FACTS AND THEORIES CONCERNING THE INSECT HEAD

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INTRODUCTION

We can feel fairly confident that the insect head has not changed since the first entomologist looked at it and described it. Yet a review of what has subsequently been written about the insect head shows that our ideas about its structure and segmental composition have changed very much. Morphology is an attempt to understand the significance of anatomical facts in their relation to one another, and to reconstruct from the known facts the evolutionary development by which the animal has come to be what it is today. Consequently as new facts come to light our morphology has to be revised to fit them, though it sometimes seems as if some morphologists find it easier to make the facts fit their theories. Ontogeny and anatomy are visible facts not always correctly observed; morphology and phylogeny are mental concepts that cannot be demonstrated. Hence, descriptions of facts by different observers may be inconsistent, and theories about them will vary according to our individual ways of thinking. The present paper, therefore, is a version of the insect head structure according to the facts now presumed to be known about it, and of morphological ideas according to the writer's personal way of interpreting the facts.

No new theory is here introduced, but critical attention will be given to some current theories about the segmentation of the insect head. It does not seem that we really need a theory on the subject, since the embryo gives us a very good idea about how the insect head has been evolved. Nevertheless, some morphologists contend that the embryo may be deceptive and itself needs to be interpreted, while some would even discard embryonic evidence as having no evolutionary value.

Elongate animals that habitually move in one direction necessarily have their principal sense organs at the forward end of the body.

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Since this end comes first in contact with whatever may serve as food, the mouth also is usually at or near the anterior end. Thus the anterior part of the animal has become structurally a head bearing the orienting sense organs and the mouth. All animals that have a stomach have a mouth; the mouth is as old as the blastopore. Yet it would seem that the primitive animals had no jaws or other special feeding organs associated with the mouth. In their later evolution the common need for such organs has been met in various ways. Among the coelenterates a circle of grasping tentacles was developed around the mouth. The earthworm ingests mud sucked in by a muscular pharynx, but some of its polychaete relatives developed teeth or jawlike organs in the pharynx, which became eversible as a proboscis. In the ancestral vertebrates two pairs of preexisting gill arches were converted into jaws, which are permanently within the mouth. The arthropods are unique in that their feeding organs have been fashioned from a pair or several pairs of legs behind the mouth. The forelimbs or fingers of some quadruped or biped vertebrates, of course, are often used for grasping food and putting it into the mouth, but they have never become modified for biting and chewing. The primitive arthropods, however, had so many legs they could well spare a few for purposes other than that of locomotion.

The adult head of an insect is a composite structure in which the segments of the feeding appendages have been intimately combined with a primitive head that was principally sensory in function. The insect head is thus superior in many ways to the head of any other animal in the number of functional units it contains. It is a cranial structure provided with sense organs of numerous kinds, and a feeding apparatus capable of being modified for feeding in various ways on different kinds of food. The sensory organs include simple and compound eyes, and a pair of antennae that are delicately sensitive to touch and odor, and, in some cases, to sound. The feeding organs in their simplest form serve for grasping, biting, and chewing, but all together they may be modified and combined in different ways to form a complex apparatus for sucking, or for piercing and sucking. The insects in general are thus enabled to diversify their diet and to get their food from many different sources. By contrast, the vertebrate animals, provided only with jaws for biting and chewing and a tongue for licking and lapping, are practically limited to one way of feeding. Moreover, to sample any substance for food the vertebrate must take it into its mouth, where the gustatory organs are located. The taste organs of insects, on the other hand, are outside the mouth, very

conveniently, in some cases, on the feet, so that an insect can select its appropriate food without first taking it into its mouth. Insects that have biting jaws masticate their food outside the mouth, and in all insects the duct of the salivary glands discharges extraorally, so that the saliva can mix with the food before ingestion.

From all this it is evident that a number of advanced ideas have been incorporated in the organization of the insect head that makes it a structure quite different from our own head, and gives the insects advantages that we vertebrates do not possess.

I. DEVELOPMENT AND EVOLUTION OF THE HEAD

The insects in their evolution, if we may rely on the embryo for historical information, did not get their modern head all at once. The head of the young embryo, particularly in the more generalized insect orders, is a large lobe at the anterior end of the body, usually itself bilobed (fig. 1 A, *emH*), on which are developed the eyes, the antennae, and the labrum. Following the embryonic head is the elongate body, which becomes segmented, and eventually on the segments appear the rudiments of paired appendages in the form of small lateroventral outgrowths. The mouth of the embryo (*Mth*) is formed ventrally at the base of the cephalic lobe by ingrowth of an ectodermal stomodaeum. In front of the mouth the labrum (*Lm*) projects usually as a small lobe on the underside of the head.

The cephalic lobe of the embryo is not limited to the insects; it is repeated in an early embryonic stage of so many of the arthropods as to suggest that it represents a primary head structure developed by the common ancestors of these animals. This theoretically primitive head might be called the archicephalon, but DuPorte (1953) has appropriately named its embryonic representative the *blastocephalon,* a term that need have no phylogenetic significance. Some writers have interpreted the embryonic head as representing the prostomium of the annelids, or of the ancestral arthropods; others contend that it includes primary body segments added to the prostomium. It contains the ocular and antennal nerve centers, which become the protocerebrum and deutocerebrum of the definitive brain. It is not to be supposed that the size of the embryonic blastocephalon means that the ancestral arthropods were big-headed animals. The blastocephalon probably is enlarged to give a precocious start to the development of the contained nerve centers.

The head of the adult insect includes at least three primarily body segments, and probably some remnant of a fourth segment, which

during embryonic development are added to the blastocephalon. The imaginal head, therefore, is a *syncephalon* and evidently is a product of evolution. The cephalized body segments include those of the mandibles (fig. 1 B, *Md*), the first maxillae (*1Mx*), and the second maxillae (*2Mx*), so that in the modern adult head the organs of feed-
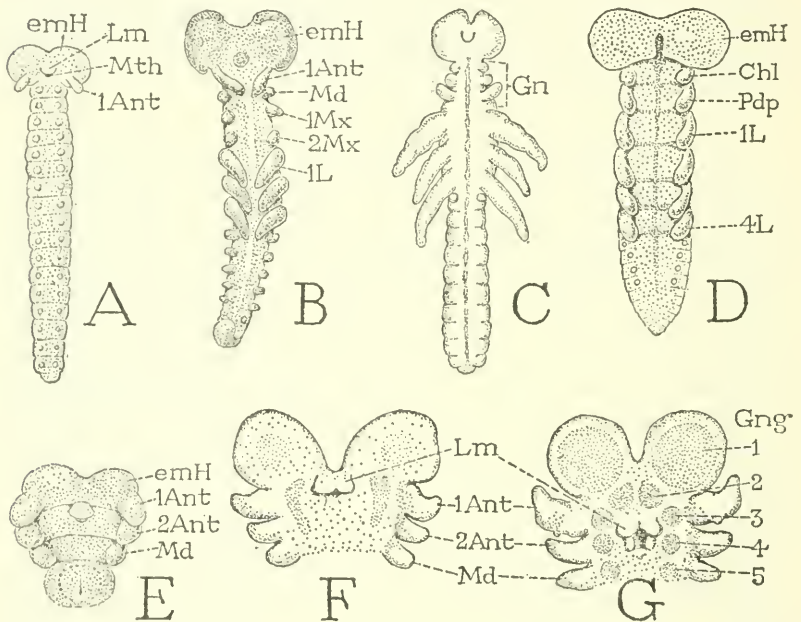

Fig. 1.—Examples of arthropod embryos, illustrating particularly the embryonic head (*emH*), or blastocephalon.

A, General structure of a young embryo, ventral, diagrammatic. B, Embryo of a mantid, *Paratenodera sinensis* (from Hagan, 1917). C, Embryo of a hemipteron *Ranatra fusca* (from Hussey, 1926) with distinct gnathal tagma (*Gn*) between head and thorax. D, Embryo of a spider, *Agelena labyrinthica* (from Balfour, 1880). E, Embryonic nauplius stage of a crustacean, *Leander serratus* (from Sollaud, 1923). F, Head region of an amphipod embryo, *Gammarus pulex pulex* (from Weygoldt, 1958). G, Later stage of same (from Weygoldt, 1958).

ing become closely associated with the mouth and the anterior sense organs.

There is no question that the three segments mentioned above, the so-called *gnathal segments,* become an intimate part of the definitive cranium in both the insects and the chilopods. It is commonly assumed that a premandibular, or first postoral body segment is also included in the adult head. The principal evidence of the existence of this segment, however, is the presence of a pair of premandibular

ganglia that become the tritocerebral lobes of the definitive insect brain. Otherwise the segment of these ganglia cannot be recognized in the composition of the adult cranium, and it is but little evident in the embryo, though embryonic vestiges of premandibular appendages have been observed in several insect species. A short region in the embryo of *Japyx* between the mouth and the mandibular segment is identified by Silvestri (1933) as the tritocerebral segment, since, though it bears no trace of appendages, it does contain rudiments of a pair of ganglia. Likewise in the embryo of a centipede, *Scolopendra,* Heymons (1901) regarded a space between the antennae and the mandibles as pertaining to the tritocerebral segment because of the presence of paired coelomic sacs and ganglion rudiments within it. In the symphylan *Hanseniella,* Tiegs (1940) says, "the pre-mandibular ectoderm curves round the stomodaeal opening, and forms much of the inferior surface of the clypeo-labrum," but he admits this has not been demonstrated in the insects.

The development of ganglia from the postoral ectoderm that become directly the tritocerebral lobes of the brain has been observed in insects by so many writers that there can be no question concerning the origin of the tritocerebral ganglia in the insects. These ganglia are always connected by a suboesophageal commissure, and give off the root nerves of the preoral frontal ganglion. The tritocerebral segment itself, however, appears to be practically eliminated. Eastham (1930), in his study of the embryogeny of *Pieris,* says that "when the premandibular ectoderm has given rise to the tritocerebral neuroblasts it loses its distinctness as a segment and is no longer distinguishable." However, a premandibular segment is present as a distinct somite in the crustacean embryo (fig. 1 E), bearing the rudiments of second antennal appendages (*2Ant*). A corresponding segment of the chelicerae is present in the embryo of Arachnida (D, *Chl*). It may be inferred, therefore, that a fully developed premandibular segment was present in the ancestors of all the mandibulate arthropods, and a corresponding cheliceral segment in the chelicerates.

The cephalic nervous system of the Crustacea appears to be more primitive than that of the insects and myriapods. In the crustaceans small premandibular ganglia are present as swellings on the nerve connectives between the brain and the mandibular ganglia. They are united by a suboesophageal commissure, and give off the root nerves of a small preoral "oesophageal" ganglion, which clearly is the frontal ganglion of the insects. In the branchiopods the nerves of the second antennae are given off from the connectives close to the ganglia. These ganglia on the connectives in the Crustacea thus appear to be the trito-

cerebral ganglia of the insects not united with the brain; they are called the tritocerebral ganglia by Henry (1948) and by Young (1959). In most of the Malacostraca, however, the second antennal nerves arise from the back of the brain, which is now termed the tritocerebrum. The terminology here is somewhat confusing, since in the insects the tritocerebral lobes of the brain are the premandibular ganglia themselves united with the primitive brain. In the higher crustaceans it would appear that only the nerves of the second antennae have been transposed to the brain, as depicted by Henry (1948) in a series of drawings of the anterior nervous system of an anostracan, a notostracan, an isopod, an amphipod, and a decapod.

Among the mandibulate arthropods the segmental composition of the definitive head is quite different in different groups. There is one case in which it appears that the embryonic blastocephalon alone becomes the functional head of the adult, and this is seen in the crustacean order Leptostraca. In *Nebalia bipes* a small head lobe (fig. 2 B) bearing the eyes, the first antennae, and ventrally the labrum projects freely from beneath the rostrum (A). The large second antennae (*2Ant*) arise close behind this head lobe but from the region of the gnathal segments, on which the carapace (*Cp*) has its attachment, and the antennal muscles here take their origins.

A distinct head lobe bearing the eyes and the first antennae is present likewise in the anostracan branchiopods, in the Syncarida, and in Malacostraca having a carapace, but in these forms the head always carries the second antennae in addition to the first antennae and the eyes. The best example of this type of head, termed the *protocephalon,* or by German writers the *Vorderkopf,* is seen in the Anostraca (fig. 2 C, *Prtc*). A similar but relatively smaller head unit is present in Anaspidacea and in the decapods (D), in the latter concealed beneath the rostrum. The muscles of the second antennae, however, as shown by Schmidt (1915) in *Astacus* and by Grobben (1919) in a stomatopod, retain their origins on the carapace as in the Leptostraca. In the anostracan (C) the antennal muscles appear to arise on the line between the protocephalon and the mandibular tergum (*II*), there being no evidence of a second antennal segment contained in the protocephalon.

The so-called protocephalon, therefore, appears to be the embryonic blastocephalon invaded by the second antennae, but it does not include the second antennal segment. Admittedly it seems an improbable assumption that a pair of appendages should migrate from one segment to another. The second antennae, however, are never developed on the embryonic blastocephalon, and pertain to the

first segment following. In a stomatopod the second antennae are membranously connected with the protocephalon, in some other crustaceans they arise just within the posterior sclerotized margin of the head, and in an amphipod they have almost come together on the midline of the face. Certainly in the amphipod the second antennae must have migrated from their own segment into the blastocephalic
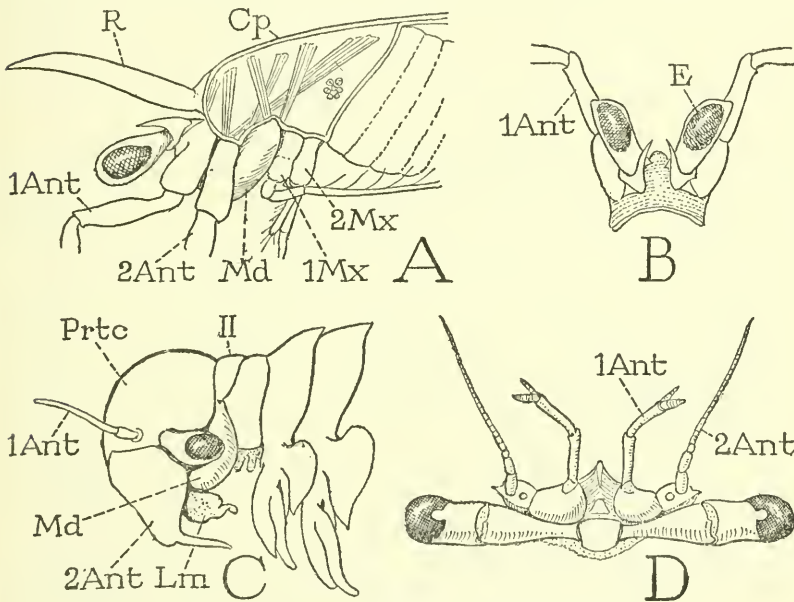

FIG. 2.—Examples of simple crustacean heads.

A, *Nebalia bipes,* anterior end of body, gnathal region opened on left side. B, Same, free head lobe, dorsal. C, *Eubranchipus vernalis,* protocephalon (*Prtc*) and anterior trunk segments, mandibular segment (*II*) not united with head. D, *Callinectes sapidus,* protocephalon, dorsal.

part of the head. The crustacean protocephalon, therefore, evidently represents the embryonic head lobe which has secondarily taken over the second antennae, while the segment of these appendages has been eliminated. The first persisting postoral segment (fig. 2 C, II) is that of the mandibles (*Md*).

If the cephalic lobe of the embryo represents the primitive arthropod head, or at least an early stage in the head evolution, it was merely a sensory outpost at the anterior end of the animal. At this period the wormlike lobopod progenitors of the arthropods and the ony-chophorans probably had no specific feeding organs outside the mouth. Some of the legs behind the mouth evidently served for grasping

food and bringing it to the mouth. These legs later become structurally modified to serve specifically as feeding organs. The labrum, when developed as a preoral lobe, must have served to stop the food passed forward where it could be taken into the mouth. The appendages utilized as feeding organs, however, differ in different arthropod groups.

In modern Onychophora the claws of the first pair of legs have been converted into a pair of flat "jaws" working in a vertical plane in front of the mouth. The ancient trilobites had no jaws or other special mouth parts, but the legs had spiny lobes on the inner sides of the coxae, by which probably food was grasped and passed forward to the mouth. In the ancestors of the chelicerate arthropods the first pair of postoral appendages became small pincerlike organs, the chelicerae, from which this group gets its name. In another early arthropod group the coxae of the second postoral legs were developed into a pair of jaws, the mandibles, working in the transverse plane, while the rest of the limb was reduced to a palpus and usually eliminated. Members of this group became the Mandibulata (crustaceans, myriapods, and insects) characterized by the possession of mandibles. The following pair of legs, or generally two pairs, were then modified as accessory feeding organs, known as the first and the second maxillae. In most of the Mandibulata the segments of these gnathal appendages were combined with the protocephalon in the adult head. In the anostracan and syncarid Crustacea, however, the gnathal segments remained as an independent group between the protocephalon and the thorax. In those crustaceans having a maxillary carapace united with the thorax, the gnathal segments were thereby anchored to the thorax, leaving the protocephalon as the functional head.

It is evident, therefore, that cephalization of the gnathal segments has taken place independently in different arthropod groups, since the tracheate mandibulates cannot be supposed to have been derived from any crustacean having the same type of syncephalon. Among the Crustacea the head of the isopods and amphipods most resembles the insect head, but it includes the segment and appendages of a fifth segment, that of the first maxillipeds. The head of the chilopods has the same segmental composition as that of the insects, as has also the symphylan head. In the pauropods, however, according to Tiegs (1947), only one maxillary segment is contained in the head, and probably the same is true of the diplopods.

Just when in the ancestry of the insects the gnathal appendages were modified for feeding and their segments added to the primitive head we cannot know, since all known fossil insects appear to have

modern heads. In some insect embryos, however, the thorax with its six legs (fig. 1 C) is already differentiated as the locomotor section of the body while the segments of the gnathal appendages (*Gn*) are still a small body section between the blastocephalon and the thorax. If we can trust the embryo, therefore, the insects may have been hexapods before the gnathal segments became a part of the head. In this respect the primitive insects must have resembled an anostracan crustacean (fig. 2 C).
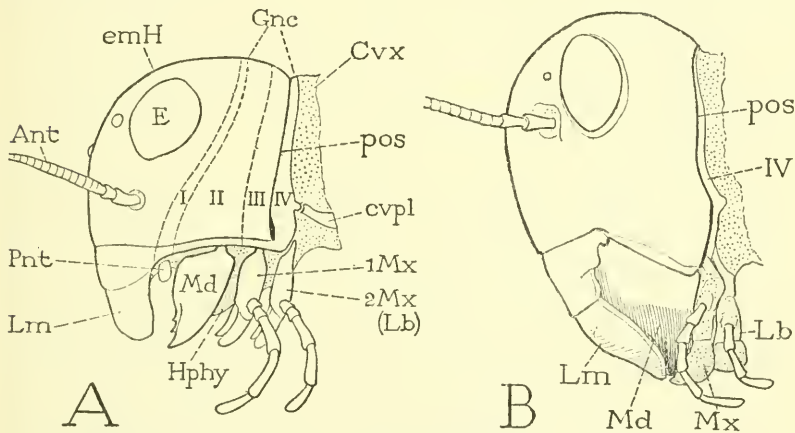

Fig. 3.—Structure and composition of the adult insect head.

A, Diagram of the head showing probable approximate regions derived from the embryonic blastocephalon (*emH*) and four postoral segments (*I-IV*). B, An adult head of generalized structure, intersegmental lines obliterated except for the persisting groove (*pos*) between third and fourth segments.

In conclusion, it appears that we may safely infer from embryonic evidence that the modern insect head has been evolved by the addition of four postoral segments (fig. 3 A) to the primary head (*emH*), represented in the embryo by the blastocephalon. This concept of the composition of the adult insect head is certainly suggested by the normal development of the embryo. It is somewhat disconcerting, therefore, when we read the results of experiments by Haget (1955) on the embryo of *Leptinotarsa*. Haget reports that when the gnathal segments of the embryo are destroyed, a complete cranium is reformed by the cephalic lobe alone. Very probably, however, this is a curious case of regeneration, and has no phylogenetic significance.

The present discussion and the diagram (fig. 3 A) allot no space to a theoretical "superlingual" segment between the premandibular and mandibular segments, the existence of which is generally discredited

by entomologists. Chaudonneret (1956), however, has revived this segment and its supposed homologue, the "paragnathal segment" in Crustacea. Accepting it as a real segment, he points out, explains the appendagelike nature of the paragnaths and superlinguae; but he admits the idea is only a hypothesis.

In the mature insect head (fig. 3 B) the cephalic components have been so completely united that, with the possible exception of a groove (*pos*) around the occipital foramen, no trace is left of the interseg-mental lines. It is suggested by Strenger (1942) that the oblitera-tion of the segmental limits is an adaptation to the need of a uniform cranial surface for muscle attachments, which have spread from one segmental area to another. The secondary development of ridge-forming grooves in the head cuticle is a device for strengthening the cranial walls.

That the groove around the occipital foramen, known as the *postoc-cipital sulcus* (figs. 3, *pos*), is a true intersegmental line is indicated by several structural features. First, it sets off behind it a narrow post-occipital flange on which the membranous neck is attached. Second, it forms a strong internal ridge that gives attachment to the muscles from the thorax that move the head, and this ridge appears to cor-respond with the intersegmental ridges of the segmental body plates on which are attached the intersegmental dorsal muscles of the trunk. Third, in a head of generalized type of structure, the maxillae are attached on the lower cranial margins *before* the postoccipital sulcus (fig. 3 A, *1Mx*), and the labium (*Lb*) is suspended from the postoc-cipital flange *behind* the sulcus. The postoccipital sulcus, therefore, appears to be the persisting intersegmental groove between the maxil-lary and labial segments of the head. The labial segment in Symphyla, according to Tiegs (1940), is the last body segment to be added to the head in embryonic development, and the groove before it is the only intersegmental line that remains on the adult head. The postoc-cipital sulcus is well said by Strenger (1952) to owe its origin to the union of segments, its retention in the adult to its functional im-portance.

Chaudonneret (1950), in his study of *Thermobia,* admits that the lower lateral parts of the postoccipital sulcus mark the intersegmen-tal line between the maxillary and labial segments. The dorsal part, however, he contends must be the line between the labial segment and the prothorax, because the prothoracic muscles are attached on its internal ridge. This interpretation creates a rather complicated situa-tion, but otherwise it must be assumed that the intersegmental groove between the labial segment and the prothorax has been lost some-

where in the neck, and that the dorsal muscle fibers attached on the head have become continuous through two consecutive segments. The true condition here is hard to understand, and probably has not yet been rightly explained, but it must be noted that muscles from both the head and the prothorax may be attached on the lateral neck sclerites.

Theories of head segmentation, including the disputed question of segments in the blastocephalon, will be discussed in a final section of this paper (p. 38).

II. GENERAL EXTERNAL STRUCTURE OF THE INSECT HEAD

The typical insect head (fig. 4 A) is a craniumlike capsule movably supported on the thorax by a short membranous neck. The head bears the eyes (E), the antennae (Ant), and the organs of feeding, or *mouth parts*. The last include an upper lip, or *labrum* (Lm), a pair of mandibles (Md), a pair of maxillae (Mx), a lower lip, or *labium* (B, Lb), and, enclosed between these parts (D), a median tonguelike lobe known as the *hypopharynx* ($Hphy$). On the back of the head (B) is a large opening (For) into the neck, analagous to the foramen magnum of the vertebrate skull, but generally called the *occipital foramen*. The only movable part of the head is the labrum, which is either articulated on the clypeal area (A, Clp) above it, or suspended from the latter by an ample membranous area, sometimes called the anteclypeus. The labrum is really an appendicular structure provided with four basal muscles, two of which are anterior and two posterior (C, 4), the latter attached on special sclerotizations (Tor) known as the *tormae*.

The cranial wall is continuously sclerotized, but it is usually marked by grooves that appear to divide it into specific areas, which the earlier entomologists regarded as sclerites united along "sutures." This concept, however, is now seen to be entirely erroneous, as will be shown in the next section, since the function of the grooves is to form internal strengthening ridges.

Enclosed by the mouth parts of insects such as the cockroach and others that feed on solid foods is a space (fig. 4 D, PrC) that serves for the intake of food and its mastication by the mandibles. This space, therefore, has been known as the "mouth cavity" or "buccal cavity" of the insect. However, the true mouth (Mth), or opening into the alimentary canal, lies in the inner wall of this cavity. The *preoral food cavity* (PrC), therefore, is merely a part of the exterior enclosed between the labrum in front, the labium behind,
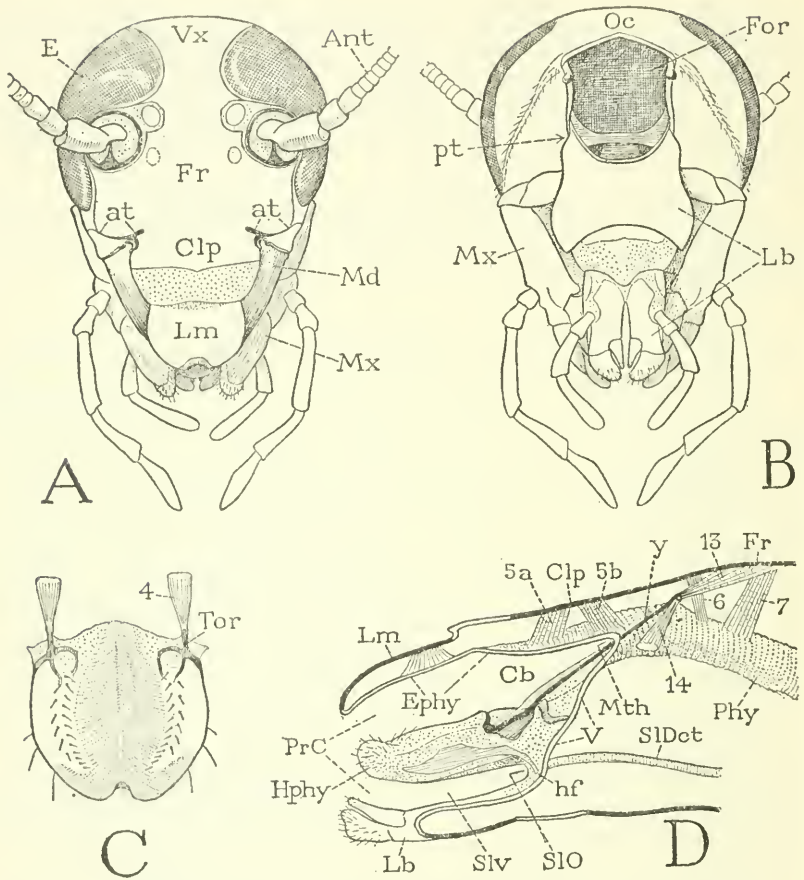
FIG. 4.—The head of a cockroach, *Periplaneta americana,* example of a generalized insect head.

A, Anterior. B, Posterior. C, Labrum, inner surface. D, Section through left side of ventral part of head, turned horizontally.

Ant, antenna; *at,* anterior tentorial pit; *Cb,* cibarium; *Clp,* clypeus; E, compound eye; *Ephy,* epipharyngeal surface; *For,* occipital foramen; *Fr,* frons; *hf,* fulcral point of hypopharynx; *Hphy,* hypopharynx; *Lb,* labium; *Lm,* labrum; *Md,* mandible; *Mth,* mouth; *Mx,* maxilla; *Oc,* occiput; *Phy,* pharynx; *PrC,* preoral cavity; *pt,* posterior tentorial pit; *SlDct,* salivary duct; *SlO,* salivary orifice; *Slv,* salivarium; *Tor,* torma; *V,* ventral wall of head; *Vx,* vertex; *y,* suspensory arm of hypopharynx.

Muscles: 4, posterior muscle of labrum; 5, dilators of cibarium; 6, 7, dilators of pharynx; 13, producer of hypopharynx; 14, reductor of hypopharynx.

and the mandibles and maxillae on the sides. Its inner wall (*V*) is the true ventral wall of the head, and from it arises the median hypopharynx (*Hphy*). The mouth (*Mth*) lies anterior to the base of the

hypopharynx, and behind the latter is the opening (*SlO*) of the salivary duct (*SlDct*).

The hypopharynx is suspended by a pair of lateral rods (*y*) in its wall that enter the head through the mouth angles and give attachment each to a pair of muscles (*13, 14*). It is supported on the labium by a pair of fulcral processes (*hf*) at the sides of the salivary orifice. Between the suspensory rods the front surface of the hypopharynx is somewhat depressed, and forms the floor of a pocket (*Cb*) of the preoral cavity immediately before the mouth. This pocket has long been called the "pharynx," regardless of the fact that it is outside the mouth. Since it serves the cockroach at least as a receptacle for masticated food to be swallowed, the pocket is now generally known as the *cibarium* (*Cb*). It becomes the sucking pump of liquid-feeding insects. Since, however, the cibarium was long ago called the "pharynx," we still use the name "epipharynx" for the anterior or dorsal wall of the preoral cavity (*Ephy*), and call the postoral lobe the "hypopharynx." No one has yet proposed suitable names for these parts. The true pharynx is an anterior part of the alimentary canal (D, *Phy*). The salivary passage between the hypopharynx and the labium (*Slv*) into which the salivary duct opens, may be termed the *salivarium*. It is thus seen that the important parts of the insect feeding apparatus lie entirely outside the mouth.

An internal skeletal structure known as the *tentorium* is present in the head of Thysanura and Pterygota. It consists of four apodemal arms, two anterior and two posterior. The posterior arms are usually joined to each other in a bridge through the back of the head, and in the Pterygota the anterior arms are united with the bridge. The points of ingrowth of the arms are marked by depressions in the head cuticle termed the *anterior* and the *posterior tentorial pits* (fig. 4 A, *at;* B, *pt*). The tentorium is highly variable in its structure and degree of development, as will be described in a special section (p. 32).

The position of the head relative to the body axis is variable. When the face is directed forward and the mouth parts hang downward (fig. 5 A) the head is said to be *hypognathous*. This should be the primitive head position since the feeding appendages are modified legs and thus have the same relative position as the thoracic legs. The hypognathous insects are mostly vegetarians that live in the open, feeding on the leaves, sap, or nectar of plants, though some are bloodsuckers.

On the other hand, in many insects the head is turned upward on the neck in line with the body axis (fig. 5 B), so that the mouth parts are directed forward, in which case the insect is said to be

prognathous. Since this condition is of common occurrence among insects of various orders, some writers have contended that the primitive insects were prognathous. This, however, seems improba-
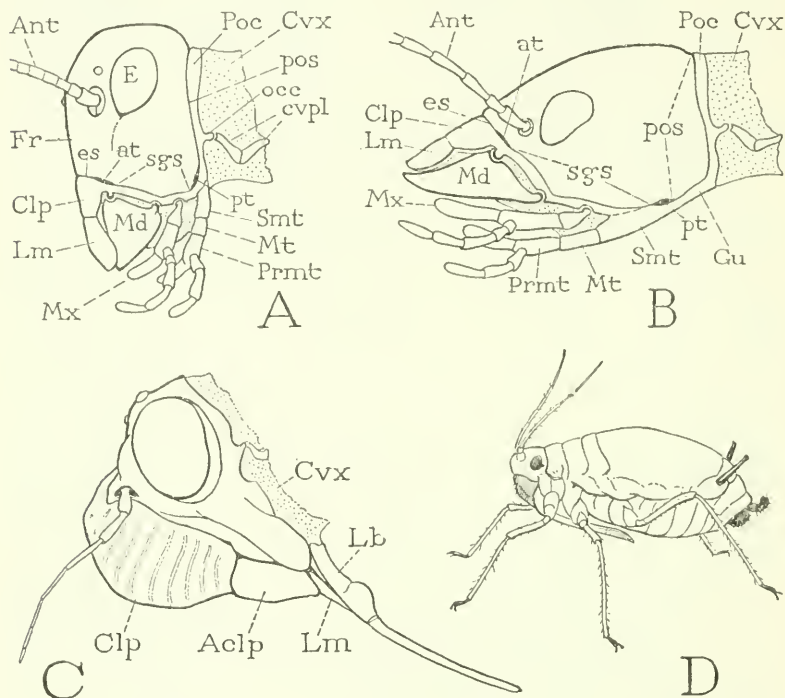

Fig. 5.—Different positions of the head or mouth parts relative to the body.

A, *Hypognathous* position of head, diagrammatic, head vertical, mouth parts hang downward. B, *Prognathous* position of head, diagrammatic, head horizontal, mouth parts anterior. C, *Auchenorhynchous* position of mouth parts, cicada, beak projects from below the neck. D, *Sternorhynchous* position of mouth parts, aphid, beak held against undersurface of thorax when not in use.

Aclp, anteclypeus; *cvpl*, cervical plates; *es*, epistomal sulcus; *Gu*, gula; *Mt*, mentum; *occ*, occipital condyle; *Poc*, postocciput; *pos*, postoccipital sulcus; *Prmt*, prementum; *sgs*, subgenal sulcus; *Smt*, submentum.
Other lettering as on figure 4.

ble, because prognathism involves extensive readjustments in the structure of the head, particularly of the undersurface, which are specializations, and are not the same in different prognathous insects. Furthermore, some insects are prognathous in the larval stage, and revert to the hypognathous condition in the adult. The structural changes correlated with prognathism will be fully discussed in a following section on the back of the head (p. 21). Prognathism,

as pointed out by Walker (1932), is particularly characteristic of carnivorous insects which chase their prey and capture it with their mandibles, of larvae that burrow with their mandibles, as wood-boring beetles, and generally of species that habitually rest on broad surfaces, or lurk in crevices.

Again, the mouth parts may be directed posteriorly, as seen in most Hemiptera (fig. 5 C, D). This condition might be termed opisthognathous, except for the fact that such insects have a beak instead of jaws. More literally, therefore, they are *opisthorhynchous*. Some, such as the cicada (C), in which the beak slopes posteriorly and downward apparently from the neck (*Cvx*) are termed *auchenorhynchous*. Others, such as the aphids (D) that hold the beak when not in use close against the undersurface of the body, are termed *sternorhynchous*. Since the beak of the aphid must be directed downward for feeding, it is evidently turned backward for convenience when not in use.

III. THE SO-CALLED "SUTURES" AND THE SURFACE AREAS OF THE HEAD

The cuticle of the insect head wall is marked by various impressed lines that divide the cranial surface into specific areas. The early entomologists, being acquainted with vertebrate anatomy, naturally saw in the areas of the insect head a likeness to the centers of ossification in the vertebrate skull united along sutures. It was a simple matter then to give names to the supposed sclerites and sutures of the insect cranium. We still use these same names, but we now realize that the sclerotization of the head cuticle is continuous, and that the so-called "sutures" are mostly lines where the cuticle has been infolded to form internal strengthening ridges or to give attachment to muscles. The external grooves, if we must have a Latin name for them, are better termed *sulci*. Strenger (1942, 1950, 1952) has strongly emphasized the functional significance of the cranial sulci (though she calls them Nähte) in that they form internal ridges for strengthening the head wall along lines of mechanical stress. The same applies to most of the "sutures" in other parts of the insect skeleton. Scientific terms should express facts rather than perpetuate errors. When errors become chronic, however, they are hard to eradicate.

There are, of course, always exceptions to any general rule. In some insects there is a true median suture on the under side of the head where the extended lateral walls have grown together. Also,

there is the so-called "epicranial suture," which is neither a suture nor a ridge-forming groove, but a pre-formed line of weakness where the head cuticle will split at ecdysis, though it may be retained on the adult head. These exceptional features will be fully discussed later.

The ridge-forming sulci of the head are variable and any of them may be absent. Since they are mechanical adaptations to resist strains, however, some of them are fairly constant in occurrence and position in response to general needs for strengthening the head wall. The surface areas separated by the sulci are given names for descriptive purposes, but in no case do they represent primitive head sclerites. Some named areas not demarked by sulci are defined on a topographical basis, and, where sulci are not present, the cranial sclerotization is continuous.

The groove perhaps most commonly present on the head is one that crosses the lower part of the face and forms a strong internal brace between the anterior articulation of the mandibles. This is the *epistomal sulcus* (fig. 6 A, *es*). Incidentally it separates a distal facial area, the *clypeus* (D, *Clp*), from the frontal area (*Fr*) above it, for which reason it is known also as the *frontoclypeal sulcus*. In some insects this sulcus is arched upward into the facial region. In others it is incomplete, and it may be absent even in insects with strong, jawlike mandibles, in which case the frontal and clypeal regions are continuous (fig. 4 A).

The head area known as the *frons* (fig. 6 D, *Fr*) can be defined only as the facial region between the compound eyes and the antennae, extending down to the clypeus. In the textbooks, however, it has commonly been defined as the area between the arms of the ecdysial cleavage line (C, *CL*). These lines, however, as will later be shown (fig. 7), are so variable in the position they take that they define no specific part of the face. Moreover, they are present in only a few adult insects (fig. 6 C). Dorsally the frons passes without interruption into the recurved top of the head known as the *vertex* (D, E, *Vx*). The vertex and the dorsal part of the frons are sometimes marked by a *midcranial sulcus* (A, *mcs*), and a pair of lateral *temporal sulci* (*ts*) convergent between the compound eyes.

Below each compound eye there is often a *subocular sulcus* (fig. 6 A, B, *sos*), which when present separates the frons from the lateral head wall termed the *gena* (D, E, *Ge*). The gena extends back to the postocciput (E, F, *Poc*). For descriptive purposes its posterior part is distinguished as the *postgena* (fig. 9 A, *Pge*). Since the mandibles and the maxillae are articulated on the lower margins of the genae,

these margins are commonly reinforced by submarginal internal ridges formed by a *subgenal sulcus* on each side of the head (fig. 6 A, B, *sgs*). This sulcus is generally continuous from the epistomal sulcus in front to the postoccipital sulcus (*pos*) behind, and sets off a
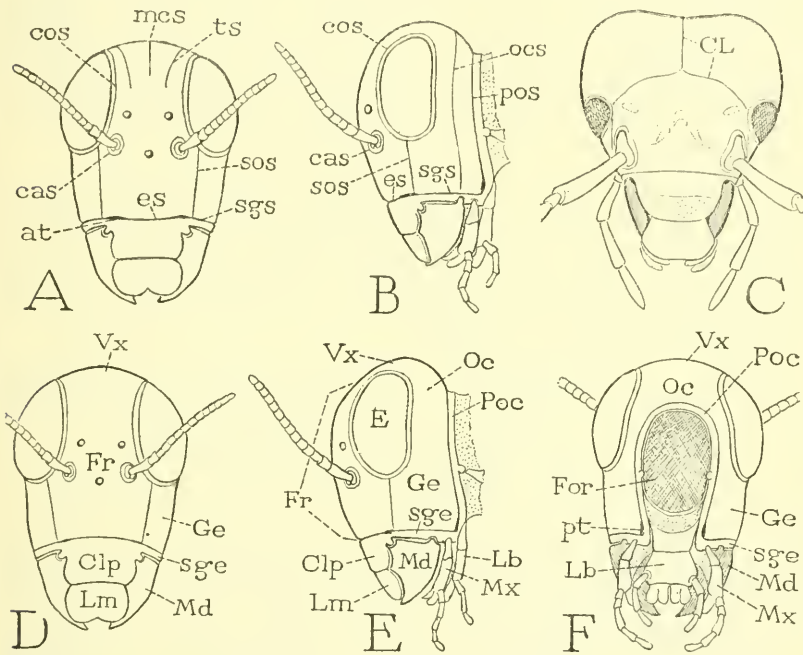
FIG. 6.—The common external sulci and defined areas of the adult insect head, diagrammatic except C.

A, B, The impressed lines, or sulci (generally called "sutures"). C, *Anisolabis maritima,* Dermaptera, example of ecdysial cleavage line (*CL*) retained on adult head. D, E, F, The commonly defined areas of the head.

Sulci on A, B: *cas,* circumantennal; *cos,* circumocular; *es,* epistomal; *mcs,* midcranial; *ocs,* occipital; *pos,* postoccipital; *sgs,* subgenal; *sos,* subocular; *ts,* temporal.

Head areas on D, E, F: *Clp,* clypeus; *Fr,* frons; *Ge,* gena; *Lm,* labrum; *Oc,* occiput; *Poc,* postocciput; *sge,* subgena; *Vx,* vertex.

Other lettering as on figure 4.

narrow marginal strip, the *subgena* (D, E, F, *sge*), from the main genal area above it. The part of the subgena over the mandible is distinguished as the *pleurostoma,* and that behind the mandible as the *hypostoma.* The corresponding parts of the subgenal sulcus are correspondingly termed *pleurostomal* and *hypostomal.* As will be seen later this distinction is only one of convenience for descriptive purposes. In some cases the subgena is obliterated by coincidence of

the subgenal ridge with the lower genal margin, and the ridge may be absent.

On the back of the head the postoccipital sulcus (fig. 6 B, *pos*), as already described, sets off the narrow postocciput (E, F, *Poc*) that arches over the occipital foramen (F, *For*). Present particularly among the Orthoptera, but not in all of them, is an *occipital sulcus* (B, *ocs*) that crosses the top of the head behind the compound eyes and extends downward on the sides. The area behind this sulcus is known as the occiput whether the sulcus is present or not (E, F, *Oc*).

Closely surrounding the compound eye is usually a *circumocular sulcus* (fig. 6 A, B, *cos*) that strengthens the cranial rim of the eye, and in some cases forms a deep internal flange protecting the inner part of the eye. Likewise the rim of the membranous antennal "socket" is generally strengthened by a surrounding ridge formed by a *circumantennal sulcus* (*cas*).

Finally, various linear grooves may occur on the head that have no relation to one another in different insects, being independent adaptations to some special need of the particular species.

There is one line on the head that must be given special attention. This is the so-called "epicranial suture," which is no suture at all and does not form an internal ridge. It is merely a pre-formed line of weakness where the cuticle will split at ecdysis, as has been shown by DuPorte (1946) and by the writer (1947). The line is properly, therefore, an *ecdysial cleavage line,* characteristic of immature insects, and retained in only a few adults. Yet it has long been described as an important structural feature of the insect head.

The cleavage line on the head has typically the form of an inverted Y when seen from in front (fig. 7 A, B, *CL*), with the stem on the top of the head and the arms spreading downward. At ecdysis the whole line breaks open (C, D, E), and the stem is then seen to be continuous from the median cleavage line on the back of the thorax (E).

The facial area between the arms of the cleavage line is often identified as the frons, but these lines do not consistently define any anatomical part of the head, since they vary greatly in their extent and position in different insects. Typically they extend down to the clypeus, but in some insects they turn laterally and at ecdysis the splits cut through the compound eyes (fig. 7 E), in others the arms of the Y end between the eyes and the antennae (A), in still others they go to the antennal sockets (B, G) or below them, and finally they may extend clear through the clypeus (D). The part of the head wall
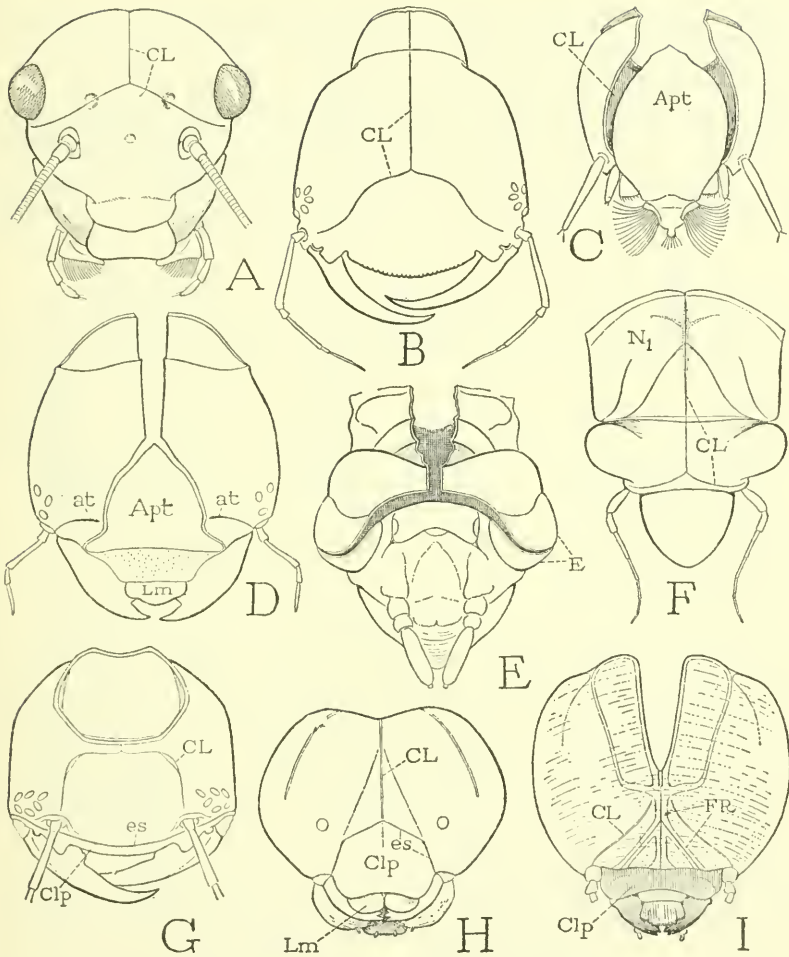
FIG. 7.—Examples of the ecdysial cleavage line on the nymphal and larval head.

A, Head of an ephemeropterous larva. B, *Dytiscus marginalis* larva, Coleoptera. C, *Anopheles farauti*, Culicidae; head exuviae. D, *Chauliodes* sp., Megaloptera, head exuviae. E, *Opisthogomphus morrisoni*, Odonata, exuviae of head and thorax. F, *Magicada septendecim*, Homoptera, nymphal head and prothorax. G, *Hydrophilus* sp., Coleoptera, head of larva. H, *Vespula* sp., Hymenoptera, head of larva. I, *Chalcophora* sp., Coleoptera-Buprestidae, head of larva.

cut out at ecdysis, therefore, cannot be identified as the frons; it may be termed the *cephalic apotome* (C, D, *Apt*). Moreover, the cleavage line does not always fork. In some hymenopterous larvae it goes straight down through the middle of the face (H), and at ecdysis the head cuticle spreads apart in a wide V-shaped opening. Many caterpillars, except at the last ecdysis, shed the head capsule

entire. The six common types of ecdysial cleavage in the head cuticle
are shown diagrammatically on figure 8.

The area between the arms of the cleavage line is sometimes rein-
forced by ridges that might easily be mistaken for the cleavage lines
when the latter are faintly marked. In a wood-boring buprestid beetle
larva, for example (fig. 7 I) an elaborate set of ridges (*FR*) in the
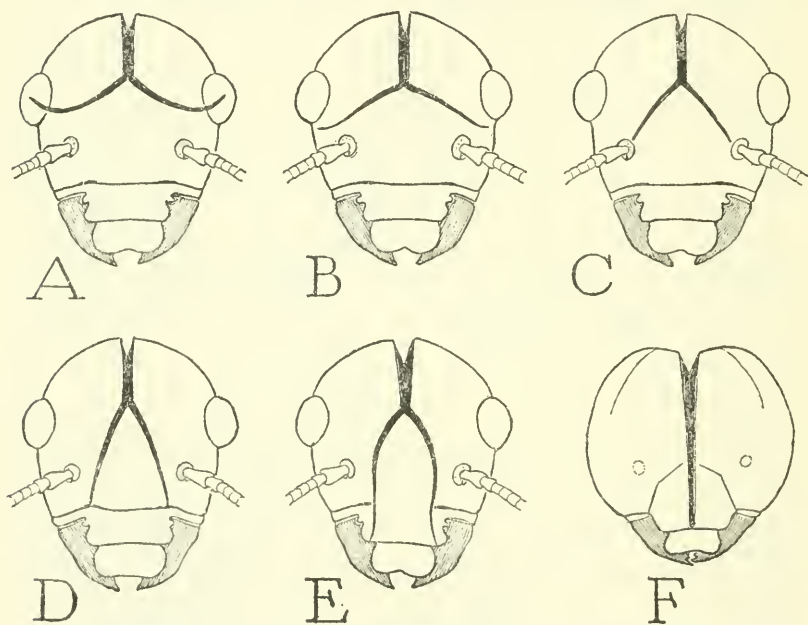otherwise weak cuticle of the head braces the clypeus for support

Fig. 8.—Diagrams of larval heads showing various positions of the ecdysial
splits along the arms of the cleavage line.

of the mandibles. The true cleavage lines (*CL*) lie laterad of these
ridges.

In a few insects, particularly in the Dermaptera and among the
Orthoptera, the cleavage line is retained on the head of the adult.
Usually it is a faint replica of the line on the nymphal head (fig. 6 C),
but in *Forficula* Strenger (1950) notes it forms an internal ridge,
which is particularly developed as a comb on the vertex. The reten-
tion of the cleavage line on the adult head might be explained as a
relict from times when the adult ancestors of the insects periodically
moulted and shed the cuticle, as do the adults of modern Thysanura
and most other arthropods. Adult moulting occurs now among the
winged insects only in the Ephemeroptera, and then but once at an

early stage. In the adult insect, as in the larva, ridge-forming grooves on the head sometimes resemble the cleavage line, and have been mistaken for the "epicranial suture." On the adult head of the water beetle *Hydrophilus* a Y-shaped groove exactly duplicates a typical cleavage line, but it is formed by a midcranial ridge that meets the ridge of the angulated epistomal sulcus.

IV. THE POSTERIOR HEAD STRUCTURE

The modifications of the insect head hardest to understand, and the most confusing to taxonomists, are those that affect the posterior surface, particularly when this surface becomes ventral in prognathous species.

The head of an acridid grasshopper is a good example of the primitive structure of the head and its position on the thorax, since the subgenal margins are approximately horizontal (fig. 6 E) and the occipital foramen occupies a large part of the posterior head surface (F). The labium hangs from the neck between the posterior tentorial pits. By contrast, in most of the higher orders of insects the foramen is much contracted by shortening from below (fig. 10). In a simple hypognathous head of this type (fig. 9 A) the hypostomal margins of the cranium have been drawn upward on the rear surface of the head. The hypostomal sulci (*hs*) extend to the tentorial pits (*pt*) as usual and become continuous with the postoccipital sulcus (*pos*) over the occipital foramen. The postocciput and the hypostomata thus form a continuous marginal band of the cranium. The labium still hangs from the neck approximately between the tentorial pits, but both the labium and the maxillae are now suspended from the back of the head. An example of this type of head structure is seen in the hymenopteron *Xyela* (B), except that the base of the labium has lost its association with the tentorial pits. Other less diagrammatic examples of the same essential structure are seen in the beetle larvae *Popillia* (C) and *Melandrya* (D), and in an adult Myrmelionid (E).

On the figures accompanying the following discussions it may seem inconsistent that the basal plate of the labium in some cases is labeled the postmentum (fig. 9 B, D, E, *Pmt*), in others the submentum (C, *Smt*). The labial sclerotization fundamentally consists of a *prementum* and a *postmentum,* but the postmentum is often subdivided into a *mentum* and a *submentum.* The basal plate, therefore, may be either a postmentum or a submentum. The prementum is always to be identified by the attachment on its base of a median

retractor muscle (E, *rprmt*). Incidentally it may be noted that the word *mentum,* meaning "chin," is incongruously applied to any part of the labium, or "lip," but we cannot stop here to reform this accepted terminology.
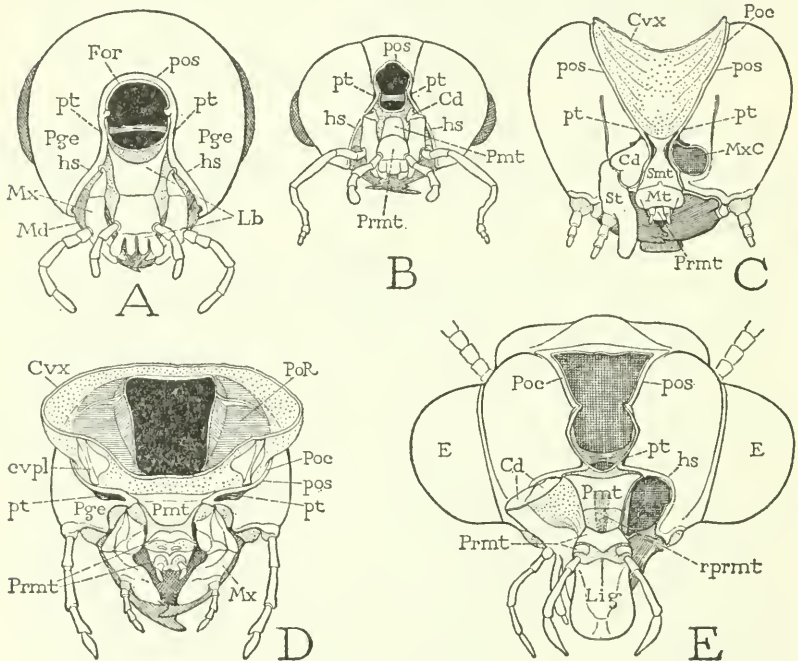

Fig. 9.—Examples of simple modifications of the relatively generalized structure (A) of the back of the head.

A, Posterior surface of a head having a relatively generalized structure associated with a centrally placed occipital foramen. B, *Xyela minor,* adult, Hymenoptera. C, *Melandrya,* larva, Coleoptera. D, *Popillia japonica,* larva, Coleoptera. E, A myrmelionid adult, Neuroptera.

A series of modifications in the posterior surface of the head, departing from the relatively generalized structure shown at A of figure 9, begins with the formation of a pair of opposing lobes of the hypostomata (fig. 10 B, *HL*) that intrude between the occipital foramen and the base of the labium. A union of these lobes then produces a *hypostomal bridge* (D, *HB*) ventral to the tentorial pits (*pt*). A suggestion of the lobes is seen on the head of *Pteronidea ribesii* (A), but they are fully developed on the head of a caterpillar (C). The bridge is a narrow bar in *Tabanus* (E); in other Diptera it becomes a wide plate, as in the asilid (F), and in a muscoid
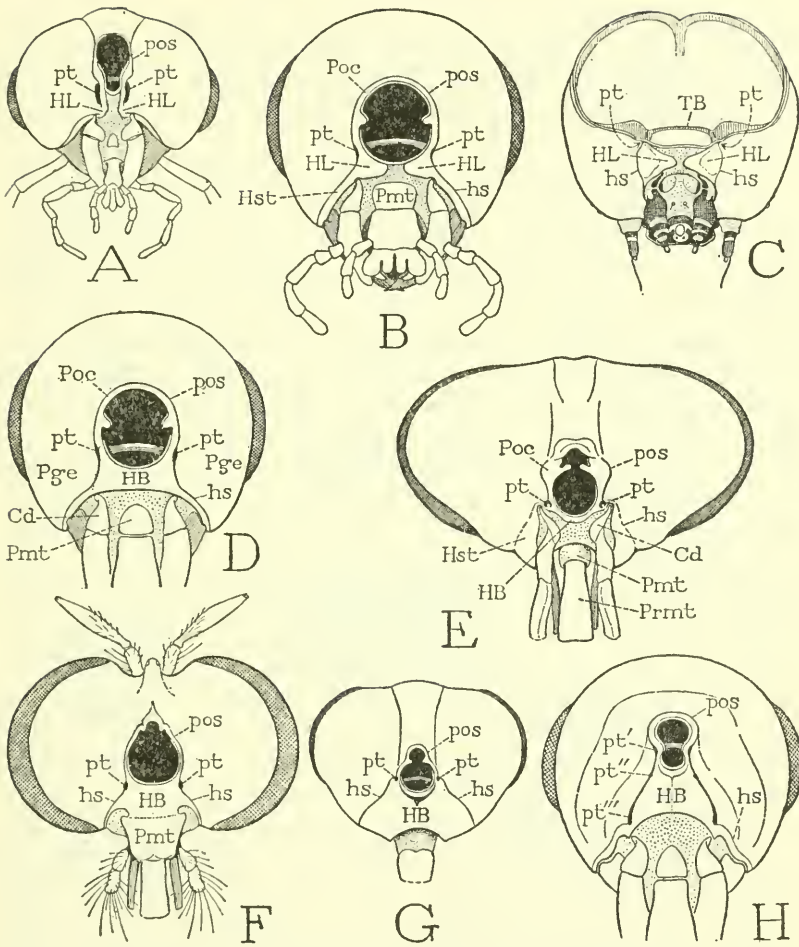
FIG. 10.—Formation of a hypostomal bridge between the occipital foramen and the labium.

A, *Pteronidea ribesii*, Hymenoptera, hypostomal lobes (*HL*) small. B, Diagram of hypostomal lobes enlarged. C, *Malacosoma americanus*, larva, Lepidoptera with hypostomal lobes. D, Diagram, hypostomal lobes united in a bridge (*HB*). E, *Tabanus sulcifrons*, Diptera, bridge narrow. F, *Deromyia discolor*, Diptera, bridge enlarged. G, *Calliphora* sp., Diptera, bridge still larger. *H*, *Pelicinus* sp., diagrammatic, Hymenoptera, bridge limited by the elongate posterior tentorial pits.

(G) it covers the whole ventral part of the head wall. Since the hypostomal sulci (D, *hs*) are continuous with the postoccipital sulcus (*pos*), the hypostomal bridge is continuous dorsally with the postocciput (*Poc*), and ventrally with the hypostomata.

An unusual condition is seen in the hymenopterons *Proctotrupes* and *Pelecinus* (fig. 10 H). The hypostomal bridge here appears to be limited laterally by the ventrally elongate posterior tentorial pits, from which are given off separately (*pt'*, *pt"*, *pt'''*) three parts of the tentorium.

By another line of modifications the posterior wall of the head becomes closed between the occipital foramen and the base of the labium by a bridge that unites the postgenae. This *postgenal bridge* has its inception in a pair of median lobes of the postgenae (fig. 11 A, F, *PgL*) below the tentorial pits, or distal to them in prognathous species. If a hypostomal bridge is already present (A, *HB*) it may be compressed between the postgenal lobes, as in the honey bee (B). A union of the lobes, as in the wasp (C), then establishes a postgenal bridge (*PgB*) between the foramen and the labium that has supplanted the hypostomal bridge. The bridge itself may then be lengthened downward (D) until it forms a large area on the back of the head, as seen in the hymenopteron *Pristocera* (E). The tentorial pits here retain their primary relation to the occipital foramen, but the labium becomes far removed from the pits by intervention of the lengthened postgenae. The postgenal bridge differs from the hypostomal bridge in that it has no connection with the postocciput (C, *Poc*), and is continuous only with the postgenae.

In other cases, particularly in nematocerous fly larvae in which there is no hypostomal bridge, a postgenal bridge may be formed by direct confluence of a pair of hypostomal lobes (fig. 11 F, *PgL*). In the same way the bridge becomes lengthened (G) between the foramen and the mouth parts. The median postgenal suture (D, *ms*) is usually retained as a groove, but it may be partly suppressed (G), and in others (H, I) it becomes entirely obliterated by complete union of the postgenae. The broad enclosure of the back of the head in *Notonecta* (H) and *Naucoris* (I) is evidently a postgenal bridge, since it is continuous with the postgenae and not with the postocciput.

In many insects, especially prognathous larval forms, the tentorial pits lie near the center of the posterior or under surface of the head (fig. 12, *pt*). Inasmuch as the pits retain their primitive association with the base of the labium (A, B) the condition here must therefore be interpreted as brought about by a lengthening and approximation of the postgenae *proximal* to the pits, since the lower ends of the postoccipital sulcus when present (A, *pos*) are continued to the pits. In some beetle larvae, as in the carabids (C, D), the postgenae are farther lengthened *distal* to the pits, and come together medially,
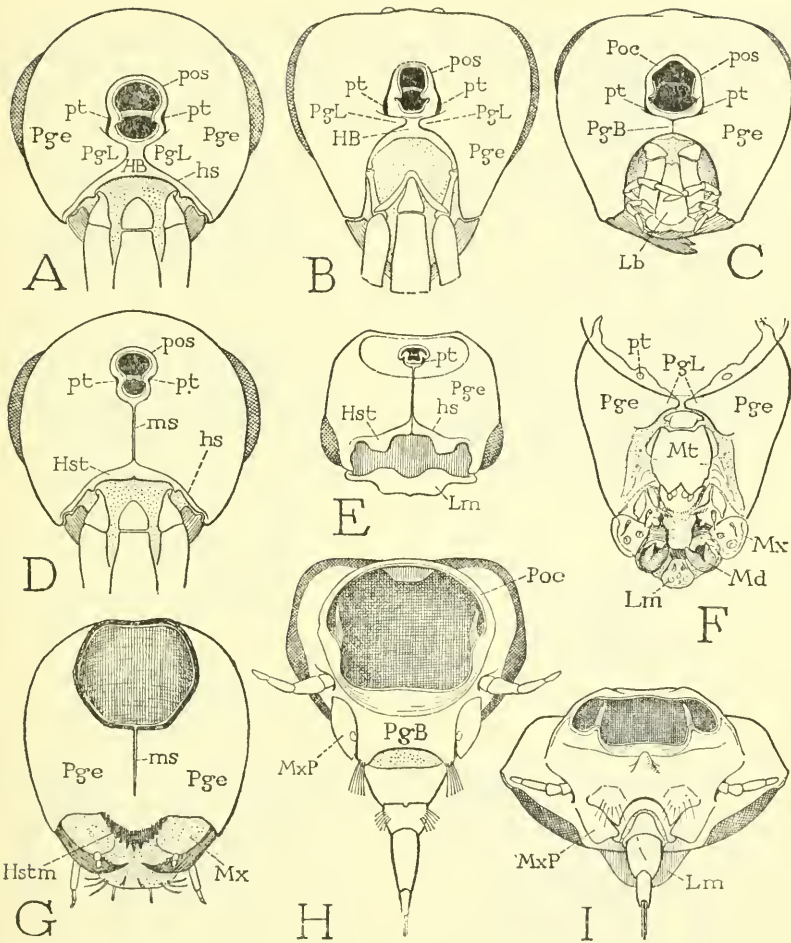
FIG. 11.—Formation of a postgenal bridge between the occipital foramen and the labium.

A, Postgenal lobes (*PgL*) encroaching on the hypostomal bridge (*HB*), diagrammatic. B, *Apis mellifera.* C, *Vespula maculata,* postgenal lobes united in a bridge (*PgB*). D, Postgenal bridge lengthened, diagrammatic. E, *Pristocera armifera,* Hymenoptera. F, *Olbiogaster* sp., a primitive dipterous larva with postgenital lobes not united (outline from Anthon, 1943). G, *Chironomus plumosus,* larva, Diptera, postgenal suture (*ms*) partly suppressed. *H, Notonecta variabilis,* Homoptera, postgenal bridge entire. *I, Naucoris cimicoides,* Homoptera.

almost (C) or entirely (D) suppressing the submentum (*Smt*) between them. In this case the head has been lengthened in both directions relative to the pits.

Finally, we may start again with a fairly generalized head struc-

ture, such as that of the larva of *Silpha* (fig. 13 A), and trace the evolution of a head plate known as the *gula*. In the silphid larva the basal plate of the labium (*Smt*) is attached on the cranial margins
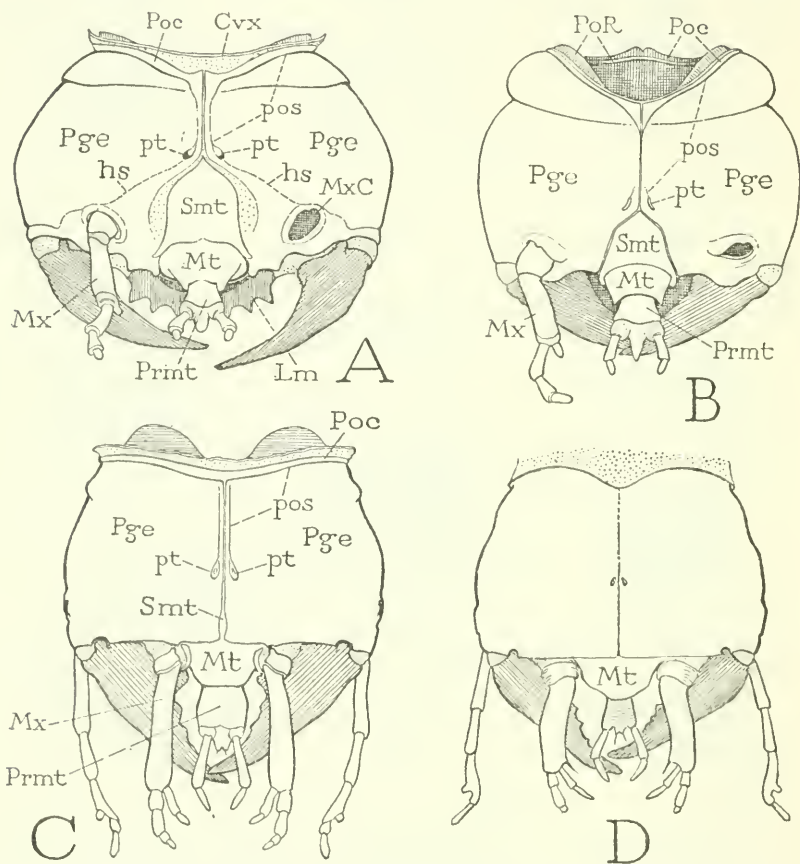
Fig. 12.—Coleopterous larvae with postgenae lengthened and united proximal to the tentorial pits (A, B), or also distal to the pits (C, D).

A, *Thinopinus pictus*, Staphylinidae. B, *Staphylinus* sp. C, *Scarites* sp., Carabidae. D, *Eufcronia stygica*, Carabidae.

immediately distal to the tentorial pits (*pt*). Proximal to it the lower ends of the postocciput are united in a median sclerotization (*Gu*) in the ventral wall of the neck. This is the beginning of the gula. In many beetles, both larval and adult (B, C) and in some other insects (D), the gula becomes lengthened distally accompanying a lengthening of the postgenae proximal to the tentorial pits. As the gula enlarges, the tentorial pits (B, C, D, *pt*) maintain their primary
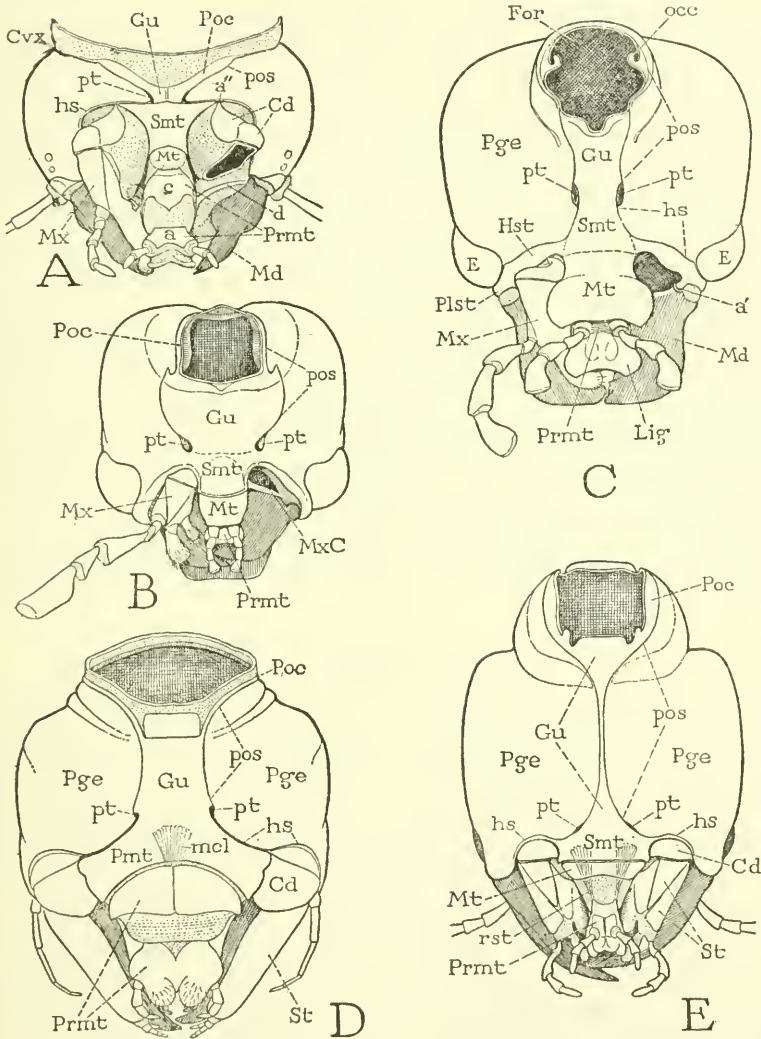
FIG. 13.—Formation of the gula. Tentorial pits (*pt*) at base of labium, under surface of head lengthened proximal to pits.

A, *Silpha* sp., larva, Coleoptera, gula (*Gu*) a ventral sclerotization of the neck, proximal to the tentorial pits (*pt*). B, *Melandrya striata*, adult, Coleoptera, gula enlarged. C, *Epicauta, marginata*, adult, Coleoptera, gula elongate, united with base of labium (*Smt*). D, *Corydalus cornutus*, larva, Megaloptera. E, *Staphylinus cinnamopterus*, adult, Coleoptera, gula compressed between post-genae (*Pge*).

relations to the base of the labium, but the gula and the labium become sclerotically continuous. The labiogular plate has been termed the "gulamentum," but the labial part involved is either the post-

mentum or the submentum, according to the number of subdivisions in the labium. The original line of confluence between the gula and the labium must be between the tentorial pits, as shown by the silphid larva (A). The gula is usually continuous proximally with the postocciput, since actually it is merely a ventral sclerotic union of the lower ends of the postocciput. The general tendency of the postgenae to come together ventrally on the prognathous head now in some cases reduces the gula to a narrow median strip between the postgenal margins (E, *Gu*), and may proceed so far as to eliminate the gula. The line of union between the postgenae is commonly termed the "gular suture," though really it is a *postgenal suture*. DuPorte in a recent paper (1960) gives a good comparative account of the gula.

A most unusual gular condition is present in the head of a soldier termite (fig. 18 A). The long gula is here limited by lateral grooves (*pt*) continuous from the postoccipital sulcus (*pos*), which superficially appear to be parts of the latter as in other insects. In the termite, however, these grooves are the greatly drawn-out tentorial pits, from which is inflected internally the long, tentlike tentorial bridge (C, *TB*).

V. THE ANTENNAE

The antennae are segmented appendages of the head characteristic of the trilobites and of all the mandibulate arthropods except the Protura, but they are absent in the chelicerates. They are freely movable by basal muscles arising in the head, and ordinarily have only a sensory function, though in the nauplius larvae of Crustacea they serve temporarily for swimming, and in the barnacles for attachment. The antennae are always of postocular origin in the embryo, and receive their innervation from the second, or deutocerebral, brain centers. Being sensory organs, however, principally tactile and olfactory, they commonly assume a facial position in postembryonic stages, where they more effectively serve as feelers or as odor receptors.

An antennal *segment,* as a leg segment, must be defined as a section of the appendage individually musculated by muscles inserted on its base, arising in the segment proximal to it, except that the muscles of the basal segment arise in the head. Segments, however, are often divided into nonmusculated subsegments, which are thus not to be confused with true segments, though they are usually counted as such in enumerating the parts of an appendage.

Among the hexapods the antennae are of two types of structure,

differing in the number of segments they contain. In the ento-
gnathous apterygotes (Collembola and Diplura) the antennae vary
in length, but are fully segmented and each segment is individually
musculated (fig. 14 A). This type of antenna is characteristic also
of the chilopods, diplopods, pauropods, symphylans, and some crus-
taceans such as the copepods and ostracods. It therefore represents
the primitive arthropod antenna. In the Thysanura and Pterygota,
on the other hand, there are muscles only in the basal segment (B)
insterted on the small second segment (*Pdc*). The rest of the antenna
in these insects is a *flagellum* (*Fl*) of various lengths subdivided into
nonmusculated annuli.

Imms (1939), who first pointed out this difference in the arthropod
antennae, distinguished the two kinds as "segmented" and "annu-
lated" antennae, but he held that the flagellar annuli are primitive
segments which have lost their muscles. The two antennal types have
been described also as "musculated" and "nonmusculated," and made
a basis for dividing the mandibulate arthropods into Myocerata and
Amyocerata (Remington, 1955). However, since the number of
annuli in the flagellum varies from one to many, it is evident that the
flagellum represents a single segment variously subdivided. This in-
terpretation follows also from Imms' (1940) observation that the
growth of a fully segmented antenna proceeds by division of the
apical segment, while growth of the flagellum results from subdivi-
sion of the basal annulus, or sometimes by division of the inter-
mediate annuli. The same thing has been noted by other writers.
Lhoste (1942), for example, shows that the antennal flagellum of
Forficula increases during growth from 8 to 14 annuli by division of
the basal annulus. The thysanuran-pterygote antenna, therefore, has
not more than three true segments, the third of which is usually a
multiannulate flagellum. The first and second segments are muscu-
lated.

The typical thysanuran and pterygote antenna (fig. 14 B) is a
slender elongate appendage composed of three parts, a basal stalk,
or *scape* (*Scp*), a small middle piece, or *pedicel* (*Pdc*), and an annu-
lated *flagellum* (*Fl*) of variable length. The scape is set on a small
membranous area of the head wall with a reinforced margin, and is
pivoted, usually from below, on a marginal point, the *antennifer* (*af*).
The antenna as a whole is thus freely movable in all directions, and
is provided with basal muscles inserted on the scape. The antennal
muscles in some insect larvae and in other arthropods arise on the
head wall, but in most insects they arise on the dorsal arms of the
tentorium where these arms make contact with the head wall.

The only intrinsic muscles of the antenna are those in the scape inserted on the base of the pedicel. The flagellum is thus moved by the pedicel muscles, and the pedicel might therefore appear to be a
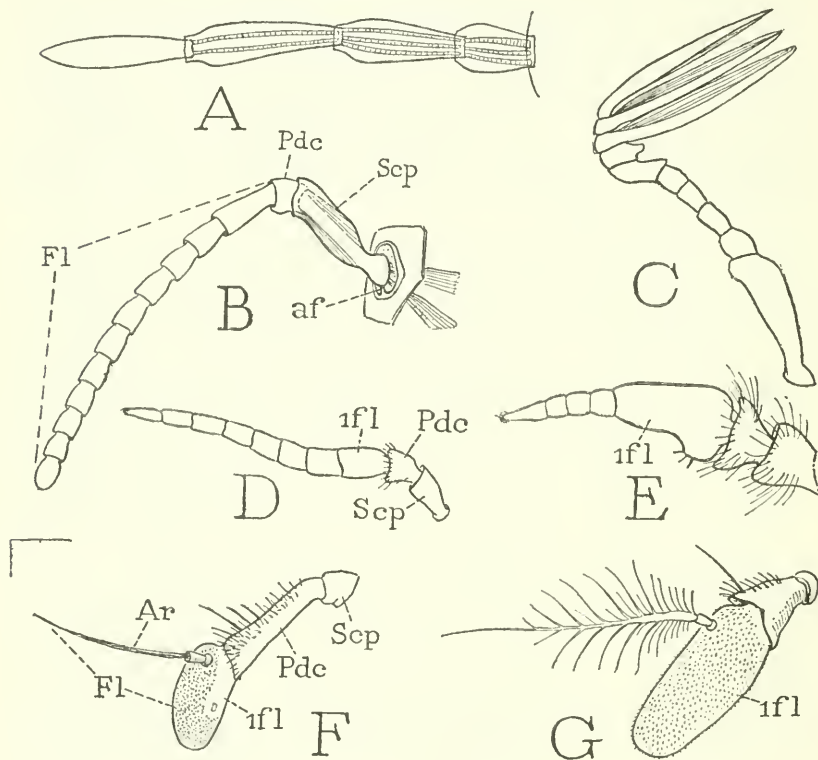
FIG. 14.—Types of adult insect antennae.

A, *Isotoma palustris,* Collembola (adapted from Imms, 1939). B, Diagram of typical thysanuran-pterygote antenna. C, *Leucopelea albescens,* lamellicorn beetle. D, *Xyloma tenthredinoides,* Diptera-Xylomyidae. E, *Tabanus affinis,* Diptera-Tabanidae. F, *Archytas apicifer,* Diptera-Tachinidae. G, *Sarcophaga bullata,* Diptera-Sarcophagidae.

basal annulus of the flagellum. It is noted by Imms (1940), however, that growth of the antenna never involves subdivision of the pedicel. The pedicel contains an elaborate sense organ known as the organ of Johnston, so it is probable that the pedicel itself is a segment from which the muscles of the flagellar segment have been eliminated. The flagellar units vary in size from short annuli to long sections. If we are not too particular about hybridizing words, they may be

termed *flagellomeres,* as suggested by Imms (1940), but they are
not "antennal segments."

Among adult Pterygota the antennae take on a great variety of
forms, produced chiefly by modifications of the flagellum, or by a
differentiation of its annuli. Typically the flagellum is slender and
cylindrical (fig. 14 B), but it may be club shaped, or extended as a
long, tapering filament. In the lamellicorn beetles some of the distal
annuli are produced at right angles to the shaft as overlapping leaf-
like plates (C). A particularly specialized type of antenna is that of
the muscoid flies. The first annulus of the flagellum has a tendency to
be larger than the others (B, D). The enlargement is much exagger-
ated in a tabanid fly (E, *1fl*). In the muscoid antenna (F, G) this
flagellomere becomes a large oval lobe (*1fl*) borne on the pedicel, and
the rest of the flagellum is reduced to an *arista* (*Ar*) consisting of two
small basal annuli, and a long, tapering, simple or usually branched
distal shaft.

The antennae of holometabolous larvae are often so different from
those of the adult that they appear to be special larval organs rather
than developmental stages of the adult antennae. It is principally
among the Neuroptera that the larval antennae resemble adult an-
tennae in having a multiannulate flagellum (fig. 15 A), though in
many species they are reduced to three small units. Antennae
of four or five units occur in the Megaloptera (B) and in Can-
tharidae, Dytiscidae, and Hydrophilidae among the Coleoptera, but
the antennae of most larval beetles are very small, three-segmented
organs (F). Similarly the antennae of lepidopterous larvae (D)
have only three segments, the third being a mere apical lobe on the
second (E). Among the nematocerous Diptera the larval antennae
are always short, but are variable. In *Chironomus* the antenna (C)
may have three short apical units on a long base, but in the mosquito
larva the very small antenna (G) is undivided. In the higher
Hymenoptera the larval antennae are represented by only slight
swellings or mere discs of the head wall. In the muscoid fly larva the
antennae are entirely eliminated externally, being formed in a pair
of long sacs from the frontal region of the head that extend back
into the thorax.

When the larval antenna is greatly reduced in size, the succeeding
pupal antenna develops either beneath the cuticle of the head, or
more commonly in a pocket of the epidermis beneath the larval an-
tenna, usually with its tip in the latter. In the mosquito, for ex-
ample, as shown by Imms (1908) the pupal antenna is formed in a
deep pocket of the head, but has no connection with the larval organ.

On emergence of the pupa the new antenna (fig. 15 H) is five times the length of the larval antenna (G), and is distinctly differentiated into scape, pedicel, and a multiannulate flagellum, but its surface is entirely devoid of hairs. During the pupal stage, the epidermis con-
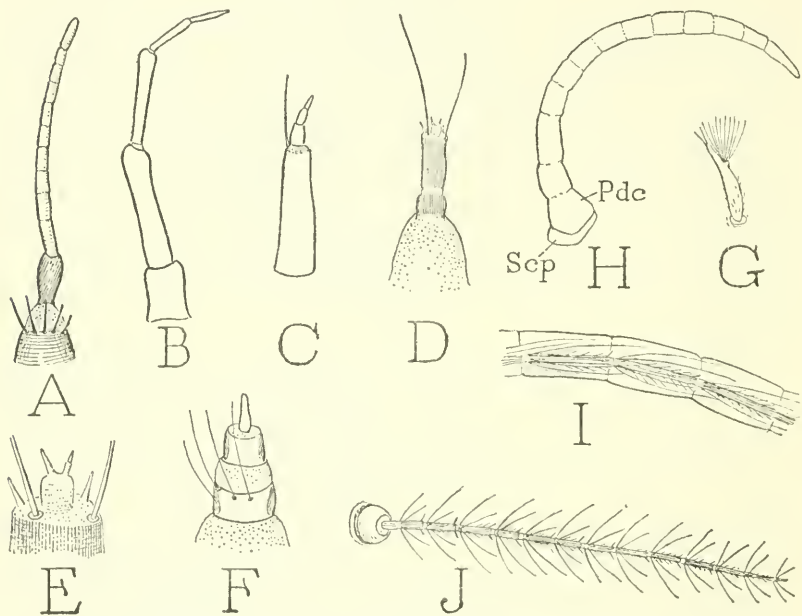
FIG. 15.—Examples of larval antennae, and developmental stages of a mosquito antenna.

A, *Palpares* sp., Neuroptera-Myrmelionidae. B, *Corydalus cornutus*, Megaloptera. C, *Chironomus plumosus*, Diptera-Chironomidae. D, *Bombyx mori*, silkworm. E, Same, apical part of antenna. F, *Trogoderma* sp., Coleoptera-Dermestidae. G, *Culex* sp., mosquito, left antenna of larva, dorsal. H, Same, pupal antenna, same magnification as G. I, Same, part of pupal antenna with adult antenna formed inside the cuticle. J, Same, adult female antenna, same magnification as G and H.

tracts to a slender, jointed shaft within the cuticle (I), having all the hairs and bristles of the adult antenna (J).

VI. THE TENTORIUM

The tentorium is an internal cuticular framework of the head of ectognathous insects formed by ingrowth and union of four apodemal arms from the exoskeleton. Two of the arms are anterior, and two posterior. The posterior arms arise at the lower ends of the postoccipital sulcus and usually unite with each other to form a transverse

bridge through the back of the head. The anterior arms are variable in their points of origin, but they project posteriorly through the head and in pterygote insects unite with the posterior bridge. The term *tentorium,* meaning a "tent," seems curiously inappropriate for this structure, but in some of the lower insects the arms are united in a central plate, which might suggest a canopy supported on four stays. Though the tentorium varies much in form and degree of development, the name has become fixed in entomological nomenclature. The points of ingrowth of the four tentorial arms are marked externally on the head by depressions known as the *anterior* and *posterior tentorial pits.* Functionally the tentorium gives attachment to the ventral muscles of the mouth parts, and, when strongly developed, probably serves to brace the lower edges of the cranial walls.

To understand the origin and evolution of the insect tentorium we must revert to the myriapods. A comparable structure is not present in the entognathous hexapods—Protura, Collembola, and Diplura. In the chilopods a pair of plates in the ventral head wall lies before the mandibles between the lateral cranial margins and the hypopharynx (fig. 16 A, B, *hF*). These plates are the *kommandibulares Gerüst* of German writers, but since their relation to the hypopharynx is more intimate than that with the mandibles, they may be termed the *hypopharyngeal fulturae.* From each plate is given off at the side of the hypopharynx an apodemal arm (*Ap*) that extends posteriorly within the head. In *Scutigera* (A) the inner ends of the arms support a wide sheet of soft tissue (*Lg*) from which are given off the ventral muscles (*mcls*) of the mouth parts. In *Lithobius* (B) the apodemal arms are connected merely by a membranous bridge (*Lg*), and most of the muscles have been taken over by the apodemes. In the diplopods premandibular ventral sclerites are present, but the apodemes are less developed than in the chilopods. In Symphyla (C) the supporting sclerites are absent; the long muscle-bearing apodemes (*Ap*) arise at the base of the hypopharynx, and have no connection with each other.

When we turn now to the Thysanura it is seen that in the Machilidae (fig. 16 D) two long apodemes (*AT*) arise ventrally mesad of the mandibles and extend posteriorly and dorsally in the head. In addition, however, a transverse bar (*TB*) forms a bridge through the back of the head. Here, therefore, are the elements of the pterygote tentorium, and there can be little doubt that the anterior arms (*AT*) are homologues of the ventral head apodemes of the chilopods and symphylans. In the Lepismatidae the structure becomes more elaborate by the union of the anterior arms in a broad
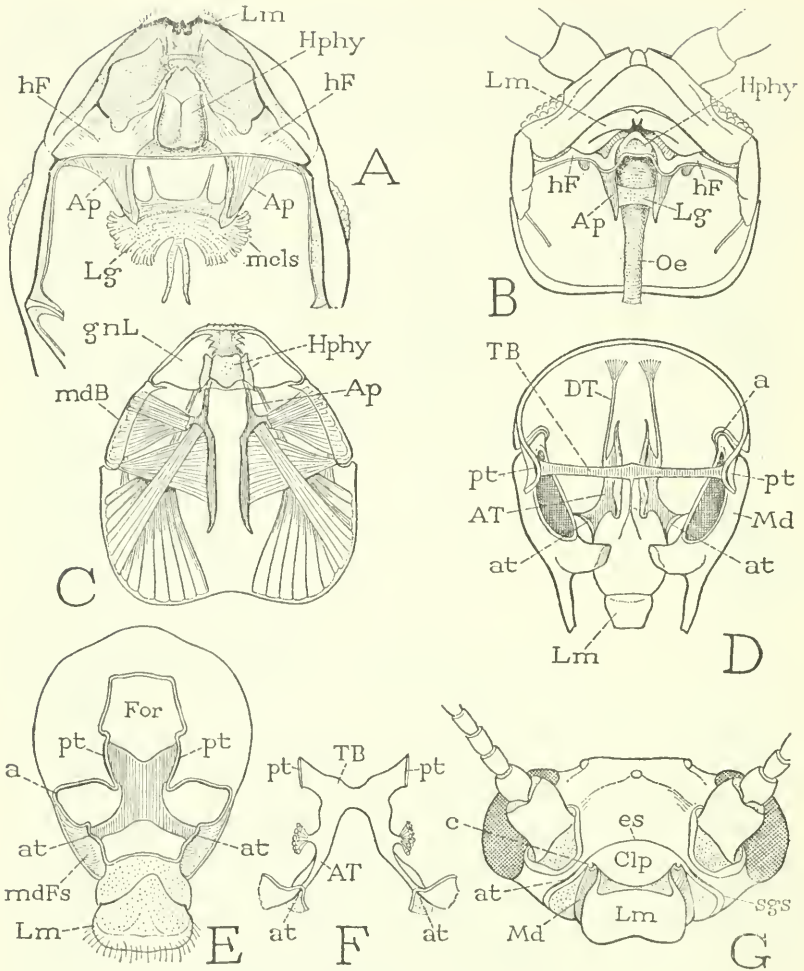
FIG. 16.—Evolution of the tentorium.

A, *Scutigera* sp., Chilopoda, ventral surface of anterior part of head with mouth parts removed, showing hypopharyngeal fulturae (*hF*) and their apodemes (*Ap*). B, *Lithobius* sp., Chilopoda, same view of head as A. C, *Scutigerella immaculata*, Symphyla, optical section of head behind mandibles. D, *Neso-machilis maoricus*, Thysanura, posterior view of interior of head, showing separate anterior tentorial arms (*AT*) and tentorial bridge (*TB*). E, *Isonychia* sp., Ephemeroptera, larval head, posterior, showing tentorium. F, *Anax junius*, Odonata, larval tentorium, dorsal. G, *Strophopteryx fasciatus,* Odonata, larval head, anterior.

central plate, which rests against the posterior bridge, or overlaps it, but does not unite with it. In both thysanuran families slender dorsal arms (D, *DT*) branch from the anterior arms and are attached on the cranial wall by small groups of muscle fibers.

From this primitive condition of the tentorium in Thysanura it is only a step to that in the Pterygota in which the anterior arms have become united with the posterior bridge (fig. 17 A). In an ephemerid larva (fig. 16 E) the anterior arms still arise on the ventral surface of the head, but in a lateral position from pits (*at*) just mesad of the mandibles, which lie in lateral fossae of the head wall (*mdFs*) but have no articulation on the clypeus. In Odonata, Plecoptera, Dermaptera, and some Orthoptera, however, the roots of the anterior
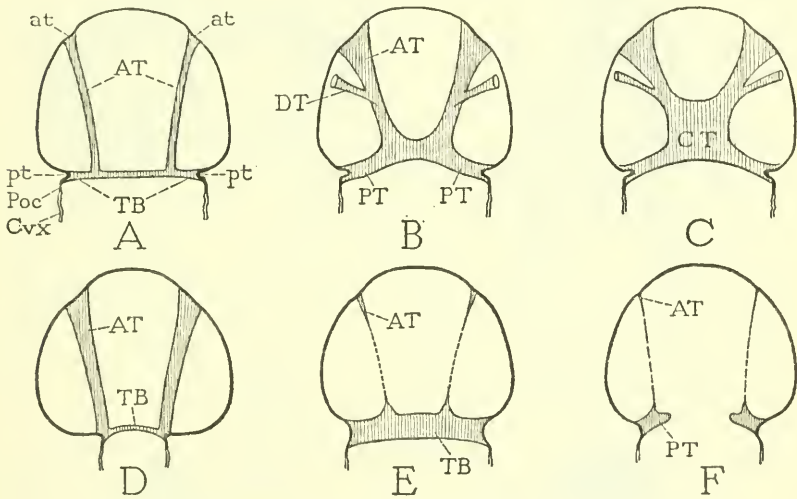
FIG. 17.—Variations of the pterygote tentorium, diagrammatic.

at, anterior tentorial pit; *AT,* anterior tentorial arm; *Cvx,* neck (cervix); *CT,* corpotentorium; *DT,* dorsal tentorial arm; *Poc,* postocciput; *pt,* posterior tentorial pit; *PT,* posterior tentorial arm; *TB,* tentorial bridge (united posterior arms).

arms (F, *AT*) are in the subgenal sulci *laterad* of the mandibles (G, *sgs*). Evidently the arms have been transposed to this position before the mandibles acquired their anterior articulations (*c*) on the clypeus. Finally in most higher insects these arms have taken a facial position on the head by migration into the epistomal sulcus, in which their pits are usually located (fig. 6 A, *at*). It may seem surprising that fixed structures should migrate in this apparent manner from a ventral to a lateral and finally to a facial position. It is hardly to be supposed, however, that the anterior tentorial arms, carrying always the same muscles, have been independently redeveloped in each of their several positions.

Once established as a unified composite structure (fig. 17 B), the pterygote tentorium undergoes numerous variations. In the orthop-

teroid and other lower insects with strong biting and chewing mandibles, the tentorium may be strengthened by the development of a central plate, the "corpotentorium," in which the four arms are united (C, *CT*). In the higher insects the tentorium retains more of the primitive form (A), but the relative thickness of the arms is variable. The anterior arms may form a pair of strong longitudi-
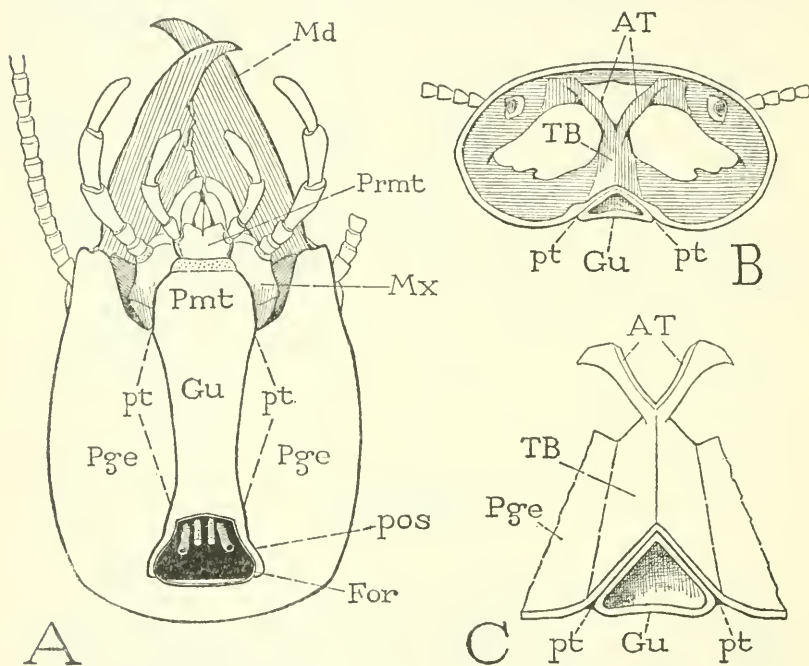
FIG. 18.—Head and tentorium of a soldier termite, *Termopsis* sp.

A, Undersurface of head, posterior tentorial pits (*pt*) greatly elongate. B, Cross section of head, posterior, showing tentorium in place. C, The tentorium, dorsal, tentorial bridge (*TB*) elongate.

nal bars through the head, connected by a narrow bridge (D), or the bridge may be strongly developed and the anterior arms reduced to mere threads (E). The bridge is nearly always retained in some form, but the component arms may be reduced to mere stubs giving attachment to very attenuated anterior arms (F). An unusual modification of the tentorium is seen in the soldier caste of a termite (fig. 18 B, C). The bridge (*TB*) is here drawn out longitudinally into a long, inverted trough, from the anterior end of which diverge the short anterior arms (*AT*). On the undersurface of the head (A) it is seen that the "pits" (*pt*) are long grooves at the sides of the gula.

The entognathous hexapods—Protura, Collembola, and Diplura—have no head structure corresponding anatomically with the tentorium of the ectognathous insects. When the cleared head of one of these forms is examined by transmitted light there is seen a pair of long skeletal arms (fig. 19 B, S) extending posteriorly from the hypo-
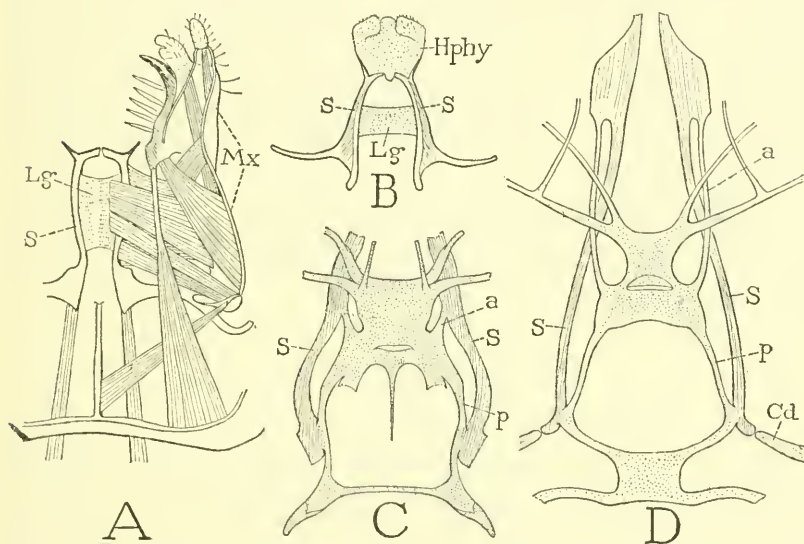
FIG. 19.—Noncuticular endosternal structures in the head of Diplura and Collembola.

A, *Heterojapyx gallardi*, Diplura, sternal arms of head (S) connected by internal arched ligament (Lg), giving attachment to maxillary muscles, dorsal. B, *Campodea* sp., Diplura, hypopharynx and sternal arms with internal ligamentous bridge, dorsal. C, *Onychiurus fimentarius*, Collembola, sternal arms of head and endosternal superstructure with supports (a, p) on sternal arms (adapted from Denis, 1928). D, *Anurida maritima*, Collembola, same parts as at C (from Denis, 1928).

pharynx. These arms have been mistaken for tentorial apodemes, but actually they are sternal arms contained in the walls of the gnathal pouches, as shown by the writer (1951) and by Tuxen (1952). Folsom (1900) described their superficial origin in the embryo of Collembola. The sclerites clearly pertain to the maxillary segment since the cardines are articulated on their posterior ends (D, *Cd*).

In the Diplura (fig. 19 A, B) an internal membranous bridge (Lg) is arched upward between the sternal arms and gives attachment to ventral muscles of the maxillae (A). In the Collembola an elaborate superstructure is built upon the sternal arms (C, D), consisting of

transverse anterior and posterior parts variously developed in differ-
ent species and supported by props (a, p) on the sternal arms. This
structure has been fully described by Denis (1928), who called it a
"tentorium." However, it has no resemblance to either the thysanuran
or the pterygote tentorium, and moreover, as shown by Tuxen (1952),
it is a mesodermal tissue soluble in caustics and lactic acid. This
collembolan "tentorium" is thus more nearly comparable to the endo-
sternum of Chelicerata. Since it gives attachment to the ventral
muscles of the mouth parts, it functionally serves the same purpose
as the chelicerate endosternum and the tentorium of the ectognathous
insects. In Protura there is no corresponding superstructure on the
maxillary sternal arms.

Incidentally it may be observed that, in the possession of a cuticu-
lar tentorium, the ectognathous hexapods appear to be more closely
related to the chilopods and symphylans than to the entognathous
hexapods.

VII. THEORETICAL CONSIDERATIONS

The accumulation of knowledge does more than simply add new
facts to old ones; it changes our ideas about the accepted facts. This
is particularly true in our study of insect anatomy and our morpho-
logical interpretation of the structural facts. We have now become
involved in interpretations and theories that never occurred to the
earlier entomologists, and hence they could write their descriptions
of insect anatomy in a more direct and simple manner than we can.
Furthermore, since morphology (the science of form) is a product
of our brains, and our brains are not standardized, we are now per-
plexed with opposing theories that purport to explain the same set of
facts in different ways. Our descriptive matter, therefore, has be-
come so mixed with argumentation that the facts often seem less im-
portant than the theoretical discussions about them. In particular,
some modern theories of insect head segmentation are so opposed to
all our former ideas as to make the insect head seem so complex that
it is hard to visualize how it ever got that way in its evolution. Even
the embryo appears to be unable to recapitulate its evolution accord-
ing to these theories, and adheres to old-fashioned ways of develop-
ment. Of course, it is always possible that theories do not represent
the truth. So in this study of the insect head we must critically re-
examine not only the evidence, but also inductions made even from
correctly observed facts.

The following discussions will be concerned with theoretical ques-

tions concerning the nature of the labrum, segmentation of the embryonic head lobe, and the homology of the antennae with trunk limbs.

The writer formerly expressed the opinion that the labrum is the anatomical anterior pole of the arthropod and that its ventral position in some cases is secondary. Dahl (1956), however, has vigorously opposed this view as turning "the available evidence upsidedown." On the other hand, Young (1959) reasserts that "the labrum is the anterior end of the arthropod." It is true, of course, that the labrum is formed on the underside of the embryonic head lobe, but in a variable position, and the fact remains that the anteriormost nerve endings are on the labrum regardless of its position.

Since the labrum in so many cases is developed from a pair of lobes that unite, and in the adult insect is often emarginate medially, some writers have expressed the opinion that the labrum represents a pair of appendages. The insect labrum is consistently provided with two pairs of antagonistic extrinsic muscles from the frons, and usually with internal compressor muscles. Judging from the anatomical literature on the arthropods it would appear that musculature of the labrum is exceptional. In the shrimp *Penaeus setiferus,* however, Young (1959) finds a highly complex labral musculature including 12 bilateral pairs of intrinsic muscles running in all directions through the labrum, and two pairs of extrinsic muscles inserted on its base. Because of its inconsistency the labral musculature gives no clue to the nature of the labrum, but the labral innervation has been invoked by several writers as evidence that the labrum is not the simple lobe of the head it appears to be. The labrum is said to be innervated from the postoral tritocerebral ganglia of the brain, but this fact has led to two quite different theories as to the morphological status of the labrum. (As will be shown, the nerves in question really go from the labrum to the tritocerebral ganglia.)

One interpretation of the labrum, the Ferris-Henry theory, is correlated with a comparative study of the annulate nervous system by Miss Henry (1948). She starts with the assumed principle that nerves are always confined to the segment of their ganglionic origin. Then she logically contends that, since the labrum is innervated from the tritocerebral ganglia, it must be the segment of these ganglia, and is therefore the *first segment* of the arthropod head, equivalent to the prostomium of the earthworm. Though in no modern arthropod,

embryonic or adult, do the tritocerebral ganglia lie in the labrum, ganglia themselves are free to move, and hence, according to Henry, the tritocerebral ganglia have been displaced posteriorly and have united with the back of the brain in the adult insect. The tritocerebral segment is commonly said to be the segment of the second antennae in the Crustacea. Henry, however, after establishing the labrum as the tritocerebral segment, asserts that this cannot be true, because, as she correctly observes, "these antennae do not occur on the labrum."

All this interpretation is so at variance with well-known and long-described facts of arthropod embryogeny and comparative anatomy that it creates a suspicion there is something wrong about it. It appears to be supported on a conviction (Henry, 1947) that the arthropods have been evolved from polychaete annelids, and that the eversible proboscis of these worms is the introverted first two trunk segments. Consequently the mouth of the polychaete is said to be apical on the first segment, and this segment becomes the labrum in the arthropods. (And yet, certainly no arthropod has its mouth on the end of the labrum.)

In conformity with her claim that the polychaete proboscis consists of the first two segments introverted, Henry relegates the polychaete prostomium to the "third segment," and denies its homology with the oligochaete prostomium. This, to say the least, creates a curious discrepancy between these two groups of annelids. Since it is assumed that the arthropods have been derived from the Polychaeta, the corollary follows that in the arthropods the oculo-antennal part of the head must be the third segment. Henry's evidence for the segmental nature of the polychaete proboscis has been critically examined by DuPorte (1958), who reports that it is inconclusive. The account by Wells (1954) of the structure and mechanism of the proboscis of *Arenicola* certainly gives no suggestion that the proboscis is anything other than an eversible anterior part of the alimentary canal.

A very different concept concerning the nature of the labrum is proposed by Butt (1957). From his own embryological work and that of others he has assembled evidence that in many insects of several orders the labrum is formed from a pair of small lateral lobes that come together and fuse before the mouth. Eastham (1930) says there is no doubt of the bifid nature of the labrum as it first appears in the embryo of *Pieris rapae,* each half of the organ being a hollow extension of the head wall containing preoral mesoderm. According to Mellanby (1936), the labrum of *Rhodnius* appears definitely to arise as a paired structure, and it is observed by Ando and Okada

(1958) that in the sawflies *Aglaostigma* and *Pteronidea* "the labrum first appears as a pair of elevations which later become united on the median line." In *Pteronidea ribesii* Shafiq (1954) says the labral lobes unite at the 28th hour of embryonic life, and the stomodaeum develops immediately behind them. Further evidence of the double origin of the labrum is claimed by Bervoets (1913) to be seen in the individual tracheation of the halves of the labrum observed in an odonate larva.

It may be conceded, then, that at least in many insects the labrum is formed from paired rudiments, and there is evidence of its similar origin in some other arthropods. The innervation of the insect labrum by nerves from the tritocerebral brain ganglia, which led Henry (1948) to conclude that the labrum is the *segment* of these ganglia, is interpreted by Butt (1957) as evidence that the paired labral rudiments are the *appendages* of the tritocerebral segment, which have moved forward to a preoral position and united with each other. Minute tritocerebral appendages have been observed in the embryo of a number of insects, but in most cases they are described as transient vestiges.

In the Crustacea the premandibular, or "tritocerebral," appendages develop into the large second antennae. Butt suggests, therefore, that it is logical to assume that the crustacean labrum represents the fused basal parts of the second antennae. Yet, in the adult crustacean the second antennae, though they have migrated forward, are usually widely separated from the labrum, and show no evidence of having given up their basal parts to form the labrum, which should have involved the loss of their basal muscles. In the lower branchiopods the second antennal nerves are given off from the brain connectives near the premandibular ganglia; in the decapods they arise from the back of the brain. The labral innervation is entirely independent of the second antennal nerves. Finally, in the early crustacean embryo (fig. 1 E) or the nauplius larva a labrum is generally recognized already present before the mouth while the second antennae are still behind the first antennae. In the amphipod *Gammarus,* Weygoldt (1958) illustrates the embryonic head region (F) with a well-developed, bilobed labrum overhanging the mouth while the second antennal lobes are yet far behind the mouth. In the Crustacea, then, there is clearly no relation of the labrum to the second antennae. Since the labrum is evidently a homologous structure in all the arthropods, its rudiments in the insects can hardly be identified with the crustacean second antennae, or the appendages of the tritocerebral segment.

Since the basic point in the arguments of both Henry and Butt concerning the nature of the labrum is the "innervation" of the insect labrum by nerves from the tritocerebral ganglia, the value of these nerves as evidence must now be examined. In the insects a nerve trunk goes forward from each tritocerebral lobe of the brain and divides into a frontal-ganglion connective and a so-called "labral" nerve. The latter nerve, however, does not restrict its branches to the labrum; it ramifies profusely to the epidermis of the frons, the clypeus, the labrum, the mouth region and the epipharynx. If Henry (1948), therefore, had taken into account the entire head area of the insect supplied by the "labral" nerves, she should have included at least the clypeus as well as the labrum in her "first segment," whereas the clypeus is regarded as the "second segment." Chaudonneret (1950) is more consistent in this respect, since he attributes the median parts of both the labrum and the clypeus to the tritocerebral segment, the lateral parts to a "superlingual" segment. However, he regards the clypeolabral area as being only the sterna of these segments which have become preoral. Likewise invalidated by the wide distribution of the "labral" nerves is the contention of Butt (1957) that the tritocerebral innervation of the labrum identifies the labral lobes with the tritocerebral appendages. Clearly the labral branches of these nerves can have no specific value of any kind related to the labrum alone.

Furthermore, the tritocerebral nerves which are said to "innervate" the fore part of the head have been shown to be integumentary *sensory* nerves. Bretschneider (1914) says those of the cockroach *Periplaneta* (*Blatta*) are entirely sensory. Jösting (1942) illustrates their elaborate sensory ramifications on the clypeus and labrum of the larva of *Tenebrio*. According to Bierbrodt (1942) these nerves in the larva of *Panorpa* come from the epidermal sense organs of the frons, the clypeus, the labrum, and the mouth region. In the malloph-agan *Myrsidea* the "labral" nerves are described by Buckup (1959) as breaking up into sensory branches to the labrum, the clypeal region, the cibarial sclerite, and the epipharynx.

While it may be true that motor nerves commonly are restricted to the segments of their respective ganglia, this is not necessarily true of integumental sensory nerves. The neurocytes of sensory nerves are peripheral, their axons grow inward to the ganglia. It has been shown by Wigglesworth (1953, 1959) that as new sense cells are developed in the epidermis of postembryonic instars of *Rhodnius,* their axons grow inward, join with the first nerves they meet, and accompany them to the central nervous system. The clypeolabral

nerves originate in sense cells of the epidermis and enter the trito-
cerebral ganglia usually by way of the frontal-ganglion connectives.
In the Mallophaga, however, Buckup (1959) shows that they enter
the ganglia independently.

Dorsal tegumentary nerves from the tritocerebrum of insects un-
doubtedly go to segmental regions of the head that are not tritocere-
bral, since this segment is practically eliminated in the adult head. In
the malacostracan Crustacea, according to Hanström (1928), a dor-
sal tegumentary nerve from the brain branches anteriorly to the eye
stalks and posteriorly to the whole cephalothorax. In *Limulus* Patten
and Redenbaugh (1899) describe and illustrate a pair of lateral
nerves from the tritocerebral ganglia that turn backward on the epi-
dermis of the leg segments and finally branch toward the first five
appendages of the abdomen.

Tegumentary sensory nerves, therefore, do not necessarily iden-
tify segments or segmental appendages by the ganglion they enter.
The neurocytes of motor nerves, on the other hand, lie in the ganglia
and in general their function is to innervate the muscles of the cor-
responding body segments. Motor nerves are thereby more reliable
indices of segmental limits than are sensory nerves, but even here
there may be exceptions. Nüesch (1954) reports that in the thorax
of the moth *Telea polyphemus* the second ganglion gives off nerves
to the three thoracic segments. The deductions of both Henry and
Butt are thus not justified, since both are based on the sensory nerves
of the labrum, which are merely a group of sensory fibers from the
general preoral region of the head. Only in the tritocerebral ganglia
can these fibers make connections with motor neurons of the ventral
nerve cord. The function of sensory stimuli is to produce movement.

Of greater significance than the sensory innervation of the fore-
parts of the head is the fact that the motor innervation of the labral
and clypeal muscles comes from the frontal ganglion, or its equiva-
lent in some arthropods known as the stomodaeal bridge. Chaudon-
neret (1950), for example, describes in *Thermobia domestica* an
elaborate innervation of the anterior head region from the frontal
ganglion. Dorsal nerves of the ganglion go to the muscles of the
mouth angles (hypopharyngeal muscles) and to the anterior dilators
of the pharynx. A median nerve goes to the labral muscles, and
lateral nerves go to the cibarial dilators (clypeal muscles) and the
transverse epipharyngeal muscles.

The frontal ganglion is developed from the anterior wall of the
stomodaeum just before the mouth. The stomodaeum, however, is
an ectodermal ingrowth at the site of the mouth. The frontal gan-

glion, therefore, is actually a preoral first ganglion of the ventral nerve cord, as becomes evident if the tritocerebral ganglia are imagined to be restored to their primitive ventral postoral position (fig. 20). In the symphylan *Hanseniella* the frontal ganglion is shown by Tiegs (1940) to be represented by a pair of ganglia connected by a preoral commissure. Nerves go to the clypeolabrum from the ganglia, and the stomodaeal recurrent nerve arises from the commissure.
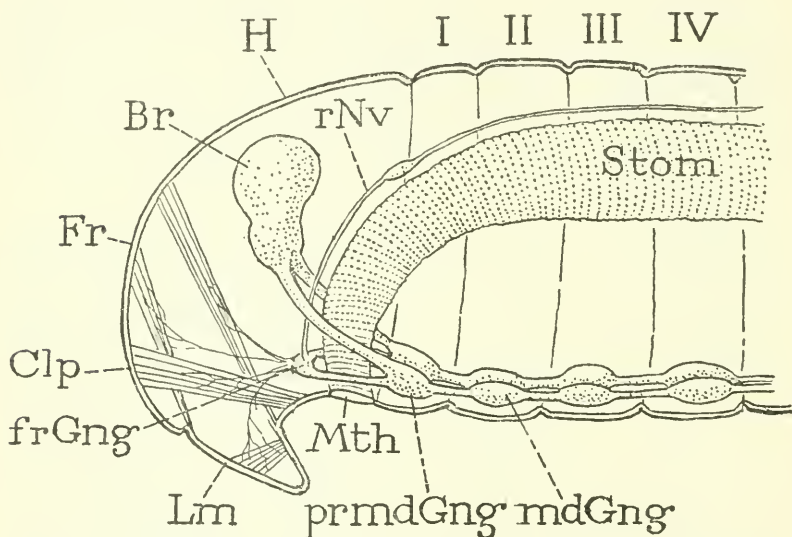
FIG. 20.—Diagrammatic theoretical reconstruction of the anterior region of a primitive arthropod before the postoral segments (*I-IV*) became a part of the head. The premandibular ganglia (future tritocerebral ganglia) are still ventral behind the mouth. The preoral frontal ganglion (*frGng*) is seen to be the first ganglion of the ventral nerve cord, innervating the clypeal and labral muscles, and the ectodermal stomodaeum.

The connection of the preoral frontal ganglion with the premandibular tritocerebral ganglia is of no more significance than the connection of these ganglia with the mandibular ganglia or the union of any other consecutive ganglia in the ventral nerve cord. As described by Orlov (1924) in the larva of *Oryctes nasicornis* the frontal ganglion is in itself a fully developed nerve center containing sensory, motor, and association neurons. The preoral ocular and antennal brain centers are primitively supraoesophageal ganglia connected with the ventral nervous system by way of the postoral tritocerebral ganglia.

Considering the difficulties encountered by theories that attempt

to identify the labrum with the tritocerebral segment or with its appendages, it seems much simpler to accept the labrum for what it appears to be in all the arthropods from trilobites to insects, namely, a preoral lobe of the head. When it is formed by the union of a pair of lobes it practically refutes the idea that it is a head segment, and a forward migration of the tritocerebral appendages that unite before the mouth is hard to visualize as a logical event in evolution. The frequent double origin of the labrum and its dual musculature in insects might suggest that the labrum represents a pair of united appendages; but the vision of a primitive arthropod having a pair of ventral appendages in front of its mouth is too fanciful to be real. Functionally the labrum is a preoral lip, which may have first served to arrest food at the site of the mouth when pushed forward by the postoral appendages.

THE EMBRYONIC HEAD LOBE

The nature of the cephalic lobe of the arthropod embryo, whether or not it is composed of consolidated primitive segments, and if so, of how many segments, has been the subject of endless discussions, arguments and counterarguments, and still the question cannot be considered as definitely answered. Our only source of evidence is the embryo itself. The embryo shows us visible facts, but it does not interpret them in phylogenetic terms, nor does the embryo give us any assurance that it fully recapitulates its ancestral history, which is the very thing we want to know. Hence, whatever phylogenetic interpretations we may deduce from embryogeny are products of our own mental processes, and differ according to our different ways of thinking. Since evolutionary theories cannot be put to an experimental test, and we cannot see backward in time, arguments continue because we are ever prone to make the known facts fit a favored theory.

The principal, externally visible facts about the embryonic head lobe are that it projects anterior to the mouth, shows no clear outward sign of segmentation, and bears the first antennae, the labrum, and the eyes when the eyes are developed. A pair of small lobes lying before the antennae, observed in a centipede (Heymons, 1901) and an orthopteroid insect (Wiesmann, 1926), have been regarded as vestiges of preantennal appendages. It is therefore contended that the head lobe includes at least a preantennal segment and an antennal segment, and some would include an ocular segment. If there is any remote ancestral relation between the arthropods and the annelid

worms, the cephalic lobe of the arthropod embryo should contain some part derived from the nonsegmental prostomium of the worms. Heymons (1901) in his study of the embryo of a centipede, *Scolopendra,* asserts that only the clypeal region and the labrum pertain to the prostomium, and that the first three postoral segments of the annelid are represented in the arthropod by an ocular segment, a preantennal segment, and an antennal segment. These alleged segments, he says, correspond with internal nerve ganglia and with mesodermal coelomic sacs.

Small paired cavities in the preantennal mesoderm have been observed in a number of arthropods, and there are usually mesodermal sacs associated with the antennae. In several cases, also, cavities have been reported in the labral mesoderm, but none has been attributed to the ocular region. Weber (1952), after a review of the various theories of head segmentation, gives his own conclusions as follows. The arthropod head consists of a prostomial acron and six segments. The acron contains the primitive brain, or archicerebrum, which innervates the eyes. Its ventral part becomes elongate posteriorly to the mouth. A *preantennal segment* follows the acron. Its ganglia, termed the prosocerebrum, unite with the archicerebrum to form the definitive protocerebrum. The preantennal coelomic sacs are often suppressed or united with the second pair. Next is the *antennal segment,* the ganglia of which become the deutocerebral component of the brain. Third is the *premandibular segment.* Its ganglia in lower Crustacea remain on the circumoesophageal connectives, but in the other groups they unite with the brain as the tritocerebrum. These are the ganglia of the second antennae of Crustacea, of the chelicerae in the Chelicerata. The fourth, fifth, and sixth segments are the mandibular, first maxillary, and second maxillary, or labial, respectively.

Weygoldt (1958) in his study of the embryonic development of the amphipod *Gammarus* arrives at essentially the same analysis of the head segmentation as does Weber. This interpretation, that the head consists of a prostomium and six segments, is probably agreeable to most students of the subject who contend that the embryonic head lobe is a formerly segmented region of the trunk. Dahl (1956), for example, says that Weber's interpretation is the one that most closely agrees with his own view on the matter.

A somewhat different scheme of head segmentation is deduced by Chaudonneret (1950) from his elaborate study of the head of *Thermobia domestica.* The prostomium he restricts to a very small apical

region before the first segment. The latter Chaudonneret calls the "preantennular" segment, the ganglia of which become the proto-cerebrum, and the appendages the eye stalks of Crustacea. The second segment is that of the first antennae, the third is the second antennal segment, the ganglia of which become the tritocerebrum. The fourth segment is the segment of the superlinguae, the next three those of the mandibles, maxillae, and labium. Chaudonneret thus, by reviving the long discredited superlingual segment and omitting the preantennal segment of other writers, makes out seven segments in the adult head.

On the other hand, from a comparative study of the internal or-ganization of the brain in the Polychaeta, Onychophora, and Arthrop-oda, Holmgren (1916) and Hanström (1928) have very reason-ably argued that the entire preoral head lobe of the arthropod embryo represents the annelid prostomium. First it is to be noted that both the prostomium of the worm and the head lobe of the arthro-pod are preoral, and show no external evidence of segmentation. Second, the part of the arthropod brain formed inside the cephalic lobe shows a striking resemblance to the prostomial archicerebrum of the polychaetes.

The brain of the Polychaeta innervates the anterior tentacles, the eyes, and the prostomial appendages known as the palps. The brain centers of the palpal nerves lie behind the optic centers and are closely associated with the corpora pedunculata. In some families the ganglia of the first postoral segment, from which arises the stomatogastric system, are united with the brain.

The brain of Onychophora consists of the primitive prostomial brain and the secondarily added first postoral ganglia. The tentacles of the annelids are absent in the Onychophora, but the forebrain in-nervates the eyes and the antennae. The antennal commissure lies behind the optic centers and the antennal nerve centers are associated with the corpora pedunculata just as are the palpal centers in the polychaete. The onychophoran antennae thus would appear to repre-sent the polychaete palpi. The onychophoran brain, as that of the arthropods, contains a central body. The hind brain innervates the feeding organs known as the "jaws," which thus correspond with the chelicerae or second antennae of the arthropods. It gives origin to the stomatogastric nerves, and its component ganglia are connected by a suboesophageal commissure.

The internal structure of the arthropod brain closely resembles that of the onychophoran brain, except that the ocular and antennal

centers are more differentiated. It is argued, therefore, by the above-named authors that the oculo-antennal part of the arthropod brain represents the prostomial brain, or archicerebrum, of the polychaetes, and that the procephalic part of the adult head is derived from the annelid prostomium. Secondarily added to the brain in the insects and myriapods are the ganglia of the first postoral body segment, which become the tritocerebral brain lobes. The commissures of the optic and antennal centers are intracerebral and suprastomodaeal. The commissure of the tritocerebral ganglia is free beneath the stomo-daeum.

This concept that the adult head consists of a primitive cephalic lobe equivalent to the prostomium of the annelids and four second-arily added postoral somites has been maintained in a recent study by Butt (1960) on the embryonic development of the arthropod head. The prostomial part of the head is represented in the embryo by the blastocephalon, within which are differentiated from the archicere-brum the ocular and antennal centers of the definitive brain.

The principal objection that has been urged against this interpre-tation is based on the occurrence of paired cavities in the mesoderm of the embryonic cephalic lobe. The presence of mesodermal cavi-ties, regarded as coelomic sacs, has been recorded in the labrum, in the preantennal region, and associated with the first antennae. Most writers discount the significance, or even the verity, of the labral cavities, but the preantennal and antennal sacs are taken as evidence of segmentation. The preoral mesoderm has been shown in Onychoph-ora and Arthropoda to be formed by forward growth of postoral mesoderms, the labral mesoderm being derived from the preantennal mesoderm. This fact cannot mean necessarily that the forward-grow-ing mesoderm represents anteriorly migrating segments, and it throws some doubt on the segmental value of the transient cavities that sub-sequently appear in it.

The mere presence of paired cavities in the trunk mesoderm is accepted by some zoologists, especially embryologists, as unques-tioned evidence of body segmentation. If, then, any pair of cavities in the mesoderm, particularly when associated with nerve ganglia, defines a segment, there is no further argment on the subject. How-ever, in the adult animal a segment is a motor unit of the body with an intrasegmental somatic musculature. In this sense, therefore, the contention that the blastocephalon is a segmented region implies the assumption that at some time in the history of the insect it consisted of individually movable rings. Clearly this assumption is purely

theoretical in the absence of concrete evidence, and it is difficult to visualize the embryonic head as having once consisted of individually movable segments. It is easier to believe that temporary cavities can occur in the preoral mesoderm without giving rise to segments. Primitive coelomic cavities must have had some primary reason for their formation, probably a physiological one. They usually set the pattern for segmentation, but that they necessarily form segments is just a convenient belief for supporting a theory when no segmentation is visible. DuPorte (1957) has well discussed the weakness of evidence for segmentation in the preoral head region derived from the presence of cavities in the mesoderm.

It is true that Nelson (1915) describes protocerebral and deutocerebral segments in the embryo of the honey bee, but it appears that he refers to surface swellings over the ganglia; no mention is made of coelomic cavities in this region. Shafiq (1954) likewise finds no coelomic sacs in the embryonic head of the sawfly *Pteronidea ribesii,* and from the lack of any other evidence of segmentation he concludes that the embryonic head is better interpreted as an unsegmented acronal lobe bearing the eyes, the antennae, and the labrum.

The occurrence of cavities in the labral mesoderm should be somewhat embarrassing to the segmental theory regarding the rest of the head lobe. Most embryologists do not accept the labrum as a segment, but they insist that the cavities in the following region denote former segments. Yet the presence of paired mesodermal cavities in the labrum appears to be as well attested as that of cavities in the preantennal and antennal mesoderm. Paired cavities in the embryonic labral mesoderm have been described by Wiesmann (1926) in *Carausius,* by Mellanby (1936) in *Rhodnius,* by Roonwal (1937) in *Locusta,* by Eastham (1930) in *Pieris,* and by Miller (1940) in *Pteronarcys.* The cavities, however, soon become disorganized and their walls reduced to irregular cell masses. That the labrum contains mesoderm in all cases is unquestioned, but the validity of the labral cavities as true coelomic sacs is disputed by some writers, particularly by Manton (1928), who cites Wiesmann as the only one who records the presence of labral sacs distinct from a pair of preantennal sacs. More recently, however, Miller (1940) has described in the stonefly *Pteronarcys* definite traces of cavities in the preantennal mesoderm, as well as cavities in the labral mesoderm.

To further support the claim of primary segmentation in the blastocephalon, it will be argued that the presence of ganglia is in itself evidence of segmentation. It is true, of course, that each pair of

ganglia in the trunk pertains to a segment. A trunk segment, however, is determined by the somatic muscles, and the ganglia are necessary to activate the muscles. In the blastocephalon, or the part of the adult head derived from it, there are no somatic muscles. This head region bears the eyes and antennae, and sense organs do not form segments as do muscles; but they also must have nerve centers. Thus the claim that nerve ganglia define segments is not valid, except theoretically, where there is no muscular segmentation.

The preoral and intracerebral position of the ocular and antennal brain commissures appears to conflict with the claim that the ocular and antennal ganglia belong to segments that were formerly postoral. It is explained, however, that these commissures are formed *after* the cephalization of the ganglia. Yet these ganglia, in common with the other body ganglia, should have had free ventral commissures before they were cephalized. If the cephalic lobe of the embryo is a segmented region, it should have ventral ganglia corresponding with its component segments, but the only ventral ganglion of this region is the preoral frontal ganglion, which innervates the clypeal and labral muscles and the ingrowth of the oral ectoderm that forms the stomodaeum. This fact in itself should suggest that the embryonic head lobe is a preoral anatomical unit. The connection of the frontal ganglion with the tritocerebral ganglia does not make this ganglion a tritocerebral element, since its circumoral connectives with the tritocerebral ganglia are equivalent to the connectives between any two consecutive ganglia of the ventral nerve cord.

Most of the theories of arthropod origins are based on the assumption that the arthropods have been derived from polychaete worms. Glaessner (1958) has described a fossil polychaete from the base of the Cambrian, but the arthropods must have originated a long time back in the Precambrian. It, therefore, does not follow that polychaetes were yet in existence at the time when the arthropod progenitors became differentiated from simple ancestral segmented worms. What the arthropods and onychophorans may have in common with modern annelids, therefore, must be traced back to some primitive common wormlike ancestor, which very probably was not a polychaete or even a chaetopod.

Until some embryo or some arthropod living or fossil is found with a preoral segmentation, we have no real evidence that this part of the animal ever was segmented. Theorists who put their faith in a few small cavities in the preoral mesoderm have yet to prove that these cavities ever belonged to true body segments. Since we shall

probably have to wait a long time for this proof to materialize, we may as well in the meantime be content with the facts as they are known. If we must have a theory, that of the prostomial nature of the embryonic blastocephalon is the simplest and the easiest to visualize. However, even if we do not know the facts concerning the segmentation of the head, and perhaps never shall know them, ignorance in this respect will have no practical effect on an understanding of the head structure in modern arthropods. And really, it would be too bad if the question of head segmentation ever should be finally settled ; it has been for so long such fertile ground for theorizing that arthropodists would miss it as a field for mental exercise.

THE ANTENNAE

The principal theoretical question pertaining to the antennae (antennules of Crustacea) concerns their possible homology with other appendages. The nature of the antennae then has an important bearing on the question of segmentation in the embryonic blastocephalon.

That the antennae are not organs equivalent to the postoral appendages would seem obvious from the fact that normally they never have a leg structure in any arthropod, and are filamentous even in the trilobites The antennules of Crustacea may be branched, but not in the manner of the second antennae or other truly biramous appendages. Furthermore, the antennal nerve centers are always closely associated in the brain with the ocular centers, and are connected by a preoral, intracerebral commissure. The only brain ganglia that are known to have a postoral origin are those that become the tritocerebral lobes of the brain. From the likeness of the first antennal nerve centers in the arthropod brain to the nerve centers of the palps in the polychaete brain it has been contended that the antennae are homologues of the annelid palps. The antennae are palplike in their embryonic origin, but since the derivation of arthropods from polychaetes is an overworked theory, the palps and antennae may be quite separate organs in their origin.

In opposition to the idea that the first antennae are primary preoral appendages of the embryonic head lobe, there is often cited the well-known fact that the insect antennae when amputated at or near the base are frequently regenerated in a form having a striking resemblance to a segmented leg with a pair of apical claws (fig. 21 D). The same results have been obtained by other methods, and leglike antennae are sometimes found in nature.

Bodenstein and Abdel-Malek (1949) submerged larvae of *Dro-*

sophila virilis in a nitrogen mustard solution for 30 minutes, then washed and dried them. Many of the emerged adults showed malformations of the antennal arista and the compound eyes, as well as of other parts of the head and body. The antennae and the eyes of muscoid flies are developed in deep pouches of the head wall (not from the "pharyngeal cavity" as the above authors state. (See Snodgrass, 1953).

The effects of the treatment on the antennae varied from an arista almost normal (fig. 21 F) except for the presence of two points on the apex, through a series of greater modifications (G), to one that somewhat resembled a jointed, two-clawed leg (H). The results varied with the age of the larvae treated, being greatest between ages of 70 to 78 hours. After 88 hours the antennae regenerated normally.

The normal antenna of *Drosophila virilis* (fig. 21 E) consists of the usual parts of a typical muscoid antenna, namely, a narrow basal scape (*Scp*), a pedicel (*Pdc*), and a large lobe (*1fl*) bearing an arista (*Ar*). The arista and the supporting lobe together constitute a four-part flagellum, the arista having a very narrow basal ring, a small second unit, and a long, branched apical shaft. It is of particular interest to note that in the regenerated appendage (G, H) it is only the arista that assumes the leglike character. Hence the term *aristapedia* given by Bodenstein and Abdel-Malek to these regenerated antennae.

Lengerken (1933) describes leglike antennae of a beetle, *Tachyderes succinctus,* found in nature. The normal antenna of this species (fig. 21 A) has a large, somewhat swollen scape, a small pedicel, and a long, slender flagellum of 10 subsegments. In the abnormal antennae (B, C) the scape, pedicel, and first section of the flagellum are approximately normal, but the rest of the flagellum is an irregular, apparently 7-segmented structure with a pair of terminal claws. As in *Drosophila* the deformity affects only the flagellum beyond its basal section (*1fl*), the proximal part of the appendage being that of a normal antenna. The resulting *Fühlerbein,* Lengerken observes, could have no locomotor function.

Perhaps the most leglike regenerates from amputated antennae are those obtained from experiments on Phasmidae. Cuénot (1921), working with *Carausius (Dixippus) morosus,* amputated the antennae through the middle of the scape or pedicel and obtained regenerates (fig. 21 D) with a typical leg tibia, a tarsus of four tarsomeres, and two apical claws with a median lobe between them. Even here, however, there is not a complete leg, and the large regenerated basal

segment is that of the antenna. Friza and Przibram (1933), from amputation experiments on *Sphodromantis* and *Drosophila,* report that the regenerated pedicel always contains an organ of Johnston,
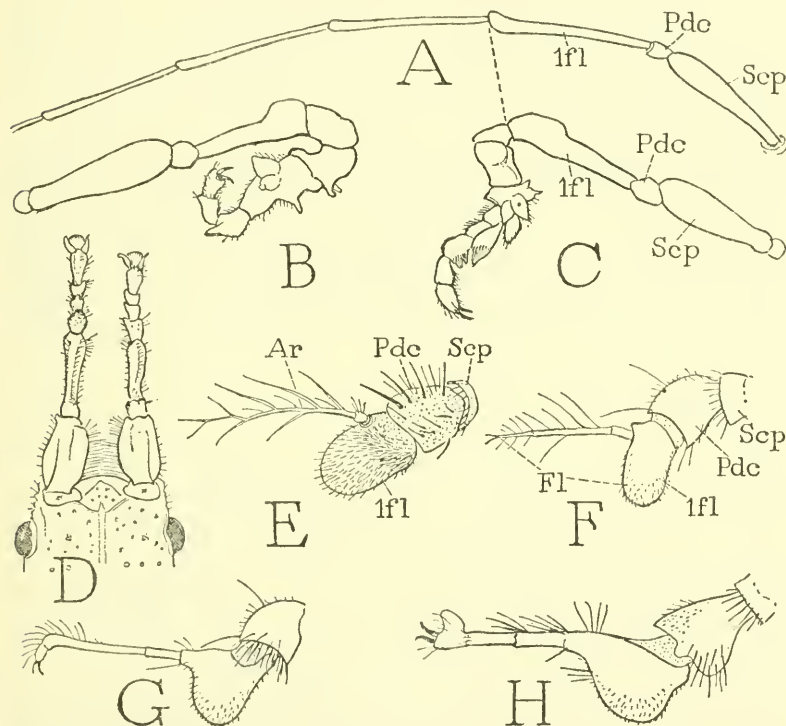

Fig. 21.—Examples of normal and leglike antennae. (A, B, C, from Lengerken, 1933; D, from Cuénot, 1921; F-H, from Bodenstein and Abdel-Malek, 1949).

A, *Trachyderes succinctus,* Coleoptera, normal antenna. B, C, Same, left and right leglike antennae found in nature. D, *Carausius morosus,* Orthoptera, adult antennal regenerates after section through middle of second segment. E, *Drosophila virilis,* Diptera, normal antenna. F-H, Same, antennae of adults reared from larvae treated with nitrogen mustard, showing various degrees of leglike regeneration.

and that the usual muscles are present in the scape. Here again, therefore, it is only the flagellum that undergoes malformation during regeneration, and the new appendage never reproduces the complete segmentation of a leg. In some insects no regeneration follows complete amputation of an antenna, as reported by Gäbler (1934) in his study of Homoptera.

It is the common presence of apical "claws" on the regenerated

antennae that gives the latter their most leglike appearance. Len-
gerken (1933) suggests that the apparent claws result from a split-
ting of the end of the flagellum. Similar processes, he says, are often
found on the apex of the normal antenna, and he gives a figure of
such an antenna in a beetle. Though the frequent occurrence of
claws on regenerated antennae is somewhat perplexing, before we
accept them as true pretarsal leg claws we should know more of their
structure, and of how they arise from the end of the appendage.

Those who discount the idea that the regenerated antenna is a re-
version to a primitive leg, usually explain its leglike form as resulting
from the influence of the "leg organizer" on the newly growing tissue.
It is surprising, then, that the basal part of the regenerate should
always be that of an antenna. The various forms of normal antennae
(fig. 14) are produced principally by modifications of the flagellum.
As already noted, the flagellum of the lower insects grows by sub-
division of its basal section.

It is quite impossible that the insect antenna was ever a leg in the
past history of the *insects*. The Crustacea are older than the insects,
and none of them has a leglike first antenna; even in the trilobites the
antennae are long filaments. If the antennal "leg" regenerate is a
return to an ancestral form of the appendage, it would have to be a
throwback through millions of years before the Cambrian, long before
insects existed, when the arthropod ancestors very improbably had
fully segmented legs with paired apical claws. The antennal "leg"
proves too much for the theory of its leg origin, and thus gives no
support to the idea that the antennae are appendages of a formerly
postoral segment of the trunk. The claim that the antennae are modi-
fied, primarily postoral legs needs stronger support than that derived
from regeneration.

Heteromorphic regenerates have followed even amputation of the
compound eyes. Experiments in eye removal on the cockroach and
Tenebrio larva by Janda (1913) and by Kříženecký (1913) produced
only small fingerlike outgrowths in place of the amputated eye, ac-
companied in most cases by a small regenerated eye. On the other
hand, in experiments by Herbst (1896, 1900, 1902) on Crustacea,
the amputation of an eye was followed by the regeneration of a truly
antennalike appendage. If the antennal regenerate is interpreted as
an ancestral reversion, we should have to assume that the primitive
crustaceans had three pairs of antennae but no compound eyes, and
that eyes were later developed on the first pair of antennae, which
then were converted into eye stalks. To accept all this as truth re-
quires great faith in imagination.

In further experiments Herbst found that in the Crustacea the formation of an antennal regenerate in place of an eye depended on the destruction of the optic ganglion, otherwise a new eye and eye stalk were regenerated. In the lower vertebrates, however, Goldfarb (1910) reports that the destruction of nerves to an amputated part has no effect on the regenerate; a salamander thus treated replaces a leg and its tail, a tadpole its tail, and an earthworm its head.

Considering the many known examples of abnormal growth of the appendages of insects, such as those recorded by Przibram (1910) in adults, and by Cappe de Baillon (1927) in the embryo, nymph, and adult of *Carausius morosus,* it is difficult to believe that any kind of abnormal growth can have any phylogenetic significance. All such things result from some disturbance of the growth factors, and would appear to have no more meaning than a two-headed rooster or a six-legged calf. I once saw in a circus a three-legged man, but I am not convinced our ancestors were tripods.

LETTERING ON THE FIGURES

Aclp, anteclypeus.
af, antennifer.
Ant, antenna (*1Ant,* first; *2Ant,* second).
Ap, apodeme.
Apt, cephalic apotome.
Ar, arista.
AT, anterior tentorial arm.
at, anterior tentorial pit.
Br, brain.
cas, circumantennal sulcus.
Cb, cibarium.
Cd, cardo.
Chl, chelicera.
CL, ecdysial cleavage line.
Clp, clypeus.
cos, circumocular sulcus.
Cp, carapace.
CT, corpotentorium.
cvpl, cervical plate.
Cvx, cervix, neck.
DT, dorsal arm of tentorium.
E, compound eye.
emH, embryonic head, blastocephalon.
Ephy, epipharyngeal surface.
es, epistomal sulcus.
Fl, flagellum.
1fl, first annulus of flagellum.

For, occipital foramen.
FR, frontal ridge.
Fr, frons.
frGng, frontal ganglion.
Ge, gena.
Gn, gnathal segments.
Gnc, gnathocephalic part of cranium.
Gng, ganglion.
gnl, gnathal lobe.
Gu, gula.
HB, hypostomal bridge.
hF, hypopharyngeal fultura.
hf, fulcrum of hypopharynx.
HL, hypostomal lobe.
Hphy, hypopharynx.
hs, hypostomal sulcus.
Hst, hypostome.
Hstm, hypostomium.
I-IV, postoral head segments.
L, leg.
Lb, labium.
Lg, ligament.
Lig, ligula.
Lm, labrum.
mcls, muscles.
mcs, midcranial sulcus.
Md, mandible.
Md B, base of mandible.

mdFs, mandibular fossa.
mdGng, mandibular ganglion.
ms, median suture.
Mt, mentum.
Mth, mouth.
Mx, maxilla (*1Mx,* first; *2Mx,* second).
MxC, maxillary cavity
N₁, pronotum.
Oc, occiput.
occ, occipital condyle.
ocs, occipital sulcus.
Pdc, pedicel.
PgB, postgenal bridge.
Pge, postgena.
PgL, postgenal lobe.
Phy, pharynx.
Plst, pleurostoma.
Pmt, postmentum.
Pnt, premandibular appendage (?).
Poc, postocciput.
PoR, postoccipital ridge.
pos, postoccipital sulcus.
PrC, preoral food cavity.
prmdGng, premandibular ganglion.

Prmt, prementum.
Prtc, protocephalon.
PT, posterior tentorial arm.
pt, posterior tentorial pit.
R, rostrum.
rNv, recurrent nerve.
rprmt, retractor muscle of prementum.
S, sternum, or sternal arms.
Scp, scape.
sge, subgena.
sgs, subgenal sulcus.
SlDct, salivary duct.
Slv, salivarium.
Smt, submentum.
sos, subocular sulcus.
St, stipes.
Stom, stomodaeum.
TB, tentorial bridge.
Tnt, tentorium.
Tor, torma.
ts, temporal sulcus.
V, ventral wall of head.
Vx, vertex.
y, suspensory rod of hypopharynx.

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