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## INTRODUCTION

The structure of insects presumably remains the same for long periods of time. A reading of entomological texts and papers, however, might give the impression that a rapid change has been going on in insects even during the last few years. The evident stability of the insect structure as compared with the diversity in the written accounts of it simply illustrates the difference between anatomy and morphology. *Anatomy* refers to the facts of structure, *morphology* is our interpretation of the facts or what we think about them. Anatomy is unchangeable, except by the slow processes of natural evolution; morphology, on the other hand, changes with each generation of morphologists, or as often as any morphologist changes his mind or thinks he sees a new light on an old subject. Sometimes the light is

deceptive, what appears as reality to one may be a mirage to another. At best, morphological interpretations can be deduced only from circumstantial evidence, and evidence is not *circum*stantial if it is one-sided.

Students of entomology have long been taught that one of the most important structural features of the insect head is a Y-shaped line on the face called the "epicranial suture." Now a paper appears (DuPorte, 1946) in which it is asserted that this "suture" has no structural significance at all, being merely a line of weakness in the head wall where the cuticle splits at ecdysis, with its arms taking quite different courses in different insects. At the same time the same idea had been elaborated in the manuscript and drawings of the present paper. The two papers are in entire agreement concerning the "epicranial suture"; in other ways they are not completely in accord. DuPorte discredits the value of muscle attachments as criteria for determining homologies of parts in the exoskeleton; he says, "the known inconsistency of muscle origins throws doubt on their value in determining the homologies of the facial sclerites." However, one unreliable member of a class does not discredit the integrity of all the others. On the face of the insect are attached two groups of muscles, separated by the frontal ganglion and its brain connectives. There is no known irregularity in the relation of these muscles to the facial wall of the head, those of one group never invade the territory of the other group. Wherever the claim is made that there has been a shift in the origins of these muscles it will be found that the claimant has merely changed the name of the external part on which the muscles are attached. The writer, therefore, contends that the facial muscles of the insect head *are* reliable criteria for determining the homologies of the surface parts of the cranium. The frontal ganglion, moreover, is an important landmark in the fundamental anatomy of the head, and the structure of the head is not to be understood from a study of its superficial features alone. A man may be characterized by the wrinkles on his face, but probably there is an underlying reason for the wrinkles.

## I. GENERAL DISCUSSION

The *cranium* of an insect is the sclerotized cuticle of the head. In discussing *sutures* it must be understood that an anatomical "suture," according to the literal sense of the word (from L. *suere,* to sew), should be a line along which two parts have united without obliterating the evidence of their union. The best examples of anatomical sutures, except those made by surgeons, are the irregular lines of

junction between bones of the vertebrate skull, which to the earlier anatomists suggested seams of stitching. In entomology the term "suture" is carelessly used for any external groove of the integument, regardless of its nature or of how it may have been formed.

Since the integument of an animal is continuous over all parts of the body in postembryonic stages, the term "suture" can be applied only to lines of union between separate centers of dermal hardening. Thus, Ferris (1942), in discussing the head of Symphyla, says of the cranial lines that they "are sutures in the strictest application of the term, being seams between the various areas of sclerotization." However, by what evidence he arrives at this positive information he does not tell us. It is probable that the postoccipital sulcus of the insect head is a line of union between primitive segments, and on the ventral side of the head of some insects there are lines which clearly indicate the union of primarily separate sclerotic areas. Otherwise there is no proof that any of the lines on the insect's cranium are true sutures; neither nymphs nor larvae show separate centers of sclerotization in the head integument, and the embryonic head is unsclerotized. Certainly most of the so-called "sutures" of the insect head are grooves incidental to the formation of ridges on the inner surface, and these endoskeletal ridges are structural features serving to strengthen the cranial walls. The external grooves, or *sulci,* of the endoskeletal ridges, therefore, are not "sutures" in any true sense. Strenger (1942), in a "functional analysis of the orthopteran head," though calling these sulci "sutures" (Nähte), concludes that they are in general strengthenings along lines of stress in the head capsule.

There is, however, on the head of nearly all immature insects, and on that of some adults, another kind of line which is not marked by a groove externally, nor does it ordinarily form a ridge on the inner surface. This line is that commonly known as the "epicranial suture." Typically it has the form of a Y, inverted if viewed from in front. The stem, called the "coronal suture" or "metopic suture," is median on top of the head; the arms, or "frontal sutures," diverge laterally and downward to different points on the face in different insects. Functionally this "epicranial suture" is the line along which the head cuticle of the immature insect splits at ecdysis. It is in no sense a suture, and is here termed the *ecdysial cleavage line of the head.* DuPorte (1946) calls it the "ecdysial line or suture." In nymphal and larval stages the cleavage line usually appears as a pale double-edged tract of the head cuticula, the stem of which is continuous from the similar mid-dorsal line on the thorax. According to Duarte (1939) the line along which the cuticle splits on the thorax of *Locusta* is

characterized by an absence of the exocuticular sclerotization, and a great elongation of the sublying epidermal cells. DuPorte (1946) says, "the ecdysial suture is a narrow line along which the sclerotic and usually pigmented exocuticle is not developed." The cleavage line, furthermore, is distinguished from other lines of the head in that of itself it does not form internally a ridge. However, as shown by DuPorte, the coronal stem of the cleavage line sometimes runs along the bottom of a ridge-forming sulcus, and thus has been confused with a coincident but independent structure.

It is generally observed that when the cuticle splits preceding ecdysis, the rupture appears first on the thorax, whence it proceeds anteriorly through the neck onto the head, where it forks (fig. 1 A); posteriorly the cleft may branch laterally behind the metathorax, or it may continue into the abdomen. Incidentally it should be noted that moulting and ecdysis are not the same thing. *Moulting,* with arthropods, is the separation of the old cuticle from the new cuticle formed beneath it; *ecdysis* is the emergence of the insect from the moulted skin. Ecdysis does not always accompany moulting, as when the larval cuticle forms a puparium. The cleavage line of the cuticle that opens to permit the escape of the insect is, therefore, a *line of ecdysis,* but not a "moulting line."

In some of the ametabolous and hemimetabolous insects the exuvial cleavage line of the head is carried over entire or partially into the adult (fig. 4 A, B, D, *CL*). As observed by Strenger (1942) in Orthoptera, however, it would appear in most cases that the retained cleavage line has no mechanical significance in the imago. Among holometabolous insects it is doubtful if the larval line of ecdysis is ever fully present on the adult head; usually it is entirely suppressed, though Y-shaped grooves of internal ridges of the cranium that have no relation to the larval cleavage line have been regarded as the "epicranial suture." Examples of such misidentification will be given in the discussion of Coleoptera and Mecoptera.

The region of the face between and below the arms of the cleavage line includes the areas commonly known as the *frons,* the *clypeus,* and the *labrum.* The labrum, however, is the only anatomically distinct part of this region, since usually it is separated from the clypeal area by a flexible, membranous or weakly sclerotized conjunctiva, and generally it is movable by muscles arising on the frons. The frontoclypeal area presents in most insects a continuously sclerotized surface, though in many insects a transverse inflection, the *epistomal,* or *frontoclypeal, sulcus,* runs between the anterior mandibular articulations and forms a strong ridge on the inner surface. This groove,

when present, separates the clypeal area from the frontal area, but it is clearly a secondary device for strengthening the head wall between the bases of the jaws, and, considering the irregularity of its occurrence, it may be suspected of having been independently developed in some cases. However, this epistomal sulcus lies posterior to the muscles that pertain to the clypeus, and separates these muscles from those which arise above it on the frons.

The frons is usually defined as the facial area above or behind the clypeus embraced by the arms of the "epicranial suture"; but, thus defined, it has no definite anatomical status because of the different courses followed by the said arms of the "suture" (fig. 1 C-G). According as the arms go behind or between the antennae, the "frons" in some cases carries the antennae, in others it does not, and this inconsistency is clearly seen on the head exuviae after ecdysis. DuPorte (1946), therefore, would bound the frons laterally by grooves present in some insects extending dorsally from the anterior mandibular articulations. These lateral grooves, however, in some insects run laterad of the antennae and in others mesad of them, and in many cases the "frontogenal sulcus" of DuPorte is part of the groove commonly known as the frontoclypeal, or epistomal, sulcus. In short, the "frons" is a name rather than an anatomical reality, but as a name without a definition it is perhaps the more useful inasmuch as any writer may apply it as he chooses. In the present paper the term *frons* is used in an indefinite sense for the facial area of the head above the clypeus, or the clypeal area, just as *vertex* applies to the top of the head, and *genae* to the sides. The areas designated by these names are topographical but not anatomical. When the arms of the cleavage line go posterior to the antennae (fig. 1 C, D) they approximately define the frons; when the arms go between the antennae the area they embrace is frontal (F), or frontoclypeal (G), but is not *the* frons or *the* frontoclypeus. The part cut out at ecdysis may be termed the *apotome,* which will be either a *frontal apotome,* or a *frontoclypeal apotome,* according to the position and extent of the cleavage lines.

Riley (1904), in his account of the embryonic development of the head of *Blatta,* contended that the labrum, the clypeus, and the frons are all derived from the "procephalon" (meaning the preoral lobe of the embryonic head terminating with the labrum). "The vertex, the compound eyes, and with them the ocular sclerites and the genae," he says, "are formed from the fused cephalic lobes and thus, with the front, clypeus and labrum, belong to the ocular or protocerebral segment." The Y-shaped "epicranial suture" of the head, Riley

claims, results from the dorsal union of the cephalic lobes (forming the coronal stem), and the inclusion within their anterior angle of the procephalic lobe (forming the divergent frontal arms). Other students of insect embryology have given the same explanation of the origin of the cleavage line on the head in orthopteroid insects, and it has been invoked by Steiner (1930) to explain the line in *Sialis,* though without any substantiating evidence. If the Y-line does thus originate, it may be regarded as a true suture.

The ecdysial cleavage line on the head, however, as it actually occurs in postembryonic stages, is much more variable than might be expected from a structure of fundamental significance. It varies with different insects in the point of forking on the face, the course taken by the arms, and the points at which the arms terminate. Thus, in some insects the clefts along the arms of the cleavage line at ecdysis cut into or through the compound eyes (fig. 1 C), in others they end between the eyes and the antennae (D), in still others they go to the antennal fossae (E), while again they run mesad of the antennae (F), and finally they may extend entirely through the clypeus (G). Also the coronal stem of the Y varies in length, and in some insects it is entirely absent (H), in which case the frontal clefts may proceed separately from the occipital margin of the cranium. On the other hand, the frontal arms in some insects are obsolete, and at ecdysis the coronal split extends to the clypeus, or to the labrum (I), cutting the head cuticle through the midline of the face.

Furthermore, the Y-shaped line of cuticular cleavage on the head is a feature peculiar to insects. If it represents so important a thing as the line of dorsal closure and union of the head components, it should be present also in other arthropods, but it is not—other arthropods have different ways of ecdysis. It seems probable, therefore, that at least the frontal arms of the cleavage Y are secondarily developed lines of weakness in the head cuticle, and hence are free to follow different courses in different insects. In any case, the embryonic dorsal closure of the head lobes, and that of the thorax as well, is purely an embryonic device for growing around the yolk, and cannot possibly represent any phylogenetic event in the evolution of the free-living ancestors of the insects, which presumably shed their skins as modern insects do.

Whatever may be the origin of the cleavage line on the insect head, however, and regardless of where the arms branch from the coronal stem or of the course they follow on the face, the arms are consistent in one respect, which is, that they invariably lie between two distinct sets of head muscles; at ecdysis the frontal clefts always separate the

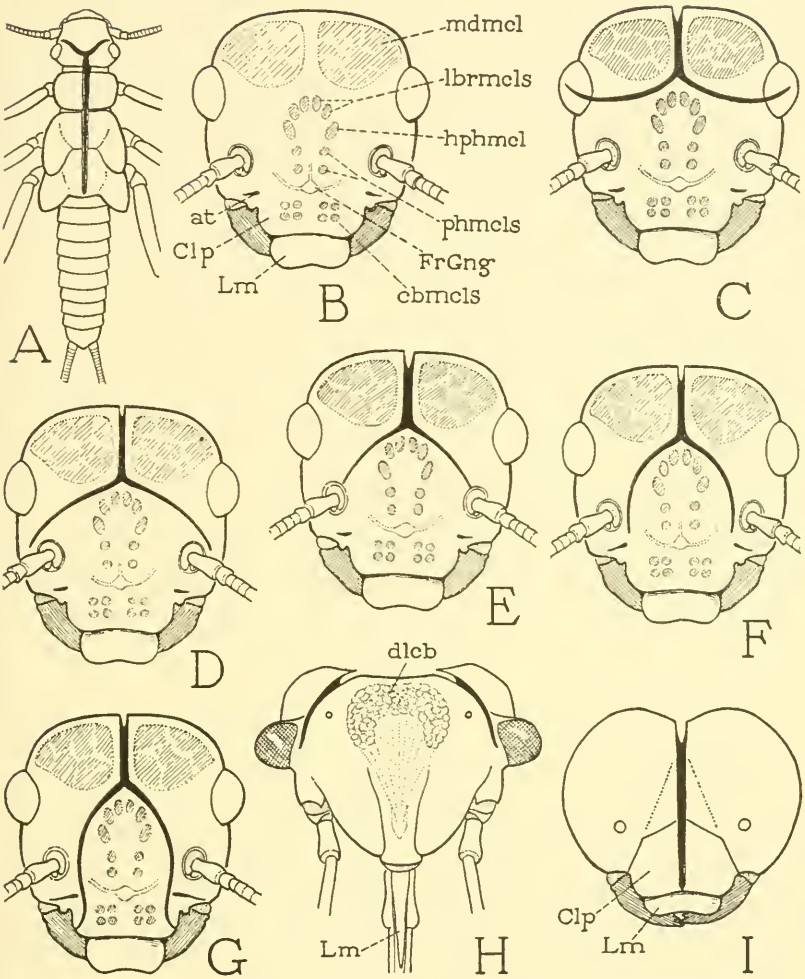


FIG. 1.—Diagrams showing the cleavage line of ecdysis, its principal variations on the head, and the relation of the frontal arms to the head muscles.

A, stonefly nymph showing entire cleavage line, with frontal forks on head. B, distribution of head muscles, with cleavage lines omitted. C, frontal splits at ecdysis extended into compound eyes. D, frontal splits going between eyes and antennae. E, frontal splits ending at antennal fossae. F, frontal splits going mesad of antennae. G, frontal splits extended to free margin of clypeus. H, coronal line absent, frontal splits proceeding separately from posterior margin of cranium (Pentatomidae). I, frontal arms of cleavage line obsolete, coronal split extended to labrum (Vespidae).

*at,* anterior tentorial pit; *cbmcls,* cibarial muscles; *Clp,* clypeus; *dlcb,* dilators of cibarium (*cbmcls*); *FrGng,* frontal ganglion; *hphmcls,* frontal muscle of hypopharynx (retractor of mouth angle); *lbrmcls,* labral muscles; *Lm,* labrum; *mdmcl,* mandibular muscle; *phmcls,* dilator muscles of pharynx.

region of the cranium on which arise the muscles of the maxillae and the mandibles (fig. 1 B, *mdmcl*) from that on which the facial muscles take their origin. The facial muscles comprise two distinct groups: an upper group, including the extrinsic muscles of the labrum (*lbrmcls*), except in adult Diptera, the precerebral dilators of the pharynx (*phmcls*), and the dorsal hypopharyngeal muscles (*hphmcl*), or "retractors of the mouth angles"; and a lower group of intraclypeal muscles, which are the dilators of the cibarium (*cbmcls*). The cibarial muscles are always separated from the hypopharyngeal and pharyngeal muscles by the frontal ganglion (*FrGng*) and its brain connectives.

In recent years it has become the custom, following Crampton (1932) and Snodgrass (1935), to give the name "postfrontal sutures" to arms of the cleavage line that diverge to points usually between the eyes and the antennae (fig. 1 D), while the term "frontal sutures" is restricted to the arms in positions mesad of the antennal bases (F). In either case, however, the divergent arms of the "epicranial suture" on the head of an immature insect are the preformed lines of the future exuvial splits that branch from the end of the coronal cleft. As DuPorte (1946) has shown, the two supposed "sutures" are the same thing in different positions.

The idea that the arms of the cleavage line on the head are two different "sutures" according as they go laterad of the antennae or between them has led to some curious interpretations of the insect head structure. Ferris (1942), for example, calls the lines in the first case the "postfrontal sutures," and connects them with the temporal sulci that in some insects run back over the top of the head mesad of the compound eyes and then downward on the posterior surface to the bases of the mandibles. The continuous line thus established he calls the "great suture" of the cranium, which he asserts is the line of union between the oculoantennal segment and the mandibular segment of the head, the tritocerebral segment being assumed to have been obliterated. The mantis is cited as an example demonstrating this alleged continuity in the parts of the "great suture," and, in fact, on the head of an *adult* mantis (fig. 4 D) the arms of the cleavage line (*CL*) do appear to turn back and become continuous with the temporal sulci (*ts*). The continuity, however, is not present in the nymph, and even in the adult the external appearance is misleading.

An examination of the inner surface of the adult mantid cranium (fig. 4G) shows that the facial area is fortified by a complex of ridges braced laterally against the circumocular ridges (*OcR*) and continued dorsally into the temporal ridges (*TR*). From the lower

end of each temporal ridge a short branch (*d*) extends mesally along the frontal arm of the persisting nymphal line of ecdysis (*CL*). The exuviae of a nymphal mantis (*F*), however, show that in the immature insect the facial ridges are much less developed than in the adult; there is here no trace of the branches from the temporal ridges invading the arms of the cleavage line, and even in the last nymphal stage the temporal sulci themselves (F, *ts*) do not reach the latter. In the first instar nymph (E) the temporal sulci end far short of the arms of the cleavage line, which are pale soft tracts of the head cuticle leading directly to the eyes. The frontal arms of the cleavage line are thus unencumbered in the nymph; at ecdysis (F) the frontal splits extend through them unobstructed, and furthermore, at least at the final ecdysis, they cut through the middle of the compound eyes (*E*).

The structure in the mantis on which Ferris bases his concept of "the great suture" is thus seen to be one that pertains only to the imago, which, being done with moulting, can undergo a structural remodeling without regard to ecdysis. If the apparent continuity of the cleavage lines and the temporal sulci in the adult mantid were real and of such fundamental structural importance as Ferris contends, the unity of the lines should be all the more evident in the nymph. Among other species of insects given by Ferris to illustrate his "great suture" he nowhere is able to find an actual continuity between the "postfrontal sutures" and the "temporal sutures," and, as will be shown later, in his discussion of the head of the symphylid *Scutigerella* he is forced to compose a "great suture" from ingredients that are not sutures at all and have no relation to one another.

The area below the so-called "postfrontal sutures," or arms of the cleavage line extending laterad of the antennal basis (fig. 1 D), is regarded by Ferris (1942) as the "frons," or later (1943) as the "antennal segment"; but when the arms go downward on the face between the antennae (F, G), as they do in most holometabolous larvae, they are together identified as the "clypeofrontal suture," and the facial area embraced by them is interpreted as that of the clypeus extended upward on the face. Yet if the cleavage lines were deleted (fig. 1 B) there would be no evident differences in the structure of the head in the two cases. The cranial muscles have always the same relative distribution, as is amply shown by Cook (1944) in his comparative study of the labral and clypeal muscles in the principal orders of insects, though Cook follows the Ferris interpretation of the skeletal areas of the head. The facts represented diagrammatically on figure 1 (C-G) show that the frontal arms of the cleavage line simply take any position in the otherwise unoccupied spaces between the

mandibular muscles and the facial group of frontoclypeal muscles. The shift in the lines from one position to another affects the manner of ecdysis, but the cranial structure is thereby no more altered than is an orange changed in structure according to the way it is peeled.

An understanding of the structure of the insect cranium must take into consideration certain facts in the basic organization of the head. Though the frons and the clypeus present externally a continuous surface, which may be indented by an epistomal sulcus for purposes of reinforcement, a real anatomical difference between the two areas arises from the fact that, while the frons is a part of the postoral anterior wall of the cranium, the clypeus, in its generalized state, is *preoral,* since it is the basal part of a hollow lobe projecting in front of the mouth (fig. 2 D) divided into clypeus (*Clp*) and labrum (*Lm*). Both the labrum and the clypeus, therefore, have an outer surface and an inner "epipharyngeal" surface. Each has a set of internal compressor muscles (*cprlm dlcb*), and the movable labrum has muscles (*lbrmcls*) arising on the frons. On the frons are attached also, as above noted, the precerebral dilators of the pharynx (*dlphy*), and a pair of muscles (*hphmcl*) inserted on the oral arms of the suspensory apparatus (*HS*) of the hypopharynx (*Hphy*). Since the clypeal muscles and the frontal muscles are invariably separated by the frontal ganglion (*FrGng*) and its brain connectives, this fact would seem to have some important significance bearing on the fundamental structure of the head.

The frontal ganglion in its embryonic origin is derived from the dorsal wall of the ectodermal stomodaeum just within the mouth; its nerve connections are with the tritocerebral lobes of the brain (fig. 2 A, *T*). The tritocerebral brain lobes, however, as shown by phylogeny and embryogeny, have been added secondarily to the primitive suprastomodaeal brain, which included only the ocular and the antennal centers (A, *P, D*) that become the protocerebrum and deutocerebrum of the definitive brain. Primarily the tritocerebral lobes (A, *T*) were the ventral ganglia of the premandibular somite (B, *GngI*). If, therefore, the head ganglia are visualized as they would be if restored to their primitive places (B), it is clear that the frontal ganglion (*FrGng*) must have been an unpaired, or possibly paired, preoral center of the ventral nerve cord with its connectives from the premandibular ganglia (*GngI*) embracing the stomodaeum just within the mouth. With the later transposition of the premandibular ganglia to the brain (A), of which they constitute the tritocerebral lobes (*T*), they carry the frontal-ganglion connectives with them, but the ganglion itself maintains its primitive position.

The frontal ganglion, therefore, always marks the dividing line between the under surface of the preoral clypeus and the postoral part

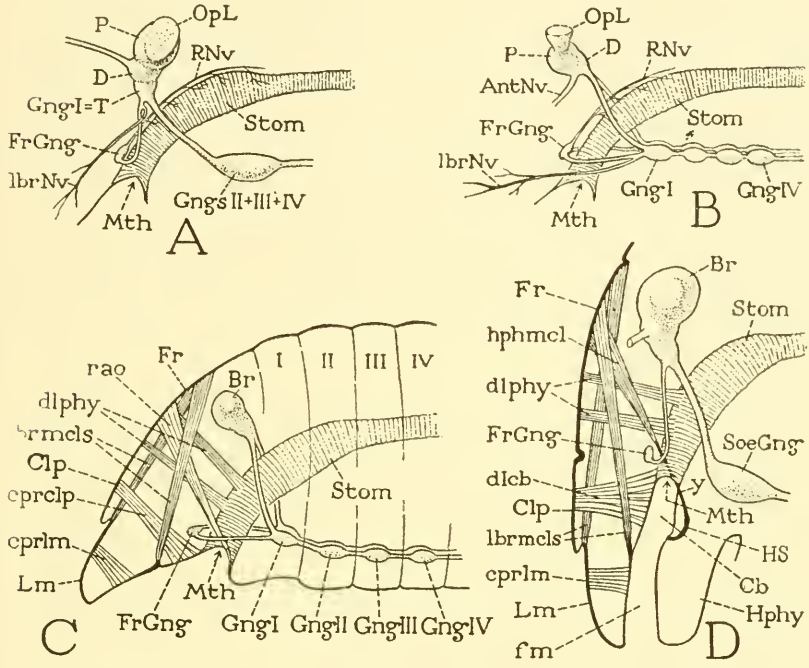


FIG. 2.—Diagrams showing the relation of the facial muscles to the frontal ganglion in the definitive structure, and in a theoretically primitive state.

A, definitive structure of the head nervous system; first postoral ventral ganglia (B, *GngI*) have become tritocerebral lobes of brain (*T*), the three following ganglia united in the suboesophageal ganglion. B, primitive relations of the same parts: the definitive tritocerebral ganglia (*GngI*) are postoral, the frontal ganglion (*FrGng*) is a preoral ganglion of the ventral nerve cord. C, theoretical facial musculature with primitive nervous system as at B. D, the same muscles as at C, with definitive nervous system as at A.

*AntNv,* antennal nerve; *Br,* brain; *Cb,* cibarium; *Clp,* clypeus; *cprclp,* compressor muscles of clypeus, prospective dilators of cibarium; *D,* deutocerebrum; *dlcb,* dilators of cibarium (compressors of clypeus); *dlphy,* dilator muscles of pharynx; *fm,* food passage; *Fr,* frons; *FrGng,* frontal ganglion; *GngI,* ganglia of first postoral somite (definitive tritocerebral lobes of brain); *GngII, III, IV,* ganglia of second, third, and fourth postoral somites; *hphmcl,* frontal muscle of hypopharynx (same as C, *rao*); *Hphy,* hypopharynx; *HS,* hypopharyngeal suspensorium; *I-IV,* first four postoral somites; *lbrmcls,* labral muscles; *lbrNv,* labral nerve; *Lm,* labrum; *Mth,* mouth; *OpL,* optic lobe; *P,* protocerebrum; *rao,* retractor muscle of mouth angle, frontal muscle of hypopharynx (D, *hphmcl*); *RNv,* recurrent nerve; *SoeGng,* suboesophageal ganglion; *Stom,* stomodaeum; *T,* tritocerebrum; *y,* oral arm of hypopharyngeal suspensorium.

of the head (fig. 2 D), and it maintains its primitive oral association regardless of whatever position the mouth may take by invagination within the head.

In the primitive condition of the nervous system, accompanied by what may be supposed to have been the primitive musculature of the anterior part of the head (fig. 2 C), the frontal ganglion (*FrGng*) must have lain between the compressor muscles of the clypeus (*cprclp*) and the postoral group of frontal muscles. The latter included dilators of the pharynx (*dlphy*), and possibly a pair of retractors of the mouth angles (*rao*). The clypeal compressors become in the modern insect (D) the dilators of the cibarium (*dlcb*), and, with the development of the hypopharynx, the mouth-angle retractors become the muscles of the hypopharyngeal suspensoria (*hphmcl*). In generalized pterygote insects the frontal muscles of the hypopharynx are functionally productors of this organ, but they are retained in Neuroptera, Coleoptera, and Hymenoptera, in which the hypopharynx is intimately united with the labium (fig. 13 A, F) and has no independent movement.

The development of the insect hypopharynx (fig. 2 D, *Hphy*) from a metastomial lobe of the head creates a food passage (*fm*) leading to the mouth between the inner wall of the labrum and clypeus and the anterior wall of the hypopharynx. At its inner end the food passage is usually enlarged by a depression of the hypopharyngeal surface to form a food pocket, the cibarium (*Cb*), beneath the clypeus. The pocket, therefore, may be expanded by the contraction of the compressor muscles of the clypeus, which thus become dilators of the cibarium (*dlcb*); it is compressible either by transverse muscles on the clypeal wall, or by elasticity of the latter. The cibarium is therefore capable of a sucking action, and in the liquid-feeding insects it is elaborated into a highly efficient ingestion pump.

With the greater development of the cibarial pump, the clypeal dilator muscles become greatly increased in size, and, to accommodate these muscles, the outer wall of the clypeus is correspondingly enlarged by an upward extension on the face. There is thus always a close correlation between the size of the clypeus and the size of the pump muscles, and in most of the insects that feed exclusively on liquid food the clypeus, or the clypeal area of the head wall, occupies a relatively large part of the facial surface of the cranium. If the clypeus is not set off from the frons by an epistomal sulcus, its proper area is always to be identified by the origins of the dilator muscles of the sucking pump, and in no such case is it necessary to suppose that the clypeus in its upward or posterior extension has taken over the muscles of the invaded frons.

## II. EXAMPLES OF THE ECDYSIAL CLEAVAGE LINE OF THE HEAD

Though the Y-line of the ecdysial cleft on the head is well known under the name of the "epicranial suture," a few examples taken from the principal orders of insects will serve to show its variations, which have not been given much consideration by entomologists. Also, it will be noted that grooves of secondary cranial ridges present in larval or adult stages of some insects have been misinterpreted as the "epicranial suture."

The names of genera and species used in the following descriptions have been furnished by the entomologists in the United States National Museum; the names of authors of species not given in the text will be found in the legends of the figures.

*Apterygote insects.*—Only a few published records are to be found on the manner of ecdysis in Protura, Collembola, Diplura, and Thysanura. Henriksen (1932) has shown that in the machilid *Petrobius balticus* Stach a rupture takes place along the midline of the back of the thorax and is continued on the head, where it ends behind the eyes in a pair of very short lateral branches. At ecdysis of the silverfish *Ctenolepisma longicaudata* Esch., Lindsay (1940) says, "a deep furrow develops in the mid-dorsal line of the thorax and along the epicranial stuture." In a personal communication to the writer, Charles L. Remington, of Harvard University, describes the exuvial split observed by him in a specimen of *Campodea* as extending from the neck upon the head as far as the bases of the antennae. Concerning ecdysis in Collembola, Handschin (1926) records that in *Onychiurus armatus* Tulb. the skin is split between the head and the thorax by alternate dorsal and ventral bending of the body; in some other species, however, he says the exuviae are not shed entire, but break up into fragments which in the course of time are rubbed off. Davis and Harris (1936), in their study of *Pseudosinella violenta* (Folsom), an entomobryid, observe merely that the insect moves the thorax up and down until the old skin begins to split along the mid-dorsal region of the thorax. Exuviae of the podurid *Achorutes* examined by the writer show the skin to have been shed in one piece, and that the insect emerged through a rent on the back of the thorax extended on the head, where it appears to be forked above the bases of the mouth parts.

From these few records it would appear that ecdysis in most of the apterygote insects takes place generally as in Pterygota through a cleft on the thorax and head, but that the frontal arms of the cleavage

line are short or absent. The Protura and Diplura commonly have an internal median ridge along the posterior part of the head. Though Tuxen (1931) in reference to Protura points out that this ridge is an apodemal structure quite unlike the thin line of ecdysis in pterygote insects, it is still possible that its component lamellae may be split apart at ecdysis.

*Ephemeroptera and Plecoptera.*—In these two orders the line of exuvial cleavage is plainly marked on the larval head, and has the typical Y-form (fig. 3 A, B, *CL*). The frontal arms diverge to points between the eyes and the antennae, and may therefore be said to delimit the frons (*Fr*). At ecdysis the head cuticle splits to the ends of the frontal lines, as shown in the plecopteron *Acroneuria* (C).

*Odonata.*—The cleavage line on the head of larval Odonata is characteristically T-shaped rather than Y-shaped, inasmuch as the frontal arms usually go almost straight laterally (fig. 3 D). According to Calvert (1934) in the first larval exuviae of *Anax junius* the transverse fissure does not reach the eyes, as in following ecdyses; the median fissure, however, extends apparently to the labrum, so that the two clefts form a cross on the top of the head. On the exuviae of subsequent instars the frontal arms of the cleavage line cut through the corneae of the compound eyes, but Calvert says the point at which they enter the corneae moves forward during larval development. While with most dragonflies the exuvial cleft at the last ecdysis cuts the cornea into an upper and a lower section (fig. 3 E, F), Calvert observes that "in at least some Libellulidae it cuts through the side of the head anterior to the eyes and in some members of this family (e. g., *Macromia, Plathemis*) farther cephalad than in others (e. g., *Libellula, Sympetrum*)." Henriksen (1932) says the cleavage line is easily seen on the eye of an odonate larva, but the writer has discovered no trace of it on the eyes of specimens examined before ecdysis.

*Dermaptera.*—The Y-line of cuticular cleavage on the head in this order is as plainly marked in the adult (fig. 4 A, B) as in the nymph. In *Anisolabis maritima* (A) the arms of the cleavage line curve outward and forward to the mesal angles of the eyes, where they are met by the lines of internal ridges extending upward laterad of the antennal sockets, but the writer has no examples of the splits as formed at ecdysis in this species. In *Forficula auricularia* also the arms of the cleavage line go to the compound eyes (B), and at ecdysis, as noted also by Henriksen (1932), the cuticular splits bisect the corneae (C). The frontal apotome (*frapt*) of the exuviae is then turned forward and downward, widely opening the corneal cleft,

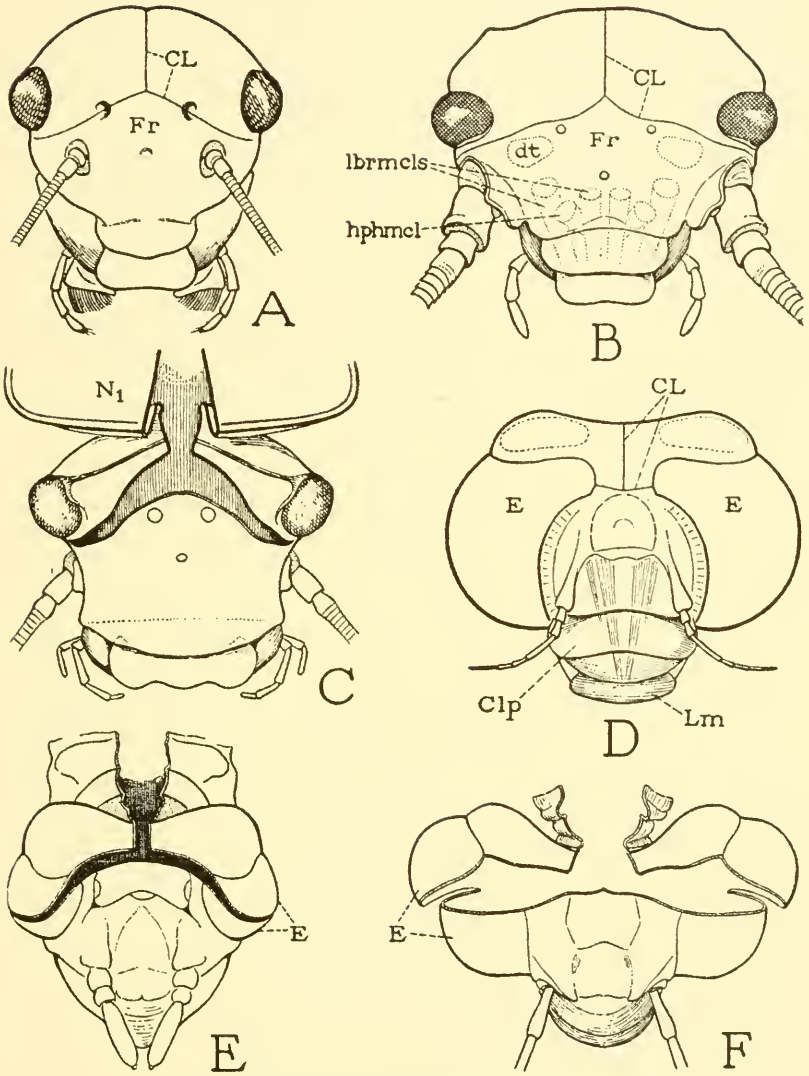


FIG. 3.—Ephemeroptera, Plecoptera, and Odonata.

A, ephemeropteron, head of larva. B, *Pteronarcys* sp., Plecoptera, head of larva. C, *Acroneuria* sp., Plecoptera, exuviae of head and prothorax. D, *Anax junius* (Drury), Odonata, head of larva. E, *Opisthogomphus morrisoni* Selys., Odonata, exuviae of head and prothorax. F, *Archilestes californica* McL., Odonata, exuviae of head.

while the mouth parts and antennae project posteriorly beneath the skin of the head.

*Orthoptera.*—Most of the Orthoptera retain at least a part of the cuticular cleavage line in the adult, though neither in the imago or the nymph do the arms always represent the full length of the exuvial splits that take place at ecdysis.

In the Mantidae (fig. 4 D) the frontal arms of the cleavage line go dorsal to the paired ocelli, and, in the adult insect, appear to be confluent with the temporal sulci (*ts*) that turn back from them over the top of the head. As already explained, however, this apparent continuity of the cleavage lines with the temporal sulci is due to the invasion of the former, on the inner surface of the head wall (G), by spurs (*d*) from the temporal ridges (*TR*). On the head exuviae of a nymphal mantis (E, F) it is seen that the temporal sulci (*ts*) do not reach the arms of the cleavage line. At ecdysis of the mantid the frontal clefts extend to the compound eyes and cut deeply into the corneae (F, *E*) as in *Forficula* (C). The lower halves of the corneae are then pulled downward with the depression of the frontal apotome (F, *frapt*), and the mouth parts and antennae project posteriorly beneath the head capsule.

In the Phasmatidae, Blattidae, and Gryllidae, the arms of the cleavage line appear to end at the lateral ocelli. In a nymph of *Periplaneta americana* undergoing ecdysis (fig. 4 H), however, it is to be seen that the frontal splits go below the ocellar spots and proceed to the mesal angles of the antennal fossae, whence they turn upward along the dorsal rims of the fossae to points above the bases of the antennae. The parietal lobes of the head exuviae are then forced to each side by the emerging head of the new instar, producing deep folds through the corneae of the compound eyes, but not splitting them. Finally, the facial region of the slough is turned flat ventrally (I) as in the mantid, forming deep infoldings of the eyes and the genae on each side, the edges of which partially overlap the bases of the antennae. The exuviae of the maxillae and labium are drawn up into deep pockets on the under side of the head.

In *Grylloblatta,* Crampton (1932) shows the cleavage line on the head of a full-grown nymph with the arms going directly to the rims of the antennal fossae, and Walker (1931) indicates the same line very faintly marked on the head of an adult.

In nymphs of Acrididae the line of the exuvial cleavage is scarcely perceptible, but at ecdysis the thoracic split extends over the top of the head and forks at the upper end of the frontal costa. Duarte (1939) says of *Locusta migratoria* that the frontal splits of the

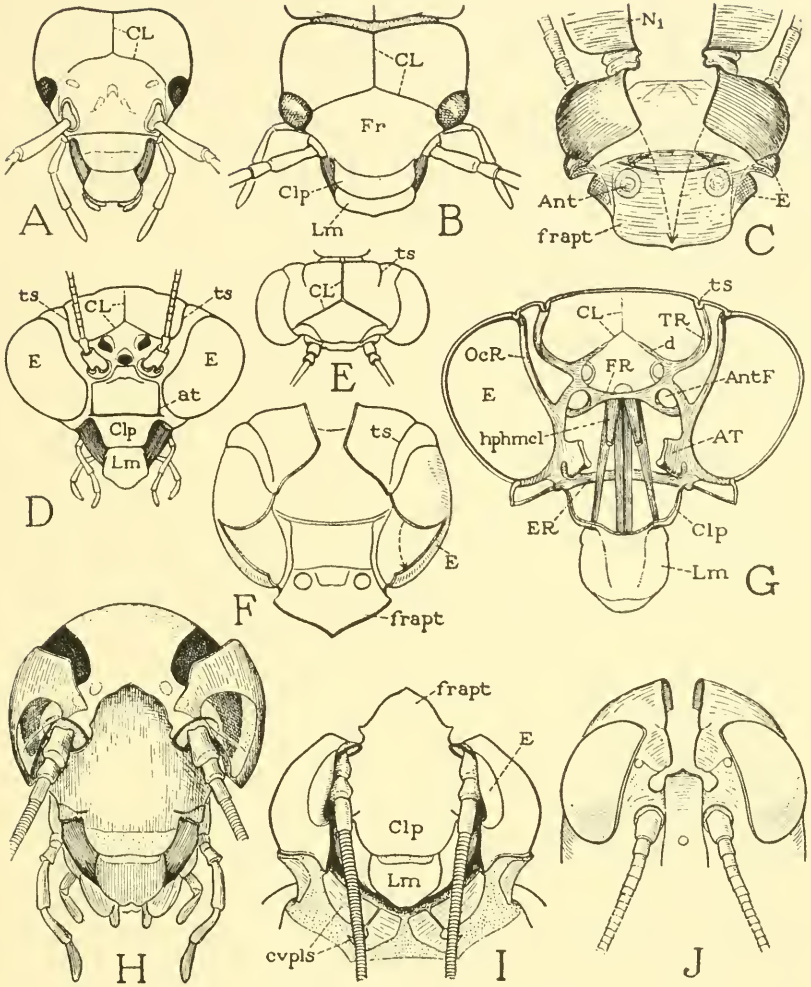


FIG. 4.—Dermaptera and Orthoptera.

A, *Anisolabis maritima* (Géné), Dermaptera, head of adult. B, *Forficula auricularia* L., Dermaptera, head of adult. C, same, exuviae of head and prothorax, frontal apotome turned downward. D, *Tenodera sinensis* Sauss., Mantidae, head of adult. E, same, head of first nymphal instar, dorsal, showing temporal sulci (*ts*) ending far from arms of cleavage line. F, same, head exuviae of last nymphal instar, frontal apotome turned downward. G, same, inner surface of facial wall of adult head, showing branch (*d*) of temporal ridge (*TR*) extending into arm of cleavage line (*CL*). H, *Periplaneta americana* (L.), Blattidae, head of adult emerging from nymphal cuticle. I, same, cast-off exuviae of head, ventral view. J, *Melanoplus differentialis* (Thos.), Acrididae, upper part of exuviae of head.

cleavage line reach the antennary sockets, but in *Dissosteira* and *Melanoplus* (fig. 4 J) the median cleft opens above the frontal costa in two short, wide lateral arms ending between the paired ocelli and the antennal sockets.

*Hemiptera.*—The line of cuticular cleavage on the head presents some interesting variations in this order. Though the frontal arms always go anterior to the eyes, and, when sufficiently extended, laterad of the antennae, the coronal stem is of variable length, and may be entirely absent. Many examples of the course of the "epicranial suture" in the Homoptera and the Heteroptera are given by Spooner (1938) in his comparative study of the head capsule of the Hemiptera. The nymphs of such species as *Ceresa* sp. (Membracidae), *Lyperonia quadrangularis* (Cercopidae), *Ranatra americana* and *Nepa apiculata* (Nepidae), *Gerris marginatus* (Gerridae), *Lampracanthus* sp. (Saldidae), *Alydus* sp. (Coreidae), and others are shown to have a typical Y-line of exuvial cleavage. In some others, however, the coronal stem is short and the frontal arms branch from it far back on the head, as illustrated by Spooner in *Cimex lectularius* (Cimicidae) and *Ischnodemus falicus* (Lygaeidae), and as shown in the present paper in *Oncopeltus fasciatus* (Lygaeidae) (fig. 6 A) and in *Cimex lectularius* (B). The ecdysial splits in *Cimex* follow the arms of the cleavage line and extend to the anterior dorsal angles of the eyes. The large frontoclypeal apotome of the exuviae (C, *frcapt*) is then turned forward and flat downward, with the beak directed posteriorly, while the narrow parietal lobes (*Prtl*) carrying the eyes and the antennae are spread out laterally.

Finally, in the Pentatomidae, as seen in *Brochymena* sp. figured by Spooner, and in *Acrosternum hilare* and *Mergantia histrionica* here illustrated (fig. 6 D, E), the coronal line is absent, and the frontal lines arise widely separated on the occipital margin of the cranium. At ecdysis of such species, the frontal splits, branching directly from the median cleft of the thorax and neck (fig. 6 D), cut off small, lateral parietal triangles of the vertex (*Prtl*) bearing the compound eyes, and leave the median part of the cranial margin unbroken.

The frontal arms of the cleavage line also are variable in length and position. They may reach to points between the eyes and the antennae (fig. 5 A; fig. 6 A), but more often they do not extend beyond the eyes (fig. 5 D, E, F; fig. 6 B, E). When the coronal stem is relatively long the arms may diverge forward on the top of the head, as in the nymphal cicada (fig. 5 A), in which at ecdysis the frontal splits cut out a small triangular frons (B). In the Fulgoroidea, however, which

have a large frontal area on the anterior surface of the head (fig. 5 G, *Fr*), the arms of the cleavage line are either transverse (D, F), or they curve posteriorly to points before the eyes (E). In such species

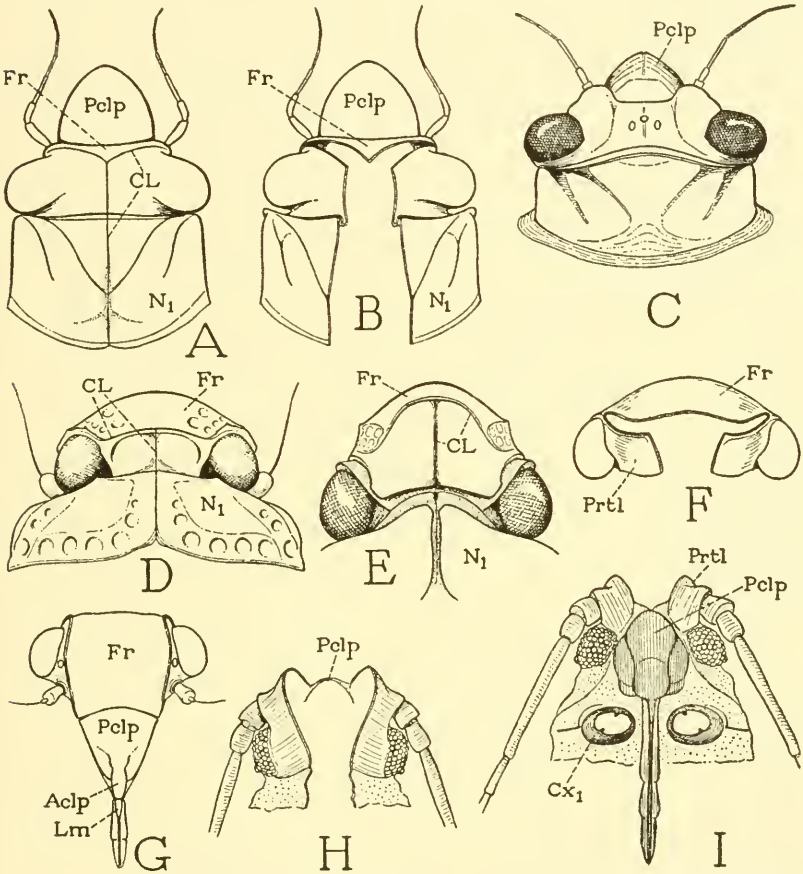


FIG. 5.—Homoptera.

A, *Magicicada septendecim* (L.), Cicadidae, head and pronotum of last nymph, dorsal view. B, same, exuviae of head and prothorax. C, same, head and pronotum of adult. D, *Catonia nava* (Say), Fulgoroidea, head and pronotum of nymph. E, *Epiptera florida* (Walk.), Fulgoroidea, head and pronotum of nymph. F, *Catonia nava* (Say), Fulgoroidea, dorsal part of exuviae of head. G, *Ormenis pruinosa* (Say), Fulgoroidea, facial view of head of adult. H, *Hyadaphis xylostei* (Schrank), Aphididae, exuviae of head, dorsal. I, same, exuviae of head and prothorax, ventral.

the vertex is cut at ecdysis into a pair of parietal plates bearing the compound eyes (F), or the eye lobes of the nymphal cuticula (B).

In the Homoptera, at least in the nymph, the frons and the post-

clypeus are usually separated by an epistomal sulcus and ridge (fig. 5 A, G); but in the Heteroptera, as noted by Spooner (1938), the frons and the postclypeus are always confluent. In the latter suborder, therefore, the respective areas of the frons and the clypeus can be determined only by an examination of the muscle attachments on their inner surfaces. The muscles of the sucking pump pertain always to the clypeus. Since the usual labral and hypopharyngeal muscles are absent in Hemiptera, only the pharyngeal muscles of the frons are present, and they are to be identified as such by their separation from the pump, or cibarial, muscles by the frontal ganglion and its brain connectives.

The variations in the point of forking of the cleavage line on the head of Hemiptera are clearly correlated with the posterior extent of the frontoclypeal muscles on the dorsal wall of the cranium, since the arms of the line always diverge from the coronal stem above or behind these muscles (fig. 1 C-G). In the lygaeid *Oncopeltus,* for example, the frontoclypeal muscles spread over a large part of the upper wall of the head (fig. 6 F, *dlcb, dlphy*), and consequently the frontal arms of the cleavage line branch far back on the head from a very short coronal line (A), leaving only a small area to the vertex. In the Pentatomidae, however, the cibarial muscles (G, *dlcb*) of the sucking pump are so large that they crowd the pharyngeal muscles (*dlphy*) to the extreme posterior edge of the cranium. In this family, therefore, the frontal arms of the cleavage line branch directly from the dorsal cleft of the thorax (D, E), leaving the median area of the cranium intact. The dorsal part of the vertex in such species is eliminated, and the frons is in contact with the neck membrane. On the other hand, in the Fulgoroidea the clypeal muscles and the clypeus itself are relatively small (fig. 5 G, *Pclp*), while the frons (*Fr*) is a large area on the front of the head, and the vertex forms the upper surface limited anteriorly by the arms of the cleavage line (D, E).

The Aphididae appear to be exceptions among the Hemiptera in their manner of splitting the head cuticle at ecdysis. According to Henriksen (1932) there is no forking of the cleavage line on the head in either the Aphididae or the Psyllidae. Exuviae of *Hyadaphis xylostei* and those of another species examined by the writer show only a median split of the head cuticle from the occipital margin to the postclypeus (fig. 5 H, I). Weber (1928) in his study of *Aphis fabae* Scop. concludes that the frons and the vertex are fused since there is no line of separation between them, but he says that in the wingless form there is a suggestion of a median line on the head. However, considering the small size of the frontal area between the arms of

the cleavage line in the nymphal cicada (fig. 5 A, B, *Fr*), it might be supposed that in the aphids the frons has been entirely obliterated.

Finally, it may be noted that a method of ecdysis having no relation to that in other insects occurs in the Aleyrodidae and Coccidae. In

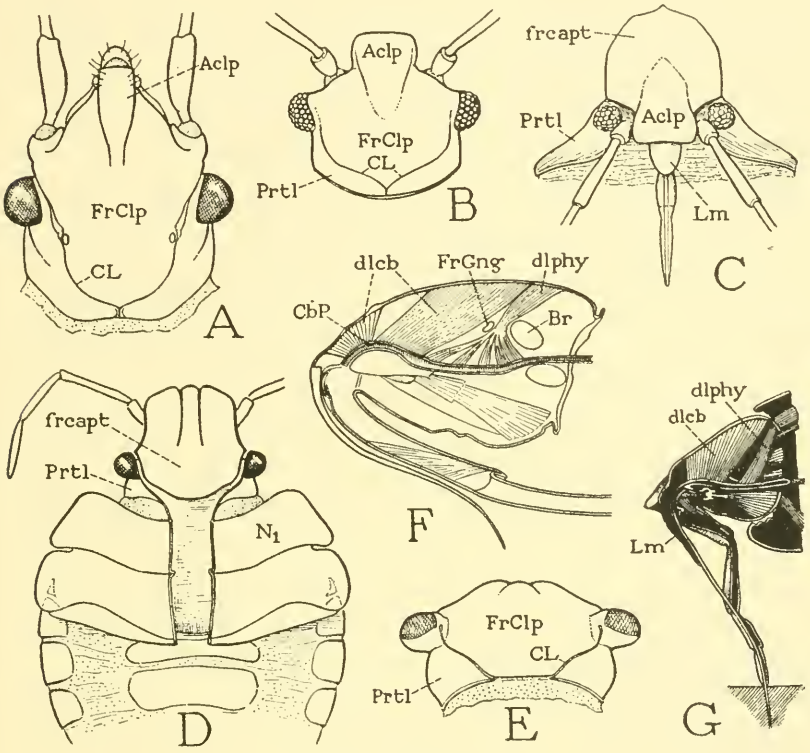


FIG. 6.—Heteroptera.

A, *Oncopeltus fasciatus* (Dallas), Lygaeidae, head of nymph. B, *Cimex lectularius* L., Cimicidae, head of nymph. C, same, exuviae of head, ventral. D, *Acrosternum hilare* (Say), Pentatomidae, exuviae, dorsal. E, *Mergantia histrionica* (Hahn), Pentatomidae, head of nymph. F, *Oncopeltus fasciatus* (Dallas), Lygaeidae, section of head (simplified from Butt, 1939), showing distribution of cibarial and precerebral pharyngeal muscles on frontoclypeal area of head. G, *Graphosoma italicum* (Müller), Pentatomidae, section of head (from Weber, 1930), showing cibarial and pharyngeal muscles occupying entire extent of dorsal wall of head.

*Trialeurodes vaporarium* (West.), as described by Weber (1931), at each of the first three larval ecdyses the cuticle is split around the anterior end of the body between the dorsal and ventral surfaces, and the emerging insect pushes the exuviae off the rear end of the abdomen. At the final ecdysis there is formed also an anterior marginal

cleft, but the adult emerges from a T-shaped dorsal opening formed by a median split through the cephalothoracic region and a transverse cleft between the thorax and the abdomen (see Weber, 1931, figs. 20, 21).

*Anoplura.*—The exuvial cleavage line on the head of the sucking lice is typically Y-shaped (fig. 7 A, C, D), with some variation in the length of the coronal stem according to the length of the head. At ecdysis, the clefts along the frontal arms go mesad of the antennae and thus take a course characteristic of holometabolous larvae, but which has not been observed to occur in other ametabolous or hemimetabolous insects.

In *Pediculus humanus corporis* the cleavage line is not visible on the head of younger nymphs; in later instars and in the adult it is present but very faintly marked, and appears as illustrated by Stojanovich (1945) in the adult (fig. 7 C). In mature nymphs evidently just before emergence of the imago, however, the cleavage line is a pale, distinctly double-edged tract of the head cuticle (A), and it may now be observed that the frontal arms extend to the basal membranes of the antennae. At ecdysis the splits along the arms are farther extended mesad of the antennae to points ($x$, $x$) at the sides of the conical fore part of the head. The discarded exuviae have the frontal apotome (B, *frapt*) turned forward on the transverse axis between the ends of the frontal clefts ($x$, $x$), together with the snoutlike cone of the head, while the parietal parts of the cuticle are spread out laterally, and in a ventral view (B) are seen to carry the eyes and the antennae.

In the lengthened head of *Haematopinus suis,* as shown by Stojanovich (fig. 7 D), the coronal stem of the cleavage line is relatively long, but the arms go mesad of the antennae to points anterior to the antennal bases. The frontal lines of cleavage are therefore the same in both *Haematopinus* and *Pediculus,* though in the latter the full length of the clefts is not evident until the ecdysial splits are formed.

The distribution of muscle attachments on the frontoclypeal region of the anopluran head is shown by Stojanovich in several species, including *Pediculus humanus* (fig. 7 C) and *Haematopinus suis* (D). It is to be seen that these muscles include, as in other insects, the cibarial dilators (*dlcb*) and the muscles of the labrum, hypopharynx, and pharynx, and in addition the antennal muscles. In *Pediculus* (A, C) a weakly sclerotized band of the cuticle crosses the head between the antennal bases, and appears to separate approximately the clypeal region from the frontal region, but it is questionable if it represents the epistomal sulcus of other insects. As between *Pediculus*

(C) and *Haematopinus* (D) there is no essential difference except in the relative length of the head and the presence of the interantennal band of weak cuticle in the former. Yet Stojanovich calls the arms

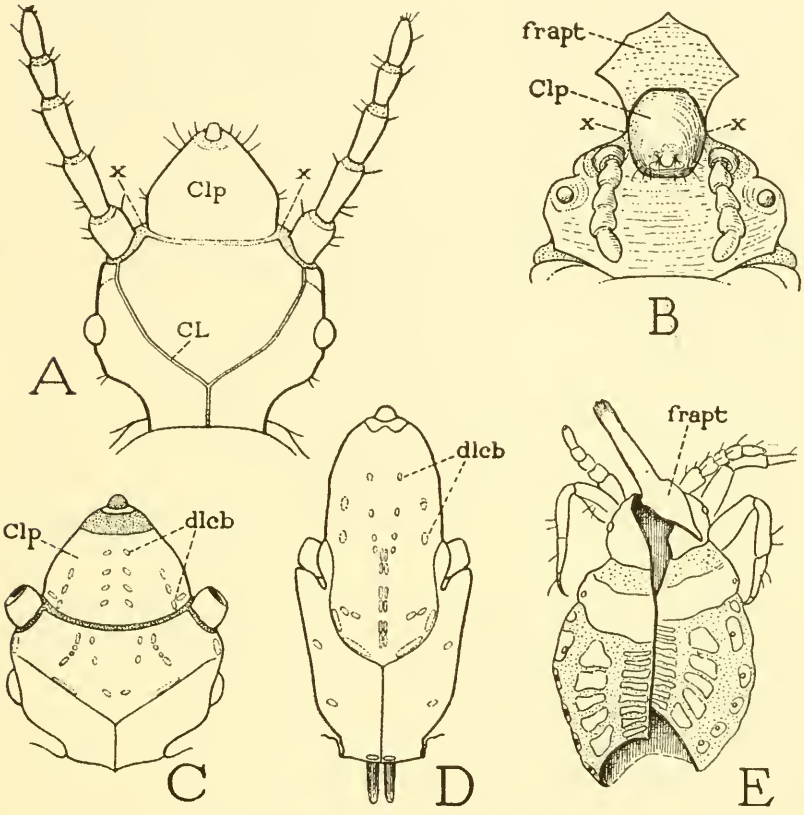


FIG. 7.—Anoplura and *Haematomyzus.*

A, *Pediculus humanus corporis* Deg., head of male nymph just before ecdysis. B, same, exuviae of head, ventral; frontal apotome turned downward between points *x, x,* parietal lobes with eyes and antennae spread laterally. C, same, head of adult (from Stojanovich, 1945), showing distribution of muscle attachments. D, *Haematopinus suis* (L.), head of adult (from Stojanovich, 1945), showing muscle attachments. E, *Haematomyzus elephantis* Piaget, exuviae of first nymphal instar (from Weber, 1939).

of the cleavage line in *Pediculus* "postfrontal sutures," and those of *Haematopinus* the "clypeofrontal suture." In the first, the facial area embraced by the arms is designated the "antennal segment," in the second the "clypeus." To reconcile the muscle attachments with this interpretation of the skeletal areas Stojanovich makes the statement

that the clypeus of *Haematopinus,* in the course of its posterior extension on the head, "has taken over the muscle origins that normally are found on the antennal segment." Why such an unnecessary and confusing interpretation should be invoked is not clear to the writer; it is scarcely to be credited that these two genera of Anoplura should differ so radically in the head structure when they appear to differ only in unessential ways. However, it should be noted that Stojanovich, earlier in his paper, says his interpretation is according to the "dictum of Ferris."

On the head of a young elephant louse, *Haematomyzus elephantis* Piaget, Weber (1939, 1939a) has shown that there is present a typical Y-shaped cleavage line, the frontal arms of which extend forward mesad of the antennae as in Anoplura. At ecdysis (fig. 7 E) the cuticle splits along the arms and there is cut out a triangular frontal apotome (*frapt*) in continuity with the dorsal wall of the elongate snout.

*Coleoptera.*—The larvae of beetles are of particular interest in a study of the lines of ecdysis on the head, inasmuch as they exhibit a transition in the position of the frontal arms from that in which the latter are called "postfrontal sutures" to that in which they become "frontal sutures," or, according to Cook (1943), the "clypeofrontal suture." A review of the many figures of heads of coleopterous larvae given by Böving and Craighead (1931) will show that in the majority of species illustrated the frontal arms of the cleavage line go either laterad of the antennae, or directly to the antennal fossae, but that in a few cases, as seen in *Dermestes* and *Eurypepla,* they run distinctly mesad of the antennae. The last condition, judging from the illustrations of Hayes (1929), evidently prevails in the larvae of Scarabaeoidea, though in this group the frontal lines may go also either to the antennal fossae, or laterad of them.

A few examples of the three courses taken by the arms of the cleavage line in coleopterous larvae are shown in figure 8 of the present paper. On the heads of *Trichodesma gibbosa* (B), *Crioceris asparagi* (C), and *Leptinotarsa decimlineata* (G) the arms end laterad of (or posterior to) the antennae; in the larvae of *Dytiscus* (A), *Chalcophora* (F), and *Hydrophilus* (I) they go directly to the antennal fossae, in *Dynastes tityus* (D) and *Alaus oculatus* (E) they run mesad of the antennae. It is clear, then, that in the Coleoptera there can be no distinction between "postfrontal sutures" and "frontal sutures"; there is here only a variation in the course taken by the arms of the exuvial cleavage line on the head. On the facial region embraced by the frontal arms (fig. 8 A) are attached the muscles of

the labrum, if these muscles are present, the precerebral dilators of the pharynx, the hypopharyngeal muscles (*hphmcl*), and the

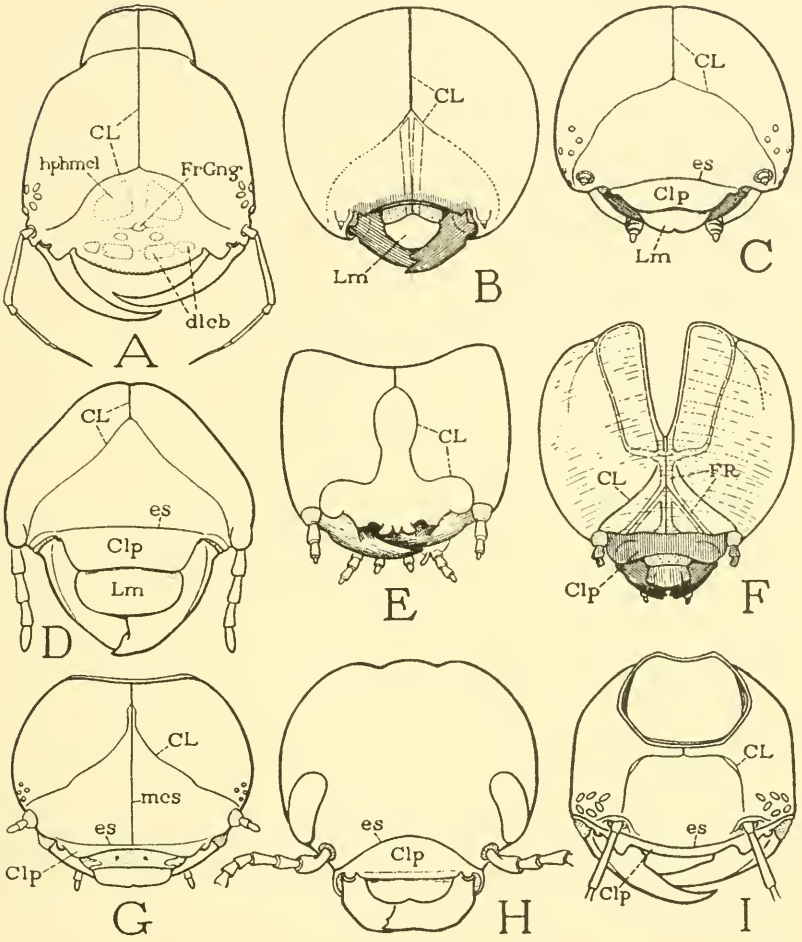


FIG. 8.—Coleoptera.

A, *Dytiscus* sp., Dytiscidae, head of larva, showing distribution of frontoclypeal muscles (see fig. 13 D). B, *Trichodesma gibbosa* (Say), Anobiidae, head of larva. C, *Crioceris asparagi* (L.), Crioceridae, head of larva. D, *Dynastes tityus* (L.), Scarabaeidae, head of larva. E, *Alaus oculatus* (L.), Elateridae, head of larva. F, *Chalcophora* sp., Buprestidae, head of larva. G, *Leptinotarsa decimlineata* Say, Chrysomelidae, head of larva. H, same, head of adult. I, *Hydrophilus* sp., Hydrophilidae, head of larva.

dilators of the cibarium (*dlcb*). The last are separated from the others by the frontal ganglion (*FrGng*) and its cerebral connectives. In some beetle larvae the frontoclypeal region is divided between frons

and clypeus by an epistomal sulcus (C, D, G, I, *es*), in others it is not so divided (A, B, E).

The larvae of Buprestidae present on the inner surface of the dorsal wall of the cranium a system of strong, branching ridges (fig. 8 F). The vertex is deeply emarginate for the insertion of long muscles from the thorax, but from the apex of the cleft a thick, median, internal ridge (*FR*) runs forward to the strongly sclerotized clypeal plate (*Clp*) and gives off a pair of diagonal side branches to the lateral parts of the clypeus. From the proximal end of the median ridge two lateral ridges turn back to the occipital margin of the cranium and are continuous around the latter with the thickened edges of the cleft of the vertex. In a surface view of the head the grooves of inflection that form these cranial ridges are visible as fine lines through the middle of the ridges. On the larval head only the frontal arms of the cleavage line are present; they are pale, weak, double-edged linear tracts of the cuticle (*CL*) diverging from the apex of the notch in the vertex to the bases of the antennae. Between the upper ends of the arms arise the muscles of the labrum.

The structural contrast between grooves of cranial ridges and the lines of cuticular cleavage is so pronounced that there can be no mistaking one for the other. Yet, Cook (1943) would identify the arms of the frontal ridge in the buprestid larva with the cleavage lines of the *Corydalus* larva (fig. 10 A), for no other reason, apparently, than that in each case the lines go mesad of the antennae. The cleavage lines of the buprestid larva Cook terms "postfrontal sutures," and the V-line formed by the branches of the median frontal ridge he calls the "clypeofrontal suture." To say the least, such an interpretation results in a most confusing inconsistency and is in no way necessary. The fact appears to be simply that the frontal area between the cleavage lines of the buprestid larval head is reinforced by ridges to brace the otherwise weakly sclerotized cranium against the strong clypeal plate, which carries the mandibles; the cranium is thus enabled to withstand the pull of the huge mandibular muscles, the bases of which cover almost the entire parietal regions. If the frontal ridges were absent, there would be little to distinguish the head of a buprestid larva from the head of any other beetle larva. A median ridge extending from the occipital margin of the head to the clypeus is present also in larvae of Chrysomelidae (fig. 8 G, *mcs*), but in the adult (H) all the larval lines except the epistomal sulcus are absent.

The lines of cuticular cleavage in the larva are probably not retained in any adult beetle, though other lines of the adult head have frequently been mistaken for them, which is to say, they have been

commonly termed the "epicranial suture." The water beetle, *Hydrophilus,* is sometimes cited as an example among the Coleoptera showing the presence of a complete "epicranial suture" in the adult insect (fig. 9 A) ; but an examination of the inner surface of the head (B) reveals the fact that the supposed "frontal sutures" form a thick internal ridge (*ER*) broadly united with a strong midcranial ridge (*mcR*) from the postocciput. The origin of the labral muscles (*lbrmcl*) above the transverse ridge demonstrates that the latter is the epistomal ridge (*ER*) and that its external sulcus (A, *es*) delimits the clypeus and not the frons. The true cleavage lines on the larval head of *Hydrophilus* (fig. 8 I, *CL*) are quite different things. Simi-

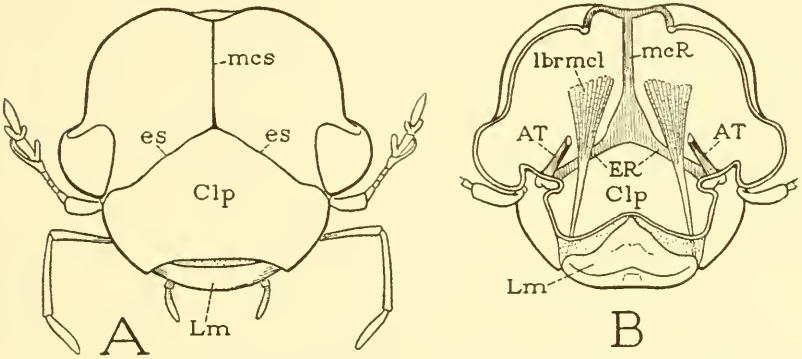


FIG. 9.—*Hydrophilus triangularis* Say, Hydrophilidae, head of adult.

A, facial view of head. B, inner surface of facial wall of head with labral muscles, showing a strong midcranial ridge (*mcR*) united with the epistomal ridge (*ER*), forming the supposed "epicranial suture" on the outer surface (A).

larly in other beetles the epistomal sulcus has often been mistaken for the arms of the "epicranial suture," as in figures by Stickney (1923), with the consequence that the clypeus is wrongly identified as the "frons."

In most of the Coleoptera, both larval and adult, the cibarium is a preoral food pocket (fig. 13 A, *Cb*) as it is in *Orthoptera* and other more generalized insects (fig. 2 D). The hypopharynx, though always united with the labium (fig. 13 A, F), retains its frontal muscles (*hphmcls*). In the dytiscid larvae, however, the cibarium becomes a closed chamber by the interlocking of the labrum with the labium, and is drawn out between the mandibular bases into a long transverse tube, the hypopharyngeal floor of which, or sitophore, takes the form of a strongly sclerotized gutter. The cibarial dilator muscles (fig. 13 D, *dlcb*) are therefore distributed transversely on the distal part

of the frontoclypeal area of the head (fig. 8 A) anterior to the frontal ganglion (*FrGng*). The large hypopharyngeal muscles (fig. 8 A; fig. 13 D, *hphmcl*), on the other hand, arise behind the frontal ganglion connectives; they are inserted on a pair of broad platelike lobes of the sitophore, representing the oral arms of the hypopharynx in other insects (fig. 2 D; fig. 13 A, F, *y*).

*Neuroptera* (*Megaloptera and Planipennia*).—The arms of the cleavage line on the head of neuropterous larvae go always mesad of the antennae in the manner characteristic of most Holometabola, and at their greatest extent they cut entirely through the clypeal area. On the adult head the cleavage line is absent.

The Megaloptera, including *Raphidia,* show very clearly the interantennal position of the frontal arms of the cleavage line (fig. 10 A, D, G). In the larva of *Sialis* (D) there is present a fully developed epistomal sulcus (*es*) setting off the clypeus from the frontal area behind it, and the arms of the cleavage line end at this groove. In *Corydalus* (A), *Chauliodes* (C), and *Raphidia* (G), however, the epistomal sulcus is represented only by short lateral grooves (A, *es'*, *es'*) containing the anterior tentorial pits (*at, at*), and in these forms the frontal arms of the cleavage line extend through the clypeal area to the distal margin of the latter. At ecdysis, as seen in *Chauliodes* (C), the frontal clefts cut out a triangular frontoclypeal apotome (*frcapt*). The frontoclypeal nature of the apotomal triangle is shown by the origin of the labral and hypopharyngeal muscles on its upper part (A, *lbrmcls, hphmcl*) and the attachment of the cibarial muscles (*dlcb*) on its lower part. In the larva of *Sialis,* in which the epistomal sulcus is complete (D), these same groups of muscles, as shown by Röber (1941), arise respectively on the frontal and clypeal areas of the prospective apotome.

The adult megalopteran head is like the larval head with respect to the development of the epistomal sulcus, the sulcus being complete in the imago of *Sialis* (fig. 10 E, F, *es*) as it is in the larva (D), but interrupted between the tentorial pits in *Corydalus* (B), *Chauliodes,* and *Raphidia* as it is in the larvae of these forms (A, C, G). The line of exuvial cleavage in the larval cuticle, however, is suppressed in the adults of all these latter genera (B). The adult head of *Sialis* presents a median groove that forks anteriorly into a pair of weakly impressed lines (E, F, *mcs*) diverging behind the antennal bases. Though these grooves of the imaginal head of *Sialis* are regarded by Röber (1941) as the "coronal suture" and the "frontal sutures," Röber notes that the latter do not have the position of the frontal lines of the larva, which he says are preformed lines for rupture of the cuticle at ecdysis.

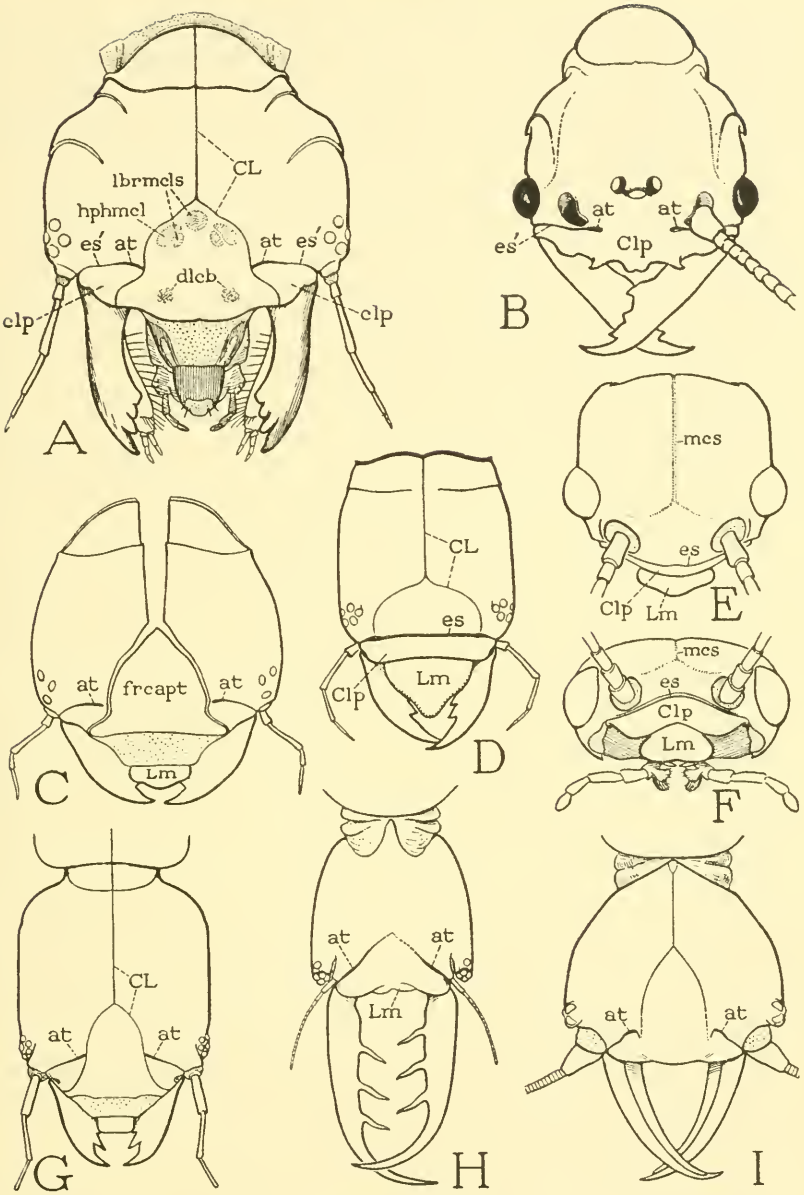


FIG. 10.—Neuroptera.

A, *Corydalus cornutus* (L.), Sialidae, head of larva, showing distribution of frontoclypeal muscles. B, same, head of adult female. C, *Chauliodes* sp., Sialidae, exuviae of head. D, *Sialis* sp., Sialidae, head of larva. E, *Sialis infumata* Newm., Sialidae, head of adult. F, same, anterior view of adult head. G, *Raphidia* sp., Raphidiidae, head of larva. H, *Myrmeleon* sp., Myrmeleonidae, head of larva. I, *Hemerobius* sp., Hemerobiidae, head of larva.

The Y-line on the adult head of *Sialis,* in fact, is merely a shallow groove of the sclerotic cranial wall, and would appear to have no direct relation to the exuvial cleavage line of the larva. Probably of the same nature is a similar head line in certain other adult Neuroptera, as that regarded by Ferris (1940) as the persisting "epicranial suture" in *Plega signata* (Hagen). A dried specimen of *Climaciella brunnea* (Say) shows a faintly impressed line on the head as in *Plega signata,* but on boiling in water the line completely disappears.

Among the Planipennia the hemerobiid larva (fig. 10 I) resembles the larvae of *Corydalus, Chauliodes,* and *Raphidia* in that the epistomal sulcus is incomplete and a Y-shaped line of ecdysis is present with the arms going mesad of the anterior tentorial pits (*at, at*), though they do not extend through the clypeal region. During ecdysis of hemerobiid larvae, Killington (1936) says, "the thorax becomes distended, and a split occurs dorsally along the thorax and extends along the epicranial and frontal sutures of the head."

In some of the other Planipennia, as *Chrysopa, Myrmeleon,* and *Ascalaphus,* the larval head shows no trace of the coronal line (fig. 10 H). Distally on the upper surface of the head, however, is a triangular area set off by the arms of a V-shaped groove containing the anterior tentorial pits (H, *at, at*). Sundermeier (1940) calls this area the "labrum," but he gives no attention to muscle attachments. In the *Myrmeleon* larva the cibarial muscles arise anteriorly on the triangle, which fact, together with the articulation of the mandibles on its lateral lobes, leaves no doubt that this area beyond the V-shaped groove is in part the clypeus. Owing to the immobility of the labrum, and the absence of a free hypopharynx, there appear to be no labral or hypopharyngeal muscles to identify the upper part of the triangle as the frons, but it should be noted that the head region above it is entirely occupied by the mandibular and maxillary muscles. The area in question, therefore, must represent the frontoclypeal region of *Hemerobius* (I) and of the Megaloptera, together with the labrum, the frontal area being reduced because of the absence of the usual frontal muscles.

There is little evidence available as to the manner of ecdysis in those Planipennia whose larvae have no apparent coronal line of exuvial cleavage on the head. Smith (1922) says of the Chrysopidae that at ecdysis the dorsal split of the thorax extends forward to the head. Henriksen (1932), in reference to Smith's observation, notes that if the cleavage line stops at the head, "this agrees with the fact

that a Y-shaped suture cannot be discovered on the head of a *Chrysopa*-larva."

*Mecoptera.*—The line of the exuvial cleft on the larval head of Mecoptera (fig. 11 A, B, C) is identical with that of the Megaloptera in that the frontal arms go between the anterior tentorial pits and extend through the clypeus to points just mesad of the anterior mandibular articulations. The same structure is shown by Steiner (1930) and by Bierbrodt (1942) in the larval head of *Panorpa communis* L. (fig. 11 C), and by Applegarth (1939) and Cook (1944) in that of *Apterobittacus apterus* (MacL.) (B).

The area embraced by the arms of the cleavage line on the larval head of *Panorpa communis* is shown by Steiner and by Bierbrodt to be itself divided into three parts by a Y-shaped groove (fig. 11 C, *FR*), the stem of which is continuous with that of the line of cleavage (*CL*). Bierbrodt contends that the arms of this inner Y are the true "frontal sutures," while those of the outer Y (*CL*) are secondary lines of splitting at ecdysis. The latter, however, clearly are to be identified with the frontal lines of cleavage in other insects, which are commonly called the "frontal sutures." The lines of the inner Y, therefore, are more reasonably interpreted by Steiner (1930) as secondary grooves forming internal ridges correlated with muscle attachments; the labral muscles take their origins in the angle between the arms. In the larva shown at A of figure 11 the frontal area between the arms of the cleavage line is marked only by a shallow pigmented groove in the form of an inverted V, and apparently something similar is present in *Apterobittacus* as illustrated by Applegarth (1939); in *Harpobittacus* and *Boreus* the frons shows no corresponding structure.

The frontal and the clypeal areas of the mecopteron larvae are separated by a broad depression or a groove (fig. 11 A, B, C). The labral and the cibarial muscles are shown both by Bierbrodt (1942) and by Cook (1944) to arise respectively on the areas above and below this groove (B), but Cook regards the entire region between the arms of the cleavage line as the "clypeus," an interpretation entirely inconsistent with his own showing of the muscle attachments.

The line of exuvial cleavage so conspicuous on the larval head is greatly reduced or obliterated in the adult mecopteron. No trace of it is shown by Ferris and Rees (1939) in *Panorpa nuptialis* Gerst., by Evans (1942) in *Nannochorista maculipennis* Tillyard, or by Crampton (1932) in *Merope*. In *Panorpa communis* L., Heddergott (1938) describes and figures a small V-shaped groove over the median ocellus, which he regards as a remnant of the "frontal

sutures," and Issiki (1933) shows a similar line in *Panorpodes paradoxa* MacL.), though he says there is a suppression of the "frontal sutures" in the Panorpidae. On the pupal head of *Panorpa communis* Bierbrodt (1942) shows the presence both of "frontal sutures" and a distinct "coronal suture." Otanes (1922) discusses

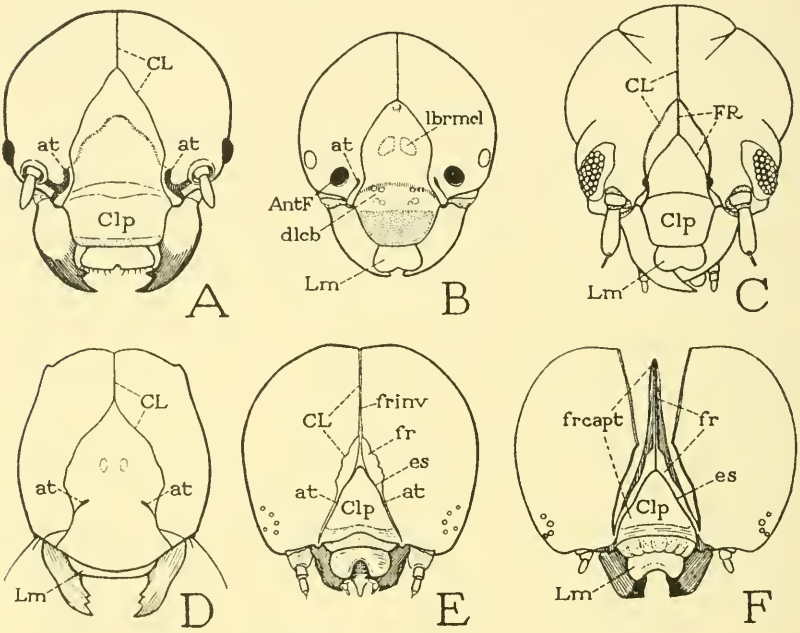


FIG. 11.—Mecoptera, Trichoptera, and Lepidoptera.

A, head of a panorpid larva. B, *Apterobittacus apterus* (MacL.), Mecoptera, head of larva (from Cook, 1944), showing distribution of frontoclypeal muscles. C, *Panorpa communis* L., Mecoptera, head of larva (from Bierbrodt, 1942), showing lines of Y-shaped frontal ridge (*FR*) between frontal arms of cleavage line (*CL*). D, head of a trichopterous larva. E, *Malacosoma americana* (F.), Lepidoptera, head of larva. F, *Hemerocampa leucostigma* (A. & S.), Lepidoptera, exuviae of head at last ecdysis.

"arms of the epicranial suture" in adult Mecoptera, but evidently he has reference to the epistomal and subgenal sulci.

*Trichoptera.*—The head of a trichopterous larva (fig. 11 D) is very similar in its facial structure to that of the larvae of Mecoptera (A, B, C) and of such Megaloptera as *Corydalus, Chauliodes,* and *Raphidia* (fig. 10 A, C, G) in that the arms of the cleavage line extend to the margin of the clypeus mesad of the mandibular articulations. It furthermore resembles the head of the megalopterous forms just mentioned in the absence of a separating groove between

the frontal and clypeal areas embraced by the cleavage lines. In two species examined by the writer, however, the anterior tentorial pits lie mesad of the arms of the cleavage line (fig. 11 D), though in a species figured by Cook (1944) the pits are seen to lie in mesal angulations of the arms. Inasmuch as it is shown by Cook that the labral muscles and the hypopharyngeal muscles (mouth-angle retractors) arise above the level of the tentorial pits, while the cibarial muscles are on the widened area below the pits, it is evident that the region of the apotome is frontoclypeal, though Cook regards the whole triangle as the "clypeus."

*Lepidoptera.*—The head of a caterpillar is characterized by an upward extension of the clypeus in the form of a triangle on the lower part of the face (fig. 11 E, *Clp*), and by a complete invagination (*frinv*) of the upper part of the frontal area embraced by the arms of the cleavage line (*CL*). Below the invaginated part of the frons, the arms of the cleavage line diverge and run down along the sides of the clypeus to the mandibular articulations, thus defining a V-shaped frontal area (*fr*) inverted over the apex of the clypeus. The two arms of the frontal V are commonly termed the "adfrontals" by students of lepidopterous larvae, who have long regarded the triangular plate of the face as the "frons." A new interpretation by DuPorte (1946) relegates the clypeus to the conjunctiva which attaches the labrum to the cranium, and defines the facial triangle as an "antefrons," the groove bounding the apex of the triangle above the anterior tentorial pits being regarded as a "transfrontal suture," and the parts below the pits as "frontoclypeal sutures."

The several conflicting opinions that have been held concerning the homologies of the external lines and enclosed areas of the caterpillar head well illustrate the diversity of interpretation that may arise from a study of external features alone. Plausible evidence may be deduced from superficial characters for at least three interpretations, but, for this very reason, none of them is convincing.

The true structure of the median facial parts of the caterpillar cranium is revealed at the final ecdysis. On the head exuviae (fig. 11 F) the frontal clefts follow the arms of the cleavage line (E, *CL*) from the top of the head to the base of the clypeal triangle. Between the separated lateral hemispheres of the cranium there is now exposed the long apotome (F, *frcapt*), which is seen to include the triangular clypeus (*Clp*) and both the exposed and the invaginated parts of the frontal component (*fr*). The same structure can be demonstrated by treating the intact head with caustic. The median groove of the caterpillar's cranium (E, *frinv*), therefore, is not the coronal stem

of the cleavage line, nor is it a midcranial sulcus; its margins are the approximated frontal arms of the cleavage line along the sides of the narrow invaginated part of the frons (F, *fr*).

Further evidence that the triangular plate of the caterpillar's head is the clypeus is seen in the fact that upon it (fig. 13 B, *Clp*) are attached the facial muscles (*cbmcls*) that lie anterior to the frontal ganglion and its brain connectives (*FrGng*). These preganglionic muscles are the cibarial dilators, though the cibarium of the caterpillar (*Cb*) appears to be continuous with the stomodaeum, and in no known insect are the cibarial muscles attached elsewhere than on the clypeus. On the other hand, the postganglionic muscles (*phmcls*), or precerebral dilators of the pharyngeal region of the stomodaeum, take their origins on the narrow strips (*fr*) between the cleavage lines and the apex of the clypeal triangle, and these muscles in all insects are consistently frontal muscles. Finally the labral muscles, which also characteristically arise on the frons, take their origins in the caterpillar far back on the median invagination of the cranium above the clypeus. All these skeleto-muscular relations, therefore, demonstrate that the exuvial apotome of the caterpillar head represents the frontoclypeal region between the arms of the cleavage line in other holometabolous larvae.

A rupture of the head cuticle does not take place at each ecdysis with all caterpillars. Many species shed the head capsule entire except at the last ecdysis, when the cranial cuticle splits in the usual manner. The head exuviae of the younger instars may be detached, or remain connected with the body skin. According to Frost (1922), in the bud moth, *Tmetocera ocellana* Schiff., the head capsule comes off separately at each ecdysis, the cuticular rupture taking place between the head and the thorax. In the Hesperidae, Henriksen (1932) says, "no opening of the head capsule takes place; the head of the new instar is drawn back through the occipital foramen of the old head capsule and out through the rent in the thorax." Usually in such cases it is to be observed that the head of the new instar develops in the thorax of the old skin before ecdysis. Hess (1937) describes the moulting of *Hemerocampa leucostigma* (A. & S.), *Hyphantria cunea* (Drury), and *Malacosoma americana* (F.) in all of which apparently the head capsule is shed entire at each ecdysis except the last, which takes place in the cocoon.

*Diptera.*—For a study of the cleavage lines on the larval head of lower Diptera, the mosquito furnishes a good subject, since many species have been described and figured, and it is easy to observe the fact that the ecdysial splits follow the lines ordinarily called the

coronal and frontal "sutures." A review of recent papers on the head of larval Diptera will show, moreover, that the structure is essentially the same in all dipterous families in which the larva has a free head capsule. Anthon (1943) has described and figured the larval head in representatives of the Rhyphiceridae, Ptychopteridae, Trichoceridae, and Psychodidae; Cook (1944b) gives a full description of the head structure and musculature in a species of *Chironomus;* Ross and Roberts, in their Mosquito Atlas (1943), illustrate the larval head structure in 33 species of *Anopheles,* besides a species each of *Aedes* and *Culex,* and Cook (1944a) describes species of *Theobaldia, Anopheles, Lutzia,* and *Armigeres,* giving both the structure and the musculature of the larval head and mouth parts.

In all the forms illustrated by the writers just mentioned, the head of the larva presents a prominent Y-line having usually a short coronal stem and widely divergent frontal arms that go mesad of the antennae and embrace most of a large facial area that continues downward without interruption to the base of the labrum (fig. 12 A-D, F). As shown here in *Aedes* (E) and *Anopheles* (G), the ecdysial splits in the head exuviae extend to points just mesad of the antennal bases. On the large shield-shaped facial area of the apotome thus separated from the parietal lobes are attached in the intact head, as shown by Cook (1944a), the muscles normal to the frons and the clypeus (D). There would hence appear to be no reason for regarding this area as other than that of the frontoclypeal region of the cranium. However, Anthon (1943) designates it the "frons," and Cook (1944a) calls it the "clypeus." The first assumes that a downward extension of the frons has crowded out the clypeus, or reduced it to a pair of lateral lobes at the base of the labrum, and presumably that the frons has taken over the clypeal muscles; the second assumes the opposite, namely, that the clypeus has invaded the region of the frons and has appropriated the frontal muscles. If either assumption is necessary, one would seem to be as good as the other, but neither is substantiated by evidence to show that a shifting or transposition of any part of the cranial surface has taken place. The muscle attachments maintain the same relative positions that they have in insects in which the frontal and clypeal areas are separated by an epistomal groove, or in other insects in which this groove is absent. Since an epistomal sulcus is not usually present in holometabolous larva, and is variable in its occurrence even in adult insects, and since we have no evidence in dipterous larvae of either the frons or the clypeus having invaded the territory of the other, there is no reason for regarding the facial region between the arms of the ecdysial line and

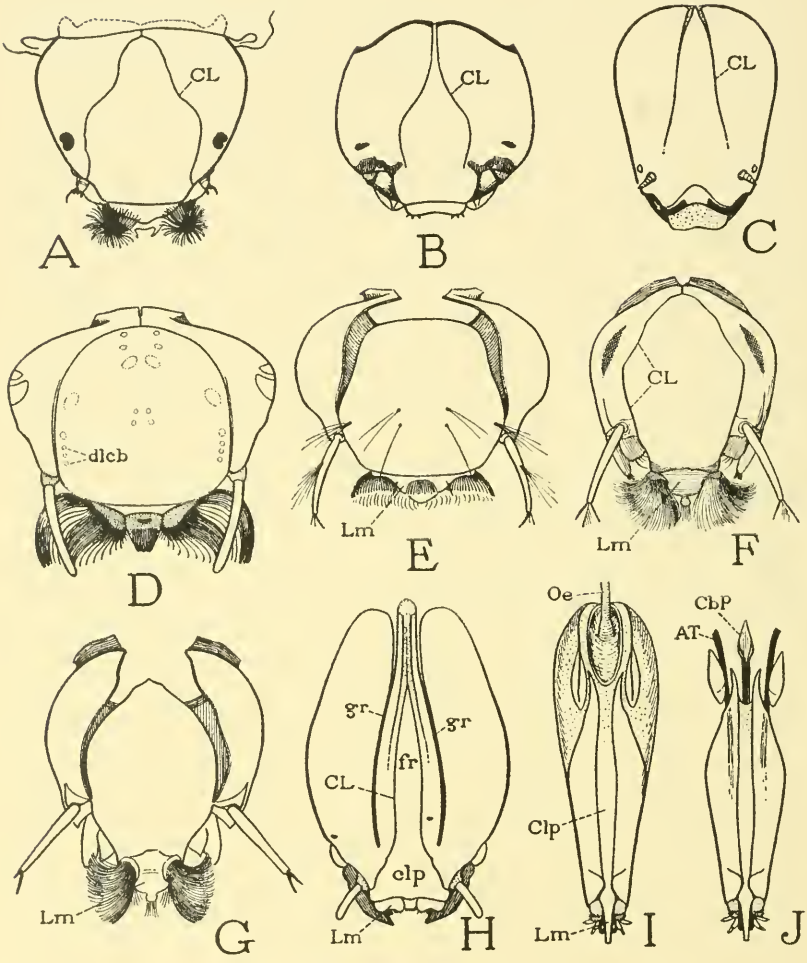


FIG. 12.—Diptera.

A, *Ptychoptera* sp., Liriopidae, head of larva (outline from Anthon, 1943). B, *Bibio albipennis* Say, Bibionidae, head of larva. C, *Lycoria* sp., Fungivoridae, head of larva. D, *Theobaldia incidens* (Thomson), Culicidae, head of larva (from Cook, 1944), showing distribution of frontoclypeal muscles. E, *Aedes increpitus* Dyar, Culicidae, exuviae of head. F, *Anopheles maculipennis freeborni* Aitken, Culicidae, head of larva. G, *Anopheles farauti* Lav., Culicidae, exuviae of head. H, *Tipula abdominalis* (Say), Tipulidae, head of larva. I, *Tabanus reinwardtii* Wied., Tabanidae, head of larva. J, same, exuviae of larval head.

the labrum as other than the unseparated areas of the frons and clypeus. If the cleavage lines were not present, it is doubtful if anyone would think of making any other interpretation. In adult Diptera the frontal and clypeal areas are usually distinctly separated, and the clypeus is identified as such by the attachments on it of the dilator muscles of the cibarial pump.

As already noted, Cook (1944a) has shown the distribution of muscle attachments on the frontoclypeal region in the head of the mosquito larva; the pharyngeal muscles are attached on the upper part (fig. 12 D), the cibarial muscles (*dlcb*) laterally on the lower part. In addition, however, are four groups of fibers, called by Cook the "messorial" muscles, which vibrate the labral mouth brushes, and which take their origin on the upper, presumably frontal, area of the frontoclypeal region. Cook concludes that these "messorial" muscles are probably specialized groups of cibarial fibers, but their functional connection with the labrum and their frontal origin would suggest that they are labral muscles, though admittedly it is difficult to identify them with muscles of the labrum in other insects.

The larva of Tipulidae may be taken as an example of the type of dipterous larvae in which the head is retracted into the thorax but still retains a relatively generalized structure. The dorsal surface of the ovoid head (fig. 12 H) presents two deep, longitudinal sclerotic grooves (*gr, gr*), between which the arms of the cleavage line (*CL*) demark a narrow frontal area (*fr*) continuous anteriorly with a wider clypeal area (*clp*) betwen their divergent distal parts, which end on the clypeal margin just beyond the bases of the antennae.

An examination of the head musculature of the tipulid larva shows a generalized arrangement of the cibarial and precerebral stomodaeal muscles (fig. 13 C), though the brain lies in the thorax. The cibarial muscles (*dlcb*) arise on the clypeal region (*Clp*), and the pharyngeal muscles of the stomodaeum (*phmcls*) take their origin on the frontal area (*fr*) between the cleavage lines. The two sets of muscles are separated by the frontal ganglion connectives, which turn back along the sides of the stomodaeum (*FrCon*) to the brain. On the frontal area are attached also the single, median pair of labral muscles (*lbrmcl*).

A quite different type of head structure is seen in the retracted head of a tabanid larva (fig. 12 I). Here the head is slender and club-shaped, thickened basally and tapering distally. On the dorsal surface two longitudinal lines separate a long, narrow median area (*Clp*), continuous distally with the labrum (*Lm*), from a pair of lateral plates of the head that end proximally in tapering points on the dorsal

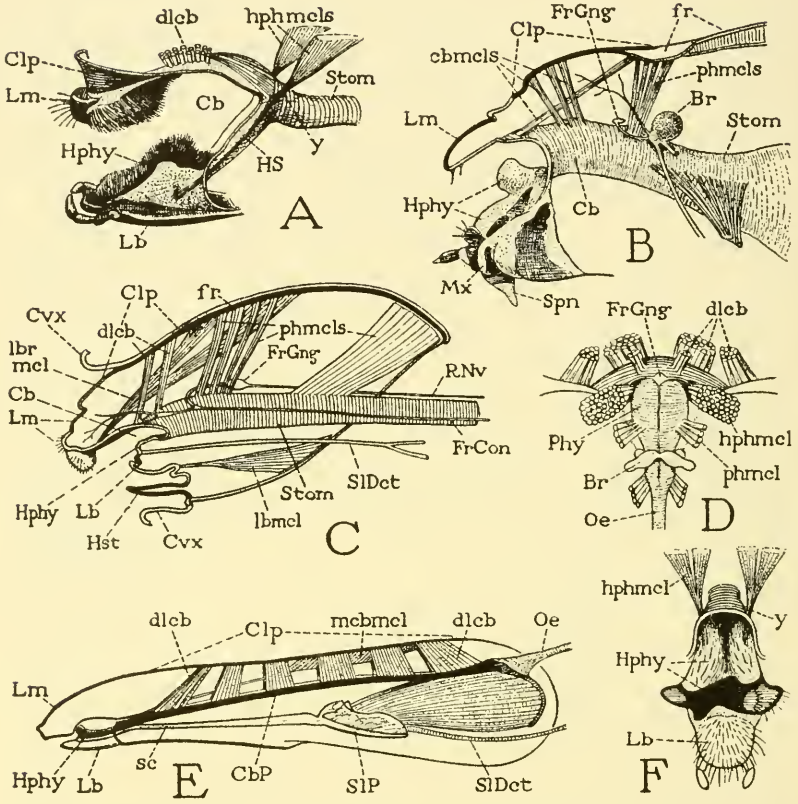


FIG. 13.—Examples of widely different head structures of various insects having the hypopharynx and labium united, showing the constant relation of the cibarial, hypopharyngeal, and stomodaeal muscles to the frontal ganglion connectives and to the clypeal and frontal areas of the head wall.

A, *Popillia japonica* Newm., Coleoptera, adult, lateral view of mouth region: cibarium (*Cb*) entirely preoral, frontal muscles of hypopharynx inserted on oral arms (*y*) of hypopharyngeal suspensoria (*HS*). B, *Malacosoma americana* (F.), Lepidoptera, larva, section of anterior part of head, showing cibarial and stomodaeal muscles; cibarium postoral, continuous with stomodaeum; brain in head. C, *Tipula abdominalis* (Say), Diptera, larva, sagittal section of invaginated head: cibarium preoral; brain in thorax. D, *Dytiscus* sp., Coleoptera, larva, dorsal view of cibarium and pharynx, with muscles: cibarium postoral, transversely elongate, its dilator muscles (*dlcb*) separated from hypopharyngeal and pharyngeal muscles by frontal ganglion connectives. E, *Tabanus reinwardtii* Wied., Diptera, larva, sagittal section of head: cibarium (*CbP*) a long sucking tube with its dilator muscles extending along entire dorsal surface of cranium; stomodaeum and brain in thorax. F, *Dynastes tityus* (L.), Coleoptera, larva, dorsal view of united hypopharynx and labium, showing frontal muscles of hypopharynx attached on oral arms penetrating the mouth angles.

surface. Laterad of the ends of these plates are two small elongate oval sclerites, but the rest of the basal part of the head is weakly sclerotized. When the head capsule is opened it is seen to contain three long, strongly sclerotic rods, two of which are lateral, and one median. The lateral rods arise at the base of the labrum and are attached posteriorly by their apodemal inflections to the posterior oval sclerites of the head surface. These rods evidently are tentorial arms. The median rod is the sclerotic floor of a tube extending the full length of the head (fig. 13 E, *CbP*), opening posteriorly into the oesophagus (*Oe*). This rod is clearly the floor (sitophore) of the greatly elongate, tubular cibarium; on the invaginated roof of the tube are inserted a series of paired muscles (*dlcb*) that arise on the median area of the dorsal head wall (fig. 12 I, *Clp*), which is thus seen to be the clypeus. In addition to the paired dilator muscles there is present also a median cibarial muscle (fig. 13 E, *mcbmcl*) inserted anteriorly by a long tendon. Confirmatory evidence that the sucking tube of the tabanid larva is the cibarium is seen in the fact that on a descending arm from the posterior end of its floor are attached the huge muscles of the unusually large salivary pump (*SlP*). The salivary pump muscles are always attached on the floor of the sucking pump in Diptera having a salivary pump, since these muscles primarily are hypopharyngeal and the floor of the pump is the sitophore of the hypopharynx in generalized insects.

At ecdysis the head of the tabanid larva shows none of the usual exuvial clefts. The soft posterior part of the head is torn off, while the sclerotic parts remain intact (fig. 12 J), with the tentorial arms (*AT*) and the sclerotic floor of the sucking pump (*CbP*) projecting from the posterior opening. It is to be noted that this exuvial remnant of the tabanid larval head is little more than the so-called "pharyngeal" skeleton of a cyclorrhaphous larva, which correctly is the combined clypeus and cibarial pump, represented in the adult fly by the composite structure commonly known as the "fulcrum."

*Hymenoptera.*—There is not much information available on the manner of ecdysis in Hymenoptera, but a few observations make it appear that the splitting of the head cuticle follows the usual lines in the Tenthredinoidea, and that in the higher Hymenoptera it is limited to a cleft down the middle of the face.

The head of a tenthredinid larva, as seen in *Neodiprion* (fig. 14 A), presents a prominent forked line of cleavage (*CL*), the widely divergent arms of which enclose a large quadrate facial region extending to the clypeal margin. The muscles attached on this region are shown by Parker (1934) in *Pseudoclavellaria amerinae* (L.), and by

Cook (1944) in *Zaraea americana* (Cress.), to include, on the upper part, the labral and pharyngeal muscles, and, on the lower part, the cibarial muscles. The two sets of muscles are separated as in other insects by the frontal ganglion and its brain connectives. The region in question, therefore, is frontoclypeal. The arms of the cleavage line, however, turn somewhat mesally at their distal ends and do not

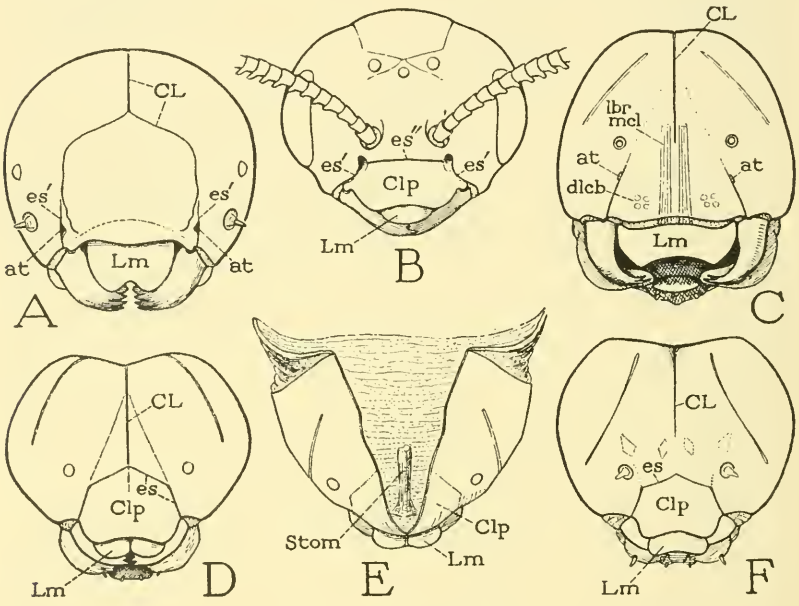


FIG. 14.—Hymenoptera.

A, *Neodiprion sertifer* (Geoff.), Diprionidae, head of larva. B, *Neodiprion dyari* Rohwer, Diprionidae, head of adult female. C, *Polistes* sp., Vespidae, head of larva. D, *Vespula* sp., Vespidae, head of larva. E, *Vespa crabro* L., Vespidae, head exuviae of last larval instar. F, *Xylocopa* sp., Apidae, head of larva.

extend entirely through the clypeal area. Just laterad of each mandibular condyle of the clypeus a short groove (*es'*) containing the anterior tentorial pit (*at*) extends upward close to the corresponding arm of the cleavage line, but does not blend with the latter. This groove and its mate on the other side evidently are larval representatives of the epistomal sulcus of the adult (B, *es*). At ecdysis the exuvial splits follow the frontal cleavage lines, so that the apotome does not carry the anterior tentorial arms.

The adult head of *Neodiprion* (fig. 14 B) differs in many respects from that of the larva (A). The larval line of ecdysis is entirely absent, the antennae have taken positions much nearer the middle of

the face, the grooves containing the anterior tentorial pits converge toward the bases of the transposed antennae, and are now connected by a transverse groove (*es''*) between the pits, there being thus established in the adult a complete epistomal sulcus setting off the clypeus from the frons. A comparison with other insect larvae in which the arms of the cleavage line go mesad of the tentorial pits (fig. 10 A, C, G, I) will show that in such cases the epistomal sulcus is either absent or represented only by short lateral grooves containing the pits. On the other hand, when the cleavage lines do not reach the level of the tentorial pits, a complete epistomal sulcus may be present in the larva (fig. 10 D). Also the sulcus may extend between the tentorial pits when the exuvial cleft does not follow the arms of the obsolete cleavage line, as seen in *Vespula* (fig. 14 D) and *Xylocopa* (F).

The head transformation of *Neodiprion* from larva (fig. 14 A) to adult (B) shows clearly that the epistomal sulcus of the latter has no relation to the cleavage line of the larva. The interpretation given by Cook (1944) in reference to *Zaraea americana* that in the larva the cleavage line of the head is the "clypeofrontal suture" seems, therefore, quite inconsistent with the facts. The groove appearing in the adult of *Neodiprion* that connects the anterior tentorial pits runs between the two sets of facial muscles that are separated by the frontal ganglion, and this groove, therefore, is the epistomal sulcus, or clypeofrontal "suture." The cleavage lines of the larva simply disappear with the transformation to the imago.

In the wasps and the bees the larval head shows no distinct arms of the cleavage line such as those of the Tenthredinoidea, but the coronal line is always present (fig. 14 C, D, F, *CL*). This fact would suggest that the exuvial split at ecdysis follows the coronal line alone. The only example of the head cleavage at ecdysis in the higher Hymenoptera here presented, however, is that of *Vespa crabo* (E), in which it is to be seen that the head exuviae are bisected by a median cleft from the occiput to the labrum. Faintly impressed lines present on the head of *Polistes* (C) and *Vespa* (D), converging upward from the tentorial pits, are possibly remnants of the unused arms of the cleavage line. The larval head of *Polistes* (C) resembles the tenthredinid larval head (A) in that there is no transverse sulcus connecting the tentorial pits. In the larvae of *Vespula* (D) and *Xylocopa* (F), however, this sulcus is present as in the adult of *Neodiprion* (B) and sets off the clypeus from the frons. The manner of ecdysis in the Hymenoptera needs further investigation.

*Symphyla.*—The symphylid head becomes of interest in connection with a study of the cranial "sutures" of insects, because the Symphyla have been much exploited as possible ancestors of the hexapods. Ferris (1942), in fact, claims to find the basic structure and even the segmentation of the insect head fully revealed in the adult head of *Scutigerella immaculata* (Newp.).

The dorsal surface of the head of *Scutigerella immaculata* (fig. 15 A) presents a prominent Y-shaped median line (*a*), and a pair of lateral lines (*b, b*) diverging from near the base of the stem of the median line. The Y-line is the external mark of a strong internal ridge, the divergent arms of which extend toward the antennae and unite with the thickened rims of the antennal fossae opposite the pivotal processes that support the antennae. This Y-shaped ridge of *Scutigerella* must serve to strengthen the otherwise thin wall of the head. The arms of the ridge are regarded by Ferris (1942, p. 29) as representing the "clypeofrontal suture" of insects. Of the external groove of the median stem, Ferris says, "it evidently is the suture, common to so many arthropods, which breaks at the time of ecdysis, and there is no reason to regard it as anything different from the 'coronal' suture of insects." A very good reason to the contrary, however, may be drawn from the description by Williams (1907) of ecdysis in *Scutigerella immaculata,* or the same as recounted by Henriksen (1932), from which it would appear that this symphylid sheds its cuticle at ecdysis in the manner of other myriapods, namely, in most cases, by a transverse rent behind the head. "The most common method," Williams says, "is to disarticulate the cast at the junction of head and first segment and to creep out forward." But the animal may escape from the moulted skin also "by tearing between the legs or just above the attachment of the legs on either side or by tearing the dorsal covering longitudinally or by disarticulating the cast somewhere on the dorsal side and extricating the body." The Y-shaped "suture" on the head of *Scutigerella,* therefore, Henriksen points out, "does not play any role in moulting." A similar Y-shaped ridge is present on the head of some diplopods (fig. 15 B), but the arms in this case go to the eyes instead of the antennae. Finally, it should be noted that a Y-line of exuvial cleavage on the head is a feature peculiar to insects, and is not "common to so many arthropods" as Ferris asserts.

The two lines that form the V on the head of *Scutigerella* (fig. 15 A, *b, b*) are of quite a different nature from the Y-line, being merely clear linear tracts of the cuticle devoid of the minute setae that thickly cover the rest of the head surface. They begin as apparent clefts in

the margins of the cranial sclerotization above the postantennal membranes containing the organs of Tömösvary (A, C), and converge posteriorly to points close to the base of the median cranial ridge.

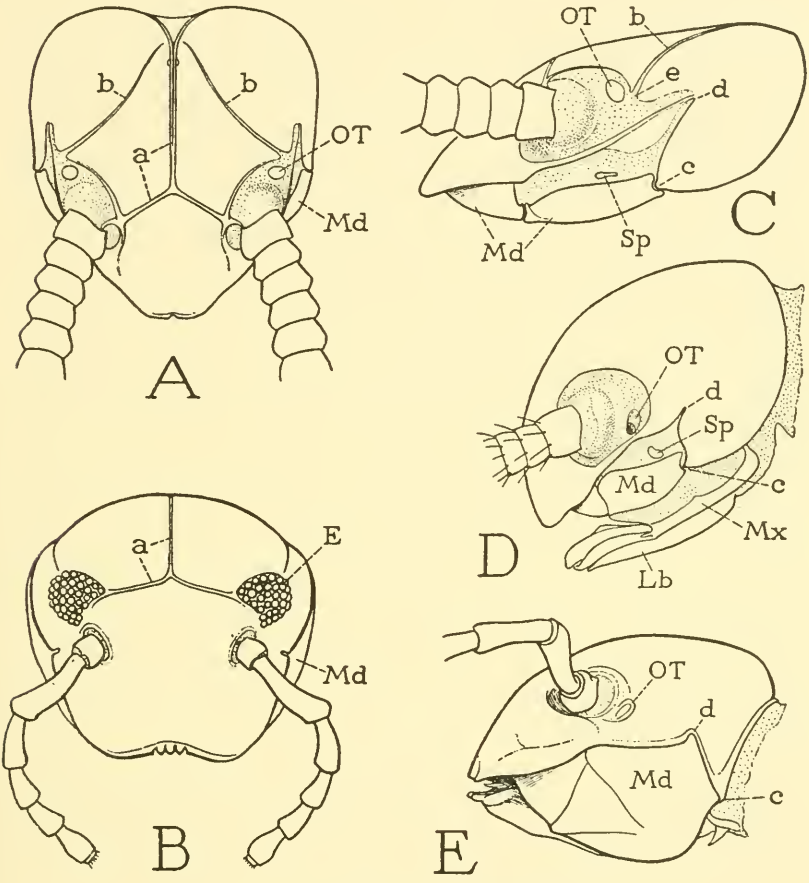


FIG. 15.—Symphyla and Diplopoda.

A, *Scutigerella immaculata* (Newp.), Symphyla, head of adult, dorsal. B, *Habrostrepus* sp., Diplopoda, head of adult. C, *Scutigerella immaculata* (Newp.), Symphyla, head of adult, lateral. D, *Hanseniella agilis* Tiegs, Symphyla, head of adult, lateral (outline from Tiegs, 1940). E, *Apheloria coriacea* (Koch), Diplopoda, head of adult, lateral.

In discussing these head lines of *Scutigerella,* Ferris (1942, p. 29) makes the following remarkable statement: "Another transverse suture begins at the side of the head, immediately in front of each primary mandibular articulation. For a short distance it coincides

with the border of the cranium which takes the form of a small V-shaped notch. Thence the suture continues over the front of the head where it forms a large, inverted V posterior to the antennae." This description can best be followed by reference to a side view of the head (fig. 15 C). Beginning at the mandibular articulation (*c*) the alleged suture "coincides with the border of the cranium" to the point *d;* here it jumps the subantennal bar (which is the true lower lateral margin of the cranial wall, but is conveniently interrupted in Ferris' illustration, fig. 11 A), and then turns forward along the edge of the postantennal membrane to *e,* whence it runs mesally and posteriorly on the dorsal surface of the head as the line *b,* forming "a large, inverted V." To the writer it is quite incomprehensible how such diverse elements strung together can be even imagined to constitute a "suture." Yet, Ferris designates this variously composed line the "great suture of the head," and furthermore asserts that it is "evidently the suture between the mandibular and antennal segments." An examination of other species of Symphyla gives no evidence of the existence of any such suture, even the V-lines on the head being absent (D).

The symphylid head in its essential structure is identical with the head of a diplopod (cf. fig. 15 C and D with E). The lateral margin of the cranium below the postantennal membrane containing the organ of Tömösvary (*OT*) is a narrow bar in *Scutigerella* (C), forming a sharp angle (*d*) with the ascending margin above the mandibular articulation (*c*). The same structure is seen in *Hanseniella* (*D*), but here the subantennal bar of the cranium is wider; in the diplopod (E) the same part is a broad sclerotic area below the antenna and the organ of Tömösvary. The deep notch of the lateral cranial margin is characteristic of both Symphyla and Diplopoda, but while it is entirely occupied by the mandible in the diplopods (E, *Md*), in the symphylids (C, D) a membranous area containing the head spiracle (*Sp*) intervenes between the mandible and the edge of the cranium. The symphylid head, in fact, has no structural likeness to an insect's head; it is clearly a slightly modified diplopod head, or vice versa. The structure of the head, the presence of a large, independently musculated gnathal lobe on the mandible, and the anterior position of the genital openings link the Symphyla with the progoneate Diplopoda.

## SUMMARY

1. The insect cranium is *not* composed of "plates" united by "sutures."

2. Most of the so-called sutures of the head are lines of cuticular

inflection forming internal ridges; the ridges are the important structural features, the external grooves, or sulci, are merely incidental to the production of ridges.

3. The postoccipital sulcus is probably a line of union between two segments, apparently the first and second maxillary segments, and lines of union between sclerotized areas may occur on the ventral side of the head, such as a median "gular suture."

4. The so-called "epicranial suture," with its coronal stem and frontal arms, is, in the immature insect, a preformed line of weakness in the head cuticle along which the cuticle will split at ecdysis. The cleavage line may be carried over into the adult, though usually it is more or less suppressed or entirely absent in the imago; other grooves of the adult cranium have frequently been mistaken for it, and designated the "epicranial suture." In some insects the exuvial cleavage line goes through the middle of the head without forking.

5. The common Y-shaped cleavage line of the head is variable in different insects both as to the length of the coronal stem and the extent and course of the frontal arms. The arms may take five different facial positions (fig. 1 C-G); at one extreme they go to the compound eyes, at the other they go mesad of the antennae to the distal margin of the clypeus. The coronal stem may be very short, and is sometimes absent, in which case the arms proceed separately from the occipital margin of the cranium.

6. The arms of the Y-shaped cleavage line, therefore, do not define any fixed part of the cranium, and in this sense they have no structural value, nor do their variations in position affect the fundamental structure of the head; the ecdysial clefts merely cut the head cuticle in different ways in different insects.

7. On the other hand, whatever may be the course of the arms of the cleavage line, the latter run always through the cranial areas that intervene between the attachments of the mandibular muscles and those of the facial muscles.

8. The facial muscles attached on the cranium between the arms of the cleavage line are consistently separated into an upper group, including the labral muscles, the precerebral pharyngeal muscles, and the dorsal muscles of the hypopharynx, and a lower group composed of the cibarial muscles. The two groups are always separated by the frontal ganglion and its brain connectives.

9. The frontal ganglion, being developed from the anterior or dorsal wall of the stomodaeum just within the mouth, and connected with the primarily postoral premandibular ganglia, must have been originally a preoral nerve center of the ventral nerve cord. The

cibarial muscles lying anterior to the ganglion are therefore primarily preoral, while the hypopharyngeal and pharyngeal muscles attached on the head wall behind it are postoral.

10. The facial area of the head on which the cibarial muscles take their origin is, in generalized insects, the outer wall of a preoral lobe of the head known as the clypeus, which supports the labrum, and carries on its basal angles the anterior articulations of the mandibles. The cibarial muscles are primarily compressors of the clypeus.

11. The facial area of the head above or behind the clypeus, on which the hypopharyngeal, pharyngeal, and labral muscles take their origin, is commonly termed the frons. In some insects the frontal area is separated from the clypeal area of the head wall by a transverse groove, the epistomal sulcus, but in others the frontal and clypeal areas are continuous. When they are not thus separated the respective areas are to be identified by the muscles attached on them, and the identity of the two sets of muscles is to be determined by the position of the frontal ganglion and its brain connectives.

12. The term "frons" cannot be given a precise anatomical meaning. If "the frons" is defined as the facial area above the clypeus embraced by the arms of the cleavage line, it will vary in extent according to the position of the arms, in some insects it would carry the antennae, in others it would not. The term "frons," therefore, is serviceable only when applied to the general facial area of the head above the clypeus or the clypeal area.

13. The clypeus, being the area of attachment of the cibarial muscles, varies in extent according to the size of these muscles; the size of the muscles depends on the development of the cibarium. The clypeus, therefore, is usually relatively large in liquid-feeding insects, in which the cibarium forms the principal sucking pump, and in these insects the clypeus is extended upward, or posteriorly, at the expense of the frons. When, in such cases, an epistomal sulcus is absent, the muscle attachments relative to the frontal ganglion still serve to identify the respective areas of the clypeus and the frons.

14. Just as the frons is usually cut into three sections by the arms of the cleavage line, so also the clypeus may be divided when the arms extend through the clypeal area. The facial apotome, or triangle of the head cuticle cut out at ecdysis, therefore, may be either the median part of the frons alone, or the median parts of the frons and clypeus, depending on the length of the ecdysial clefts.

## ABBREVIATIONS USED ON THE FIGURES

*Aclp,* anteclypeus.
*Ant,* antenna.
*AntF,* antennal foramen of cranium.
*AntNv,* antennal nerve.
*AT,* anterior tentorial arm.
*at,* anterior tentorial pit.

*Br,* brain.

*Cb,* cibarium.
*cbmcls,* cibarial muscles (same as *dlcb*).
*CbP,* cibarial pump.
*CL,* cleavage line ("epicranial suture").
*Clp,* clypeus.
*clp,* median part of clypeus between arms of cleavage line.
*cprclp,* compressor muscles of clypeus (dilators of cibarium).
*cprlm,* compressor muscle of labrum.
*cvpls,* cervical plates.
*Cvx,* neck, cervix.
*Cx*$_1$, prothoracic coxa.

D, deutocerebrum.
*dlcb,* dilator muscles of cibarium, primarily compressors of clypeus.
*dlphy,* dilator muscles of pharynx.
*dt,* attachment point of dorsal arm of tentorium on cranium.

*E,* cornea of compound eye.
*ER,* epistomal ridge.
*es,* epistomal sulcus.
*es'*, lateral parts of incomplete epistomal sulcus.
es", median part of epistomal sulcus.

*fm,* food meatus.
*FR,* frontal ridge.
*Fr,* frons.
*fr,* median part of frons between arms of cleavage line.
*frapt,* frontal apotome.
*frcapt,* frontoclypeal apotome.
*FrClp,* frontoclypeal region of head.
*FrCon,* brain connective of frontal ganglion.
*FrGng,* frontal ganglion.

*GngI,* first postoral ganglion of ventral nerve cord, becomes tritocerebral lobe of brain.
*GngII, III, IV,* second, third, and fourth ganglia of ventral nerve cord.
*gr,* groove of cranial wall.

*hphmcl,* frontal muscle of hypopharynx.
*Hphy,* hypopharynx.
*HS,* hypopharyngeal suspensorium.
*Hst,* hypostoma.

*I-IV,* postoral somites.

*Lb,* labium.
*lbmcl,* labial muscle.
*lbrmcl,* labral muscle.
*lbrNv,* labral nerve.
*Lm,* labrum.

*mcbmcl,* median cibarial muscle.
*mcR,* midcranial ridge.
*mcs,* midcranial sulcus.
*Md,* mandible.
*mdmcl,* mandibular muscle.
*Mth,* mouth.
*Mx,* maxilla.

*N*$_1$, pronotum.

*OcR,* ocular ridge.
*Oe,* oesophagus.
*OpL,* optic lobe of brain.
*OT,* organ of Tömösvary.

*P,* protocerebrum.
*Pclp,* postclypeus.
*phmcls,* pharyngeal muscles.
*Phy,* pharynx.
*Prtl,* parietal area of cranium.

*rao,* retractor muscle of mouth angle, frontal muscle of hypopharynx (*hphmcl*).
*RNv,* recurrent nerve.

*sc,* salivary canal, outlet tube of salivary pump.
*Sit,* sitophore, floor of cibarial pump.
*SlDct,* duct of salivary glands.
*SlP,* salivary pump.
*SoeGng,* suboesophageal ganglion.
*Sp,* spiracle.
*Spn,* spinneret.
*Stom,* stomodaeum.

*T,* tritocerebrum.
*TR,* temporal ridge.
*ts,* temporal sulcus.

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