterior and posterior elements are still independent of each other. A two-branded fiber (*q*) extends downward in the head from the middle of the posterior bar. A similar tentorial bar is strongly developed in the crustacean, *Gammarus* (fig. 28 B, *PT*).

In all the pterygote insects the anterior and the posterior arms of the tentorium are united with each other, and typically the lateral elements are fused across the median line to form the central plate-like body of the tentorium (figs. 21 F, 39 B, *Tnt*). The median plate, however, is not developed in all cases; in the caterpillars the posterior arms form only a slender bar through the back of the head, to which the anterior arms are attached on each side (fig. 53 D, *Tnt*), and a similar condition exists in adults of the higher Hymenoptera, where the posterior bar appears as a slender yoke between the posterior ends of the large anterior arms. In all insects of the orthopteroid branch of the Pterygota, the roots of the anterior tentorial arms lie in the fronto-clypeal suture (figs. 18 A, B, 36 A, B, 46 A, B, D, F, *at, at*). So constantly do they have this position that they become diagnostic marks of the suture, or of the fronto-clypeal line when a suture is absent. In the Ephemerida (*nymphs*), however, the roots of the broad anterior arms (fig. 21 F, *at*) lie at the edges of the inflected ventral areas of the genae (*Ge*), before the bases of the mandibles. Here, clearly, is a more primitive condition, differing from that of the Myriapoda and Apterygota only in that the bases of the hypopharyngeal apodemes have moved outward from the hypopharynx to the lateral walls of the cranium. In the Odonata the roots of the anterior tentorial arms lie on the sides of the head, above the bases of the mandibles, in the subgenal sutures. This is a second step toward the orthopteroid condition, in which finally the tentorial roots have migrated anteriorly into the fronto-clypeal suture on the facial aspect of the head.

The writer believes that the facts presented in the foregoing descriptions solve the riddle of the insect tentorium, and explain the seeming anomalies of the gnathal musculature, though he has not shown the mode of union between the anterior and the posterior arms in forming the characteristic tentorium of pterygote insects, and though the method of the change in the connections of the anterior arms from the base of the hypopharynx to the facial aspect of the head may still be held as not exactly determined. The origin of the *anterior tentorial* arms as *apophyses of the sternal region of the gnathal segments,* however, shows that the adductor muscles of the gnathal appendages, which arise on the tentorium in pterygote insects, are the true sternal muscles of the head appendages, and this relation brings the musculature of these appendages directly in line with that of the thoracic legs, which are moved by sets of muscles arising on the tergum and the sternum in each segment. In the Pterygota, it will further be shown, the mandibles lose their primitive sternal adductors, and, by a change in the nature of the mandibular articulation with the head, the primitive tergal promotor and remotor muscles of the jaw become the functional abductors and adductors.

III. THE HEAD APPENDAGES

The segmental appendages of the head in an adult insect are the antennae, the mandibles, the maxillae, and the labium. The antennae belong to the second, or deutocerebral, segment of the protocephalon, the other appendages to the gnathal segments. In many insect embryos there is present a pair of small lobes on the third protocephalic segment, which lobes are unquestionably rudiments of the tritocerebral appendages. Preantennal appendages have been reported in Scolopendra and in the phasmid insect, *Carausius* (fig. 14 A, B *Prnt*). As already pointed out, there is some reason for regarding the crustacean eye stalks as being the appendages of the preantennal segment, though the true status of these organs has not yet been demonstrated.

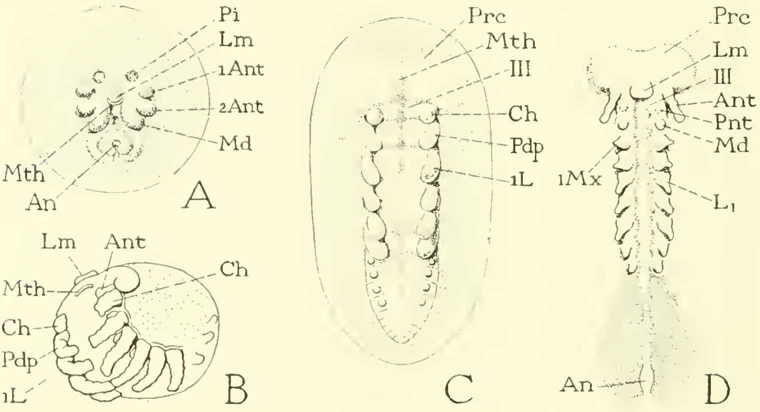

FIG. 22.—Arthropod embryos showing relative development of the tritocerebral appendages.

A, embryo of a crayfish, *Astacus* (*Potamobius*) *astacus* (from Reichenbach, 1877). B. embryo of a spider, *Trochosa singoriensis* (from Jaworowski, 1891). C, embryo of a spider, *Angelena labyrinthea* (from Balfour, 1880). D, embryo of an apterygote insect, *Anurida maritima* (from Wheeler, 1893).

An, anus; *Ant*, antenna; *1Ant*, first antenna; *2Ant*, second antenna; *Ch*, chelicera; *III*, tritocerebral segment; *1L*, first leg; L_1, prothoracic leg; *Lm*, labrum; *Md*, mandible; *Mth*, mouth; *Pdp*, pedipalp; *Pi*, pit on head region; *Pnt*, postantennal appendage; *Prc*, protocephalon.

The eye stalks of the decapod crustaceans arise from the ends of a transverse ridge on the top of the protocephalon, and project laterally from under the base of the rostrum, the latter being a process of the anterior edge of the carapace, and, therefore, from the tergum of the mandibular segment. Each eye stalk (fig. 17 B) consists of two movable segments, a narrow basal one forming a short peduncle, and a large terminal one capped by the hemispherical compound eye. Schmidt (1915) enumerates ten individual muscles for each eye stalk in the crayfish, the basal segment being provided with muscles arising on the head walls that move the appendage as a whole, while muscles from the basal segment move the terminal eye-bearing segment. The eye muscles are innervated by an oculo-motor nerve arising from the brain near the base of the sensory optic nerve.

THE ANTENNAE

The insect antenna is typically a many-jointed filament. Usually the first two basal segments are differentiated from the rest of the shaft (fig. 23 A). The first segment serves to attach the antenna to the head, and, being often thicker and longer than the others, forms a basal stalk, or *scape* (*Scp*), of the appendage. The second segment, or *pedicel* (*Pdc*), is short, and in nearly all insects contains a special sensory apparatus known as the organ of Johnston. The part of the antenna beyond the pedicel is termed the *flagellum* or *clavola* (*Fl*). The flagellum may be long and tapering and made up of many small segments, or it may be abbreviated, and reduced even to a single segment. The scape is set upon a small membranous area of the head wall, sometimes depressed to form a cavity, or *antennal socket*.

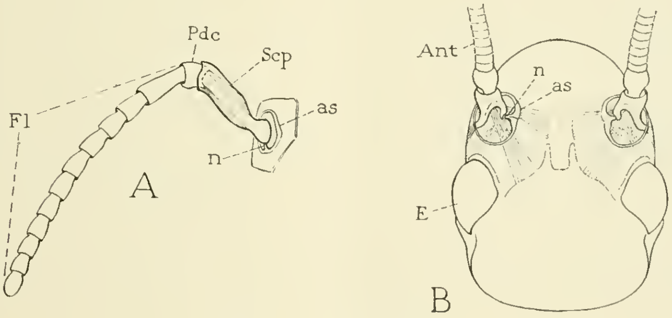

FIG. 23.—The antenna.

A, diagram of typical segmentation and articulation of an insect antenna. B, head of a chilopod, *Scutigera forceps*, dorsal, showing dorsal articulation of antennae, and origin of antennal muscles on walls of cranium.

Ant, antenna; *as,* antennal suture; *E,* eye; *n,* articular pivot of antenna; *Pdc*, pedicel; *Scp,* scape; *Fl,* flagellum.

The head wall surrounding the antennal base is strengthened by an internal ridge, the line of which is marked externally by a suture (fig. 23, *as*), setting off a circular, marginal rim known as the antennal sclerite. Usually a pivot-like process (*n*) from the rim of the sclerite forms a special support and articular point for the base of the scape, and allows the antenna a free motion in all directions. In its single point of articulation with the head wall, the antenna resembles the maxilla, or the mandible of those apterygote insects in which the jaw does not have a double hinge with the cranium. In most pterygote insects the antennal pivot is ventral or postero-ventral in position, relative to the base of the antenna (fig. 23 A), while the single mandibular or maxillary articulations are dorsal. The ventral position of the antennal articulation might be supposed to have shifted during the forward and upward migration of the appendage from its primitive ventral and postoral situation; but in *Japyx* the antennal pivot is *dorsal,* as it is also in the Chilopoda (fig. 23 B, *n*).

Each antenna is moved by muscles inserted upon the base of the scape. The origin of the antennal muscles in adult pterygote insects is commonly on the dorsal, or dorsal and anterior arms of the tentorium (fig. 38 D, *DT, AT*), but in the caterpillars (fig. 50 B, C, E, F) and in some coleopteran larvae, the antennal muscles arise upon the walls of the epicranium. The cranial origin of the muscles is probably the primitive condition, for, as already shown, the tentorium belongs to the gnathal segments only. The attachment of the antennal muscles on the tentorium, therefore, appears to be a secondary condition that has resulted from the migration of the muscle bases to the dorsal tentorial arms when the latter make contact with the dorsal wall of the head. In Crustacea and Chilopoda the antennal muscles have their origin on the head wall. In *Scutigera* (fig. 23 B) a dorsal set to each antenna arises on the dorsal wall of the cranium mesad and posterior to the antennal base, and a ventral set arises on the lateral walls below the antenna, and below the eyes. The insertion points of these muscles, distributed on three sides of the articular pivot (*n*), allow the muscles to act as levators, depressors, and rotators of the appendage. The part of the insect antenna distal to the scape is moved by muscles arising within the scape and inserted on the base of the pedicel (fig. 23 A). The segments of the flagellum in insects, however, so far as known to the writer, are never provided with muscles, and their lack of muscles suggests that the flagellum is a single segment secondarily subsegmented, corresponding with the flagellum of a crustacean antenna (fig. 24 B, *Fl*), which is a many-jointed dactylopodite. In the Myriapoda, however, all the antennal segments may be individually provided with muscles (*Scolopendra, Spirobolus*). The first antenna, or antennule, of the crayfish, according to Schmidt (1915), has paired antagonistic muscles for each of its first three proximal segments, and the third segment contains a single reductor inserted on the base of the dorsal branch of the flagellum, but otherwise none of the flagellar segments is provided with muscles.

The Arachnida and Xiphosura lack antennal appendages in the adult stage. Croneberg (1880) describes a pair of head lobes in the arachnid embryo, which he says fuse into a median rostrum in the mites and in the higher arachnids, and which he believes represent the antennal appendages. Jaworoski (1891) likewise describes in the embryo of a spider, *Trochosa singoriensis,* a pair of lobes situated before the chelicerae, which he claims are rudiments of the antennae (fig. 22 B, *Ant*), but he says the lobes disappear during later development.

THE POSTANTENNAL APPENDAGES

The pair of postantennal appendages on the tritocerebral segment of the head, known also as the antennae (Crustacea), second antennae, premandibular appendages, and intercalary appendages, are at best rudimentary in all insects. According to Uzel (1897), two small lobes in the adult head of *Campodea,* lying between the labrum and the maxillae, in the space left free by the retracted mandibles, are the tritocerebral appendages; the writer has found a pair of small papillae in *Dissosteira* between the bases of the mandibles and the angles of the mouth (fig. 42 B, *Pnt*) that might be vestiges of these organs. Otherwise tritocerebral appendages are known in insects only as evanescent rudiments in the embryo (fig. 22 D, *Pnt*). In the Myriapoda, likewise, the postantennal appendages are lacking, or possibly are present as temporary premandibular lobes on the head of the embryo (" rudiments of lower lip " in *Geophilus*, Zograf, 1883). In the Crustacea, on the other hand, the appendages of the tritocerebral segment, though sometimes reduced or lacking, are commonly highly developed, biramous organs, the second antennae, or " the antennae " according to the terms of carcinology. In the decapods each appendage consists of a two-segmented base (fig. 24 B, *Prtp*), of a large, one-segmented exopodite (*Exp*), and of a long, slender endopodite (*Endp*), of which the terminal segment is the many-jointed flagellum (*Fl*). The exopodite is independently movable by abductor and adductor muscles arising in the second segment of the base.

In Xiphosura and Arachnida, the chelicerae (fig. 24 A) are generally regarded as the appendages of the tritocerebral segment. Their rudiments in the embryo of a spider (fig. 22 C, *Ch*) bear a relationship to the head so similar to that of the tritocerebral rudiments in the insect embryo (D, *Pnt*), that the identity of the two sets of organs can scarcely be questioned. Holmgren (1916), furthermore, claims that the histology of the arachnid brain shows that the chelicerae are innervated from the tritocerebral region of the brain. If this homology is correct, there is no reason for calling the tritocerebral appendages "second antennae" except in the Crustacea. The arachnid chelicera is a uniramous organ, that of a scorpion (fig. 24 A) having three well-developed segments.

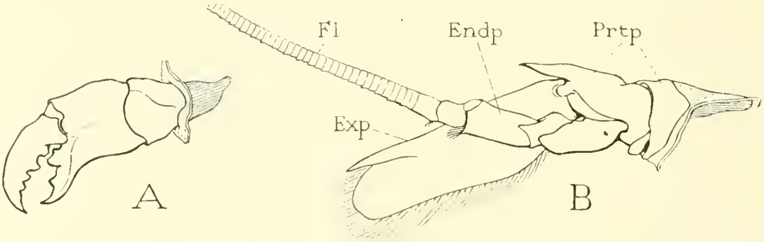

FIG. 24.—Postantennal appendage of adult arthropods.

A, chelicera of a scorpion, left, ventral view, showing uniramous structure and three segments. B, second antenna of a decapod crustacean (*Spirontocaris groenlandicus*), left, ventral view, showing biramous structure, consisting of two-segmented base (*Prtp*) bearing an exopodite (*Exp*) and an endopodite (*Endp*).

THE GNATHAL APPENDAGES

There can be no doubt that the gnathal organs—the mandibles, the first maxillae, and the second maxillae—constitute a distinct group of appendages in the eugnathate arthropods. The mandibles are the most highly modified of the gnathal appendages, and, in most cases, their structure has lost all resemblance to that of the more generalized insect maxillae. A maxillary appendage, therefore, should be studied first as affording a better example of the basic structure of the gnathal organs, and, in insects, the first maxilla preserves most nearly the primitive structure, since the second maxillary appendages are united to form the labium.

The first maxilla of an insect with typical biting mouth parts, of which the roach offers a good example (fig. 25 A), consists of a basal stalk, two terminal lobes, and a palpus. The base is divided into a proximal *cardo* (*Cd*), suspended from the head by a single point of articulation (*c*), and a distal *stipes* (*St*). The cardo and stipes are freely flexible on each other by a broad hinge line, and their planes may form an abrupt angle at the union, but neither has an inner wall, the two being merely strongly convex sclerites set upon the membranous lateral wall of the head, and their cavities are a part of the general head cavity. Only the terminal maxillary lobes and the palpus are free parts of the appendage. The lobes arise from the distal end of the stipes, one, the *lacinia* (*Lc*), being internal, the other, the *galea* (*Ga*) external. The galea is also anterior to the lacinia (or dorsal to it in insects with the head flattened and held horizontal). The galea is usually a soft lobe; the lacinia is more strongly chitinized, and ends in a strong incisor point provided with one or more apical teeth curved inward. Both lobes are movable on the end of the stipes; the galea can be deflexed, and the lacinia can be flexed inward. The palpus (*Plp*) arises from the lateral surface of the stipes, a short distance proximal to the base of the galea. The palpus of the roach is five-segmented.

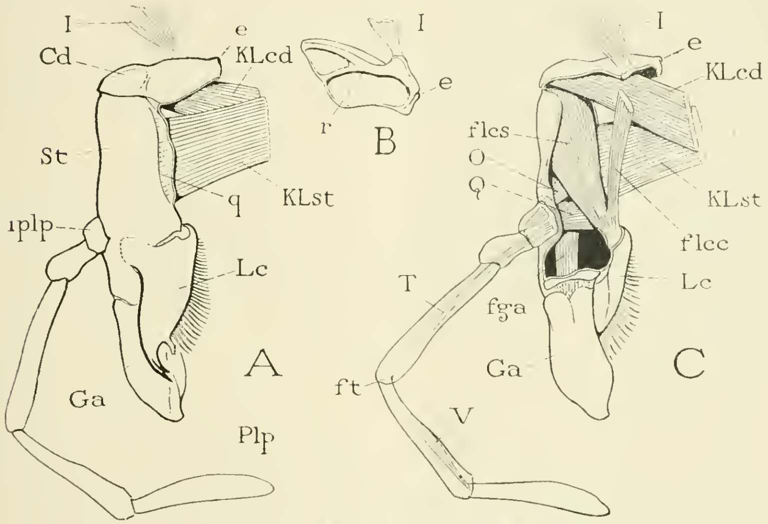

Fig. 25.—Maxilla of *Periplaneta*.

A, left maxilla, posterior (ventral) surface. B, internal surface of cardo. C, right maxilla, anterior (dorsal) view, showing muscles.

Cd, cardo; *e*, articulation of cardo with cranium; *fga*, flexor of galea; *flcc*, cranial flexor of lacinia; *flcs*, stipital flexor of lacinia; *ft*, femoro-tibial joint of palpus; *Ga*, galea; *I*, promotor of cardo; *KLcd*, adductor of cardo (origin on tentorium); *KLst*, adductor of stipes (origin on tentorium); *Lc*, lacinia; *O*, levator of palpus; *Plp*, palpus; *1plp*, first segment of palpus; *Q*, depressor of palpus; *q*, submarginal suture (and internal ridge) near inner margin of stipes; *r*, internal ridge of cardo; *St*, stipes; *T*, depressor of fourth segment (tibia) of palpus; *V*, depressor of fifth segment (tarsus) of palpus.

The musculature of the maxilla (fig. 25 C) comprises muscles that move the appendage as a whole, and muscles that move the terminal lobes and the palpus. The first group includes a tergal muscle (*I*) arising on the posterior dorsal wall of the head, and two sets of sternal muscles (*KLcd, KLst*) arising on the tentorium in most insects, or on the homologous hypopharyngeal apodemes in some apterygote insects (fig. 30 B, *HA*). The single tergal muscle (fig. 25 C, *I*) is inserted on the proximal end of the cardo just before the articulation of the latter with the head (*c*); it is probably a promotor, serving to swing the appendage forward. The sternal muscles (i. e., the tentorial or hypopharyngeal muscles) consist of two large flat bundles of fibers, one group (*KLcd*) inserted on the inner face of the cardo, the other (*KLst*) on an internal ridge of the stipes near the mesal border of the posterior face of the latter (A, *q*). These muscles are the adductors of the maxilla; the fibers of the cardo muscle arise anterior (or dorsal) to those of the stipes muscle and cross them obliquely.

The muscles of the movable parts of the maxilla include muscles of the galea, the lacinia, and the palpus. The galea has a single muscle (fig. 25 C, *fga*) arising on the posterior wall of the stipes and inserted on the posterior rim of the base of the galea; it is a reductor in as much as it serves to flex the galea posteriorly (or ventrally). The lacinia has a large flexor (*flcs*) arising in the base of the stipes, and a second muscle (*flcc*) arising on the posterior dorsal wall of the cranium. In the roach these two muscles are inserted by a common broad tendinous base on the inner proximal angle of the lacinia; in other insects they usually have separate insertions (fig. 30 B, *flcs* and *flcc*, fig. 40 B, *14*, *15*). The palpus is provided with two muscles (fig. 25 C, *O*, *Q*), both of which arise within the stipes and are inserted on the base of the first segment of the palpus (A, *1plp*). The two palpus muscles are more distinct in most other insects than in the roach (fig. 31 A, B, C, E), and since one is dorsal and the other ventral, relative to the morphologically vertical axis of the maxilla, they are clearly a levator and a depressor, or abductor (*O*) and adductor (*Q*), of the palpus. The muscles within the palpus vary somewhat in different insects. In the palpus of the roach, a levator of the second segment arises in the first, where also a long depressor of the fourth segment (*T*) has its origin. A depressor of the terminal segment (*V*) arises ventrally in the penultimate segment.

THE MANDIBLES

The most generalized mandibular appendage in the arthropods, i. e., one corresponding most closely in structure and musculature with a typical maxilla, is to be found, not in the insects or crustaceans, but in the myriapods, and best developed in the Diplopoda.

The diplopod mandible consists of a large basal plate, which appears to form an extensive part of the lateral head wall (fig. 17 K, *Md*), and of a movable terminal lobe mostly concealed in the normal condition by the gnathochilarium (*Gch*). The basal plate is subdivided into several regions, but particularly there is a proximal piece (fig. 26 A, *Cd*) and a distal piece (*St*), separated by a line of flexibility. The proximal piece is loosely articulated to the head wall by a single point on its dorsal posterior angle (*a*). The entire mandibular base is slightly movable by its membranous union with the head, but it is not of the nature of a free appendicular structure, since it has no inner wall—it is merely a convex plate in the lateral wall of the head, but separated from the cranium by a membranous suture. The free terminal lobe of the mandible is a strongly chitinized, jaw-like structure with a proximal molar area and terminal incisor point (fig. 26 A, *Lc*). It is hinged by a dorsal articulation at its base with the end of the basal plate.

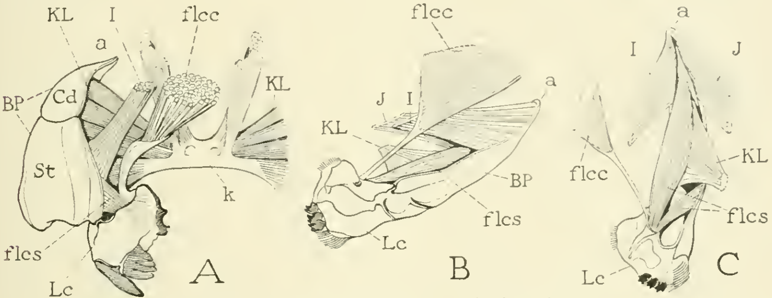

FIG. 26.—Mandibles of Myriapoda.

A, right mandible of a diplopod, *Thyropygus* (*Spirostreptus*), dorsal, showing large dumb-bell adductors (*KL, KL*) from opposite mandibles, united by median tendon (*k*). B, left mandible of a chilopod, *Scutigera forceps*, lateral view. C, right mandible of *Scutigera*, dorsal, somewhat diagrammatic.

a, articulation of mandible with cranium; *BP*, basal plate of mandible; *Cd*, "cardo" of mandible; *flcc*, cranial flexor of lacinia; *flcs*, stipital flexor of lacinia; *I*, promotor of mandible; *J*, remotor of mandible; *k*, median tendon of mandibular adductors; *KL*, mandibular adductors, united by median tendon in diplopod (A, *k*) to form dumb-bell muscle; *Lc*, lacinia; *St*, "stipes" of mandible.

So closely do the parts of the diplopod mandible (fig. 26 A) resemble the cardo, the stipes, and the lacinia of an insect maxilla (fig. 25 A), that the imagination at once sees in the diplopod jaw an appendage similar to the maxilla, lacking only a galea and a palpus. That the fancied resemblance is real is easily demonstrated by a study of the musculature.

The musculature of the diplopod mandible consists of muscles that move the appendage as a whole, and of muscles that move the lacinial lobe. As in the insect maxilla, the muscles that move the entire organ include a tergal promotor and a group of ventral adductors. The promotor (fig. 26 A, *I*) arises on the wall of the cranium dorsal and posterior to the articulation of the basal plate with the head. It is inserted on the dorsal (anterior) margin of the distal division (*St*) of the basal plate, and in its point of insertion alone does this muscle differ from the promotor of the insect maxilla, which is inserted on the edge of the cardo (fig. 25 C, *I*). Functionally, however, the two muscles are the same, and a shift in the point of attachment is not a morphological difference.

The adductor muscles of the diplopod mandible consist principally of a great mass of fibers (fig. 26 A, *KL*) filling the cavity of both divisions of the basal plate (*Cd* and *St*). These muscles are clearly the homologues of the adductors of the cardo and the stipes in the insect maxilla (fig. 25, *KLcd*, *KLst*), which have their origins on the tentorium, or on the hypopharyngeal apodemes. In the diplopod mandibles, however, the fibers of the adductor muscles converge medially from each jaw upon a large, tough, transverse ligament (fig. 26 A, *k*), and the two conical fiber masses, together with the connecting ligament, form a great dumb-bell-shaped muscle uniting the two mandibles. The two sets of fibers pull against each other to close the jaws. Clearly, the inner ends of these muscles have become detached from the hypopharyngeal apodemes, and the fibers from opposite sides have been united across the middle of the head by means of a transverse ligament. There is also, however, a small group of adductor fibers to each mandible (not seen in the figure) that still retains a connection with the corresponding apodeme of the hypopharynx. Besides the mandibular muscles, other muscles have their origin on the transverse ligament, including muscles to the gnathochilarium, which is either the united second maxillae, or the combined first and second maxillary appendages. In the Diplopoda, therefore, the ventral adductors of all the gnathal appendages have lost their sternal connections by their detachment from the hypopharyngeal apodemes. This is a specialized condition, and the ligamentous bridge on which the muscles arise has no relation to the insect tentorium.

The muscles of the free terminal lobe of the diplopod mandible (fig. 26 A, *Lc*) include a muscle inserted directly on the base of the lobe (*flcs*) arising within the stipes (*St*), and a large cranial muscle (*flcc*) arising on the dorsal wall of the head and inserted by a strong, chitinous apodeme on the inner basal angle of the lobe. These muscles correspond exactly with the lacinial flexors of the insect maxilla, one of which (fig. 25 C, *flcs*) arises within the stipes, the other (*flcc*) on the dorsal wall of the cranium. In most insects the second muscle is inserted, as in the diplopod, on a chitinous apodeme from the inner angle of the lacinia (fig. 30 B, *flcc*). There can be little question, therefore, that the single lobe (*Lc*) of the diplopod mandible is the lacinia, and that the jaw of the Diplopoda has a structure identical with that of the insect maxilla, except for the lack of a galea and a palpus.

The mandible of the Chilopoda is more specialized in structure than is that of the diplopods, but in its musculature it is in some respects more generalized. In *Scolopendra, Lithobius, Scutigera,* the jaw is slender and greatly elongate. In *Scutigera* (fig. 17 G, *Md*) its tapering base is exposed on the side of the head where it is articulated to the cranial margin (*a*), but in *Scolopendra* (fig. 21 B) the end of the mandible is buried in a pocket of the head wall lying mesad of the base of the maxilla (*MxC*). The long basal plate of the chilopod jaw is undivided (fig. 26 B, *BP*), and is articulated to the head wall by its apical point (*a*). In some chilopods there is an anterior articulation between the mandible and the suspensorial plate of the hypopharynx, but this articulation is a mere contact between external surfaces. As in the diplopods, the basal plate has no inner wall. The distal part of the mandible is a free lobe (*Lc*) movable on the base, but not so definitely hinged to the latter as is that of the diplopod mandible.

The musculature of the chilopod mandible is practically alike in both the Pleurostigma and the Notostigma, and is essentially the same as in the diplopods, though the muscles differ in relative size. The basal plate is provided with both tergal and sternal muscles. Of the former, there are two sets of fibers, one inserted on the dorsal (anterior) edge of the proximal part of the plate (fig. 26 B, C, *I*), the other (*J*) on the ventral (posterior) edge; both have their origins on the dorsal wall of the cranium. These muscles apparently serve to rotate the mandible on its long axis, and they probably act as protractors where the mandible is capable of a longitudinal movement; but clearly the first would be a promotor, and the second a remotor in an appendage with primitive relations to the head. The sternal muscles of the mandible consist of a conical mass of adductor fibers (fig. 26 B, C, *KL*) spreading upon the inner wall of the basal plate from their median origin (fig. 21 B, *KL*), which is on the ligamentous bridge uniting the two apodemes of the hypopharynx (fig. 21 A, C, *j*). The adductors of the chilopod mandibles are unquestionably homologues of the dumb-bell muscle of the diplopods. The condition of the mandibular adductors, therefore, is more primitive in the Chilopoda, for here the muscles retain their connections with the sternal, hypopharyngeal apodemes.

The movable terminal lobe of the chilopod mandible (fig. 26 B, C, *Lc*) is provided with the same muscles as is the corresponding lobe of the diplopod mandible (A, *Lc*) and the lacinia of the insect maxilla (figs. 25 C, 30 B, *Lc*). The muscle from the lobe to the basal plate in the chilopod jaw is very large (fig. 26 B, C, *flcs*), suggesting that of *Japyx* (fig. 30 B, *flcs*), and is composed of two groups of fibers. The cranial muscle (*flcc*) arises by a broad base on the dorsal wall of the head, and is inserted on a slender apodeme from the inner angle of the lobe. In the chilopod mandible, therefore, there is a basal plate (fig. 26 B, *BP*) corresponding with the cardo and stipes of the insect maxilla, but not divided as in the diplopods, and a free terminal lobe (*Lc*) which represents the lacinia. In retaining the connection of the adductor muscles with the hypopharyngeal apodemes, the chilopod mandible preserves the primitive condition shown by the maxilla of *Japyx* (fig. 30 B).

In the Crustacea and Hexapoda, the mandible, or the jaw part of the mandibular appendage, which may bear a palpus, consists of a single piece. Whatever may be the primitive elements that have entered into its composition, these elements are fused into a solid gnathal organ. There are, hence, never muscles entirely within the mandible, except those that pertain to the palpus, when a palpus is present. The mandibular musculature consists exclusively of the muscles that move the appendage as a whole, and these muscles correspond with the muscles of the basal plate of the myriapod mandible, or with those of the cardo and stipes of the insect maxilla.

In the phyllopod crustacean *Apus*, the large mandibles (fig. 27 A, *Md*) hang vertically from the wall of the mandibular segment (*IV*). Each is a strongly convex, elongate oval structure, attached to the lateral membranous wall of the head by most of its inner margins, leaving only a ventral masticatory part projecting below as a free lobe. A single, dorsal point of suspension (*a*) allows the base of the mandible to turn on its vertical axis, or to swing inward and outward as far as the membranous lateral head wall will permit. The musculature is correspondingly simple: two dorsal muscles from the tergum of the mandibular segment (*IV*) are inserted on the base of the jaw, one (*I*) on the anterior margin, the other (*J*) on the posterior margin; the hollow of the mandible is filled with a great mass of fibers (*KL*) which converge upon a median transverse ligament (*k*) that receives likewise the muscles from the opposite jaw. Here, then, is a ventral dumb-bell adductor, as in the diplopods, and two dorsal muscles, which may function either as productors and reductors, or as anterior and posterior rotators. It is not clear as to what constitutes the mechanism of abduction in appendages with this type of articulation and musculature.

The *Apus* type of mandible is probably characteristic of most of the more generalized Crustacea; it is present also in some of the decapods (*Virbius, Spirontocaris*). In *Spirontocaris* (fig. 27 B), the median ligament (k) of the dumb-bell adductors (KL) is connected with the hypodermis of the dorsal wall of the body by a branched arm (m) on each side. As before pointed out, however, the adductor liga-

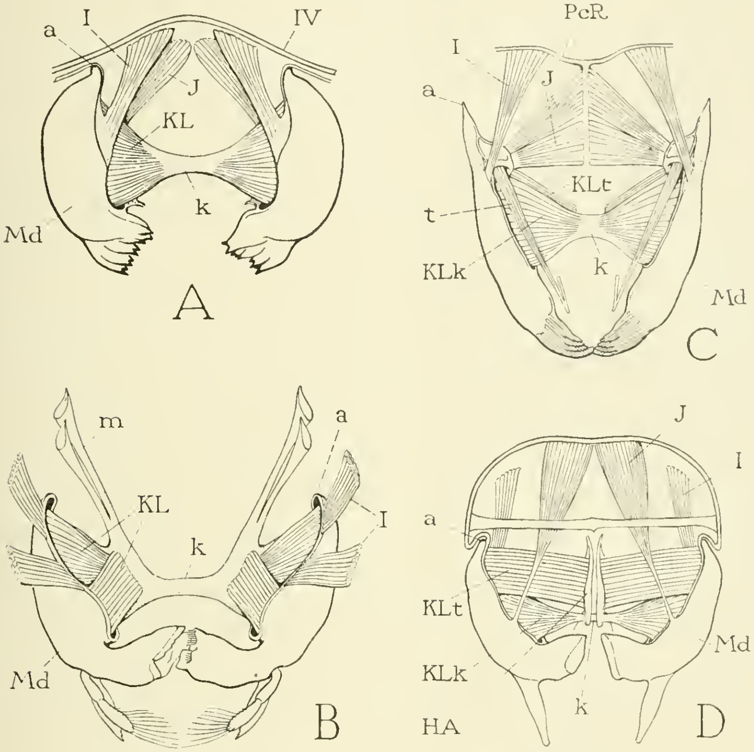

Fig. 27.—Mandibles of Crustacea and Apterygota.

A, mandibles of *Apus longicaudata* (phyllopod), anterior. B, mandibles of *Spirontocaris groenlandicus* (decapod), anterior. C, mandibles of *Heterojapyx gallardi* (apterygote insect), anterior (dorsal). D, mandibles of *Nesomachilis maoricus* (apterygote insect), posterior.

a, articulation of mandible with cranium, or with wall of mandibular segment (*IV*); *HA*, hypopharyngeal apophysis; *I*, promotor of mandible; *J*, remotor of mandible; *k*, median tendon of mandibular adductors of dumb-bell muscle (*KL* or *KLk*); *KLk*, fibers of mandibular adductors united by tendon (*k*); *KLt*, fibers of mandibular adductors retaining origin on hypopharyngeal apophyses (D, *HA*); m, suspensory tendons of mandibular adductors; *Md*, mandible; *PcR*, posterior cranial ridge; *t*, branch of labral muscle attached on mandible.

ment is in no sense to be homologized with the tentorium as developed in some of the higher crustacea and in the pterygote insects. Each mandible of *Spirontocaris* is provided with two dorsal productor muscles (*I*), but a reductor was not observed. *Spirontocaris* preserves the primitive single dorsal point of articulation of the mandible (*a*) with the wall of its segment. In higher decapods, the amphipods, and the isopods, where the mandible may have a double hinge with the wall of the head, the musculature of the organ is modified in a manner to be described later.

The simple mechanism of the mandible of the higher pterygote insects is well understood; the complicated musculature of the mandible in Apterygota has been given scant attention, and the derivation of the pterygote jaw mechanism from that of the Apterygota has been almost ignored. Börner (1909) has given the first comparative account of the mandibular musculature in the more generalized insects, and has pointed out certain points of similarity with the musculature of higher crustaceans. He did not, however, carry his comparisons to the myriapods, and thereby missed some fundamental relations.

The mandibles of the Machilidae will serve best as an example of the more generalized apterygote jaw. The mandible of *Machilis* or of *Nesomachilis* (fig. 27 D, *Md*) is surprisingly similar in form to that of the crustacean *Apus* (*A*), except that it has a long incisor point in addition to a broad molar lobe. In this latter character the machilid jaw resembles the mandibles of some of the decapod crustaceans, such as *Sprirotocaris* and *Virbius*, as has been pointed out by Crampton (1921b). The mandible of *Machilis* is suspended by a single dorsal point of articulation (*a*) against the lateral wall of the head. The cavity of the elongate base of each organ is filled by a mass of muscle fibers (*KLk*), and these fibers from the two mandibles converge upon the ends of a common transverse tendon (*k*) that passes through the base of the hypopharynx. Here, in an insect, therefore, we find the same type of dumb-bell adductor uniting the two mandibles as occurs in the Diplopoda and in lower Crustacea. In *Machilis*, however, there is a second and larger set of adductor fibers (*KLt*) which has its origin on the hypopharyngeal apodemes (*HA*). *Machilis*, therefore, in the possession of two differentiated sets of mandibular adductor fibers, combines the primitive condition of the chilopods with the specialized condition of the diplopods and lower crustaceans. The tergal musculature of the mandible in *Machilis* is simple, consisting of an anterior promotor (*I*) and a posterior remotor (*J*). The two muscles are disposed exactly as in *Apus* (A), and are in entire conformity with the tergal musculature of the basal plate of the jaw of *Scutigera* (fig. 26 B, C, *I*, *J*) and other chilopods.

The machilid type of mandibular musculature appears to be characteristic of most apterygote insects except the Lepismatidae. In *Japyx* and *Campodea*, the bases of the elongate mandibles and maxillae are deeply retracted into the head above the labium, and the edges of the labium are fused to the postgenal margins of the head, so that the distal edge of the labium appears as the ventral lip of a pouch containing the other gnathal appendages and the hypopharynx.

The mandibles of *Heterojapyx* (fig. 27 C, *Md*) are simple, slender organs, each consisting of a long, hollow basal piece, and of a more strongly chitinized free terminal lobe with a toothed incisor edge. The proximal tapering end of each jaw is set off from the rest by a thick internal ridge, superficially suggesting the division of the maxillary base into cardo and stipes; but the "division" in the Japyx mandible gives rigidity instead of flexibility. The two mandibles of *Heterojapyx* are connected by a large dumb-bell adductor muscle (*KLk*), the spreading fibers of which fill the basal cavities of the organs. Besides this muscle there are also sets of ventral fibers (*KLt*) to the mandible that arises on the hypopharyngeal apophyses. The tergal muscles of the mandibles are large: they include for each jaw an anterior muscle (*I*) arising against a dorsal cranial ridge (*PcR*), and a wide fan of posterior fibers (*J*) arising along a median coronal ridge. Because of the retraction of the mouth appendages, the hypopharyngeal muscles of the mandibles (*KLt*) would appear to function as protractors, and the tergal muscles as retractors; but the former are clearly the hypopharyngeal adductors of *Machilis* (D, *KLt*), and the latter the tergal promotors (*I*) and remotors (*J*). A peculiarity noted in *Heterojapyx*, if the writer observed correctly, is the attachment of a branch of the retractor of the labrum (*t*) on the base of the mandible.

In the Collembola, which also have retracted mandibles and maxillae, the mandibular musculature would appear, from Folsom's (1899) account of *Orchesella cincta*, to be of the same essential nature as that of *Japyx*. Folsom enumerates ten muscles for each mandible of *Orchesella*, but they all fall into three groups according to their origins, namely, muscles arising on the walls of the head, muscles arising on the "tentorium" (hypopharyngeal apodemes), and fibers from one mandible to the other. The second and third groups constitute the adductors of the jaw; their fibers are inserted, Folsom says, on the inside of the lateral wall of the mandible, and most of them have their origin on the "tentorium," but a few of the fibers, he adds, "pass under the tentorium and become continuous with similar fibers from the opposite mandible." Folsom, it will be noticed, says the adductor fibers connecting the mandibles pass *beneath* the tentorial arms. In *Japyx* the tendon of the dumb-bell muscle distinctly lies dorsal to the hypopharyngeal apodemes. In *Machilis* the apodemes are so loosely connected with the base of the hypopharynx and so strongly united with the lateral inflections of the head wall, that in dissections their hypopharyngeal connections are easily lost, and the impression is given that the tendon of the dumb-bell adductor lies ventral to the apodemes. It does lie ventral to the suspensorial plates uniting the apodemes with the lateral walls of the head, but it passes anterior, *i. e.,* dorsal, to the ends of the apodemes themselves. Folsom's statement, therefore, should be verified, for a discrepancy in the relations of the parts in question seems hardly permissible if we are dealing with homologous structures.

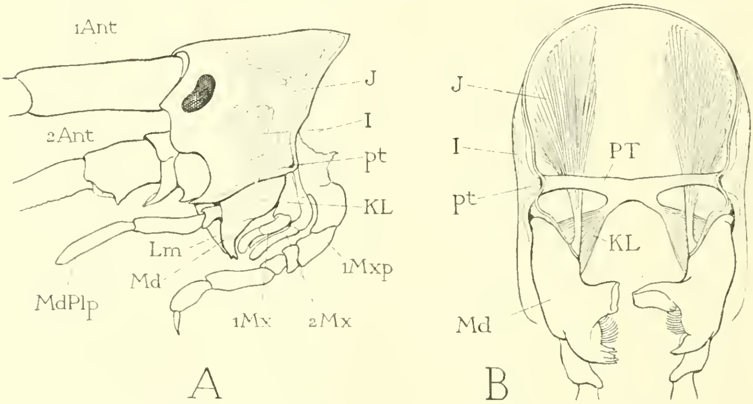

FIG. 28.—Head of *Gammarus locusta* (amphipod crustacean).

A, lateral view of head, showing tergal abductors (*I*) and adductors (*J*) of left mandible, and base of ventral adductor (*KL*). B, postero-ventral view of back of head, showing origin of ventral adductors (*KL*) on posterior tentorial bar (*PT*).

1Ant, first antenna; *2Ant,* second antenna; *I,* abductor of mandible; *J,* dorsal adductor of mandible; *KL,* ventral adductor of mandible; *Lm,* labrum; *Md,* mandible; *MdPlp,* mandibular palpus; *1Mx,* first maxilla; *2Mx,* second maxilla; *1Mxp,* first maxilliped; *pt,* posterior tentorial pit; *PT,* transverse posterior tentorial bar.

The mandibles of the Protura, as described by Berlese (1909), are provided each with retractors and protractors that have their origins on the head wall, and with a protractor arising on the tentorial apodeme. Berlese, however, does not mention a muscle continuous between the two mandibles. The muscles present clearly represent the usual tergal muscles, and the hypopharyngeal adductor.

In all the apterygote forms thus far described, the mandible has a free attachment to the head, being implanted by most of its length in the ventro-lateral membranous part of the head wall, and articulated to the margin of the chitinous cranium by only a single dorsal point of contact. In the Lepismatidae, a new condition is established in the mandible through the elongation of its dorsal base line forward and ventrally to the anterior end of the lower genal margin of the epicranium. The jaw thus becomes hinged to the head on a long basal axis extending from the primitive dorsal articulation, which is now *posterior,* to the angle between the genal margin of the head and the clypeus. At the latter point a secondary, *anterior* articulation is established between the mandible and the cranium. Börner (1909) describes the articulation of the mandible of *Lepisma,* but he does not observe that its type of structure is characteristic of the Lepismatidae only, not of the Apterygota in general. The alteration in the mandibular articulation involves a change in the entire mechanism of the jaw, and initiates the series of modifications that have led to the evolution of the pterygote type of mandibular musculature from that of *Machilis, Japyx,* and the Collembola.

The musculature of the mandible of *Lepisma,* as described by Börner (1909), is apparently almost the same as that of *Machilis.* The adductor muscles inserted within the body of the mandible consist of a large dorsal set of fibers (fig. 29 B, *KLt*) from the tentorium representing the fibers that arise on the hypopharyngeal apodeme of *Machilis* (figs. 27 D, 29 A, *KLt*), and of a small ventral set (*KLh*) arising directly from the hypopharynx. The tergal muscles comprise a pair of abductors (*I*) inserted on the outer margin of the mandibular base between the two articular points (*a, c*), and a large dorsal adductor (*J*) inserted on the inner margin mesad of the posterior articulation. The tergal abductors and adductor, however, are clearly the promotor and the remotor of the mandible of *Machilis* (fig. 29 A, *I, J*) and of all other generalized forms, which have assumed a new function by reason of the change in the nature of the mandibular articulation.

The structure and musculature of the mandible in nymphs of Ephemerida is essentially the same as in *Lepisma.* Börner describes and figures the nymph of *Cloëon dipterum,* showing the presence of a large tentorial adductor and a very small hypopharyngeal adductor, in addition to the dorsal abductors and adductors; the writer has verified the existence of all these muscles in another ephemerid species. In a dragonfly nymph, *Aeschna,* a small hypopharyngeal adductor was found, but no tentorial fibers were observed. In the orthopteron, *Locusta,* Börner shows two small tentorial adductors of the mandible (fig. 29 C, *KLt*), and a small hypopharyngeal adductor (*KLh*). The same muscles the writer has found in *Microcentrum,* the hypopharyngeal fibers being attached medially on the tips of the rudimentary suspensorial arms of the hypopharynx (fig. 20 D, *KLh*); but no trace of either set could be discovered in the acridid, *Dissosteira.* Mangan (1908) described in the roach, *Periplaneta australasiae,* both a tentorial adductor and a hypopharyngeal adductor. The first mention of either of these muscles is by Basch (1865), who found the tentorial adductor in the mandible of *Termes flavipes.*

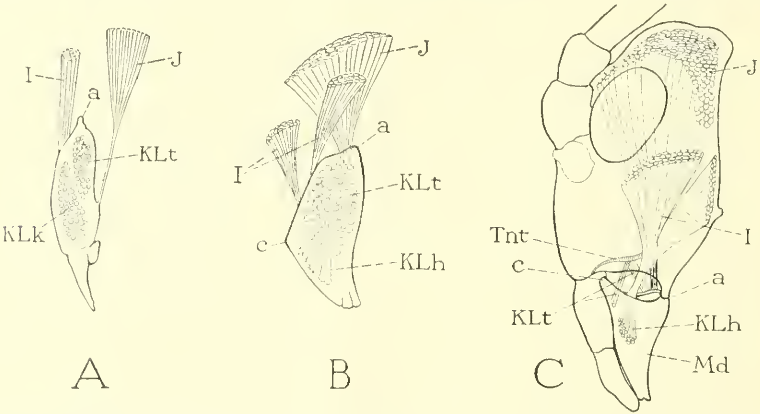

FIG. 29.—Three stages in the evolution of the mandibular mechanism in biting insects.

A, mandible of *Machilis,* outer surface, with single dorsal point of articulation (*a*) with cranium; the jaw moved by tergal promotor (*I*) and remotor (*J*), and by ventral adductors (*KLk, KLt,* see fig. 27 D).

B, mandible of *Lepisma* (from Börner, 1909), articulated with cranium on long basal hinge inclined downward anteriorly from dorsal articulation (*a*) to anterior articulation (*c*); the promotors (*I*) here become abductors, and the remotor (*J*) becomes a tergal adductor; ventral adductor (*KLh, KLt*) retained.

C, head of *Locusta* (from Börner, 1909), showing common type of mandibular articulation in pterygote insects, with hinge line inclined downward posteriorly from anterior articulation (*c*) to posterior articulation (*a*); tergal abductors and adductors (*I, J*) highly developed, ventral adductors (*KLh, KLt*) rudimentary. In higher Pterygota the ventral adductors disappear.

The adductor fibers arising directly from the base of the hypopharynx are evidently remnants of the primitive sternal adductors that have retained their original connections. *In the insects, therefore, the primary, sternal adductor muscles (KL) of the mandibles have become differentiated into three groups of fibers, the fibers of one group (KLh) retaining the primitive sternal connection, those of the second (KLt) being carried inward upon the sternal (hypopharyngeal) apophyses, those of the third (KLk), after having united medially* *with the corresponding set from the opposite mandible, having been detached from all connections except their points of insertion on the mandibles.* With the change in the mandibular articulation from a single dorsal suspensory point to a long basal hinge, the primary adductors have lost their importance, and the function of adduction has been secondarily taken over by the primary tergal remotor, while the original tergal promotor becomes the abductor. Remnants of the primary adductors in insects having a hinged mandible persist in the Lepismatidae, Ephemerida, Orthoptera, and Isoptera, but in the higher orders they have disappeared.

A still further evolution in the mandibular base has reversed the tilt of the hinge line. Instead of sloping from the posterior articulation downward and forward, as it does in *Lepisma* and in some ephemerid nymphs, the base of the jaw in all higher insects is inclined from the anterior articulation downward and posteriorly (fig. 29 C). This change in the slope of the axis of the hinge causes the apex of the jaw to swing inward and posteriorly during adduction, instead of inward and anteriorly as in the first condition.

In the higher decapod crustaceans, and in the amphipods and isopods, the mandible has undergone an evolution parallel to that which has taken place in insects. Börner (1909) has described the mandible and mandibular musculature of *Gammarus*, an amphipod, and has shown the structural similarity with the mandible of *Lepisma*. In *Gammarus locusta* (fig. 28 A) the mandible is hinged to the cranium by its long base, which slopes downward and forward from the posterior point of articulation. The primitive tergal promotor muscle (*I*) has then become an abductor, and the remotor (*J*) has become a dorsal adductor. The primitive ventral adductor (*KL*) has its origin on a well-developed transverse tentorial bar (B, *PT*) passing through the back of the head; a hypopharyngeal branch of the adductor is lacking. In the crayfish (*Astacus*), Schmidt (1915) describes an anterior ventral adductor of the mandible arising on the anterior end of the ventral head apodeme. In the isopods the mandible attains a stage almost exactly comparable with that of the higher pterygote insects (fig. 17 F)—the basal hinge line of the jaw slopes posteriorly and downward, and the only muscles present, so far as the writer could find, are the tergal abductors and adductors.

The homologues of the mandibles in Xiphosura and Arachnida, the so-called pedipalps (fig. 17 J, *Pdp*), scarcely need consideration here. The pedipalps never attain a jaw-like form, but retain always the structure of a jointed limb, though the basal segment may develop a strong gnathal lobe.

THE FIRST MAXILLAE

The leading features of the first maxilla have been sufficiently noted in the description of a generalized gnathal appendage (page 60) based on the maxilla of *Periplaneta* (fig. 25). In none of the other arthropods are the maxillary appendages so highly developed as in the insects, but, in all the arthropods, it appears that the mandible has been evolved from an appendage that was originally very similar to the generalized insect maxilla. In many of the higher insects the maxillae, too, have become specialized, always in adaptation to special modes of feeding, but a description of the modifications involved is beyond the scope of the present paper. The musculature of the organ is essentially the same in all groups of biting insects, except as it suffers a reduction where the appendages become reduced or united with the labium.

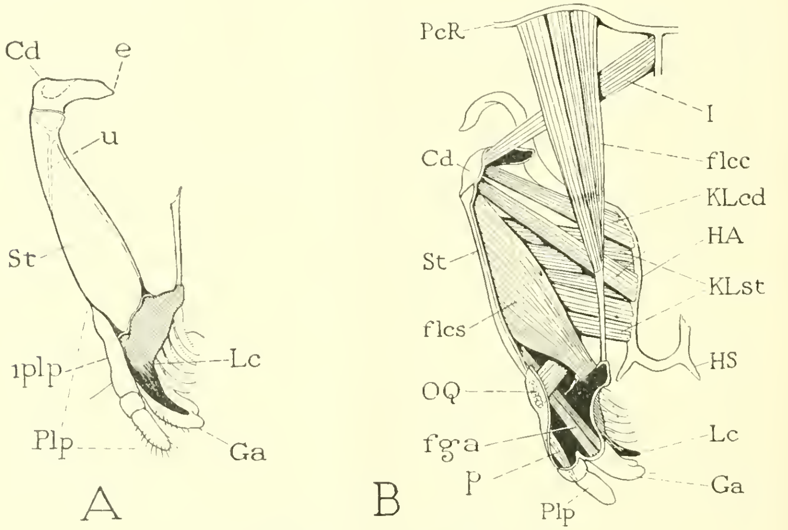

FIG. 30.—Maxilla of Heterojapyx gallardi.

A, left maxilla, posterior (ventral) surface. B, right maxilla and muscles, anterior (dorsal) view.

Cd, cardo; *c*, articulation of cardo with cranium; *fga*, flexor of galea; *flcc*, cranial flexor of lacinia; *flcs*, stipital flexor of lacinia; *Ga*, galea; *HA*, hypopharyngeal apophysis; *HS*, rudiment of suspensorial arm of hypopharynx; *I*, promotor of cardo; *KLcd*, adductors of cardo; *KLst*, adductors of stipes; *Lc*, lacinia; *OQ*, muscle of base of palpus; *p*, muscle of terminal segment of palpus; *PcR*, posterior cranial ridge; *Plp*, palpus; *1plp*, first segment of palpus; *St*, stipes; *u*, line of internal ridge of stipes.

The maxilla of *Japyx* (fig. 30) presents a more generalized condition in its relation to the head than does the maxilla of the roach, in that the head apophyses (B, *HA*) upon which the adductor muscles of the appendages arise are still connected with the hypopharynx, whereas in *Periplaneta* the corresponding endoskeletal arms have lost their primitive sternal connections and have become a part of the tentorium. The adductors of the cardo in *Heterojapyx* (fig. 30 B, *KLcd*) are well differentiated from those of the stipes (*KLst*), and cross obliquely the inner ends of the latter. The promotor of the cardo (*I*) arises against a median ridge of the dorsal wall of the cranium. The lacinia (*Lc*), which is mostly covered dorsally by the galea, has a broad flexor arising within the stipes (*flcs*), and a large cranial muscle (*flcc*) arising against the dorsal cranial ridge (*PcR*) on the top of the head, and going dorsal to the other muscles of the appendage to be inserted on a slender apodeme from the inner angle of the lacinial base. The galea (*Ga*) is provided with a single long flexor (figs. 30 B, 31 D, *fga*) arising within the stipes, which splits into two bundles of fibers toward its insertion on the ventral wall of the base of the galea. The palpus (*Plp*) is reduced and otherwise modified as compared with that of the roach (fig. 25), consisting of only three segments, of which the basal one (figs. 30 A, 31 D, *1plp*) is much elongate and is united with the outer wall of the base of the galea (*Ga*). There might be some question as to the homology of this basal region of the palpus of *Japyx,* but the insertion upon its base of the muscle (*OQ*) from the stipes, evidently representing the usual pair of palpal muscles, and the origin within it of a muscle (*p*) going to the distal segment of the palpus identify the part in question as the true basal segment of the palpus.

The cardo and the stipes of many insects appear externally to be divided into sub-sclerites, but in most such cases it is found that the so-called " sutures " are but the external lines of inflections that have formed internal ridges, the ridges being developed either for giving strength to the sclerite, or to furnish special surfaces for muscle attachment. The cardo of *Periplaneta,* for example (fig. 25 A, *Cd*), has a " divided " appearance externally, but when examined from within (B) it is seen that the regions apparent on the surface result from the presence of a strong Y-shaped ridge (*r*) on the inner wall, which extends distally from the base to reinforce with its diverging arms the extremities of the hinge line with the stipes. This structure of the cardo is characteristic of other orthopteroid insects. Crampton (1916) distinguishes the area of the cardo between the arms of the ridge as the " veracardo," and calls the rest of the sclerite the " juxtacardo." The terms may have a descriptive convenience, but they are misleading if taken to signify a division of the cardo into two parts.

The stipes is usually marked by a prominent groove parallel to its inner edge (fig. 25 A, *q*), setting off a narrow marginal strip. The groove is here likewise but the external line of an internal ridge or plate upon which are inserted the adductor muscles of the stipes (B, *KLst*). Crampton designates the area of the stipes external to the ridge as the "verastipes," and that mesad to it as the "juxtastipes." In *Heterojapyx* the basal part of the stipes is strengthened by an internal ridge (fig. 30 A, *u*) that forks proximally to the ends of the hinge line with the cardo.

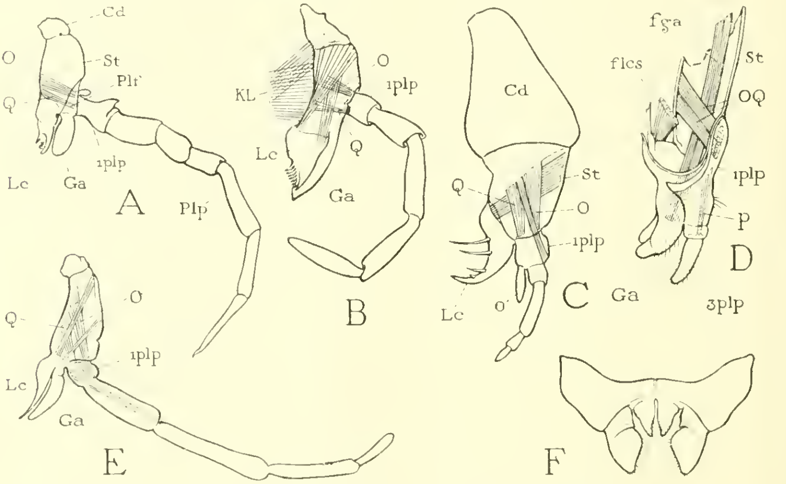

FIG. 31.—Maxillae of insects and of a chilopod.

A, maxilla of *Nesomachilis*. B, maxilla of *Thermobia* (Lepismatidae). C, maxilla of larva of *Sialis*. D, terminal part of maxilla of *Heterojapyx*. E, maxilla of an adult stonefly (*Pteronarcys*). F, first maxillae of a chilopod (*Lithobius*).

Base of palpus to be identified by insertions of levator and depressor muscles (*O, Q*); the palpifer (*Plf*) has no muscles, and appears as a mere subdivision of stipes; in *Sialis* larva (C), lobe *o* is not the galea, but an endite of first segment of palpus (*1plp*), the latter identified by its muscles (*O, Q*).

The ventral, or distal, end of the stipes bears the lacinia and galea, and to its lateral surface is attached the palpus. The lacinia and galea are movable lobes, each being provided with muscles having their origin in the stipes, by which they can be flexed posteriorly (or ventrally if the mouth appendages are horizontal). The lacinia, in addition, has a muscle from the cranial wall inserted on the inner angle of its base, which gives it a mesal flection, or adduction. The base of the galea commonly overlaps anteriorly the base of the lacinia.

The maxillary palpus arises from the outer wall of the stipes, usually only a short distance proximal to the base of the galea. The area supporting the palpus is frequently differentiated from the rest of the stipes, and is then distinguished as the palpifer (fig. 31 A, *Plf*). When the delimiting suture of the palpifer region extends to the galea, the palpifer appears to support both the galea and the palpus. *That the palpifer is not a segment of the appendage is shown by the fact that muscles neither arise within it nor are inserted upon it.* The muscles that move the palpus as a whole have their origins within the main part of the stipes, and always pass through the palpifer, if the latter is present, to be inserted on the proximal segment of the palpus (figs. 25 C, 31 A-E, *O, Q*). The palpus muscles, then, may be taken as identification marks of the true basal segment of the palpus. Since they are typically inserted one dorsally and the other ventrally, relative to the vertical axis of the appendage, they are evidently a levator (*O*) and a depressor (*Q*) of the palpus. The number of segments in the maxillary palpus varies much in different insects. *Machilis* perhaps presents the maximum number of seven (fig. 31 A) : the palpus of the roach with five segments is more typical (fig. 25). Evidence will later be given indicating that the palpus is the telopodite of the maxillary appendage, and that its basal articulation with the stipes, or palpifer, is the coxo-trochanteral joint of a more generalized limb (fig. 35 A, B, C, *ct*). A joint near the middle of the palpus (figs. 25 C, 35 A, B, *ft*) often suggests the femero-tibial flexure.

THE SECOND MAXILLAE

The second maxillae of insects are unquestionably united in the labium. The correspondence in external relations between the parts of each half of a typical labial appendage and those of an entire maxilla is so close that most entomologists have not hesitated to assume an homology of the submentum (figs. 32 A, 40 D, *Smt*) with the cardines, of the mentum (*Mt*) with the stipites, of the glossae (*Gl*) with the laciniae, and of the paraglossal (*Pgl*) with the galeae. Some writers, however, have contended that the submentum, or both the submentum and the mentum represent the sternum of the labial segment. Thus, Crampton in a recent paper (1928) adopts the idea of Holmgren (1909) that the submentum and mentum are derived from the sternum of the labial segment.

In an orthopteroid labium (fig. 40 D), the muscles of the palpi (*28, 29*), and the muscles of the terminal lobes (*25*) arise in the mentum (*Mt*), and this relation, together with the presence of muscles from the mentum to the tentorium (*23, 24*), must certainly identify the region of the mentum in the labium with that of the stipes in a first maxilla (fig. 40 B, *St*). The wall of the mental region, however, may not be entirely or continuously chitinized (fig. 32 A), and, hence, a distinction must be drawn between the entire region of the mentum, and the area occupied by one or more mental sclerites. The labium may contain muscles not represented in the maxillae, such as the muscles associated with the orifice of the salivary duct in the grasshopper (fig. 40 D, *26, 27*), or with the silk press in the caterpillar (figs. 53 C, D, 54, A, B, C, *17, 18, 19*).

The submentum corresponds functionally at least with the cardines of the maxillae, since it serves to attach the labial appendage to the walls of the head. The lateral articulation of its basal angles to the margins of the cranium in orthopteroid insects (figs. 18 B, C, 36 C, *f*) suggests, moreover, that the points of attachment are the true basal articulations of the second maxillae with the cranium, corresponding with the articulations of the cardines (*e*) in the first maxillae. It is possible, of course, that a median part of the labial sternum has been incorporated into the submentum. To accept the proposal, however, that the entire submentum is the sternum of the labial segment, is to assume that the sternum itself has become articulated laterally to the tergum of its segment, and that it alone bears the segmental appendages. Such assumed relations violate the basic principles of segmental morphology, and thus throw suspicion on the evidence given in their support.

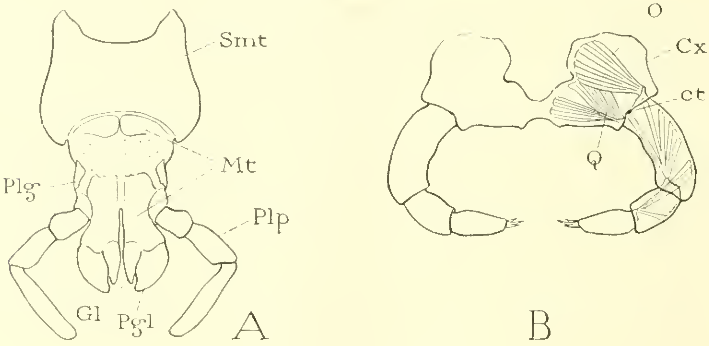

FIG. 32.—Second maxillae.

A, typical second maxillae of an insect (*Periplaneta*) united to form the labium. B, second maxillae of a chilopod (*Lithobius*) united by inner angles of coxae.

ct, coxo-trochanteral joint; *Cx,* coxa; *Gl,* glossa; *Mt,* mentum; *O,* levator muscle of telopodite (palpus); *Pgl,* paraglossa; *Plg,* palpiger; *Plp,* palpus; *Q,* depressor muscle of telopodite (palpus); *Smt,* submentum.

It will be shown in the next section of this paper that the *cardines* of the maxillae are not true proximal segments of the maxillary appendages, but are secondary subdivisions of the bases of these appendages. It appears probable, therefore, that the submentum represents likewise proximal subdivisions of the bases of the second maxillae, retaining the lateral articulations with the margins of the cranium in generalized insects (fig. 36 C, *f*), and perhaps including between them a median part of the labial sternum.

If the insect labium (figs. 32 A, 40 D) is compared with the second maxillae of a chilopod (fig. 32 B), it will be seen that the united basal segments of the latter (*Cx*), containing the origins of the palpal muscles (*O, Q*), correspond at least with the mentum of the labium. The large proximal segments of the chilopod maxillae are clearly the bases of a generalized limb, the coxae, according to Heymons (1901), and the limb base, or a subcoxal division of it, bears the primitive dorsal articulation of the appendage with the body. The mentum, and at least the lateral parts of the submentum, therefore, appear to be subdivisions of the primary bases of the second maxillary appendages, corresponding with the stipites and cardines of the first maxillae in insects, and with the similar subdivisions of the bases of the mandibles in the diplopods (fig. 26 A, *Cd, St*).

The median, terminal duct of the labial, or " salivary," glands opens anterior to the labium, and, in typical forms, at the base of the mentum (figs. 18 D, 19, *SlO*). The position of the orifice, anterior to the submentum, however, does not argue that the latter is entirely the sternum of the labial segment, but rather the reverse, for it is likely that the orifice of the duct has not left the sternal region of its segment, and that it has been crowded forward in the latter by the median approach of the labial cardines. The common duct of the labial glands results during embryonic development from the union of the two primary ducts of paired lateral glands of the labial segment.

MORPHOLOGY OF THE GNATHAL APPENDAGES

It has often been assumed that the segmental appendages of all arthropods are derived from a primitive limb having a biramous type of structure. A two-branched limb, however, occurs actually only in the Crustacea, and there is no certain evidence of a biramous limb structure ever having prevailed in other arthropod groups. In all forms, including the Crustacea, the segmental appendages first appear in the embryo as simple protuberances of the body wall, and some zoologists now believe that the exopodite branch, when present, is merely a specially developed exite lobe of a single shaft. Borradaile (1917) expresses the opinion that "probably the primitive crustacean appendage resembled that of the Branchiopoda in being uniramous." Movable lobes individually provided with muscles, however, may be developed along both the outer and the inner margin of the limb, and an excessive development of one of the outer lobes might give rise to a secondary biramous structure of the appendage. Hansen (1925) recognizes the definitive two-branched structure of the typical crustacean appendage, but he says it seems "impossible to deny the possibility that the exopod may be analogous with the epipod, and if so the primitive appendage is uniramous."

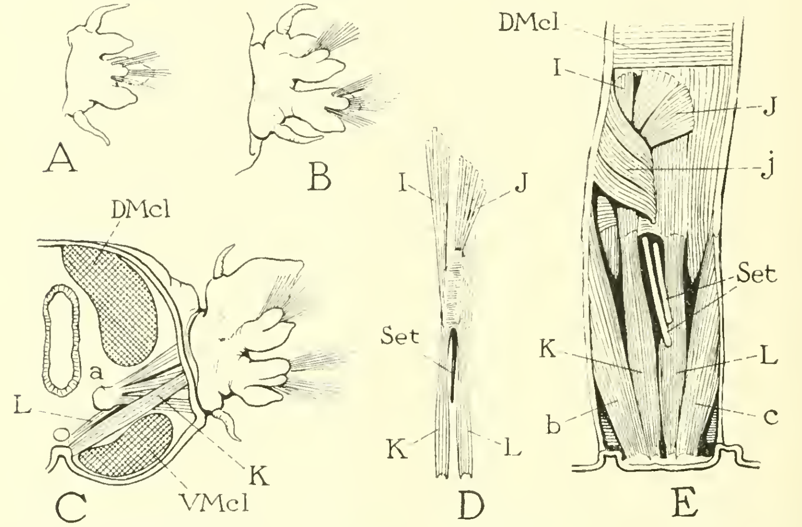

Fig. 33.—Parapodium and parapodial musculature of an annelid worm (*Nereis virens*).

A, B, first and third parapodia, left, anterior surfaces.

C, cross section of left half of a segment from middle of body, cut anterior to base of parapodium, showing muscles of setae inserted on end of setal pouch (*a*), and ventral promotor (*K*) and remotor (*L*) muscles of parapodium. *DMcl, VMcl,* dorsal and ventral bands of longitudinal body muscles.

D, musculature of third parapodium, right, inner view, showing tergal promotor (*I*) and remotor (*J*), and sternal promotor (*K*) and remotor (*L*).

E, musculature of right side of a segment from middle of body, internal view, lateral oblique muscles and setal muscles removed: *b, c,* anterior and posterior pleuro-sternal muscles; *DMcl,* part of dorsal longitudinal muscles; *I,* tergal promotor of parapodium; *J,* tergal remotor; *j,* accessory remotor arising anteriorly from intersegmental fold; *K,* sternal promotor; *L,* sternal remotor; *Set,* bases of setae.

The segmental appendages, or parapodia, of the polychaete annelids are in some cases simple lobes; in others they are of a two-branched structure owing to the presence of two groups of setae on each (fig. 33 B, C). In *Nereis virens,* though most of the parapodia are distinctly cleft, those of the first and second segments do not have the double structure (fig. 33 A). Whatever relations, however, may be traced, or assumed to exist, between the annelids and the arthropods, the relationship must be presumed to have come through a remote worm-like ancestor common to both groups, for none of the highly organized modern annelids can be taken to represent the ancestral form of the arthropods.

A comparative study of the legs of mandibulate arthropods will show that in each group there is a maximum of seven limb segments, beyond a subcoxal base, that are individually provided with muscles. The relative size and form of the segments, the character of the articulations, and the nature of the musculature present many variations, and it is not to be assumed that segments are to be homologized in all cases by their numerical order beyond the base of the limb.

The gnathal appendages undoubtedly constitute a group of organs that are individually homologous in arthropod groups, whether their segments are united with the protocephalon to form a larger head, or with the body segments following. The similarity of the structure of the mandible in all the eugnathate arthropods, and the common plan of its musculature, allowing for modifications of which the evolution can easily be followed, leave no doubt concerning the identity of the jaw in the various groups, or that the jaw attained its basic structure in some very remote common ancestor. The primitive structure of the mandible is not entirely preserved in any arthropod: in the Diplopoda and Chilopoda the movable lacinia is retained, but the palpus has been lost; in the Crustacea and Hexapoda, the lacinia has lost its independent mobility and has become solidly fused with the base of the appendage, but in many crustaceans a mandibular palpus persists.

The first maxilla of the Hexapoda has the structure of a generalized mandible, *i. e.*, it consists of a base supporting a palpus and at least one movable lobe, the lacinia, though generally there is present a second lobe, the galea. The insect labium consists of a pair of appendages that probably once had the structure of the first maxillae. In the Chilopoda the maxillary appendages appear to have undergone but little modification of structure, and those of the second pair still retain a form similar to that of the body appendages. The corresponding appendages of the Diplopoda are now so highly specialized that it is useless to speculate as to their earlier form. In the Crustacea both pairs of maxillae have been reduced in size and modified in structure to serve as organs accessory to the mandibles, but they have not attained the highly specialized form of the corresponding appendages of insects.

We may conclude, therefore, that in the common ancestor of the several groups of modern eugnathate arthropods, the mandible alone had attained a gnathal function, and that in form and structure it resembled the maxilla of a present day insect, though perhaps lacking a galea, or outer endite lobe of the base. The two maxillae at this period were more or less modified to serve as organs accessory to the mandibles.

When the modern groups of arthropods were differentiated, the mandible, in the Diplopoda and Chilopoda, retained the movable lacinia, but lost the palpus; in the Crustacea and Hexapoda, the lacinia fused with the base of the appendage to form a solid jaw, while the palpus was preserved by the crustaceans, and lost by the insects. The two maxillary appendages retained the leg-like form in the Chilopoda; in the Diplopoda they became highly specialized in a manner peculiar to the diplopod group; in the Crustacea and Hexapoda they were modified for an accessory gnathal function, but in the insects they acquired a form almost identical with that of a primitive mandible. Finally, in the insects, the second maxillae united basally to form the labium. While the insect maxilla appears to be a highly specialized appendage, it will be shown that its basic structure is not far removed from that of a thoracic leg.

While the status of the gnathal appendages relative to one another in the various groups of the eugnathate arthropods seems fairly clear, it is a more difficult matter to homologize their parts with the segments of the ambulatory appendages. The structure of the first and second maxillae of a chilopod, or of the first maxilla of an insect, suggests that the gnathal appendages have been derived from an appendage of the ambulatory type—the insect maxilla is certainly more like the leg of an insect, a chilopod, or a decapod than it is like one of the body appendages of *Apus* (fig. 35 C), or of any other of the lower crustaceans in which the appendages are used for swimming. This condition suggests, therefore, that the ambulatory leg more nearly represents the primitive type of arthropod limb than does an appendage, such as that of *Apus*, clearly modified for purposes of purely aquatic locomotion. If we consider, furthermore, that the appendages of the chelicerate arthropods (Xiphosura and Arachnida) are also of the ambulatory type, the evidence becomes all the more convincing that the primitive arthropod limb was a walking leg and not a swimming organ. If this deduction is acceptable, we must conclude that the Crustacea represent a group of arthropods that have secondarily adopted an aquatic life, and that, while certain forms have become thoroughly adapted to a free life in the water, others have retained, with but little modification, some of the organs that were developed primarily for terrestrial locomotion. This view, perhaps, is contrary to generally accepted ideas concerning the evolution of the arthropods, but it is clearly futile to attempt to derive the appendages of arthropods in general from the swimming appendages of Crustacea.

If the ambulatory limb be taken as more nearly representative of the basic structure of an arthropod appendage than is the natatory limb, we have only to inquire as to what was its probable form in the ancestors of terrestrial arthropods. The primitive appendage undoubtedly turned forward and backward on a vertical axis through its base (fig. 34 A, *a*, *b*), as does the parapodium of a modern polychaete annelid (fig. 33 A, B, C). For walking purposes, however, the limb must have acquired joints, and, as Börner (1921) has shown, the simplest practical condition would demand at least *two* joints with vertical movements (fig. 34 A), one near the union of the leg with the body (*ct*), dividing the limb into a *basal piece* (*LB*) and a *telopodite*

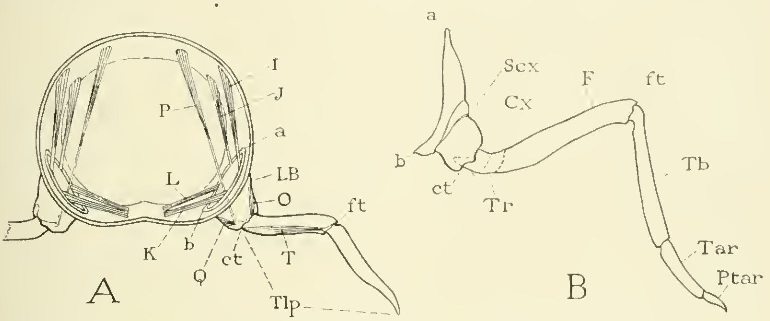

FIG. 34.—Generalized segmentation and musculature of an insect leg, diagrammatic.

A, theoretical segmentation and musculature of a primitive arthropod leg, anterior view: the appendage, consisting of a *limb base* (LB), and a *telopodite* (*Tlp*) of two segments, moved forward and backward on vertical basal axis (*a-b*) by tergal and sternal promotors (*I*, *K*), and tergal and sternal remotors (*J*, *L*).

D, definitive segmentation of an insect leg by division of limb base (A, *LB*) into subcoxa (*Scx*) and coxa (*Cx*), and by subsegmentation of first part of telopodite into trochanter and femur, and of second part into tibia, tarsus, and praetarsus.

a-b, basal axis of limb base; *ct*, coxo-trochanteral joint; *Cx*, coxa; *F*, femur; *ft*, femoro-tibial joint; *I*, tergal promotor; *J*, tergal remotor; *K*, sternal promotor; *L*, sternal remotor; *O*, levator of telopodite; *P*, tergal depressor of telopodite (characteristic of insects); *Ptar*, pretarsus; *Q*, depressor of telopodite; *Scx*, subcoxa; *T*, depressor of distal segment of telopodite; *Tar*, tarsus; *Tb*, tibia.

(*Tlp*), and one (*ft*) near the middle of the telopodite. These primary joints persist, evidently, as the coxo-trochanteral joint (B, *ct*) and the femero-tibial joint (*ft*) of the leg (*Hüftgelenk* and *Kniegelenk*, according to Börner). The type of leg-segmentation resulting from two joints so placed applies at least to the Chilopoda, Diplopoda, Hexapoda, and Crustacea; in the Xiphosura and Arachnida, however, it is possible that the mechanism of the leg is given by three primary joints, the second and third setting off a horizontal middle section of the leg (patella).

The further segmentation of the limb has been produced by the subdivision of the principal parts of the telopodite. In the mandibulate arthropods (fig. 34 B), one or two small segments cut off from the basal end of the proximal piece of the telopodite form the trochanters (*Tr*), while the rest of this part becomes the femur (*F*); the distal section beyond the knee joint (*ft*) subsegments into the tibia (*Tb*), tarsus (*Tar*), and praetarsus (*Ptar*). This type of segmentation is clearly shown also in the maxillipeds or in any of the anterior body appendages of *Apus*. In the third maxilliped (fig. 35 C) there are two principal flexures, one (*ct*) between the limb base (*LB*) and the telopodite (*Tlp*), the other (*ft*) beyond the middle of the latter. The part between the two points of flexure is the femur (*F*) with two indistinctly separated trochanters (*Tr*); that beyond consists of two shortened segments, and the terminal praetarsus, or dactylopodite. The limb base of *Apus* is entire, but in some arthropods the basis appears to have become subdivided into a coxa (fig. 34 B, *Cx*) and a subcoxa (*Scx*). The coxa may then become the free functional base of the appendage, since the subcoxa usually forms a chitinization in the pleural or the sternal wall of the segment.

The primitive musculature of the limb base was such as to swing the appendage forward and backward; it must have comprised, therefore, promotor and remotor muscles. Probably there was a tergal promotor (fig. 34 A, *I*) and a tergal remotor (*J*), and a sternal promotor (*K*) and a sternal remotor (*L*). In a thoracic leg of an insect, the base of the telopodite is provided with a depressor muscle (*P*) having its origin on the tergum of the segment, which greatly increases the lifting power of the appendage, but this muscle is not to be considered as a primitive element of the limb musculature. The usual levator and depressor muscles of the telopodite (*O, Q*) have their origin within the limb base.

The simple type of musculature shown in figure 34 A, and here assumed to be the primitive musculature of an arthropod limb base, is actually present in typical form in the simpler anterior parapodia of the annelid, *Nereis virens* (fig. 33 D). Here a dorsal promotor and a remotor (*I, J*) arise on the tergal wall of the segment, and a ventral promotor and a remotor (*K, L*) on the midline of the sternal wall. The ventral muscles are repeated regularly in all the segments of the worm (C, E, *K, L*), but in the more posterior segments the dorsal muscles, though present (E, *I, J*), are less symmetrical in arrangement, and the primary remotor (*J*) is subordinated to a large oblique remotor (*j*) that arises on the anterior margin of the segment. This last muscle is described by Börner (1921) as being the typical dorsal remotor of the parapodium, but by comparison with the simpler anterior appendages (D) it appears to be a secondary acquisition, for the muscle (E, *J*) dipping beneath it has the same insertion on the parapodial base as that of the tergal promotor of the anterior parapodium (D, *J*). Börner's claim, however, that this simple type of limb musculature presented by *Nereis* must represent the primitive motor mechanism of an appendage turning forward and backward on a vertical axis through its base is scarcely to be questioned.

The basal muscles of an appendage do not necessarily retain their original functions, nor their primitive simplicity, for an alteration in the basal articulation of the appendage may change the fundamental movements of the limb, and thereby give quite a different action to the muscles, which, in turn, may shift in position, or become split up into segregated groups of fibers, thus multiplying the number of individual muscles actually present.

Returning now to a further consideration of the muscles of the gnathal appendages of the arthropods, it is not difficult to draw a parallel between the musculature of a mandible, or of an insect maxilla, and that of the annelid parapodium (fig. 33 D, E), or with the hypopthetically primitive musculature of an arthropod limb base as expressed in figure 34 A. In the mandible of *Scutigera* (fig. 26 B, C), *Apus* (fig. 27 A), *Heterojapyx* (fig. 27 C), *Nesomachilis* (fig. 27 D), a tergal promotor (*I*) and a remotor (*J*) have the typical relation to the appendage. In some forms the tergal remotor appears to be lacking (Diplopoda, fig. 26 A; *Spirontocaris*, fig. 27 B). The cranial flexor of the mandibular lacinia in diplopods and chilopods (fig. 26 A, B, C, *flcc*) is probably derived from the tergal promotor, since it arises on the dorsal wall of the head and goes dorsal (anterior) to the ventral muscles. The sternal promotor and remotor, which are distinct muscles in the annelid parapodium (fig. 33 C, D, E, *K, L*), are united in the gnathal appendages of the arthropods, where they become ventral adductors (*KL*) as a result of the free movement of the base of the appendage on a single dorsal point of articulation (*a*).

The adductor fibers of the mandible may all retain their connection with the sternal, or hypopharyngeal, apophyses (Chilopoda, fig. 21 B), or they may become detached from the apophyses and united with the fibers from the opposite jaw to form a transverse dumb-bell muscle (Diplopoda, fig. 26, A, *KL*; some Crustacea, fig. 27 A, B; most Apterygota, fig. 27 C, D, *KLk*), though at the same time some of the fibers may retain their connections with the apophyses, or with the tentorium (Apterygota, fig. 27 C, D, *KLt*; Orthoptera, fig. 29 C, *KLt*) or with the base of the hypopharynx (*Lepisma,* fig. 29 B, *KLh*; *Locusta,* fig. 29 C, *KLh*; *Microcentrum,* fig. 20 D, *KLh*; ephemerid nymph, fig. 20 A, *KLh*). The evolution of the mandibular muscles in the higher insects has been detailed in an earlier paragraph, wherein it was shown that the ventral adductors are reduced and finally obliterated after the jaw has acquired a double hinge with the edge of the cranium, and that the tergal promotor and remotor muscles then become respectively the functional abductors and adductors.

The basal musculature of the insect maxilla, as already shown, coincides almost exactly with the basal musculature of the mandible of a diplopod or a chilopod, and may be derived from the simple plan of the musculature of the annelid parapodium. The tergal promotor is evidently separated into two groups of fibers inserted on the dorsal and ventral extremities of the anterior rim of the appendage base, the upper set being the muscle of the cardo (figs. 25 C, 30 B, *I*), the lower set the cranial flexor of the lacinia (*flcc*). A tergal remotor is lacking in the insect maxilla, but so it appears to be also in the diplopod mandible (fig. 26 A). The sternal promotor and remotor muscles (figs. 33 D, E, 35 B, *K, L*) are united, as in the mandible, to form a ventral adductor (*KL*), the fibers of which almost always retain their origin on the hypopharyngeal apophyses, or on the corresponding part of the tentorium, and are distributed to both the cardo and the stipes (figs. 25 C, 30 B, *KLcd, KLst*). In *Machilis* the maxillary adductors from opposite appendages are united with each other medially, and appear to be detached from the ventral apophyses.

The margin of the basal cavity of the maxilla (fig. 35 A) includes the region of the cardo, the stipes, and the lacinia; and the tergal and sternal muscles (*I, J, KL*) of the appendage are distributed to these three parts. *The entire base of the maxilla, therefore, has the fundamental character of a single segment,* and there can be no doubt that this segment is the true primitive base of the appendage (fig. 34 A, *LB*). The base of a leg appendage may be divided into a coxa and a subcoxa (fig. 34 B, *Cx, Scx*), and Börner (1909, 1921) would identify the cardo of the maxilla with the subcoxa of a leg. The suture separating the cardo from the stipes, however, terminates at both ends in the marginal rim of the maxillary base (fig. 35 A) instead of running parallel with it; *the cardo, therefore, does not have the relation of a true segment to the rest of the appendage.* It is perhaps, though, to be questioned if the subcoxal chitinization, the pleuron, at the base of a thoracic leg is not also a mere subdivision of the basal limb segment similar to the cardo, rather than the remains of a true independent segment. If the cardo does, in any sense, represent the thoracic subcoxa, it is to be noted that the hinge line between it and the stipes has a horizontal position with reference to the axis of the appendage, and this, the writer has argued (1927), must have been the primitive position of the subcoxo-coxal hinge in a thoracic leg.

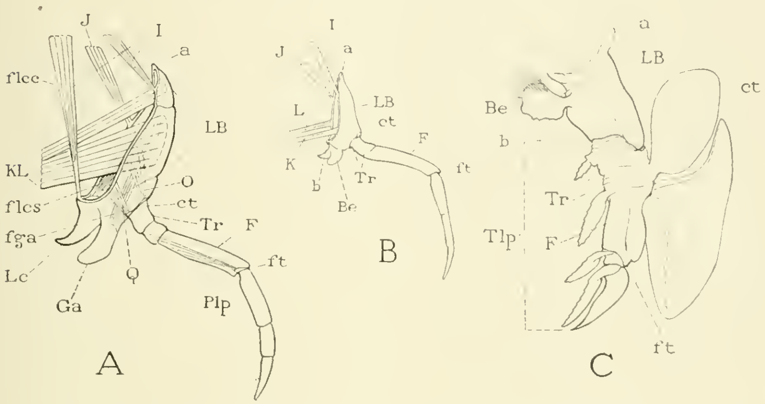

FIG. 35.—The relation of a maxilla to a generalized limb.

A, theoretical generalized structure of a gnathal appendage, consisting of a limb base (*LB*), bearing a divided basendite (*Lc, Ga*), and a six-segmented telopodite, or palpus (*Plp*), with the principal downward flexure at the femoro-tibial joint (*ft*). The limb base provided with tergal promotor and remotor muscles (*I, J*), and sternal adductors (*KL*).

B, showing basal musculature of a gnathal appendage analysed into the functional elements of the musculature of an annelid parapodium (fig. 33 D).

C, third maxilliped of *Apus longicaudata,* left, anterior surface, showing division into a limb base (*LB*) and a telopodite (*Tlp*); the base movable on a transverse axis (*a-b*), the telopodite with a principal flexure (*ft*) between its third and fourth segments.

a-b, basal axis of limb base; *Be,* basendite; *ct,* coxo-trochanteral joint; *F,* femur; *fga,* flexor of galea; *flcc,* cranial flexor of lacinia; *flcs,* stipital flexor of lacinia; *ft,* femoro-tibial joint; *Ga,* galea; *I,* tergal promotor; *J,* tergal remotor; *K,* sternal promotor; *KL,* ventral adductors (*K* and *L* united); *L,* sternal remotor; *LB,* limb basis; *Lc,* lacinia; *O,* levator of telopodite; *Plp,* palpus (telopodite); *Q,* depressor of telopodite; *Tlp,* telopodite; *Tr,* trochanters.

Though the homology of the cardo must be left in question, the writer would agree with Börner (1909, 1921) that the part of the maxilla bearing the lacinia, galea, and palpus represents the coxal region of the leg base, and that the basal segment of the palpus is a trochanter (fig. 35 A, *Tr*). The lacinia and galea, then, are *coxal endites,* and, as Börner proposes, *the stipes and palpifer are corresponding secondary subdivisions of the coxa,* or of the coxal region of the maxillary base. In the maxillae and maxillipeds of the Crustacea, Börner claims, the segments bearing the lobes homologous with the insect lacinia and galea are also subdivisions of the coxa. By this interpretation, the palpus (fig. 35 A, *Plp*) becomes the telopodite of the maxillary appendage (B) ; its basal union with the stipes or palpifer is the coxo-trochanteral joint (*ct*), and its principal distal articulation having a ventral flexure is the femoro-tibial joint (*ft*).

Other writers have held somewhat divergent views concerning the homologies of the maxillary segments. Göldi (1913) interpreted the cardo as the coxopodite, the stipes as the basipodite, to which he assigned the lacinia and galea as endite lobes, and the basal segment of the palpus as the ischiopodite. Crampton (1922) gave a modification of this view in that he proposed that the palpifer represents a segment, the ischiopodite, and that the galea is an endite of this segment. Uzel (1897) appears to give confirmation to this view in his description of the development of the maxilla of *Campodea* ; the maxillary rudiment, he says, is first divided into an outer and an inner lobe, and then the outer lobe splits into two parts, one of which becomes the palpus, the other the galea. If the maxilla of *Campodea* resembles that of *Japyx* (fig. 30 A), however, it is easy to believe that the structure in the embryo might be misinterpreted, in as much as the adult structure is misleading until the muscle relations are taken into consideration (fig. 31 D) ; then it is seen that the basal region of the palpus, which is united with the base of the galea, is the true basal segment of the palp, and not the palpifer—clearly a secondary modification.

It has already been pointed out that the entire lack of muscle connections in the palpifer is a condition that disavows the segmental nature of the palpifer region. Crampton's best example among insects of a structure corresponding with his idea of the segmentation of a maxillary appendage is the maxilla of the larva of *Sialis* (fig. 31 C), in which there is a small lobe (*o*) borne on the apparent first segment of the palpus. This lobe Crampton would identify as the galea, making the supporting segment the palpifer. The muscles (*O, Q*) inserted on the base of this segment, however, clearly demonstrate that it is the true base of the palpus (*1plp*)—therefore, not the palpifer, which lacks muscles—and that the lobe in question is not the galea, as also the absence of a muscle to it would indicate. The maxilla of the *Sialis* larva, then, is not a generalized appendage in the sense that Crampton would infer, since it lacks a true galea and is provided with an accessory lobe on the first segment of the palpus. Similar lobes of the palpus segments occur in other insects, particularly in larvae of Coleoptera; they have a suggestion of the endite lobes of the telopodite in such crustaceans as *Apus* (fig. 35 C).

In the thoracic legs the limb is always flexible at the union between the basis and the telopodite, *i. e.,* at the coxo-trochanteral joint, and in no appendage, where the facts can be clearly demonstrated, is there a union between the coxa and the trochanter. It does not seem reasonable, therefore, to suppose that the proximal segment of the telopodite (the trochanter) should have been incorporated into the limb base in the case of a maxillary appendage. Especially is such a supposition unreasonable in the face of much specific evidence to the contrary. The whole body of evidence bearing on the limb mechanism points to a primitive uniformity of flexure in all the appendages, whereby the limb is divided into a *basis* and a *telopodite*, and indicates that the articulation between these two parts is preserved in the entire series of appendages, except, of course, where the telopodite is lost.

The maxillipeds and the anterior body appendages of *Apus* bear each five endite lobes. The first lobe (fig. 35 C, *Be*) is a basendite, the second is carried by the proximal division of the trochanter, the third by the femur, the fourth by the tibia, and the fifth by the tarsus. Each endite is independently movable by muscles inserted upon or within its base. The maxillae of *Apus* are reduced to single lobes, but the first maxilla appears to represent the rudimentary limb base with the large basendite, since it falls exactly in line with the series of basal endites on the following appendages. The basal endites of arthropod limbs in general, including the "gnathobases" of the trilobite appendages, the gnathal lobes of the pedipalps in Xiphosura and Arachnida, and the "styli" of the legs of *Scolopendrella,* are almost certainly analogous lobes in all cases, and they must be represented by the laciniae (at least) of the insect maxillae, by the laciniae of the mandibles of diplopods and chilopods, and by the incisor and molar lobes of the mandibles in all arthropods. It is a question, therefore, whether the galea of the insect maxilla is an accessory lobe of the limb base, or a subdivision of the primary basendite (fig. 35 B, C, *Be*) The latter seems probable, since, in the more generalized insects, the lacinia and galea overlap each other basally, and both are flexed by the muscles inserted upon their bases that have their origin in the stipes.

It is impossible at present to arrive at final conclusions on the many problems connected with the morphology of arthropod appendages, and the most that the writer would claim for the present attempt at advancing the subject is that the material here presented gives at least a substantial enlargement to the foundation of known facts from which future work must proceed. There is no question that students of arthropods have given far too little attention to the relationship between skeletal structure and musculature. The more the subject is looked into, the more it will be seen that the characters of the arthropod skeleton are in large part adaptations to the strain of muscle tension, and that they are to be correctly interpreted only through an understanding of the entire mechanism of which they are a part. The sclerites of the insect cuticula, in particular, have been studied as if they were skeletal elements deftly fitted together in such a manner as to cover the outside of the animal, and we entomologists have played with them, as we might with the sections of a picture puzzle, without looking for their significance in the mechanics of the insect. The arthropod skeleton, it is true, has been formed from a few major centers of increased chitinization, but the minor "divisions" are in almost all cases adaptations to flexion, or the opposite, namely, the strengthening of the skeleton by the development of internal ridges. The scientific study of the comparative anatomy of insects must look for its advance in the future to a wider knowledge of muscles and mechanism.

IV. SUMMARY OF IMPORTANT POINTS

1. The arthropods have been derived from creeping animals, not from forms specially modified for swimming; their immediate progenitors were annelid-like in structure.

2. The stomodeum marks the anterior end of the blastopore. There are, therefore, no true mesodermal segments anterior to the mouth. The unsegmented preoral part of the animal is the prostomium, and constitutes the most primitive head, or *archicephalon,* of segmented animals, since it contains the first nerve center, or "archicerebrum," and bears the primitive sense organs.

3. The first stage in the development of a composite head in the arthropods, as represented in the embryo, comprises the prostomium and the first two or three postoral segments. The head in this stage may be termed the *protocephalon;* it is represented by the cephalic lobes of the embryo, which may or may not include the third segment.

4. The protocephalon carried the labrum, the mouth, the eyes, the preantennae, and the antennae, also the postantennae when it included the third body segment.

5. During the protocephalic stage of insects, as shown by the embryo, the thorax was differentiated as a locomotor center of the body, and the region between the head and the thorax, consisting of the fourth, fifth, and sixth body segments, became a distinct gnathal region.

6. The gnathal region was eventually added to the protocephalon to form the definitve head, or *telocephalon*. In the Crustacea, in which there was no thoracic region corresponding with that of the insects, the gnathal region was not definitely limited posteriorly, and the definitive head in this group may include as many as five segments following the protocephalon. In some of the crustaceans the gnathal segments have united with segments following to form a gnathothorax, leaving the protocephalon as a separate anterior head piece. In the Arachnida the protocephalon included the prostomium and two postoral metameres, and it has combined with the following six segments to form the cephalothorax.

7. In the definitive insect head, the prostomium, according to some embryologists, contributes the clypeus and frons and the region of the compound eyes; according to others it forms the clypeus and frons only. The labrum is a median preoral lobe of the prostomium.

8. The arthropod brain probably always includes the median prostomial ganglion, combined with the ganglia of the preantennal segment to form the protocerebral lobes. It may still be questioned whether the optic lobes are derived from the prostomium or from the preantennal segment. The ganglia of the antennal segment form the deutocerebrum. The commissures of the protocerebrum and the deutocerebrum are formed above the stomodeum, and unite with the archicerebral rudiment to form the median part of the brain. The ganglia of the postantennal segment, when united to the preceding ganglia, become the tritocerebral brain lobes, but they remain separate from the brain in some crustaceans, and their uniting commissure always preserves its sub-stomodeal position.

9. The prostomial region of the adult arthropod is innervated from the postantennal ganglia, but this is probably a secondary condition owing to the loss of the true prostomial nerves.

10. The appendages of the definitive insect and myriapod head are the preantennae, the antennae, the postantennae, the mandibles, the first maxillae, and the second maxillae. Rudimentary, evanescent preantennae have been reported only in the embryo of *Scolopendra*

(Heymons) and in the embryo of *Carausius* (Wiesmann). Postantennae are commonly present in insect embryos, but their rudiments persist in only one or two doubtful cases in the adult. The postantennal appendages are the second antennae of Crustacea, and probably the chelicerae of Arachnida and Xiphosura. Endites of their bases may have been the functional jaws of the insectan and myriapodan ancestors in the protocephalic stage.

11. The gnathal appendages have been derived from organs having the structure of uniramous ambulatory legs. All the primitive arthropod appendages were probably uniramous ambulatory limbs. Biramous and natatory appendages are characteristic of the Crustacea only, and are probably secondary adaptations to an aquatic life.

12. The mandible is a common inheritance from an early ancestor of the eugnathate group of arthropods. Its primitive structure resembled that of the first maxilla of modern insects, and is best preserved in the Myriapoda.

13. The diplopod mandible consists of a base subdivided into cardo and stipes, bearing a large movable lacinia, but lacking a galea and a palpus. In the typical chilopod mandible, the division between cardo and stipes has been lost, and the lacinia is less free. The musculature of the chilopod mandible is more primitive than that of the diplopod mandible. In the crustaceans and insects the mandibular lacinia is either lost, or is fused with the base to form a solid jaw. The mandibular palpus is retained in many Crustacea. The mandible is represented by the pedipalp in Arachnida.

14. The first maxillary appendage is best developed in the insects, and probably here preserves the primitive structure of the mandible. Its musculature is exactly duplicated in the musculature of the mandibles in the diplopods and chilopods. Neither the first nor the second maxillae of the chilopods gives any evidence of ever having attained the special structure of the primitive mandibles and the insect maxillae.

15. A primitive gnathal appendage had the structure of a generalized ambulatory appendage, consisting of a *limb basis* and a *telopodite*. The basis represents the coxa and subcoxa of a thoracic leg, but its division into cardo and stipes is not a true segmentation. The galea and lacinia are movable endites of the basis, with the origin of their muscles in the stipital region of the latter. The telopodite becomes the palpus of the gnathal appendage, and its basal articulation is the homologue of the coxo-trochanteral joint in the leg. The palpifer is not a segment of the limb, but a subdivision of the stipes

bearing the palpus and the galea (as claimed by Börner); the muscles of the palpus and the galea pass through the palpifer, but never arise within it.

16. The primitive appendage was implanted in the soft lateral wall of its segment, and turned forward and backward on a vertical axis through its base, as does an annelid parapodium. The first joint set off the telopodite, and gave the latter a mobility in a vertical plane.

17. The primitive muscles inserted on the base of a generalized limb, as on an annelid parapodium, consisted of a dorsal promotor and a remotor, and of a ventral promotor and a remotor. When tergal plates were developed, the gnathal appendages of the arthropods became attached to their lateral margins, each by *single* point of articulation. The ventral muscles of the appendages then became sternal adductors.

18. The points of origin of the ventral adductors of the gnathal appendages in myriapods and insects were probably crowded together when the gnathal segments were added to the protocephalon. They have since become supported on a pair of apophyses arising at first from the base of the hypopharynx. In the myriapods and in most of the apterygote insects, the apophyses still maintain their hypopharyngeal connections; but in the pterygote insects their bases have migrated laterally to the margins of the cranium, and in all but some of the lower forms have finally moved to a facial position in the epistomal suture. Their posterior ends have united with the transverse tentorial bar developed in the back part of the head. The hypopharyngeal apophyses of the Myriapoda and Apterygota have thus come to be the anterior arms of the pterygote tentorium.

19. The adductor muscles of the insect maxillae, arising on the tentorium, are the sternal adductors of the appendages, corresponding with the sternal adductors or rotators of the thoracic legs, and are derived from the primitive ventral promotors and remotors of the limb.

20. The ventral adductors of the mandibles in the Chilopoda retain their connections with the sternal, or hypopharyngeal, apophyses. In the Diplopoda, Crustacea, and Apterygota, groups of the adductor fibers from the mandibles have lost their sternal connections and have united with each other by a median ligament to form a dumb-bell muscle between the two jaws. Other groups of fibers may retain their connections with the apophyses, or direct with the base of the hypopharynx. In the Pterygota, the ventral adductors of the mandibles have been lost, except for a few rudiments in some of the lower orders.

21. The mandible of *Lepisma* and of pterygote insects is hinged to the head on a long base line with anterior and posterior articulations.

The posterior articulation is the primitive one, the anterior a secondary one. By this change in the articulation and movement of the jaw, the primitive tergal promotor muscle becomes an abductor, and the primitive tergal remotor becomes an adductor. The base line of the mandible slopes downward and forward in *Lepisma* and in a few of the lower pterygotes; in all others its slope is reversed, allowing the tip of the jaw to swing inward and posteriorly during adduction. A similar evolution of the mandible has taken place in the Crustacea.

22. The ridge of the base of the insect cranium, on which the prothoracic and neck muscles are inserted, is probably a chitinization of the intersegmental fold between the maxillary and labial segments. The posterior tentorial arms arise from its ventro-lateral ends by invaginations in the external suture. The neck of the insect, therefore, may be unchitinized parts of both the labial and the prothoracic segments.

V. THE HEAD OF A GRASSHOPPER

After laying down the general principles worked out in the preceding sections, it will be well to test them with a few specific examples. The head of a grasshopper is a good subject for an elementary study of the structure of the pterygote insect head, because it preserves the generalized orientation in having the face directed forward and the mouth appendages hanging downward. Terms of direction, therefore, do not have to be qualified—*ventral* is downward, *dorsal* is upward, and *anterior* is forward. The descriptions here given are based on the Carolina locust (*Dissosteira carolina*), a fairly large grasshopper to be obtained in almost any part of the United States.

The muscles are designated numerically for convenience of reference only, and the same numbers do not refer to corresponding muscles in the grasshopper and in the caterpillar (Section VII). The myology of insects is as yet too little advanced to furnish a satisfactory general nomenclature for insect muscles, and no attempt is made here to use a set of names for the muscles of the grasshopper that could in all cases be applied to the muscles of other insects. The usual method of naming muscles according to their function, or their supposed function, gives terms fitting for the species described; but in many cases, by a change in the articulation between the skeletal parts involved, muscles that are clearly homologous have their functions completely altered. Again, it is impossible to name muscles consistently according to their points of origin and insertion, for either end of a muscle may shift and may migrate into a territory quite foreign to its original connections. A third feature disturbing to a uniform muscle nomenclature is the fact that any muscle may break up into groups of fibers, or, at least, a single muscle in one species may be represented functionally by several muscles in another. Finally, there are muscles that are evidently new acquisitions developed in connection with special mechanisms. The importance of the study of musculature for the understanding of the insect skeleton, however, can not much longer be ignored.

STRUCTURE OF THE CRANIUM

The walls of the head in the grasshopper are continuously chitinized on the anterior, dorsal, and lateral surfaces (fig. 36 A, B), and the dorsal and lateral walls are reflected upon the posterior surface (C) to form a narrow occipito-postgenal area surrounding the foramen magnum (*For*). The foramen is closed below by the neck membrane, in which is suspended the base of the labium (*Lb*). The ventral wall of the head, between the bases of the gnathal appendages, is occupied mostly by the large median hypopharynx, it being otherwise reduced to the narrow membranous areas between the lateral margins of the hypopharynx and the bases of the mandibles and maxillae.

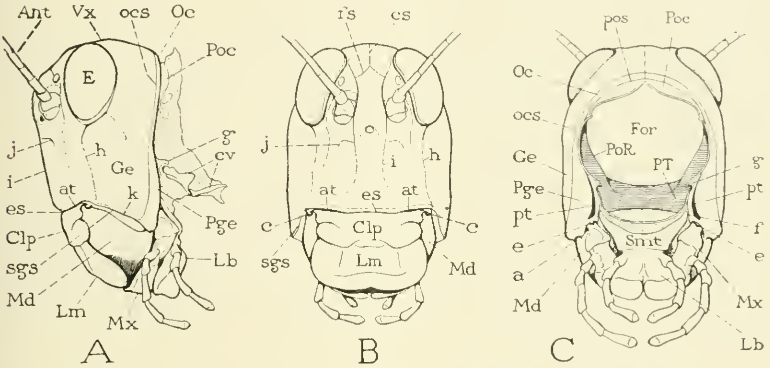

FIG. 36.—Head of a grasshopper, *Dissosteira carolina*.

A, lateral. B, anterior. C, posterior.

a, posterior articulation of mandible; *Ant*, antenna; *at*, anterior tentorial pit; *c*, anterior articulation of mandible; *Clp*, clypeus; *cs*, coronal suture; *cv*, cervical sclerites; *E*, compound eye; *e*, articulation of maxilla with cranium; *es*, epistomal suture; *f*, articulation of labium with cranium; *For*, foramen magnum; *fs*, frontal suture; *g*, condyle of postocciput for articulation with cervical sclerite; *Ge*, gena; *h*, subocular ridge; *i*, frontal carina; *j*, subantennal suture; *k*, flexible area between lower edge of gena and base of mandible; *Lb*, labium; *Lm*, labrum; *Md*, mandible; *Mx*, maxilla; *O*, ocellus; *Oc*, occiput; *ocs*, occipital suture; *Pge*, postgena; *Poc*, postocciput; *PoR*, postoccipital ridge; *pos*, postoccipital suture; *PT*, posterior arm of tentorium; *pt*, posterior tentorial pit; *sgs*, subgenal suture; *Vx*, vertex.

The facial aspect of the cranium is distinctly separated by the epistomal suture (fig. 36 A, B, *es*) from the clypeus, but there is no demarked frontal sclerite. The apex of the frons, however, is defined in *Dissosteira* by two short remnants of the frontal sutures (B, *fs*) diverging from the end of the coronal suture (*cs*). The facial area of the head is limited on each side by an impressed line (*h*) extending from the lower angle of the eye to the anterior articulation of the mandible. The median part of this area forms a broad *frontal costa,* margined laterally by a pair of sinuous carinae (*i*) reaching from the top of the head to the lower part of the face. A short, transverse *subantennal suture* (*j*) lies on each side of the frontal costa just below the level of the median ocellus. The inner ridges of these subantennal sutures have a close relation to the attachments of the more important muscles of the frons (fig. 38 D, *j*). The true frontal area of the grasshopper, therefore, must include the region of these sutures and extend dorsal to them between the bases of the antennae into the angle between the short remnants of the frontal sutures.

The lateral areas of the head (fig. 36 A) have no special characteristics. The subgenal suture (*sgs*) on each side is continuous anteriorly with the epistomal suture (*es*). The compound eye is surrounded by a distinct suture forming a high ridge internally (fig. 39 A, *OR*), and setting off a narrow rim, or ocular sclerite, around the base of the eye (fig. 36, A, B, C).

On the posterior surface of the head (fig. 36 C), the occipito-postgenal area (*Oc, Pge*) is included between the well-marked occipital suture (*ocs*) and the postoccipital suture (*pos*). In *Dissosteira* the occiput and postgenae are continuous; in *Melanoplus* the occipital arch is separated from the postgenae by a short groove on each side on a level with the lower angles of the compound eyes. Posterior to the postoccipital suture is the postoccipital rim of the head (*Poc*), widened above and below on each side, to which the membrane of the neck is attached. The postoccipital suture forms internally the ridge on which the muscles of the neck and prothorax that move the head are inserted (fig. 45 A, *PoR*). Laterally the postoccipital ridge is elevated as a high plate (fig. 36 C, *PoR*), from the ventral ends of which the posterior arms of the tentorium (*PT*) proceed inward. The roots of the tentorial arms appear externally as long open slits in the lower ends of the postoccipital suture (*pt, pt*).

The clypeus and labrum form together a broad free flap (fig. 36 A, B, *Clp, Lm*) hanging before the mandibles from the lower edge of the frontal region. The fronto-clypeal, or epistomal, suture (*es*) is a deep groove forming internally a strong epistomal ridge (fig. 39 A, B, C, *ER*), from the lateral parts of which arise the anterior tentorial arms (*AT*). The roots of these arms appear externally as lateral slits in the epistomal suture (figs. 36 B, 37 A, *at, at*), just mesad to the anterior articulations of the mandibles (*c, c*). The clypeus of *Dissosteira* is partially divided by transverse lateral grooves into anteclypeal and postclypeal areas. The labrum is a broad oval plate, notched at the middle of its ventral margin, freely movable on the lower edge of the clypeus. A median quadrate area on its basal half is limited below by a sinuous transverse groove (fig. 37 A) that forms a low ridge on the inner surface of the anterior wall (B, *l*.) On the posterior surface of the clypeo-labral lobe, the area of the clypeus is separated from that of the labrum by two small chitinous bars, the *tormae* (figs. 37 B, 42 A, *Tor*). A median Y-shaped thickening (fig. 42 A, *m*) of the cuticula of the labrum makes a ridge on the inner surface of the posterior labral wall.

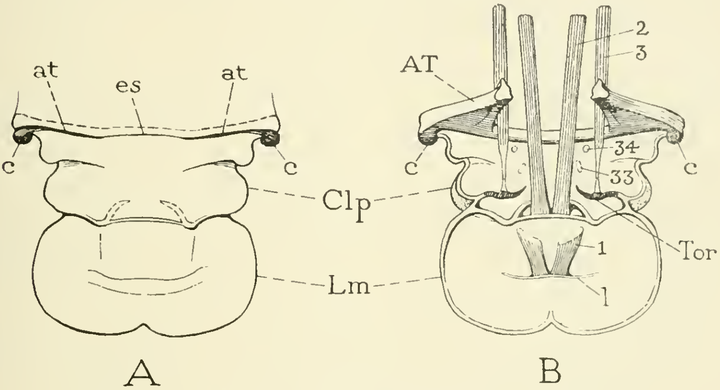

FIG. 37.—Clypeus and labrum of *Dissosteira carolina.*

A, anterior surface. B, posterior surface of anterior wall, showing muscle attachments, and bases of anterior tentorial arms.

AT, anterior arm of tentorium; *at,* anterior tentorial pit; *c,* anterior articulation of mandible; *Clp,* clypeus; es, epistomal suture; *l,* ridge of anterior labral wall; *Lm,* labrum; *Tor,* torma; *1,* labral compressors; *2,* anterior retractors of labrum; *3,* posterior retractors of labrum; *34, 35,* points of origin of anterior dilators of buccal cavity (figs. 41, 44).

The clypeus has no muscles for its own movement, but the first two pairs of anterior dilators of the buccal cavity (figs. 41, 44, *33, 34*) are inserted on the inner surface of its anterior wall (fig. 37 B, *33, 34*). The labrum is provided with three sets of muscles, as follows:

1.—Compressors of the labrum (fig. 37 B).—A pair of short muscles arising medially on transverse ridge of anterior labral wall (*l*); diverging to arms of Y-shaped ridge in posterior wall (fig. 42 A, *m*).

2.—Anterior retractors of the labrum (fig. 37 B).—A pair of long muscles arising on subantennal ridges of frons (fig. 38 D, *j*); converging downward to insertions on base of anterior wall of labrum (fig. 37 B).

3.—Posterior retractors of the labrum (fig. 37 B).—A pair of long muscles arising on subantennal ridges of frons, each laterad of *2* (fig. 38 D); inserted on dorsal processes of tormae at base of posterior wall of labrum (figs. 37 B, 42 A).

The articulations of the gnathal appendages occupy typical positions along the lower lateral margins of the cranium. The mandible articulates anteriorly with a condyle (fig. 39 A, *c*) supported at the junction of the epistomal and subgenal ridges (*ER, SgR*), but projecting on the external surface of the head. Posteriorly the jaw articulates with a facet on the ventral edge of the postgena (figs. 36 C, 39 A, C, *a*). This articulation as the first is outside the membranous connection of the mandible with the head. The axis of the mandible slopes strongly downward and posteriorly between the articular points. The lateral edge of the mandibular base is separated from the margin of the gena by a narrow, flexible strip of weakly chitinized articular membrane (fig. 36 A, *k*), at the ventral margin of which arises the abductor apodeme of the mandible (fig. 39 D, *8 Ap*).

The maxilla articulates by a single point on the base of the cardo with a shallow facet on the edge of the postgena (figs. 36 C, 40 C, *c*) almost directly below the posterior tentorial pit (*pt*). The maxillary articulation is thus crowded unusually far posteriorly in the grasshopper. In most generalized insects it lies well before the line of the postoccipital suture, as in a roach or a termite, and is often much farther forward.

The labium is loosely articulated by the elongate basal angles of the submentum with the posterior margin of the postocciput at points a short distance above the posterior lower angles of the latter (figs. 36 C, 40 C, *f*).

The tentorium of the grasshopper has the form of an X-shaped brace between the lower angles of the cranial wall (fig. 39 B). The anterior arms (*AT*) arise from the lateral parts of the epistomal ridge (*ER*), their broad bases extending from points above the mandibular articulations half way to the median line of the face. In this respect *Dissosteira* shows an advance over *Periplaneta*, in which the bases of the anterior tentorial arms arise from the subgenal ridges and extend only a short distance mesad of the mandibular articulations. The posterior tentorial arms of *Dissosteira* (fig. 39 B, *PT*) arise from the lower ends of the postoccipital ridge (fig. 45 A, *PoR*). The median body of the tentorium is concave below (fig. 39 B, C, *Tnt*). A thin, flat dorsal arm of the tentorium (fig. 39 C, *DT*) arises from the base of the inner end of each anterior arm and extends upward and anteriorly to the wall of the cranium just before the lower angle of the compound eye. The dorsal tentorial arms are attached to the hypodermis of the head wall, but make no connection with the cuticula in *Dissosteira*.

THE ANTENNAE

Each antenna consists of two larger basal segments, and of a long slender flagellum broken up into about 24 small subsegments. In *Dissosteira* the antenna of the male is a little longer than that of the female. Of the two basal segments, the proximal one, or scape (fig. 38 A, *Scp*), is the larger. It is articulated to the rim of the antennal socket by a small process on the lateral ventral angle of its base that touches upon the margin of the socket (*n*). The motion of the scape on the head, however, is that of a hinge joint moving in a vertical plane on a transverse axis. The base of the scape is provided

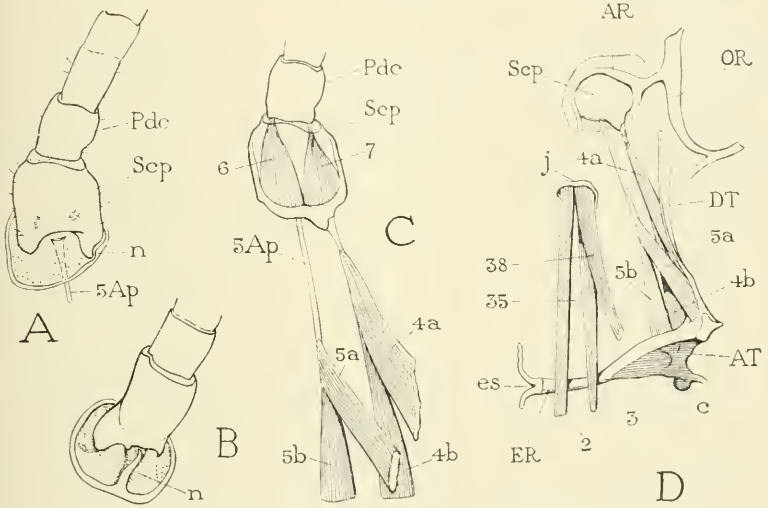

FIG. 38.—Antenna of *Dissosteira carolina* and of *Periplaneta*.

A, base of left antenna of *Dissosteira*, ventral surface. B, the same of *Periplaneta*. C, base of right antenna and antennal muscles of *Dissosteira*, dorsal view. D, base of right antenna, antennal muscles, anterior tentorial arm, muscles arising on frons, and associated structures of *Dissosteira*, interior view.

5Ap, apodeme of depressor muscles of antenna; *AR*, antennal ridge; *At*, anterior arm of tentorium; *c*, anterior articulation of mandible; *DT*, dorsal arm of tentorium; *ER*, epistomal ridge; *es*, epistomal suture; *j*, subantennal ridge; *n*, pivot of antenna; *OR*, ocular ridge; *Pdc*, pedicel; *Scp*, scape.

with levator and depressor muscles (C, D). In other insects the antenna is more commonly pivoted on a ventral point of articulation with the rim of the socket, as in *Periplaneta* (fig. 38 B, *n*), and thus has greater freedom of movement. As already noted, however, the articular point may be dorsal, as in *Japyx,* and in the Chilopoda (fig. 23 B, *n*). The thickened rim of the antennal socket (fig. 38 D, *AR*) is braced by a short arm against the anterior margin of the heavy circumocular ridge (*OR*). A crescentic area of the head wall just above and mesad to the antennal socket is depressed externally, and the inflection tilts the place of the antennal socket somewhat dorsally, giving the antenna a more upward play than it otherwise would have.

The second basal segment of the antenna, the pedicel (fig. 38 A, B, *Pdc*), is movable in a horizontal plane on the end of the scape by means of muscles arising within the scape. The other segments of the antenna are flexible but have no muscles.

The muscles of the antenna comprise muscles inserted on the base of the scape that move the antenna as a whole, and the muscles of the pedicel that move the pedicel and flagellum. They are as follows:

4.—Levators of the antenna (fig. 38 C, D).—Two muscles arising on tentorium, one (D, *4a*) on dorsal arm, the other (*4b*) on anterior arm; both inserted by a short tendon on a lobe of dorsal side of base of scape (C, D).

5.—Depressors of the antenna (fig. 38 C, D).—Two muscles arising on dorsal arm of tentorium (D, *5a*) and on anterior arm (*5b*); both inserted on a long slender tendon arising near ventral margin of scape (A, *5Ap*) in articular membrane of antenna.

6.—Extensor of the flagellum (fig. 38 C).—Arises dorsally and medially in base of scape; inserted medially on base of pedicel.

7.—Flexor of the flagellum (fig. 38 C).—Arises dorsally and laterally in base of scape; inserted laterally on base of pedicel.

THE MANDIBLES

The mandible of the grasshopper is a strongly chitinous jaw—a short, hollow appendage with triangular base, thinning down to the cutting margin. The anterior and the posterior angles of the lateral base line carry the articular points with the head, and the apodeme of the adductor muscles arise at the median angle.

The distal edge of each mandible presents an incisor and a molar area. The first (fig. 39 D, *o*) forms the compressed and toothed apical part of the jaw, the second (*p*) forms a broad grinding surface on the anterior median face closer to the base of the mandible. The incisor and molar areas are not exactly alike on the two jaws, each being best developed on the right. The molar area of the right mandible consists of strong, heavy ridges forming a projecting surface; the ridges of the left jaw are low and their area does not project. The two molar surfaces, therefore, fit one upon the other without interference when the jaws are closed. The incisor lobes of the mandibles close upon the ventral end of the hypopharynx, the molar surfaces over its base, and the anterior contour of the hypopharynx is modeled according to the irregularities of the mandibular surfaces. The posterior slope of the mandibular hinge lines cause the points of the jaws to turn inward, upward, and posteriorly during adduction. At the base of each molar area of the mandibles a flat brush of hairs (fig. 39 C, D) projects inward, and the two brushes come together anterior to the mouth opening when the mandibles are closed, serving thus evidently to prevent the escape of masticated food material from between the jaws. The anterior surfaces of the mandibles are overlapped by the epipharyngeal surface of the clypeus and labrum, and the

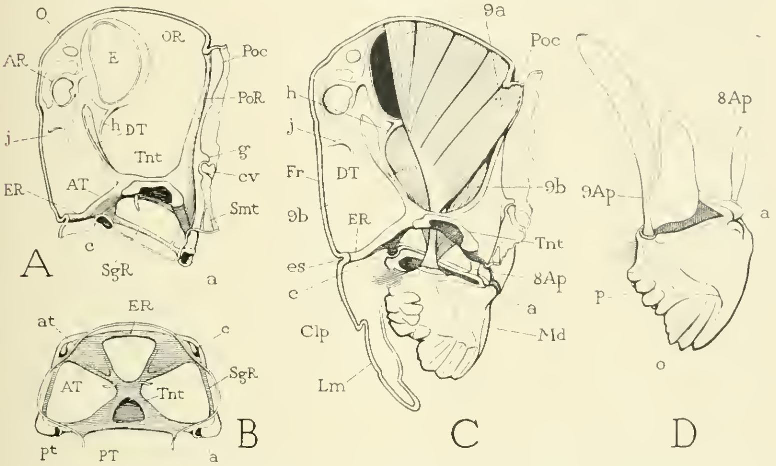

FIG. 39.—Internal structure of the head of *Dissosteira carolina,* and the mandible and its muscles.

A, inner surface of right half of epicranium. B, tentorium and lower margin of epicranium, ventral view. C, inner view of right half of head, with right mandible and its muscles in place. D, right mandible, postero-mesal view.

a, posterior articulation of mandible; *8Ap,* abductor apodeme of mandible; *9Ap,* adductor apodeme of mandible; *AR,* antennal ridge; *AT,* anterior tentorial arm; *at,* anterior tentorial pit; *c,* anterior articulation of mandible; *Clp,* clypeus; *cv,* cervical sclerite; *DT,* dorsal tentorial arm; *E,* compound eye; *ER,* epistomal ridge; *es,* epistomal suture; *Fr,* frons; *g,* condyle of articulation of cervical sclerite; *h,* subocular ridge; *j,* subantennal ridge; *Lm,* labrum; *Md,* mandible; *O,* ocellus; *o,* incisor lobe of mandible; *p,* molar area of mandible; *Poc,* postocciput; *PoR,* postoccipital ridge; *PT,* posterior tentorial arm; *pt,* posterior tentorial pit; *SgR,* subgenal ridge; *Smt,* submentum; *Tnt,* body of tentorium.

asymmetry of the mandibular surfaces and contours is reflected in that of the epipharyngeal surface (fig. 42 A).

The mandibles of *Dissosteira* are moved, so far as the writer could discover, only by tergal abductor and adductor muscles, which, as already explained, are the primitive tergal promotors and remotors transformed in function by the change from a monocondylic to a dicondylic articulation in the mandible (fig. 29 A, B, C). Small ventral adductors of the mandibles arising on the hypopharynx and on the tentorium persist in some of the Tettigoniidae (figs. 20 D, *KLh*, 29 C, *KLh*, *KLt*), but these muscles appear to be lost in the Acrididae, as they are in all higher pterygote insects. The fibers of the functional abductors and adductors arise on the walls of the cranium and are inserted on flat apodemal plates of the jaws. The abductor apodeme is a small plate (fig. 39 D, *8Ap*) arising from the articular membrane close to the outer margin of the mandibular base and near the posterior articulation (*a*). The adductor apodeme (*9Ap*) consists of two large thin plates borne upon a common stalk, which arises from the articular membrane at the inner angle of the mandibular base, and lies in the lateral angle between the anterior and posterior arms of the tentorium (C). One plate extends dorsally in a longitudinal plane, the other, which is smaller, lies in a transverse plane. Each mandibular apodeme is a chitinous invagination from the articular membrane close to the base of the jaw. The muscles of the mandible correspond with the apodemes. They are as follows:

8.—Abductor of the mandible.—A small fan of fibers, arising on ventral part of postgena and on extreme posterior part of ventral half of gena; inserted on abductor apodeme of the mandible.

9.—Adductors of the mandible (fig. 39 C).—Two sets of fibers corresponding with the two divisions of the adductor apodeme. The fibers of one set (*9a*) arise on dorsal wall of cranium, from a point between compound eyes to occiput, with one bundle attached on postocciput (*Poc*); inserted on both sides and on posterior margin of the median apodemal plate. Those of the other set (*9b*), inserted on the transverse plate of the apodeme, arise on lateral walls of cranium from subocular ridge (*h*) to postgena, and some of the posterior fibers encroach upon outer end of posterior tentorial arm.

THE MAXILLAE

The maxilla of the grasshopper (fig. 40 A) is so similar to that of the roach (fig. 25 A), already described, that its major features will need no special description. It consists of a triangular cardo (fig. 40 A, *Cd*), a quadrate stipes (*St*), with a well-developed palpifer

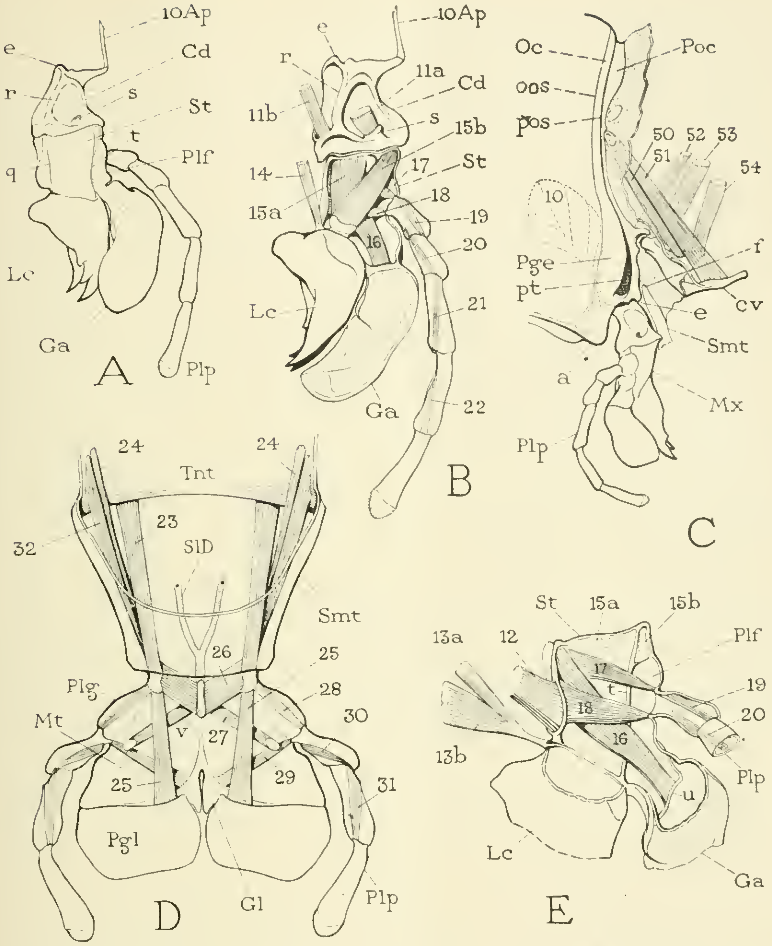

FIG. 40.—Maxilla and labium of *Dissosteira carolina.*

A, right maxilla, posterior surface. B, left maxilla, anterior view, exposing muscles of cardo and stipes. C, posterior region of cranium, with cervical sclerites and maxilla, left side. D, labium and its muscles, posterior view. E, stipes and palpifer with bases of palpus, galea and lacinia, lacinial muscles removed, anterior view.

a, posterior articulation of mandible; *10Ap*, apodeme of promotor of cardo; *Cd*, cardo; *cv*, cervical sclerite; *e*, articulation of maxilla with cranium; *f*, articulation of labium with cranium; *Ga*, galea; *Gl*, glossa; *Lc*, lacinia; *Mt*, mentum; *Mx*, maxilla; *Oc*, occiput; *ocs*, occipital suture; *Pgc*, postgena; *Plf*, palpifer; *Plg*, palpiger; *Plp*, palpus; *Poc*, postocciput; *pos*, postoccipital suture; *pt*, posterior tentorial pit; *q*, suture and internal ridge near inner margin of stipes; *r*, internal ridge of cardo; *s*, apophysis of cardo for muscle insertion; *SlD*, salivary duct; *Smt*, submentum; *St*, stipes; *t*, suture and internal ridge separating palpifer from stipes; *Tnt*, body of tentorium; *u*, inner ridge at base of posterior wall of galea; *v*, keel of salivary cup.

(*Plf*), and two terminal lobes, lacinia (*Lc*) and galea (*Ga*), and a five-segmented palpus (*Plp*).

The cardo presents an irregular topography on its external surface, and is marked into several areas by the lines of a strong branching ridge on its internal surface (fig. 40 B, *r*). Crampton (1916) calls the part proximal and posterior to the ridge the *juxtacardo* and the rest of the sclerite the *veracardo,* but the inference that these areas are " divisions " of the cardo is scarcely warranted, since the ridge is clearly a mere strengthening device. The articular point (*e*) of the cardo with the cranial margin is a knob on the posterior angle of its base, anterior to which is a long arm to which is attached the apodeme (*10Ap*) of the promotor muscle (C, *10*). A pit in the distal part of the external surface of the cardo (A, *s*) marks the site of an internal process on which one of the adductor muscles is inserted (B, *11a*). The distal margin of the cardo is articulated by a long, flexible hinge line with the base of the stipes, but there are no muscles extending between the cardo and stipes.

The quadrate stipes (fig. 40 A, *St*) has a strong plate-like ridge on its internal surface near the inner margin (*q*), on which is inserted one of the adductor muscles (E, *12*). Crampton distinguishes the body of the stipes as the *verastipes,* and the flange mesad of the muscle-bearing ridge as the *juxtastipes*. The region of the palpifer (A, *Plf*) is well separated from that of the stipes by an internal ridge (E, *t*), but the muscles of the palpus (*17*, *18*), as well as the muscle of the galea (*16*), have their origin in the stipes, suggesting that the palpifer is a subdivision of the stipes, and not a basal segment of the palpus.

The lacinia (fig. 40 A, B, *Lc*) is borne by the distal end of the stipes, and is capable of flexion anteriorly and posteriorly on an oblique axis with the latter. Distally it tapers and ends in two claws turned inward. The lacinia is flexed by a pair of strong muscles arising within the stipes (B, *15a*, *15b*), and by a slender muscle (*14*) having its origin on the wall of the cranium.

The galea (fig. 40 A, *Ga*) is carried by a distal subdivision of the palpifer, which Crampton (1916) calls the *basigalea.* In form, the galea (A, B, C, *Ga*) is an oval, flattened lobe ; its walls are but weakly chitinized. Its inner margin lies against the lacinia, and its outer surface is modeled to fit the outer part of the posterior surface of the mandible, against which it can be tightly closed. The base of the galea is marked on the posterior wall by an internal ridge (E, *u*), upon which is inserted its single flexor muscle (*16*).

The maxillary palpus consists of five segments (fig. 40 A, B, C, *Plp*). The basal segment is provided with levator and depressor muscles (B, E, *17*, *18*) arising within the stipes; each of the other segments has a single muscle arising in the first or second segment proximal to it.

The muscles of a maxilla are as follows:

10.—Promotor of the cardo (fig. 40 C).—A small fan of fibers arising on lower posterior part of postgena, external and anterior to the mandibular abductor; inserted on slender apodeme of basal arm of cardo.

11.—Adductors of the cardo (fig. 40 B).—Two muscles arising on posterior end of anterior arm of tentorium, extending ventrally, posteriorly, and outward; one (*11a*) inserted on process (*s*) of inner face of cardo, the other (*11b*) mesad to distal end of ridge (*r*) of cardo.

12.—Proximal adductor of the stipes (fig. 40 E).—Arising on extreme posterior end of anterior arm of tentorium; inserted on ridge of inner margin of stipes.

13.—Distal adductors of the stipes (fig. 40 E).— Two muscles arising on tentorium, the first (*13a*) a slender muscle arising, along with *11a, 11b,* and *12,* on posterior end of anterior arm of tentorium, the second (*13b*) a large, thick, digastric muscle arising laterally on concave ventral surface of body of tentorium; both muscles inserted on a slender apodeme attached to inner distal angle of stipes.

Muscles *11, 12,* and *13* correspond with the adductors of the cardo and stipes that in Apterygota arise on the hypopharyngeal apodemes (fig. 30 B, *KLcd, KLst*), representing the sternal adductors, or sternal promotor and remotor, of a primitive appendage (fig. 35 B, *K*, *L*).

14.—Cranial flexor of the lacinia (fig. 40 B).—Arises on gena just before upper end of promotor of cardo (C, *10*); inserted on inner angle of base of lacinia. This muscle is the homologue of the cranial flexor of the maxillary lacinia in Apterygota (fig. 30 B, *flcc*), and of the corresponding flexor of the mandibular lacinia in Myriapoda (fig. 26 A, B, C, *flcc*).

15.—Stipital flexor of the lacinia (fig. 40 B).—A large two-branched muscle arising in base of stipes, one branch (*15a*) medially, the other (*15b*) in outer basal angle; both inserted on anterior margin of base of lacinia. These muscles flex the lacinia forward. Berlese (1909) describes the posterior branch of this muscle in *Acridium* as attached to the posterior wall of the lacinia, and as being an antagonist to the anterior branch, but in no insect has the writer observed an antagonist to the lacinial flexor.

16.—Flexor of the galea (fig. 40 B, E).—A large muscle arising mesally in base of stipes, external to lacinial muscles and depressor of palpus; inserted posteriorly on ridge (E, *u*) at base of galea. This muscle probably flexes the galea forward and inward, the point of flexion being at the base of the subgalea.

17.—Levator of the maxillary palpus (fig. 40 B, E).—Origin in median basal part of stipes; insertion on dorsal margin of basal segment of palpus.

18.—Depressor of the maxillary palpus (fig. 40 B, E).—Origin on inner edge of stipes; crosses anterior to muscle of galea (*16*) to insertion on ventral margin of basal segment of palpus.

If the basal segment of the palpus (fig. 35 A) corresponds with the trochanter of the leg (fig. 34 B, *Tr*), then muscles *17* and *18* represent the levator and depressor of the telopodite (fig. 34 A, *O*, *Q*) arising in the coxal region of the leg base (*LB*).

19, 20, 21, 22.—Muscles of the maxillary palpus (fig. 40 B).—A single muscle for each segment, the first (*19*) a levator of second segment, the second (*20*) a productor of third segment, the third (*21*) a depressor (adductor) of fourth segment, the fourth (*22*) a reductor of terminal segment.

The joint between the third and fourth segments of the palpus apparently represents the femero-tibial flexure of a leg (figs. 34, 35 A, *ft*), the two small basal segments of the palpus being trochanters.

THE LABIUM

The labium of the grasshopper (fig. 40 D) is simple in construction, and typical of the labium of biting insects, except in the reduction of the glossæ. It consists of a large submentum (*Smt*) with the elongate basal angles loosely attached to the posterior margin of the cranium behind the roots of the posterior tentorial arms (C, *f*). The mentum (D, *Mt*) is broad, with imperfectly differentiated palpus-bearing lobes, or palpigers (*Plg*), at the sides of its base. On its ventral margin the mentum bears a pair of large flat lobes, the paraglossae (*Pgl*), with a pair of rudimentary glossae (*Gl*) between them. Each palpus is three-jointed.

At the base of the anterior surface of the mentum, where the wall of the mentum is reflected into that of the hypopharynx (fig. 41), there is a small, median, oval, cup-shaped depression into which opens the duct from the salivary glands (*SlD*). A small prominence on the base of the hypopharynx fits into the salivary cup and apparently closes the latter when the labium is pressed against the hypopharynx.

The walls of the salivary cup are chitinous, and its posterior inner surface bears a strong chitinous keel (figs. 40 D, 41 *v*) projecting into the interior of the labium in the base of the mentum. Two pairs of muscles (figs. 40 D, *26*, *27*) are attached upon the keel and the walls of the salivary cup.

The musculature of the labium is in general similar to that of the maxillae. It includes the following muscles:

23.—Proximal retractors of the mentum (fig. 40 D).—A pair of muscles arising on ventral surfaces of posterior tentorial arms; inserted on lateral basal angles of mentum.

24.—Distal retractors of the mentum (fig. 40 D).—A pair of muscles arising on posterior surfaces of posterior tentorial arms; extending through submentum and mentum to be inserted on anterior wall of labium at inner basal angles of the glossae. The distal parts of these muscles are not seen in figure 40 D, being covered posteriorly by muscles *23* and *25*. The labial muscles *23* and *24* evidently correspond with the tentorial adductors of the maxillae (E, *12*, *13*).

25.—Flexors of the paraglossae (fig. 40 D).—A pair of large muscles arising in lateral basal angles of mentum; inserted on bases of paraglossae, to posterior walls, near inner ends. Each of these muscles corresponds with the flexor of the galea in the maxilla (E, 16).

The small labial glossae of *Dissosteira* have no muscles.

26, 27.—Muscles of the salivary cup (fig. 40 D).—Two pairs of muscles: one pair (*26*) arising on basal angles of mentum, converging to insertions on keel of salivary cup; the other pair (*27*) arising on posterior wall of mentum near bases of palpi, converging proximally to insertions on sides of salivary cup. These muscles apparently have no homologues in the maxillae; perhaps they are special labial muscles having something to do with the regulation of the flow of saliva from the salivary duct.

28.—Levator of the labial palpus (fig. 40 D).—Origin in lateral basal angle of mentum; insertion on dorsal rim of base of palpus.

29.—Depressor of the labial palpus (fig. 40 D).—Origin in distal median angle of mentum; insertion on ventral rim of base of palpus.

30, 31.—Muscles in the labial palpus (fig. 40 D).—The first (*30*) a levator of second segment; second (*31*) a depressor (adductor) of third segment.

THE PREORAL CAVITY AND THE HYPOPHARYNX

The intergnathal space, or preoral cavity, of the grasshopper (fig. 41, *PrC*) is of large size, but it is mostly filled by the thick, tongue-like hypopharynx suspended from its roof (*Hphy*). Its anterior wall is the posterior surface of the clypeus and labrum (*Clp*, *Lm*), which in the grasshopper is not produced into a specially developed lobe, or epipharynx. The lateral walls are the inner faces of the mandibles and maxillae; the posterior wall is the anterior surface of the labium (*Lb*). The dorsal wall of the cavity represents the true sternal region of the head, sloping downward and posteriorly from the mouth opening to the base of the labium. It is mostly produced into the large, median hypopharynx (*Hphy*), leaving otherwise only a narrow membranous area on each side between the base of the hypopharynx and the bases of the mandible and maxilla.

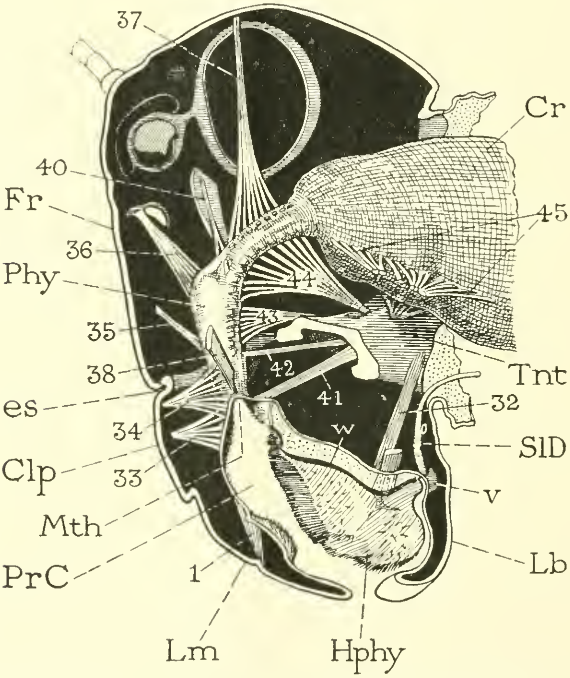

FIG. 41.—Stomodeum, and its dilator muscles in right half of head of *Dissosteira carolina*.

Clp, clypeus; *Cr*, crop; *es*, epistomal suture, *Fr*, frons; *Hphy*, hypopharynx, *Lb*, labium; *Lm*, labrum; *Mth*, mouth; *Phy*, pharynx; *Prc*, preoral cavity; *SlD*, salivary duct; *Tnt*, tentorium; *v*, salivary cup.

The anterior or epipharyngeal wall of the preoral cavity presents a number of features of special interest (fig. 42 A). The lateral parts of the labral region of this wall are concave and fit closely over the smooth, rounded, anterior surfaces of the mandibles. The bands of hairs directed inward on the labral surface guard the exits from between the mandibles, and the asymmetrical forms of the hair-covered areas here correspond with the different shapes of the two mandibles. Minute sense organs are scattered over this labral surface, especially on the bare lateral regions. A special group of similar but somewhat larger sense organs lies at each side of the notch in the ventral border of the labrum. The median area of the basal half of the labral surface forms a low elevation, the sides of which are thickly covered with long spine-like hairs curved inward and upward. This elevation projects between the inner edges of the closed mandibles, and its irregular contours fit with the lines of the opposing jaws. Its median surface is depressed and embraces the region of the internal **Y**-shaped ridge (*m*). The elevation is continued upward on the clypeal region, above the spreading arms of the **Y**-shaped ridge, and between the inner recurved ends of the tormae (*Tor*), and then into the mouth (*Mth*) and upon the anterior wall of the buccal cavity. A sinuous groove begins upon the elevation ventrally between the tormae, which extends dorsally and enlarges into a deep, median channel continued into the anterior wall of the mouth and pharynx. At the sides of the lower end of the channel, between the slender arms of the tormae, are four asymmetrically placed, oval groups of small peg-like sense organs with large circular bases, partly covered from the sides by fringes of long recumbent hairs.

The hypopharynx is a large median lobe suspended, as already noted, from the ventral wall of the head between the mouth and the base of the labium (fig. 41, *Hphy*). Its posterior end is closely covered by the paraglossal lobes, and its sides are concealed by the mandibles and maxillae. In form, as seen from below (fig. 42 C), the hypopharynx is somewhat ovate, with the smaller end anterior, but its posterior end is set off as a narrowed lobe by lateral constrictions. The lateral surfaces of the anterior division fit into the posterior concavities of the mandibles, those of the posterior lobe are embraced by the concave inner faces of the laciniae. The posterior, basal extremity of the hypopharynx projects as a small median process into the salivary cup on the base of the labium (fig. 41). The lateral line of the hypopharyngeal base is marked by a slender, sinuous, chitinous bar on each side (*w*). The arrangement of the hairs clothing the hypopharynx is sufficiently shown in the figures (figs. 41, 42 C). On its sides and at the posterior end near the salivary cup are a few small sense organs similar to those of the labrum.

Dorsal to the anterior end of the hypopharynx is an area that leads directly upward into the floor of the mouth. It possibly represents the sternal region of the protocephalic segments of the head. On its median surface (fig. 42 B, C) is a ridge, bordered by long hairs directed inward and upward, that continues dorsally from the narrowed end of the hypopharynx, and which is excavated by a median channel where it enters the mouth. At each side of this channel is an oval group of sense organs. Flanking the ridge are two chitinous bars (*HS*), the ventral ends of which articulate with the anterior extremities of the lateral basal rods of the hypopharynx (*w*). Dorsally each bar forks into two arms, of which one (*x*) goes posteriorly to the base of the adductor apodeme of the mandible (*9Ap*), and the other (*y*) goes anteriorly, laterally, and dorsally into the angle of the mouth, where it forms a support for the insertion of the retractor muscle of the mouth angle (A, B, *38*).

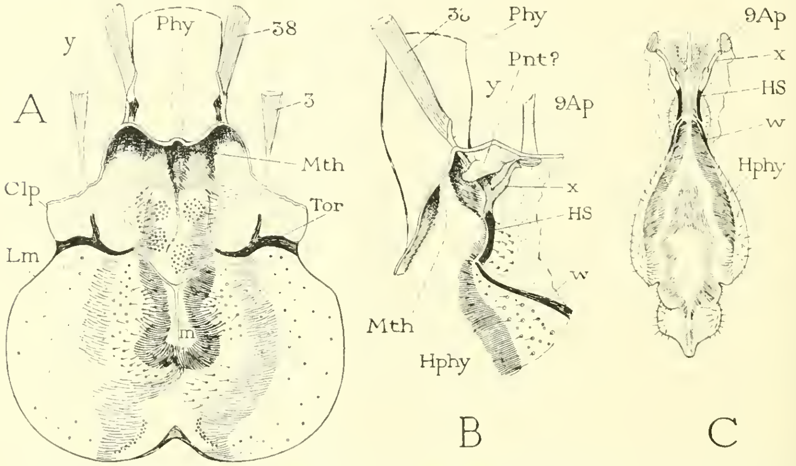

FIG. 42.—The epipharyngeal surface, and the hypopharynx of *Dissosteira carolina*.

A, epipharyngeal surface of clypeus and labrum, and ventral extremity of pharynx. B, lateral view of mouth opening, and of suspensorial apparatus of hypopharynx. C, antero-ventral view of hypopharynx and its suspensory rods. *9Ap*, apodeme of adductor muscle of mandible; *Clp*, clypeus; *Hphy*, hypopharynx; *HS*, suspensorial bar of hypopharynx; *Lm*, labrum; *m*, Y-shaped ridge in epipharyngeal wall of labrum; *Mth*, mouth; *Phy*, pharynx; *Pnt*, small lobe behind angle of mouth, possibly rudiment of tritocerebral appendage; *Tor*, torma; *w*, lateral basal bar of hypopharynx; *x*, mandibular branch of suspensorial bar (*HS*) of hypopharynx; *y*, oral branch of same.

The two lateral bars (fig. 42 B, *HS*) in the space between the hypopharynx and the mouth, with their posterior dorsal arms (*x*) braced against the bases of the mandibular apodemes, and their ventral ends articulated with the basal rods (*w*) of the hypopharynx, constitute a movable suspensorial apparatus of the hypopharynx. It is evident that a contraction of the mouth angle muscles (*38*) inserted on the anterior dorsal arms (*y*) of the bars must effect a movement of the hypopharynx, and that the latter would be lifted and swung forward beneath the mouth opening. The pull of the mouth muscles, however, also retracts the mouth angles, and there is probably thus accomplished a closing of the mouth upon the food mass accumulated in the preoral space above the anterior end of the hypopharynx. In the grasshopper, the mouth is closed also by the opening of the jaws, but, so far as can be observed in a dead specimen, the closing of the mouth in this case results mechanically from the transverse stretching of the oral aperture between the separating bases of the adductor apodemes of the mandibles.

Posteriorly the hypopharynx is fixed to the base of the labium, where its wall is reflected into that of the latter (fig. 41). The hypopharynx, therefore, can swing forward only in unison with the labium, but otherwise it is free to move to the extent permitted by the membranous areas laterad of its base. The only muscles properly belonging to the hypopharynx are the following:

32.—Retractors of the hypopharynx (figs. 40 D, 41)—A pair of muscles arising posteriorly on extreme lateral ends of anterior arms of tentorium (fig. 40 D); inserted on posterior parts of basal rods of hypopharynx (fig. 41).

The contraction of these muscles probably retracts the hypopharynx, and pulls the hypopharynx and labium posteriorly. The mouth aperture is opened by the contraction of the dilator muscles inserted on its anterior and posterior walls (figs. 41, 44, *33, 34, 41*).

The rods (*HS*) of the suspensory apparatus of the hypopharynx in the grasshopper are evidently remnants of the much larger suspensory plates of the hypopharynx in Apterygota and Myriapoda (fig. 21 A, B, C, E, *HS*). In *Microcentrum,* as already shown (fig. 20 D), a small hypopharyngeal adductor muscle of the mandible is attached to the end of each rod. In the roach (*Periplaneta*) the chitinous parts of the hypopharyngeal suspensorium are more strongly developed than in the grasshopper, and their action can be more clearly demonstrated. In the bees, though the hypopharynx itself may be lacking, the oral arms of the suspensory bars are prolonged as slender rods into the lateral walls of the pharynx, and their basal ends are bridged by a wide plate on the pharyngeal floor.

In *Dissosteira* there is at each side of the mouth, in the angle between the dorsal arms of the suspensorial bar of the hypopharynx, a very small but distinct membranous lobe of a definite form (fig. 42 B, *Pnt*), but having no apparent function, and bearing neither hairs nor sense organs. The position of these lobes between the mouth and the adductor apodemes of the mandibles strongly suggests that they are rudiments of the postantennal appendages of the tritocerebral segment, which have otherwise not been observed in the adult of any pterygote insect.

THE STOMODEUM

At the upper end of the preoral cavity (fig. 41, *PrC*), anterior to the base of the hypopharynx, and immediately behind the base of the clypeus is the true mouth (*Mth*), or external opening of the stomodeum. The mouth of *Dissosteira* is a transverse aperture having acute lateral angles, but without definite "lips," for the epipharyngeal and the supra-hypopharyngeal walls are directly continued into the anterior and posterior walls of the buccal cavity and pharynx.

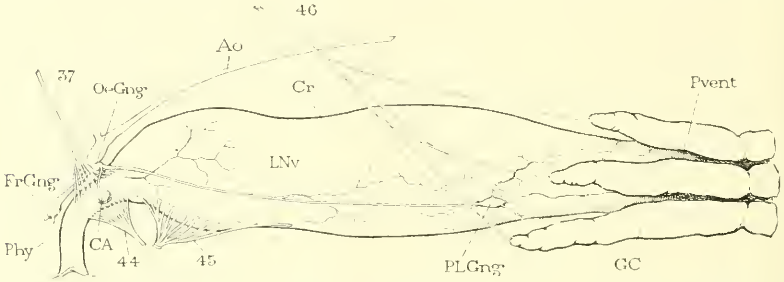

FIG. 43.—Pharynx, crop, anterior gastric caeca, and associated organs of *Dissosteira carolina*.

Ao, aorta; *CA,* corpus allatum (?); *Cr,* crop; *FrGng,* frontal ganglion; *GC,* gastric caecum; *LNv,* lateral stomodeal nerve; *OeGng,* posterior median or oesophageal ganglion; *Phy,* pharynx; *PLGng,* posterior lateral stomodeal ganglion; *Pvent,* proventriculus.

The stomodeum of the grasshopper extends from the mouth upward in the anterior part of the head (fig. 41), then turns posteriorly above the tentorium, and continues rearward through the head and thorax into the base of the abdomen (fig. 43). By differences in its diameter and in the character of its walls, the stomodeum is differentiated into several parts, but only three parts are well defined in the grasshopper; these are the *pharynx,* the *crop,* and the *proventriculus.*

The pharynx, or first division of the stomodeum, is a narrow, muscular-walled tube bent downward to the mouth between the anterior arms of the tentorium (figs. 41, 43, 44, *Phy*). The region of the mouth, including the upper end of the preoral cavity (fig. 41, *PrC*) and the part of the stomodeum just within the oral aperture, may be distinguished as the *buccal cavity* because the muscles inserted on it (figs. 41, 44, *33, 34, 38, 41*) function in connection with the mouth. The dorsal dilators (*33, 34*) arise upon the clypeus (fig. 41, *Clp*).

The true pharyngeal region of the stomodeum of the grasshopper is differentiated into an *anterior pharynx* and a *posterior pharynx*, the two parts being thus named by Eidmann (1925) in the roach. The principal differences between the two parts of the pharynx, however, are in the conformations of the cuticular lining, though the posterior end of the anterior pharynx is marked externally by a slight bulging of the lateral walls. The circumoesophageal connectives (fig. 44, *CoeCon*) lie approximately between the two pharyngeal sections.

The crop (fig. 43, *Cr*) is a large, rather stiff-walled sack, representing probably both oesophagus and crop in insects with a long oesophageal tube, though the posterior section of the pharynx in the grasshopper appears to be the oesophageal region in the caterpillar (fig. 55). The anterior end of the crop in *Dissosteira* lies in the back of the head where it rests upon the bridge of the tentorium (fig. 41); the ventral surface of the thoracic part of the organ is supported by the spreading apophyses of the thoracic sterna. The anterior third of the crop (fig. 43) is somewhat set off from the rest by a slight narrowing of the walls; the posterior part tapers between the large anterior caecal pouches of the ventriculus, and ends in the proventriculus (*Pvent*). The proventriculus is a small, cup-shaped enlargement of the posterior end of the stomodeum, mostly concealed between the bases of the ventricular pouches (*GC*).

The frontal ganglion of the stomodeal (stomatogastric) nervous system (fig. 43, *FrGng*) rests against the anterior wall of the pharynx, and the posterior median oesophageal ganglion (*OeGng*) lies over the posterior end between the spreading bases of the last pair of dorsal dilator muscles of the pharynx (*37*). From this second median ganglion a long lateral nerve (*LNv*) goes posteriorly on each side of the crop, ending on the rear part of the latter in a posterior lateral ganglion (*PLGng*). A pair of short anterior lateral nerves from the oesophageal ganglion go laterally to a pair of globular bodies, possibly the corpora allata (*CA*), lying at the sides of the posterior pharynx. The anterior dilated end of the aorta (*Ao*) rests upon the oesophageal ganglion, and its open, trough-like lower lip is extended forward beneath the brain.

The Inner Wall of the Stomodeum.—The surface of the intima, or cuticular lining, of the pharynx, crop, and proventriculus is diversified by various folds and ridges, most of which are clothed with hairs or are armed with small chitinous teeth.

The channels on the walls of the preoral cavity that lead into the mouth are continued upon the inner walls of the anterior pharynx. The median epipharyngeal groove proceeds upward on the anterior pharyngeal wall between two converging ridges, but it soon ends in a thick median fold which follows the midline of the roof of the posterior pharynx to the end of the latter. Likewise, the median channel leading upward from the base of the hypopharynx is continued on the rear wall of the anterior pharynx, between two converging ridges, and ends in a median ventral fold on the floor of the posterior pharynx. From the lateral angles of the mouth, wide channels go dorsally in the side walls of the anterior pharynx, but these again end each in a lateral fold of the posterior pharynx. Thus the relative positions of the principal ridges and grooves in the walls of the two parts of the pharynx are reversed. In the posterior pharynx there is a slenderer intermediate fold between each two of the major dorsal, lateral, and ventral folds. These eight folds of the posterior pharynx end at the entrance of the crop, giving the aperture a stellate appearance when seen from the lumen of the crop. All the pharyngeal folds, except the midventral fold of the posterior pharynx, are clothed with hairs directed backward.

In the crop, a wide dorsal channel proceeds from the pharyngeal opening posteriorly on the anterior third of the upper wall between converging folds of the intima. A narrower ventral channel follows the midline of the floor between a pair of folds that diverge posteriorly and are lost beyond the middle of the organ. The lateral walls of the anterior half of the crop are closely corrugated by obliquely transverse ridges, which bear rows of small, slightly curved, sharp-pointed, chitinous teeth projecting backward. The anterior three or four transverse ridges on each side are particularly conspicuous by reason of their greater width, and because they are thickly beset with similar but slightly larger teeth than those of the other ridges. In the posterior, narrowed part of the crop the transverse ridges are replaced by fine, parallel, lengthwise folds, following the lines of the longitudinal muscle fibers. Numerous teeth are present here also, but they are smaller and blunter than those of the anterior region, and are mostly arranged in small groups, usually two or three together, on elevations of the intima along the folds. The interior characters of the crop are better developed and the teeth are more numerous in the larger organ of the female grasshopper than in that of the male. They can be studied best on pieces of the intima stripped from the tough muscular sheath of the crop.

The walls of the short proventriculus are produced into six flat, triangular elevations having their bases contingent anteriorly, and their apices directed backward, where they all end on the rim of the wide, round orifice into the ventriculus. The proventricular ridges are not mere folds of the intima, for each is formed by a thick mass of the underlying epithelial cells. The surface of the intima in the proventriculus is smooth, except for a few very small teeth on the edges of the triangular ridges, and areas of minute granulations on the distal halves of the latter. The posterior margin of the proventricular wall is reflected outward upon itself to form a short circular fold projecting into the anterior end of the ventriculus, reaching just past the openings of gastric caeca. The intima covers the outer surface of the fold, but terminates at the base of this surface. The line of the latter, therefore, marks the end of the stomodeal or anterior ectodermal section of the alimentary canal.

The Muscular Sheath of the Stomodeum.—The stomodeal walls are everywhere covered with flat bands of muscles, which in general take a transverse and a longitudinal direction, the transverse bands being external and the longitudinal internal; but the distribution of the two sets is not such as to form a regular net-pattern on all parts of the stomodeum. On the posterior two-thirds of the crop, the external transverse fibers have the form of continuous rings encircling the organ, and the longitudinals run with its length. On the anterior third, however, the ring muscles are interrupted laterally and dorsally, and their layer is continued only on the ventral surface as a series of ventral arcs; but the fibers of a latero-ventral tract of the posterior longitudinal muscles on each side curve upward on the lateral wall of the crop where the circular bands are interrupted, and are continuous with those from the opposite side over the dorsal surface as an external layer of obliquely transverse fibers reaching to the base of the pharynx. On the pharyngeal tube the muscles again take the pattern of regularly arranged external circular and internal longitudinal fibers. The circular fibers of the pharynx may belong to the interrupted set of circular fibers of the crop, but the longitudinal fibers are continued irregularly into the walls of the crop on the inner surface of the anterior circular fibers of the latter, and they do not, therefore, belong to the same layer as the posterior longitudinal crop muscles. A close study of the stomodeal musculature of the grasshopper would show some complexity of detail in the arrangement and relationship of the muscle fibers, but nothing approaching the intricacy of the fiber connections in the muscular layers on the pharynx and crop of the caterpillar, to be described later.

The Dilator Muscles of the Stomodeum.—Thirteen paired sets of muscle fibers and one median unpaired muscle arising on the skeletal parts of the head or thorax are inserted on the stomodeal walls in *Dissosteira* (figs. 41, 43, 44). These muscles may be classed as *dorsal, lateral,* and *ventral* according to their insertions, though because of the downward flexure of the pharynx, the first "dorsal" and "ventral" muscles are anterior and posterior. The dilator muscles of the stomodeum, sometimes called also suspensory muscles, enumerated from *33* to *46* inclusive, are as follows:

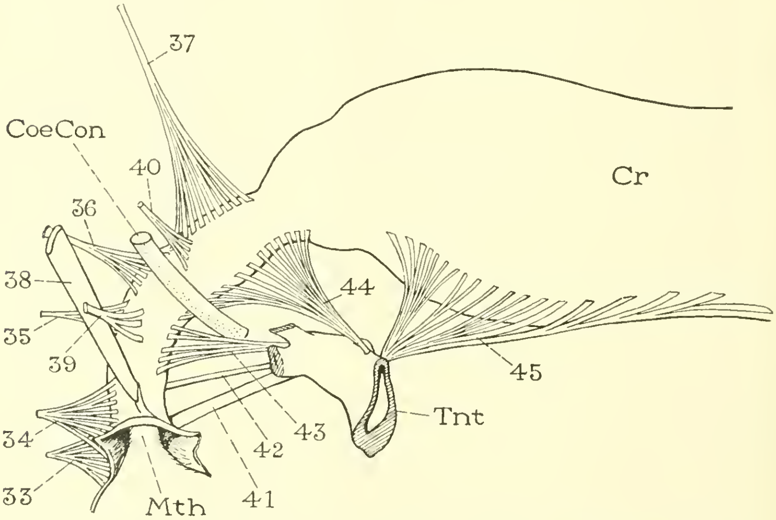

FIG. 44.—Dilator muscles of the buccal region, pharynx, and crop of *Dissosteira carolina.*

CoeCon, circumoesophageal connective; *Cr,* crop; *Mth,* mouth; *Tnt,* tentorium.

33.—First anterior dilators of the buccal cavity (figs. 41, 44).—A pair of fan-shaped muscles arising on inner wall of clypeus (fig. 37 B), the fibers spreading to their insertion on anterior wall of buccal cavity (fig. 44) mostly distal to oral aperture.

34.—Second anterior dilators of the buccal cavity (figs. 41, 44).—A pair of fan-shaped muscles similar to *33*, arising on clypeus near epistomal ridge (fig. 37 B); inserted laterad of *33* and mostly proximal to oral aperture.

35.—First dorsal dilators of the pharynx (figs. 41, 44).—A pair of slender muscles arising on frontal area of head wall, each attached between labral retractors of same side (fig. 38 D); inserted on anterior wall of pharynx.

36.—Second dorsal dilators of the pharynx (figs. 41, 44).—Each arises by a slender stalk on subantennal ridge of frons (fig. 41); inserted by spreading base on upper end of anterior pharynx.

37.—Third dorsal dilators of the pharynx (figs. 41, 43, 44).—Each arises by slender stalk on vertex near inner rim of compound eye just anterior to first dorsal fibers of mandibular adductor; inserted by widely spreading base on dorsal wall of posterior pharynx.

38.—Retractors of the mouth angles (figs. 41, 44).—These, the largest muscles of the stomodeum, and the first of the lateral series, arise on the subantennal ridges of the frons (fig. 38 D), and extend downward and posteriorly to their insertions on the oral arms of the hypopharyngeal suspensorial rods (figs. 42 A, B, 44) in the lateral angles of the mouth.

39.—First lateral dilators of the pharynx (fig. 44).—A pair of slender muscles arising laterally on frontal region; inserted on sides of anterior pharynx.

40.—Second lateral dilators of the pharynx (figs. 41, 44).—A slender muscle on each side, arising on posterior face of distal end of dorsal arm of tentorium (fig. 41); inserted by spreading base on upper end of anterior pharynx (fig. 44).

41.—Ventral dilator of the buccal cavity (figs. 41, 44).—A median, unpaired, strap-like muscle arising on ventral face of body of tentorium; inserted on median groove of posterior wall of mouth.

42.—First ventral dilators of the pharynx (figs. 41, 44).—A pair of fibers arising on ventral surface of tentorium; going anteriorly to insertions medially on lower end of posterior wall of anterior pharynx.

43.—Second ventral dilators of the pharynx (figs. 41, 44).—A group of diverging fibers on each side, arising on anterior edge of tentorium; inserted latero-ventrally on anterior pharynx.

44.—Third ventral dilators of the pharynx (figs. 41, 43, 44).—A large fan of fibers on each side, arising on dorsal edge of posterior arm of tentorium; the spreading fibers inserted ventro-laterally along entire length of posterior pharynx.

45.—Anterior dilators or protractors of the crop (figs. 41, 43, 44). —A large group of fibers arising on each posterior tentorial arm, behind origin of *44*; spreading posteriorly to insertions ventro-laterally along anterior third of crop. These are the last of the stomodeal muscles that have their origin in the head.

46.—Posterior protractors of the crop and gastric caeca (fig. 43).—A pair of long, branched muscles, each arising by a slender stalk on inner surface of prothoracic tergum, just anterior to base of trochantinal muscle; branching downward and posteriorly, one branch inserted on lateral wall of crop just above posterior lateral stomodeal ganglion (*PLGng*), the others on tips of the gastric caeca (*GC*) of same side.

THE MECHANISM FOR MOVING THE HEAD

The head of the grasshopper is freely attached to the prothorax by a membranous neck, but its movements are somewhat limited by the overlapping anterior edges of the protergum, and by the pair of cervical sclerites on each side (fig. 45 B, *1cv, 2cv*) which link the head with the concealed episternal plate of the prothorax (Eps_1).

The cervical sclerites, however, constitute an important part of the mechanism for moving the head The two plates of each pair are articulated end to end, and ordinarily they are bent downward at an angle to each other (fig. 36 A, *cv*). The first is articulated anteriorly to the posterior margin of the postoccipital rim of the head (fig. 45, *g*), the second posteriorly to the anterior edge of the prothoracic episternum (Eps_1). The neck plates thus constitute a fulcrum on each side between the head and the thorax, giving a leverage to the dorsal and ventral muscles extending from the postoccipital ridge and tentorium to the prothorax and the first thoracic phragma. Moreover, upon each plate are inserted strong levator muscles (fig. 45 B) arising on the back of the head and on the prothoracic tergum, and the contraction of these muscles, with the consequent straightening of the angle between the two plates of each pair, must cause the protraction of the head. From each anterior plate a horizontal muscle extends to the prosternal apophysis of the opposite side (fig. 45 A, B, *54*). Besides the muscles that connect the skeletal parts of the head, neck, and prothorax, there are two muscles on each side inserted directly upon the neck membrane (A, *56, 57*).

It is difficult to give names signifying function to the neck muscles, for it is evident that the function will depend on whether the two muscles of any pair act in unison, or as antagonists. The neck muscles of *Dissosteira* are as follows, on each side:

47.—First protergal muscle of the head (fig. 45 A).—A slender muscle arising dorsally on prothoracic tergum; inserted dorso-laterally on postoccipital ridge of head (*PoR*).

48.—Second protergal muscle of the head (fig. 45 A).—A larger muscle arising on principal ridge of protergum (*e*); inserted with *47* on postoccipital ridge of head.

49.—Longitudinal dorsal muscle of the prothorax (fig. 45 A).—Extends from first thoracic phragma (*1Ph*) to postoccipital ridge (*PoR*) just below *48*.

50, 51.—Cephalic muscles of the cervical plates (fig. 45 A, B).—Origin on postoccipital ridge below *49*; both extend ventrally and posteriorly, the first (*50*) inserted on first cervical plate, the second (*51*) on second plate.

52, 53.—Protergal muscles of the cervical plates (fig. 45 B).—Origin dorso-laterally on prothoracic tergum; both extend ventrally and anteriorly, crossing internal to *50* and *51*, to be inserted on first cervical plate, the first (*52b*) with a branch (*52a*) to articular process (*g*) of postoccipital ridge.

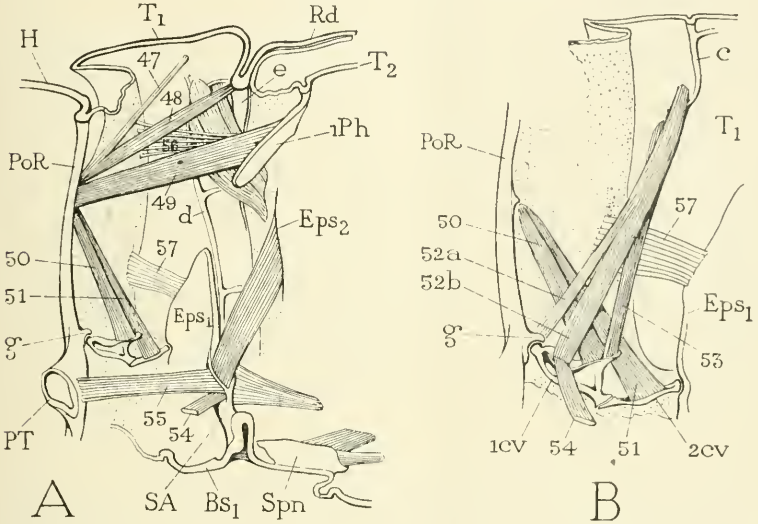

FIG. 45.—Muscles of the neck of *Dissosteira carolina*, right side, internal view.

A, muscles extending between head and prothorax, omitting 52, 53 and 54, inserted on cervical sclerites (B). B, head and prothoracic muscles of cervical sclerites.

Bs_1, basisternum of prothorax; *c*, first ridge of protergum; *1cv*, first cervical plate; *2cv*, second cervical plate; *d*, second ridge of protergum; *e*, third ridge of protergum; *Eps_1*, episternum of prothorax; *Eps_2*, episternum of mesothorax; *g*, process of head articulating with first cervical sclerite; *H*, head; *1Ph*, first thoracic phragma; *PoR*, postoccipital ridge; *PT*, base of posterior arm of tentorium; *Rd*, posterior fold of protergum; *SA*, apophysis of prothoracic sternum; *Spn*, spina; *T_1*, tergum of prothorax.

54.—Prosternal muscle of the first cervical plate (fig. 45 A, B).—A diagonal, horizontal muscle arising on apophysis of prothoracic sternum (A, *SA*), crossing its fellow to insertion on inner edge of first cervical plate of opposite side (B).

55.—Longitudinal ventral muscle of the prothorax (fig. 45 A).—A broad, flat muscle from prosternal apophysis (*SA*) to base of posterior arm of tentorium (*PT*).

56.—Dorsal lateral neck muscle (fig. 45 A).—A band of slender fibers from first phragma (*1Ph*), inserted on base of neck membrane.

57.—Ventral lateral neck muscle (fig. 45 A, B).—A short, flat muscle from anterior edge of prothoracic episternum (Eps_1), inserted on base of neck membrane.

VI. SPECIAL MODIFICATIONS IN THE STRUCTURE OF THE HEAD

The important structural variations in the head of biting insects affect principally the fronto-clypeal area, and the posterior lateral and ventral regions. Modifications of the facial plates are often to be correlated with variations in the relative size of the buccal and pharyngeal parts of the stomodeum, or with a special development of the mouth cavity. Modifications in the posterior ventral parts of the head are correlated with a flattening and elongation of the cranial capsule, usually resulting from an upward tilting of the head on the neck by which the mouth parts become directed forward, and, in certain orders, are accompanied by an elongation of the submentum anteriorly, with a differentiation of this plate into a posterior gular sclerite and a secondary anterior submental sclerite.

MODIFICATIONS IN THE FRONTO-CLYPEAL REGION

The prostomial part of the insect head includes the frons, the clypeus, and the labrum. Whether or not it comprises also the region of the compound eyes may be regarded as an open question, and one for the embryologists to settle. If the compound eyes belong to the first true segment of the head, it is probable that the frontal sutures define the posterior limit of the prostomium; otherwise the sutures must be secondary formations within the area of the prostomium. The frontal sutures do not always mark the lines of cleavage in the head cuticula at the time of a molt. In an odonate nymph, for example (fig. 46 I), the facial clefts (*t*) of the molting cuticula extend from the coronal suture outward and downward on each side between the eyes and the bases of the antennae, far outside the possible limits of the frons (*Fr*).

The part of the postembryonic head that may be defined as the *frons* is the area included between the frontal sutures, where these sutures are fully developed (fig. 46 B, *Fr*). The frontal sutures (*fs*) extend typically from the coronal suture (*cs*) to the neighborhood of the anterior articulations of the mandibles (*c, c*). The true frontal region, therefore, can not include the bases of the antennae, which organs belong to the second head segment behind the prostomium. and acquire their facial positions secondarily by a forward and upward migration. Ventrally the frons is limited, and separated from the clypeus, by the epistomal suture (fig. 46 B, *es*), except when this suture is lacking. If a median ocellus is present, it is situated in the upper angle of the frons (figs. 46 E, 47 B). The muscles of the labrum, some of the dilator muscles of the pharynx, and the retractors of the mouth angles, when present, have their origins on the frons. By

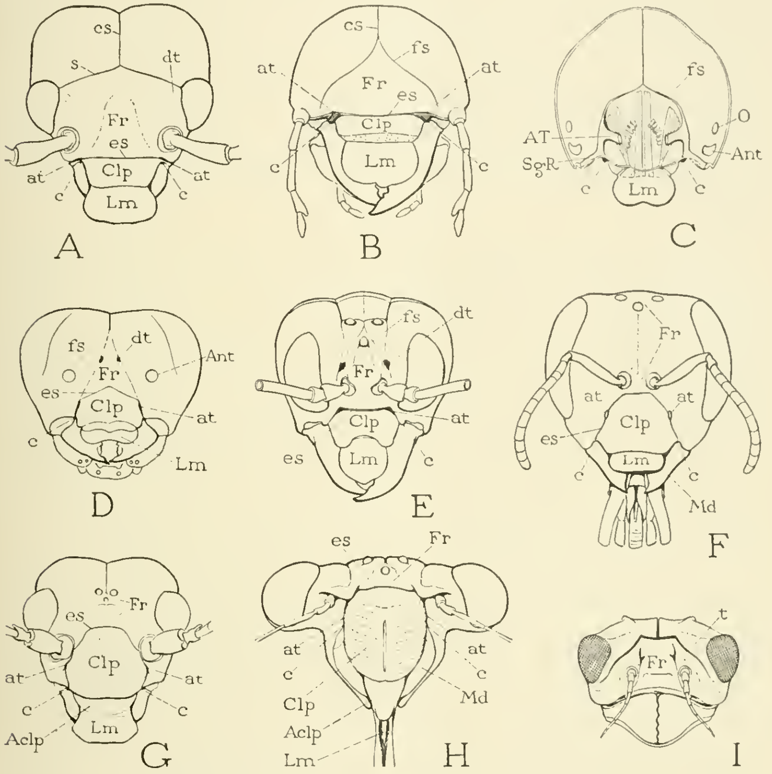

FIG. 46.—Modifications in the facial structure of the insect head.

A, *Forficula auricularia.* B, *Popillia japonica*, larva. C, *Pteronidea ribesi*, larva, inner surface of front of head. D, *Vespa maculata,* well-chitinized larva. E, *Pteronidea ribesi,* adult. F, *Apis mellifica.* G, *Psocus venosus.* H, *Magicicada septendecim.* I, molted skin of an *Aeschna* larva.

Aclp, anteclypeus; *Ant,* antenna; *AT,* anterior arm of tentorium; *at,* anterior tentorial pit; *c,* anterior articulation of mandible; *Clp,* clypeus; *dt,* attachment of dorsal tentorial arm to head wall; *es,* epistomal suture; *Fr,* frons; *fr,* "adfrontal"; *Lm,* labrum; *O,* ocellus; *s,* suture of *Forficula* diverging from end of coronal suture; *SgR,* subgenal ridge; *t,* molting split in *Aeschna* larva diverging from end of coronal suture, but is not frontal suture.

these characters, especially the position of the median ocellus and the origin of the labral muscles, the true frontal region is to be identified when the frontal sutures are imperfect or obsolete (fig. 46 E, F, *Fr*).

As was shown in the study of the grasshopper (fig. 36 B), the frontal region of the face may present a number of secondary lines formed by ridges of the inner surface. In the Dermaptera two sutures (fig. 46 A, *s*) diverge widely from the end of the coronal suture (*cs*) and extend outward to the compound eyes. It appears doubtful that these are the frontal sutures, for the true frontal region should be the smaller triangular area indistinctly defined on the median part of the face.

The *clypeus* (fig. 46 B, *Clp*) is a distinct area of the prostomial region, and is to be identified by the origin of the dilator muscles of the mouth and buccal cavity on its inner wall. It is almost always in biting insects separated from the labrum by a flexible suture, and it is demarked from the frons whenever the epistomal suture is present. The clypeus is sometimes divided into an anteclypeus and a postclypeus by a partial or complete transverse suture; but often the term "anteclypeus" is given to a more or less membranous area between the clypeus and the labrum (fig. 46 G, *Aclp*), and it is likely that regions named "anteclypeus" are not equivalent in all cases.

The *labrum* (fig. 46 B, *Lm*) hangs as a free flap before the mouth. It is a preoral lobe of the prostomium characteristic of insects, myriapods, and crustaceans. The insect labrum is usually movable, and is provided with one or two pairs of muscles (though both may be absent), which, as above noted, have their origin on the frons. The labral muscles, therefore, are strictly muscles of the prostomium.

The principal departure from the typical structure in the prostomial sclerites arises from variations in the development or in the position of the epistomal suture, and from a partial or complete suppression of the frontal sutures.

The epistomal suture is the external groove formed incidentally to the development of an internal transverse ridge across the prostomial area. Since this ridge in generalized insects lies approximately between the anterior articulations of the mandibles, its primitive position suggests that it was developed to strengthen the lower edge of the face between the mandibular bases. The epistomal ridge itself is a continuation of the subgenal ridges, and the epistomal suture is, therefore, continuous with the subgenal sutures. In the Ephemerida and Odonata, as we have seen, the anterior arms of the tentorium arise in the subgenal sutures laterad of the bases of the mandibles. In some of the Orthoptera, as in the roach, and in larvae of Coleoptera, the tentorial arms have moved forward to a position above the mandibular articulations, and their external openings, the anterior tentorial pits, appear in these positions (fig. 46 B, *at, at*).

In some of the more generalized insects, the epistomal ridge and its suture are lacking, as in the roach, and there is then present only a single fronto-clypeal sclerite (fig. 47 A, *Fr-Clp*). In such cases, the tentorial pits (*at*) lie in the anterior extremities of the subgenal sutures (*sgs*), above the anterior articulations (*c*) of the mandibles. Where an epistomal ridge unites the subgenal ridges across the face, separating the clypeus from the frons, the tentorial pits may retain their positions above the mandibular articulations (fig. 46 A, B, *at, at*); but more commonly they move into the epistomal suture (fig. 47 B). In any case, the tentorial pits identify the epistomal suture, when this suture is present. The mandibular articulations (*c, c*) are carried by the ventral margin of the epicranium and are not true landmarks of the epistomal suture, as has been pointed out by Yuasa (1920), and by Crampton (1925).

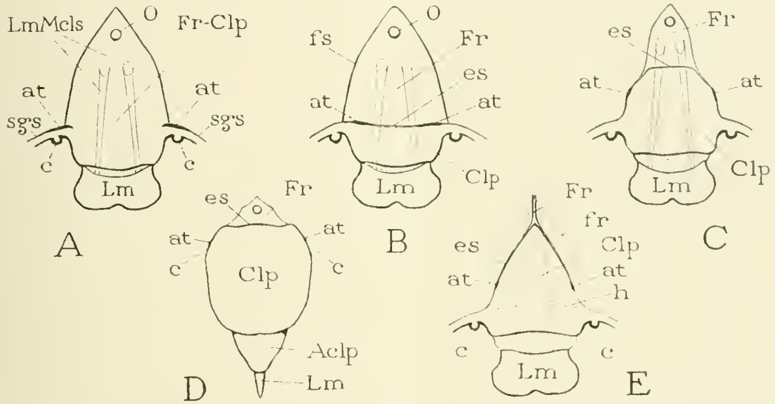

FIG. 47.—Diagrams showing variations in the position of the epistomal suture (*es*), and the relations of the frons and the clypeus.

Aclp, anteclypeus; *at,* anterior tentorial pit; *c,* anterior articulation of mandible; *Clp,* clypeus; *es,* epistomal suture; *Fr,* frons; *fr,* "adfrontal"; *Fr-Clp,* fronto-clypeus; *fs,* frontal suture; *h,* line of secondary ridge across lower part of clypeus; *Lm,* labrum; *LmMcls,* labral muscles, with origin always on frons; *O,* median ocellus.

As long as the epistomal suture maintains its direct course across the face, no complications arise; but the suture is frequently arched upward, and this shift in the position of the suture extends the clypeus into the facial region above the bases of the mandibles, and reduces the area of the frons (fig. 47 C). A modification of this kind has taken place in the Hymenoptera. In the larval head of *Vespa* (fig. 46 D) the clypeus has clearly encroached upon the area of the frons by a dorsal arching of the epistomal suture (*es*). In an adult tenthredinid (E), the same condition is observed, but the lower parts of the frontal sutures (*fs*) are lost, and the bases of the antennae have approached each other mesally, and have constricted the frontal area between them. In the adult of *Apis* (F) the condition is more exaggerated—the epistomal suture (*es*), identified by the tentorial pits (*at, at*), is arched upward almost to the bases of the antennae, and the frontal sutures are obsolete. The frontal area (*Fr*), however, is to be identified by the position of the median ocellus, and the points of origin of the labral muscles between and just above the antennal bases. The head of a larval tenthredinid (fig. 46 C) presents a specialized condition, for the single large facial plate is here clearly a fronto-clypeus, as shown by the origin of the labral muscles on its upper parts, and by the origin of the tentorial arms (*AT*) from the ridges at its sides. Evidently, the median part of the epistomal ridge and its suture has been suppressed. A similar condition is to be observed in some trichopteran larvae.

A still greater degree in the upward extension of the clypeus is shown on the face of a psocid (fig. 46 G). Here the epistomal suture (*es*) is arched high above the tentorial pits (*at, at*), and the clypeus (*Clp*) becomes the large, prominent, shield-shaped plate of the face between the bases of the antennae. The frontal sutures are lacking, but the frontal area (*Fr*) is that between the bifid end of the coronal suture and the clypeus, on which is located the median ocellus. A weakly chitinized area below the clypeus is sometimes called the anteclypeus (*Aclp*), but it appears to be only a chitinization of the connecting membrane between the clypeus and the labrum.

The clypeus, finally, attains its greatest development at the expense of the frons in the Homoptera (fig. 47 D). In the cicada (fig. 46 H), the clypeus is the great bulging, striated plate of the face upon which arise the dilator muscles of the mouth pump. The dorsal arch of the epistomal suture (*es*) lies on a level with the antennal bases, and the anterior tentorial pits (*at, at*) are in its upper lateral parts, just above the dorsal extremities (*c, c*) of the mandibular plates (*Md*). The frons is a small, indistinctly defined triangular area (*Fr*) bearing the median ocellus in the adult. It is more strongly marked in the nymph, and is cut out by the opening of the frontal sutures at the time of the molt. The plate below the principal clypeal sclerite is probably an anteclypeus (*Aclp*), because in some Hemiptera it is not distinctly separated from the area above it, but it is questionable if it is homologous with the preclypeal area of the psocid (fig. 46 G, *Aclp*). The terminal piece in the cicada (H, *Lm*) that closes the groove in the upper part of the labium would appear to be the labrum by comparison with Heteroptera. The "mandibular plates" (*Md*) on the sides of the head must be the true bases of the mandibles. Their upper ends (*c, c*) have the same relations to the surrounding parts that the anterior mandibular articulations have in biting insects. The mandibular bristles are chitinous outgrowths from the ventral posterior angles of the plates, and the protractor apparatus of each bristle in the adult is differentiated from the posterior margin of the mandibular plate, as the writer has elsewhere shown (1927).

In the larvae of Lepidoptera, a somewhat different type of modification has produced an unusual distortion in the relation between the frons and the clypeus. The caterpillar head shows no essential variation within the order, but the homologies of the facial structures are clear if interpreted by the characters which serve as identification marks in the other orders. The triangular facial plate (fig. 50 A) thus becomes the clypeus, because the suture (*cs*) bounding it is identified as the epistomal suture by the origin of the anterior tentorial arms from its lateral parts (fig. 50 I, *AT*). Upon this plate arise the muscles of the buccal region of the stomodeum. The median part of the frons is invaginated and forms the thick internal ridge (*Fr*) dorsal to the apex of the clypeus, which is to be identified as the frons by the origin of the labral muscles upon it. The so-called "adfrontals" (A, *fr*) are probably lateral remnants of the frons at the sides of the clypeus, and the "adfrontal" sutures are the true frontal sutures (*fs*). That the relations of the plates of the caterpillar's head, as thus established, are identical with those in other insects is made clear in the diagram given at E of figure 47. The clypeus (*Clp*) has simply extended into the area of the frons, and the median part of the latter plate (*Fr*), bearing the origins of the labral muscles, has been inflected, while its distal parts, the so-called "adfrontals" (*fr*), maintain the original lateral ground of the primitive frontal area. The lower part of the clypeus is sometimes strengthened between the bases of the jaws by a secondary thickening forming a submarginal ridge (*h*) on its inner surface.

MODIFICATIONS IN THE POSTERIOR VENTRAL REGION OF THE HEAD

The structural changes in the posterior parts of the head described here are associated with an elongation of the postgenal regions, resulting in the production of a long interval between the foramen magnum and the posterior articulations of the mandibles. Two different types of structure follow from this style of modification, one shown in adult Hymenoptera and in the larvae of Lepidoptera, the other in those orders in which a gular plate is developed.

The morphology of the posterior surface of the hymenopteran head is comparatively easy to understand, for, in the larval stages, the rear aspect of the head presents the same structure as does that of an adult orthopteron (fig. 36 C). In the head of the larva of *Vespa,* for example (fig. 48 A), the details of the structure are exactly as in the grasshopper. There is a distinct postoccipital suture (*pos*) ending below in the invaginations of the posterior arms of the tentorium (*pt, pt*). The postocciput (*Poc*) is very narrow, but it forms the marginal lip of the head capsule behind the postoccipital suture. The labium (*Lb*) is suspended from the ventral neck membrane, and the cardines of the maxillae (*Cd*) are articulated to the ventral cranial margins just anterior to the tentorial pits.

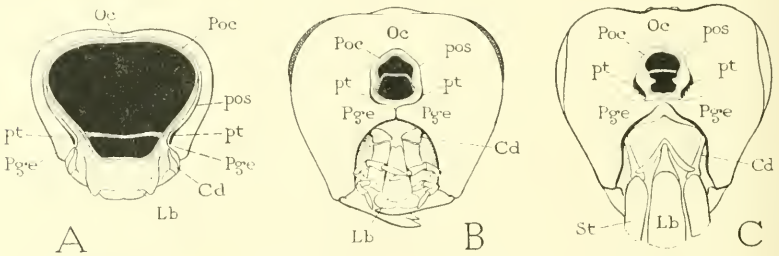

Fig. 48.—Development of the posterior head region in Hymenoptera.

A, posterior surface of head of larva of *Vespa maculata.* C, same of the adult. D, corresponding view of head of adult *Apis mellifica.*

Cd, cardo; *Lb,* labium; *Oc,* occiput; *Pge,* postgena; *Poc,* postocciput; *pos,* postoccipital suture; *pt,* posterior tentorial pit; *St,* stipes.

In the adult wasp (fig. 48 B) the back of the head presents a quite different appearance from that of the larva. The foramen magnum is greatly contracted and is reduced to a small aperture in the center of a broad occipito-postgenal field. It is surrounded by a wide postoccipital collar (*Poc*) set off by the postoccipital suture (*pos*), in which suture are located the posterior tentorial pits (*pt, pt*). The labium (*Lb*) is detached from the neck and displaced anteriorly (ventrally), and the space between its base and the neck is closed by mesal extensions of the inner angles of the postgenae (*Pge, Pge*). The articulations of the cardines (*Cd*) are also far removed from the tentorial pits (*pt, pt*), and are separated from them by the intervening bridge of the postgenae. In the wasp the postgenal bridge preserves a median suture, but in the honeybee (C) the line of union between the postgenal lobes is obliterated, and the bridge presents a continuous surface in the space between the foramen magnum and the fossa containing the bases of the labium and maxillae. In an adult tenthredinid (*Pteronidea*), on the other hand, the foramen magnum, though greatly reduced in size by the development of a wide occipito-postgenal area, is still " open " below, that is, it is closed by a narrow remnant of the neck membrane between the approximated angles of the postgenae. The labium, however, is displaced ventrally and united with the bases of the maxillae.

In the Hymenoptera, then, there can be little question as to the line of evolution that has produced the structure of the back of the head in the higher forms. The resulting condition has been correctly observed by Stickney (1923), who says: " In many Hymenoptera the mesal margins of the postgenae are fused between the occipital foramen and the articulation of the labium." A very similar modification of the head has taken place in the caterpillars, as will be shown later, in which the parts constituting the " hypostoma " (fig. 51 A, *Hst*) correspond with the postgenal bridge of adult Hymenoptera. In either case, an unusual thing has happened in that the labium, after being moved forward to unite with the maxillae, has been separated from its own segment by the intervention of parts of the first maxillary segment. If the postgenae are lateral tergal elements of the head wall, their ventral union finds a parallel in the prothorax of the honeybee, which is completely encircled behind the bases of the legs by the prothoracic tergum.

The modifications in the posterior ventral parts of the head in those orders in which a " gula " is developed are difficult to explain if studied only in the higher phases of their evolution, but they can be understood if traced from forms that show the simpler earlier stages of departure from the normal.

In the Blattidae, the cranium is much flattened, but the essential head structure has not been altered, its posterior parts retaining the same form as in the less movable head of the grasshoppers. In many insects, especially in the Neuroptera and Coleoptera, however, the flattened head is not only turned upward on the neck, causing the true anterior surface to become dorsal and the mouth parts to be directed forward, but the ventral surface of the head has been elongated to preserve the vertical plane of the foramen magnum. In such insects the bases of the mouth parts become separated from the foramen magnum by a wide space, and in this space there appears a median plate called the "gula." The nature of the gula has long been a puzzle to entomologists, but Crampton (1921, 1928) has given reasons for believing that it is a differentiation of the base of the labium, and a few examples taken from the Coleoptera will amply substantiate this view.

In a scolytid or scarabaeid beetle larva the structure of the head does not differ essentially from that of the grasshopper. The face is directed forward, the mouth parts hang downward, and the under surface of the head is short. In the scarabaeid larva (fig. 49 A) the occipital and postgenal regions terminate in a postoccipital suture (*pos*), in the ventral ends of which are situated the large invaginations (*pt, pt*) of the posterior arms of the tentorium. Beyond the suture is a narrow postoccipital rim of the cranium (*Poc*), best developed ventrally, where the lateral cervical sclerites (*cv*) are articulated to it. The postoccipital ridge is developed on each side of the foramen magnum into a broad apodemal plate (*PoR*), the two plates constricting the foramen laterally, and uniting ventrally in the broad tentorial bridge, which is concealed in the figure by the ventral part of the neck membrane (*NMb*). The labium, the maxillae, and the mandibles of the scarabaeid larva are suspended from the ventral edges of the cranium exactly as in the grasshopper (fig. 36 C), but the two forms differ by the elongation in the beetle (fig. 49 A) of the postgenal margins of the head between the articulations of the cardines (*c*) and the posterior articulations of the mandibles (*a*).

The basal part of the submental region of the labium in the scarabaeid larva, *Popillia japonica* (fig. 49 A), is chitinized to form a triangular plate (*Smt*). This plate is attached to the mesal points of the postgenae (*Pge*), and has its extreme basal angles prolonged behind the tentorial pits to points (*f, f*) corresponding with the basal articulations of the submentum with the postocciput in an orthopteron (fig. 36 C, *f*). There can be no doubt that this plate in the beetle head is the submentum, or a chitinized basal part of the submentum. It is marked by a transverse groove between the tentorial pits (*pt, pt*).

In a silphid larva (fig. 49 B) the general structure of the head is similar to that in the scarabaeid larva, but the ventral postgenal margins between the articulations of the cardines (*c, c*) and the mandibles (*a*) are much longer, and the posterior tentorial pits (*pt, pt*) are approximated in the mesally prolonged basal angles of the postgenae. The submentum (*Smt*) is large; its base is narrowly constricted between the tentorial pits, which here almost cut off a small but distinct proximal area (*Gu*). The lateral angles of this extreme basal area of the submentum are prolonged behind the tentorial pits and become continuous with the postocciptal rim of the cranium (*Poc*), which is set off by the postoccipital suture (*pos*) ending ventrally in the tentorial pits (*pt, pt*).

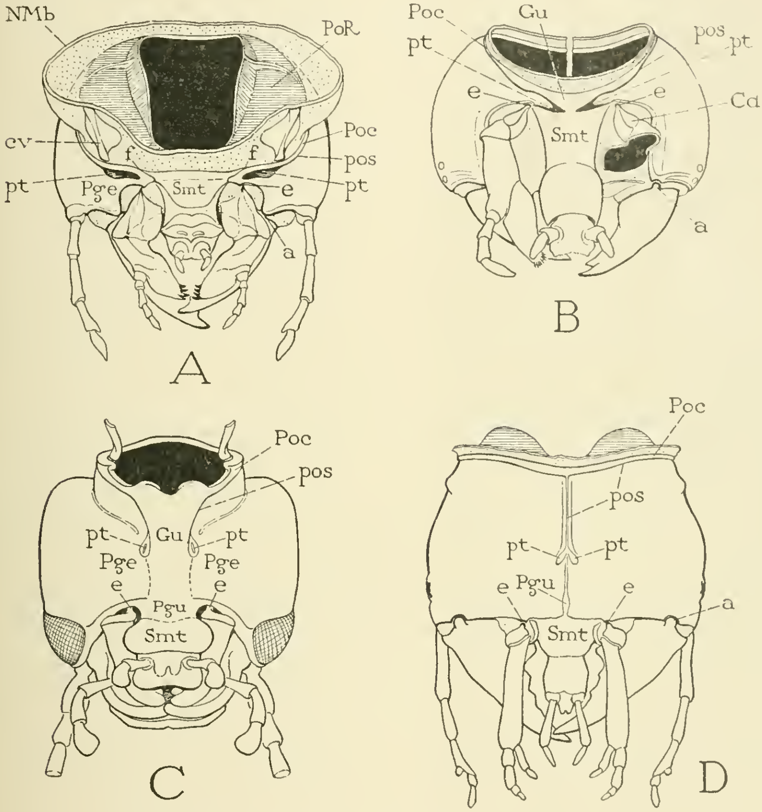

FIG. 49.—Evolution of the "gula" in Coleoptera.

A, Postero-ventral view of the head of a scarabaeid larva, *Popillia japonica.* B, same of a silphid larva, *Silpha obscura.* C, ventral surface of an adult meloid, *Epicauta pennsylvanica.* D, same of a carabid larva, *Scarites.*

a, posterior articulation of mandible; *Cd,* cardo; *cv,* cervical sclerite; *e,* anterior articulation of mandible; *Gu,* gula; *Pge,* postgena; *Poc,* postocciput; *PoR,* postoccipital ridge; *pos,* postoccipital suture; *pt,* posterior tentorial pit; *Smt,* submentum.

The characteristic structure of an adult coleopteran head is well illustrated in the head of a meloid beetle (fig. 49 C). The form of the cranial capsule here differs principally from that of the scarabaeid or silphid larva in the lengthening of the postgenal regions between the foramen magnum and the articulations of the cardines (*e, e*).

The extension of the ventral surface of the cranial wall accommodates the head to its horizontal position, and has involved a great elongation in that part of the submentum which lies between the posterior tentorial pits (*pt, pt*) and extends forward to the articulations of the cardines (*c, c*). This region of the submentum is known as the *gula*. In *Epicauta* (fig. 49 C) the tentorial pits lie at about the middle of the lateral margins of the gula, and the ventral ends of the postoccipital suture (*pos*) are, consequently, turned anteriorly and lengthened in the same direction behind the pits. The ventral parts of the postoccipital suture, terminating in the tentorial pits, now become the so-called " gular sutures." It is evident that the large gular region in the adult meloid head (fig. 49 C) lying posterior to the tentorial pits and continuous basally with the postoccipital rim of the cranium (*Poc*) is produced from the small but corresponding area in the larval silphid head (B, *Gu*), and that this area, in turn, is merely the basal strip of the submentum in the scarabaeid larva (A, *Smt*), attached to the postocciput by its lateral extremities (*f, f*).

In adult Coleoptera the distal end of the gula may be differentiated as a " pregula " or " gular bar " (C, *Pgu*). It supports the terminal part of the original submental plate (*Smt*), which lies between the bases of the maxillae, and which, in a restricted sense, is usually called " the submentum " by coleopterists. The pregular region may fuse laterally with the " hypostomal " regions of the postgenae, and in other ways the more primitive structure may become so obscured that the relations of the parts are difficult to determine except by studying them in a gradient series of simpler forms. The comparative studies made by Crampton (1921, 1928) on the gula in various orders show fully its numerous variations, and demonstrate its origin from the proximal part of the primitive submental plate. Stickney (1923) also has well illustrated the structure of the gula and associated parts in a large number of coleopteran forms. Stickney fails to recognize, however, that the " gular sutures " are direct continuations of the ventral ends of the postoccipital suture, and that, therefore, the gular plate between them must be the basal part of the submentum. He would explain the gular bridge in the Coleoptera as a product of the ventral fusion of the edges of the postgenae, and the gular sclerite as a plate cut out of this newly-formed region by the anterior extension of the " gular sutures." As we have seen, the ventral bridge of the cranial walls is formed in this manner in the Hymenoptera (fig. 48), as Stickney has pointed out, but in the Hymenoptera the tentorial pits have remained at the sides of the foramen magnum, and the labium has lost its original connection with the postoccipital region.

The facts are quite otherwise in the Coleoptera, for here the labium retains its postoccipital connections, and its base has been drawn out between the lengthened postgenal margins to form the gula.

In certain Coleoptera the postgenal margins do become closely approximated (fig. 49 D), but, in such cases, the gula is compressed between the postgenae, and sometimes almost obliterated. The gular sutures may then be partially or wholly united into a median gular suture, with which are closely associated the two tentorial pits (*pt, pt*). Intermediate stages of this condition are well shown in some of the Rhyncophora, in which the head is drawn out into a " snout."

In the Neuroptera, both larvae and adults, and in larval Trichoptera, a gular plate is developed showing essentially the same structure and variations of form as in the Coleoptera. The gular structure has been described in various members of these orders and others in addition to the Coleoptera by Crampton (1921, 1928). In the Termitidae, Crampton shows, the gular region of the submentum may be very much elongated, and in the soldier of *Termopsis* its margins become united with the lengthened edges of the postgenae to form a typical gular plate.

The question of the derivation of the gula, the answer to which is, that the gula is a part of the submental region of the labium, is not to be confused with the question as to the origin of the submentum itself. The various views concerning the nature of the submentum have been already discussed in an earlier section of this paper (page 77), and the writer will reiterate here only his own personal opinion that, since the submentum in generalized insects is attached laterally to the postoccipital tergal region of the head, it comprises the basal parts of the second maxillary appendages, to which, however, there may be added a median field of the sternum of the corresponding segment. If the submentum is regarded as entirely the labial sternum, then the sternum becomes suspended directly from the tergum of its segment, and bears the appendages—a condition so at variance with ordinary morphological relations as to discredit the premises from which it is deduced.

VII. THE HEAD OF A CATERPILLAR

The caterpillars are remarkable for their standardization of structure. In none of the other larger groups of insects is there such uniformity in fundamental organization as in the larvae of the Lepidoptera. Some species are superficially specialized, but apparently there is no " generalized " caterpillar. Ontogenetically, the caterpillars probably represent a stage below that of the larvae of Neuroptera, and of the larvae of the more generalized adult Coleoptera (Adephaga), since the young of these insects are closer in form to that of a typical adult insect. The caterpillars show primitive conditions in the origin of the antennal muscles on the walls of the cranium, in the musculature of the thoracic legs, in the monocondylic leg joints, in the dactylopodite-like end segments of the legs, and in the retention of the abdominal " legs," if these organs are remnants of true abdominal appendages, as they appear to be. The general form of the alimentary canal, of the tracheal system, and of the nervous system are fairly generalized, though the brain is specialized by an extreme condensation of its ganglia. On the other hand, the head, the maxillary appendages, the muscle sheath of the alimentary canal, and the body musculature are all highly specialized. While the form of the caterpillar's body is worm-like, it is not to be supposed that it represents a worm stage or even a primitive stage in the insect ancestry, for the structure of the head shows that the caterpillar belongs to the highly evolved stage of the pterygote insects. The caterpillar's form is merely one that adapts the insect to a wide feeding environment. The extremely complicated body musculature must be regarded as acquired through an excessive multiplication of the segmental muscles to give unlimited mobility to a soft-bodied animal. The fly maggot likewise has an intricate body musculature, but of quite a different pattern from that of the caterpillar.

STRUCTURE OF THE HEAD CAPSULE

The caterpillar head is an example of the type of head structure in which the lower genal and postgenal regions of the cranium (fig. 51 E) are lengthened to give a long ventro-lateral area on each side between the foramen magnum and the posterior articulation of the mandible. The facial aspect of the head (fig. 50 A) is characterized by the extension of the clypeus into the area of the frons, and by the invagination of the median part of the frons dorsal to the clypeus.

The prominent triangular plate so characteristic of the facial aspect of a caterpillar's head is unquestionably the clypeus (fig. 50 A, B, C, F, H, *Clp*), though it has usually been called the " frons." Its margins are defined internally by a strong **V**-shaped ridge (E, I, *ER*), the inverted apex of which is continued into a thick median ridge of the dorsal wall of the cranium. From the arms of the **V**-ridge arise the anterior tentorial apophyses (*AT*), and the latter identify the **V**-ridge as the epistomal ridge (*ER*). The space between the diverging arms, therefore, is the true clypeus (*Clp*). It has already been shown that the clypeus in other orders of insects may be extended into the facial region dorsal to the mandibular articulations (figs. 46 D, F, G, 47 C).

Further evidence that the area thus designated the clypeus in the lepidopteran larva is the true clypeal area, and not the frons, is given

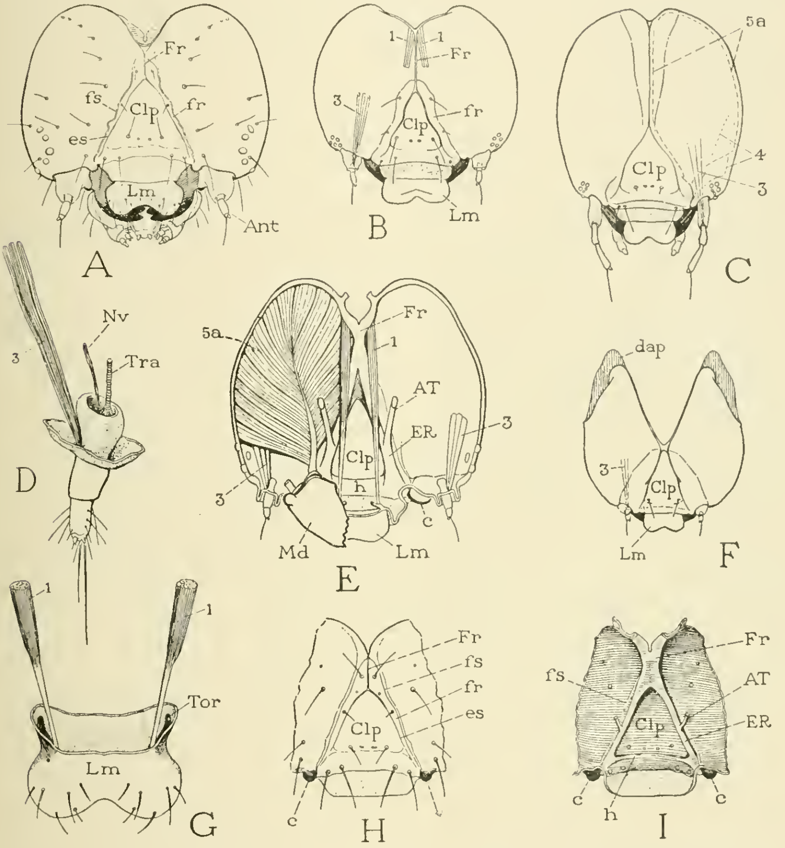

Fig. 50.—Head structure of caterpillars: anterior cranial wall, labrum, antenna, and mandibular muscles.

A, anterior surface of head of *Lycophotia* (*Peridroma*) *margaritosa*. B, same of *Thrydopteryx ephemeraeformis*. C, same of *Sibene stimulea*, showing areas of origin of mandibular muscles (*4*, *5a*). D, antenna of *Malacosoma americana*, left, anterior view. E, interior view of anterior wall of head of *Prionoxystus robiniae* (Cossidae), with labral muscles and adductor of left mandible in place. F, anterior surface of head of *Mnemonica aurocyanea*. G, labrum of *Lycophotia margaritosa*, anterior view, showing muscle insertions. H, fronto-clypeal area of same. I, inner view of same.

AT, anterior arm of tentorium; *c*, anterior articulation of mandible; *Clp*, clypeus; *ER*, epistomal ridge; *es*, epistomal suture; *Fr*, frons; *fr*, "adfrontal"; *fs*, frontal suture; *h*, submarginal thickening of clypeus; *Lm*, labrum; *Md*, mandible; *Nv*, antennal nerve; *Tra*, antennal trachea.

by the origin of the clypeal dilator muscles of the stomodeum upon it (fig. 55, *20, 21*). Finally, it is to be observed, the muscles of the labrum, which, in all cases where the identity of the facial plates is clear, arise on the frons, are never attached to the triangular plate of the caterpillar face, but take their origin from the median ridge dorsal to it (fig. 50 B, E, *1*). In many caterpillars the lower part of the clypeus is strengthened by an internal submarginal thickening (E, I, *h*) forming a bracing ridge between the articulations of the mandibles (c, *c*).

The frontal area of the head, as has been shown, is to be identified by the origin of the labral retractor muscles upon its inner surface (fig. 47 B, C). In the caterpillar the labral muscles arise either upon the median internal ridge of the cranium that extends between the apex of the posterior emargination of the vertex and the apex of the clypeus, or upon the dorsal bifurcations of this ridge that are continued into the margins of the vertical emargination (fig. 50 B, E, 53 E, *1*). This ridge, then, is at least a part of the frons. It is formed by a deep inflection of the median line of the cranium dorsal to the apex of the clypeus, which appears externally as a median suture (fig. 50 A, B, C, H, *Fr*). In a softened specimen this frontal invagination can often be widely opened, when it is seen that its inflected surfaces are continuous with the so-called "adfrontal" strips lying laterad of the clypeus and extending ventrally to the bases of the mandibles. The sutures, or membranous lines, along the outer margins of the "adfrontals" thus become the true frontal sutures (fig. 50 A, H, I, *fs*).

The frontal region of the caterpillar, therefore, includes the invaginated frontal groove (fig. 50 A, E, *Fr*), the "adfrontals" (*fr*), and perhaps the apical margins of the vertical emargination. When the mature caterpillar sheds its skin at the pupal molt, the head cuticula splits along two lines, which, beginning at the notch of the vertex, follow the external lips of the median frontal invagination and then diverge along the "adfrontal" sutures to the bases of the mandibles. An elongate piece is thus cut out which includes the median frontal inflection, the "adfrontals" and the clypeus. In some caterpillars the molting cleft follows only one of the adfrontal sutures, the other remaining closed.

The median part of the vertex in the caterpillar's head is obliterated by the dorsal emargination, and the angle of the emargination usually extends into the frontal invagination (fig. 50 I); in some cases the notch is so deep that the latter is reduced to a very small area dorsal to the apex of the clypeus (F).

The labrum of the caterpillar (fig. 50 A, B, *Lm*) is commonly separated from the lower edge of the clypeus by a wide, flexible membranous area. Some writers, having mistakenly identified the true clypeus as the frons, have regarded this membranous area as the clypeus, but the error of this interpretation is shown by the fact that none of the stomodeal muscles arise upon the membrane, the clypeal dilators having their origin on the triangular plate above. The caterpillar labrum has but a single pair of muscles:

1.—Retractor muscles of the labrum (figs. 50 E, G, 53 E).—A pair of long slender muscles arising on the inflected frons (figs. 50 E, 53 E, *Fr*); inserted by long tendons on bases of tormae (figs. 50 G, 53 E)

The ventral surface of a caterpillar's head presents a number of secondary modifications that, at first sight, somewhat obscure the basic structure; but, when the general head "landmarks" are once recognized, it is not difficult to see that the fundamental structure is no different from that in an orthopteroid head.

As we have noted, the caterpillar head is characterized by an elongation of the postgenal regions between the foramen magnum, or the end of the neck membrane (fig. 51 E, *NMb*), and the posterior articulations of the mandibles (*a*). On each side, a posterior median part of the postgena (A, E, *Hst*) is separated from the more lateral postgenal region (*Pge*) by a suture (*j*).

The median area thus set off is called the *hypostoma* (*Hst*), and the inner angles of the two hypostomal areas are approximated and sometimes united on the median line behind the base of the labium, which is thus separated from its usual basal connection with the neck membrane, or with the postoccipital rim of the cranium. In this manner a condition has been evolved which is almost a replica of that in the head of adult Hymenoptera (fig. 48 B, C), except that in the latter the hypostomal areas are not separated from the rest of the postgenal regions.

In some caterpillars a well-developed subgenal ridge (fig. 51 D, *SgR*) follows the outer margin of the membranous area of the antennal base from the anterior articulation of the mandible (*c*) to the posterior (*a*), and is then continued along the anterior mesal margin of the hypostoma (*Hst*). Some entomologists distinguish the part of the subgenal ridge that skirts the mandibular area as the "pleurostomal ridge," or "pleurostoma," and that part which follows the hypostomal margin as the "hypostomal ridge." The external suture that defines the hypostomal area on each side (E, *j*) forms internally a strong ridge (D, *j*) extending from the subgenal ridge at the posterior mandibular articulation (*a*) to the postoccipital ridge (*PoR*). The subgenal ridge, especially its hypostomal part, is lacking or but weakly developed in some caterpillars (C), but the ridge of the hypostomal suture (*j*) is always well developed, and apparently serves to brace the genal area between the mandible and the posterior rim of the head. The maxillae are suspended in the usual manner by the articulations of the cardines against the margins of the hypostomal areas of the postgenae (C, *Cd,* E, *e*).

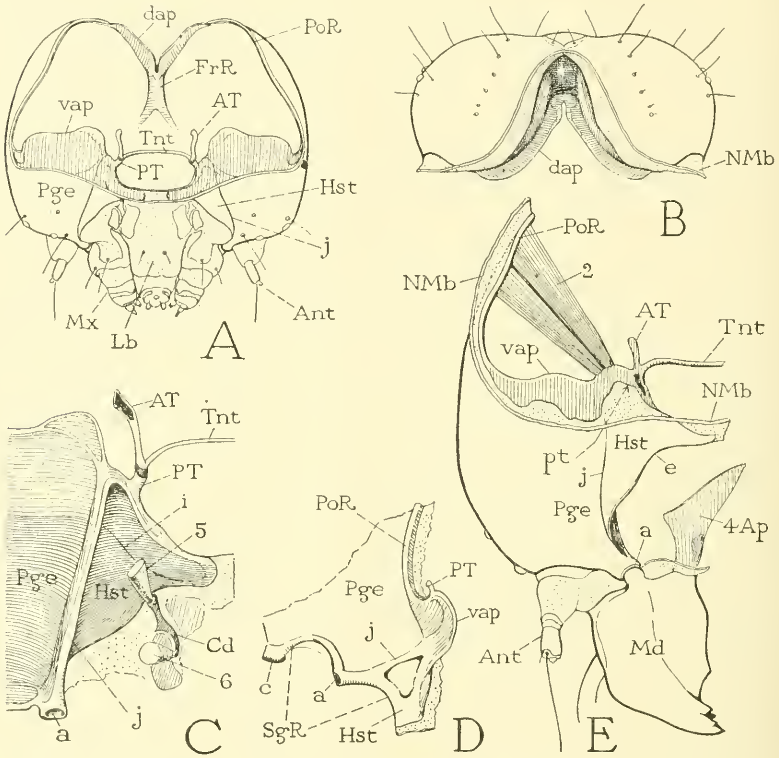

Fig. 51.—Structure of the posterior and ventral parts of the head of a caterpillar.

A, postero-ventral view of head of a noctuid (*Lycaphotia margaritosa*). B, dorsal view of same. C, interior view of postgenal and hypostomal regions, showing posterior arm of tentorium (*PT*), and articulation of cardo (*Cd*). D, inner face of same region in *Malacosoma americana.* E, ventral view of right half of cranium, with mandible and antenna, of *Estigmene acraea.*

a, posterior articulation of mandible; *Ant,* antenna; *4Ap,* base of adductor apodeme of mandible; *AT,* anterior arm of tentorium; *c,* anterior articulation of mandible; *Cd,* cardo; *dap,* dorsal apodemal plate of postoccipital ridge; *e,* articulation of cardo to cranium; *FrR,* frontal ridge; *Hst,* hypostoma; *i,* line of base of neck membrane; *j,* hypostomal suture, hypostomal ridge; *Lb,* labrum; *Md,* mandible; *Mx,* maxilla; *NMb,* neck membrane; *Pge,* postgena; *PoR,* postoccipital ridge; *PT,* posterior arm of tentorium; *Tnt,* transverse bar of tentorium; *vap,* ventral apodemal plate of postoccipital ridge.

The foramen magnum is extraordinarily large in the caterpillar, being almost as wide as the cranium, and is extended forward dorsally in the median notch of the vertex (fig. 51 A). The postoccipital ridge (*PoR*) is inflected from the rear margin of the cranial walls, there being no perceptible chitinization beyond it to form a postoccipital rim in the neck region. The postoccipital ridge gives origin to platelike apodemes that constrict the actual opening of the head cavity into that of the neck. Usually there is a pair of dorsal apodemes (A, B, *dap*) in the notch of the vertex, and a pair of larger ventral apodemes (A, D, E, *vap*) arising from the postgenal and hypostomal parts of the postoccipital ridge. The apodemes vary much in size and shape in different species, but those of the ventral pair are usually the larger and the more constantly developed. The apodemes furnish surfaces of attachment for the anterior ends of prothoracic muscles inserted on the back of the head (fig. 57 A, C). In the caterpillars the foramen magnum is crossed laterally by oblique foraminal muscles, which are the following:

2.—*Muscles of the foramen magnum* (figs. 51 E, 57 A).—Attached below on each side to ventral postoccipital apodeme (fig. 51 E, *vap*) laterad of posterior root of tentorium; spreading dorsally and laterally, sometimes as a broad fan (fig. 57 A), to the dorso-lateral parts of postoccipital ridge. The foraminal muscles are of the nature of the transverse muscles of the intersegmental folds in the body of the caterpillar. From their position it would appear that they must produce a tension on the hypostomal regions of the head wall. Foraminal muscles are not present in insects generally.

The tentorium of the caterpillar is a simple structure consisting of two slender longitudinal bars, and of a delicate transverse posterior bridge. The longitudinal bars, which represent the anterior arms of the tentorium (fig. 53 D, E, *AT*), arise from the lateral parts of the epistomal ridge at the sides of the clypeus (fig. 50 E, I, *AT*). They extend horizontally through the head (fig. 53 E), and are united posteriorly with the ends of the posterior bridge (figs. 51 A, C, E, 53 D, *Tnt*). The bridge represents the united median parts of the posterior tentorial arms (fig. 51 A, C, *PT*), the origins of which (E, *pt*) are at the posterior angles of the hypostomal plates in the deep inflections that form the inner ends of the ventral postoccipital apodemes (*vap*). The positions of all the tentorial roots in the caterpillar, thus, are identical with those of the tentorial roots in an orthopteroid head, notwithstanding the considerable alterations which the surrounding parts have suffered.

THE ANTENNAE

The antennae are much reduced in all caterpillars, being so small by comparison with the adult organs that the latter are forced to develop by recession, and during the propupal stage their tips only lie within the antennae of the larva. The antennae of the caterpillar are situated on membranous areas just laterad of the bases of the mandibles, while the antennae of the adult arise from the facial region above the compound eyes. The ventro-lateral position of the larval antennae, therefore, appears to be a primitive character in the caterpillars.

Each antenna of the caterpillar consists of three segments, of which the middle one is usually the largest, the proximal segment being often reduced to a mere basal ring (fig. 51 E, *Ant*), and the terminal one appearing as a minute apical papilla of the second. The membrane of the antennal base may form a large mound with the antenna retractile into it, or sometimes a long cylindrical projection simulating a basal segment (fig. 50 C). A hypodermal fold projects inward from the base of the antenna (fig. 50 D) which receives the antennal nerve and trachea. Each antenna is moved by a single set of muscle fibers, which are:

3.—The retractor muscles of the antenna (fig. 50 B—F).—A group of slender fibers arising on the parietal walls of the cranium laterad of adfrontal area; inserted on anterior inner angle of base of proximal antennal segment. Extension of the antennae is probably effected by blood pressure from within the head.

THE MANDIBLES

The mandibles of the caterpillar are typical insect jaws suspended from the lower margins of the cranium by a hinge line sloping downward posteriorly, with well-developed anterior and posterior articulations. The anterior articulation of each mandible consists of a condyle on the cranial margin placed just laterad of the clypeus (fig. 52 A, *c*), received into a socket on the base of the jaw; the posterior articulation (*a*) is the reverse, consisting of a socket on the cranial margin receiving a condyle of the mandible. As in all insects, the articular points of the jaw lie *outside* the membrane that connects the base of the mandible with the head. A line between the two articulations divides the base of the jaw unequally (fig. 52 B), the larger part being mesad to the axis.

The muscles of the mandibles are inserted on large but weakly chitinized apodemal inflections arising at the outer and inner margins of each jaw. The muscles take their origin on the walls of the cranium and on the ventral apodemes of the postoccipital ridge. Their fibers occupy most of the cavity of the head, and the cranial hemispheres appear to model their form on that of the bases of the great adductor muscles of the jaws.

4.—The abductor muscles of the mandible (figs. 50 C, 52 B).—A group of fibers, small by comparison with the adductor group, arising on lower lateral and posterior walls of cranium, and on ventral apodeme of postoccipital ridge laterad of posterior root of tentorium; fibers converging ventrally, anteriorly, and mesally to insertion on abductor apodeme of mandible.

5.—The adductor muscles of the mandible (figs. 50 C, E, 52 B, 53 E).—An enormous mass of fibers disposed in two sets (figs. 52 B, 53 E, *5a, 5b*). The fibers of one group arise from almost entire dorsal, anterior, lateral, and posterior walls of corresponding half of epicranium above the ocelli (figs. 50 C, E, 53 E, *5a*); they converge downward upon both surfaces of the broad adductor apodeme of mandible. The fibers of the other group (figs. 52 B, 53 E, *5b*) arise on ventral apodeme of postoccipital ridge (fig. 53 E, *vap*) mesad of bases of abductor fibers, and extend horizontally to posterior edge of adductor apodeme of mandible.

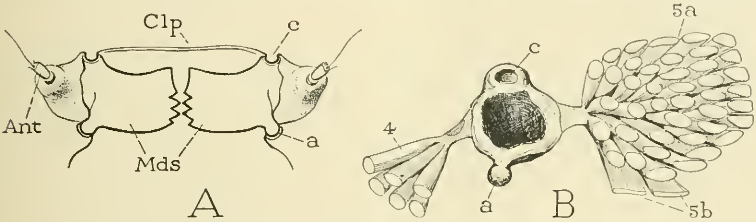

FIG. 52.—Mandibles of a caterpillar.

A, mandibles and antennae of *Estigmene acraea*, ventral view. B, left mandible of a noctuid, with bases of muscles, dorsal view.

a, posterior articulation of mandible; *Ant*, antenna; *c*, anterior articulation of mandible; *Clp*, edge of clypeus; *Mds*, mandibles; *4*, abductor muscle of mandible; *5a*, fibers of adductor arising on wall of cranium; *5b*, adductor muscles arising on ventral apodeme of postoccipital ridge (see fig. 53 E).

The obliquity of the mandibular axes causes the points of the jaws to turn upward and somewhat posteriorly during adduction. When the mandibles are closed, the teeth on the cutting edges of the two jaws are opposed to each other (fig. 52 A), not interlocked; but usually one mandible closes first and its toothed edge passes inside that of the other. Live caterpillars examined by the writer always closed the right mandible over the left, and species of several families preserved in alcohol were found to have the jaws in the same position.

THE MAXILLAE AND LABIUM

The basal parts of the maxillae and labium are united, and their chitinous areas are reduced or variously broken up into small plates (figs. 51 A, 53 A), which may differ much in different species. With the anterior wall of the labium, apparently, is united also the hypopharynx (fig. 54 D, *Hphy*), and the duct of the silk gland opens through a hollow spine, the spinneret, at the tip of the labium.

Each maxilla includes a cardinal area (fig. 53 A, *Cd*), a stipital area (*St*), both united with the basal part of the labium, and a free terminal lobe (*Lc*), which appears to be the lacinia. A maxillary palpus is lacking. The area of the cardo includes one principal sclerite (fig. 53 A, B, E, F, *Cd*), and generally one or two accessory plates (A, E, F, *k, k*). The principal sclerite is always articulated to the hypostomal margin at a point (*e*) corresponding with the articulation of the cardo to the cranium in orthopteroid insects. The area of the stipes (*St*) is variously chitinized, or unchitinized, but it always preserves the ridge (*q*) of its inner margin, upon which are attached all the stipital muscles. The homology of the terminal lobe of the maxilla is difficult to determine.

The musculature of the maxilla of a caterpillar comprises muscles pertaining to its three parts, most of which are comparable to the maxillary muscles of the grasshopper or other generalized insects, though there is little similarity in the general appearance of the structure in the two cases. The cardo, in the caterpillar, is provided with two or three muscles (fig. 53 B, E, F, *6, 7, 8*), all of which arise on the anterior arm of the tentorium (D, E), and, therefore, represent the tentorial adductors of the cardo in orthopteroid insects. The usual cranial muscle of the cardo (fig. 25, *I*, fig. 40 C, *10*) is lacking in the caterpillar. The stipes is provided likewise with tentorial adductors (fig. 53 B, D, E, F, *9, 10, 11*) inserted on its mesal chitinous ridge (*q*). The terminal maxillary lobe is moved by muscles that arise within the stipes (B, F, *12, 13*), and also by a long muscle (B, *14*) having its origin in the posterior angle of the hypostomal plate (*Hst*) of the epicranium. These three muscles are inserted upon a basal sclerite in the ventral wall of the maxillary lobe (A, B, *l*). The first two suggest the ordinary stipital muscles of the lacinia, but the third (*14*) appears to have no homologue in more generalized insects, since the usual cranial flexor of the lacinia (fig. 30 B, *flcc*) is inserted on the median angle of the latter. The insertion of the three muscles on a single sclerite in the base of the maxillary lobe leaves no evidence to indicate the presence of a galea, and suggests that the lobe is the lacinia alone, complicated in form by the development of large sensory papillae. Certainly, the musculature of the lobe shows that none of the papillae can be a palpal rudiment.

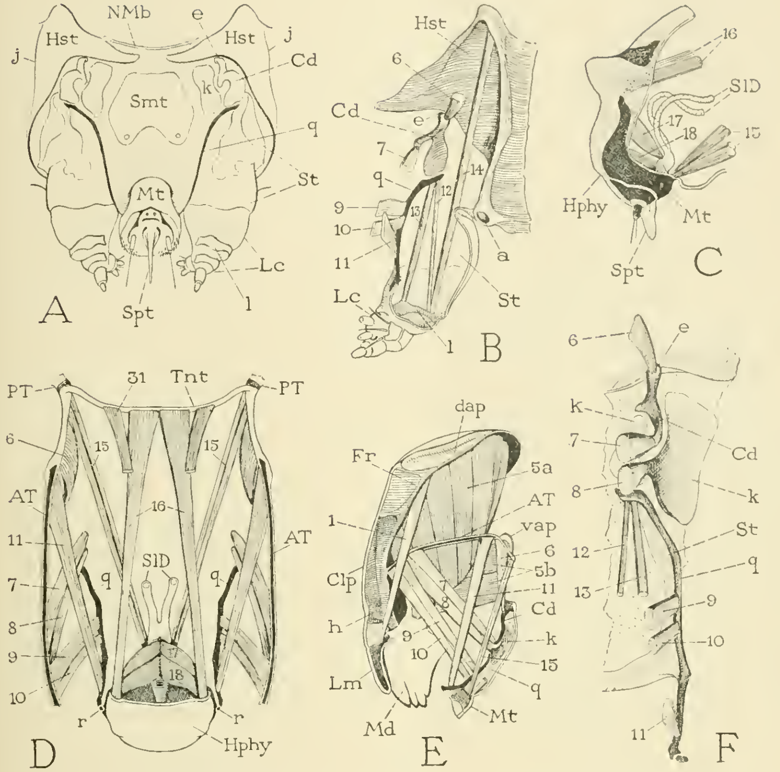

FIG. 53.—Maxilla, labium, and silk press of a caterpillar.

A, *Estigmene acraea*, maxillae and labium, with hypostomal plates of head, posterior (ventral) view. B, internal view of left maxilla and hypostomal region of same, showing muscles. C, *Malacosoma americana*, distal part of labium and hypopharynx, lateral view, showing silk press and muscles. D, *Lycophotia margaritosa*, muscles of maxillae, labium, and hypopharynx, internal (dorsal) view. E, the same, right side of head, internal view, showing muscles of labrum, mandible, maxilla, and labium. F, cardo and lateral parts of stipes of right maxilla, showing bases of muscles, dorsal (anterior) view. (Compare with E.)

a, anterior articulation of mandible; *AT*, anterior arm of tentorium; *Cd*, cardo; *Clp*, clypeus; *dap*, dorsal apodeme of postoccipital ridge; *e*, articulation of cardo with cranium; *Fr*, frons; *h*, submarginal ridge of clypeus; *Hphy*, hypopharynx; *Hst*, hypostoma; *j*, hypostomal suture; *k*, accessory plates of cardo; *l*, basal sclerite of lacinia; *Lc*, lacinia; *Lm*, labrum; *Md*, mandible; *Mt*, mentum; *NMb*, neck membrane; *PT*, posterior tentorial arm; *pt*, posterior tentorial pit; *q*, ridge on inner edge of stipes; *r*, articular nodule between end of stipital ridge (*q*) and mentum; *SlD*, silk gland ducts; *Smt*, submentum; *Spt*, spinneret; *St*, stipes; *Tnt*, transverse bar of tentorium; *vap*, ventral apodeme of postoccipital ridge.

The muscles of the maxilla may be enumerated as follows, and they will probably be found to differ but little in different species of caterpillars:

6.—First adductor of the cardo (fig. 53 B, D, E, F).—Origin on posterior end of anterior arm of tentorium (*AT*); goes ventrally to insertion on base of cardo.

7.—Second adductor of the cardo (fig. 53 B, D, E, F).—Origin anteriorly on tentorial arm (D, E); insertion on distal end of cardo.

8.—Third adductor of the cardo (fig. 53 D, E, F).—This muscle found in noctuid larvae, perhaps a subdivision of *7*. Origin anterior to *7* on tentorial arm (D, E); insertion on accessory plate (E, F, *k*) mesad to the articulating sclerite of cardo (*Cd*).

9.—First adductor of the stipes (fig. 53 B, D, E, F).—Arises near anterior end of anterior tentorial arm (D, E); goes obliquely ventrally and posteriorly to insertion on marginal ridge (B, D, E, F, *q*) of stipes.

10.—Second adductor of the stipes .(fig. 53 B, D, E, F).—Origin at anterior end of tentorial arm, just before *9* (D, E); insertion on stipital ridge (D, E, F, *q*) anterior to *9*.

11.—Third adductor of the stipes (fig. 53 B, D, E, F).—Arises posteriorly on anterior tentorial arm, just before first adductor of cardo (*6*); goes obliquely ventrally and anteriorly (D, E), internal to *7*, *8*, *9*, and *10*, to insertion on anterior end of stipital ridge (B, D, E, F, *q*)

12.—External retractor of the lobe (fig. 53 B, F).—Origin on base of stipital ridge (*q*); insertion laterally on basal plate (A, B, *l*) of terminal lobe of maxilla.

13.—Internal retractor of the lobe (fig. 53 B, F).—Origin on base of stipital ridge (*q*); insertion mesally on basal plate (A, B, *l*) of terminal lobe of maxilla.

14.—Cranial abductor of the lobe (fig. 53 B).—Origin in basal angle of hypostomal plate of epicranium (*Hst*); insertion on outer end of basal plate (*l*) of terminal lobe of maxilla. A corresponding muscle is not present in orthopteroid insects.

The labium of the caterpillar (fig. 53 A) lies between the maxillae. The broad membranous surface of its large submental region is united on each side with the marginal ridges (*q*) of the stipites, and its basal part is continuous laterally with the membrane of the cardinal areas. Proximally the labium may be continuous with the neck membrane (*NMb*) between the approximated ends of the hypostomal plates (*Hst*), but, when the latter are united, the labium becomes separated from the neck. A large submental plate occupies the median basal part of the submental region in some species (A, *Smt*).

The distal, free lobe of the labium probably represents the mentum and ligula of other biting insects, combined with the hypopharynx, which forms its anterior surface (fig. 54 A). Evidence of this interpretation is found in the fact that the labial and hypopharyngeal

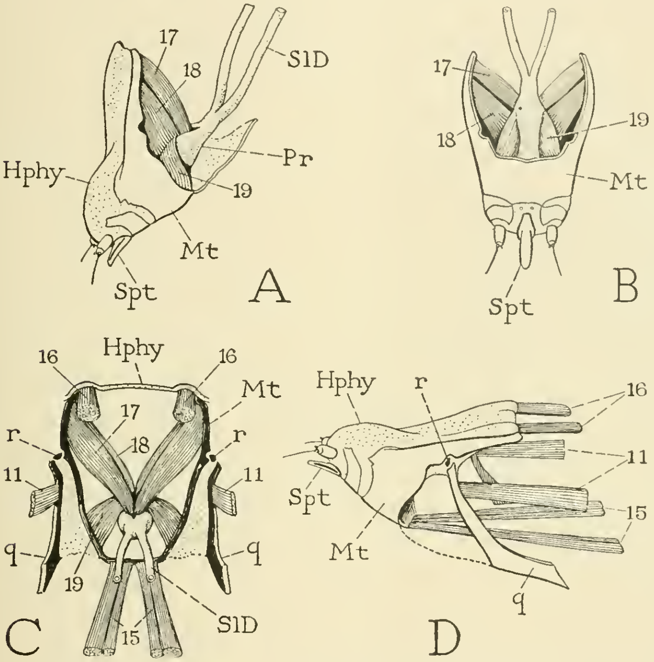

Fig. 54.—Distal part of labium, hypopharynx, and silk press of a noctuid caterpillar.

A, mentum and hypopharynx, with silk press partly exposed, lateral view. B, the same, dorsal view. C, the same, posterior view, showing support on arms of stipites (*q*, *q*). D, lateral view, showing muscle attachments.

Hphy, hypopharynx; *Mt*, mentum; *Pr*, silk press; *q*, *q*, ridges of stipes; *r*, *r*, articular nodules between stipital arms and mentum; *SlD*, silk duct; *Spt*, spinneret.

muscles are inserted on the base of the lobe (figs. 53 C, D, 54 C, D, *15*, *16*), and in the position of the spinneret (fig. 54 A, D, *Spt*), which contains the opening of the silk duct (salivary duct), the latter being normally situated between the labium and the hypopharynx (fig. 18 D, *SlO*).

The mental region of the mento-hypopharyngeal lobe appears to be that occupied by the large proximal plate (fig. 53 A, *Mt*) that embraces the base of the lobe ventrally and laterally, but which is not continued across the hypopharyngeal surface (figs. 53 C, 54 A, C, D, *Mt*). This plate is supported upon the distal ends of the ridges of the stipites (fig. 54 C, D, *q, q*), which are turned forward and articulated with the dorsal arms of the mentum (*Mt*) by small, chitinous nodules (*r, r*). By this mechanism, the mentum-hypopharynx, which carries the spinning apparatus, is freely movable on a transverse axis between the ends of the supporting stipital ridges. The motion in a vertical plane is the only movement that can be given to the spinning apparatus, except by the action of the entire head; but the head of the caterpillar is highly mobile by reason of the great number of muscles inserted upon its posterior margin (fig. 57). The musculature of the mentum-hypopharynx, or spinning organ, is as simple as its mechanism, consisting of two pairs of muscles, as follows:

15.—Reductors of the spinning organ (figs. 53 C, D, E, 54 C, D)—A pair of double muscles arising at posterior ends of tentorial arms (fig. 53 D, E); converging ventrally and anteriorly to insertions on ventral edge of mentum (figs. 53 C, E, 54 C, D, *Mt*). These muscles probably represent the mento-tentorial muscles of orthopteroid insects (fig. 40 D, *23*), which are primitive adductors of the second maxillae.

16.—Productors of the spinning organ (figs. 53 C, D, 54 C, D).—A pair of broad muscles arising medially on transverse bridge of tentorium (fig. 53 D, *Tnt*), diverging ventrally and anteriorly to base of hypopharynx (figs. 53 C, D, 54 C, D, *Hphy*). These muscles are probably the retractors of the hypopharynx in orthopteroid insects (fig. 41, *32*).

The silk press of the caterpillar is a special development of the common duct of the labial glands (here, the silk glands). The deeply invaginated dorsal wall of the organ exerts a pressure on the silk material, which is regulated by two sets of opposing muscles that, probably acting together, effect a dilation of the lumen of the press by elevating the invaginated roof. The muscles of the press arise within the mentum, and the two sets may be distinguished as follows:

17, 18.—Dorsal muscles of the silk press (fig. 54 A, B, C).—Two lateral series of muscles, the number on each side varying in different species of caterpillars, arising on dorsal arms of mentum; converging to insertions on chitinous raphe in dorsal (anterior) wall of press.

19.—Ventral muscles of the silk press (fig. 54 A, B, C).—Origin in ventrolateral parts of mentum; insertion on dorso-lateral edges of silk press. These muscles are antagonists to the dorsal muscles, since the fibers of the two sets oppose each other in the crossed lines of an X (fig. 54 C) ; but in function the ventral muscles are probably accessory to the dorsals by counteracting the pull of the latter on the press.

It is difficult to discover a parallelism between the muscles of the silk press in the caterpillar and muscles of the labium in other insects. However, it may be possible that the two sets of muscles in the labium of the grasshopper (fig. 40 D, *26, 27*) inserted on the salivary cup (*v*) are the prototypes of the silk press muscles, though their insertion points are ventral instead of dorsal.

THE STOMODEUM

The stomodeum of the caterpillar (fig. 55) is differentiated into four parts. The first part is a bucco-pharyngeal region (*BuC, Phy*) ; the second, a cylindrical tube with strong transverse muscle rings, constitutes an oesophagus (*OE*) in the caterpillars, but it evidently corresponds with the posterior section of the pharynx in Orthoptera ; the third part is the large sack-like crop (*Cr*) ; the fourth is the constricted posterior region of the stomodeum (fig. 56 F, *Pvent*), which may be termed the proventriculus, though it has no special development of the lining intima, such as usually distinguishes the proventricular region in other insects.

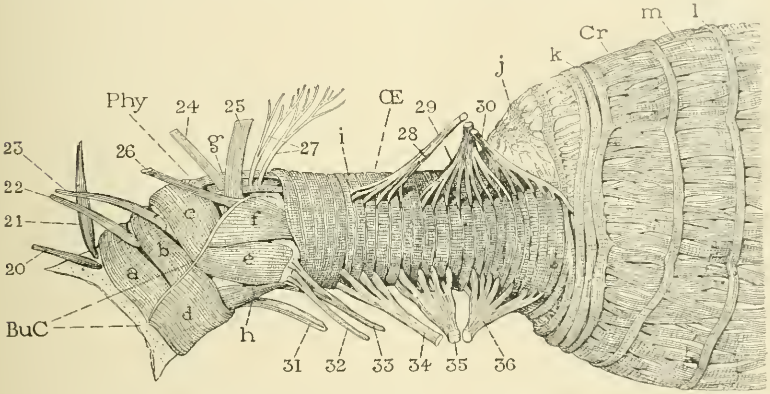

Fig. 55.—Anterior part of the stomodeum of a noctuid caterpillar, showing muscles of the stomodeal wall, and the dilator muscles arising in the head.

a-m, muscles of stomodeal wall; *BuC*, buccal cavity; *Cr*, crop; *OE*, oesophagus; *Phy*, pharynx; *20-23*, muscles of buccal region, arising on clypeus; *24-27*, dorsal dilators of anterior pharyngeal region; *28-30*, dorsal dilators of oesophagus (posterior pharyngeal region) ; *31-36*, ventral dilators.

The muscular sheath of the entire alimentary canal of the caterpillar is strongly developed, and in some parts becomes highly complicated in structure. The alimentary muscles are particularly strong in the noctuids, and the following descriptions are based mostly on *Lycophotia margaritosa*.

The lateral walls of the bucco-pharyngeal region are marked on each side by an oblique ridge (fig. 55), formed by a specially chitinized groove of the intima, which gives a firm line of insertion for the external muscles. The latter consist of thick, broad bands of strongly fibrillated muscle tissue, for the most part lying in one plane, though varying in position from transverse to longitudinal. The anteriormost muscles consist of two dorsal arcs (*a*, *b*), and of a corresponding wide ventral arc (*d*), their ends inserted laterally on the oblique ridges. This part of the stomodeum may be defined as the buccal region because its dilator muscles (*20-23*) have their origins on the clypeus. The anterior end of the pharyngeal region following is covered dorsally by a broad transverse muscle (*c*) attached laterally on the oblique ridges. The frontal ganglion lies over the posterior border of this muscle. Each side of the pharynx presents two muscle plaques (*e, f*) attached to the ventral margins of the upper half of the oblique ridge, but extending posteriorly to the oesophagus. The posterior dorsal wall of the pharynx is covered with several longitudinal muscles, the most prominent of which is a wide, median, external band of fibrils (*g*) deflected from the posterior part of the broad anterior transverse muscle (*c*). Concealed by this muscle are two longitudinals of a deeper set, arising anteriorly on the buccal region beneath the first transverse muscle (*a*) and extending posteriorly to the anterior end of the oesophagus. Several superficial longitudinal fibers lie more laterally.

The buccal region of the stomodeum is thus distinguished by its strong circular musculature, which evidently gives it a powerful constrictor action. The pharynx is provided principally with longitudinal muscles, and its action, except for that produced by the anterior dorsal transverse muscle, must be one of lengthwise contraction.

The entire length of the oesophageal tube is sheathed in a close series of strong circular fibers (*i*) which are complete rings, except a few of the most posterior interrupted dorsally at the anterior end of the crop.

The inner walls of the pharynx and oesophagus form four longitudinal folds—one dorsal, one ventral, and two lateral. The dorsal fold is broad, flat, and straight-edged. It arises at the base of the labrum, where its margins begin at the tormae, and continues to the posterior end of the oesophagus, where it is lost with the sudden widening of the stomodeal tube in the crop. Between the pharynx and the oesophagus, the continuity of the dorsal fold is interrupted by a transverse fold. The ventral and lateral folds are less definite, rounded inflections of the stomodeal wall, continuous from the pharynx into the oesophagus. In *Lycophotia margaritosa* each of these folds ends at the opening of the crop in a prominent fleshy papilla covered with small chitinous points. Between the folds are four deep channels extending from the mouth to the crop, two dorso-lateral, and two latero-ventral. Possibly it is through these channels that the alimentary liquid, which caterpillars frequently eject from the mouth when irritated, is conveyed forward from the crop.

The muscles of the crop (fig. 55, *Cr*) are arranged longitudinally and circularly. The circular muscles (*l*), except for a few closely placed anterior bands (*k*), are widely spaced, external circular fibers. They all completely surround the crop like the hoops of a barrel. At the junction of the crop with the oesophagus, there are several short transverse fibers (*j*) confined to the dorsal surface. All the muscles of the crop are strongly fibrillated (fig. 56 A, B, C, D). The circular bands have distinct nuclei, but nuclei were not observed in the longitudinal muscles of noctuid species examined.

The longitudinal muscles of the crop (fig. 55, *m*) have their origin in single fibrillae (fig. 56 A) or small bundles of fibrillae (B) given off from the posterior margins of the circular fibers. They are, therefore, of the nature of branches of the circular fibers, and this fact may account for their lack of nuclei. Moreover, the longitudinal muscles are not continuous, individual bands, but are everywhere branched and intimately united by intercrossing bundles of fibrillae in such a manner that the entire layer becomes a plexus of muscle tissue (fig. 56 C). Most of the fibrillae of this layer spring from the anterior circular fibers, but probably all the circular fibers contribute at least a few elements to the longitudinal plexus. On the anterior end of the crop, the longitudinal fibrillae appear as simple connectives between the transverse fibers (fig. 55, *j*). On the posterior end of the crop (fig. 56 F), the longitudinal muscles again break up into smaller fibril bundles, and at last into fine strands that reunite with the external circular fibers of the crop or the proventriculus.

The proventricular region (fig. 56 F, *Pvent*) resembles the oesophagus in being surrounded by a close series of strong circular muscle fibers (*n*). There is no distinct inner muscular sheath here, but the circular fibers are all connected by small bundles of fibrillae going from one to another (G), some to the first neighboring fibers, others to the second, third, or fourth removed in either direction. The proventriculus has a special feature in the presence of an external layer of fine, widely-spaced, longitudinal muscles, stretched freely between its two ends (fig. 56 F, *o*). These threadlike strands arise anteriorly from branches that spring from the posterior ends of the longitudinal crop muscles, and from the anterior circular fibers of the proventriculus. Posteriorly they again break up into branches that are lost in a plexus of fibers at the junction of the proventriculus with the ventriculus (*Vent*).

A study of the stomodeal muscle sheath of the caterpillar thus shows that the usual brief statement that the insect stomodeum is surrounded by an external layer of circular fibers and an internal layer of longitudinal fibers must be considerably modified and amplified to fit conditions in the caterpillar. The proctodeal muscles of the caterpillar are even more complicated than are those of the stomodeum. The high degree of development in the alimentary musculature of the caterpillars accords with the general specialization of the caterpillar as an animal most efficient in feeding, and the extreme development of the somatic musculature is only another adaptation to the same end.

The dilator muscles of the stomodeum are inserted dorsally and ventrally on the stomodeal walls. The dorsal muscles are grouped into three sets corresponding with the buccal, pharyngeal, and oesophageal regions of the stomodeum. The dilator muscles of the dorsal and central series, enumerated according to the order of their insertions, are as follows:

20.—First dorsal dilators of the buccal cavity (fig. 55).—A pair of slender muscles arising on submarginal ridge of clypeus (fig. 50 I, *h*); extending posteriorly to insertions laterally on roof of mouth cavity just before first band of circular stomodeal muscles.

21.—Second dorsal dilators of the buccal cavity (fig. 55).—Origins on clypeus, above middle and close to lateral margins; insertions medially on dorsal wall of mouth cavity between insertions of *20*.

22, 23.—Third and fourth dorsal dilators of the buccal cavity (fig. 55).—Two pairs of slender muscles: those of each side arising together in ventral angles of clypeal triangle just above ends of submarginal ridge; inserted dorso-laterally on buccal region, *22* before second band of transverse muscles (*b*), *23* behind it.

A wide space occupied by the third transverse muscle band (*c*) intervenes between the dilators of the buccal region and those of the true pharyngeal region.

24.—First dorsal dilators of the pharynx (fig. 55).—Origin on upper part of clypeus just internal to epistomal ridge; insertion medially on dorsal wall of pharynx laterad of frontal ganglion. These are clearly true pharyngeal muscles; their points of origin have evidently crossed the epistomal ridges to the clypeus.

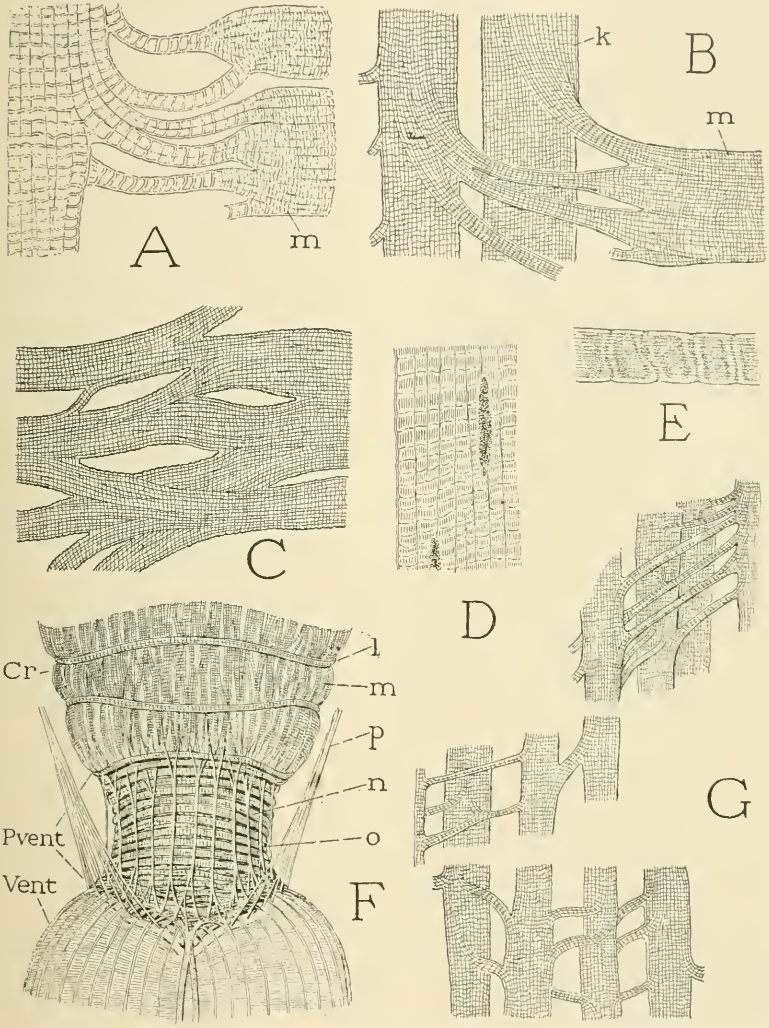

FIG. 56.—Muscles of the stomodeum of a noctuid caterpillar.

A, B, origin of longitudinal muscles (*m*), of crop (see fig. 55) from fibrils deflected from the anterior circular muscles (*j*, *k*). C, plexus of longitudinal muscles, anterior part of crop. D, piece of circular fiber from anterior part of crop. E, a connecting fiber between circular and longitudinal muscles. F, posterior end of crop (*Cr*), proventriculus (*Pvent*), and anterior end of ventriculus (*Vent*): *l*, *m*, circular and longitudinal muscles of crop; *n*, circular muscles of proventriculus; *o*, external longitudinal fibers of proventriculus; *p*, first suspensory muscles of ventriculus. G, parts of seven consecutive circular fibers of proventriculus, showing bundles of uniting fibrils, external.

25.—Second dorsal dilators of the pharynx (fig. 55).—Origins on epistomal ridges near union with frontal ridge; insertions dorsolaterally on pharynx.

26.—Third dorsal dilators of the pharynx (fig. 55).—Each arises on cranial wall laterad of origins of antennal muscles; extends medially, posteriorly, and downward to insertion on pharynx just laterad of *25*.

The insertions of muscles *24*, *25*, and *26* all lie posterior to the frontal ganglion connective.

27.—Fourth dorsal dilators of the pharynx (fig. 55).—A group of fibers on each side, arising on outer surface of lower end of frontal ridge; converging to one or two stalks inserted on dorsal wall of pharynx just before brain.

The following dorsal muscles are inserted behind the brain and on the region of the stomodeum that may be distinguished in the caterpillar as the oesophagus, but which is the so-called posterior pharynx in Orthoptera.

28, 29, 30.—Dorsal dilators of the oesophagus (fig. 55).—Three fans of muscles arising on posterior margin of cranial walls on each side of vertical emargination; the spreading fibers inserted dorsolaterally on oesophagus from brain to crop.

31.—First ventral dilators of the pharynx (fig. 55).—A pair of long slender muscles arising on transverse bar of tentorium (fig. 53 D, *Tnt*), converging to ventral wall of pharynx where inserted just behind first ventral transverse muscle (*d*).

32, 33.—Second and third ventral dilators of the pharynx (fig. 55).—A pair of small muscles on each side arising on extreme outer ends of transverse tentorial bar; fibers spreading at insertion ventro-laterally on pharynx just before anterior circular muscles of oesophagus.

34, 35, 36.—Ventral dilators of the oesophagus (fig. 55).—Three large fans of fibers arising on postoccipital apodemes on each side laterad of posterior roots of tentorium; the spreading fibers inserted ventro-laterally on oesophagus from circum-oesophageal nerve connective to crop.

THE MUSCULATURE OF BACK OF HEAD, AND NATURE OF THE INSECT NECK

The head of the caterpillar is remarkably mobile. It is provided with a wonderful system of muscles, the fibers of which arise mostly in the prothorax and are distributed at their insertions upon the postoccipital ridge of the head in such a manner as to enable the caterpillar to make all possible head movements of which it conceivably might have need (fig. 57 A, B, C).

The muscles of the prothorax of the American tent caterpillar, *Malacosoma americana,* are illustrated in figure 57. At A are shown the lateral and ventral muscles as seen from a posterior dorsal view, with the head turned somewhat downward on the neck; B shows the dorsal muscles as seen from below; C presents an inner view of all the muscles in the right half of the prothorax inserted on the head; and D gives the muscles of the same side that lie external to those shown in C, except the single fiber arising just dorsal to the spiracle, which is shown in both figures.

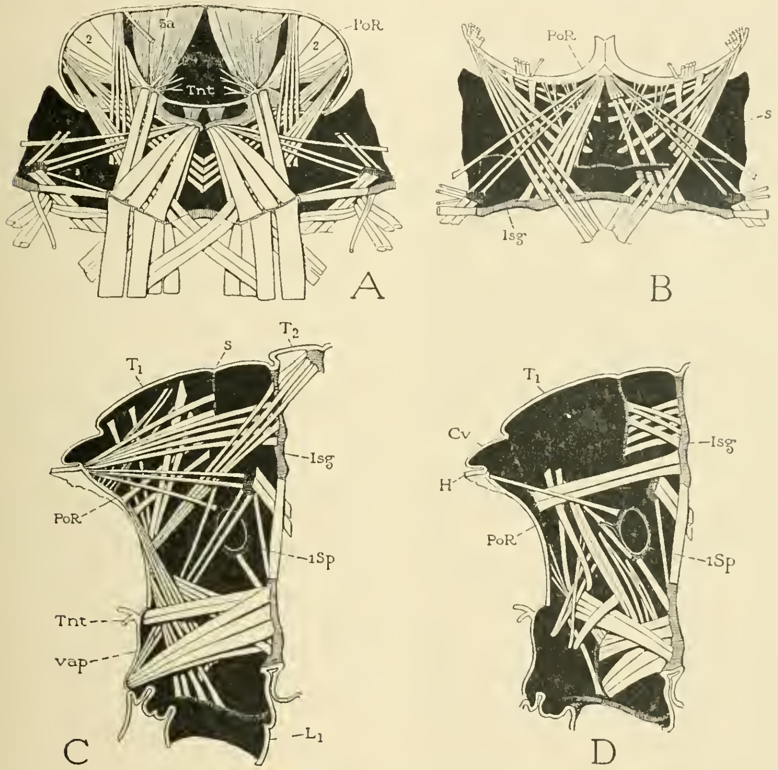

Fig. 57.—Muscles of the prothorax of a caterpillar, *Malacosoma americana.*

A, prothoracic muscles inserted on lateral and ventral parts of back of head, and ventral muscles of mesothorax, posterior view. B, dorsal muscles of prothorax and mesothorax inserted on dorsal half of back of head, seen from below. C, innermost layers of muscles of right half of prothorax, internal view. D, external muscles of right half of prothorax.

Isg, intersegmental fold; L_1, base of prothoracic leg; *PoR,* postoccipital ridge of head; *s,* edge of tergal plate of prothorax; *1Sp,* first spiracle; *Tnt,* transverse bar of tentorium; *vap,* ventral apodemal plate of postoccipital ridge.

The various fibers of the head muscles are mostly arranged in groups, and it is easiest to trace them from their points of insertion on the back of the head. Inserted in the median notch of the vertex there is a dorsalmost group of long fibers that diverge posteriorly to the dorsal wall of the prothorax (B, C), the middle fibers of each group going to the posterior margin of the segment. External to these muscles, a group of short fibers, inserted serially on each side, extends posteriorly and dorsally to the tergal plate of the prothorax. Laterally there are inserted on the postoccipital ridge several fibers that spread to their origins on the tergal plate, and a group of four long fibers going dorsally and medially to the intersegmental fold (*Isg*), with the two median fibers crossing the latter to the dorsum of the mesothorax. Three lateral groups of fibers (A, C) go ventrally and posteriorly from their head insertions, one to the sternal intersegmental fold, another to the region just before the base of the prothoracic leg, and the third to the median longitudinal fold between the legs. Ventrally there are inserted on the ventral apodeme of the hypostomal region (C, *vap*) the anterior ends of the ventral longitudinal muscles of the prothorax (A, C), and a group of four long fibers on each side that arise on the region above the spiracle.

It is of particular interest to observe that, in the caterpillar, the ventral longitudinal muscles of the prothorax are *not* inserted on the tentorium (fig. 57 A, C) as they are in orthopteroid insects, and furthermore, that all the principal longitudinal ventral muscles of the thorax have their origin on the *intersegmental* folds, and not on intrasegmental apophyses. The primitive anterior insertion of these muscles in the prothorax, therefore, should be on a ventral intersegmental fold between the prothorax and the last head segment. We have already seen that there is evidence of the loss of the true labio-prothoracic intersegmental fold, since the postoccipital ridge, which bears the anterior attachments of the prothoracic muscles in all known insects, appears to be the fold between the maxillary and the labial segments. If so, the original attachments have been lost and the muscles now extend through the length of two primary segments.

Furthermore, the attachment of the ventral muscles of the caterpillar on the hypostomal regions of the head must signify a migration of the muscles from their primitive sternal insertions, for the hypostomal lobes clearly belong to the postgenae, and are, therefore, ventral extensions of the tergal area of the head wall. In any case, an attachment of the ventral muscles on the bridge of the tentorium certainly represents a farther displacement of the muscle insertions by a final migration from the tergal postoccipital ridge to the posterior tentorial apophyses.

The question of the morphology of the cervical region of the insect must yet remain a puzzle; but the musculature gives no evidence of the existence of a neck segment. On the other hand, the fold in the integument of the caterpillar between the neck (fig. 57 D, *Cv*) and the prothoracic tergum (T_2) is suggestive of being the true intersegmental line between the labial segment and the prothoracic segment, and several muscles of the prothorax have their anterior attachments upon it (D). If the primitive insect is conceived as a continuously segmented, vermiform animal, the neck, or any other secondary intersegmental area, must be a part of a primary segmental region. From the evidence at hand it seems more probable that the region of the insect neck belongs to the labial segment, than to an anterior part of the prothoracic segment.

ABBREVIATIONS USED ON THE FIGURES

Ab, abdomen.
obplp, abductor of palpus.
adplp, adductor of palpus.
Am, amnion.
AMR, anterior mesenteron rudiment.
An, anus.
Ant, antenna.
AntNv, antennal nerve.
Ao, aorta.
AP, apical plate.
AR, antennal ridge.
Arc, archicerebrum.
as, antennal suture.
AT, anterior arm of tentorium.
at, anterior tentorial pit.

BC, body cavity.
Bdy, body.
Blc, blastocoele.
Bld, blastoderm.
Bp, blastopore.
1Br, protocerebrum.
2Br, deutocerebrum.
3Br, tritocerebrum.
Bs, basisternum.
BuC, buccal cavity.

CA, corpus allatum.
Cd, cardo.
Cer, cercus.
Ch, chelicera.
Cho, chorion.
Clp, clypeus.
CoeCon, circumoesophageal connective.
Com, commissure.
3Com, commissure of tritocerebral lobes.
Con, connective.
cs, coronal suture.
ct, coxo-trochanteral joint.
Cth, cephalothorax.
Cv, neck, cervix.
cv, cervical sclerite.
Cx, coxa.

dap, dorsal apodemal plate of postoccipital ridge.
DMcl, dorsal longitudinal body muscle.
DNv, dorsal longitudinal nerve.
DT, dorsal arm of tentorium.
dt, attachment of dorsal tentorial arm to wall of cranium.

E, compound eye.
Ecd, ectoderm.
End, endoderm.
Endp, endopodite.
Ephy, epipharynx, epipharyngeal surface.
Eps, episternum.

ER, epistomal ridge.
es, epistomal suture.
Exp, exopodite.

F, femur.
fga, flexor of galea.
Fl, flagellum.
flc, flexor of lacinia.
flcc, cranial flexor of lacinia.
flcs, stipital flexor of lacinia.
For, foramen magnum, or "occipital" foramen.
Fr, frons.
fr, "adfrontal"
FrGng, frontal ganglion.
fs, frontal suture.
ft, femoro-tibial joint.

Ga, galea.
GC, gastric caecum.
Gc, gastrocoele, archenteron.
Gch, gnathochilarium.
Ge, gena.
Gl, glossa.
Gn, gnathal segments.
Gnc, gnathocephalon.
Gng, ganglion.
Gu, gula.

H, head.
Hphy, hypopharynx.
Hst, hypostoma.

I, tergal promotor muscle of an appendage.
I-VI, segments of the head.
Isg, intersegmental fold.

J, tergal remotor muscle of an appendage.

K, sternal promotor muscle of an appendage.
KL, ventral adductor muscles.
KLh, ventral adductors arising on hypopharynx.
KLk, ventral adductors united by ligament (*k*) forming "dumb-bell muscle."
KLt, ventral adductors arising on tentorium, or hypopharyngeal apodemes.

L, leg. *1L,* first leg. L_1, prothoracic leg.
sternal remotor muscle of an appendage.
LB, primitive limb base (coxa and subcoxa).
Lb, labium.
LbNv, labial nerve.
lbmcl, labial muscles.
Lc, lacinia.
Lm, labrum.
LNv, lateral stomodeal nerve.

Md, mabdible.
MdC, mandible cavity.
MdNv, mandibular nerve.
Ment, mesenteron.
Mps, mouth parts.
Msb, primary mesoblast.
Msc, mesenchyme.
Msd, mesoderm.
Mst, metastomium.
Mt, mentum.
Mth, mouth.
Mx, maxilla.
1Mx, first maxilla.
2Mx, second maxilla.
MxC, maxilla cavity.
MxNv, maxillary nerve.

NC, nerve cord.
NMb, neck membrane.
Nph, nephridium.

O, ocellus.
levator muscle of palpus, or of trochanter.
Oc, occiput.
OcR, occipital ridge.
ocs, occipital suture.
OE, oesophagus.
OeGng, oesophageal, or posterior median stomodeal ganglion.
OpL, optic lobe.
OR, ocular ridge.
os, ocular suture.

P, thoracic depressor muscle of trochanter.
PcR, posterior cranial ridge.
Pdc, pedicel.
Pdp, pedipalp.
Pge, postgena.
Pgl, paraglossa.
Ph, phragma.
Phy, pharynx.
PLGng, posterior lateral stomodeal ganglion.
Plp, palpus
Pnt, postantennal appendage.
Poc, postocciput, postoccipital rim of foramen magnum.
PoR, postoccipital ridge.
pos, postoccipital suture.
Pp, "pleuropodium," specialized appendage of first abdominal segment.
Ppd, parapodium.
Ppt, periproct.
PrC, preoral cavity.
Prc, protocephalon.
Prnt, preantennal appendage.
Proc, proctodeum.
Prst, peristomium.
Prtp, protopodite.
Pst, prostomium.
PT, posterior arm of tentorium.
pt, posterior tentorial pit.
Ptar, praetarsus.

Q, depressor muscle of palpus, or of trochanter.
Rd, posterior fold of tergum.

rh, retractor of hypopharynx.
RNv, recurrent nerve.
SA, sternal apophysis.
Scp, scape.
Scx, subcoxa.
Ser, serosa.
Set, seta, setae.
SgR, subgenal ridge.
sgs, subgenal suture.
SlD, salivary duct, silk gland duct.
SlO, opening of salivary duct.
Smt, submentum.
SoeGng, suboesophageal ganglion.
Sp, spiracle, 1*Sp*, first thoracic spiracle.
Spn, spina.
Spt, spinneret.
St, stipes.
Stom, stomodeum.

T, tergum.
depressor muscle of tibia.
Tar, tarsus.
Tb, tibia.
Th, thorax.
Tl, tentacle.
Tlp, telopodite.
Tnt, tentorium.
Tor, torma.
Tr, trochanter.

V, fifth head segment.
vap, ventral apodemal plate of postoccipital ridge.
VI, sixth head segment.
VMcl, ventral longitudinal body muscle.
VNC, ventral nerve cord.
VNv, ventral longitudinal nerve.
Vx, vertex.

REFERENCES

Attems, C. (1926). Myriapoda. Krumbach's *Handbuch der Zoologie*, 4. Berlin, Leipzig.

Balfour, F. M. (1880). Notes on the development of the Araneina. *Quart. Journ. Micr. Sci.*, n. s., **20**: 1-23, pls. 19-21.

——— (1883). The anatomy and development of Peripatus capensis. *Quart. Journ. Micr. Sci.*, n. s., **23**: 213-259, pls. 13-20.

Basch, S. (1865). Untersuchungen über das Skelet und die Muskeln des Kopfes von Termes flavipes (Kollar). *Zeit. wiss. Zool.*, **15**: 56-75, pl. 5.

Berlese, A. (1909). Gli Insetti, **1.** Milan.

——— (1910). Monografia dei Myrientomata. *Redia,* **6:** 1-182, pls. 1-17.

Bidder, G. P. (1927). The ancient history of sponges and animals. *Rep. British Assoc. Adv. Sci.,* **1927:** 58-71.

Börner, C. (1909). Neue Homologien zwischen Crustaceen and Hexopoden. Die Beissmandibel der Isekten und ihre phylogenetische Bedeutung. *Zool. Anz.,* **34:** 100-125, 9 figs.

——— (1921). Die Gleidmassen der Arthropoden. Lang's *Handbuch der wirbellosen Tiere,* 4: 649-694, 57 figs. Jena.

Borradaile, L. A. (1917). On the structure and functions of the mouth-parts of the palaemonid prawns. *Proc. Zool. Soc. London,* **1917:** 37-71, 51 figs.

Comstock, J. H., and Kochi, C. (1902). The skeleton of the head of insects. *Amer. Nat.,* **36:** 13-45, 29 figs.

Crampton, G. C. (1916). A comparative study of the maxillae of the Acridiidae (Oedipodinae and Tettiginae), Phasmidae and Phylliidae. *Psyche,* **23:** 83-87, pl. 11.

——— (1921). The sclerites of the head, and the mouth parts of certain immature and adult insects. *Ann. Ent. Soc. Amer.,* **14:** 65-103, pls. 2-8.

——— (1921a). The origin and homologies of the so-called "superlinguae" or "paraglossae" (paragnaths) of insects and related arthropods. *Psyche,* **28:** 84-92, pl. 5.

——— (1921b). The phylogenetic origin of the mandibles of insects and their arthropodan relatives. A contribution to the study of the evolution of Arthropoda. *Journ. New York Ent. Soc.,* **29:** 63-100, pls. 6-8.

——— (1922). A comparison of the first maxillae of apterygotan insects and Crustacea from the standpoint of phylogeny. *Proc. Ent. Soc. Washington,* **24:** 65-82, pls. 8, 9.

——— (1925). The external anatomy of the head and abdomen of the roach, Periplaneta americana. *Psyche,* **32:** 195-220, pls. 5-7.

——— (1928). The eulabium, mentum, submentum and gular region of insects. *Journ. Ent. and Zool.,* **21:** 1-15, 3 pls.

——— (1928a). The evolution of insects, chilopods, diplopods, Crustacea and other arthropods indicated by a study of the head capsule. *Canad. Ent.,* **60:** 129-141, pls. 8-12.

Croneberg, A. (1880). Ueber die Mundtheile der Arachniden. *Arch. Naturgesch.,* **46** (1): 285-300, pls. 14-16.

Daiber, Marie (1921). Crustacea. Lang's *Handbuch der Morphologie der wirbellosen Tiere,* 4: 9-252. Jena.

Eidmann, H. (1925). Vergleichend-anatomische Studien über die Pharynxmusculatur der Insekten. *Zool. Anz.,* **62:** 49-64.

Evans, A. M. (1921). On the structure and occurrence of maxillulae in the orders of insects. *Journ. Linn. Soc. Zool.,* **34:** 429-456, pl. 31.

Folsom, J. W. (1899). The anatomy and physiology of the mouth-parts of the collembolan, Orchesella cincta. *Bull. Mus. Comp. Zool.,* **35:** 7-39, pls. 1-4.

——— (1900). The development of the mouth-parts of Anurida maritima Guer. *Bull. Mus. Comp. Zool.,* **36:** 87-157, pls. 1-8.

Göldi, E. A. (1913). Die bisherige Anschauung bezuglich der Homologie der Insekten-Mundteile mit der Derivaten des Spaltfusses der Crustaceen und eine notwendig gewordene Modification. *Mitt. Schweiz. Entom. Gesells.*, **12:** 146-151, 1 fig.

Goodrich, E. S. (1898). On the relation of the arthropod head to the annelid prostomium. *Quart. Journ. Micr. Sci.*, n. s., **40:** 247-268, 12 figs.

de Gryse, J. J. (1915). Some modifications of the hypopharynx in lepidopterous larvae. *Proc. Ent. Soc. Washington*, **17:** 173-178, pls. 17-19.

Hansen, H. J. (1893). Zur Morphologie der Gliedmassen und Mundtheile bei Crustaceen und Insekten. *Zool. Anz.*, **16:** 193-198, 201-212.

Hatschek, B. (1888-'91). Lehrbuch der Zoologie (first to third parts). Jena.

Henriksen, K. L. (1926). The segmentation of the trilobite's head. *Saert. Medd. Dansk. geolog. For.*, **7:** 1-32, 27 figs.

Heymons, R. (1895). Die Embryonalentwickelung von Dermapteren und Orthopteren. 136 pp., 12 pls. Jena.

——— (1897). Entwicklungsgeschichtliche Untersuchungen an Lepisma saccharina L. *Zeit. wiss. Zool.*, **62:** 581-631, pls. 29, 30.

——— (1901). Die Entwicklungsgeschichte der Scolopender. *Zoologica. Orig.-Abhandl. Gesammt. Zool.*, **33**, 244 pp., 8 pls.

Hoffmann, R. W. (1911). Zur Kenntnis der Entwicklungsgeschichte der Collembolen. (Die Entwicklung der Mundwerkzeuge von Tomocerus plumbeus L.) *Zool. Anz.*, **37:** 353-377, 7 figs.

Holmgren, N. (1909). Termitenstudien. 1. Anatomische Untersuchungen. *Kungl. Svenska Vetenskapsakad. Handl.*, **44**, No. 3, 215 pp., 3 pls.

——— (1916). Zur vergleichenden Anatomie des Gehirns von Polychaeten, Onycophoren, Ziphosuren, Arachniden, Crustaceen, Myriopoden, und Insekten. *Kungl. Svenska Vetenskapsakad. Handl.*, **56**, No. 1, 303 pp., 12 pls.

Hussey, Priscilla B. (1926). Studies on the pleuropodia of Belostoma flumineum Say and Ranatra fusca Palisot de Beauvais. *Entomologica Americana*, **7:** 1-59, pls. 1-11.

Janet, C. (1899). Essai sur la constitution morphologique de la tête de l'insecte. 74 pp., 7 pls. Paris.

——— (1911). Constitution morphologique de la bouche de l'insecte. 35 pp., 2 pls. Limoges.

Jaworowski, A. (1891). Ueber die Extremitäten bei den Embryonen der Arachniden und Insecten. *Zool. Anz.*, **14:** 164-169, 173-176, 4 figs.

Korschelt, E. and Heider, K. (1895). Text-book of embryology of invertebrates. English transl., Vol. 1.

Kowalevsky, A. (1883). Embryogénie du Chiton polii (Philippi). *Ann. Mus. Hist. Nat. Marseille*, Zool., **1**, 46 pp., 8 pls.

Kowalevsky, A. and Marion, A. F. (1883). Documents pour l'histoire embryogénique des Alcyonaires. *Ann. Mus. Hist. Nat. Marseille*, Zool., **1**, 50 pp., 5 pls.

Lankester, E. R. (1881). Observations and reflections on the appendages and on the nervous system of Apus cancriformis. *Quart. Journ. Micr. Sci.*, n. s., **21:** 343-376, 3 figs.

MacGillivray, A. D. (1923). External insect-anatomy. Urbana, Ill.

Mangan, J. (1908). On the mouth-parts of some Blattidae. *Proc. R. Irish Acad.*, **27**, B: 1-10, pls. 1-3.

MEINERT, F. (1867). On the Campodeae, a family of Thysanura. English transl., *Ann. Mag. Nat. Hist.,* ser. 3, **20:** 361-378, 3 figs.

PATTEN, W. (1912). The evolution of the vertebrates and their kin. Philadelphia.

PRELL, H. (1913). Das Chitinskelett von Eosentomon. *Zoologica Orig.-Abhandl. Gesammt. Zool.,* **25,** 58 pp., 6 pls.

RAMME, W. (1913). Die Bedeutung des Proventriculus bei Coleopteren und Orthopteren. *Zool. Jahrb., Anat.,* **35:** 419-456, pls. 22-24.

REICHENBACH, H. (1877). Die Embryonalanlage und erste Entwicklung des Flusskrebses. *Zeit. wiss. Zool.,* **29:** 123-196, pls. 10-12.

RILEY, W. A. (1904). The embryological development of the skeleton of the head of Blatta. *Amer. Nat.,* **38:** 777-810, 12 figs.

SCHMIT-JENSEN, H. O. (1913). Homeotisk Regeneration af Antennen hos en Phasmide, Carausius (Dixippus) morosus. *Vidensk. Med. Dansk. naturh. Foren.,* **65:** 113-134. English transl., *Ann. Rep. Smithsonian Inst.* for 1914: 523-536, 7 figs.

SCHMIDT, W. (1915). Die Muskulature von Astacus fluviatilis (Potamobius astacus L.) *Zeit. wiss. Zool.,* **113:** 165-251, 26 figs.

SNODGRASS, R. E. (1927). The head and mouth parts of the cicada. *Proc. Ent. Soc. Wash.,* **29:** 1-16, pl. 1.

——— (1927a). Morphology and mechanism of the insect thorax. *Smithsonian Misc. Coll.,* **80,** No. 1, 108 pp., 44 figs.

STICKNEY, F. S. (1923). The head-capsule of Coleoptera. *Illinois Biol. Monographs,* **8,** No. 1. 51 pp., 26 pls.

VON STUMMER-TRAUNFELS, R. (1891). Vergleichende Untersuchungen über die Mundwerkzeuge der Thysanuren und Collembolen. *Sitz. Kaiserl. Akad. Wiss. Wien.,* math.-natur., **100,** Abth. I: 216-235, 2 pls.

UZEL, H. (1897). Vorlaufige Mitteilung über die Entwicklung der Thysanuren. *Zool. Anz.,* **20:** 125-132.

——— (1897a). Beiträge zur Entwicklungsgeschichte von Campodea staphylinus Westw. *Zool. Anz.,* **20:** 232-237.

WALTON, L. B. (1927). The polychaete ancestry of the insects. I. The external structure. *Amer. Nat.,* **61:** 226-250, 11 figs.

WHEELER, W. M. (1889). The embryology of Blatta germanica and Doryphora decimlineata. *Journ. Morph.,* **3:** 291-386, pls. 15-21.

——— (1893). A contribution to insect embryology. *Journ. Morph.,* **8:** 1-160, pls. 1-6.

WIESMANN, R. (1926). Zur Kenntnis der Anatomie und Entwicklungsgeschichte der Stabheuschrecke Carausius morosus Br. III. Entwicklung und Organogenese der Cölomblasen, pp. 123-328, 86 figs. Published by Zool.-vergl. anat. Inst. Univ. Zürich.

YUASA, H. (1920). The anatomy of the head and mouth-parts of Orthoptera and Euplexoptera. *Journ. Morph.,* **33:** 251-290, 9 pls.

ZOGRAF, N. (1883). Contributions to a knowledge of the embryological development of Geophilus ferrugineus L. K. and Geophilus proximus L. K. (in Russian). *Studies Lab. Zool. Mus. Moscow Univ.,* **2,** pt. 1, 77 pp., 108 figs.