

## THE SKELETON OF THE HEAD OF INSECTS.

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THE skeleton of the head of an insect is composed of several sclerites more or less closely united, forming a capsule, which includes a portion of the viscera, and to which are articulated certain appendages.

The early entomologists, among whom were Fabricius (1775), Illiger (1800, 1806), Kirby (1802, 1826), Savigny (1816), Straus-Durckheim (1828), Burmeister (1832), Newman (1834), and Newport (1839), laid the foundation of our knowledge of the structure of this skeleton; and it is remarkable, considering the extent of entomological literature, how little has been added in this particular field since the publication of the article "Insecta" by the last-named writer.

Although comparatively little progress has been made in the study of the sclerites of the head during the last sixty years, very much has been learned by the workers of to-day regarding the development of this region of the body; and the time has come when, using the known facts of embryology as a starting point, one can hope, by comparative anatomical studies, to gain a clearer idea of the structure of the skeleton of the head than has been set forth as yet. To do this has been the aim of the writers of this paper.

### THE AREAS OF THE EXTERNAL SKELETON.

In descriptions of insects it is necessary to refer to the different regions of the surface of the head. This has resulted in the establishment of a nomenclature, which, although based on the work of the early insect anatomists, is really of comparatively little morphological value; for but few of the primitive sclerites of the head have remained distinct, and some of them greatly overshadow others in their development. The result

is that in some cases a named area includes several sclerites, while in other cases only a portion of a sclerite is included.

This nomenclature, however, is sufficient for the needs of describers of species, and will doubtless continue in use. It is worth while, therefore, to review it briefly and to attempt where necessary to make it more definite.

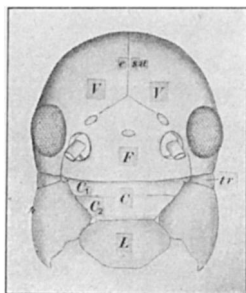


FIG. 1. — Head of a cricket.

The best landmark from which to start for this purpose is the *epicranial suture*, the inverted Y-shaped suture on the dorsal part of the head, in the more generalized insects (Fig. 1, *e.su.*). Behind the arms of this Y there is a series of *paired* sclerites, which meet on the middle line of the dorsal wall of the head, the line of union being the stem of the Y; and between the arms of the Y and the mouth there are typically three *single* sclerites (Fig. 1, *F, C, L*). It is with these unpaired sclerites that we will begin our definitions of the areas of the head.

*The Front* (*frons*, Kirby; *clypeus posterior*, Newport). — The unpaired sclerite between the arms of the epicranial suture (Fig. 1, *F*).

In the more generalized insects at least, if not in all, the front bears the median ocellus; and in the Plecoptera, the paired ocelli also. Frequently the suture between the front and the following sclerite, the clypeus, is obsolete; but as it ends on each side in the invagination which forms the anterior arms of the tentorium (Fig. 2, *at*), its former position can be inferred, at least in the more generalized insects, even when no other trace of it remains. In Fig. 2 this is indicated by a dotted line.

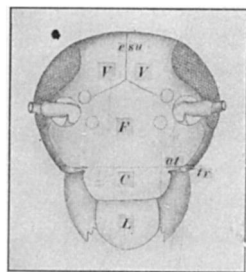


FIG. 2. — Head of a cockroach.

*The Clypeus* (*clypeus*, Fabricius; *chaperon*, Straus-Durckheim; *clypeus anterior*, Newport). — The intermediate of the three unpaired sclerites between the epicranial suture and the mouth (Fig. 1, *C*). To this part one condyle (the ventral) of the mandible articulates.

Although the clypeus almost always appears to be a single sclerite, except when divided transversely as indicated below, it really consists of a transverse row of three sclerites, — one on the median line and one on each side articulating with the mandible. The median sclerite may be designated the *clypeus proper*, and each lateral sclerite, the *antecoxal piece of the mandible*. Usually there are no indications of the sutures separating the clypeus proper from the antecoxal pieces; but in some insects they are distinct. In the larva of *Corydalis* the antecoxal pieces are not only distinct but are quite large (Fig. 3, *ac, ac*).

In some insects the clypeus is completely or partly divided by a transverse suture into two parts (Fig. 1). These may be designated as the *first clypeus* and the *second clypeus*, respectively; the first clypeus being the part next the front (Fig. 1, *C<sub>1</sub>*) and the second clypeus being that next the labrum (Fig. 1, *C<sub>2</sub>*).

There is a great lack of uniformity in the application of the term *clypeus*, arising from the fact that many writers apply it to the entire area between the epicranial suture and the labrum; either overlooking the fact that the part here designated as the front is a distinct sclerite, or, following Newport, terming it the *clypeus posterior*. But as the front and the clypeus (in the more restricted sense) pertain to different segments of the head, it is desirable to use distinct names for them; and as the names proposed by Newport are morphologically incorrect, the so-called clypeus posterior being in front of the so-called clypeus anterior, as will be shown later, it is doubtless better to use the older term *frons*, or *front*, for the sclerite next the epicranial suture, and to restrict the term *clypeus* to the part termed *clypeus anterior* by Newport.

*The Labrum (labrum, Illiger).* — A movable flap which constitutes the upper lip of the mouth (Fig. 1, *L*). The labrum is the last of the series of unpaired sclerites between the

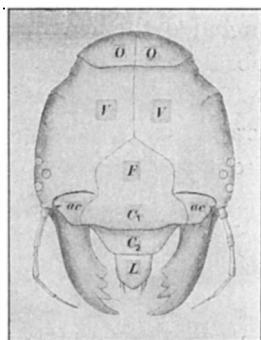


FIG. 3. — Head of the larva of *Corydalis*, dorsal aspect.

epicranial suture and the mouth. It has the appearance of an appendage but is really a portion of one of the head segments.

*The Epicranium (épicrâne, Straus-Durckheim).* — Under this term are included all of the paired sclerites of the skull, and sometimes also the front. The paired sclerites constitute the sides of the head and that portion of the dorsal surface that is behind the arms of the epicranial suture. The sclerites constituting this region are so closely united that they were regarded as a single piece by Straus-Durckheim, who also included the front in this region, the epicranial suture being obsolete in the May beetle, which he used as a type.

*The Vertex (vertex, Kirby).* — The dorsal portion of the epicranium; or, more specifically, that portion which is next the front and between the compound eyes (Fig. 1, *V, V*). In many insects the vertex bears the paired ocelli. It is not a definite sclerite; but the term *vertex* is a very useful one and will doubtless be retained.

*The Occiput (occiput, Kirby).* — The hind part of the dorsal surface of the head. When a distinct sclerite, it is formed from the tergal portion of the united postgenæ described below (Fig. 3, *O, O*).

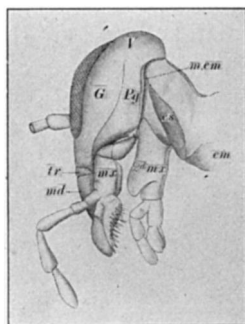


FIG. 4. — Head and neck of a cockroach.

*The Genæ (genæ, Kirby).* — The lateral portions of the epicranium. Each gena, in the sense in which the word was used by the older writers, includes a portion of several sclerites. Like *vertex*, however, the term is a useful one.

*The Postgenæ.* — In many insects each gena is divided by a well-marked suture. This led Comstock<sup>1</sup> to restrict the term *gena* to the part in front of the suture (Fig. 4, *G*), and to propose the term *postgenæ* for the part behind the suture (Fig. 4, *Pg*).

*The Gula (gula, Kirby; pièce basilaire, Straus-Durckheim).* — A sclerite forming the ventral wall of the hind part of the head in certain orders of insects, and bearing the labium or second

<sup>1</sup> Comstock and Kellogg. *Elements of Insect Anatomy*. 1895.

maxillæ (Fig. 5, *Gu*). In the more generalized orders, the sclerite corresponding to the gula does not form a part of the skull.

*The Cervical Sclerites (cervical sclerites, Huxley).*— Small sclerites found in the neck of many insects. Of these there are dorsal, lateral, and ventral sclerites; the lateral cervical sclerites have been termed the *jugular sclerites* (*pièces jugulaires*, Straus-Durckheim) (Fig. 4, *es, em*).

*Other Sclerites.*— In addition to the areas and sclerites named above, the following sclerites will be described in later pages of this essay: the *ocular sclerite*, the *antennal sclerite*, the *trochantin of the mandible*, and the *maxillary pleurites*. These terms should be added to the list of those available for the purposes of systematic entomology.

#### THE SEGMENTS OF THE HEAD.

The determination of the number of segments in the head of an insect is a problem that has been much discussed since the early days of entomology. The first important step towards its solution was made by Savigny (1816), who suggested that the movable appendages of the head were homodynamous with legs. This conclusion has been accepted by all; and as each segment in the body of an insect bears only a single pair of appendages, there are at least four segments in the head; *i.e.*, the antennal, the mandibular, the maxillary, and the second maxillary or labial.

As the compound eyes are borne on movable stalks in certain Crustacea, it was held by Milne-Edwards that they represent another pair of appendages; but this view has not been generally accepted. It is not necessary, however, to discuss in this place whether the eyes represent appendages or not; the existence of an ocular segment has been demonstrated in another way, to be discussed later.

This is the point to which the solution of the problem was carried by the methods of comparative anatomy. The existence

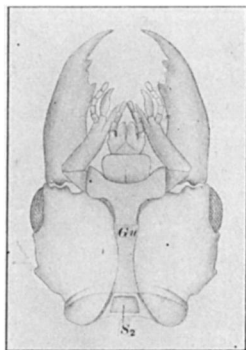


FIG. 5.— Head of *Corydalis*, adult, ventral aspect.

of four segments was demonstrated, and the presence of a fifth (the ocular) suggested. From this point the work has been carried on chiefly by the embryologists.



FIG. 6. — Embryo of a damselfly (*Calopteryx*), after Brandt.

The existence in the embryo of distinct segments, each corresponding to a pair of mouth parts, was early shown. Among the better of the older figures for this purpose are those of Brandt ('69, Fig. 12) and of Packard ('71). Fig. 6, which is copied from Brandt, represents an early stage in the development of the embryo of a damsel fly (*Calopteryx*). In this stage the labial and maxillary segments are quite distinct, appearing to be body segments rather than cephalic. This doubtless represents a phylogenetic stage, in which the head proper consisted of fewer segments than it does in existing insects.

It was also found that the subœsophageal ganglion, which innervates the mandibles, maxillæ, and labium, is formed by the union of at least three pairs of primitive ganglia. Fig. 7, from Heider ('89), represents a stage in the development of *Hydrophilus*, in which these ganglia are still distinct, each pair of ganglia corresponding to a pair of mouth parts.

So far the results of embryology merely confirm the conclusions of comparative anatomy. But the embryologists have also demonstrated the existence of vestiges of segments, which had not been recognized as such by the early writers.

In his work on the embryology of the honey-bee, Bütschli ('70) described a pair of evanescent appendages situated between the antennæ and the mandibles. Later these were observed by others, and writers began to refer to a "pre-mandibular," or "intercalary," segment in the head of insects. More recently the appendages of this vestigial segment, which is properly termed the second antennal segment, were observed in the embryo of *Anurida* by Wheeler ('93) and by Claypole ('98).

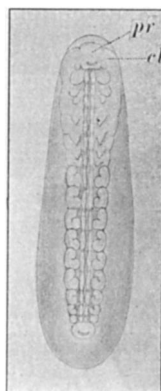


FIG. 7. — Embryo of *Hydrophilus*, after Heider.

They were also observed in Campodea by Uzel ('97). The last writer states that these appendages persist in the adult Campodea, and Folsom ('99b) says, "I may add that rudimentary chitinized intercalary appendages persist in adults of *Tomocerus*, *Orchesella*, and other *Collembola*."

Equally important evidence as to the existence of a second antennal segment in insects has been furnished by studies of the nervous system. It was shown by Viallanes ('87a) in his study of the structure of the brain (supra-œsophageal ganglion) of *Vespa* that there are three principal divisions in the brain of insects. These he named the *protocerebrum*, the *deutocerebrum*, and the *tritocerebrum*. Almost immediately after Patten ('88) demonstrated that the brain is formed from three pairs of primary ganglia; and the same fact was shown by Wheeler ('89). Viallanes also showed that the protocerebrum innervates the compound eyes and ocelli; the deutocerebrum, the antennæ; and the tritocerebrum, the labrum. This demonstrates the existence of three premandibular segments: first, an ocular or protocerebral segment, without appendages, unless the compound eyes represent them (the supposed discovery of other appendages on the ocular segment by Carriere ('90) has not been confirmed); second, an antennal or deutocerebral segment, bearing antennæ; and third, a second antennal, or tritocerebral segment, of which the labrum is a part, and to which the so-called intercalary appendages doubtless belong. As Viallanes has shown that the tritocerebrum of Crustacea innervates the second antennæ, we are warranted in considering the tritocerebral segment of insects to be the second antennal segment.

The evidence thus far brought forward demonstrates the existence of six cephalic segments, — three innervated by the brain and three by the subœsophageal ganglion. We have now to refer to the evidence indicating the existence of a seventh cephalic segment.

The hypopharynx of insects is usually, in the Pterygota, a tongue-like organ lying below and projecting in front of the beginning of the alimentary canal. In the Apterygota it consists of three distinct parts, — a median organ termed the

"lingua" and a pair of organs termed "paraglossæ" by writers on the Thysanura and Collembola. As the term "paraglossæ" has long been used for a part of the labium or second maxillæ, Folsom ('00) justly maintains that it should not be applied to a part of the hypopharynx, and proposes for these paired organs the term *superlinguæ*.

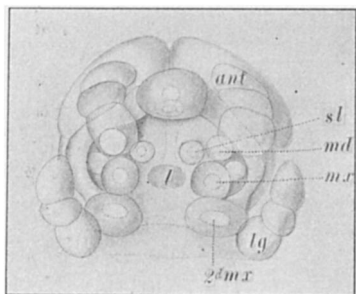


FIG. 8.—Head of embryo of Anurida, after Folsom.

In his work on the development of apterygote insects, Uzel ('98) showed that the lingua arises between the rudiments of the maxillæ; hence it may be regarded as pertaining to the sternum of the maxillary segment. Uzel also showed that the superlinguæ arise

as a pair of appendages between the mandibles and the maxillæ. This indicates the existence of a segment between the mandibular and the maxillary segments.

Similar results were obtained by Folsom ('00) in his work on the development of the mouth parts of Anurida. Fig. 8 is copied from Folsom and illustrates the relative positions of the rudiments of the mouth parts. To Folsom also belongs the credit of completing the evidence of the existence of a superlingual segment, by demonstrating the existence of a pair of primary ganglia between those of the mandibular and of the maxillary segments (Fig. 9, 5). And in a preliminary paper ('99b), he set forth the first complete account of what promises to be our final view regarding the segmentation of the head.

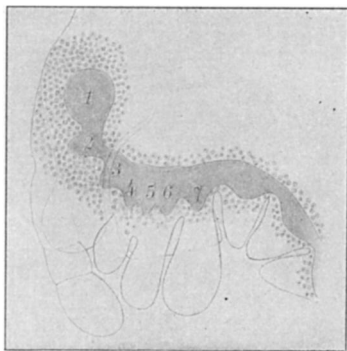


FIG. 9.—Section of the head of an embryo of Anurida, after Folsom.

In confirmation of the view that the subœsophageal ganglion consists of four pairs of primary ganglia, it should be mentioned that long ago Patten ('88) figured these ganglia. It has been believed, however, that



the pair immediately in front of the maxillary ganglia were the mandibular ganglia (see Korschelt and Heider, '99b, p. 326); but it is more probable that the first of these four pairs of ganglia (Fig. 10, 4) pertains to the mandibular segment and that the second pair are the homologues of the superlingual ganglia figured by Folsom.

The seven segments of the head are designated as follows :

- First, ocular, or protocerebral.
- Second, antennal, or deutocerebral.
- Third, second antennal, or tritocerebral.
- Fourth, mandibular.
- Fifth, superlingual.
- Sixth, maxillary.
- Seventh, labial, or second maxillary.

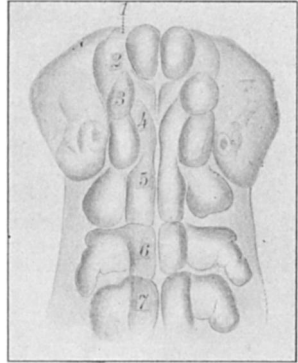


FIG. 10. — Head of embryo of *Acilius*, after Patten.

#### DIAGRAMS OF THE ELEMENTS OF THE HEAD.

The head of an insect consists of seven segments closely consolidated, greatly reduced in length, and, in the case of some, bent out of the original line. The morphological relations of these segments can be shown by representing them as distinct, of uniform size, and in a direct line. This is done in the accompanying diagram (Fig. 11, A).

Let us trace the steps by which this diagram was made. First, the outlines of the seven segments were drawn as if no



FIG. 11. — Diagrams of the elements of the head: A, lateral aspect; B, ventral aspect.

reduction or consolidation of any of them had occurred; at this stage the diagram might represent the cephalic end of an earthworm, except that the prostomium is not represented.

Second, a longitudinal line was drawn representing the line of separation of the sternal from the pleural elements of the segments; it is along this line that the appendages are borne. Third, the chain of ganglia were added, a pair of ganglia in each segment; as the nervous system is developed from the ectoderm on the ventral side of the body between the appendages, it is represented in the sternal portion of the preoral segments as well as in the postoral segments. The diagram being of a side view, only a single member of each pair of ganglia and longitudinal commissures are shown. Fig. 11, *B*, is a diagrammatic representation of a ventral view of the nervous system. Fourth, the compound eyes and the ocelli were represented in the first segment (Fig. 11, *A*), because they are innervated by the protocerebrum. The reasons for the exact positions within the segment assigned to these organs will be discussed later. Fifth, the position of the appendages was indicated, a pair to each segment except the first. It will be remembered that the antennæ are innervated by the deutocerebrum; hence they pertain to the second segment. Sixth, the mouth was represented as opening in the ventral wall of the third segment; this is in accordance with the results of the studies of Viallanes ('87a), who has shown that, although the third pair of ganglia enter into the composition of the supra-œsophageal ganglion, the commissure which connects them passes behind the œsophagus. This is shown in the second diagram. Although the position assigned to the mouth in these diagrams was suggested by the results of the studies of Viallanes, it is not in accordance with his conclusions; for he evidently believes that the mouth opens between the third and fourth segments.<sup>1</sup> Our view is based on the well-known fact that the mouth of the embryo is formed *in* the labral rudiment and not behind it.

The determination of the position of the mouth is one of the most striking of the results of the later studies of the head. Naturally the older entomologists believed that the mouth-opening was at the cephalic end of the body, and this effectually

<sup>1</sup> "La tête de l'insecte est formée par six zoonites; trois sont prebuccaux et trois post-buccaux." — Viallanes ('87b, p. 117).

prevented a correct homologizing of the sclerites of the head. It is evident that the old belief is still held by many; thus Heymons ('95) designates what he believes to be the first segment the *primäres Kopfsegment oder Oralstück*.

The earliest suggestion of a different position of the mouth that we have met was by E. Ray Lancaster ('73), who refers to an "adaptational shifting of the oral aperture." The later writings contain many references bearing upon this, although the full force of them is evidently not appreciated by the writers. Thus it has been said by many that although the antennæ were doubtless originally postoral they have become preoral. The facts would be more accurately stated by saying that although the mouth was doubtless originally preantennal it has become postantennal. This, however, would only partially indicate the change that has taken place; for, as will be shown later, the antennæ have moved cephalad at the same time that the mouth has moved caudad.

#### THE STRUCTURE OF A TYPICAL SEGMENT.

In order to determine the homologies of the sclerites of the head, it is necessary to decide what sclerites were probably present before the consolidation and reduction of its segments took place. We have decided that the head is composed of seven segments; let us now determine the elements in the skeleton of a single segment. This necessitates a study of segments in other regions of the body.

In the abdomen it is evident that a reduction of certain parts has taken place, correlated with the loss of the abdominal appendages; it is to the thorax, therefore, that we must look for the more typical insectan segment.

The parts of a thoracic segment that are commonly recognized are those described by Audouin ('24): a ventral part, *sternite*; two lateral parts, *pleurites*; and a dorsal part, *tergite*.

These are most easily seen in the wing-bearing segments; but they can be recognized also in the prothorax of certain generalized insects. This is especially the case in many Orthoptera, as cockroaches and walking-sticks, where the

pleurites of the prothorax are distinct from the sternum on the one hand and from the tergum on the other; more often, however, the tergite of the prothorax is not separated from the pleurites. This is also the case in the segments of the head: sometimes the tergite is distinct from the pleurites; but more often the tergite is merely a continuation of the pleurites over the dorsal side of the segment. In such cases the combined lateral and dorsal parts are designated as the pleurites; for we find that they bear the most characteristic feature of the pleurites, the lateral apodemes, to be described later.

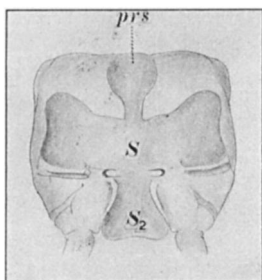


FIG. 12.—Ventral aspect of the metathorax of a nymph of *Pteronarcys*.

Equally important for the purposes of this study is the fact that each thoracic segment is composed of two subsegments. It is not necessary for us to decide in this place whether or not this indicates a fusion between two primary metameres, as has been suggested by various writers<sup>1</sup>; the essential fact which must be taken into account is the transverse division of each segment. The line separating the subsegments passes, on the pleural aspect, between the episternum and the epimeron; and, on the tergal aspect, between the scutum and the scutellum. On the sternal aspect, in most insects, the division is not easily recognized; but in certain Plecoptera and Orthoptera it can be readily seen.

Fig. 12 represents the sternite of the metathorax of a nymph of *Pteronarcys*, and Fig. 13 the same part of *Stenopelmatus*. In each

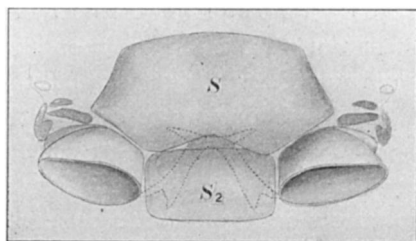


FIG. 13.—Ventral aspect of the metathorax of *Stenopelmatus*. The position of the furca within the body is represented by a dotted line.

case it can be seen that the sternite is composed of two distinct sclerites,—one lying between the episterna and one

<sup>1</sup> The reasons for believing that each segment is composed of two primary metameres have been well stated by Patten ('90, pp. 319, 320).

between the coxæ; the former pertains to the first subsegment, the latter, to the second.

In the furrow or suture between these two sclerites are the invaginations forming the furca of that segment. The position of the furca is, therefore, a good landmark for determining the line of union of the two sclerites forming a sternite, or, in other words, the division between the subsegments.

The second of the sclerites forming a sternite is smaller than the first, even in those insects where it is best developed; and in most insects it is greatly reduced or obsolete, so that the furca appears to arise from the caudal margin of the segment

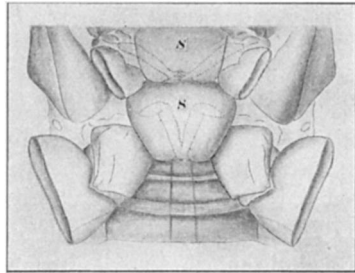


FIG. 14.—Ventral aspect of the meso- and metathorax of *Gryllus*; the positions of the furcæ within the body are indicated by dotted lines.

(Fig. 14). It is for this reason that the sternite of the second subsegment has been overlooked heretofore. The sternite of the first subsegment is retained in all insects, and is the sclerite to which the term *sternum* has been universally applied. The smaller sternite of the second subsegment may be termed the *sternellum* (Fig. 12, *S*<sub>2</sub>; Fig. 13, *S*<sub>2</sub>).

Sometimes, as in *Pteronarcys*, the cephalic portion of the sternum is more or less separate from the main part; this detached portion may be termed the *præsternum* (Fig. 12, *prs*).

A *poststernellum*, corresponding to the postscutellum, has not been observed.

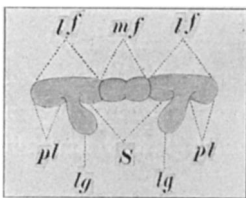


FIG. 15.—Diagram of a segment of an embryo, after Heymons.

It has been shown by Haase ('89) and Heymons ('95) that in a comparatively early embryonic stage each segment of the body is composed of three parts,—a median field and two lateral fields (Fig. 15),—and that the appendages are developed as evaginations of the lateral fields. Each sternite is therefore composed of three parts,—the portion derived from the median field of the segment, and, on each side, a portion derived from that part of the lateral field which lies

between the appendage and the median field. This portion may be designated the *lateral element of the sternite*. Such a division is well shown in the abdominal sternites of the adult *Gryllus* (Fig. 14).

More frequently, however, when a sternum in an adult insect is divided longitudinally it is by a single median suture, which perhaps represents the neural groove of the embryo.

A sternite of a subsegment may be composed, therefore, of either two or three elements: in the one case the sutures between the median field and the lateral fields are preserved; in the other, a trace of the neural groove is indicated. But as a rule, each sternite is an undivided sclerite.

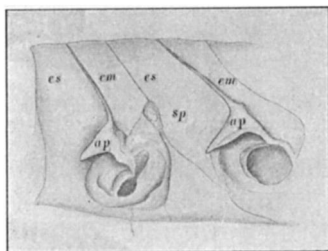


FIG. 16. — Ental surface of the pleurites of the meso- and metathorax of *Melanoplus*, showing the lateral apodemes.

In the same way that the position of the furca determines the line of union of the subsegments on the ventral aspect of a thoracic segment, the line of union of the subsegments on the pleural aspects is determined by the position of the lateral apodemes. Each of these is an invagination of the

body-wall between the episternum and the epimeron. Fig. 16 represents the inner surface of the pleurites of the meso- and metathorax of *Melanoplus* and shows the form of the lateral apodemes (*ap*).

For the purposes of this paper, it is not necessary to discuss the structure of the tergal aspect of the typical segment beyond a reference to the median suture, which represents the line of the closure of the embryo. This suture has been well preserved in the head and thorax, as it is the chief line of rupture of the cuticle at the time of molting.

The relations of the appendages to a typical segment are illustrated by the accompanying figure (Fig. 17) of the base of a leg of a cockroach. Near the point marked *x* the coxa articulates with the ventral end of the foot of the lateral apodeme of the segment, *i.e.*, with the ventral end of the episternum and the epimeron. This may be termed *the pleural articulation*

of the coxa. In front of the coxa there is a triangular *trochantin* (*tr*), with its apex pointing towards the middle line of the body. Between the trochantin and the ventral arm of the episternum there are two sclerites, — one next the trochantin, the *antecoxal piece*; and one next the episternum, not yet named, which may be termed the *second antecoxal piece*. The antecoxal piece at its mesal extremity (*y*) articulates with the coxa. This articulation may be termed the *ventral articulation of the coxa*.

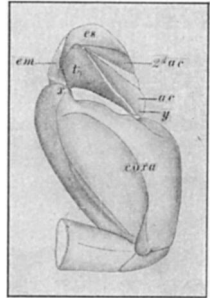


FIG. 17. — The base of a leg of a cockroach.

### THE SCLERITES OF THE HEAD AND NECK.

The segments of the body of an insect do not fall into three well-marked groups, — head, thorax, and abdomen, — as commonly defined in the text-books. Between the head and the thorax there is a more or less distinct neck, which in some insects contains several sclerites. As we believe that these cervical sclerites form a part of the second maxillary or labial segment, it is necessary to include them in a discussion of the sclerites of the head. We shall return to them later.

If an embryo insect be examined after the appearance of the mouth and the appendages, the cephalic end of the body will be found to consist of a central swelling, the *procephalon* (Fig. 7, *pr*), and a large lobe on each side, the *cephalic lobes* (Fig. 7, *cl*).

The procephalon has been commonly described as the rudiment of the clypeus and the labrum. This is doubtless correct if the term *clypeus* be taken in the broader sense by which it includes the clypeus anterior and the clypeus posterior of Newport; and this is evidently the sense in which it has been used by nearly all writers on the embryology of insects. Hence, according to the nomenclature adopted in this paper, the procephalon is the rudiment of the front, clypeus, and labrum.

This conclusion makes evident the significance of the episcranial suture. The sclerites lying in front of the arms of

this inverted Y-shaped suture are those developed from the procephalon, while the stem of the Y represents the line of union of the cephalic lobes.

When we take into account the position of the mouth (see Fig. 11), it is evident that the parts developed from the procephalon pertain to the ventral aspect of the body. In the course of development there is a dorsal flexure of the cephalic region by which the preoral sterna are bent up towards the tergal aspect (Huxley, '78, p. 343); this has been described by several observers (see Korschelt and Heider, '99b, p. 302).

As a result of this dorsal flexure, the former most anterior part of the procephalon assumes a more backward position, which led to the part derived from it being termed by Newport the *clypeus posterior*. As this term is morphologically incorrect, we have adopted the name *front* for this part, and restrict the term *clypeus* to the clypeus anterior of Newport.

It seems obvious that the three sclerites derived from the procephalon, — the front, the clypeus, and the labrum, — represent the sternites of the three preoral segments.

As to the front, it bears the median ocellus, and, in the Plecoptera, the paired ocelli also; and as the ocelli are innervated by the protocerebrum, it is evident that the front is a part of the protocerebral segment.

In this connection reference should be made to a migration of the paired ocelli. The condition in the Plecoptera, where the front bears all the ocelli, is probably the most generalized; for in this order, as will be shown later, the most nearly primitive position of the antennæ is found; and, too, in this order the most generalized condition of the tracheation of the wings exists (Comstock and Needham, '98, p. 237). In the Orthoptera (Blattidæ and Gryllidæ) the paired ocelli are in the suture between the front and the vertex. In certain Ephemerida the paired ocelli are in this suture, while in others they have passed on into the vertex. In the more specialized orders, wherever we have been able to distinguish between the front and the vertex, we have found the paired ocelli in the vertex.

The labrum is innervated by the tritocerebrum; for this reason we regard it as the sternite of the tritocerebral segment,



or rather as a part of this sternite; for, as the invagination of the stomodæum is surrounded by the labral rudiment, the labrum represents only that part of this sternite that lies cephalad of the mouth.

The clypeus (clypeus anterior) is a sclerite between the front and the labrum; for this reason, we believe it to be the sternite of the intermediate of the three preoral segments, the deutocerebral.

We have described the sclerites derived from the procephalon as representing the sternites of the preoral segments. But strictly speaking, we believe that each represents only the median field of a sternite (Fig. 15, *mf*), and that the lateral elements of the sternites have not been separated from the pleural portions of the lateral fields of the segments; in other words, that the early embryonic divisions of the segments have been retained, and that those parts derived from the lateral fields of the segments form a single sclerite on each side of each segment.

In the ocular segment each lateral sclerite constitutes one-half of the vertex and the corresponding gena, the line of union of the lateral sclerites being the stem of the Y-shaped epicranial suture.

Each lateral sclerite of this segment bears a compound eye, except in cases where they have been lost and except in the larvæ of metabolous insects, in which the development of these organs is retarded; this is obviously a secondary condition, like the internal development of the wings in the same forms.

The position of the compound eye, in the lateral sclerite slightly removed from the middle field of the sternite (the front), is that in which one would expect to find an appendage, and it seems to us that the question whether or not the compound eyes represent the appendages of the ocular segment is still an open one.

Heretofore the chief reason for regarding the compound eyes as representatives of appendages has been the stalked condition of them in certain Crustacea; but later writers are inclined to regard the eye-stalks "as secondarily abstricted lateral portions of the head which have become independently movable" (Korschelt and Heider, '99a, p. 165).

We are inclined, however, to return to the old view; for we find that in many insects each compound eye is situated in the axis of an annular sclerite, which may be the basal segment of the ocular appendage. Certainly if the eyes were merely specialized portions of the lateral sclerites, we should not expect

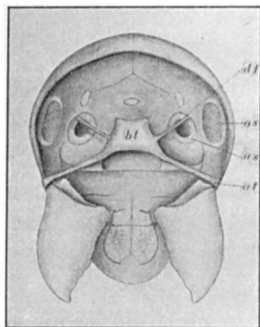


FIG. 18. — Head of a cricket, ventral surface of the dorsal wall.

them to be surrounded by a ring-like suture, which in some cases is comparatively remote from the specialized portion of the body-wall that forms the eye.

These sclerites bearing the compound eyes may be termed *the ocular sclerites*; they are represented in Fig. 18, *os*.

Passing to the second segment, we find at the base of each antenna an annular sclerite (Fig. 18, *as*), which is distinct in comparatively few insects and which has not been described. It is most clearly shown in the Plecoptera (Fig. 19, *as*). This we believe represents the lateral field of the antennal segment, *i.e.*, the lateral element of the sternite and what is left of the pleural element of the segment, which is greatly reduced. This sclerite may be termed *the antennal sclerite*.

The position of the antennal sclerites should be discussed. If the clypeus represents the median field of the sternite of the antennal segment, as we believe, the primitive position of the antennal sclerites was laterad of the clypeus, and we should expect to find the rudiments of them in this position, *i.e.*, laterad of the procephalon, in the early stages of the embryo. Many observers, however, have described the antennæ as arising in a postoral position; how can this be explained? A study of the figures given by these authors<sup>1</sup> shows that while a line connecting the two antennæ would pass in some cases behind the mouth, it is by no means so clear that the basal part of the rudiment of the antennal sclerite does not abut against the procephalon. In fact, the very figures given to

<sup>1</sup> Weismann, '63, Fig. 22; Graber, '88, Figs. 1 and 2; Heider, '89, Fig. 102 (Fig. 7 above); Patten, '88 (Fig. 10 above).

support the view that the antennæ are postoral in the early embryo support the opposite view.

A migration cephalad of the antennæ has been noted by many observers; and it is obvious that the position of the antennæ in adult insects is more or less remote from the primitive position.

In the Plecoptera is to be found the most generalized condition of the antennal sclerites yet observed in postembryonic stages of insects (Fig. 19); here they are distinct sclerites, and are only slightly removed from the clypeus, compared with their position in the more specialized insects. Even here, however, they are opposite the front, having been pushed out of place by a migration of the mandibles and the antecoxal pieces, to be described later.

In most insects each antenna has migrated along the suture between the front and the gena, and occupies a position on the lateral border of the front remote from the clypeus. Even in so generalized an insect as a cockroach (Fig. 2), the antenna has reached a point opposite the cephalo-lateral angle of the vertex. Here it is remote from the anterior arm of the tentorium; while in *Pteronarcys* it is very close to it.

In the case of the second antennal segment, the reduction has been so great that we have been able to find in the Pterygota no trace of the parts derived from the lateral fields of the segment; the labrum is the only well-marked remnant of this segment represented in the skeleton; it is possible that the lateral elements are fused with the genæ. It is probable that a study of those Apterygota in which the second antennæ are retained will reveal the presence of distinct lateral sclerites pertaining to this segment.

In taking up the study of the postoral segments of the head, the subject can be treated most easily by beginning with the labial segment and proceeding forward to the point reached in the above discussion.

In the early embryonic stages the labial segment is obviously a body segment (Fig. 6, 2<sup>nd</sup> *mx*); but in the course of the

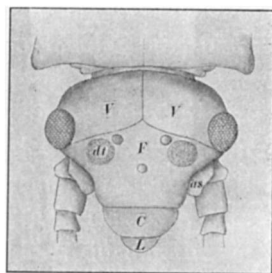


FIG. 19. — Head of a nymph of *Pteronarcys*.

development of the embryo it moves forward, and in adult insects it constitutes the dividing line between the head and the thorax, forming the neck. Its appendages, the second maxillæ or labium, however, have moved forward so that they are either loosely attached to the ventral wall of the head (Plecoptera, Orthoptera, *et al.*) or, in the more specialized orders, they contribute to the formation of the fixed parts of the head.

While the appendages of this segment have been retained and play an important rôle as a part of the mouth organs, the segment itself is greatly reduced, being represented by small and more or less detached sclerites, the cervical sclerites.

Straus-Durckheim ('28) suggested that the cervical sclerites represent the remains of two segments situated originally between the head and prothorax. Newport ('39) regarded

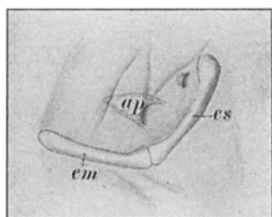


FIG. 20. — Lateral cervical sclerites of *Melanoplus*.

them as detached portions of the prothorax; and Huxley ('78) wrote: "I think it probable that these cervical sclerites represent the hindmost of the cephalic somites." But we find no account of these sclerites that contains more than a suggestion regarding their homologies. No evidence has been

brought forward to support any of the conclusions, beyond the position between the head and thorax occupied by these sclerites. We have been led to adopt the view put forth by Huxley for reasons that seem to us conclusive, and which we will now state.

The cervical sclerites are best preserved in the Orthoptera. In this order a variable number occur in the ventral wall of the neck; two in each lateral wall; and in some forms, two in the dorsal wall.

Between the two lateral cervical sclerites there is in certain forms, as *Melanoplus* and *Stenopelmatus*, a prominent apodeme (Fig. 20, *ap*). This apodeme we regard as homodynamous with the lateral apodemes of the thoracic segments. Each of these apodemes is an invagination between an episternum and an epimeron; we, therefore, conclude that the anterior lateral

cervical sclerite is the episternum of the labial segment, and the posterior one the epimeron. This conclusion is confirmed by the fact that the posterior of the two lateral cervical sclerites articulates with the episternum of the prothorax, and the anterior one with what we believe to be the epimeron of the maxillary segment.

The ventral cervical sclerites in this order are either two in number, *Periplaneta* (Fig. 21), or constitute two transverse series, *Stenopelmatus* (Fig. 22), *Gryllus* (Fig. 23). We regard these as constituting the sternites of the two subsegments of the labial segment. If this view be correct, the anterior sclerite or series

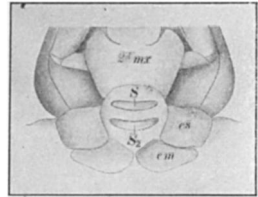


FIG. 21. — Ventral and lateral cervical sclerites of *Periplaneta*.

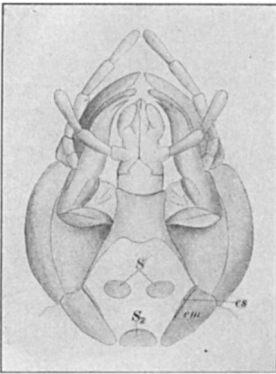


FIG. 22. — Head of *Stenopelmatus*, ventral aspect.

of sclerites represents the sternum of the labial segment, and the posterior the sternellum. The division of a sternite into a transverse series of either two or three sclerites is comparable with what frequently takes place in the sternites of the thorax and of the abdomen, already discussed on an earlier page.

The appendages of this segment, the second maxillæ, project forwards from the front margin of the segment as a single organ, the labium. This anomalous condition is the result of a migration of the appendages forwards and towards each other and of a coalescence, which has been figured by many writers and often described, lately in detail by Deegener ('00). As a result of this coalescence the united cardines become the submentum, and the stipites the mentum.

In the more generalized insects a gula is not developed as such. We have devoted much study to the question of the homology of the gula and conclude that

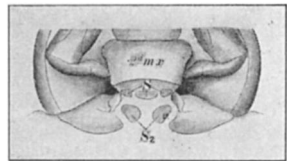


FIG. 23. — Ventral cervical sclerites of *Gryllus*.

it is the sternum of the cervical segment which has migrated cephalad and become a part of the skull. In *Corydalis* the sternellum of the cervical segment is retained back of the gula (Fig. 5,  $S_2$ ).

Although the maxillæ are well-developed organs, the maxillary segment itself is greatly reduced. The most conspicuous element of it is the lingua, the unpaired portion of the hypopharynx. This, as has been shown (Fig. 8,  $l$ ), arises between the rudiments of the maxillæ and evidently pertains to the sternite of this segment.

The opening of the salivary glands is in the lingua. Carrière has shown that these glands arise as the spiracular invaginations of the prothorax, and that their openings migrate cephalad, and towards each other, finally forming a single opening in the lingua (Carrière and Bürger, '97). This explains the absence of spiracles in the prothorax, and is one of the most remarkable instances of the migration of organs and change in function yet described.

Regarding the maxillary pleurites of the completed head, almost nothing has been published. Huxley, in his description of the structure of the cockroach ('78), stated that the cardo of the maxilla is articulated "with a thin skeletal band which runs round the posterior margin of the epicranium." He made no suggestion regarding the homology of this sclerite; and subsequent writers do not appear to have done so.

This lateral band (Fig. 4, *m.em.*) is one of two sclerites, between which is the invagination which forms the posterior arm of the tentorium; the other of these two sclerites, the anterior one, is much more reduced than this one, still it can be seen in *Periplaneta* and in *Gryllus*. The articulation of the maxilla is at the ventral end of these sclerites just ventrad of the invagination between them, the open mouth of which is very conspicuous in the more generalized insects.

The relation of these parts corresponds exactly with what exists in a thoracic segment, where each leg is articulated just ventrad of the lateral apodeme, which is an invagination between the episternum and the epimeron. Evidently the band described by Huxley is the epimeron of the maxillary segment,

the thinner band in front of the invagination is the episternum, and the invagination itself is the lateral apodeme of this segment.

From this it will be seen that the posterior arms of the tentorium are to be homologized with lateral apodemes instead of with spiracles, as is often done. It should be borne in mind, however, that the spiracles are lateral invaginations between segments, and that the lateral apodemes are invaginations in a similar position between subsegments (Fig. 16). If each segment consists of two consolidated metameres, the lateral apodemes and spiracles are homodynamous structures. The solution of this question must wait, however, the solution of the larger question, the structure of the segment in air-breathing arthropods; we need not dwell upon it here.

The superlingual segment is so greatly reduced that we are able to find no trace of the lateral elements of it in the skeleton; if they exist, they are inseparably united with the mandibular pleurites. The sternal elements are represented by that part of the floor of the mouth cavity that bears the superlinguæ; and the appendages of the segment, by the superlinguæ themselves. In the Pterygota these parts are greatly reduced and have received but little attention. Fig. 24 represents the hypopharynx of *Melanoplus*, in which the lingua is very prominent, and what we regard as the superlinguæ are reduced to a pair of small sclerites. As the superlinguæ have been carried into the mouth cavity by its invagination, they lie behind the lingua, although they originated in front of it. The superlinguæ are connected with the skull by a membranous portion of the body-wall, which, on each side, extends between the attachments of the maxilla and of the mandible.

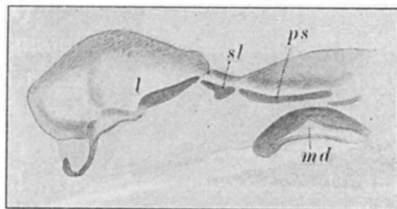


FIG. 24. — Hypopharynx of *Melanoplus*.

In the mandibular segment the pleurites are represented by the postgenæ, which, excepting the vertex and genæ, are the most prominent sclerites of the head in many Orthoptera.

The suture separating the postgenæ from the genæ is well-marked on the lateral aspect of the head in the Orthoptera. In most forms it is obsolete on the dorsal aspect but in a large South American cockroach that we have studied the postgenæ are separated from the genæ and vertex throughout their entire extent. Upon the presence or absence of this suture on the dorsal wall of the head depends the presence or absence of the so-called occiput; the occiput being the tergal portions of the postgenæ (Fig. 3, *O*, *O*).

In the ventral end of each postgena there is an acetabulum into which a condyle of the mandible fits (Fig. 25). Beginning

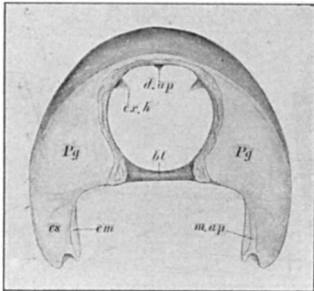


FIG. 25. — Head of a cricket, caudal aspect.

in this acetabulum and extending dorsad there is a suture which divides the postgena into two parts; this suture is the more or less open mouth of an apodeme which extends into the cavity of the head.

Here again the same relation of parts exists that is found in a thoracic segment. The mandible is the basal segment (coxa) of an appendage, which articulates with the ventral ends of two sclerites (episternum and epimeron), between which there is a lateral apodeme.

Thus we see that three of the head segments — the labial, the maxillary, and the mandibular — closely resemble a thoracic segment, in having on each side two sclerites, with an apodeme between, and an appendage below except in the case of the labial segment, where there has been a cephalization of the appendages.

In the floor of the mouth cavity of *Melanoplus* there is on each side just behind the superlinguæ a sclerite (Fig. 24, *ps*) which may represent a sternal element of the mandibular segment. The position of this sclerite farther in the mouth cavity than the superlinguæ is that which would be occupied by a mandibular sternite, as such a sternite must precede the superlinguæ in the course of the invagination of the mouth; equally suggestive is the fact that this sclerite is closely connected



with the mandible, joining it near the insertion of the flexor muscle. But in the present state of our knowledge little stress can be laid on supposed homologies of the parts of the pharyngeal skeleton; for it is evident that in this region sclerites are frequently developed secondarily.

The articulation of the mandible with the postgenæ is its pleural articulation; the ventral articulation appears to be with the clypeus in *Periplaneta* (Fig. 2), *i.e.*, with the sternite of the second segment in front of the mandibular segment. It is difficult to imagine the steps by which, in the course of the phylogenetic development of cockroaches, this condyle of the mandible could pass from one segment to another without interfering with the usefulness of the mandible during the transition period. This was for us a perplexing problem for a long time.

Later it was found that in *Gryllus* (Fig. 1) the mandible articulates with a small sclerite which is sometimes distinct from the clypeus. The same thing was found in the larva of *Corydalis*, except that here (Fig. 3, *ac*) the sclerite is large and clearly distinct.

As the ventral articulation of a coxa is with an antecoxal piece (see page 27), we regard this sclerite as the antecoxal piece of the mandible. In the course of the consolidation of the segments of the head and of the dorsal flexure of the sternites of the first three segments (the procephalon), the antecoxal piece of the mandible has been pushed out of its own segment past the labrum (the sternite of the second antennal segment) and, in *Gryllus*, nearly past the clypeus. Such a migration of the antecoxal piece could take place without interfering with the action of the mandible.

Doubtless a factor in bringing about these changes is the fact that while there has been a marked reduction in the length of the head segments (the entire head composed of seven segments being approximately of the same length as a single segment elsewhere), there has been no reduction in the width of the base of the mandible in biting insects. It is not strange, therefore, that the least firmly fixed point of articulation, the antecoxal piece, should be pushed out of its primitive position.

In most insects the antecoxal piece of the mandible coalesces with the clypeus, so that the mandible appears to articulate with this sclerite.

In some insects, as Orthoptera, there is a distinct sclerite between the mandible and the gena (Fig. 1, *tr*). This from its position on the cephalic side of the base of the mandible between the pleural and ventral articulations must be regarded as the *trochantin* of the mandible.

This completes our account of the sclerites found in the external skeleton of the head of the more generalized insects. A *résumé* of the conclusions reached is indicated by the following table.

#### SEGMENTS, SCLERITES, AND APPENDAGES OF THE HEAD.<sup>1</sup>

SEGMENTS.	SCLERITES.	APPENDAGES.
I. Ocular (Protocerebral).	Vertex and genæ. · · · · · Front.	Ocular sclerites.
II. Antennal (Deutocerebral).	Antennal sclerites. · · · · · Clypeus proper.	Antennæ.
III. 2d Antennal (Tritocerebral).	· · · · · Labrum (Mouth).	2d Antennæ of Campodea <i>et al.</i>
IV. Mandibular.	Postgenæ. · · · · · Antecoxal pieces. Pharyngeal sclerites.	Mandibles. Trochantin.
V. Superlingual.	· · · · ·	Superlinguæ.
VI. Maxillary.	Maxillary pleurites. · · · · · Lingua.	Maxillæ.
VII. Labial.	Dorsal cervical sclerites. Lateral cervical sclerites. · · · · · Ventral cervical scl. (Gula).	Labium.

<sup>1</sup> In each section of the middle column the dotted line indicates the division between the sternal and the lateral elements of the segment.

## THE ENDOSKELETON OF THE HEAD.

The endoskeleton of the head, like that of the thorax, consists of invaginations of the body-wall and of chitinized tendons. Some of these invaginations may be homodynamous with thoracic tracheæ, but others are obviously apodemes.

In many insects the mouths of some of the invaginations of the wall of the head remain open in the adult ; in *Corydalidæ*, for example, they are very conspicuous.

Some of the apodemes remain separate, and are comparatively simple ; but in the case of two or three pairs of invaginations, they meet and coalesce. In this way there is formed in the interior of the head a complicated structure which is known as the *tentorium* (Burmeister, '32, Vol. I, p. 25).

The three pairs of invaginations which may enter into the formation of the tentorium are known as the *anterior*, the *posterior*, and the *dorsal arms of the tentorium* respectively. The coalesced and more or less expanded tips of these invaginations constitute the central portion of the tentorium, and may be designated as the *body of the tentorium*. From the body of the tentorium there extends a variable number of processes or chitinized tendons.

*The Posterior Arms.* — The posterior arms of the tentorium (Figs. 26, 28, 29, *pt*) are the lateral apodemes of the maxillary segment. In many Orthoptera the open mouth of the apodeme can be seen on the lateral aspect of the head, just above the articulation of the maxilla (Fig. 4). In the Acrididæ (Fig. 28) these apodemes bear a striking resemblance to the lateral apodemes of the thorax (Fig. 16), except that the ventral process of the maxillary apodeme is much more prominent, and the two from the opposite sides of the head meet and coalesce, thus forming the caudal part of the body of the tentorium.

*The Anterior Arms.* — Each anterior arm of the tentorium (Figs. 26, 27, 29, *at*) is an invagination of the body-wall which opens on the cephalic margin of the antecoxal piece of the mandible (Fig. 2, *at*),<sup>1</sup> or, when the antecoxal piece is not distinct,

<sup>1</sup> Note that owing to the flexure of the head in those insects, like *Corydalidæ*, in which the mouth is at the anterior end of the body, the opening of the anterior arm appears to be on the caudal side of the antecoxal piece.

usually on the cephalic side of the cephalo-lateral angle of the clypeus (Fig. 2, *at*). (It should be borne in mind that the cephalic margin of the clypeus is that margin which joins the front; that morphologically the labrum is caudad of the clypeus.)

It has been shown by Carrière and Bürger ('97) that the position of this invagination in the young embryo indicates that it is the spiracle of the mandibular segment. It is easy to see that the migration cephalad of the antecoxal piece of the mandible, already described, would push this invagination into the position which it occupies in the adult insect.

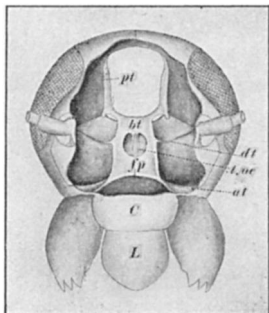


FIG. 26. — Tentorium of a cockroach, dorsal aspect.

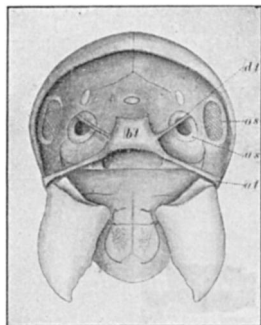


FIG. 27. — Part of the tentorium of a cricket, ventral aspect.

Bearing on this point is the fact that in *Smynthurus*, according to Lubbock ('73), the spiracles "open on the inner side of the bases of the mandibles." It remains to be determined whether in this case the anterior arms of the tentorium are wanting or not. Folsom ('00) found that, although the three pairs of arms are present in the collembolan *Orchesella*, the anterior arms are wanting in *Anurida*. In *Orchesella* where the anterior arms are present they are described by Folsom ('99a) as being joined to the paraglossæ (superlinguæ). But as the invaginations forming the anterior arms arise cephalad of the mandibles (Carrière and Bürger, '97), they cannot pertain to the superlingual segment.

Usually the invagination forming the anterior arms is extended to a greater or less degree along the sutures that converge upon it. This is well shown in *Gryllus*, where it is furnished with three buttress-like extensions: one along the suture between the front and the clypeus; another between the front and the gena; and a third between the gena and the trochantin of the mandible.

In the cockroach (Fig. 26) the buttress of the anterior arm that extends along the suture between the front and the gena is twisted in a way that suggests that it has been pulled out of place by the migration of the antenna. If we imagine the antennal sclerite pushed into a position which would untwist this buttress, it would bring this sclerite opposite the clypeus, that is, in its assumed primitive position.

In the forms upon which the study is chiefly based, — the Plecoptera, the Orthoptera, and the Neuroptera (Sialidæ), — the antecoxal piece of the mandible is joined to the clypeus near its cephalo-lateral angle as described above. But in the Hymenoptera that we have studied it is joined to the caudo-lateral angle of the clypeus very near the labrum. A result of this in some forms is that the point of invagination of the anterior arm is remote from the front, as in the ants, although even here the buttress-like extension follows the margin of the clypeus and extends along the suture between the clypeus and the front. In other Hymenoptera the opening of the invagination has migrated to the cephalo-lateral angle of the clypeus and is thus remote from the articulation of the mandible ; this is the case in *Bombus*.

*The Dorsal Arms.* — Each dorsal arm of the tentorium arises from the side of the body of the tentorium between the anterior and posterior arms and extends either to the front or to the margin of the antennal sclerite (Figs. 26, 27, 29, *dt*).

In the Plecoptera it appears to be merely a chitinized tendon, the peripheral end of which is less chitinized than the base and is only loosely attached to the skull. Here the point of attachment is on the front, some distance from the antennal sclerite, beneath a spot in the cuticle, which is marked by numerous polygonal areas. This spot is very distinct and bears some

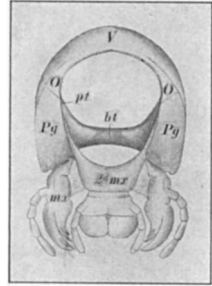


FIG. 28. — Head of *Melanoplus*, caudal aspect.

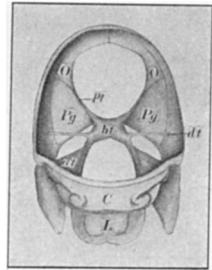


FIG. 29. — Tentorium of *Melanoplus*, cephalic aspect. The distal end of the dorsal arms detached.

resemblance to an ocellus (Fig. 19, *dt*). In the Orthoptera the peripheral end is more strongly chitinized than in the Plecoptera and firmly attached to the skull between the front and the antennal sclerite. It is small in the cockroaches, but is larger and easily seen in *Gryllus* (Fig. 27). In this case it bears some resemblance to an apodeme.

The resemblance to an apodeme is much more marked in some other insects. Thus in the Hymenoptera each dorsal arm is firmly attached to the skull near the antennal sclerite, and, in *Cimbex* for example, it is hollow and has an open mouth, appearing exactly like an apodeme.

It remains to be determined whether or not the dorsal arms in the Plecoptera are homologous with the apodeme-like dorsal arms in other insects, and, if so, which type is the more generalized.

*The Body of the Tentorium.*—This is the part to which the name *tentorium* was originally applied. It is the prominent bridge which divides the occipital foramen into two parts. The alimentary canal in entering the head passes above it, and the nervous system below it. It is formed of the coalesced and expanded tips of the arms of the tentorium (Fig. 28, *bt*).

*The Frontal Plate of the Tentorium.*—In the cockroaches the anterior arms of the tentorium meet and fuse, forming a broad plate situated between the crura cerebri and the mouth; this plate may be termed the *frontal plate of the tentorium* (Fig. 26, *fp*). On each side, an extension of this plate connects it with the body of the tentorium; these enclose a circular opening through which pass the crura cerebri.

*The Tendons of the Œsophageal Muscles.*—Muscles extend from the body of the tentorium to the Œsophagus, passing between the crura cerebri. The tendons connecting these muscles with the body of the tentorium are frequently chitinized. In *Pteronarcys* there is a single chitinized tendon; in *Periplaneta* there are two (Fig. 26, *t.oe*).

*The Tendons of the Flexors of the Head.*—These arise from the lower surface of the body of the tentorium and extend caudad. Sometimes, as in *Stenopelmatus*, they are large and strongly chitinized.

*The Tendons of the Extensors of the Head.*—These are strongly developed in *Gryllus*; they project into the occipital foramen (Fig. 25, *ex.h.*).

*The Dorsal Apodeme of the Head.*—This is also well developed in *Gryllus* (Fig. 25, *d.ap.*).

*The Lateral Cervical Apodemes.*—These have been described above (see Fig. 20, *ap.*).

*The Mandibular Apodemes.*—These also have been described above (see Fig. 25, *m.ap.*).

In this study of the skeleton of the head our attention has been confined almost entirely to representatives of the more generalized orders of insects. We have felt that to do so was the surest way to gain an idea of the fundamental plan of structure. The working out of the ways in which this plan has been modified in the more specialized groups of insects must be left for the future and perhaps for other workers.

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#### LIST OF ABBREVIATIONS.

<i>ac.</i>	Antecoxal piece.	<i>lg.</i>	Leg.
<i>ant.</i>	Antenna.	<i>md.</i>	Mandible.
<i>ap.</i>	Apodeme.	<i>m. em.</i>	Maxillary epimeron.
<i>as.</i>	Antennal sclerite.	<i>mf.</i>	Middle field.
<i>at.</i>	Anterior arm of the tentorium.	<i>mx.</i>	Maxilla.
<i>bt.</i>	Body of the tentorium.	<i>O.</i>	Occiput.
<i>C.</i>	Clypeus.	<i>os.</i>	Ocular sclerite.
<i>C<sub>1</sub>.</i>	First clypeus.	<i>Pg.</i>	Postgena.
<i>C<sub>2</sub>.</i>	Second clypeus.	<i>pl.</i>	Pleurite.
<i>cl.</i>	Cephalic lobes.	<i>pr.</i>	Procephalon.
<i>d. ap.</i>	Dorsal apodeme.	<i>prs.</i>	Præsternum.
<i>dt.</i>	Dorsal arm of the tentorium.	<i>ps.</i>	Pharyngeal sclerites.
<i>em.</i>	Epimeron.	<i>pt.</i>	Posterior arm of the tentorium.
<i>es.</i>	Episternum.	<i>S.</i>	Sternum.
<i>e. su.</i>	Epicranial suture.	<i>S<sub>2</sub>.</i>	Sternellum.
<i>ex. h.</i>	Extensors of the head.	<i>sl.</i>	Superlingua.
<i>F.</i>	Front.	<i>sp.</i>	Spiracle.
<i>fp.</i>	Frontal plate of the tentorium.	<i>t. oe.</i>	Tendons of the œsophageal muscles.
<i>G.</i>	Gena.	<i>tr.</i>	Trochantin.
<i>Gu.</i>	Gula.	<i>V.</i>	Vertex.
<i>L.</i>	Labrum.	<i>2d mx.</i>	Second maxillæ or labium.
<i>l.</i>	Lingua.		
<i>lf.</i>	Lateral field.		

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