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A COMPARATIVE STUDY OF THE LABIUM OF COLEOPTEROUS LARVAE

(With Eight Plates)

BY
W. H. ANDERSON
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CONTENTS

INTRODUCTION

The study reported on in this paper 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 origins and insertions. It is hoped that students of systematic entomology may gain some help, either directly or indirectly, from the facts herein reported.

The paper represents the major part of a thesis presented to the faculty of the Graduate School of the University of Maryland in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

The author wishes to express his appreciation of the kindness and help of R. E. Snodgrass and Dr. A. G. Böving, of the United States Bureau of Entomology.

I. GENERAL DISCUSSION OF THE INSECT LABIUM

The labium of insects in its simplest generalized form consists 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 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, pp. 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 inasmuch 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 submental plate	Mentum
Submentum	Submental-platte		Primary submental plate	Submentum
				Postmentum

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. 1, B; cricket, Snodgrass, 1931, fig. 24) is shown in the diagrammatic representation (pl. 1, 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. 1, 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 generalized labium follows:

The depressors of the palpus (pl. 1, A, *dplp*) 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 (*lplp*). These also originate in the prementum close to its posterolateral angles. In some cases (*Periplaneta,* pl. 1, 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 (*adlb*) 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 *Periplaneta*) 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. 1, B) and the labium of adult *Harpalus* (pl. 1, 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 principal regions of the labium. The postmentum is made up of two distinct subdivisions in *Orthosoma* (pl. 7, A) and in *Ptilodactyla* (pl. 6, B), but it may be a single area as in *Byrrhus* (pl. 1, 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 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 subdivision 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.

Labium
- Prementum
  - First prementum
  - Second prementum
  - Prementum
- Postmentum
  - Postmentum
    - Mentum
    - Submentum

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 in nearly all forms the ventral adductors of the labium are inserted 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 "gulamental 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. 5, 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. 7, 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 THE VARIOUS TYPES OF LABIAL STRUCTURE

As has been previously stated, the labium of insects in its primitive state (pl. 1, 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. 1, 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 the segmentlike bases of the palpi (*Plp*).

As a typical example of the labium of coleopterous larvae, *Byrrhus* was chosen (pl. 1, 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 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 (*1adlb*) 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 *Pytho* sp. (pl. 5, D), Lagriidae (pl. 5, F), *Cucujus clavipes* (pl. 3, F), and *Languria laeta* (pl. 3, 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. 6, 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. 1, D).

II. DESCRIPTIONS OF LABIA OF COLEOPTEROUS LARVAE

Cicindelidae[1] (pl. 2, A, B).

The labium of *Cicindela* sp. is made up of a rather compact and firmly united prementum (A, *Prmt*) 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 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, *lplp*), one on either side, arise from this bar, within the head capsule. They insert on the

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

sclerite at the base of the palpus, their points of insertion being indicated by the 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 barlike 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 maxillary 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. 2, C).

The labium of *Harpalus* sp. is separated into a well-marked prementum (*Prmt*), a membranous mentum (*Mt*), and a much narrowed submentum (*Smt*) 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. 2, E).

The labium of *Dytiscus* sp., as in 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 (*1adlb*) 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.

Gyrinidae (pl. 2, F).

In *Dineutes* the two parts of the labium that 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 it was 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 to judge from their position, no doubt act as depressors of the palpuslike structure, which is made up of a palpus (*Plp*) and one-half the prementum (*Prmt*).

The dorsal adductors (*1adlb*) have their origins on the tentorial invaginations and insert on the bases of the divided prementum. Fulfilling their usual rôle of opposing the ventral adductors, they apparently act as levators of the combined palpus and half prementum.

Silphidae (pl. 3, 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. 1, D), the first prementum (pl. 3, 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. 1, D). In the form studied the tentorial pits (pl. 3, 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 retractor muscles 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. 3, 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. 3, 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. 3, 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. 1, 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 mentioned it would be expected that there are two ventral pairs of muscles, the ventral adductors of the labium (pl. 3, 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. 3, 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. 3, 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. 3, 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 *Byrrhus,* 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. 3, H).

In *Eunausibius* 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 (*Pmt*) 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. 4, 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. 4, 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 bases of the palpi. The postmentum (*Pmt*) extends posteriorly 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. 4, 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 state definitely whence 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. 4, 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 division of the labium is set off from the others by sutures or grooves.

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.

Byturidae (pl. 4, F).

The labium of *Byturus* is like that of the preceding family in that it consists of three divisions, the postmentum (*Pmt*), the second prementum (*IIPrmt*), and the first prementum (*IPrmt*). 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. The retractors of the prementum (*rst*) originate from the posterior margin of the postmentum and insert on the base of the second prementum.

The ventral adductors of the labium (*2adlb*) arise from the tentorial bridge (*Tent*) and insert at the base of the first prementum.

Colydiidae (pl. 4, 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 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. 4, 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 area of 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. 5, 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 (*2adlb*) 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. 5, 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. 5, 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 from the postmental sclerite and insert on the base of the first prementum.

Alleculidae (pl. 5, 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. 5, 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. 5, 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 subdivision by a membranous strip. The postmentum, lying behind the second prementum, is separated from the latter by a distinct membranous area. The lateral margins of the postmentum diverge toward 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. 5, 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. 1, D). It shows the three divisions of the labium definitely, the first prementum (pl. 5, 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. 5, 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. 1, B).

Nosodendridae (pl. 6, A).

The labium of *Nosodendron* consists of three clearly marked divisions. From a study of the musclature 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, obliquely directed comblike tufts 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 trianglar area previously mentioned.

Ptilodactylidae (pl. 6, 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 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. 6, C).

The labium of *Chauliognathus* shows only two parts, the terminal prementum (*Prmt*) and a median oval sclerite surrounded by mem-

brane, 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 region.

Cebrionidae (pl. 6, D).

A study of the labium of *Cebrio* 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. 6, H).

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. 6, F).

The labium of *Passalus* is made up of three distinct areas: 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. 1, 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 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. 6, 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. 6, 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 rather 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. 8, G, *PT*). They insert on the base of the first prementum (pl. 6, 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. 6, 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. 7, 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 ridgelike tentorial arms and insert on the base of the first prementum.

Cerambycidae (pl. 7, A).

The labium of *Orthosoma* shows the divisions which are typical of adult Coleoptera and of Orthoptera (pl. 1, B, C): a distal prementum (pl. 7, 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 (*1adlb*) 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. 7, 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*) 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. 7, B).

The representative of this family which was used in the study has the 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. 7, 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. 7, 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 the anterior margin of which 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 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.

III. 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 invaginations from the anterior tentorial pits. The second pair of arms results from invaginations from the posterior tentorial pits. 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 the 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 pos-

terior arms (pl. 8, A, B, *PT*) arising from the posterior tentorial pits 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, 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. 8, B, *AT*). The dorsal arms (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. 5, C, *2adlb*).

Tenebroides (pl. 8, 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 the 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. 6, 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. 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 perpendicularly into the head. The inner ends are slightly separated, which indicates that the tentorium, as it

is at present, has resulted from 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.

IV. 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 that showed a typical 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 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 fairly safe criteria for separating parts of the external anatomy.

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

ABBREVIATIONS USED ON THE FIGURES

ACd, apodeme of cardo.
adcd, adductor of cardo.
adlb, adductor of labium.
adst, adductor of stipes.
AT, anterior arm of tentorium.
at, anterior tentorial pit.
b, secondary sclerite of prementum in *Periplaneta.*
Cd, cardo.
Cvx, neck, cervix.
dplp, depressor of palpus.
DT, dorsal arm of tentorium.
fgl, flexor of glossa.
For, foramen magnum.
fpgl, flexor of paraglossa.
Gl, glossa.
gs, gular suture.
Gu, gula.
gu, much narrowed gula.
HB, hypopharyngeal bracon.
Lb, labium
LbPlp, labial palpus.
Lig, ligula.
lplp, labial palpus.
MAnt, antennal muscle.
Mt, mentum.
Pgl, paraglossa.
Plp, palpus.
Pmt, postmentum.
pos, postoccipital suture.
Prmt, prementum.
IPrmt, anterior subdivision of prementum.
IIPrmt, posterior subdivision of prementum.
PT, posterior arm of tentorium.
pt, posterior tentorial pit.
rhphy, retractor of hypopharynx.
rst, retractor of prementum.
Smt, submentum.
St, stipes.
TB, cross bar of tentorium.
Tent, tentorium.

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EXPLANATION OF PLATES

Plate 1

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. *Harpalus* sp. (adult). External view of muscles of labium.
D. *Byrrhus* sp. (larva). External view of muscles of labium.

Plate 2

A. *Cicindela hirticollis* Say (larva). Ventral view of labium.
B. *Cicindela hirticollis* Say (larva). Ventrolateral view of left tentorial 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 3

A. *Silpha* 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. *Oryzaephilus surinamensis* (L.) (larva). Ventral view of labium.
H. *Eunausibius wheeleri* Schwartz and Barber (larva). Ventral view of labium.

Plate 4

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 5

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. *Prioncyphon discoideus* (Say) (larva). Ventral view of labium.

Plate 6

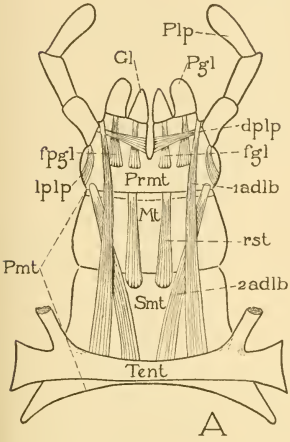
A. *Nosodendron* sp. (larva). Ventral view of labium.
B. *Ptilodactyla serricollis* (Say) (larva). Ventral view of labium.
C. *Chauliognathus* sp. (larva). Ventral view of labium and maxillae.
D. *Cebrio* sp. (larva). Ventral view of labium.
E. *Ochrosidia villosa* (Burm.) (larva). Ventral view of labium.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

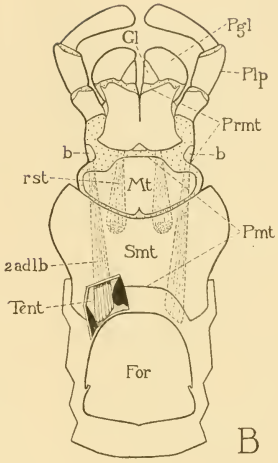
Plate 7

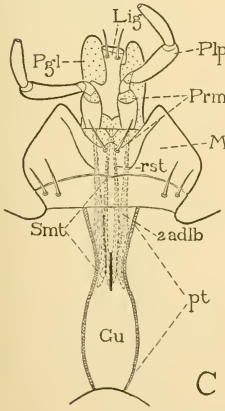
A. *Orthosoma* sp. (larva). Ventral view of labium.
B. Camptosomatidae (Cryptocephalinae) (larva). Ventral view of labium.
C. *Henous confertus* Say (larva). Ventral view of labium.
D. *Galerucella* sp. (larva). Ventral view of labium.
E. Eumolpidae (larva). Ventral view of labium.
F. *Spermophagus robiniae*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

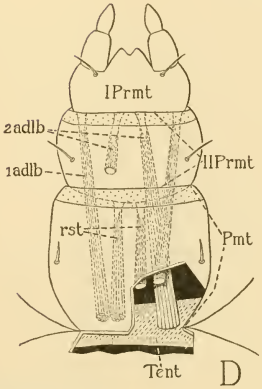
Plate 8

A. *Silpha* sp. (larva). Dorsal view of posterior tentorium.
B. *Silpha* sp. (larva). 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. *Synchroa punctata* Newm. (larva). Tentorial bar and postmentum cut in the midline.
G. Cetoninae (larva). Dorsal view of posterior tentorial bridge.
H. Cetoninae (larva). Tentorial bridge cut through the midline.
I. *Hesperus baltimorensis* Grav. (larva). Dorsal view of posterior tentorium.
J. *Hesperus baltimorensis* Grav. (larva). Lateral view of one of the elements of the posterior tentorium.
K. *Cicindela* sp. (larva). Anterodorsal view of posterior tentorium.



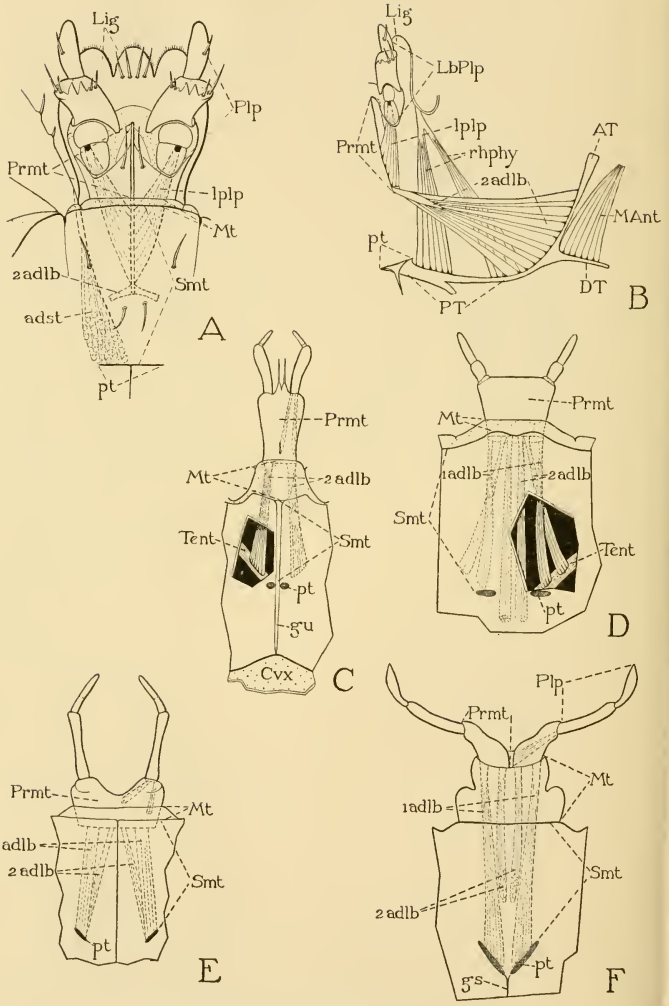






THE LABIUM OF COLEOPTEROUS LARVAE

(For explanation, see page 28.)



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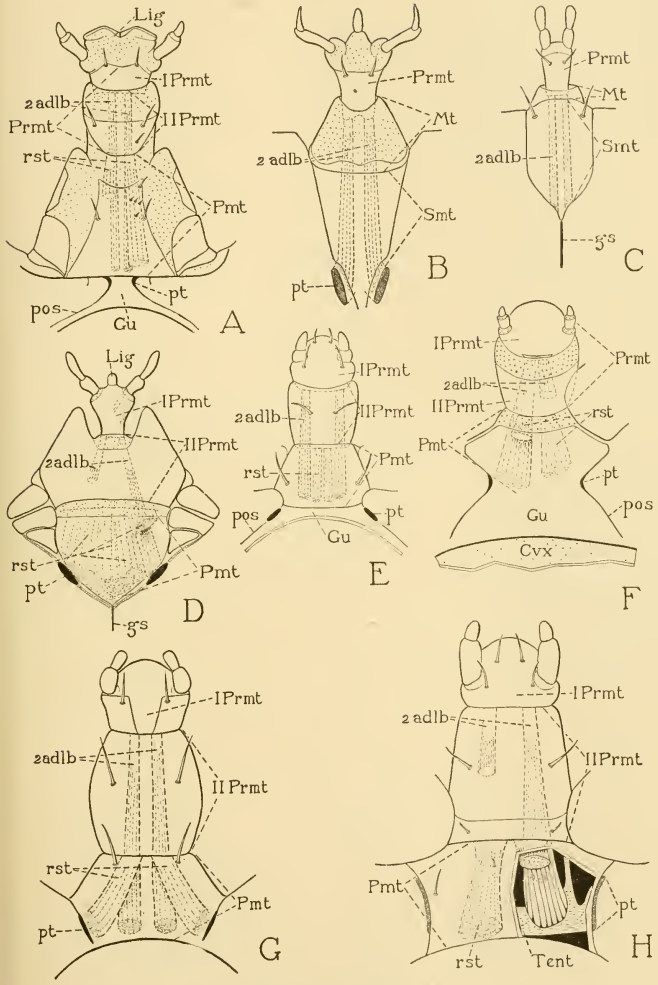

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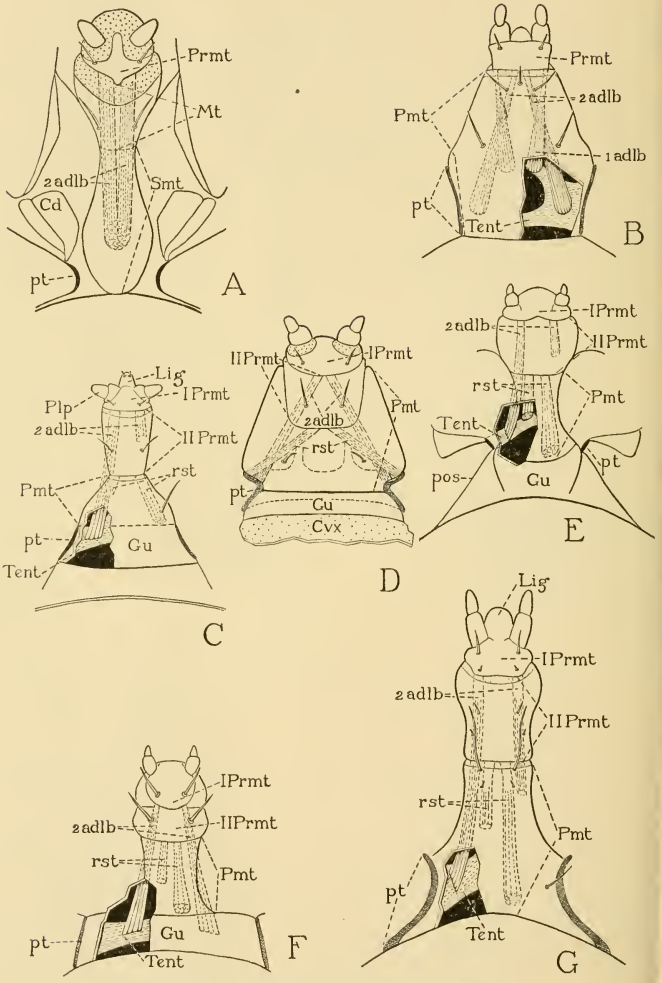

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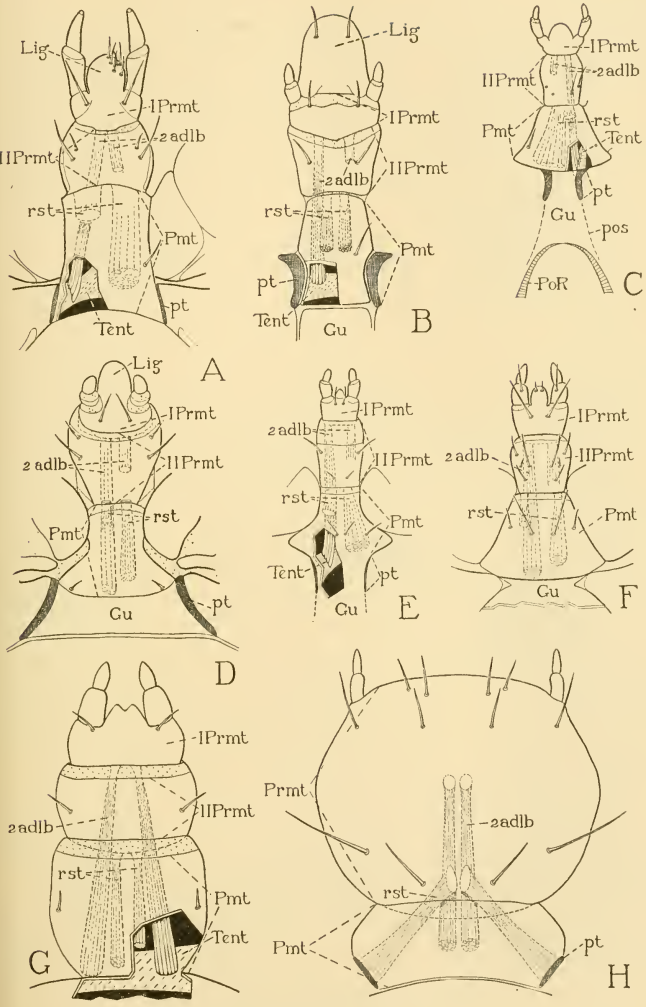

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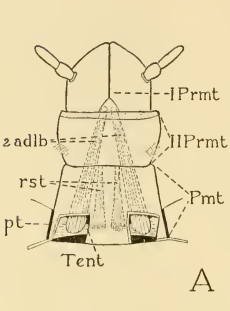

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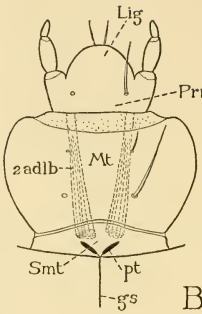

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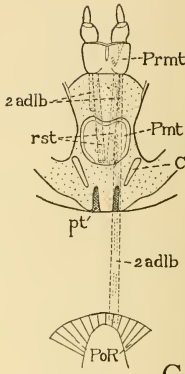

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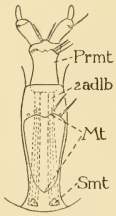

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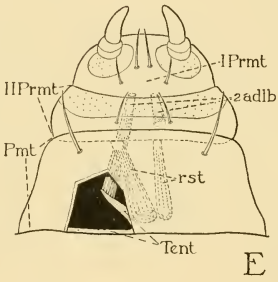

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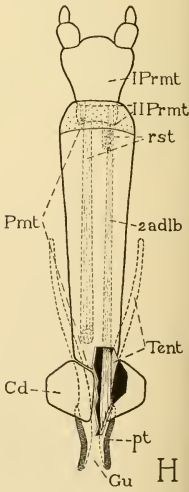

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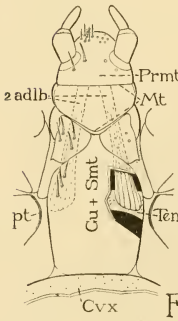

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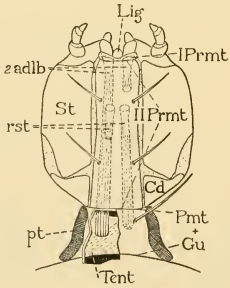

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THE LABIUM OF COLEOPTEROUS LARVAE

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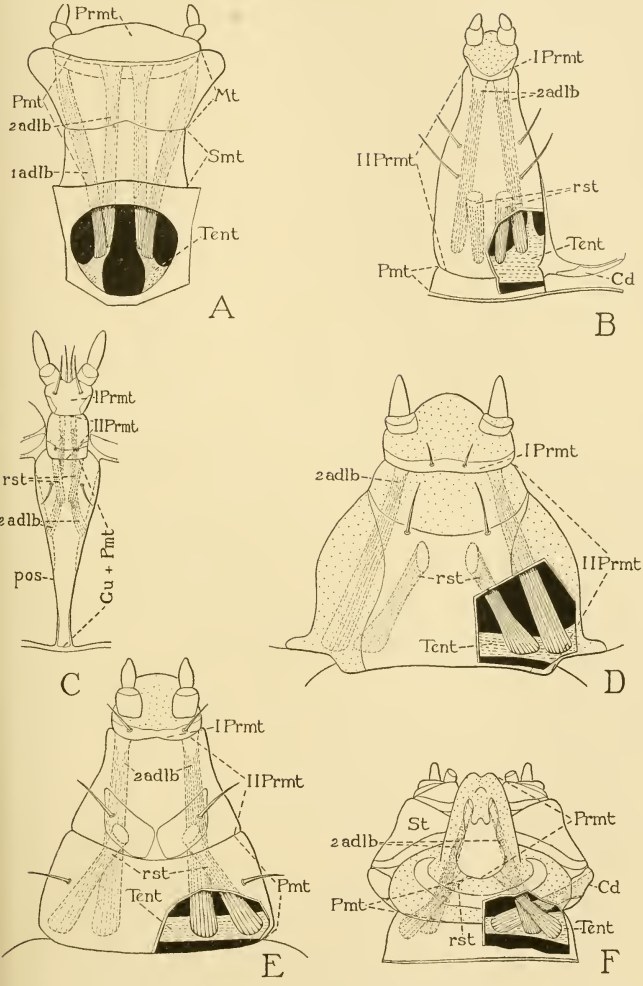

THE LABIUM OF COLEOPTEROUS LARVAE

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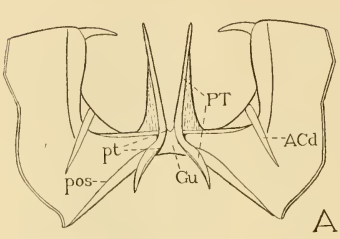

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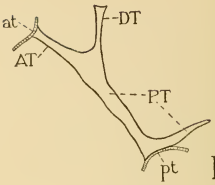

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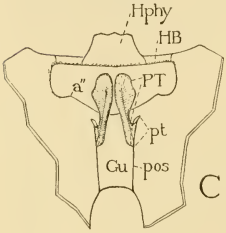

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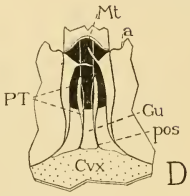

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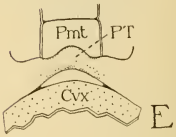

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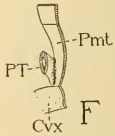

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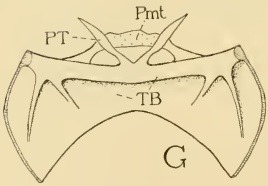

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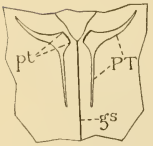

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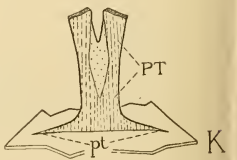

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THE TENTORIUM OF COLEOPTEROUS LARVAE

(For explanation, see page 29.)