The Musculature of the Mouth-parts of Insect Larvae.

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1. INTRODUCTION.

Various papers have been published on the morphology of the mouth-parts of adult and larval insects, but there still exist great discrepancies in the interpretation of the sclerites and lobes of the mouth-parts, especially of the labium.

Not only are the sclerites of the labium misinterpreted by many entomologists, but the real homology of the sclerites
when compared with those of the maxilla has not been properly understood.

Comparative study of the skeletal structure alone fails in certain cases to give a correct interpretation of the sclerites, lobes, &c., of the mouth-parts, but the musculature seems to be a much safer guide. Snodgrass (1935) has tried to clear up certain difficulties on the basis of musculature, but left many of the controversial points still unsettled.

In view of this, and also to find out the real homologies of the sclerites, I have studied the musculature of the mouth-parts of larval insects prior to the study of adults.

The conclusions put forward here are based on the study of about thirty species of larval insects.

2. Material and Technique.

The material was fixed in 90 per cent. alcohol for three to ten days, according to the size of the larva and the nature of its food. The fixed material could be kept for a long time without distortion of the muscles, if an incision was made in the thorax or if the head with a part of the thorax was severed from the body.

The dissections were made in 70 per cent. alcohol and the dissected mouth-parts with their muscles were stained overnight in light borax carmine. The stain was removed from the sclerotized parts in 70 per cent. alcohol. Permanent preparations were made of the mouth-parts with their muscles intact.

To study the details of the mouth-parts, the specimens were boiled in weak caustic potash solution for a short time. In order to get rid of muscles easily, they were treated with boiling water for some time, prior to the boiling in caustic potash.

In a few cases to verify certain controversial points, microtome sections were cut and the parts reconstructed.

The following larval insects were studied:

Coleoptera.

1. Tenebrio molitor, L.
2. Tenebrio obscurus, F.

Tenebrionidae
<table>
<thead>
<tr>
<th>Number</th>
<th>Species</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.</td>
<td><em>Ptinus tectus</em>, Boield</td>
<td>Ptinidae</td>
</tr>
<tr>
<td>4.</td>
<td><em>Dermestes vulpinus</em>, F.</td>
<td>Dermestidae</td>
</tr>
<tr>
<td>5.</td>
<td><em>Tenebroides mauritanicus</em>, L.</td>
<td>Trogositidae</td>
</tr>
<tr>
<td>6.</td>
<td><em>Thanatophilus</em> sp.</td>
<td>Silphidae</td>
</tr>
<tr>
<td>7.</td>
<td><em>Agriotes</em> sp.</td>
<td>Elateridae</td>
</tr>
<tr>
<td>8.</td>
<td><em>Rhagium</em> sp.</td>
<td>Cerambycidae</td>
</tr>
<tr>
<td>9.</td>
<td><em>Hydrophilus piceus</em>, L.</td>
<td>Hydrophilidae</td>
</tr>
<tr>
<td>10.</td>
<td><em>Sinodendron cylindricum</em>, L.</td>
<td>Lucanidae</td>
</tr>
<tr>
<td>11.</td>
<td><em>Lucanus cervus</em>, L.</td>
<td>Lucanidae</td>
</tr>
<tr>
<td>12.</td>
<td><em>Calandra granaria</em>, L.</td>
<td>Lucanidae</td>
</tr>
<tr>
<td>13.</td>
<td><em>Caulophilus latinasus</em>, Say</td>
<td>Curculionidae</td>
</tr>
</tbody>
</table>
| 14.    | *Cenorrhynchus pleuro-
  stigma*, Marsh.          | Curculionidae  |
| 15.    | *Carabus* sp.            | Carabidae      |
|        |                          | Neuroptera-Megaloptera. |
| 17.    | *Raphidia* sp.           | Tenthredinidae |
|        |                          | Neuroptera-Megaloptera. |
| 19.    | *Panorpa communis*, L.   | Limnophilidae  |
| 20.    | *Panorpa germanica*, L.  | Hydroptilidae  |
|        |                          | Hydroptilidae  |
|        |                          | Philopotamidae |
|        |                          | Diptera.       |
| 21.    | *Clisiocampa neustria*, L. | Lasiocampidae |
| 22.    | *Galleria mellonella*, L. | Galleriidae    |
| 23.    | *Agrotis* sp.            | Noctuidae      |
| 24.    | *Anabolia nervosa*, Leach | Limnophilidae  |
| 25.    | *Hydropsyche* sp.        | Hydropsychidae |
| 26.    | *Hydroptila* sp.         | Hydroptilidae  |
| 27.    | *Philopotamus* sp.       | Philopotamidae |
| 28.    | *Tipula flavolineata*, Mg. | Tipulidae      |
| 29.    | *Bibio* sp.              | Bibionidae     |
In addition some other larvae were also dissected for certain special points. The following adult types were also examined.

1. *Periplaneta americana*, L.
2. *Tenebrio molitor*, L.
3. *Chrysopa* sp.
4. *Panorpa communis*, L.
5. *Boreus hiemalis*, L.

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3. THE LABRUM.

The labrum or upper lip (figs. 1–8, *lm.*, Pl. 1; figs. 9–11, *lm.*, Pl. 2) of insects is typically a broad plate at the ventral margin of the cranium. It commonly overlies the mandibles and is suspended from the clypeus. Its posterior (inferior) wall, which is called the epipharynx (fig. 10, *ep.*, Pl. 2), is provided with gustatory papillae.

It varies much in shape and size in adult insects, but in the larval insects it is usually a broad flap which is roughly elliptical or quadrate with or without a notch at its anterior margin.

In larval Carabidae and Elateridae it seems superficially to be absent, but a careful examination shows that it is drawn towards the epipharyngeal side (fig. 4, *lm.*, Pl. 1). The musculature, however, reveals its true identity. In larval *Hydrophilus* it is absent, unless fused with the hard sclerite at the proximal margin of the head, which is most probably the clypeus.

On the lateral angles of the labrum there is a pair of darkly pigmented sclerites, called the tormae (figs. 1, 2, 3, 8, *t.*, Pl. 1; fig. 9, *t.*, Pl. 2). They extend a considerable distance on the epipharyngeal side of the clypeus and may run even to the frontal region (fig. 5, Pl. 1). Snodgrass (1931) regards these processes as the landmark of the proximal limit of the labrum,
but in the larvae of Curculionidae they are situated entirely on the epipharyngeal surface, their distal end being near the anterior margin of the labrum (fig. 2, t., Pl. 1). In certain larval insects such as Panorpa and Thanatophilus they are totally absent (fig. 7, Pl. 1; fig. 10, Pl. 2).

The tormae are sclerotized rods on which the labral muscles (3) from the frons (f.) are inserted.

The musculature of the larval labrum comprises the following muscles (figs. 1–8, Pl. 1; figs. 9–11, Pl. 2):

(1) A group of small fibres joining the anterior and posterior walls of the labrum.

(2) Anterior labral muscles—arising on the frons, inserted on the anterior walls of the labrum.

(3) Lateral labral muscles—arising on the frons, inserted on the tormae.

(4) Posterior labral muscles—arising on the frons, inserted on the posterior wall of the labrum, i.e. on the middle of the epipharyngeal side of the labrum.

The muscles joining the anterior and posterior walls of the labrum are present in many larvae, but it is very difficult to detect them owing to their small size. All of the muscles that arise on the frons are not present in the same larva, either one or two sets may be absent. In larval Neuroptera, Trichoptera, and Hymenoptera (figs. 1, 3, Pl. 1; figs. 9, 11, Pl. 2) both anterior and lateral muscles (2, 3) are present, while in larval Thanatophilus (fig. 10, Pl. 2) and Lucanidae only the posterior muscles (4) are retained. In all larval Lepidoptera (fig. 8, Pl. 1) and most Coleoptera (figs. 2, 5, 6, Pl. 1), only the lateral muscles (3) are present.

In larval Carabidae and Elateridae the labrum has been drawn towards the epipharyngeal side. In the former (fig. 4, Pl. 1) both anterior and posterior walls are represented by two sclerites on the same side, the distal sclerite (lm.) representing the anterior wall, and the proximal sclerite (eph.), to which the posterior muscles (4) are attached, the posterior (epipharyngeal) wall of the labrum. In larval Elateridae the labrum is likewise situated on the epipharyngeal side, closely apposed to the
clypeus, but here it is a semilunar bar fringed with hairs and provided with tormae to which the lateral muscles from the frons are inserted. The origin of these muscles upon the frons, and their insertion upon the tormae, suggest the identity of the labrum.

All muscles (2, 3, 4) of the labrum except those joining the anterior and posterior walls have their origin on the frons (figs. 1–8, Pl. 1; figs. 9–11, Pl. 2). In certain cases (figs. 3, 5, 6, Pl. 1) when only the lateral muscles (3) are retained they arise on an internal ridge of the frons.

The origin of the labral muscles, according to Snodgrass (1928, 1931, 1935), identifies the frontal sclerite in all insects with the exception of the adult Diptera in which they have their origin upon the clypeus. In larval Lepidoptera (fig. 8, Pl. 1) the labral muscles (3) arise on a median ridge (fr.) behind the triangular plate (cl.). This ridge, according to Snodgrass, is the inflected part of the frons and the so-called frons in lepidopterous larvae is really the clypeus (cl.).

4. THE HYPOPHARYNX.

The hypopharynx (figs. 50, 55, hph., Pl. 10; fig. 57, hph., Pl. 11) is a tongue-like median projection arising on the floor of the mouth between the bases of the mouth-appendages. According to embryologists it is formed from the sterna of the mandibular and first maxillary segments, but some authors suppose that a part of the sternal element of the second maxillary segment has been incorporated.

In the larval insects the hypopharynx becomes fused with the dorsal surface of the labium and in certain larvae (e.g. in Trichoptera, Lepidoptera, and Hymenoptera) it may become fused with the ligula so as to form a composite structure (figs. 50, 52, sp., Pl. 10) bearing the orifice of the labial glands. In many larvae it lies proximally to the dorsal surface of the prementum just behind the insertion of the dorsal muscles of the prementum.

On the sides of the hypopharynx are a few strongly sclerotized plates, called the suspensoria (figs. 57, 58, cl., Pl. 11), which support the hypopharynx and on which the muscles from the frons
are inserted. According to Snodgrass (1935) the suspensorial area should not be regarded as a part of the hypopharynx, and details of this structure and of its muscles are not dealt with here. A pair of muscles (5) arising on the tentorial bridge (figs. 41, tb., Pl. 8; 52, 55, tb., Pl. 10) are sometimes inserted on the hypopharynx.

The insertion of the dorsal premental muscles is very helpful in determining the anterior limit of the hypopharynx. In the larvae of Thanatophilus (fig. 24, Pl. 4) the dorsal surface of the prementum (prm.) simulates the hypopharynx, but the insertion of the dorsal muscles (27) at its posterior region shows its true nature.

In certain insects (e.g. larval Lucanidae) the hypopharyngeal region has become highly sclerotized, forming a structure like the molar area of the mandible. In the larvae of Tenebrio only the posterior region of the hypopharynx forms such a structure, but it is supported on the hypopharyngeal bracon—a rod attached to the hypostomal lobes of the head capsule near the mandibular articulations. The hypopharyngeal bracon is developed in many cases, even when the hypopharynx remains membranous. In the hypopharynx of larval Dascillus, Carpenter and MacDowell (1912) describe a similar structure which works against teeth on the epipharyngeal surface of the labrum. The present author could not find such teeth on the epipharynx of the larvae of Lucanidae, but there are two strongly sclerotized plates to which the posterior muscles of the labrum are attached.

The superlinguae are a pair of lateral lobes attached to the hypopharynx. Following the interpretation of Hansen (1893) the superlinguae have been homologized with the maxillulae of Crustacea by many authors, e.g. Carpenter (1903), Evans (1921), and Henriksen (1928), but Crampton (1921) contradicts this view, believing that they correspond to the paragnaths of Crustacea. No muscles, however, could be found at the bases of the superlinguae so that the question must be decided on other evidence.

The superlinguae in larval Tenebrio are very well developed, with fine hairs at their distal borders.
5. The Mandibles.

The mandibles (figs. 12–19, Pl. 2) are a pair of strongly sclerotized jaws, situated on each side of the mouth immediately behind the labrum. They represent the basal segment or coxo-podite of the typical Arthropod limb (Crampton, 1921). According to the nature of the food and the mode of feeding, they are highly modified into biting, chewing, sucking, and piercing organs. They may be functionless or even completely absent.

In larval insects the mandibles usually preserve the generalized biting and chewing type of structure (fig. 18, Pl. 2). Each mandible has a broad triangular base, a mesal surface produced into incisor lobes (in.), and a molar or crushing surface (mo.) near the base. In many cases the right and left mandible differ in the number of incisor points.

The mandibles are attached to pleurostomal margin of the cranium by the outer edge of the triangular base and have an articulation with the head at each end of the hinge line. Anteriorly they are articulated by means of a ginglymus or groove (figs. 14, 15, gr., Pl. 2) which fits into a convex process of the head, and posteriorly by means of a condyle (c.) which fits into a socket at the lower margin of the gena or post-gena.

In the predacious larval forms, however, the mandible loses its crushing area, while its incisor surface becomes very sharp and may be toothed. In the larvae of Sialidae, Raphidiiidae, Carabidae, &c., the mandibles are elongated with sharp points but without any molar area (figs. 15, 19, Pl. 2). In the larvae which feed on the juices of their prey the mandibles exhibit a special modification for sucking. In the predacious larvae of Chrysopidae each mandible (fig. 16, Pl. 2) is fang-shaped and along the entire length of the ventral surface is a groove (gr.) which fits against the maxilla, thus forming a channel through which the juices of the prey can be sucked. In the larvae of Dytiscus (Rungius, 1911; Korschelt, 1924) the mandibles are also fang-like, each being traversed by a canal through which the poison from the stomach is injected into the body of the prey, dissolving the soft body-tissue. The liquefied emulsion thus formed is sucked in through the mandibles by a special mechanism involving the other mouth-parts (Blunck, 1916).
In many insects there is a brush-like process fixed to the inner side or base of the mandible. This process is called the penicillus (fig. 17, Pl. 2). In a few cases a movable plate fringed with hairs is articulated at the inner base of the mandible. This is called the prostheca or lacinia mobilis (fig. 18, pr., Pl. 2). The prostheca is incorrectly homologized with the lacinia. The projecting terminal lobe of the mandible, according to Snodgrass (1934), is an endite of the basis; he states, ‘in Diplopoda this lobe is freely movable and in both diplopods and chilopods it is provided with muscles corresponding to the muscles of the lacinia of a generalized insect maxilla. In other groups the terminal lobe loses its mobility and becomes solidly fused with the basis, in consequence of which its muscles have disappeared.’ The lacinia mobilis is present in a well-developed condition in the larva of Diptera (Tipulidae and Bibionidae), where it is attached to a flexible area at the inner base of the mandible. There is no muscle inserted upon it.

Each mandible in larval insects is moved by means of powerful abductor and adductor muscles (figs. 12, 17, Pl. 2).

(6) Abductor muscle.—A small muscle arising on the lateral wall of the cranium and inserted on a small apodeme, attached to the outer margin of the mandibular base.

(7) Adductor muscle.—This is a very large muscle arising on the dorsal and posterior wall of the cranium and inserted on a large apodeme at the inner angle of the mandibular base.

These two muscles (abductor and adductor) represent the dorsal muscles of the generalized insect limb, but the ventral muscles of such a limb are absent in the mandible of most larval insects. They are, however, stated to be present in well-developed condition in the early stages of Ephemeroptera and Odonata, having their origin on the tentorium. With the increased size of the dorsal muscles, the ventral muscles become of secondary importance and are usually reduced or absent (Snodgrass, 1935).

6. The Maxillae.

The maxillae (fig. 62, Pl. 12) of an insect are the appendages of the fifth cranial segment, each having the typical structure of
a limb with a basal shaft, two lobes, and a telopodite. The basis is composed of a proximal sclerite, the cardo (cd.), and a distal sclerite, the stipes (st.). The cardo is attached to the head by the pleural membrane and articulated to the hypostomal margin of the cranium by a small condyle (c.). The inner side of the cardo near the condyle is inflected so as to form a process (p.) to which the promotor muscle (8) of the cardo is attached. Crampton (1925) calls this the cardo-process. Running from the cardo-process in many insects there is an internal ridge which subdivides the cardo into a proxicardo and a disticardo. The stipes (st.) at the distal end bears two lobes. The inner lobe is the lacinia (lc.) and the outer is the galea (ga.). Lateral of the galea is the maxillary palpus or telopodite (mp.).

The lateral area of the stipes bearing the palpus is sometimes differentiated as a small sclerite called the palpifer. The number of segments in the palpus varies.

The maxilla is attached at its base to the labium by an articulating membrane, the basi-maxillary membrane (fig. 24, bm., Pl. 4). Occasionally the articulating area is strongly sclerotized, forming a definite sclerite or sclerites, called the basimaxillary sclerites (fig. 29, ms., Pl. 5).

The maxilla in most larval insects has the typical structure mentioned above, but in a few cases it suffers a great reduction and loss of component parts. The suppression of one or both lobes is very common.

In larval insects the cardo (fig. 28, cd., Pl. 3; fig. 24, cd., Pl. 4; fig. 34, cd., Pl. 6; figs. 41, 44, cd., Pl. 8) is generally triangular in shape, articulated to the head by the condyle. In larval Rha-gium (fig. 23, Pl. 3), however, it is devoid of a condyle, but attached to the head by the pleural membrane only. In larval Diptera and in certain Trichoptera it is rather rod-shaped (fig. 45, Pl. 9; figs. 56, 59, 60, Pl. 11).

The cardo in many larval insects is subdivided by an internal ridge which strengthens the sclerite but rarely gives insertion to the tentorial adductors of the cardo. With the absence of promotor muscle the cardo loses its cardo-process. The latter is absent in larval Diptera, Trichoptera, Lepidoptera, Mecoptera, and also in certain Coleoptera such as larval Elateridae and
Trogositidae (figs. 28, 29, Pl. 5; fig. 40, Pl. 7; fig. 46, Pl. 9; figs. 54, 55, Pl. 10; figs. 56, 60, Pl. 11).

The two cardines in larval Elateridae have become mesally approximated; consequently, with the displacement of the postmentum (fig. 31, pmt., Pl. 5) forward there is left only a suture between the two cardines.

The direction of the cardo varies with the prognathous and hypognathous conditions of the head. In typical prognathous larval insects (figs. 28, 31, Pl. 5; fig. 37, Pl. 7; fig. 41, Pl. 8) it runs straight forward, while in the typical hypognathous type (fig. 30, Pl. 5; fig. 34, Pl. 6) it is directed outwards and forms an angle with the stipes. With the reduction in size of the labium in larval Mecoptera, the distal end of the cardo is turned inwards (fig. 40, Pl. 7).

The stipes is suspended from the cardo in the hypognathous type. In the prognathous type it runs straight forward in the same line as the cardo.

Yuasa (1920) states that the stipes has two points of articulation with the cardo in Orthopterous insects. The same condition exists in most larval insects, but in larval Diptera the cardo (figs. 56, 59, 60, cd., Pl. 11) is attached to the stipes by a single articulation.

The distal area of the stipes bearing the palpus is sometimes differentiated into a distinct sclerite, the palpifer (fig. 37, pf., Pl. 7), but in many cases the area remains membranous (fig. 45, Pl. 9). The basal segment of the palpus in many insects is misinterpreted as the palpifer.

The lacinia in most larval insects is spined or toothed on its inner border. The galea is sometimes two-segmented as in larval Carabidae and Elateridae (figs. 29, 31, ga., Pl. 5). In certain cases the galea is partially fused with the basal segment of the palpus. When this happens the outer part of the compound structure is sometimes mistaken for the palpifer. An examination of the palpal muscles would reveal its true identity.

In the larvae of Sialis the lobe (fig. 41, ga., Pl. 8), apparently borne by the basal segment of the palpus, is undoubtedly a part of the galea. The unusually dilated basal segment (b.)

1 Teeth not shown in many figures.
of the palpus tends to show that the galea has most probably two segments, the proximal segment being fused with the basal segment of the palpus, while the distal one remains free. The musculature also supports this view.

In the larvae of Raphidia, Panorpa, Thanatophillus, and Ptinus the lacinia and galea are fused to form a single structure, but its distal end remains notched, thus revealing the presence of both lobes (figs. 24, 25, lc., ga., Pl. 4; fig. 34, lc., ga., Pl. 6; figs. 37, 39, 40, lc., ga., Pl. 7). In larval Raphidia (fig. 40, Pl. 7) the presence of stipital flexors (13, 14) of the lacinia and galea further supports this view.

In many larvae either one or both lobes may be suppressed. In the larvae of Trichoptera, Diptera, Curculionidae, Tenebrio, and Tenebroides, only the lacinia (figs. 20, 21, lc., Pl. 3; fig. 28, lc., Pl. 5; fig. 32, lc., Pl. 6; figs. 45, 46, lc., Pl. 9; figs. 56, 59, 60, lc., Pl. 11) is present, while in the larvae of Cerambycidae and Carabidae only the galea (fig. 29, ga., Pl. 5) is retained. Both lobes are totally absent in larval Hydrophilus (fig. 27, Pl. 4), and the lobe (el.) borne by the basal segment of the palpus is the endite of that segment.

In Lepidopterous larvae (figs. 50, 51, 54, 55, Pl. 10) both lacinia and galea are absent. The lobe (1.) borne by the second segment of the palpus can in no way be regarded as either lacinia or galea. It is most probably a secondary outgrowth of the palpal segment.

The palpus is variously segmented. In larval Diptera it is composed of a single segment (figs. 56, 59, 60, mp., Pl. 11).

The detailed identities of the sclerites and lobes will be dealt with in relation to musculature.


The musculature of the typical larval maxillae comprises the following muscles (figs. 20, 21, 23, Pl. 3; figs. 24, 25, 27, Pl. 4; figs. 28, 29, 30, 31, Pl. 5; fig. 34, Pl. 6; figs. 39, 40, Pl. 7; figs. 41, 44, Pl. 8; fig. 46, Pl. 9; figs. 54, 55, Pl. 10; figs. 56, 60, Pl. 11; fig. 62, Pl. 12):

1 The spine-like process (lc. ?) on the mesal side of the stipes may represent the remnant of the lacinia.
(8) Promotor of the cardo.—A group of fibres, generally arranged in a fan-shaped manner; origin on the postgena, insertion on the cardo-process.

(9) Adductors of the cardo.—Generally two muscles; origin on the tentorium, insertion of one on the lateral side, of the other on the mesal side of the cardo. When the cardo is subdivided, one is inserted on the proxicardo and the other on the disticardo.

(10) Adductor of the stipes.—Origin on the tentorium, insertion either in one or in two groups on the stipes.

(11) Retractor of the stipes.—Origin on the basal part of the tentorium, insertion on the stipital ridge.

(12) Cranial flexor of the lacinia.—Origin just dorsal to the origin of the promotor of the cardo, insertion on the inner base of the lacinia.

(13) Stipital flexor of the lacinia.—Origin on the outer angle of the stipital base, insertion on the inner base of the lacinia near the insertion of the cranial flexor. In many cases the stipital flexor and cranial flexor of the lacinia have a common insertion through a tendinous cord.

(14) Cranial flexor of the galea.—Origin on the mesal side of the stipes, insertion on the base of the galea.

(15) Levator of the maxillary palpus.—Origin on the median basal part of the stipes, insertion on the dorsal margin of the basal segment of the palpus.

(16) Depressor of the maxillary palpus.—Origin near the origin of the levator, insertion on the ventral margin of the basal segment of the palpus.

The additional muscles of the larval maxilla (fig. 40, Pl. 7; fig. 46, Pl. 9; fig. 54, Pl. 10; figs. 56, 60, Pl. 11):

(17) Cranial flexor of the maxillary palpus.—Origin on the hypostoma in larval Lepidoptera or dorsal region of the postgena in larval Trichoptera; insertion near the levator of the maxillary palpus.

(18) Cranial flexor of the stipes.—Origin on the gena, insertion on the anterior (dorsal) side of the stipes; present in larval Panorpa and Bibio.
8. The Musculature in Relation to the Sclerites, Lobes, etc., of the Larval Maxilla.

The cardo can be distinguished by the insertion of the promotor (9) and adductor muscles (10) upon it. The adductors of the cardo are generally two groups of fibres arising on the tentorium. One group is inserted on the outer side and the other on the mesal side of the cardo (fig. 23, Pl. 3), or when the cardo is subdivided by the internal ridge each subdivision has the insertion of one group (fig. 20, Pl. 3). Rarely, the internal ridge itself has the insertion of a few fibres. In larval Elateridae, Crampton (1928) calls the disticardo (fig. 31, dc., Pl. 5) the basimaxillary sclerite. The insertion of the tentorial adductors of the cardo on both sclerites, labelled pc. and dc., shows that they are subdivisions of the cardo, and the sclerite, dc., cannot be a basimaxillary sclerite which always lacks muscles.

In larval Lepidoptera the sclerite labelled msc. in fig. 50, Pl. 10, lying on the mesal side of the cardo is called the submental sclerite by Crampton (1921, 1928), but Snodgrass (1928) labels it as the accessory plate of the cardo. The sclerite is separated by suture from the postmentum and has no insertion of any muscles upon it. The above condition suggests that it is neither a part of the postmentum nor of the cardo, but from its position I am inclined to regard it as the basimaxillary sclerite of the same nature as that of larval Carabidae (fig. 29, msc., Pl. 5) and Tenebrionidae.

In many larval insects the cardo is devoid of its promotor muscle and in larval Mecoptera and Diptera it entirely lacks muscles (fig. 40, cd., Pl. 7; figs. 56, 60, cd., Pl. 11).

The stipes (fig. 63, st., Pl. 12) can be distinguished by the origin of the muscles of the palpus (15, 16) and of the lobes (13, 14). The insertion of the adductor (10) and retractor (11) of the stipes is very helpful in finding the mesal limit of the stipes (fig. 20, Pl. 3; fig. 25, Pl. 4; fig. 84, Pl. 6). The dorsal cranial muscle (18) of the stipes, in the absence of other muscles, is the last resource for the interpretation of the sclerite (fig. 40, st. Pl. 7; fig. 60, st., Pl. 11) from the point of view of musculature. This muscle is most useful in interpreting the stipes in larval Bibionidae (fig. 60, st., Pl. 11).
In many insects the stipes has on the mesal side a small sclerite, apparently demarcated from the main one. This is mainly due to the insertion on that area of the tentorial adductor and the retractor of the stipes.

The lacinia (fig. 30, lc., Pl. 5; fig. 39, lc., Pl. 7; fig. 62, lc., Pl. 12) has a cranial flexor (12) and a stipital flexor (13), and the galea has only the stipital flexor (14). In adult Orthoptera (fig. 62, Pl. 12) the stipital flexor of the lacinia (13) lies dorsal (anterior) to the palpal muscles (15, 16), and the flexor of the galea (14) runs ventral (posterior) to the palpal muscles. The same condition exists in many adult insects and most larval stages, but in the latter the flexor of the galea arises near the origin of the palpal muscles or rather on their mesal side (fig. 23, Pl. 3; fig. 30, Pl. 5; fig. 40, Pl. 7, fig. 41, Pl. 8). These muscles are very important in distinguishing the lobes. The flexor of the galea is not present in many larval stages, but when the lacinia is present, its muscles, or at least the cranial flexor, are always retained. The cranial flexor of the lacinia undoubtedly plays an important part in interpretation of the lobes or of the lobe when one of them is absent; even in the absence of the lacinia as in larval Hydrophilus (fig. 27, Pl. 4) the cranial flexor of the lacinia (12) is retained, but its point of insertion is changed, being removed to the dorsal middle of the stipital base.

Otanes (1922) describes the two lobes in adult Mecoptera as subdivisions of the galea, the lacinia being completely absent. In view of this, and to study the modification, I have also examined adult Panorpa and Boreus and found that the lobes were definitely the lacinia and galea, since the typical muscles of the lacinia are retained in the former lobe.

The palpus has a levator (15) and a depressor muscle (16) arising upon the stipes (fig. 25, Pl. 4; figs. 28, 31, Pl. 5; fig. 84, Pl. 6; fig. 54, Pl. 10; fig. 62, Pl. 12). An accessory muscle (17) of the palpus arising on the cranium is found in larval Trichoptera and Lepidoptera (fig. 46, Pl. 9; fig. 54, Pl. 10). This muscle is not found in any other group. In larval Diptera the palpal muscles are absent (figs. 56, 60, Pl. 11).

The maxilla of larval Diptera suffers a great loss in its mus-
culature, but it retains most of its component parts in reduced condition. The only muscle present in larval Tipulidae (fig. 56, Pl. 11) is the cranial flexor of the lacinia (12) which controls the whole maxilla; in larval Bibio (fig. 58, Pl. 11) there is an additional muscle, the dorsal muscle of the stipes (18).

The maxilla in larval Diptera (figs. 56, 59, 60, Pl. 11) has a rod-shaped cardo (cd.) articulating with the hypostoma, a stipes (st.), a lacinia (lc.), and a single segmented palpus (mp.).

It is quite improbable that the palpifer represents a segment of the mouth-part limb with the lacinia as its endite, as is claimed by Hansen (1893, 1980) and Crampton (1925). The musculature does not provide any evidence for this view. Börner (1921) and Snodgrass (1928) regard the palpifer as a secondarily demarcated portion of the stipes. The latter author states, 'that the palpifer is not a segment of the appendage is shown by the fact that muscles neither arise within it nor are inserted upon it'. The origin of the muscles of the palpus and of the flexor of the galea upon the stipes adds much weight to the view of Börner and Snodgrass. On the other hand, the origin of the muscle of the galea upon the stipes shows that the galea cannot be an endite of the so-called palpiferal segment, but it belongs to the stipes.

In support of his view, Crampton (1925) cites the larva of Sialis and through it he tries to bridge the gulf between Crustacea and Insecta and to show the modification of the 'palpiferal segment'. He calls the segment b, in Sialis larva (fig. 41, Pl. 9), the palpifer, representing the ischiopodite of the Crustacean appendage, and its endite, the galea. An examination of the musculature, however, shows that the typical palpal muscles (15, 16) are inserted at the base of this segment (b.), which is undoubtedly the basal segment of the palpus. Snodgrass has also interpreted the segment on the basis of musculature. The inner lobe (ga.), apparently borne by the basal segment of the palpus, is called the galea by Crampton, on the assumption that the segment labelled b is the palpifer, but according to Snodgrass it is an endite lobe of the first segment of the palpus. The latter author criticizes Crampton, stating that 'it cannot be galea since it lacks muscles'. On this
point I do not agree with Snodgrass's interpretation, for the galea in many larval insects has been found to be without muscles. Besides, in larval Sialis the lobe undoubtedly has a muscle (14) inserted at its apparent base (this has been confirmed by cutting sections and reconstructing). This muscle is homologous with the flexor of the galea (14) of other larval insects (fig. 28, Pl. 3; fig. 30, Pl. 5; fig. 39, Pl. 7) and has a similar origin; but in Sialis larva it passes through the basal segment of the palpus to be inserted on the apparent base of the lobe (fig. 41, ga., Pl. 8). The unusually dilated basal segment of the palpus, and the insertion of the typical muscles of the galea on the apparent base of the lobe, tend to prove that the galea in Sialis larva like that of the Carabidae and Elateridae (figs. 29, 31, ga., Pl. 5) is two-segmented, but the proximal segment has become fused with the basal segment of the palpus, while the distal segment remains free.

In larval Trichoptera (figs. 45, 46, Pl. 9) the lobe (Ic.) is the lacinia. The cranial flexor of the lacinia (12) is inserted on its inner base, but the stipital flexor of the lacinia is absent. Crampton (1928) calls the lobe (Ic.) the galea, while Belton (1934) suggests it is the fused lacinia and galea. The lobe does not show any sign of external demarcation as is found in the fused lacinia and galea of larval Thanatophilus, Panorpa, and Raphidia and, therefore, probably the lacinia only.

In Lepidopterous larvae (figs. 50, 51, 54, 55, Pl. 10), Snodgrass (1928) suggests that the entire structure (mp.) distal to the stipes (st.) is the lacinia. The insertion of the palpal muscles (15, 16) at the base of the structure shows that it is the maxillary palpus, and the lobe (L.) borne by the second segment of the palpus cannot be the galea as it was supposed to be by Crampton (1921). For the galea could not be borne by a distal segment of the palpus, unless it is proximally fused with the two basal segments of the palpus, which is improbable. It also lacks muscles and most probably is an outgrowth of the second segment of the palpus. In the larval Micropterygid Sabatinca, however, there is a well-developed three-segmented palpus, a slender, sharply pointed galea, and a broader, rounded lacinia, as described by Tillyard (1922).
The partial fusion of the basal segment of the palpus with the galea in many insects has led many authors to misinterpret the basal segment of the palpus as the palpifer. The basal segment of the palpus has been called the palpifer in many insects by Crampton (1921, 1925, 1928), in larval Panorpa by Steiner (1930), in larval Rhamium by Boving and Craighead (1931), and in larval Noctuidae by Ripley (1924).

The origin of the muscles of the galea upon the stipes is against the view of Crampton (1925) and Hansen (1898, 1900) that the galea is an endite lobe of the "palpiferal segment". Snodgrass's view that the lacinia and galea are the subdivisions of the endite of the stipital segment is based on the substantial evidence that the muscles of both lobes arise upon the stipes.

9. The Labium.

The labium of insects is a composite structure formed by the union of two maxilla-like appendages. It has been homologized with the second maxillae of Crustacea, but certain authors regard it as the appendages corresponding to the first maxillipeds of Crustacea. The union of the bases of the first maxillipeds of certain Crustacea and the interpretation of the superlinguae of insects as appendages homologous with the maxillulae (first Maxillae) of Crustacea are the main evidence for the view that the labium of insects corresponds to the first maxillipeds of Crustacea. Crampton (1921), however, homologizes the superlinguae of insects with the paragnaths of Crustacea and the first and second maxillae of insects with the first and second maxillae of Crustacea respectively.

The labium of insects is composed of two segments. The distal segment bearing the palpi and lobes is called the prementum and the proximal segment the postmentum. The suture or flexible area between the prementum and the postmentum is the labial suture. The postmentum in many insects contains two plates with a suture or flexible area between them. The proximal plate is the submentum and the distal the mentum.

There is no doubt that the prementum is the result of union of two stipites of a pair of maxilla-like appendages, hence it is called the labiostipites, but the homology of the postmentum is
still a matter of controversy. Many authors regard it as the united labio-cardines, while certain authors such as MacGillivray (1923) have not even hesitated to compare the submentum and mentum with the proxicardo and disticardo respectively. The detailed discussion will be found in the section dealing with the musculature.

10. The Prementum.

The prementum or labiostipites is formed by the union of two stipites of a pair of maxilla-like appendages. The paired nature of the prementum is suggested by the distal cleft between its stipital components in primitive insects or by the presence of paired sclerites in the ventral wall in certain adult insects, e.g. Pterosticus (Snodgrass, 1935), and also by the origin of the muscles of the palpi and lobes upon it.

The size of the prementum (figs. 22–3, prm., Pl. 3; figs. 24, 26–7, prm., Pl. 4; figs. 28–31, prm., Pl. 5; figs. 32–3, 35–6, prm., Pl. 6; figs. 37–8, 40, prm., Pl. 7; fig. 45, prm., Pl. 9; figs. 61, 62, 64, prm., Pl. 12) varies in different insects and even in the same insects in different stages. In most larval insects it is very small as compared with the postmentum, but in larval Odonata it is larger than the postmentum.

The sclerotization of the ventral part of the prementum forms a single ventral plate in larval insects. The lateral areas bearing the palpi are sometimes demarcated as distinct sclerites, known as the palpigers (fig. 23, pg., Pl. 3) which are counterparts of the palpifers of the maxillae. In certain adult insects the premental sclerotization forms two lateral sclerites, but it is never subdivided into a distal and a proximal plate, the latter bearing the insertion of the ‘median muscles’. This has been supposed to be the case in larval Coleoptera and larval adult Neuroptera by Snodgrass (1935), but his ‘proximal and distal plates’ are really the mentum and prementum respectively and the so-called ‘median muscles’ inserted upon the ‘proximal plate’ are the submentomental muscles.

In larval Diptera (figs. 56–60, Pl. 11) the prementum is a strongly sclerotized plate without palpi and lobes. In larval Bibio it is most probably fused with the mentum (figs. 59, 60, p., Pl. 11).
The labial palpus (lp.) is shorter than the maxillary palpus and composed of fewer segments. In most larval Coleoptera it is two-segmented and in larval Neuroptera it is three-segmented. Crampton (1921) states that the number is a distinctive characteristic of larval Coleoptera and Neuroptera and maintains that in certain larval Neuroptera such as Chrysopa, the many-segmented condition of the palpus is due to secondary division of the primary three-segmented palpus. However, the larva of Pteronidea has a three-segmented palpus, while larval Mecoptera have again a two-segmented palpus. On the other hand, certain larval Coleoptera such as Ptinus (fig. 35, Pl. 6) have only one segment in the palpus. It is doubtful, therefore, if the number of palpal segments is of fundamental importance.

In larval Lepidoptera and Trichoptera (figs. 45–9, Pl. 9; 50–5, Pl. 10) again, the palpus is one-segmented and is represented by a small lobe on each side of the spinneret. In larval Tipula and Bibio (figs. 56–60, Pl. 11) the labial palpus is absent, unless it is fused with the prementum.

The typical number of terminal lobes borne by the distal part of the prementum is four. The median pair form the glossae, the lateral pair the paraglossae. They are undoubtedly the counterparts of the laciniae and galeae respectively. They vary much in different insects. The median lobes or the pair on each side may be united; again, all lobes may be fused to form a single structure which may be variously modified according to the mode of feeding. There may be a reduction in number, either the glossae and paraglossae being absent, or even all lobes may be totally atrophied.

In larval insects they generally form a single lobe, the ligula (fig. 22, li., Pl. 3). In certain cases (figs. 24–6, Pl. 4; fig. 36, Pl. 6) the pair on each side is fused. In larval Trichoptera, Lepidoptera, and Hymenoptera the terminal lobe bearing the orifice of the labial glands is regarded as the ligula (figs. 48, 49, li., Pl. 9; figs. 50, 52, sp., Pl. 10).

11. THE POSTMENTUM.

The postmentum is the basal part of the labium. The sclerotization of the postmentum is extremely variable. In
certain larval insects it forms a single plate as shown by the larvae of *Tenebroides* and of the Elateridae (figs. 28, 31, *pmt.*, Pl. 5). In the larval sawfly it forms a triangular median plate; in most cases it forms a proximal plate, the submentum (figs. 22, 23, *sm.*, Pl. 3), and a distal plate, the mentum (*m.*).

In larval Trichoptera of the families Hydropsychidae, Hydroptilidae, and Philopotamidae (figs. 47–9, Pl. 9) the postmentum has a definite submentum (*sm.*) lying between the two hypostomal areas and a mentum (*m.*), but in the family Limnophilidae (fig. 45, Pl. 9) the postmental sclerotization forms a single proximal plate (*sm.*) which is homologous with the submentum (*sm.*) of figs. 47–9, Pl. 9. Therefore the plate *sm.*, in fig. 45, Pl. 9, is the submentum and the distal membranous area is most probably the mentum (*m.*).

Again, the entire postmentum may be membranous, e.g. in larval Carabidae, Curculionidae, Panorpa, and Tipula (fig. 29, *pmt.*, Pl. 5; fig. 40, *pmt.*, Pl. 7; fig. 57, *pmt.*, Pl. 11). In larval Panorpa and in the Curculionidae the postmental area merges imperceptibly into the basimaxillary membrane and it is rather difficult to determine its outer limit.

It is most interesting to note that the mentum (figs. 37, 38, *m.*, Pl. 7) is sometimes formed of two sclerites, one on each side, each with a submentomental muscle (22) inserted upon it. This distinctive feature is exhibited by certain Neuropterous larvae. In the Trichopterous larvae of the family Hydropsychidae (fig. 47, Pl. 9) the mentum (*m.*) is deeply notched distally, the notch extending up to the middle of the plate.

In certain larval insects the postmentum or submentum is partially or wholly adherent to the head capsule between two hypostomal processes (fig. 37, Pl. 4; fig. 37, Pl. 7; figs. 45–9, Pl. 9). They may also be fused with the gula to form a single gulamental plate (figs. 37, 38, Pl. 7; fig. 64, Pl. 12).

12. THE MUSCULATURE OF THE LARVAL LABIUM.

The musculature of the larval labium comprises the following muscles (figs. 22, 23, Pl. 3; figs. 24, 26, 27, Pl. 4; figs. 29, 30, 31, Pl. 5; figs. 33, 35, 36, Pl. 6; figs. 38, 39, Pl. 7; figs. 41,
(19) Median muscles of the prementum.—Origin on the post-
mentum or submentum, or on the tentorium, insertion
ventrally on the middle of the proximal border of the
prementum.

(20) Lateral muscles of the prementum.—Same origin, in-
sertion ventrally on the sides of the proximal border of
the prementum.

(21) Dorsal muscles of the prementum.—Same origin, in-
sertion on the proximal border of the dorsal side of
the prementum.

(22) Submentomental muscles (retractors or flexors of the
mentum).—Origin on the posterior region of the sub-
mentum, insertion on the proximal border\(^1\) of the
mentum.

(23) Eetractor of the palpus.—Origin on the prementum,
insertion on the base of the palpus. In most larval
insects the labial palpus is not provided with antagon-
istic muscles, but in larval Odonata it has two
muscles, a levator and a depressor (Munscheid, 1931).

(24, 25) Dorsal muscles of the silk press. A pair of muscles
arising on the dorsal side of the prementum, inserted
on the sclerotized raphe of the anterior wall of the
press.

(26) Ventral muscle of the silk press.—Origin on the ventro-
lateral side of the prementum, insertion on the lateral
side of the silk press.

The following additional muscles are found in certain
larval insects:

(27) Cranial flexors of the prementum.—Arise on the post-
occipital ridge of the cranium, run ventral to the body
of the tentorium to be inserted on the dorso-lateral
sides of the prementum; present in larval sawflies.
Parker (1934) suggests that these muscles should be
called the dorsal retractors of the prementum (dorsal

\(^1\) Except larval Dermestes in which they are inserted in the middle
of the mental plate.
MUSCULATURE OF THE MOUTH-PARTS OF INSECT LARVAE

(28, 29) Dorsal and ventral retractors of the spinneret.—Origin on the body of the tentorium, insertion on the dorsal and ventral side of the spinneret; present in larval sawflies.

(30) Transverse muscle of the mentum.—A stout muscle attached to the sides of the mentum; a fine thread runs from the middle of the muscle and is inserted on the dorsal side of the prementum; present in larval Sialis.

(31) A pair of muscles arising on each side of the premental cone, inserted on the hypopharyngeal bracoon; present in larval Curculionidae.

Owing to the atrophy of the lobes or their union to form a single small lobe in larval insects, the muscles of the lobes are absent. The typical lobes of the adult insects are described here to show their homologies. The muscles of the glossa and paraglossa (fig. 61, fgl., and fpgl., Pl. 12) in adult insects are almost similar to those of the lacinia and galea, each having a flexor arising upon the prementum, but the muscle corresponding to the cranial flexor of the lacinia is not present in the glossa.

In many larval insects, if it is desired to interpret the homologies of the sclerites, it is absolutely necessary to give a detailed description of the point of origin of the muscles of the prementum and also to describe the submentomental muscles (when present).

In larval Neuroptera, as shown by the larvae of Raphidia and Sialis (fig. 38, Pl. 7; figs. 41, 42, Pl. 8), all muscles of the prementum, i.e. median, lateral, and dorsal muscles (19, 20, 21), have their origin on the tentorium. The submentomental muscles (22) are also present, having their origin upon the posterior region of the submentum and their insertion on the proximal border of the mentum. In larval Raphidia each submentomental muscle is inserted upon each lateral sclerite of the mentum.

In larval Thanatophilus (figs. 24, 26, Pl. 4), however, the dorsal and lateral muscles (21, 20) arise upon the tentorium,
but the median muscles (19) of the prementum and also the submentomental muscles (22) have their origin on the submentum. The same condition of the premental muscles exists in larval Elateridae (fig. 31, Pl. 5), but the median muscles arise upon the postmentum, there being one plate; consequently the submentomental muscles are absent.

In larval Tenebrio and Ptinus (fig. 23, Pl. 3; fig. 85, Pl. 6), on the other hand, the median and dorsal muscles (19, 21) arise from the tentorium, but the lateral muscles (20) of the prementum and also the submentomental muscles (22) arise from the submentum (sm.).

In certain larvae all muscles of the prementum are not retained, either one or two sets being absent. In larval Dermestes (fig. 36, Pl. 6) the median muscles are absent, but the lateral and dorsal muscles (20, 21), including the submentomental muscles (22), have their origin upon the submentum (sm.). In Lucanidae (fig. 30, Pl. 5) the lateral muscles are absent, but the median and dorsal muscles (19, 21) of the prementum arise upon the tentorium. The submentomental muscles (22) are also retained.

It seems from the point of origin of the premental muscles and submentomental muscles that all of these muscles represent the sternal muscles of the labial appendages, having their primary origin upon the submentum. The shifting of the bases of the premental muscles on to the tentorium is probably rather a secondary condition.

13. THE MUSCULATURE IN RELATION TO THE SCLERITES OF THE LARVAL LABIUM.

The insect labium shows so much variation and modification of its sclerites and lobes that it is very difficult in some cases to homologize the sclerites and lobes without examining the musculature.

The prementum can be identified by the origin of the muscles (when present) of the palpi and lobes upon it and also by the insertion of the premental muscles upon its proximal border. The points of insertion of the median, lateral, and dorsal muscles (19, 20, 21) limit the proximal border of the prementum.
(fig. 22, prm., Pl. 3; fig. 35, prm., Pl. 6; fig. 38, prm., Pl. 7; fig. 41, prm., Pl. 8), and the portion of the labium proximal to the insertion of these muscles is the postmentum. When the postmentum is a single plate (figs. 28, 31, pmt., Pl. 5) no muscle is inserted upon it, but when it has two plates, the submentum and mentum, the latter has the insertion of the submentomental muscles (22) upon its proximal border in many larval insects (fig. 22, Pl. 3; figs. 26, 27, Pl. 4; fig. 30, Pl. 5; fig. 35, Pl. 6; fig. 38, Pl. 7; figs. 41, 42, Pl. 8). The mental plate (m.), therefore, lies distal to the insertion of the submentomental muscles (22) and proximal to the insertion of the premental muscles (19, 20, 21). The plate (sm.), proximal to the insertion of the submentomental muscles, is evidently the submentum. The origin of the submentomental muscles (22) and some of the premental muscles upon the posterior region of the submentum identifies the submental plate. Similarly, the origin of some of the premental muscles (especially the median muscles (19)), identifies the postmentum (fig. 31, pmt., Pl. 5) when it is a single plate. Therefore, almost the whole of the postmentum is included between the origin of some of the premental muscles upon the posterior region of the postmentum and their insertion upon the proximal border of the prementum.

The point of origin of the median muscles (19) upon the posterior border of the postmentum and their insertion upon the proximal border of the prementum definitely shows that the entire plate (fig. 31, pmt., Pl. 5) in larval Elateridae is the postmentum. Ford (1917) describes the plate, pmt., as the mentum. Roberts (1921) and Crampton (1928) regard this elongated plate as the submentum and the membranous part distal to the plate as the mentum. It is more probable that, as in many other insects, the membranous part is the flexible area between the prementum and postmentum.

In many cases the postmentum has been wrongly called either mentum or submentum, but an examination of the musculature can hardly fail to indicate its true identity.

When the postmentum or submentum is fused with the gula

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1 Except larval Derastes (fig. 36 Pl. 6) in which the submentomental muscles (22) are inserted upon the middle of the mental plate (m.).
so as to form a single gulamental plate, it is not difficult to find out the approximate proximal limit of the postmentum or submentum by the points of origin of the submentomental muscles (22) or some of the premental muscles (especially the median muscles, (19)). The points of origin of these muscles correspond approximately with the pregular suture (when the gula and submentum are separated by a suture) (fig. 22, Pl. 3) or with the line drawn across the two tentorial pits (figs. 37, 38, Pl. 7) which always corresponds with the pregular suture when the latter is present.

Crampton (1921, 1923, 1925, 1928) labels the plate (sm.) in larval Hydrophilus (fig. 27, Pl. 4) as the gula and the flexible area distal to it as the submentum, but the origin of the submentomental muscles (22) upon the conical proximal border of the plate (sm), and their insertion upon the proximal border of the mentum (m.), show that the plate (sm.) is the submentum with a distal flexible area between it and the mentum.

In larval Eaphidia (figs. 37, 38, Pl. 7), where the submentum (sm.) is fused with the gula (gu.), Crampton (1928) calls the entire plate (sm. and gu.) the gula and the flexible area distal to the plate the submentum. The point of origin of the submentomental muscles, which also approximately corresponds with the line drawn across the two tentorial pits (pt.), shows that the part of the big plate distal to the two tentorial pits is the submentum (sm.), and the part proximal to the pits is the gula (gu.). The broad plate, labelled sm., in Sialis larva (figs. 41, 42, Pl. 8), is the submentum alone, as revealed by the origin and insertion of the submentomental muscles (22). The plate (sm.) cannot be a gulamental plate as it is supposed to be by Crampton (1921, 1928).

Snodgrass's view (1935) that the only muscles having their origin upon the postmentum are the median muscles of the labium that extend from the postmentum to the prementum is not upheld in many of the species I have examined. As I have already stated, in addition to submentomental muscles (which are quite different from the median muscles) some of the muscles of the prementum in many larval insects have their origin upon the submentum (fig. 22, Pl. 3; fig. 26, Pl. 4; figs. 35, 36,
In larval *Thanatophilus* (fig. 26, Pl. 4) both median and submentomental muscles (19, 22) arise upon the submentum (sm.). In larval *Dermeestes* (fig. 36, Pl. 6) the lateral and dorsal muscles (20, 21), including the submentomental muscles (22), and in larval *Tenebrio* and *Ptinus* (fig. 22, Pl. 3; fig. 35, Pl. 6), the lateral and submentomental muscles (20, 22) have their origin upon the submentum (sm.).

Snodgrass (1935) does not distinguish the median muscles from the submentomental muscles and calls the submentomental muscles the 'median muscles' in many larval Coleoptera and larval and adult Neuroptera. This led him to misinterpret the mentum as the 'proximal sclerite of the prementum' and consequently the submentum as the postmentum in such cases. He states that in many larval Coleoptera and larval and adult Neuroptera the prementum is composed of two principal plates, on the proximal one of which are inserted the 'median muscles' and on the distal one the tentorial adductors. A comparative study of the musculature in a wider range of larval insects shows that the so-called 'median muscles' in such cases are the submentomental muscles which are morphologically quite different from the median muscles, the latter being sometimes present at the same time and both having their origin upon the submentum (fig. 26, Pl. 4), and the so-called 'proximal plate' of the prementum is, therefore, really the mentum, and the so-called 'postmentum' is the submentum. In adult *Chrysopa* (fig. 63, Pl. 12) the plate, labelled m., is the mentum, having the insertion of the submentomental muscles (22) at its proximal border, and the plate, labelled sm., is the submentum. Therefore, the prementum is never subdivided into a proximal and a distal plate, though it may have two lateral sclerites.

In larval Lepidoptera (fig. 50, Pl. 10) the plate (pmt.) is evidently the postmentum as it lies proximal to the insertion of the premental muscles. In many Lepidopterous larvae the postmentum remains membranous like that of the sawfly larva.

In larval Trichoptera (figs. 45, 49, Pl. 9) the postmental

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1 Anderson (1936), supporting Snodgrass's view, states that the prementum in Coleopterous larvae is very often subdivided into a first and a second prementum.
sclerotization forms a single plate in some cases, two in others. No muscles arise from or are inserted upon it, but the entire postmental area lying between the insertion of the premental muscles (19) and the two tentorial pits (pt.) can easily be recognized. Therefore, the plates (sm. and m.) in figs. 47-9, Pl. 9, are the submentum and mentum respectively, but in the case where the postmentum forms a single proximal plate (fig. 45, Pl. 9), the plate (sm.) undoubtedly represents the submentum which is homologous with the submentum of figs. 47-9, Pl. 9, in shape and position, and the membranous area distal to the plate (sm.) is the mentum. In all Trichopterous larvae the submentum (figs. 45-9, Pl. 9) lies either partially or wholly between the two hypostomal processes of the head capsule. Many authors regard the plate (sm.) as the gula, but the gula is never situated distal to the tentorial pits.

In larval Diptera (figs. 56-60, Pl. 11) it is rather difficult to interpret the labium with the help of the musculature, since the muscles of the labium arise upon the head capsule. In larval Tipula (figs. 56-8, Pl. 11) the plate (prm.) has the insertion of the muscles (19, 20) which are homologous with the median and lateral muscles of the prementum, but they arise upon the posterior region of the head. From the insertion of these muscles upon the proximal border of the plate (prm.) it can be inferred that the plate represents the prementum, and the membranous area connecting the plate with the hypostoma cannot be anything but the postmentum (fig. 57, pmt., Pl. 11). In Tipulidae Becker (1910) describes the ventral hypostomal plate (figs. 56, 59, hst., Pl. 11) as the submentum and the upper plate (prm.) as the mentum. In Chironomus larvae Miall and Hammond (1900) also describe the similar ventral plate as the submentum and the upper plate as the mentum. In larval Bibio (fig. 58, Pl. 11) only the lateral muscles (20) are retained, but they are inserted at a point half-way from the proximal border of the plate (pl.), suggesting that some element from the postmentum, most probably the mentum, has entered into the composition of the plate (pl.); the plate sm. is, therefore, the submentum.

The homology of the postmentum is still uncertain. The view that the postmentum contains the sternal element of the labial
segment is strongly supported by the origin of the premental and submentomental muscles upon the postmentum or rather upon the submentum. These muscles represent the sternal muscles of the labial appendages, having their primary origin upon the sternal area of the postmentum. The shifting of the bases of the premental muscles on to the tentorium so as to provide a stronger base for muscles is a secondary condition. In Mačílis Snodgrass states that the median triangular area which is separated by faint lines from the lateral areas of the postmentum is the sternum of the labial segment. This triangular area seems to correspond with the points of origin of the submentomental muscles and the premental muscles upon the postmentum. Imms (1934) suggests that the postmentum, though representing the united cardines, also has a sternal element in its composition.

Crampton (1921, 1928), following the interpretation of Holmgren (1909), regards the entire postmentum as the sternal derivative of the labial segment, and his hypothetical mid-labium representing the united cardines lies between the prementum and postmentum. However, from the insertion of the submentomental muscles upon the proximal border of the mentum, it is difficult to justify the inclusion of the mentum in the sternum, for the sternal element must always lie proximal to the insertion of the submentomental muscles. Evidently the mentum is the representative of the united cardines in the labium. The presence of paired sclerites in the mentum of certain Neuropterous larvae is especially suggestive of this theory. If this is the case, then the entire submentum is a sternal derivative. This view seems to agree with the fact that all premental muscles (including submentomental muscles) have their primary origin upon the submentum. The presence of submentomental muscles when there are two plates in the postmentum, and their complete atrophy in a single postmental plate, show that the fusion of the submentum and mentum has taken place.

1 Compare also incomplete fusion of the two sclerites of the mentum in larval Hydropsychidae (Trichoptera).

2 It might be objected to this view that many generalized insects have the postmentum represented by a single plate. In certain Orthoptera
late in phylogeny. These facts are scarcely compatible with the inclusion of portions of the labial cardines in the submentum. Therefore, the submentum is entirely a derivative of the sternum of the labial segment, and the only part comparable to the cardines is the mentum. The insertion of the submento-mental muscles representing the sterno-cardinal muscles of the labial appendages on the proximal border of the mentum also strongly supports this interpretation.

A further comparative study of the musculature and sclerites of the labium and embryological data are needed before speculating further.

14. **The Musculature of the Mouth-parts of Larval Insects in Relation to Classification.**

The musculature of the mouth-parts is very helpful in grouping the larval insects, since each group has its own characteristic muscles, but it is more uniform in some orders, such as Lepidoptera and Trichoptera than in others. On the other hand, in Coleoptera and Neuroptera, so far as I have studied them, each family is in some way peculiar in the musculature of the mouth-parts.

The larvae of Lepidoptera and Trichoptera can at once be distinguished from others in having an additional muscle of the maxillary palpus, which arises upon the cranium and also by the loss of the promotor of the cardo. The cranial muscle of the palpus is characteristic of these two groups and is found nowhere else. The larvae of Trichoptera can be separated from those of Lepidoptera in having both anterior and lateral muscles of the labrum, while in the latter only the lateral muscles are retained. The origin of the cranial muscles of the palpus upon the hypostomal region is again characteristic of larval Lepidoptera, this muscle arising upon the posterior region of the cranium in larval Trichoptera.

The larvae of Mecoptera and Diptera are conspicuous by the absence of all muscles of the cardo. They are also characterized (e.g. *Periplaneta*, *Gryllus*, &c.), however, the postmentum is divided though apparently without muscles. I hope to study this point at a later date.
by having the dorsal cranial flexor of the stipes (except Tipula). Larval Diptera (Nematocera) can be distinguished by the absence of tentorial adductor and retractor of the stipes and also of the muscles of the maxillary palpus, which are retained in larval Mecoptera. In larval Mecoptera only the anterior labral muscles are present, while in larval Diptera only the lateral labral muscles are retained.

Larvae of Hymenoptera, Neuroptera, and Coleoptera\(^1\) can be distinguished from other larvae so far studied in having the promotor of the cardo. The larvae of Hymenoptera and Neuroptera have both anterior and lateral muscles of the labrum, and larval Coleoptera have either lateral or posterior labral muscles.

The fact that all premental muscles have their origin on the tentorium is characteristic of the larval Neuroptera. The submentomental muscles are not present in any order besides Coleoptera and Neuroptera. Larval Hymenoptera have distinctive dorsal cranial flexors of the prementum. These muscles most probably represent the tergal muscles of the labial appendages.

15. **The Gula.**

The gula (fig. 22, gu., Pl. 3; figs. 24, 26, gu., Pl. 4; fig. 28, gu., Pl. 5; figs. 37, 38, gu., Pl. 7) is the median ventral plate, formed by the sclerotization of the neck membrane proximal to the postmentum or submentum, and bounded on each side by the extension of the postgenae but demarked from them by the gular suture (figs. 37, 38, gs., Pl. 7). Snodgrass (1928, 1935) considers that the origin of the gula is generally associated with the prognathous condition of insects, in which the head is turned upwards upon the neck, with the result that the original posterior surface becomes the ventral. In such cases the ventral parts of the head become elongated with the extension of the postgenal areas. The membrane on the ventral side of the head behind the postmentum or submentum becomes sclerotized and forms a single median plate, the gula, which gives more rigidity to the head. The membrane forming the gula was originally

\(^1\) Except larval Elateridae and Trogositidae.
in the neck region behind the postmentum or submentum, but
with prognathism has become a part of the head.

That the gula is developed from the cervical membrane is
shown by the fact that a pair of muscles (fig. 22, gum., Pl. 3)
arising upon the posterior border of prothoracic segment is
inserted on a crescent-shaped groove at the anterior margin of
the gula, just behind the pregular suture (pgs.) in larval Tene-
brio. These muscles are homologous with muscles having the
same origin but inserted on the proximal border of the mem-
brane just behind the submentum in certain larval insects,
where the gular area is not sclerotized.

Comstock and Kochi (1902) consider that the gula is the
sternum of the cervical segment which has migrated cephalad.
They cite Corydalis as their example and state that the
sternum of the cervical segment forms the gula but the sternel-
num remains behind it. Stickney (1928) contradicts them, stating
that both sternum and sternellum of the 'cervical segment'
are retained behind the gula in Corydalis. Henriksen (1928)
maintains that the sternum of Dermaptera forms the gula, but
that in beetles the gula is a quite different thing and has nothing
to do with the sternum. Stickney (1928) defines the gula as the
sclerite formed by the migration of the posterior tentorial pits
from the occipital foramen towards the submentum and em-
phasizes that it must be derived from the postgenae. From
the condition exhibited by the larvae of Tenebrio we can
scarcely derive the gula from the postgenae. Besides, there
are many insects (e.g. larval Carabidae) where the tentorial
pits lie far forward from the occiput, yet the gula is not de-
veloped.

The presence of a gula is not strictly characteristic of pro-
ognathous insects, since it is also found in certain hypognathous
types in a reduced condition. On the other hand, in certain
prognathous insects, such as the larva of Sialis, the gula is
not developed at all, i.e. the area behind the submentum remains
membranous. A well-developed gula (fig. 29, gu., Pl. 5; figs. 37,
38, gu., Pl. 7) is found in typical prognathous insects, such as
the larvae of Raphidia and Tenebroides.

The gula is primarily demarked from the submentum by a
suture, the pregular suture (fig. 22, pgs., Pl. 3). In certain insects the gula is fused with the postmentum or submentum, so as to form a single gulamental plate (fig. 37, sm. and gu., Pl. 7; fig. 64, pmt. and gu., Pl. 12). A line drawn across the two tentorial pits (fig. 37, pt., Pl. 7) can be taken as defining the anterior limit of the gula in the gulamental plate.

In many insects the two tentorial pits are much elongated and run towards the submentum from near the occipital foramen. The anterior ends of these two elongated tentorial pits (fig. 22, pt., Pl. 3) correspond exactly with the pregular suture in the larvae of Tenebrio and Tenebroides in which the gula is distinctly separated from the submentum and postmentum respectively. Therefore, the gula can also be defined as the plate lying between the two tentorial pits when the latter are elongated.

The points of origin of the submentomental muscles (22) or median muscles (19) are very useful in defining the gular limit in larval insects (fig. 26, Pl. 4). The submentomental muscles (22) arise upon the posterior region of the submentum, slightly in front of its proximal border or pregular suture, in larval Tenebrio (fig. 22, Pl. 3). In larval Raphidia (fig. 38, Pl. 7), where the gula is fused with the submentum, the point of origin of the submentomental muscles (22) approximately corresponds with the line drawn across the two tentorial pits (pt'). Although it is not possible to define in this way the exact anterior limit of the gula in the single gulamental plate, one can at least rest assured of its not being extended beyond the point of origin of these muscles. Crampton (1921, 1928) wrongly interprets the gulamental plate as the gula alone in larval Raphidia.

In the soldier termite (Termopsis sp.) the gula (fig. 64, gu., Pl. 12) lies between the two elongated pits (pt.), but it is fused with the postmentum (pmt.) so as to form a big plate. The portion of the gulamental plate distal to the elongated pits is evidently the postmentum (pmt.). Snodgrass (1935) designates the entire plate (pmt. and gu.) as the postmentum, although he states that 'in some of the Scarabaeidae the gula is likewise demarked by the greatly elongated tentorial pits'. The point
of origin of the median muscles also approximately corresponds with the anterior ends of the tentorial pits.

In certain insects the hypostomal lobes of the head lie in front of the two tentorial pits and the postgenal lobes behind them; and the basal part of the labium becomes fixed to the head capsule in front of the two tentorial pits. The membrane behind the two tentorial pits may form a gula or it may be completely obliterated by the median approximation of the postgenal areas, leaving only a suture, the mid-genal suture. The characteristic modification of the former condition is exhibited by the larva of Raphidia (fig. 37, Pl. 7), in which the submentum (sm.) lies between the hypostomal lobes of the cranium but in front of the two tentorial pits, while the gula (gu.) lies behind them. The second type of modification is shown by larval Hydrophilus (fig. 27, Pl. 4). The submentum (sm.) is similarly fixed to the head capsule but the gular area is obliterated by the median approximation of the postgenal areas, leaving only the mid-genal suture (mgs.). This median approximation has altered the shape of the submentum into a cone which lies slightly behind the two tentorial pits, but the origin and insertion of the submentomental muscles (22) may be relied on in the interpretation of the submentum.

A further modification of the median approximation of both hypostomal and postgenal areas is shown by the larvae of Panorpa, of the Carabidae, and of the Elateridae, in which there is left only a suture (figs. 29, 31, mgs., Pl. 5) between the approximated ventral parts of the head capsule.

In larval Cerambycidae the median approximation has gone a step farther than that exhibited by the larva of Panorpa, &c., resulting in the complete fusion of the ventral parts of the head, which thus forms a bridge, the hypostomal bridge (fig. 28, hst.b., Pl. 8), sometimes wrongly called the gula. However, the tentorial pits lie at the posterior margin of the head capsule and consequently the gula is absent.

In Trichopterous larvae the tentorial pits (fig. 46, pt.', Pl. 9) lie at the posterior margin of the head capsule and the gula is

1 The median muscles and submentomental muscles have the same point of origin upon the submentum.
totally absent. The so-called gula in larval Trichoptera is really the submentum (figs. 45, 46, 47, 48, 49, sm., Pl. 9) which lies between the two hypostomal lobes but varies much in shape and relative position. Siltala (1907) maintains that in certain Trichopterous larvae of the families Hydroptilidae and HydroPsychidae the so-called gula is the submentum, and in other families there are two parts of which the posterior one is the gula, but Belton (1934) could not find a suture and states that there is a thickened ridge in the middle of the plate and a distinction in colour. I have also examined a few types of certain families and thoroughly agree with Belton.

Crampton's attempt (1921, 1928) to define the gula by drawing a line between the bases of the maxillary cardines is responsible for many of his misinterpretations of the sclerites of the labium, although he states that the point of origin of the submento-mental muscles is very helpful in defining the gula and submentum.

Crampton's view (1921, 1928) regarding the formation of the gula and submentum in the adult by the secondary division of the primary gulamental plate of the larva is not supported by any substantial evidence. The best example brought forward by him is that the single gulamental plate of the larva of Sialis forms the gula and submentum in the adult by secondary division. I have already shown that the plate (figs. 41, 42, sm., Pl. 8) which is called the gulamentum by Crampton is the submentum alone, as revealed by the origin and insertion of submentomental muscles (22). In adult Sialis, if there is any gula at all (I did not study adult Sialis) it must have been secondarily formed by the sclerotization of the membrane behind the submentum of the larva. Secondly, the presence of single gulamental plate in a larval Pyrochroid and a distinct gula and submentum in the adult, though the dividing line between them is obliterated (i.e. in effect a single gulamental plate in the adult also), does not prove that the presence of gulamentum as a single plate is a primitive condition, since in certain beetle larvae (e.g. Tenebrio) the gula and submentum are distinct but in the adults they are fused to form a single plate. Again, in certain larvae there is no gula at all, but in their adults a well-developed
gula is formed. Thirdly, the supposed presence of a gula as a part of the broad plate, labelled _mu_, _sub_, and _gu_, in the termite embryo (vide Crampton's fig. 12, 1928) is evidently due to misinterpretation.

Walker (1932) states that the prognathous insects are more primitive than the hypognathous type, but the latter may revert to prognathism with a change of habits. The absence of a gula in hypognathous insects, which retain the primitive ventral position of the mouth appendages, is undoubtedly a generalized condition, since in typical prognathous insects having a well-developed gula the mouth appendages are directed forward. The fusion of the gula with the basal sclerite of the labium is a secondary condition.

16. **Summary.**

The principal points brought out in the foregoing discussion may be summarized as follows:

1. The points of origin of the anterior, lateral, and posterior labral muscle identify the frons in larval insects.
2. The hypopharynx is proximal to the insertion of the dorsal muscles (when present) of the prementum.
3. The direction of the cardo varies with the prognathous and hypognathous conditions of the insect head.
4. The palpifer is a secondarily demarcated portion of the stipes (Börner and Snodgrass), and cannot be a definite segment of the mouth-part limb, since no muscles take their origin from or are inserted upon it.
5. The lacinia can be recognized by the stipital and cranial flexors, and the galea by the stipital flexor only.
6. The cranial flexor of the lacinia is always retained and is a very important muscle in identifying the single maxillary lobe when one of the two is absent.
7. The origin of the flexors of the lacinia and galea upon the stipes shows that the lobes belong to the stipes.
8. The basal segment of the maxillary palp is often misinterpreted as the palpifer owing to its partial or complete fusion with the basal part of the galea, but it can be definitely identified by the insertion of the palpal muscles upon its base.
9. The premental sclerotization may form two lateral sclerites, but it is never subdivided into a proximal and a distal sclerite.

10. The mentum represents the united cardines of a pair of maxilla-like appendages.

11. The submentum is a derivative of the sternum of the labial segment.

12. The fusion of the submentum and mentum to form a single postmental sclerite is a secondary condition.

13. The sternal muscles of the labial appendages are represented by the premental muscles having their primary origin upon the submentum, and also by the submentomental muscles.

14. With the prognathous condition of the insect head the gula is developed from the cervical membrane.

15. The prognathous insects having a well-developed gula are more specialized than the hypognathous insects in which the gula is either reduced or absent.

16. The larval insects could be classified by the musculature of the mouth-parts, since each group has its characteristic musculature.

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EXPLANATION OF PLATES 1-12.

ABBREVIATIONS.

a., antenna; adfr., adfrons; b., basal segment of the palpus; bm., basimaxillary membrane; c., condyle; cl., clypeus; dc., disticaldo; eph., epipharynx; el., endite; fgl., flexor of the glossa; fgpl., flexor of the paraglossa; fr., frons; frcl., frontoclypeus; g., ginglymus; ga., galea; gc., gena; gl., glossa; gm., gular suture; gu., gula; gum., gular muscles; hcl., suspensoria; hph., hypopharynx; hst., hypostoma; hst.b., hypostomal bridge; in., incisor area; i., accessory lobe; lc., lacinia; li., ligula; lm., labrum; lp., labial palpus; md., mandible; mdc., mandibular cavity; mgs., midgenal suture; m., molar area; mp., maxillary palpus; mpmt., maxillary papal muscles; ms., basimaxillary selerite; p., cardo process; pc., proxicardo; pcl., postclypeus; pf., palpifer; pg., palpgl.; pgpl., paraglossa; pgu., paragula; pl., plate formed by the fusion of the mentum and prementum; pmt., postmentum; pr., prosthca; prm., prementum; pt., posterior tentorial pit; pt.', position of the posterior tentorial pit; sld., salivary duct; sm., submentum; st., stipes; t., torna; ta., tentorial arm; th., tentorial bridge; 2, anterior labral muscles; 3, lateral labral muscles; 4, posterior labral muscles; 5, hypopharyngeal muscles; 6, adductor muscle of the mandible; 7, adductor muscle of the mandible; 8, promotor of the cardo; 9, adductors of the cardo; 10, adductors of the stipes; 11, retractor of the stipes; 12, cranial flexor of the lacinia; 13, stipital flexor of the lacinia; 14, stipital flexor of the galea; 15, levator of the palpus; 16,