

A COMPARATIVE STUDY OF THE LABIUM OF
COLEOPTEROUS LARVAE.

by

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PREFACE.

Herewith I wish to express my appreciation to Mr. R. E. Snodgrass of the United States Bureau of Entomology. He has been an unfailing source of guidance and assistance, and his encouragement has been little short of inspirational.

To Dr. A. G. Böving of the United States National Museum I also express deep gratification. He has helped me not only by making valued suggestions but also by identifying larvae which I collected and by loaning me representatives of families which I could not have studied otherwise.

In nearly all cases the drawings were made from material dissected under a binocular. In a few instances mounts were made on microscope slides and studied with the compound microscope.

INTRODUCTION.

The present problem was undertaken with the idea of comparing the labia of coleopterous larvae and giving the proper connotation to the various parts and plates thereof. The naming of the divisions has been based on a study of muscle insertions and origins. It is hoped that students of systematic entomology may gain some help, either directly or indirectly, from the facts brought out in this study.

The mouth parts, or organs of feeding, in some insects are directed downwards, that is the plane in which they move is vertical. Insects which move the gnathal appendages in this manner are spoken of as hypognathous. In other forms however, the head capsule is turned upwards on the neck, through approximately ninety degrees, and the mouth parts are directed forward. In this condition they move in a horizontal plane. An insect in this group is said to have a prognathous head.

In order that this forward and upward rotation should not change the plane of the foramen magnum (Pl. I, B, For), modifications in the form of elongation of the posteroventral region of the head was essential. This lengthening took place at the base of the labium or by the addition of a gula to the proximal part of the labium. Thus in coleopterous larvae, which in nearly all cases have the prognathous type of head, the gula (Pl. I, B, Gu) is generally well developed.

Except for the modifications brought out by the above mentioned revolution, the head capsule of coleopterous larvae conforms in general with that of a generalized insect such as the roach.

THE STRUCTURE OF THE HEAD CAPSULE OF COLEOPTEROUS LARVAE.

The head of Silpha sp.

Silpha is an excellent subject for a morphological study of the generalized coleopterous larval head. The larvae are easily obtained in quantity and are sufficiently large to permit of ease of dissection.

The head (Pl. I) is robust, somewhat wider than long, the greatest width being behind the middle. In dorsal view (A) the coronal suture (cs) and the frontal sutures (fs) are readily visible and unmistakable. The epistomal suture (es), although its central portion has become lost, aids further in the delimitation of the areas of the dorsal surface of the head. In it are found the anterior tentorial pits (at). It serves to divide the area in front of the frontal sutures into the clypeus (Clp) and the frons (Fr). The clypeus and labrum (lm) are not united as in some forms but are clearly separated by the clypeolabral suture (cls).

The antennae (Ant) are comparatively long and consist of three segments. There are, on the dorsal surface of the head, four ocelli (Oc) on each side just behind the bases of the antennae, and on

the ventral surface there are two more ocelli (B, Oc) on either lateral margin. The postoccipital suture (A, pos) is found along the posterior margin of the head capsule and behind it lies the rather narrow postocciput (Poc).

The ventral surface of the head (B) shows the maxillae and labium to be retracted, leaving a narrow bridge between the foramen (For) and the posterior articulations of the cardines (a''). In this bridge are the posterior tentorial pits (pt) which lie in the ends of the anteriorly extended postoccipital suture (pos). Behind and between the tentorial pits is the gula (Gu), which although somewhat small, is a true example of this structure. The maxillae and the labium are seen to be united for approximately half their lengths by a large membranous area which, however, allows of separate action. Discussion of these parts is given elsewhere.

In order that the relationship between the labial and hypopharyngeal muscles may be more readily understood, a lateral view of the labium is shown (C). In addition to the retractors of the prementum (rst) and the ventral adductors of the labium (2adlb), which are described below (Pg. 30) there are present the dorsal adductors of the labium (Pl. I, C, ladlb). These arise on the base of the postmental sclerite (Pmt) very close to the ventral adductors, and insert on the base of the first prementum (IPrmt), dorsal to the ventral adductors. The retractors of the hypopharynx (E, rhphy) arise from the tentorial arms (Tent) close to their bases. This set of muscles inserts on the hypopharynx about midway between the anterior margin of the ligula (Lig)

and the mouth (Mth).

The maxilla of Silpha (D) shows only a slight indication of a division between the lacinia (Lc) and galea (Ga). With their rather complete fusion into one part there have been lost the stipital flexors of these parts. However the cranial flexor of the lacinia (flcc) is present. It arises on the postocciput and is a short muscle attached to a long apodeme which inserts on the inner margin of the base of the lacinia, slightly anterior to the insertion of the adductor of the stipes (adst).

In the stipes (St) arise two opposing muscles, the depressor (dpdp) and levator (lpdp) of the palpus. The tentorial muscles of the stipes consist of a large bundle having its origin on the tentorial arm (Tent). This muscle, the adductor of the stipes (adst) inserts just within the stipes, close to its inner margin.

Near the origin of the latter muscle there arises from the tentorium a muscle of the cardo, the adductor of the cardo (adcd). It inserts in the cardo on its lateral surface. Also inserting on the cardo, or more properly on an apodeme from the base of the cardo, is a short muscle the promotor of the cardo (pmcd). It originates from the postgena about halfway between the cardo and the posterior angle of the head.

As was stated above in the discussion of the external view of the head, the areas are well set off by sutures. The delimitation of these areas is further aided by a study of the muscles of the anterior part of the stomodaeum. The presence of the frontal ganglion

(E, FrGng) separates the muscles arising on the clypeus from those arising on the frons. The former insert on the stomodeum anterior to the ganglion, the latter posterior to the ganglion. In Silpha there is only one pair of muscles which arises on the clypeal region. These, the dilators of the buccal cavity (dlbc), insert on the stomodeum just posterior to the true mouth opening (Mth). The function of this pair of muscles is, of course, to enlarge the buccal cavity to admit passage of food.

The anterior (ldlphy) and posterior (2dlphy) dilators of the pharynx arise on the frons and insert on the dorsolateral surface of the pharynx. The anterior set attaches in very close proximity to the frontal ganglion. The posterior dilators arise somewhat behind the former and insert on the pharynx just before the brain (Br). Between the origins of these two groups of muscles there arise the retractors of the mouth angles (rao) which insert on the posterior end of the oral branch of the suspensorial sclerite of the hypopharynx (HS). This muscle, as its name implies, serves to retract the margins of the mouth opening.

The ventral muscles of the pharynx have their origin on the tentorium, but not on the same part as that from which the retractors of the hypopharynx (rhphy) originate. The ventral dilators of the pharynx (vdphy) arise from a posterior extension of the tentorium, on which are also attached the ventral muscles from the prothorax. A tentorium with this posterior extension seems unique in this larva and it will be discussed in another part of the paper.

The posterior labral muscle (mlro) has been included in this figure (E) to show the relationship of its origin with that of the dorsal pharyngeal muscles.

The head of Chauliognathus sp.

The head of Chauliognathus viewed dorsally (Pl. II, A) has the general form of a rectangle, with the two lateral margins nearly parallel but inclined slightly towards one another on the posterior half of the head. Its length, including the maxillae and palpi, is approximately one and one-half times its greatest width measured immediately behind the ocelli (A, Oc). The head capsule is not set deeply into the prothorax and the cervical membrane (Cvx) attaches close to the posterior margin of the head.

There are no boundary markers in the form of sutures which would assist in the definite separation of the areas on the dorsal surface of the head. By a study of the pharyngeal muscles (F) however, the general region of the frons (A, Fr) is shown by the origins of the dilators of the pharynx (F, dlphy). The clypeus and labrum (A, Clp + Lm) are completely fused and the clypeal margin of the head is nearly transverse, with a series of five teeth on either side.

There is only one pair of ocelli (Oc). They are placed on the lateral margins of the head capsule, immediately posterior to the bases of the antennae.

The antennae (Ant) are three segmented. The second segment is slightly longer than the first. The third has become greatly

reduced and appears to be little better than a terminal sensory appendix with a seta.

The mandibles (Md) are comparatively long and slender. An accessory tooth or retinaculum is found about midway on the inner face of each mandible. There is no molar area present and none would be expected, considering the systematic relationship, the nature of the food, and the method of feeding of this insect. The mandibles articulate dorsally at the dorsal condyle (c).

On the ventral surface of the head (B) there appear to be no indications of sutures which would separate the two epicranial halves, which are thus considered as being completely fused. The post-occipital suture has lost all connection with the posterior tentorial pits (pt), which usually lie in the former. The tentorial pits, except where their posterior margins are joined with the head capsule, are surrounded by membrane.

Immediately in front of the pits are the cardines (Cd) of the maxillae. They are much reduced in size and are of a shape nearly elliptical. The stipes (St) have a rather typical shape but they bear, in this species, no evidence of a galea and only a rudimentary lacinia (D, Lc). Other members of this family, however, possess both galea and lacinia. The stipes lie on a level with the postmental sclerite (Pmt) of the labium, and the maxillae together with the labium, are projected noticeably from the head (C). The maxillary palpi (E, MaxPlp) are three segmented, the third segment being slightly shorter than the other two which are nearly equal in length.

A description of the labium of Chauliognathus is given separately, with that of the various other labia.

The dorsal labial muscles and the maxillary muscles are shown (D) as viewed from within. The tentorial arms (Tent) extend anteriorly from their union with the head wall and flatten out into rather broad plates. From them originate two pairs of muscles, the adductors of the cardo (adcd) inserting on the cardines (Cd) and the adductors of the stipes (adst) which insert on the stipes (St).

Arising from the sclerite of the stipes, three bundles of muscle fibers are found. Two of these are long and slender and cross one another between their origins and insertions. These muscles are the depressor (dplp) and levator (lplp) of the palpus. The point of origin of the depressor is lateral to that of the levator. It lies ventral to the latter and inserts on the base of the palpus in the region of the medial surface of the latter. The levator muscle attaches on the base of the palpus and in keeping with its function of opposing the depressor its point of insertion is on the lateral surface of the basal segment.

As was stated above both galea and lacinia are suppressed in this species except for a remnant of the latter in the form of a small sclerite (D, Lc). On this sclerite two muscles are inserted which are, as customarily found when the lacinia is well developed, the stipital flexor of the lacinia (flcs) and the cranial flexor of the lacinia (flcc). The former originates on the stipital sclerite near its posterolateral margin and proceeds diagonally to its attachment

on the sclerotic remnant described above. The cranial flexor, a comparatively long and slender muscle, originates from the postoccipital ridge (B, PoR). Its point of origin is in the neighborhood of that of the ventral adductor of the labium (Pl. IX, C, 2adlb)

The dorsal adductors of the labium (Pl. II, D, ladlb) have their origin together with the ventral adductors on the postoccipital ridge. Close to their point of insertion the dorsal adductors unite and attach on a median sclerite.

In order to describe more clearly the tentorial muscles of the cardo and of the stipes a lateral view is shown (E). The posterior end of the cardo (Cd) very closely approaches the tentorial arm (Tent) and, in function at least, articulates with the latter. Since the tentorial muscle of the cardo (adcd) inserts close to the anterior margin of the latter it can be seen that when the muscle contracts the cardo swings in an arc, with its posterior end as a pivot, and thus forces the stipes and connected parts anteriorly. Retraction is accomplished by the adductor muscle of the stipes (adst) which, when it contracts, withdraws the labiomaxillary complex to its original position. Without doubt the cranial flexor of the lacinia (D, flcc) is of some assistance in this latter procedure.

The dorsal muscles of the pharynx are quite readily seen and the frontal nerve connective (F, FrCon) makes it possible to determine their homologies. The compressors of the labrum (clpr) arise on the anterior margin of the united clypeus and labrum (A, Clp + Lm). The lateral halves of this muscle are closely

approximated at their points of origin, being attached on a short internal median ridge (A, r). As they proceed to their insertion the two halves diverge laterally and insert on a transverse sclerotized plate lying immediately dorsal to the hypopharyngeal sclerome (F, Hphys). The dilators of the buccal cavity (dlbc) originate from the posterior part of the clypeolabral region and insert on the dorsal wall of the pharynx, just posterior to the mouth (Mth).

The muscles lying behind the frontal nerve connective consist of two bundles of fibers on each side. These, the dilators of the pharynx (dlphy), originate from the frontal region of the head (A, Fr) and insert dorsally and laterally on the pharynx.

In comparison with most other coleopterous larvae studied the hypopharyngeal sclerome (F, Hphys) in Chauliognathus is developed to a rather unusual degree. No doubt this is an adaptation to the habits of feeding on a liquid or semiliquid diet, the food being conducted to the mouth by mandibular canals or grooves. Thus there is no necessity for a large opening from the mouth to the exterior, and it has been partially closed by the development of the hypopharyngeal sclerome.

The head of Orthosoma sp.

The dorsal surface of the head capsule of Orthosoma (Pl. III, A) is divided by the frontal sutures (fs) which extend diagonally, approaching the anterior margin of the head in close proximity to the antennae (Ant). The triangular area between and in front of these

sutures is the frons (Fr) although included in this area is a portion of the clypeus (Clp) as may be seen from a study of the pharyngeal muscles. The labrum (Lm) is semicircular and partially covers the mandibles when in repose (B, Lm). The mandibles (A, Md) are robust and well fitted for gnawing the passageways which this insect makes through solid timbers.

The foramen magnum (B, For) is divided by the cross bridge of the tentorium. Through the anterior opening thus formed passes the ventral nerve cord. The digestive tract proceeds into the thorax through the posterior and larger of these two openings. The hypostomal suture (hs) is very apparent on the ventral surface of the head and is marked internally by a strong ridge.

The muscles of the maxilla (C) are strong and well developed. From anterior extensions of the posterior tentorium (Tent) arise adductors of the cardo and of the stipes. The adductor of the cardo (adcd) inserts on the medial edge of the sclerite of the cardo (Cd). In this respect Orthosoma differs somewhat from the generalized form in which this muscle inserts on the lateral boundary of the cardo (Pl. I, D, adcd). The adductor of the stipes (Pl. III, C, adst) consists of a double muscle, the elements of which are entirely separate. One branch of this muscle inserts on the very posterior limit of the lateral margin of the stipes (St). The medial part of this muscle originates directly dorsal to the adductor of the cardo, on the tentorium, and inserts at the bottom of the fold between the stipes and the membranous part of the cardo, i.e., at the posterior margin of the stipes.

The lacinia (Lc) is represented by a thumblike extension of the internal margin of the maxilla and extends posteriorly, on the dorsal surface of the maxilla, nearly to the level of the edge of the head capsule. Inserted on the posterodorsal margin of the lacinia is a large muscle, the cranial flexor of the lacinia (flcc), which arises from the ventral wall of the head. Its point of origin is approximately on a level with the center of the anterior part of the foramen (B, For).

Arising also from the head wall, just anterior to the above muscle, is the promotor of the cardo (C, omcd). This muscle lies ventral to the lacinia muscle and inserts on a short apodeme extending backwards from the membranous part of the cardo.

Originating on the ventral surface of the stipes are the muscles of the palpus (Flp). These muscles are the levator (lplp) and depressor (dplp) of the palpus.

As indicated previously, a portion of the clypeus is included in the dorsal wall of the head capsule and is to be definitely separated from the frons only by the insertion of the dilators of the buccal cavity (D, dlbc). Just posterior to this muscle there arise the robust anterior dilators of the pharynx (ldlphy). Between the insertion of these muscles and the brain (Br) there attach the posterior dilators of the pharynx (2dlphy) consisting of rather slender strands, diverging toward their origin on the frons (Fr).

The ventral dilators of the pharynx (vd1phy) are several slender strands originating on the tentorial bridge (Tent) and inserting on the ventrolateral surface of the pharynx (Phy).

The posterior labral muscles (E, mlrp) arise on the frons, more specifically from an internal ridge which divides the frons in the midline. They insert on the posterior margin of the ventral surface of the labrum. The relationship with the dilators of the buccal cavity (dlbc) is indicated in the figure.

The salivary ducts (F, S1D) in Orthosoma consist of two completely separated tubes. Because of the openings of these glands (S1O) which lie in the fold between the maxillae and the labium, they are known as maxillary glands. Such glands occur in many coleopterous larvae but they are usually small and inconspicuous (Snodgrass, 1935). In Orthosoma they extend well into the thoracic cavity as long convoluted tubes.

The brain of this insect (D, Br) is small. From it arise the nerves of the simple eyes (G, OpNv), the antennae (AntNv), the labrum (LmNv), and the frontal connective (FrCon) by which it connects with the frontal ganglion.

The suboesophageal ganglion (H, Gng) lies just without the head capsule, its position being directly ventral to the tentorial bridge (B, Tent). From it, as customarily, arise the nerves of the ventral mouthparts and it connects with the brain by the circumoesophageal connective (CoeCon). The labial nerve (LbNv) and the hypopharyngeal nerve (HphyNv) have a common root. The maxillary nerve (MxNv) and the mandibular nerve (NdNv) arise separately from the ganglion, the latter nerve being more robust, as would be expected considering the comparative amount of muscle fiber which it innervates.

GENERAL DISCUSSION OF THE INSECT LABIUM.

The labium of insects in its simplest generalized form consist of two major divisions. These parts have been given various names by previous workers, as is shown in the table following, but the most logical system of terminology is that suggested by Snodgrass (1931) because it results from comparative studies of these structures in all insects and signifies homologous parts through the entire class. For the proximal division of the labium he suggests the term postmentum. This division supposedly includes the fused cardines of the second maxillae and the part of the labial sternum which is generally accepted as being united with the cardines. The distal division of the labium, that part which always carries the palpi and ligular lobes when these parts are present, is now rather generally known as the prementum. It unquestionably represents the stipites of the second maxillae.

The main divisions of the labium may remain as single parts or each may be subdivided into two or more sclerites. Snodgrass (1931, p. 483-484) states in regard to the postmentum that "its sclerotization may take the form of one, two, or even three distinct plates."

The terminology of the labium of insects in general seems somewhat more complicated than the morphology. Perhaps more attention has been given the sclerites than they deserve, considering their secondary significance. The origin of the term mentum and its connection with a definite region of the labium is rather obscure but in as much as it means "chin" it was doubtless intended to apply to that

part of the fused second maxillae which supports the "lip." Since the word labium has a common derivation with "lip" it would seem better, perhaps, to refer to the distal region of the second maxillae, that part which is movable by muscles, as the labium. Crampton (1921) has apparently the same idea when he calls the distalmost division of the underlip region the "eulabium."

In order to assist in understanding and correlating the systems of terminology for the parts of the labium, the following table has been compiled. It shows the names that have been applied to the same divisions by the indicated workers.

Comstock (1924)	Kadić (1902)	Snodgrass (1928)	Walker (1931)	Modern usage adopted in this paper
Ligula - -	Mentum - - -	Mentum - -	Mentum - - - - -	Prementum
Mentum - -	Vorderplatte of submentum	Submentum	{ Secondary sub- mental plate - - Mentum { Primary sub- mental plate - - Submentum }	Postmentum
Submentum -	Submental- platte			

The complete musculature of the labium (salivary pump muscles omitted) based on the condition as found in some of the more generalized forms (Roach, Pl. IV, B. Cricket, Snodgrass, (1931) Fig. 24) is shown in the diagrammatic representation (Pl. IV, A). It shows the labium as made up of two main divisions, the prementum (Prmt), and the postmentum (Pmt). The postmentum is in turn divided by a suture into the mentum (Mt) and the submentum (Smt). These are the parts in the usual three-part labium, although this seems infrequently

to be the case in coleopterous larvae, as will be shown later.

Kadić (1902) showed that the mentum and submentum are to be considered as secondary subdivisions of the basal part of the labium and that therefore the labium is fundamentally made up of two regions. Walker (1931), after a study of the labial muscles, substantiates Kadić's view, namely that the mentum is in reality a sclerite of the basal region. While holding to the same viewpoint as to the importance of the divisions it has been thought best in this paper to use the terms mentum and submentum for the two basal subdivisions, and adopt the term postmentum for the combined areas as suggested by Snodgrass (1931).

The prementum bears the palpi (Pl. IV, A, Plp) and the ligula (Lig). The latter consists typically of four lobes, a median pair of glossae (Gl) and a lateral pair of paraglossae (Pgl). The postmentum is subdivided into two divisions, the mentum (Mt) and the submentum (Smt).

A description of the seven pairs of muscles found in the primitive labium follows:

The depressors of the palpus (Pl. IV, A, dplo) arise in the prementum near or on the margin of a median slit which in some cases divides the prementum nearly to its base. These muscles insert on the distal margin of the basal segment of the palpus (Plp).

Opposing the muscles just described are the levators of the palpus (lplo). These also originate in the prementum close to its posterolateral angles. In some cases (Periplaneta, Pl. IV, B) these muscles arise from a pair of small separate sclerites which lie close

to the base of the prementum. In keeping with their function of opposing the depressors they insert on the proximal margin of the basal segment of the palpus.

The flexors of the glossae (fgl) have their origin ventrally (posteriorly) on the prementum. They insert on the base of the glossae. The flexors of the glossae and those of the paraglossae lie ventral (posterior) to the depressors of the palpi.

The flexors of the paraglossae (fpgl) originate also on the prementum and extend more or less parallel to the flexors of the glossae. They insert on the base of the paraglossae.

The dorsal (anterior) adductors of the labium (ladlb) arise on the tentorium (Tent) close to the point of origin of the ventral adductors, but as a rule lateral to the latter. They insert on the dorsal (anterior) surface of the prementum near the bases of the paraglossae. In the large majority of cases their points of insertion are distal to those of the ventral adductors.

The ventral (posterior) adductors (2adlb) usually originate, as stated above, on the tentorium medially to the dorsal adductors. They insert on the base of the prementum, usually on the main sclerite but sometimes (as in Perioplaneta) on a pair of smaller sclerites (B, b,b). This pair of muscles and that described in the preceding paragraph may work together or oppose one another.

The retractors (or flexors) of the prementum (rst) are median muscles which originate from the submental subdivision (A, Smt) of the postmentum (Pmt). They insert on the base of the prementum, and in

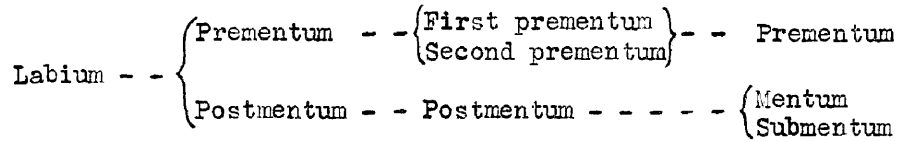
nearly all cases their points of insertion are posterior to those of any other pair of labial muscles.

From the preceding descriptions it can be seen that the typical labium may be separated into its two major divisions, the prementum and the postmentum, on the basis of the insertions of the dorsal and ventral adductors of the labium, and the retractors of the prementum. It has become well established by previous investigators that the retractors and adductors insert in all cases only on the prementum. That the mentum, a subdivision of the postmentum, contains no muscle insertions is shown by examples: Periplaneta (Pl. IV, B) and the labium of adult Harpalus (Pl. IV, C). It is necessary to accept this interpretation if we are to gain the consistency essential to a comprehensive understanding of the labial structure.

In the larvae of Coleoptera the prementum and the postmentum are again the principle regions of the labium. The postmentum is made up of two distinct subdivisions in Orthosoma (Pl. X, A) and in Ptilodactyla (Pl. IX, B), but it may be a single area as in Byrrhus (Pl. IV, D). The prementum in coleopterous larvae is very often subdivided so that confusion has arisen in giving the proper connotation to the parts. Taking Byrrhus as a typical example of this condition we find the prementum made up of two sclerites or divisions which are here called the first prementum (IPrmt) and the second prementum (IIPrmt). Neither one of these is to be considered as secondary to the other since they both have the same value morphologically. The second prementum, in all species studied, serves as the area on which the retractors

of the prementum insert. In general this subaivision has been considered by previous investigators to be the mentum, but the fact that muscles do insert on it shows that it is impossible correctly to call it the mentum in the sense of the term as applied to the more generalized forms. The term second prementum shows that it is a part of the prementum, to which it belongs.

In order to clear up any confusion that the preceding discussion may have caused, the possibilities of subdivision in the labium of the larvae of Coleoptera, based on the facts as actually observed, are shown in the following table.



Gula

In the forms studied there was found no example of a labium consisting of four parts, i.e., a first prementum, a second prementum, a mentum, and a submentum. In no case did a true mentum occur together with a second prementum. The first prementum corresponds to the prementum of previous students of these larvae. It carries the palpi, and the ventral adductors of the labium are inserted in nearly all cases on its base.

In the drawings of the labia, representing the various families, the ventral muscles only have been shown, with a few exceptions. These, the ventral adductors of the labium and the retractors of the prementum

(when present) definitely determine the morphological relationships of the divisions of the labium and serve as criteria for defining them.

The gular region in the larvae of Coleoptera has been the subject of considerable difference of opinion as to its definite boundaries. Crampton (1921) shows that in certain insects (termites and others) the gula and submentum are fused into a single "gularmental plate," and that the posterior portion of this sclerite, fused with the head, is the gula. The conspicuous elongation of this region in certain coleopterous larvae (as for example Tenebrionidae Pl. VIII, C) has been shown by Snodgrass to be an adaptation for preserving the vertical plane of the foramen magnum in the development of the prognathous type of head.

The gula is defined by Böving and Craighead (1932) as the "area behind submentum, separated from this by a real or imaginary suture between posterior articulations of the two cardines." Since, however, there are numerous cases (Meloidae Pl. X, C) in which the retractor muscles of the prementum originate on the anterior portion of this area, that part from which these muscles arise should be considered as at least making up a part of the postmentum. For this reason it is preferable to consider the gula as the area between the anteriorly extended lower ends of the postoccipital suture lying behind a line drawn between the posterior tentorial pits.

Comparison of various types of labial structure.

As has been previously stated, the labium of insects in its

primitive state (Pl. IV, A) is made up of two major divisions, the prementum (Prmt) lying distal to the insertions of all labial muscles, and the postmentum (Pmt) lying proximal to the insertions of all labial muscles.

The roach, Periplaneta, (Pl. IV, B) conforms to this scheme, although the ventral adductors of the labium (2adlb) insert on small lateral sclerites (b, b). These are, however, unquestionably but secondary subdivisions of the prementum (Prmt). The submental (Smt) division of the postmentum (Pmt) which is made up in the roach and the adult Coleoptera (C) of the submentum and the mentum (Mt), serves as the area from which the retractors of the prementum (B, rst) originate. The ventral adductors of the labium (2adlb) arise in the typical arrangement from the tentorium.

In adult Coleoptera, of which Harpalus (C) serves us as an example, the muscles again correspond to the primitive condition. The retractors of the prementum (rst) arise from a short and low internal ridge, which is common to the two components of the muscle. This ridge is marked externally by a slender band of extra heavy sclerotization lying in the submentum (Smt). The ventral adductors (2adlb) again arise from the tentorium, but their point of origin is nearly contiguous with the submentum, being in the angle formed internally between the latter and the tentorial arms. These muscles insert on the prementum at the posterior margins of segment-like bases of the palpi (Flp).

As a typical example of the labium of coleopterous larvae, Byrrhus was chosen (Pl. IV, D). "Typical" is used here in the sense

that the conditions of muscular arrangement and labial division, as shown in Byrrhus, represent those found in the majority of the larvae studied. That is, more larvae conform to this arrangement than to any other.

The prementum of Byrrhus is made up of two divisions, the first and the second prementum (D, IPrmt, IIPrmt). The postmentum (Pmt), however, is not subdivided and consists of a single sclerite. Either the mentum, as found in the generalized forms and in some larvae, has been lost or is inseparably fused with the submental sclerite to form the postmentum.

On the base of the second prementum are inserted the retractors of the prementum (rst), which in common with the generalized condition, arise from the postmentum. The ventral adductors of the labium (2adlb) insert on the base of the first prementum, close to the midventral margin of the latter. They likewise conform with the primitive labium in having their origin on the tentorium (Tent).

The dorsal adductors (ladlb) are typical in so far as their insertion is concerned, since they attach on the first prementum. Their point of origin, however, shows considerable divergence, since they arise, not from the tentorial bar but from the internal surface of the postmentum, near the point of origin of the retractors of the prementum.

That Byrrhus is not alone in having muscles other than the retractors of the prementum, arising from the postmentum, is shown by several outstanding examples, among which are Fytho sp., (Pl. VIII, D),

Lagriidae (Pl. VIII, F), Cucujus clavipes (Pl. VI, F), and Languria laeta (Pl. VI, E). Such findings are in direct contradiction to the statement of Snodgrass (1935, p. 149) and to make the facts agree we must consider that the origins of muscles may migrate to a certain degree. It is to be noted, however, that except in very unusual cases of migration (Chauliognathus Pl. IX, C) the muscular origins have not moved very far. In most cases when the point of origin is on the postmentum, it is directly ventral to the tentorial bar which extends across the head between the tentorial pits, as shown in Byrrhus (Pl. IV, D).

DESCRIPTIONS OF LABIA OF COLEOPTEROUS LARVAE.

Cicindelidae* (Pl. V, A, B)

The labium of Cicindela sp. is made up of a rather compact and firmly united prementum (A, Prmt) which is attached to the head capsule by a membranous area which, as in other representatives of the Adephaga, is called the mentum (Mt). The submentum (Smt), if it should be considered as being present, has lost what membranous connection it may have had with the head capsule and is inseparably united with the ventral wall of the head.

At the base of each palpus (Plp) in the species studied there is a small sclerotic area divided by a suture which acts as a hinge. This sclerite is in very close union with the palpus and also

* The families of Coleoptera have been arranged in the systematic order of Böving and Craighead (1930), pp. 70-80.

with the basal sclerite of the prementum, which partially surrounds it at the base and extends forward, as a bar, beyond the bases of the palpi. The latter sclerite stops at the margin of the head capsule to which it is connected by the membranous mentum, but the above-mentioned bar extends posteriorly into the head for some distance. Thus we must consider the bar as a continuation of the basal sclerite of the prementum.

Two bundles of muscle fibers (A, B, lclp), one on either side, arise from this bar, within the head capsule. They insert on the sclerite at the base of the palpus, their points of insertion being indicated by a black spot on each sclerite just posterior to the hinge or suture, previously mentioned.

No other muscles within the labium may be found, and with the palpi as well developed as they are, it is apparent that these are levators of the palpus. At least this is certainly their functional significance.

Inserted on the inner end of the bar-like structure above described, is a pair of muscles (A, B, 2adlb). These muscles originate from the tentorium, but not from its base near the posterior tentorial pits. Instead, the origins have migrated dorsally along the posterior arms and even onto the anterior arms (B, AT). That they do originate from the anterior arms, in part at least, is shown by the fact that the dorsal arms (DT) of the tentorium which arise as secondary outgrowths of the anterior arms, are given off ventral to the attachment of the dorsalmost fiber of this labial muscle. That the dorsal arm is present

is proven by the fact that the antennal muscles (MAnt) arise therefrom.

Apparently, therefore, the labium consists entirely of a prementum with its appended parts, connected with the head by a membranous mentum. The sclerite of the basal segment of the palpus has become secondarily broken up. Whether or not the submentum is present is difficult to state since from what is considered this region in closely related forms (see below), there arise the adductors of the stipes (A, adst), although a portion of this muscle originates also from the posterior tentorial arm close to the posterior tentorial pit (pt).

When the ventral adductors of the labium contract they cause the prementum to tip outward from the head, or ventrally, with the fulcrum of the lever at the margin of the head capsule.

Carabidae (Pl. V, C)

The labium of Harpalus sp. is separated into a well-marked prementum (Prnt), a membranous mentum (Mt) and a much narrowed submentum (Snt) and gula (gu). The posterior tentorial pits (pt) lie close together, just lateral to the sutures which mark off this narrowed area.

The ventral muscles of the labium consist of only one pair, the ventral adductors of the labium (2adlb). They arise on the arms of the posterior tentorium (Tent) and insert at the base of the prementum. Since the sclerotization of the mentum is lacking, these muscles serve to retract the prementum.

Dytiscidae (Pl. V, E)

The labium of Dytiscus sp., as in the other representatives of the Adephaga, has the prementum (Prmt) and the mental (Mt) subdivision of the postmentum distinguishable from the head capsule. The remainder of the postmentum, i.e., the submentum (Smt), has become immovably united with the head. The prementum bears the palpi. The mentum is short and does not show in a live specimen when the prementum is retracted. Korschelt (1924) states, in regard to Dytiscus marginalis, that, "Das Mentum is rudimentär. Das Submentum fehlt ganz, und ebenso ist die Ligula vollständig rückgebildet." The submentum (Smt) as a separate sclerite has disappeared but it is interpreted as lying anterior to the tentorial pits (pt).

The muscles inserting on the prementum consist of two pairs of adductor muscles. The ventral adductors (2adlb) originate on the tentorium, at or close to the point of invagination of the latter, and insert on the base of the prementum. Their points of insertion are closer to the midline than is the case in many larvae. The dorsal adductors of the labium (ladlb) originate also on the tentorium but, contrary to their custom, they insert ventrally on the base of the prementum. Proof that these are really the migrated dorsal adductors lies in the fact that their point of origin is as usual, ventral to that of the ventral adductors. Furthermore the point of insertion of the ventral adductors has migrated perceptibly toward the midline of the base of the prementum, allowing room for the dorsal adductors.

Amphizoidae (Pl. V, D)

Amphizoa shows the typical external structure of the labium of the Adephaga. The prementum (Prmt) is movable and joined to the head capsule by a rather short, membranous mentum (Mt). The submentum (Smt) is fused with the exoskeleton of the head. There is no ligula in the labium of this insect, the prementum bearing only the palpi.

The ventral muscles are somewhat more complex than is the case in the above species. The ventral adductors (2adlb) apparently consist of double muscles, appearing as two pairs. One of these arises on the tentorium (Tent) and inserts on the base of the prementum slightly lateral to the median pair. The latter originate on the head wall, posterior to the tentorial pits and thus behind the submentum. It seems apparent, therefore, that half this muscle has migrated posteriorly from the usual position. That both these sets of muscle fibers should be considered as ventral adductors is shown by the presence of the dorsal adductors of the labium (ladlb) which originate on the tentorium and insert dorsally on the base of the prementum.

Gyrinidae (Pl. V, F).

In Dineutes the two parts of the labium which are present and separate from the head capsule are the mentum (Mt) and a split prementum (Prmt). The submentum (Smt) has become completely fused with the skeleton of the head and is not distinguished from the latter by any indication of a suture. The prementum in Dineutes is unique among the larvae studied in that it is very deeply furcate in the

midline. The two parts have the appearance of basal segments of a three segmented palpus, but their musculature proves them to be halves of a cleft prementum. The mentum (Mt) is better developed than was the case in the larvae previously discussed.

The muscles of the labium are the two pairs of adductor muscles which usually insert on the prementum. The ventral adductors (2adlb) originate on the submentum, apparently having migrated there from their more primitive position on the tentorial arms. They insert on the bases of the halves of the prementum and judging from their position, no doubt act as depressors of the palpus-like structure, which is made up of a palpus (Plp) and one half the prementum (Prmt). The dorsal adductors (ladlb) have their origins on the tentorial invaginations and insert on the bases of the divided prementum. Fulfilling their usual role of opposing the ventral adductors, they apparently act as levators of the combined palpus and half prementum.

Silphidae (Pl. VI, A)

The labium of the larva of Silpha shows for the first time, in our study of the labia by families, a three part labium, all components of which are distinctly separated from the head. As in Byrrhus (Pl. IV, D) the first prementum (Pl. VI, A, IPrmt), the second prementum (IIPrmt) and the postmentum (Pmt) cooperate in the formation of the three part labium. They are set off from one another by distinct membranous areas. Furthermore the postmentum is definitely separated by a suture from an incipient gula (Gu).

Silpha differs from Byrrhus in that the ventral adductors of the labium (2adlb) arise on the postmentum rather than on the tentorium (Pl. IV, D). In the form studied the tentorial pits (Pl. VI, A, pt) lie very closely approximated and immediately behind the base of the postmentum. Apparently the ventral adductor muscles have moved their points of origin from the tentorial arms to the base of the postmentum. Up to this point in our consideration of the labium of the various families no retractors of the prementum have been observed. In Silpha however these muscles (rst) are present. They originate from the postmentum and insert on the base of the second prementum.

Staphylinidae (Pl. VI, B)

The labium of Hesperus appears to consist of only two parts which are distinct from the head. The submentum (Smt) is again combined with the head capsule, as in the representatives of the Adephaga. It differs from them however in having the submentum definitely marked off laterally by sutures or grooves. The prementum (Prmt) bears the palpi and a simple ligula. The mentum (Mt) is membranous almost throughout but has a narrow sclerite at its base.

There is present only one pair of ventral muscles. These, the ventral adductors of the labium (2adlb), originate on the bases of the tentorial arms and insert on the base of the prementum.

Histeridae (Pl. VI, C)

In Hololepta the labium is similar to several of the preceding

in that it consists of a clearly marked prementum (Prmt) set off from the head capsule by a membranous mentum (Mt). Also the submentum (Smt) is completely fused with the head capsule although demarcated by definite lateral grooves or sutures. The gula is narrowed to the extent that the sutures which usually bound it laterally have fused completely, forming a so-called gular suture (gs).

There is only one pair of ventral muscles to be found in the labium of this insect. These, the ventral adductors of the labium (2adlb), originate from the posterior tentorium. They insert on the base of the prementum.

Hydrophilidae (Pl. VI, D)

The postmentum (Pmt), the second prementum (IIPrmt), and the first prementum (IPrmt) cooperate in the formation of the labium of Hydrous. The first prementum bears the palpi and the ligula (Lig). The latter is smaller than in most members of this family but it is nevertheless clearly differentiated. The second prementum is broad and its lateral anterior margins are greatly extended. In this respect it resembles the mentum of many adult beetles (Pl, IV, C). It is separated by a well-defined membranous area from the postmentum. About midway of the lateroposterior margins of the latter are found the tentorial pits (pt).

From the condition of the labium as above described it would be expected that there are two ventral pairs of muscles, the ventral adductors of the labium (Pl. VI, D, 2adlb) and the retractors of the

prementum (rst). The adductor muscles originate from the tentorial arms near their bases, the posterior tentorial pits (pt). They converge somewhat and insert on the base of the first prementum. The retractor muscles consist of a single broad bundle in place of the more usual two strands. They originate from nearly the complete posterior width of the postmentum and insert along the base of the second prementum.

Languriidae (Pl. VI, E)

The labium of Languria is divided into three distinct divisions, the first prementum (IPrmt), the second prementum (IIPrmt), and the postmentum (Pmt). Posterior to the base of the distal division is the gula (Gu). The parts of the labium are separated by distinct sutures but not by areas of membrane as in some forms.

There are two pairs of ventral muscles which serve as criteria for properly naming the constituents of this labium. The shorter of these, the retractors of the prementum (rst), arise from the postmentum and insert on the base of the second prementum. The second pair, the ventral adductors of the labium (2adlb), as in Byrrhus, originate from the postmentum and not from the tentorium. They insert on the base of the first prementum.

Silvanidae (Pl. VI, G)

The customary division of the labium into a first prementum (IPrmt), a second prementum (IIPrmt) and a postmentum (Pmt) is found

in Oryzaephilus. The first prementum carries the palpi and one pair of setae. The second prementum also bears a pair of setae situated just before the middle. The postmentum is shorter than the second prementum and at its posterolateral margins are located the posterior tentorial pits (pt). On the postmentum also are found two setae, near its anterior boundary.

The ventral muscles consist of two pairs, the ventral adductors of the labium (2adlb) and the retractors of the prementum (rst). The latter have their origin on the postmentum in the region of the tentorial pits and insert on the base of the second prementum. The adductor muscles also arise from the inner surface of the postmental sclerite, medial to the retractor muscles. They insert on the base of the first prementum.

Cucujidae (Pl. VI, F)

The labium of Cucujus shows the usual three subdivisions. The distal part, which bears the palpi and is separated from the proximal parts by a distinct membranous area, is the first prementum (IPrmt). The second prementum (IIPrmt) is separated from the postmentum by a second membranous area. The postmentum (Pmt) and the gula (Gu) are fused into one sclerite with no dividing suture. This sclerotized area is bounded laterally by the posterior tentorial pits (pt) and the postoccipital suture (pos), and posteriorly by the margin of the foramen. The gula is interpreted as that portion of this sclerite which lies posterior to an imaginary line connecting the posterior

tentorial pits.

The ventral adductors of the labium (2adlb), as in Pyrrhus, arise from the postmentum instead of from the tentorium. These points of origin, however, are on a line with the posterior tentorial pits and it is apparent that they have migrated from the tentorial bridge to their present location. Their points of insertion, on the base of the first prementum, are consistent. The retractors of the prementum (rst) arise from the customary place on the postmentum, slightly anterior to a line connecting the tentorial pits.

Laemophloeidae (Pl. VI, H)

In Eunaisibius the labium is separated into three regions, the first and second subdivisions of the prementum, and the postmentum. The first prementum (IPrmt) bears the palpi. The second prementum (IIPrmt) is marked off anteriorly and posteriorly by distinct sutures. The latter area bears a pair of setae which are situated slightly before the middle, and a smaller pair located near the posterolateral margins. The postmentum (Fmt) is marked laterally by the posterior tentorial pits (pt) and posteriorly by the ventral margin of the foramen.

The ventral adductors of the labium (2adlb) arise on the cross bar or bridge of the tentorium and insert on the base of the first prementum. The retractors of the prementum (rst) arise on the proximal part of the postmental area and insert on the base of the second prementum.

Nitidulidae (Pl. VII, A)

The labium of this family is made up of three divisions, only one of which belongs to the prementum. The posterior two parts are subdivisions of the postmentum. The prementum (Prmt) bears one pair of setae which arise from the rather distinctly shaped sclerite of the prementum. It also carries the palpi which consist of only one segment in contrast to the usual condition of two segments. The mentum (Mt) is separated from the preceding division by a comparatively broad membranous area. It bears one pair of large setae. In the species figured the mentum and submentum (Smt) are separated by a weakly indicated groove but in other species of the family the separation is very clearly marked (Böving and Craighead (1930) Pl. 35, Fig. B). The submentum has a rather peculiar urn shape and extends to the posterior margin of the head.

There is only one pair of ventral muscles in the labium. The lateral elements of this muscle, the ventral adductors of the labium (2adlb), at their point of origin, unite in the midline of the submentum and diverge slightly to their insertion on the sclerite at the base of the prementum.

Endomychidae (Pl. VII, B)

The labium of Endomychidae shows two divisions, the prementum (Prmt) and the postmentum (Pmt). The prementum bears the palpi and a short ligula. It also has on its ventral surface a pair of setae which are situated slightly proximal to the neck membrane and makes up

the larger portion of the labium. On it are located two pairs of setae and an unpaired median seta near the distal margin. Bounding the postmentum on its posterolateral margins are the posterior tentorial pits (pt).

The ventral muscles, as would be expected, are only one pair, the ventral adductors of the labium (2adlb). They originate on the tentorium (Tent) and proceed obliquely from their points of origin to insert on the base of the prementum, where they nearly meet in the midline.

Dacnidae (Pl. VII, D)

The representative of this family, Tritoma unicolor Say, agrees with the general type in having a three part labium made up of the first prementum (IPrmt), the second prementum (IIPrmt) and the postmentum (Pmt). The first prementum carries the palpi and one pair of setae. It is separated from the second prementum by a suture. The postmentum is somewhat unusual in that its lateral margins are extended anteriorly to the level of the base of the first prementum. The posterior margin of the postmentum is marked by a definite suture, separating it from the gula (Gu).

The ventral adductors of the labium (2adlb) originate on the posterior arms of the tentorium, close to the tentorial pits (pt). They insert on the base of the first prementum. The retractors of the prementum (rst) originate at or very near the tentorial pits. Their point of origin so closely approaches the tentorium that it is impossible to definitely state from where they arise. It is thought that

they originate in the angle between the tentorial arms and the postmentum. They insert on the base of the second prementum.

Anthicidae (Pl. VII, E)

Anthicus has a labium which shows the usual three divisions of first prementum (IPrmt), second prementum (IIPrmt), and postmentum (Pmt). In addition there is present a distinct gula (Gu) separated from the postmentum by a definite suture. Each of the divisions of the labium is set off from the others by a suture or groove.

There are two pairs of ventral muscles, the retractors of the prementum (rst) and the ventral adductors of the labium (2adlb). They have the generalized origins and insertions. The adductor muscles arise on the tentorium (Tent) and insert on the base of the first prementum. The retractors have their origin on the postmentum, just anterior to the posterior margin of the latter, and insert on the base of the second prementum.

Eyturidae (Pl. VII, F)

In Eyturus we again have a three part labium but in this case the divisions are the prementum (Prmt), the mentum (Mt), and the submentum (Smt). The two latter divisions together form the postmentum (Pmt). Behind the postmentum and marked laterally by the posterior tentorial pits (pt) is the gula (Gu).

There are two pairs of ventral muscles in this species, both of which insert on the prementum. The retractors of the prementum (rst)

arise from the submental division of the postmentum from whence they proceed to their insertion medially on the base of the prementum. The ventral adductors of the labium (2adlb) arise from the tentorium (Tent) and insert on the prementum, laterally to the retractor muscles.

Colydiidae (Pl. VII, G)

The labium of the representative of the family *Colydiidae* shows no departure from the customary structure of this group. The usual three divisions are clearly marked and readily interpreted from a study of the musculature. The first prementum (IPrmt) bears the palpi and in addition two pairs of setae, the proximal pair much shorter than the distal pair. The second prementum (IIPrmt) likewise carries two pairs of setae. It is separated by membranous areas from the first prementum distally, and from the postmentum (Pmt) proximally. The latter bears, near its anterior margin, two pairs of setae the distal pair of which is exceptionally long and slender. The lateroposterior margins of the postmentum are marked by the posterior tentorial pits (pt).

There are two pairs of ventral labial muscles, neither of which presents any unusual features. The ventral adductors of the labium (2adlb) originate from the tentorial bridge (Tent) and insert on the base of the first prementum. The retractors of the prementum (rst) arise from the posterior region of the postmentum and insert on the base of the second prementum.

Mycetophagidae (Pl. VII, C)

The prementum of *Mycetophagus* is subdivided into the first prementum (IPrmt) and the second prementum (IIPrmt). Each of these divisions bears one pair of setae and is separated from the other by a membranous area. The second prementum is set off from the postmentum (Pmt) by a second membrane. The postmentum has one pair of setae, located slightly before and mesal to the anterior ends of the tentorial pits (pt). There is a slight indication of a groove or suture (indicated in the figure by a broken line) which connects the anterior ends of the tentorial pits. This may be a rudiment of a previously well-marked boundary line between the postmentum and the gula (Gu). This is quite possible because of the fact that the retractors of the prementum originate on the postmentum just anterior to this line.

The ventral adductors of the labium (2adlb) have their origin on the tentorium (Tent) and insert on the base of the first prementum. The retractors of the prementum (rst) arise from the posterolateral portion of the postmentum and insert on the base of the second prementum.

Synchroidae (Pl. VIII, A)

The first prementum (IPrmt), which is clearly set off from the second prementum by membrane, bears a pair of setae situated just behind the bases of the palpi. The ligula is rather more enlarged than ordinarily and it has a considerable group of sensory setae distributed on its distal portion. The second prementum (IIPrmt) has two pairs of setae located close to the lateral margins about midway from the distal

to the proximal boundary. The postmentum (Pmt) is separated anteriorly from the prementum by a suture and is interpreted as extending to the posterior margin of the head. The proximal portion of the postmentum lies between the tentorial pits (pt) and probably includes an undifferentiated gular region.

The ventral muscles have the customary origins and insertions. The ventral adductors of the labium (Zadlb) arise on the tentorium (Tent) and insert on the base of the first prementum near the midline. The sclerite of the first prementum has become extended slightly posteriorly in the center to form a point of attachment for these muscles. The retractors of the prementum (rst), a comparatively large pair of muscles, arise on the postmentum and insert on the base of the second prementum.

Pyrochroidae (Pl. VIII, B)

The customary division of the labium into the first prementum and the second prementum, together with the postmentum, is shown by this species. The labium is somewhat unusual in that it has a considerably elongated ligula (Lig). The postmentum (Pmt) is separated from the second prementum (IIPrmt) by a membranous area, and extends posteriorly as far as the proximal ends of the posterior tentorial pits (pt). The gula (Gu) is a separate sclerite lying posterior to the tentorial pits and the postmentum.

There are the usual muscles in this species. The retractors of the prementum (rst) arise on the postmentum in line with the anterior ends of the tentorial pits and insert on the base of the second

prementum. The ventral adductors of the labium (2adlb) originate from the posterior tentorium (Tent) and insert on the base of the first prementum (IPrmt).

Pythidae (Pl. VIII, D)

In external appearance the labium of Pytho shows no unusual features although it does carry a prominent ligula (Lig). The first prementum (IPrmt) carries the palpi and is set off from the second prementum (IIPrmt) by a membrane. The postmentum (Pmt) is likewise separated from the latter subdivision by a membranous area.

There are two pairs of ventral muscles to be found in the labium of this species. The retractors of the prementum (rst) originate on the postmentum and insert on the base of the second prementum. Their points of insertion are noticeable from the exterior as small ovals more heavily sclerotized than the surrounding integument. The ventral adductors of the labium (2adlb) arise also from the postmental sclerite and insert on the base of the first prementum.

Alleculidae (Pl. VIII, E)

The first and the second prementum, in this labium, are clearly marked off from each other by a membranous area. The second prementum (IIPrmt) is likewise set off from the postmentum (Pmt) by a membrane. The postmentum has as its posterior limit an imaginary line connecting the posterior tentorial pits (pt). Behind the postmentum, but in no way marked off from it, is the gula (Gu). The latter is

bounded along the sides by faint indications of the postoccipital suture.

The ventral muscles again consist of two pairs. The ventral adductors of the labium (2adlb) originate on the tentorium (Tent) and insert on the first prementum (IPrmt). The retractors of the prementum (rst) arise on the postmentum slightly anterior to the tentorial pits and insert on the base of the second prementum.

Tenebrionidae (Pl. VIII, C)

The divisions of the labium of Merinus are consistent with the basic scheme of the three part labium of coleopterous larvae. The gula is definitely separated from the postmentum (Pmt) by a suture. It is marked laterally by the posterior tentorial pits (pt) and the postoccipital suture (pos) and posteriorly by the ventral margin of the postoccipital ridge (PoR).

The ventral adductors of the labium (2adlb) originate on the tentorial arms (Tent) and insert on the base of the first prementum. The usually paired retractors of the prementum (rst) are united in this species into a comparatively large median bundle which arises from the posterior margin of the postmentum. It inserts on the base of the second prementum.

Lagriidae (Pl. VIII, F)

There are seen in the representative of this family the usual three divisions of the labium, the postmentum (Pmt), the second prementum (IIPrmt) and the first prementum (IPrmt). The first prementum

carries the palpi and a distinct ligula. The second prementum is separated from the preceding subdivisions by a membranous ring. The postmentum, lying behind the second prementum is separated from the latter by a distinct membranous area. The lateral margins of the postmentum diverge towards the proximal margin.

The ventral muscles consist of two pairs, the retractors of the prementum (rst) and the ventral adductors of the labium (2adlb). The retractor muscles, as is their custom, originate from the postmental sclerite and insert on the base of the second prementum. The ventral adductors also arise on the postmentum, instead of on the tentorium. Their point of origin is almost directly posterior to that of the retractor muscles. As is the usual condition they insert on the base of the first prementum.

Byrrhidae (Pl. VIII, G)

Since this family shows a type of labium which might be considered generalized for coleopterous larvae it was adopted as a basic example (Pl. IV, D). It shows the three definite divisions of the labium, the first prementum (Pl. VIII, G, IPrmt), the second prementum (IIPrmt), and the postmentum (Pmt). The two segmented palpi, conforming to the general condition, are borne on the first prementum. The latter is marked off from the second prementum by a membranous ring, and the second prementum is separated from the postmentum in a similar manner.

Inserted on the base of the first prementum are found the ventral adductors of the labium (2adlb). They originate on the cross-

bar of the tentorium (Tent). The retractors of the prementum (rst) insert on the base of the second prementum, with their origin on the postmental sclerite.

Helodidae (Pl. VIII, H)

The labium of Prioncyphon consists of but two well-marked divisions. Most of the labium is made up of a large prementum (Prmt) which bears several pairs of scattered setae. From its anterior margin arise the palpi, which are rather small in comparison with other larvae. Between the prementum and the posteroventral margin of the head capsule is the postmentum (Pmt). At its posterolateral margins are the posterior tentorial pits (pt).

There are two pairs of ventral muscles, both of which insert on the prementum. The retractors of the prementum (rst) originate from the tentorial arms and go diagonally to the base of the prementum where they insert close together in the midline. The ventral adductors of the labium (2adlb) are also present. They originate, however, from the postmentum. Their point of insertion is slightly anterior of the center of the premental sclerite. Thus in this insect the origins of the two pairs of ventral muscles are reversed from the more primitive condition as found in the roach (Pl. IV, B).

Nosodendridae (Pl. IX, A)

The labium of Nosodeadron consists of three clearly marked divisions. From a study of the musculature it is seen that these are

the postmentum (Pmt), the second prementum (IIPrmt), and the first prementum (IPrmt). The first prementum carries the palpi and is divided by a distinct groove almost to its base, where the groove joins the apex of a definite triangular piece. The second prementum is marked distally by a membranous band which separates it from the first prementum. It bears near its lateral margins, slightly behind the middle, an obliquely directed comb-like tuft of hairs. The postmentum lies behind the parts described above. It is nearly square and at its posterolateral margins are found the tentorial pits (pt).

The ventral muscles in the labium consist of the usual two pairs, the ventral adductors of the labium (2adlb) and the retractors of the prementum (rst). The latter originate from the postmental sclerite, approximately on a level with the internal tentorial bridge (Tent). They insert on the base of the second prementum. The ventral adductors arise on the tentorial bar and proceeding to their insertion at the base of the first prementum, converge and nearly meet in the midline at their point of attachment on the small triangular area previously mentioned.

Ptilodactylidae (Pl. IX, B)

In the labium of Ptilodactyla are found the prementum (Prmt), a median mentum (Mt), and a proximal submentum (Smt). The two latter parts together form the postmentum. The prementum bears the palpi and a prominent ligula (Lig). The mentum, separated from the prementum by a membranous area, is considerably broader than the distal division.

It is separated from the submentum by a distinct suture and hinge. The latter division is firmly united with the head although it is set off from it by a suture. In connection with this union it is interesting to note that the posterior tentorial pits (pt) have invaded the submentum. The lateral elements of the postoccipital suture have become united into a median suture (gs) and unite with the ends of the posterior ends of the posterior tentorial pits.

Although the tentorial invaginations are located in an unusual position it is definitely assured that this posterior division is the submentum because from it originate the ventral adductors of the labium (2adlb). They insert on the base of the prementum.

Cantharidae (Pl. IX, C)

The labium of Chauliognathus shows only two parts, the terminal prementum (Prmt) and a median oval sclerite surrounded by membrane, the postmentum (Pmt). All signs of a gula have become obliterated. The posterior tentorial pits (pt), which at their posterior ends are firmly united with the head capsule, extend into the membranous area at the base of the labium.

There are two pairs of ventral muscles, both of which insert on the base of the prementum. The first pair, the retractors of the prementum (rst), originate near the posterior margin of the postmental sclerite (Pmt). They lie ventral to the second pair, the ventral adductors of the labium (2adlb) which arise on the postoccipital ridge (PoR). These latter muscles are long and slender, and their points of

origin have apparently migrated to their present location, possibly in connection with the loss of the gular area.

Cebrionidae (Pl. IX, D)

A study of the labium of Cebrion shows it to consist of three parts, a prementum (Prmt), a mentum (Mt), and a submentum (Smt). The prementum bears the palpi and close behind the bases of these are found three pairs of setae, the ones on either side arranged in a straight line. The mentum is an elongate oval sclerite taking up the central region of the labium. The submentum consists of two small, triangular sclerites. They are separate from one another and located near the posterior margin of the labium.

The ventral muscles are only one pair, the ventral adductors of the labium (2adlb). They arise from the triangular submental plates and insert on the base of the prementum.

Elateridae (Pl. IX, E)

The labium of the Elateridae shows externally two distinct parts, the first prementum (IPrmt) and the postmentum (Pmt), but upon dissection there is found a third division, the second prementum (IIPrmt). This latter subdivision is firmly united with the first prementum but is completely invaginated into the distal end of the postmentum. Between the posterior margin of the postmentum and the posterior tentorial pits (pt) lie the closely approximated cardines (Cd) of the maxillae. Present also is a gular region (Gu) lying between and behind the

tentorial pits.

There are two pairs of ventral muscles present in the labium of these larvae. The retractors of the prementum (rst) originate from the distal region of the postmentum. They insert on the ventral margin of the second prementum. The ventral adductors (2adlb) arise from the tentorial arms (Tent) and insert on the base of the first prementum.

Passalidae (Pl. IX, F)

The labium of Passalus is made up of three distinct areas which are the prementum (Prmt), the mentum (Mt), and the submentum which is not separated from the gula and hence forms a combined region (Gu + Smt). The prementum carries, as usual, the palpi. The mentum is triangular and devoid of setae. It lacks the typical shape as found in adult beetles (Pl. IV, C, Mt) since its anterolateral angles are not extended. There seems to be no membranous area between it and the prementum but the suture separating them undoubtedly allows flexibility. More than half the ventral surface of the labium consists of the submentum. The distal part is flanked by a pair of sclerites which are set off from the remainder of the region by sutures, but it is doubtful if they have any significance beyond being a part of the submentum. Slightly behind the middle and somewhat removed from the lateral margins of the submentum are found the posterior tentorial pits (Pl. IX, F, pt), from which arise the internal tentorial bridge (Tent).

The ventral muscles are only one pair, the ventral adductors of the labium (2adlb). They arise from the tentorial bridge and insert on the base of the prementum.

Scarabaeidae (Pl. IX, E)

In Ochrosidia we have a three part labium made up of a first prementum which has two pairs of setae, a second prementum bearing one pair of setae, and the postmentum, likewise having one pair of quite large setae. The divisions are readily distinguished by a membranous area between the first two and a flexible suture between the second prementum and the postmentum.

The ventral adductors of the labium (2adlb) arise from the tentorium (Tent) on the remnants of the posterior tentorial arms (Pl. XI, G, PT). They insert on the base of the first prementum (Pl. IX, E, IPrmt). The retractors of the prementum (rst) arise on the postmentum near the midline and insert on the base of the second prementum (IIPrmt). They are slightly asymmetrical in that the right muscle is considerably stouter than its fellow. This is an adaptation, in Ochrosidia, to the unusually asymmetrical hypopharyngeal sclerotization.

Melyridae (Pl. IX, G)

The labium of Melyridae consists of a rather insignificant first prementum (IPrmt), an elongate second prementum (IIPrmt) and an area lying completely between the posterior tentorial pits (pt) which would appear to be a combined postmentum and gula (Pmt + Gu).

The ventral labial muscles again consist of two pairs. The ventral adductors of the labium (2adlb) originate from the tentorial bar (Tent) and insert on separate sclerites in the small first prementum. The retractors of the prementum (rst) arise from the postmentum and insert beyond the middle of the elongate second prementum.

Meloidae (Pl. X, C)

The first prementum (IPrmt) and the second prementum (IIPrmt) are clearly set off from one another and from the remainder of the labium. The postmentum and gula (Gu + Pmt) form a continuously sclerotized area and neither one is to be easily differentiated from the other. Since the bases of the tentorial arms have become greatly elongated into low ridges the tentorial pits are not clearly marked and can not be used to separate the postmentum from the gula.

Corresponding to the division of the prementum there are two ventral pairs of muscles. The retractors of the prementum (rst) arise on the postmental area and insert on the base of the second prementum. The ventral adductors of the labium (2adlb) arise on the ridge-like tentorial arms and insert on the base of the first prementum.

Cerambycidae (Pl. X, A)

The labium of Orthosoma shows the divisions which are typical of adult Coleoptera and of Orthoptera (Pl. IV, B, C): a distal prementum (Pl. X, A, Prmt), and a postmentum (Pmt) subdivided into a mentum (Mt) and a submentum (Smt).

The muscles of the labium consist of one ventral and one dorsal pair, the ventral adductors of the labium (2adlb) and the dorsal adductors of the labium (ladlb) respectively. They both have their origin on an extension from the tentorial bridge (Tent). The ventral adductors insert on the base of the prementum near the ventral midline. The dorsal adductors attach dorsally near the lateral margins of the base of the prementum.

Bruchidae (Pl. X, F)

The labium of Spermophagus shows a remarkable departure from the labia of coleopterous larvae in general in that the labial palpi are entirely lacking. The prementum (Prmt) simply ends bluntly. The first and second prementa are completely united although the united region has two pairs of ventral muscles. The postmentum (Pmt) also contains a sclerite which has a shape much resembling that of a new moon. The postmentum is considerably broader than the prementum and extends laterally nearly to the median margin of the cardo (Cd).

In common with the labia of Chrysomeloidea (see below) there are two ventral pairs of muscles. These are the ventral adductors of the labium (2adlb) and the retractors of the prementum (rst). As stated above, both pairs insert on the prementum, on the single sclerite. The retractors of the prementum also arise on the tentorial bridge lateral to the points of origin of the adductor muscles. They attach on the base of the sclerite of the prementum.

Camptosomatidae (Cryptocephalinae) (Pl. X, B)

The representative of this family which was used in the study has a labium very similar to that of Eumolpidae (see below). The labium shows a first prementum (IPrmt), and a considerably elongated second prementum (IIPrmt), the elongation apparently having resulted at the expense of the postmentum (Pmt) which is rather short and small.

The muscles are similar to those of the preceding family, both ventral pairs originating from the tentorium. The retractors of the prementum (rst) insert at a point considerably removed distally from the base of the second prementum. The ventral adductors of the labium (2adlb) are long and extend to the first prementum where they insert on the base of that division.

Eumolpidae (Pl. X, E)

The labium of Eumolpidae shows a distinct division into three parts, the first prementum (IPrmt), the second prementum (IIPrmt), and the postmentum (Pmt). The first prementum bears the palpi. The second prementum has, near its base and closely approaching one another in the midline, a pair of sclerites, each of which bears a seta. There is no gula present and the base of the postmentum connects directly with the neck membrane. The two halves of the head are firmly held together ventrally by the tentorial bar (Tent).

The ventral muscles consist of two pairs, the ventral adductors of the labium (2adlb), and the retractors of the prementum (rst). The former originate from the tentorium and insert on the sclerotized

area at the base of the first prementum, near its lateral margins. The retractors of the prementum (rst) likewise arise on the tentorial bar but insert near the base of the second prementum on the sclerites referred to in the preceding paragraph.

Galerucidae (Pl. X, D)

In Galerucella the labium consists, apparently, of but two divisions, the first prementum (IPrmt) and the second prementum (IIPrmt). The first prementum carries the palpi and has across its base a narrow sclerite on which two setae are situated near the midline. The second prementum (IIPrmt) makes up the major portion of the labium. Covering much of the median part of this division is a sclerite near whose anterior margin are located two setae. The postmentum has become reduced, even more so than in Cryptocephalinae (B), and does not show in the figure. The labium in this group is very prominent and protrudes from the ventral level of the head as a large flap. The postmentum has become adapted for connecting the posterior margin of the second prementum with the neck membrane, and thus extends more or less vertically.

The ventral muscles consist of two pairs, the ventral adductors of the labium (D, 2adlb) and the retractors of the prementum (rst). The former originate from the tentorium (Tent) and insert on the sclerite at the base of the first prementum. The retractors also arise from the tentorium, medially to the origin of the ventral adductors, and insert in about the center of the sclerite of the second prementum.

THE TENTORIUM OF COLEOPTEROUS LARVAE.

The tentorium of insects in general is of considerable interest, and a few examples of the structure as found in coleopterous larvae are included here. The probable evolutionary development of this internal "skeleton" has been given by Snodgrass (1935) and no repetition of the present day views will be included in this paper.

The tentorium of apterygote insects at least is composed of two pairs of braces or arms. One pair consists of two invaginations arising from the anterior tentorial pits (Pl. I, A, at) in the epistomal suture (es). The second pair of arms results from invaginations from the posterior tentorial pits (Pl. I, B, pt). These component parts may be united in various ways, as Snodgrass has shown (1935, Fig. 62) or the four parts may be entirely separate and greatly reduced. Oftentimes there is, in addition to the two pairs of arms above mentioned, a third pair of dorsal arms. These, however, are considered to be secondary outgrowths of the anterior arms and not invaginations from the dorsal wall of the head, since their connection with the head is usually membranous or at times entirely lacking.

In addition to its function of bracing the walls of the head, the tentorium serves as a very important region for muscle attachments. From it usually originate the adductor muscles of the maxillae and labium, the retractors of the hypopharynx and the ventral dilators of the stomodaeum. The antennal muscles are also attached to the tentorium, usually to the dorsal arms when present.

Of the tentoria of coleopterous larvae which were studied

that of Silpha is the most nearly similar to the generalized type. The posterior arms (Pl. XI, A, B, PT) arising from the posterior tentorial pits (Pl. I, B, pt) are closely approximated at their bases but as they proceed anteriorly and dorsally they diverge somewhat. Also they are continued posteriorly beyond the pits. On this posterior extension are attached the ventral dilators of the pharynx (Pl. I, E, vdiphy) and on it also are inserted the ventral muscles which extend from the prothorax into the head. United with the distal ends of the posterior arms are the anterior tentorial arms (Pl. XI, B, AT). These arise from the anterior tentorial pits (Pl. I, A, at) which lie in the epistomal suture (es). The dorsal arms (Pl. XI, B, DT) originate from the anterior arms and extend dorsally to the head wall. The lateral elements, each consisting of a posterior, anterior, and dorsal arm, are not united across the median line in Silpha.

In Merinus laevis (C) the posterior arms (PT) have lost connection with the anterior arms. They are short and have broadened out into rather flat plates which although close together in the midline, are completely separate. On these arms are attached at least the ventral adductors of the labium (Pl. VIII, C, 2adlb).

Tenebroides (Pl. XI, D) shows a condition very similar to that of Merinus, the posterior arms (PT) being separate and not connected with the anterior arms.

The posterior tentorium of Synchroa (E, F, PT) consists merely of a transverse bar between the posterior tentorial pits and is somewhat concave ventrally. No projections or extensions, which might

indicate connection with the anterior arms are observable. On this transverse bar are attached the ventral adductors of the labium.

A somewhat similar case to the above is found in Ochrosidia villosa (G, H) where the tentorium consists essentially of a bridge. It is, however, not invaginated into the head but is continuous with the lateral walls in such a manner as to form a smooth arch. From the inner dorsal margin of this bar two extensions (G, H, PT) arise which are evidently parts, at least, of the posterior tentorial arms. On these are attached the strong adductor muscles of the maxillae and the ventral adductors of the labium (Pl. IX, E, 2adlb).

The posterior tentorial apparatus of the staphylinid larva, Hesperus baltimorensis (I, J), is made up of two "Y" shaped structures, the base of the "Y" being directed ventrally and connected with the posterior tentorial pits (I, pt). (See also Pl. VI, B, pt) These lateral elements are completely separated. On the base of each is attached its corresponding portion of the ventral adductors of the labium.

In Cicindela (K) the lateral elements of the posterior tentorium have grown together at their bases and there has resulted a flat transverse plate extending nearly perpendicular into the head. The inner ends are slightly separated which indicates that the tentorium as it is at present, has resulted by a coalescing of what was originally two posterior arms.

The tentorium of coleopterous larvae, although it may show various forms, can be homologized with the primitive structure, as has been shown above.

CONCLUSION.

The muscles of the head capsule of the larvae of Coleoptera conform, for the most part, with those of a generalized insect such as the roach. There are, of course, various modifications which have taken place in connection with the habits of the particular species. The ligula, when present, was not observed to be divided into glossae or paraglossae in any case, as it is in the orthopteroid insects. There were found no larvae which showed an hypognathous head, all the forms having the prognathous type, which has resulted in a conspicuous elongation of the postmentum or in the addition of a gular region behind the base of the labium. In some cases the postgenae have completely united and this has caused a lengthening of the ventral wall of the head.

From the study thus far it does not appear that any particular form of labium is more generalized than another. It seems, however, that the labium of Byrrhus or of Silpha is typical. This type of labium consists of a prementum subdivided into a first and a second prementum, and of a postmentum made up of only one division or sclerite. Too much emphasis should not be placed upon sclerites as indices of primary morphological areas, since they are but the result of secondary hardening processes in the integument; but until some better method is devised for delimiting or describing a part of the insect it is essential that they be used. When they are studied together with muscle origins and insertions, they become a fairly safe criterion for separating parts of the external anatomy.

The tentorium of the larvae studied shows various specializations but by means of a comparative study, it may be homologized with the conditions as found in more generalized insects.

ABBREVIATIONS USED ON THE FIGURES.

<u>a</u> , posterior articulation of mandible.	<u>CoeCon</u> , circumoesophageal connective.
<u>a"</u> , articulation of cardo.	<u>cs</u> , coronal suture.
<u>ACd</u> , apodeme of cardo.	<u>Cvx</u> , neck, cervix.
<u>adcd</u> , adductor of cardo.	<u>dlbc</u> , dilator of buccal cavity.
<u>adlb</u> , adductor of labium	<u>dplp</u> , depressor of palpus.
<u>adst</u> , adductor of stipes.	<u>diphy</u> , dilator of pharynx.
<u>Ant</u> , antenna.	<u>DT</u> , dorsal arm of tentorium.
<u>AntNv</u> , antennal nerve.	<u>es</u> , epistomal suture.
<u>AT</u> , anterior arm of tentorium.	<u>fgl</u> , flexor of glossa.
<u>at</u> , anterior tentorial pit.	<u>flcc</u> , cranial flexor of lacinia.
<u>b</u> , secondary sclerite of prementum in <u>Periplaneta</u> .	<u>flcs</u> , stipital flexor of lacinia.
<u>Br</u> , brain.	<u>For</u> , foramen magnum.
<u>c</u> , anterior articulation of mandible.	<u>fpgl</u> , flexor of paraglossa.
<u>Cd</u> , cardo.	<u>Fr</u> , frons.
<u>Clp</u> , clypeus.	<u>FrCon</u> , frontal connective.
<u>clbr</u> , compressor of labrum.	<u>FrGng</u> , frontal ganglion.
<u>cls</u> , clypeolabral suture.	<u>fs</u> , frontal suture.

- Ga, galea.
Gl, glossa.
Gng, ganglion.
gs, gular suture.
Gu, gula.
gu, much narrowed gula.
- HB, hypopharyngeal bracon.
Ephy, hypopharynx.
EphyNv, hypopharyngeal nerve.
EphyS, hypopharyngeal sclerome.
HS, suspensorial sclerite of hypopharynx.
hs, hypostomal suture.
hy, hypostomal margin.
- Lb, labium.
LbNv, labial nerve.
LbPlp, labial palpus.
Lc, lacinia.
Lig, ligula.
Lm, labrum.
LmlNv, labral nerve.
lulp, levator of palpus.
- MAnt, antennal muscle.
Md, mandible.
- MdNv, mandibular nerve.
mlro, posterior labral muscle.
Mt, mentum.
Mth, mouth.
MxNv, maxillary nerve.
MxPlp, maxillary palpus.
- Oc, ocellus.
OpNv, optic nerve.
- Pgl, paraglossa.
Phy, pharynx.
Plp, palpus.
pmcd, promotor of cardo.
Pmt, postmentum.
Poc, postocciput.
PoR, postoccipital ridge.
pos, postoccipital suture.
Prmt, prementum.
IPrmt, anterior subdivision of prementum.
IIPrmt, posterior subdivision of prementum.
PT, posterior arm of tentorium.
pt, posterior tentorial pit.
- r, ridge.
rac, retractor of mouth angle.

rhphy, retractor of hypopharynx.

rst, retractor of prementum.

Sfs, subfacial sinus.

SLD, salivary duct.

SLC, opening of salivary duct.

Smt, submentum.

SoeGng, suboesophageal ganglion.

St, stipes.

TE, cross bar of tentorium.

Tent, tentorium.

vdiphy, ventral dilator of pharynx.

PLATES I - XI.

Explanation of Plate I.

- A. Silpha sp. (larva) Dorsal view of head.
- B. - Ventral view of head.
- C. - Lateral view of labial and hypopharyngeal muscles.
- D. - Muscles of maxilla, ventral view.
- E. - Muscles of left side of pharynx, lateral view.

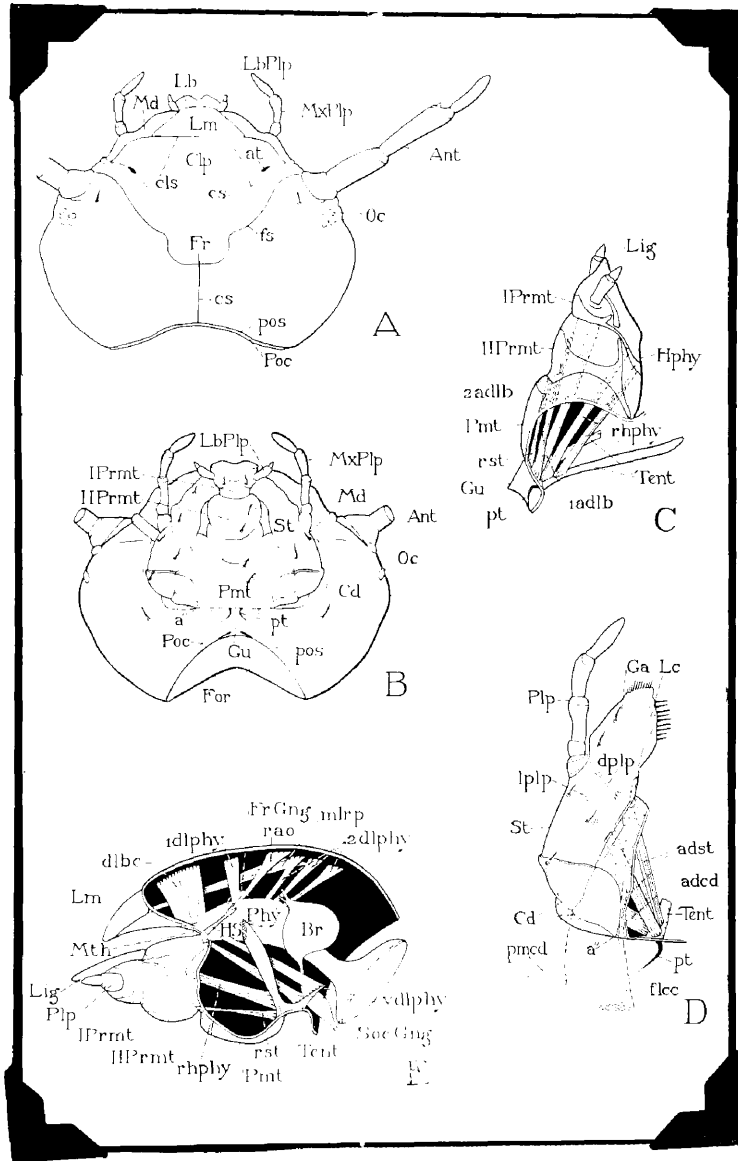


PLATE I.

Explanation of Plate II.

- | | | |
|----|-----------------------------------|--|
| A. | <u>Chauliognathus</u> sp. (larva) | Dorsal view of head. |
| B. | - | Ventral view of head. |
| C. | - | Lateral view of head. |
| D. | - | Dorsal view of the muscles of the ventral mouthparts, ventral premental muscles omitted. |
| E. | - | Lateral view of the tentorial muscles of maxillary cardo and stipes. |
| F. | - | Lateral view of dorsal muscles of pharynx. |

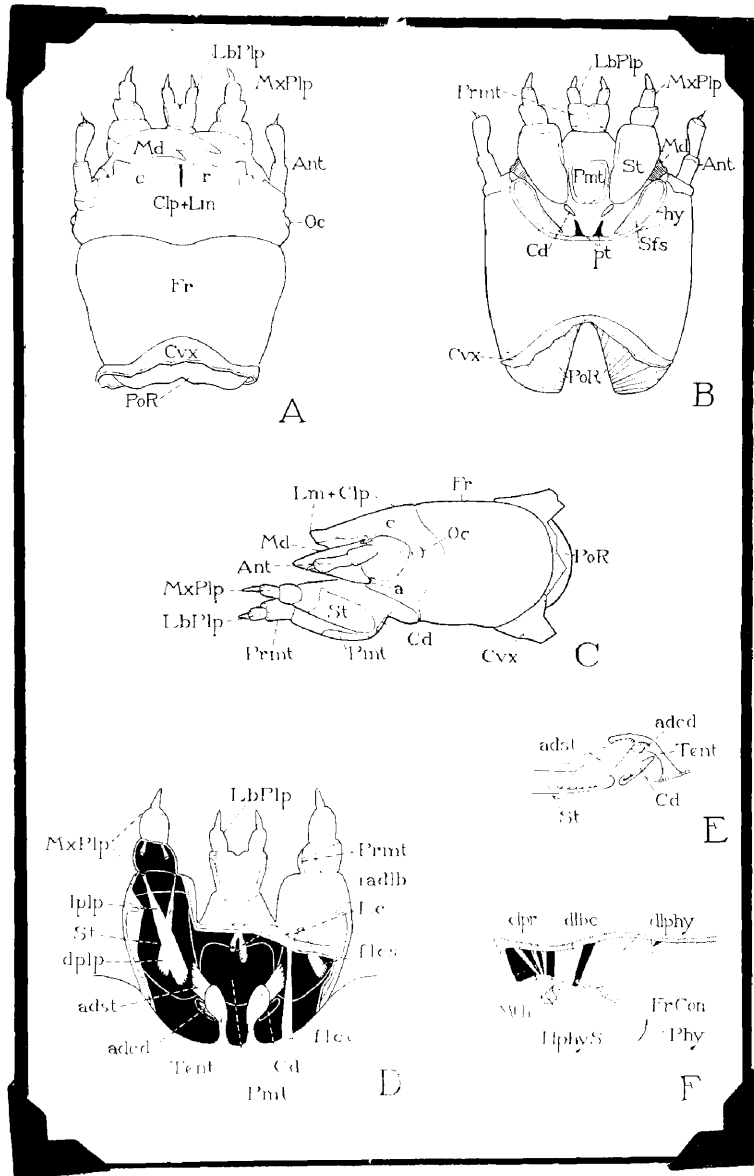


PLATE II.

Explanation of Plate III.

- A. Orthosoma sp. (larva) Dorsal view of head.
- B. - Ventral view of head.
- C. - Muscles of maxilla, ventral view.
- D. - Muscles of left side of pharynx,
lateral view.
- E. - Muscles of labrum, lateral view.
- F. - Opening of maxillary gland, lateral
view.
- G. - Brain, dorsal view.
- H. - Suboesophageal ganglion, ventral
view.

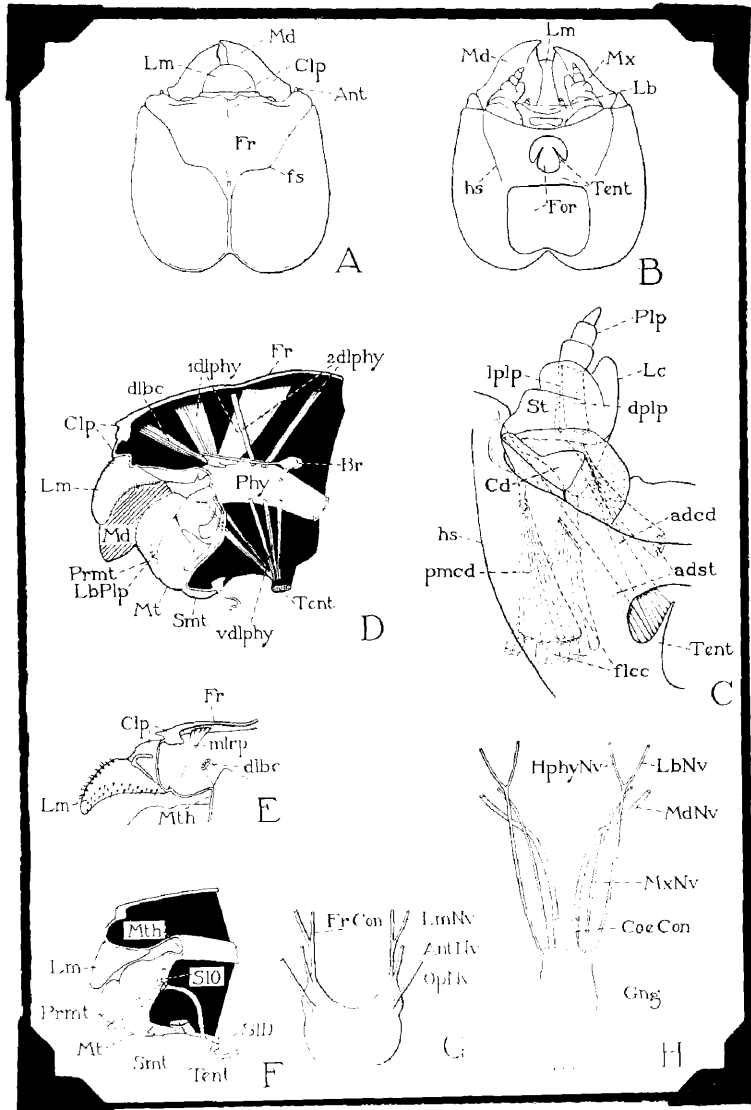


PLATE III.

Explanation of Plate IV.

- A. Internal view of hypothetical labium showing origins and insertions of all labial muscles.
- B. Periplaneta americana L. (adult) External view of muscles of labium.
- C. Haropalus sp. (adult) External view of muscles of labium.
- D. Byrrhus sp. (larva) External view of muscles of labium.

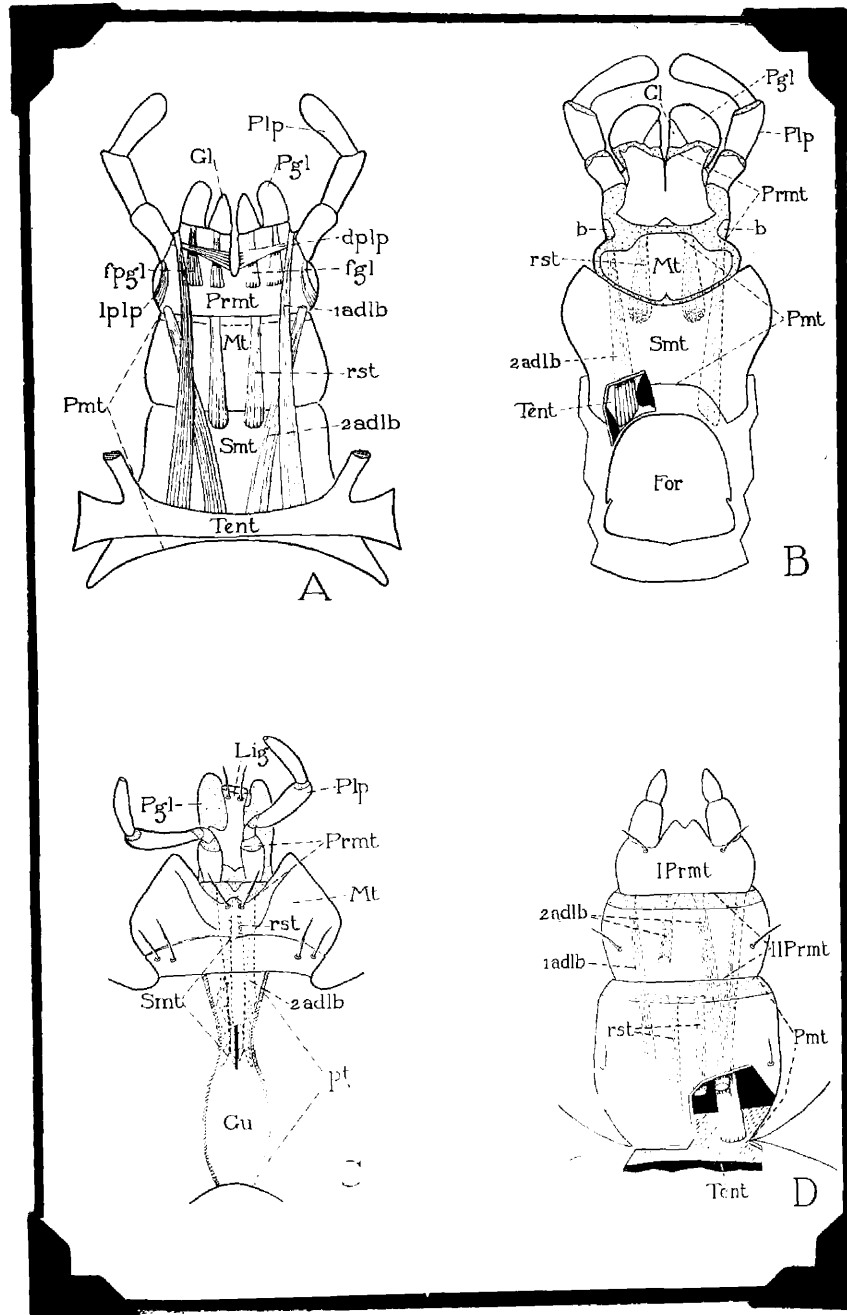


PLATE IV.

Explanation of Plate V.

- A. Cicindela hirticollis Say. (larva) Ventral view of labium.
- B. - Ventrolateral view of left ten-
torial muscles of labium and
hypopharynx.
- C. Harpalus sp. (larva) Ventral view of labium.
- D. Amphizoa (insolens Lec.)? (larva) Ventral view of labium.
- E. Dytiscus sp. (larva) Ventral view of labium.
- F. Dineutes sp. (larva) Ventral view of labium.

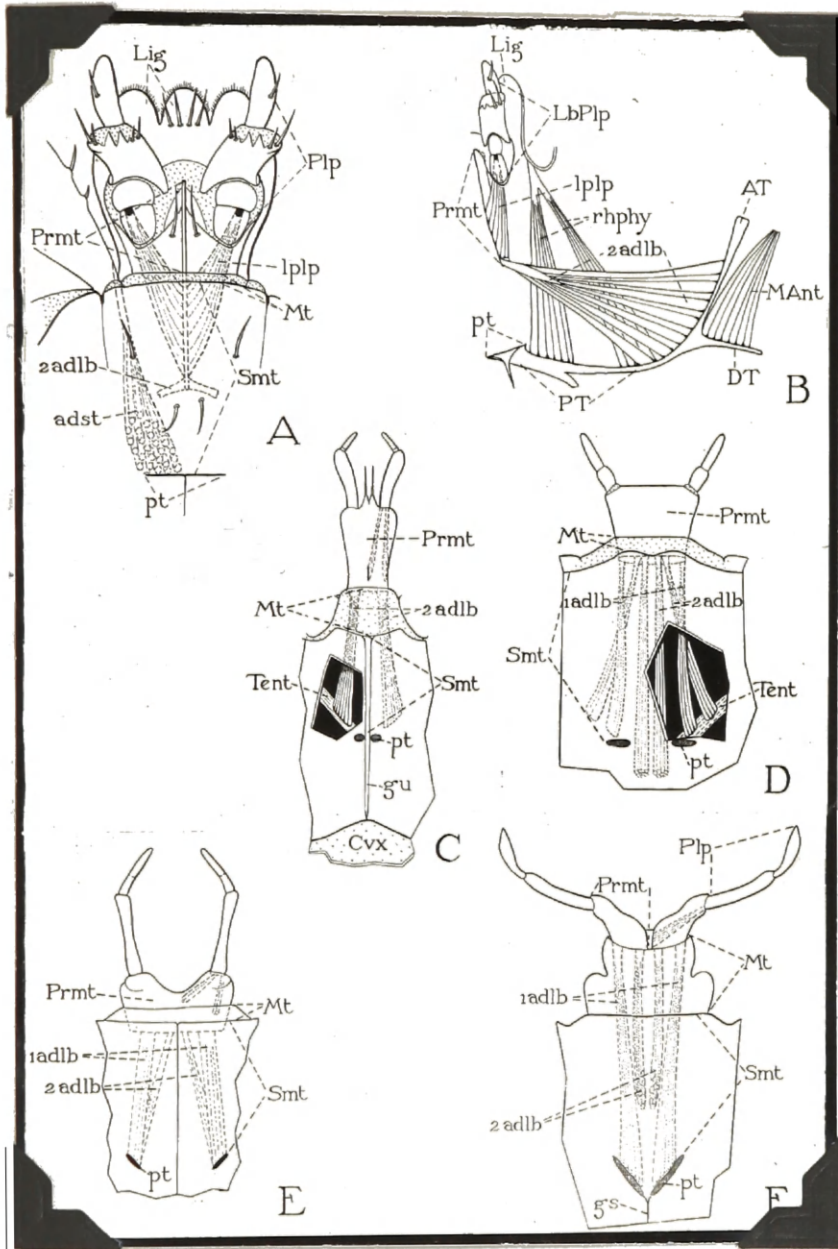


PLATE V.

Explanation of Plate VI.

- A. Siloha sp. (larva) Ventral view of labium.
- B. Hesperus baltimorensis Grav. (larva) Ventral view of
labium.
- C. Hololepta sp. (larva) Ventral view of labium.
- D. Hydrous triangularis Say. (larva) Ventral view of labium.
- E. Languria laeta Lec. (larva) Ventral view of labium.
- F. Cucujus clavipes Fab. (larva) Ventral view of labium.
- G. Oryzaophilus surinamensis (L) (larva) Ventral view of labium.
- H. Eunausibius wheeleri Schwartz and Barber. (larva) Ventral
view of labium.

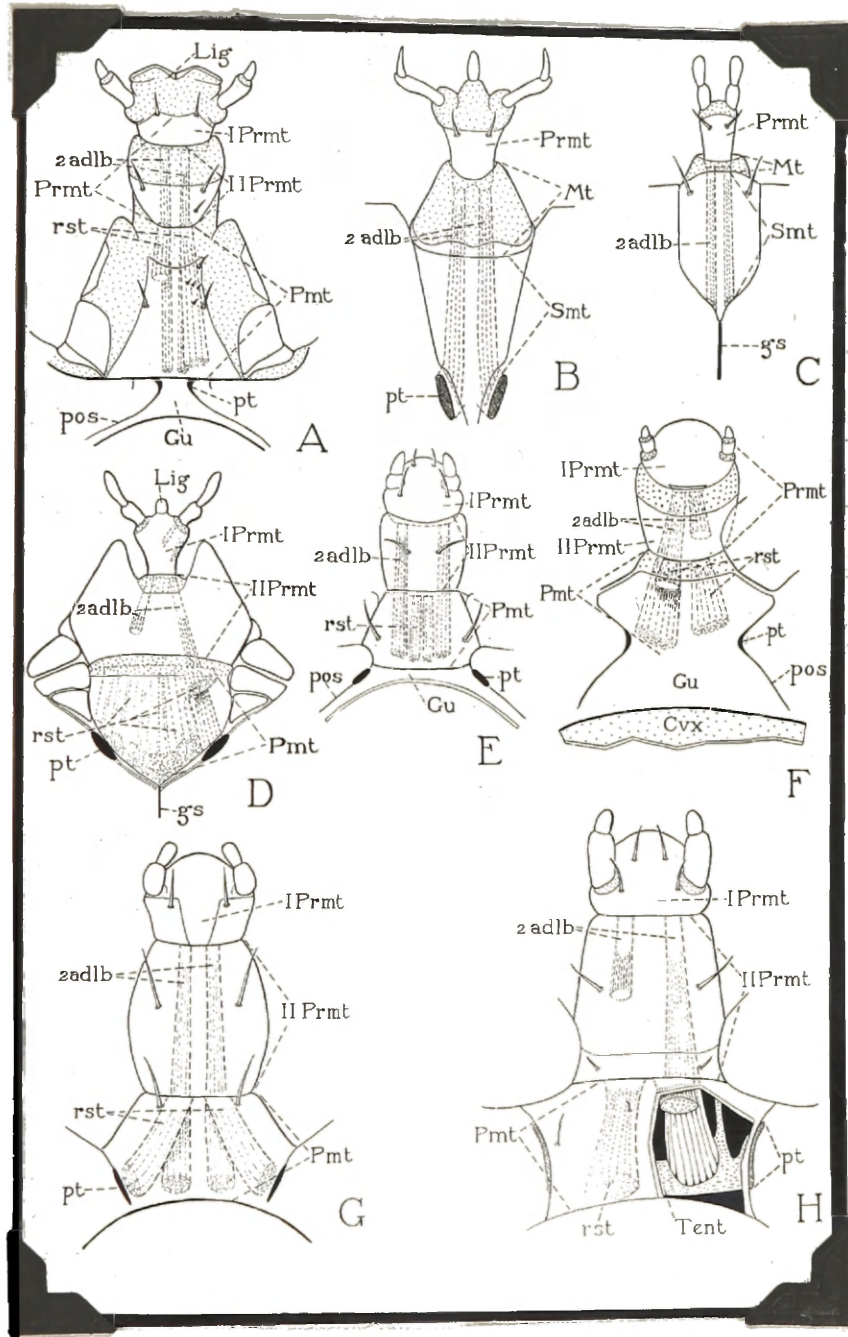


PLATE VI.

Explanation of Plate VII.

- A. Nitidulidae (larva) Ventral view of labium.
- B. Endomychidae (larva) Ventral view of labium.
- C. Mycetophagus sp. (larva) Ventral view of labium.
- D. Tritoma unicolor Say. (larva) Ventral view of labium.
- E. Anthicus sp. (larva) Ventral view of labium.
- F. Byturus (unicolor Say)? (larva) Ventral view of labium.
- G. Colydiidae (larva) Ventral view of labium.

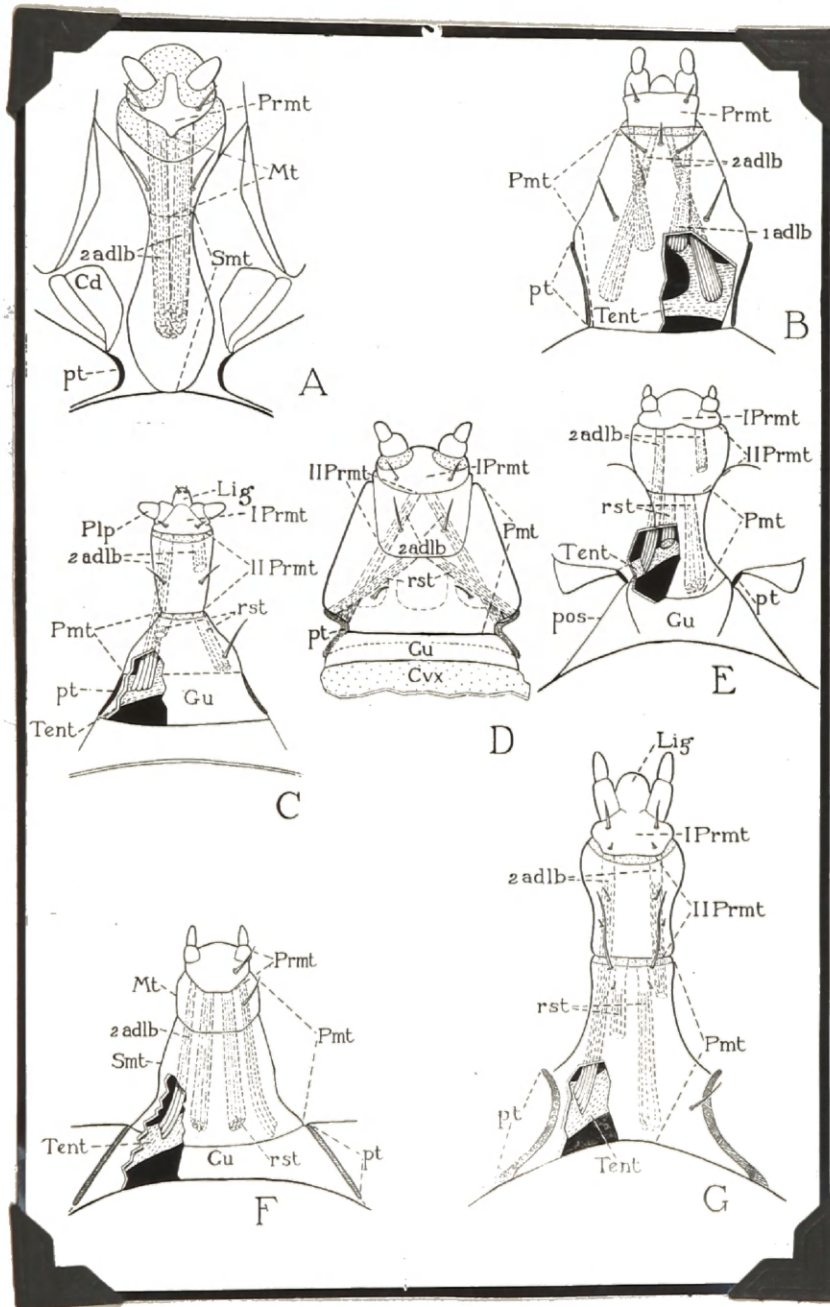


PLATE VII.

Explanation of Plate VIII.

- A. Synchroa punctata Newm. (larva) Ventral view of labium.
- B. Dendroides bicolor Newm. (larva) Ventral view of labium.
- C. Merinus laevis (Oliv.) (larva) Ventral view of labium.
- D. Pytho sp. (larva) Ventral view of labium.
- E. Hymenorus sp. (larva) Ventral view of labium.
- F. Lagriidae (larva) Ventral view of labium.
- G. Byrrhus sp. (larva) Ventral view of labium.
- H. Prionocyphon discoideus (Say) (larva) Ventral view of labium.

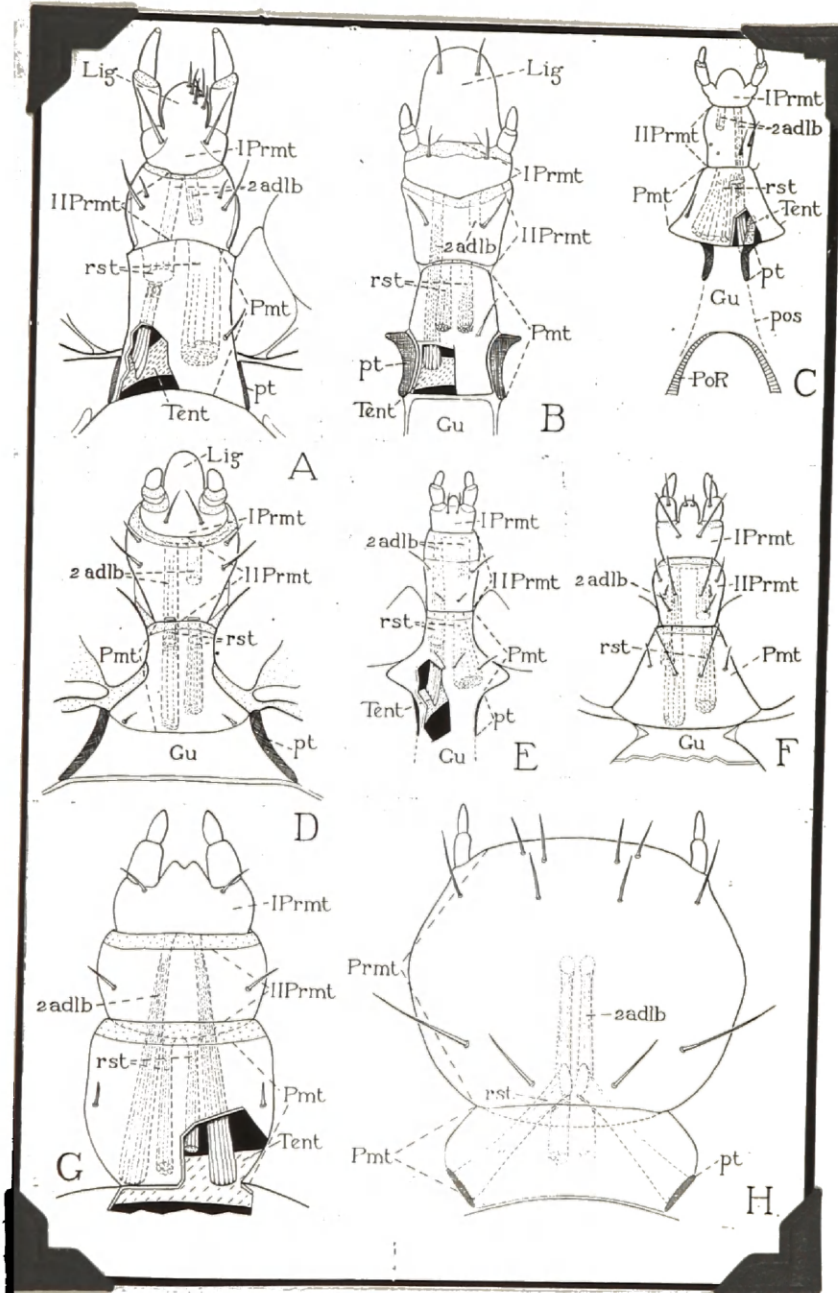


PLATE VIII.

Explanation of Plate IX.

- A. Nosodendron sp. (larva) Ventral view of labium.
- B. Ptilodactyla serricollis (Say) (larva) Ventral view of labium.
- C. Chauliognathus sp. (larva) Ventral view of labium.
- D. Cebrio sp. (larva) Ventral view of labium.
- E. Ochrosidia villosa (Burm.) (larva) Ventral view of labium.
- F. Passalus cornutus F. (larva) Ventral view of labium.
- G. Melyridae (larva) Ventral view of labium.
- H. Melanotus sp. (larva) Ventral view of labium.

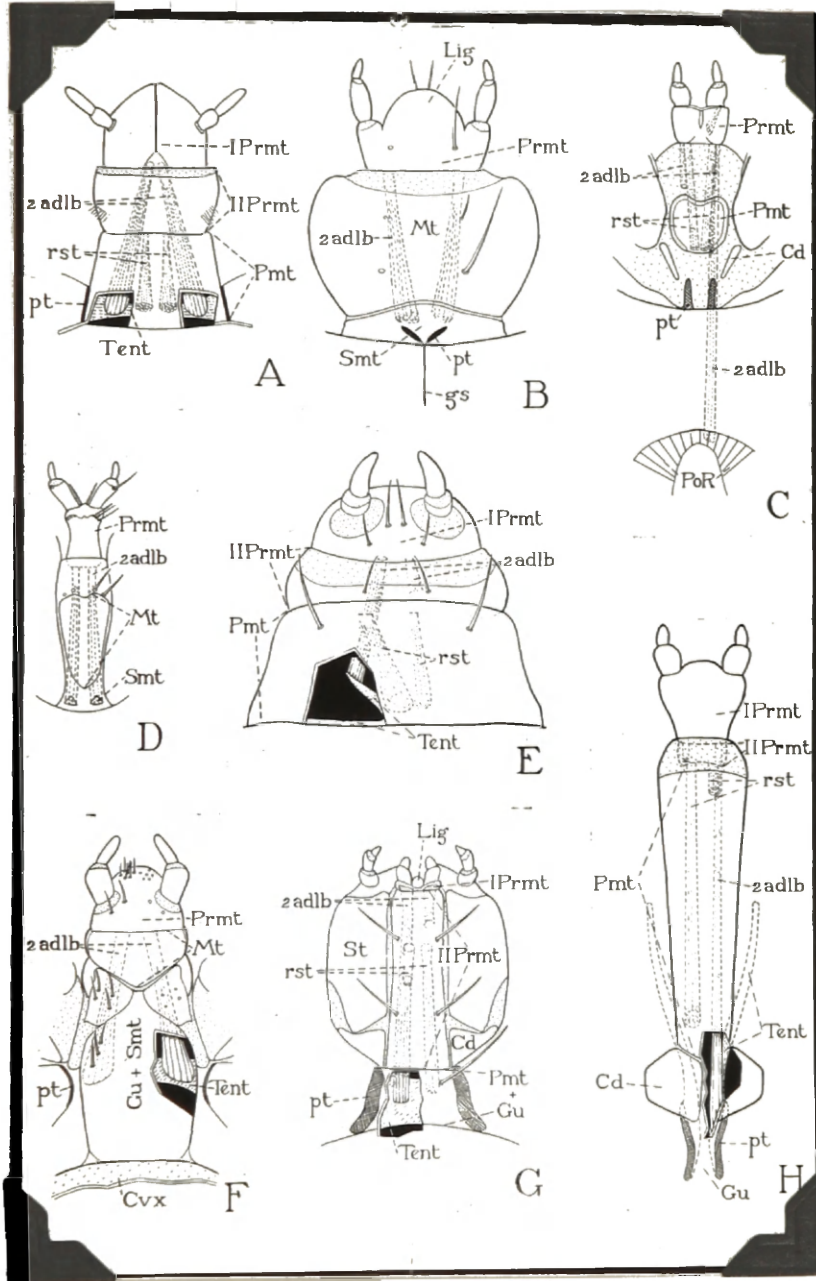


PLATE IX.

Explanation of Plate X.

- A. Orthosoma sp. (larva) Ventral view of labium.
- B. Caeptosomatidae (Cryptocephalinae) (larva) Ventral view
of labium.
- C. Henous confertus Say. (larva) Ventral view of labium.
- D. Galerucella sp. (larva) Ventral view of labium.
- E. Eumolpidae (larva) Ventral view of labium.
- F. Spermophagus robinae Sch. (larva) Ventral view of labium
and maxillae.

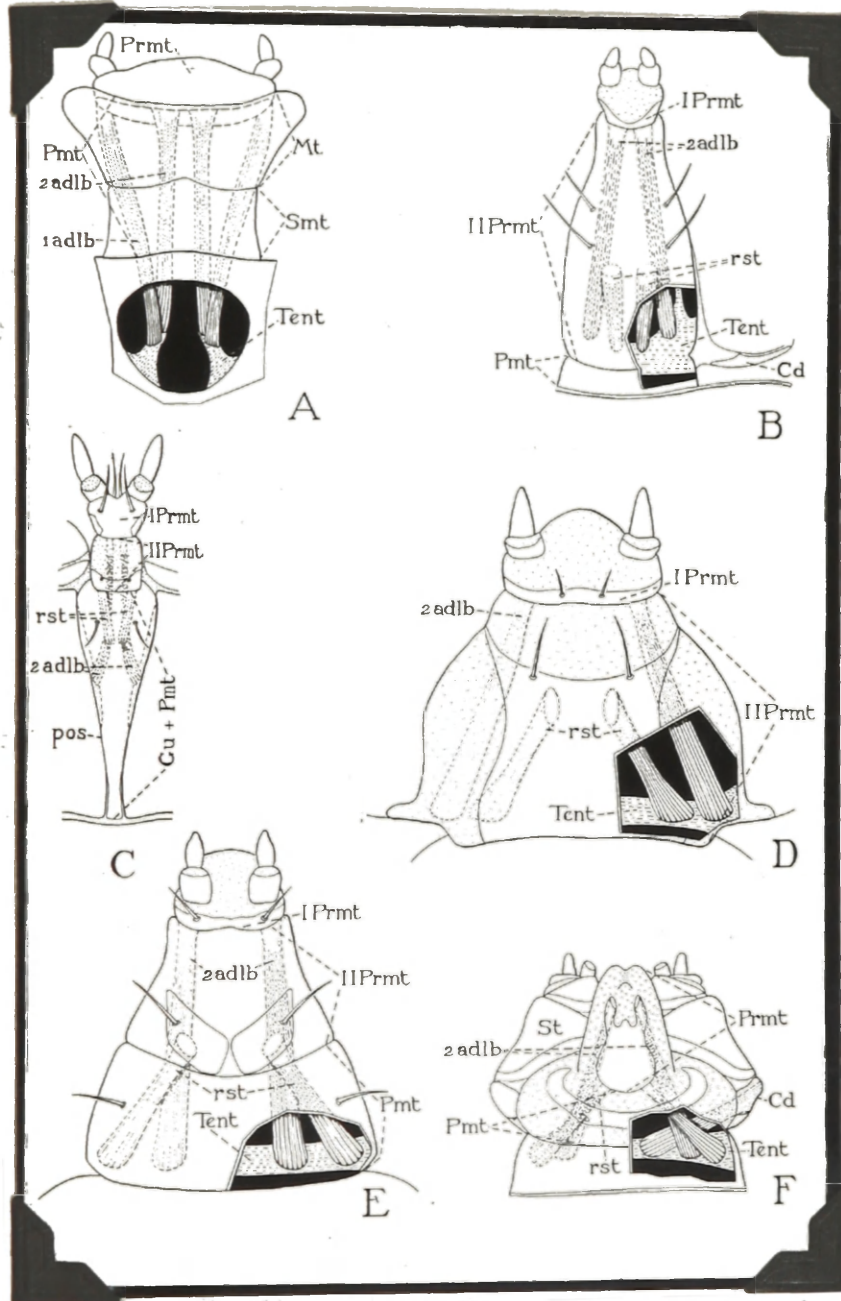


PLATE X.

Explanation of Plate XI.

- A. Silpha sp. (larva) Dorsal view of posterior tentorium.
- B. - Lateral view of left half of tentorium.
- C. Merinus laevis (Oliv.) (larva) Dorsal view of posterior tentorium.
- D. Tenebroides mauritanicus (L.) (larva) Dorsal view of posterior tentorium.
- E. Synchroa punctata Newm. (larva) Dorsal view of posterior tentorial bar.
- F. - Tentorial bar and postmentum cut in the midline.
- G. Cetoninae (larva) Dorsal view of posterior tentorial bridge.
- H. - Tentorial bridge cut through the midline.
- I. Hesperus baltimorensis Grav. (larva) Dorsal view of posterior tentorium.
- J. - Lateral view of one of the elements of the posterior tentorium.
- K. Cicindela sp. (larva) Anterodorsal view of posterior tentorium.

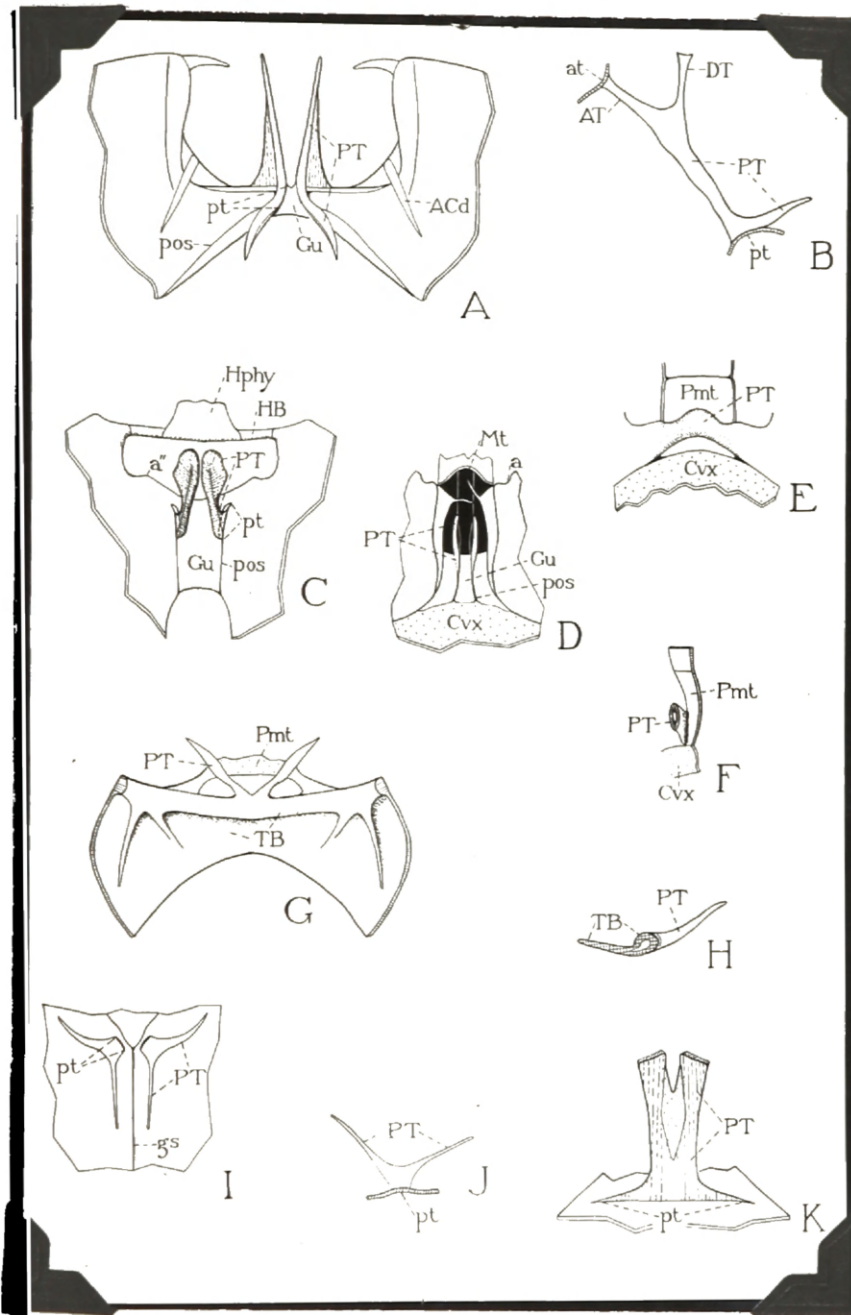


PLATE XI.

REFERENCES.

- Böving, Adam G., and Craighead, F. C. (1930). An illustrated synopsis of the principal larval forms of the order Coleoptera. Entomologica Americana, 11 (n.s.): 351 pp., 125 pls.
- Crampton, G. C. (1921). The sclerites of the head, and the mouth parts of certain immature and adult insects. Ann. Ent. Soc. Amer., 14: 65-103, pls. 2-8.
- Kadić, Otokar. (1902). Studien über das Labium der Coleoptern. Jenaische Zeitschrift für Naturwissenschaft, 36: 207-228.
- Korschelt, E. (1924). Bearbeitung einheimischer Tiere der Gelbrand Dytiscus marginalis L. Vol. 2, p. 510. Leipzig.
- Snodgrass, R. E. (1928). Morphology and evolution of the insect head and its appendages. Smithsonian Misc. Coll., 81, No. 3, 158 pp. 57 pls.
- (1932). Evolution of the insect head and the organs of feeding. Ann. Rep. Smithsonian Institution 1931: 443-489, 25 pls.
- (1935). Principles of insect morphology. 667 pp., 319 pls., New York.
- Walker, E. M. (1931). On the clypeus and labium of primitive insects. Canadian Entomologist 63: 75-81.