NEURO-MUSCULAR STUDY OF THE MOUTH-PARTS OF *COCCINELLA SEPTEMPUNCTATA*, WITH A COMPARISON OF THE MOUTH-PARTS IN CARNIVOROUS AND HERBIVOROUS COCCINELLIDS.

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(Plate VI.)

Contents.

Introduction.

Smith (1893) was the first to compare the mouth-parts in carnivorous and herbivorous Coccinellids. He was curious to know just what, if any, differences in the mouth-structures accompanied this divergence in habit, and dissected out the parts " in *Coccinella 9-notata* and *Epilachna borealis*" He gave a very brief description of the mouth-parts in these two species and concluded by saying, " I have made no detailed comparison between the parts preferring to let the figures speak for themselves but it gives an indication of differences *remaining to be studied*[1] and contradicts a generalisation which I had been inclined to make that compound mandibles would be rarely found in predaceous forms" It is surprising that this suggestive remark of Smith did not prompt any worker during the last half a century to take up a detailed investigation of this subject. I took up this suggestion of Smith and have already obtained interesting results by a study of the alimentary canals of these beetles (Pradhan, 1937) and have compared their mouth-parts in this paper.

Coccinella septempunctata was the first form to be studied both on account of its economic importance and its abundance at the time, when the studies began.

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[1] The italics are mine.

The first important result in the study of the mouth-parts of this species was the discovery of well-developed labial glands, a short note on which has already been published (Pradhan, 1937). Encouraged by this result I worked out all the structures associated with the mouth-parts, *i.e.*, muscles, nerves and glands. The present paper embodies the results of my studies of the neuro-muscular system of the mouth-parts, the work on glands having been incorporated in a separate paper on account of their special importance.

The studies incorporated herein have been carried out under the direct guidance and supervision of Prof. K. N. Bahl. His helpful criticism throughout, painstaking correction of manuscripts, and in short his constant watchful interest in the progress of this work have been indispensable for these investigations. It has also been my privilege to receive valuable instructions, criticism and help from Dr. H. S. Pruthi, Imperial Entomologist to the Government of India. I am greatly indebted to Mr. M. L. Bhatia, University Lecturer in Zoology, who has always been ungrudgingly ready to help me in various ways.

My appreciative thanks are due to the University of Lucknow for encouragement in the form of a research fellowship during the course of these investigations.

MATERIAL AND TECHNIQUE.

The insects used during these studies were either brought fresh from the fields or reared in the laboratory, the species which were kept in the laboratory for fairly long periods being *E. indica*, *E. vingintioctopunctata*, *C. septempunctata*, and *Chilomenes sexmaculata*. The former two of these species were fed on the solanaceous and cucurbitaceous leaves while the latter two flourished well on every available species of aphids.

The points worthy of mention in the technique employed during these studies are as follows :—

Free-hand sections.—The strong chitin of the head-capsule of these beetles offers almost insurmountable difficulties in getting microtome sections. In order to get over this difficulty I began trying to cut free-hand sections of the ordinary paraffin blocks which were prepared exactly as if they were to be sectioned with a microtome. After a little practice I could get fairly good sections for anatomical studies. Further treatment of these sections was as in the case of microtome sections, although sometimes they were not fixed to the slide but treated further in a watch glass with much advantage. With these modifications the study of the internal structure of the hard head of these beetles became fairly easy.

Bleaching of chitin.—Strongly sclerotised and densely pigmented structures like the mandibles ordinarily do not show any of their internal structures. In order to examine the interior of such structures I have been bleaching the whole head of these beetles in Hydrogen peroxide. By this treatment the opaque chitin becomes almost transparent and the soft structures inside not only remain absolutely undamaged but begin to take specially brilliant stain with Borax carmine.

Dissection of muscles and nerves.—For the dissection of muscles and nerves of the mouth-parts I have used specimens which have been kept in 90 per cent. alcohol for some months. These specimens become specially suitable for dissection after soaking in water for 12–24 hours or more.

MOUTH-PARTS OF *COCCINELLA SEPTEMPUNCTATA*.

The mouth-parts of *Coccinella septempunctata* include as usual: (1) an unpaired *labrum-epipharynx,* (2) a pair of *mandibles,* (3) a pair of *maxillae,* (4) an unpaired *labium,* and (5) an unpaired *hypopharynx.*

Labrum-epipharynx.—As in other generalised insects, the labrum-epipharynx in *C. septempunctata* forms the anterior or the upper lip of the extra-oral cavity. It is transversely elongate as shown in Plate VI, figure 1 ; when cleared in KOH solution it looks like a hollow bag, continuous with the general haemocoel ; its anterior or upper flap is comparatively much more chitinised and forms the labrum proper (*lbr.*), and is connected above with the clypeus ; the posterior or the lower flap is quite membranous and forms the epipharynx which is continuous with the roof of the fore-gut. At the junction of the epipharynx with the fore-gut there is, on either side, a chitinised hook-shaped structure called the *torma.* The labrum is densely fenestrated, the fenestrae (not shown) being distributed in irregular groups some of which lie at the bases of the long bristles. The bases of the bristles are comparatively less chitinised and appear like large fenestrae. The epipharynx, on the other hand, is comparatively smooth, there being only a few bristles along its anterior border and only a few about the middle of its surface.

Mandibles.—These are, as usual, the strongest of the mouth-parts (Pl. VI, figs. 2 and 3). Each mandible is strongly chitinised and is hollow, with a more or less triangular basal part and a bifid hook-shaped pointed tip. One angle of the basal part is directed inwards and is situated adjacent to the oral orifice, while the other two point outwards, each of them bearing a condyle for articulation with the head-capsule. The posterior or the ventral of these two condyles (*co.*) is much stronger and larger and is much more chitinised than the anterior or dorsal condyle. A little *distal* to the inner angle of the base there are two pointed teeth (*b. t.*), of which the antero-dorsal is distinctly larger than the postero-ventral. Arising a little distally to the postero-ventral tooth is the *prostheca* (*prs.*), a very small and frail chitinous structure fringed mesially with minute bristles. When examined in refracted light, the mandibles show innumerable minute pores on their thick chitinous surface but there are no pores on the teeth, condyles, the rim of the basal opening and the prostheca. A few bristles arise distally to the outer angles of the basal part and there are also a few on the inner angle of the base proximally to the basal teeth, where the chitin is rather membranous. There are two chitinised tendons (*md. abd.* and *md. add.*) associated with the mandibles for the attachment of the muscles ; of these, the mesial one arises from the inner angle of the basal part, while the outer one arises between the two condyles. Thus the two condyles form the fulcrum-line and the two tendons represent the points of application of forces in a lever-like arrangement. It is thus clear that the mesial arm of the lever is extremely long, while the outer one is extremely small.

Maxillae.—The maxillae are (Pl. VI, figs. 4 and 5) too complicated in structure for a final interpretation of their parts from a study of their chitinous structures alone. They are, therefore, described here as they appear in a cleared specimen.

The maxilla generally consists of the cardo (*ca.*), the stipes (*st.*), the lacinia (*lc.*), the galea (*ga.*), and the palpus. The cardo (*ca.*), in this species as seen from inside, *i.e.*, antero-dorsally, looks like a deep cup-like structure lodged like a condyle into a shallow external depression on either side of the labium (*vide infra*). The proximal rim of the cardo bears three pointed apodemes projecting into the head-capsule; two of them are directed mesially while the third which is the longest is directed outwards. The two mesial apodemes are situated more or less dorso-ventrally to each other. These apodemes provide surfaces for the attachment of muscles. Distally the rim of the cardo is rather low and is connected with the stipital portion of the maxilla.

The stipital portion forms a hollow, drum-shaped structure which opens proximally into the head capsule, the opening lying in common with that of the cardo; distally the stipital portion is continued into the two lobes of the maxilla. The stipes consists of three separate sclerotised pieces, namely, dorso-lateral (*d.l.*), ventro-lateral (*v.l.*) and ventro-mesial (*sg.*).

From the dorso-mesial side of the stipes arises the lacinia which is hollow and sabre-shaped; its distal portion is fringed mesially with long bristles. Only the dorsal wall of the lacinia is well sclerotised and forms the lacinia proper.

The galea arises from the distal margin of the stipes ventrally to the lacinia, and consists of two segments; the proximal segment is small and tubular and appears neck-like as compared with the bigger head-like distal segment bearing long bristles.

The palpus arises from the distal margin of the stipes at the level of the galea. It consists of four segments which become wider and wider towards the distal end, the distalmost segment forming a big triangle, only one angle of which articulates with the penultimate segment.

Almost the whole of the body of maxilla is covered with bristles while the pores are rather rare.

Labium.—The labium (Pl. VI, figs. 6 and 7) is very much simplified. The pre-labium is a hollow, more or less triangular structure with a pair of palpi, there being no separate glossae and para-glossae. In a cleared specimen, one can sometimes distinguish a faint suture (not shown) on the ventral chitinised flap of the pre-labium running obliquely and just mesially to the origin of each palpus, thus demarcating the median pre-mentum from the lateral palpiger. The dorsal (inner) flap of the pre-labium is quite membranous and spreads out like a cushion to form the ventral (posterior) lip of the extra-oral cavity. This lip, which is the only representative of the ligula, is furnished with very minute bristles and pores. Proximally the ventral (outer) chitinised flap is continued dorsalwards into a pair of curved chitinous processes which meet dorsally in the middle line. Each palpus is three-jointed, the proximal joint being the smallest.

The post-labium is separated from the pre-labium by a wide membranous area which allows considerable flexion of the pre-labium upwards. The post-labium consists of two chitinised plates: (1) the proximal sub-mentum, and (2) the distal mentum. The sub-mentum is rigidly fixed to the median sclerotised plate extending between it and the foramen magnum ; each of its lateral sides forms part of the cavity which receives the cardo of the maxilla. The mentum is only slightly moveable on the sub-mentum ; its sides are curved upwards and the curved portions bend towards the median line and are then continued into the skeleton of the hypopharynx.

Hypopharynx.—The hypopharynx (Pl. VI, fig. 7) is a flat membranous fold of the dorsal flap of the post-labial region supported by a set of strong sclerites. The fold begins just proximally to the pre-labium and extends distally almost up to the middle of that structure. The skeleton of the hypopharynx consists of a pair of basal bars on the floor and a fork-shaped suspensorium in the roof of the hypopharynx. Distally each bar almost meets an arm of the fork and proximally the arms of the suspensorial fork are continued beneath the buccal cavity where they converge to form a small median rod. Ventrally the fork is connected through vertical chitinisations with the mentum, while dorsally it is connected with a pair of apophyses (*ap.*) which arise near the dorsal articulation of the mandible and lie along the lateral walls of the buccal cavity and the pharynx. The proximal ends of these basal bars lie within small curvatures of the vertical chitinisations between the suspensorial fork and the mentum.

MUSCULATURE OF THE MOUTH-PARTS.

Recent studies of Snodgrass (1935) have considerably enhanced the importance of musculature in determining the homology of the sclerotised parts, although Imms (1931) has given a warning that "too exclusive reliance upon this one criterion is undesirable" The study of the musculature is also helpful in understanding the functional significance of the various sclerites.

The musculature of the mouth-parts may be described under two heads, namely (1) the *intrinsic muscles*, and (2) the *extrinsic muscles.*

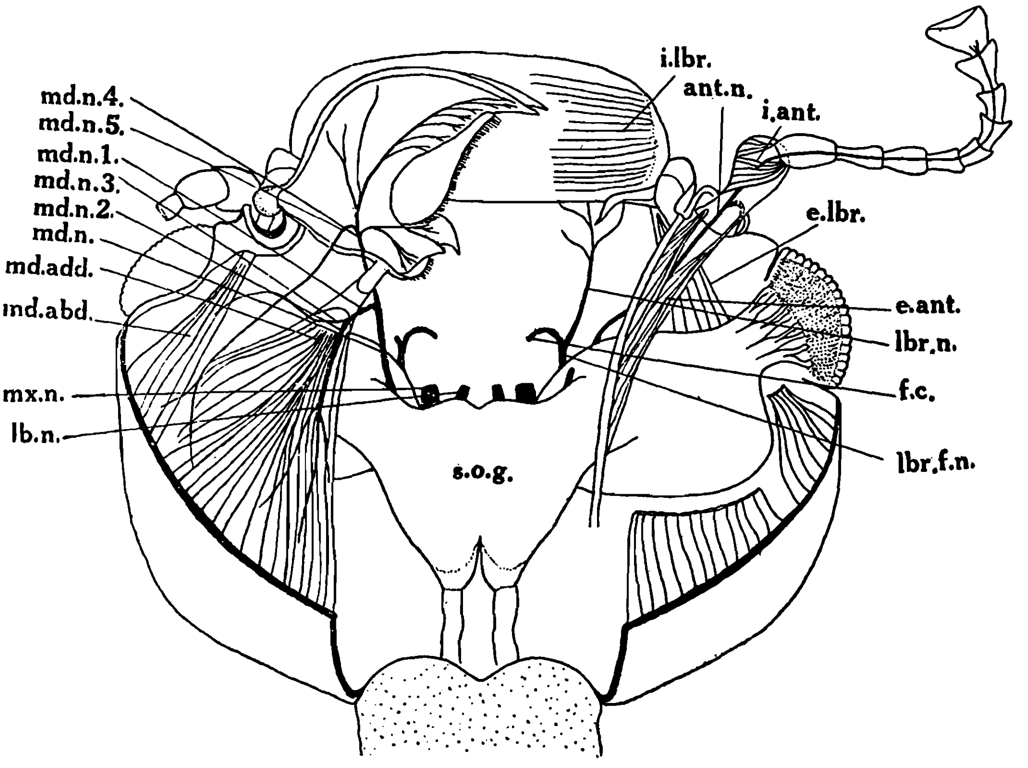
MUSCLES OF THE LABRUM.

The intrinsic labral muscles.—The intrinsic musculature of the labrum consists of two sets of fibres :—

(*a*) The first set of muscles, named as *Compressores labri* by Snodgrass, consists of small thin fibres running across and between the anterior and posterior walls of the labrum as sketched by Snodgrass in *Gryllus* or as described by Das (1937) in insect larvae in general. These muscles are so small that their contraction can hardly be effective in any way except in reducing the thickness of the labrum.

(*b*) The second set of muscles (text-fig. 1, *i, lbr.*) consists of fairly long fibres running almost parallel to the plane of the labrum. They arise from the epipharyngeal membrane about half the way between the median line and the lateral margin, and are inserted close to the lateral margin of the anterior sclerotised plate of the labrum. The contraction of these muscles brings about a curvature of the labrum inwards, thus keeping the *mandibles* steady while grasping the prey.

The extrinsic labral muscles.—The extrinsic musculature of the labrum (text-fig. 1, *e.lbr.*) consists of only a single pair of muscles. They originate from the frons and are inserted on the basal angles of the anterior sclerotised wall of the labrum. The contraction of these muscles is capable of effecting (1) an outward flexion, and (2) a lateral movement of the labrum, according as both the muscles of the pair contract simultaneously or each of them separately. The insertion of these muscles does not conform to Das's generalisation (1937) that the lateral muscles are always inserted on the tormae.



TEXT-FIG. 1.—Muscles and nerves of the mandible and labrum as seen from below after removing the labium and the maxillae (reconstructed from dissections and whole-mounts).

ant. n. antennal nerve; *e. ant.* extrinsic antennal muscles; *e. lbr.* extrinsic labral muscle; *f. c.* frontal connective; *i. ant.* intrinsic antennal muscles; *i. lbr.* intrinsic labral muscles; *lb. n.* labial nerve; *lbr. f. n.* labro-frontal nerve; *lbr. n.* labral nerve; *md. abd.* mandibular abductor muscle; *md. add.* mandibular adductor muscle; *md. n.* and *md. n. 1-5.* mandibular nerve and its branches; *mx. n.* maxillary nerve; *s. o. g.* sub-oesophageal ganglion.

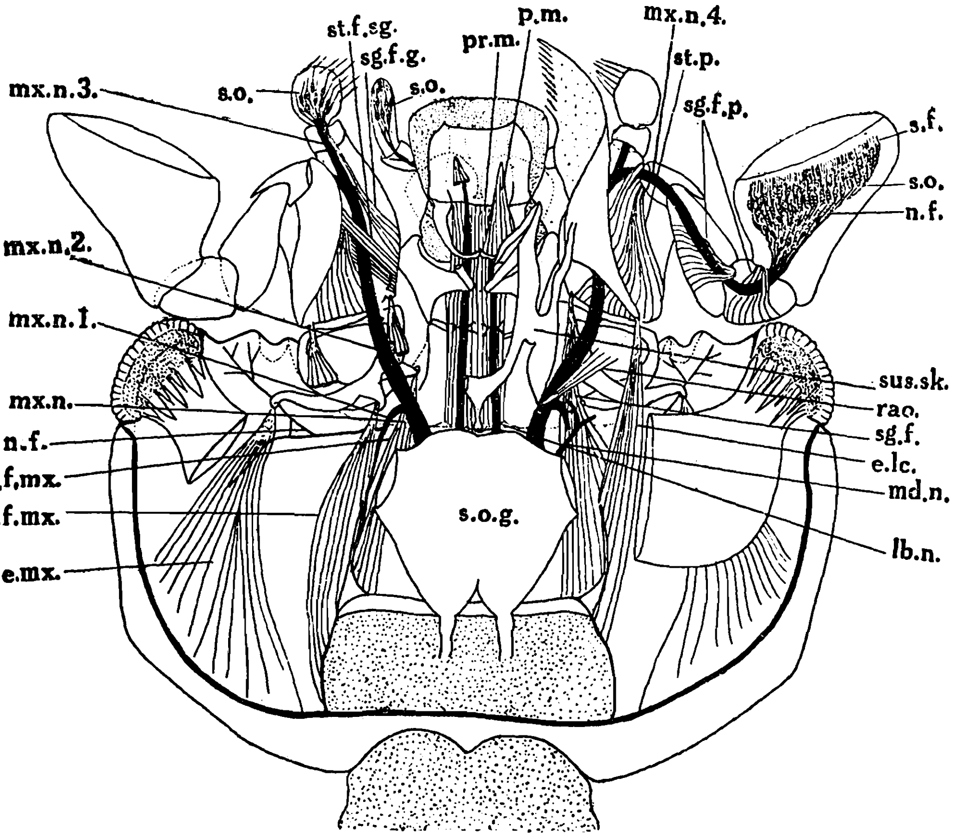
MUSCLES OF THE MANDIBLE.

There are no *intrinsic muscles* in the mandibles (text-fig. 1).

The extrinsic muscles of the mandible.—These consist of a strong adductor and a comparatively small abductor muscle. The fibres of the adductor muscle (*md. add.*) take their origin from the postero-lateral walls of the cranium and converge to form a chitinous cone-shaped tendon which is inserted on the inner angle of the basal triangle of the mandible. The origin of the abductor muscle (*md. abd.*) is antero-lateral to that of the adductor muscle and its insertion is on the outer side of the basal triangle, *i.e.*, between the condyles of the mandible, just a little outside the hinge-line. The distance of the abductor from the hinge-line is negligible in comparison with the distance between the adductor muscle and the hinge-line. Thus the adductor muscles are infinitely more effective than the abductor muscle.

MUSCLES OF THE MAXILLA.

(*a*) *The extrinsic muscles of the maxilla.*—There are five extrinsic muscles (text-fig. 2) associated with each maxilla ; three of these are inserted on the cardo and two on the stipital portion. The muscles of the cardo are not inserted into the interior of the cardo as is the case in Orthoptera and in the majority of other insects, but on long sclerotised hook-shaped apodemes, the direction and length of the apodeme



TEXT-FIG. 2.—Muscles and nerves of the maxillae and labium as seen from above after removing the dorsal wall of the cranium, labrum, mandible, etc.

d. f. mx. dorsal flexor of maxilla ; *e. lc.* extensor of lacinia ; *e. mx.* extensor of maxilla ; *lb. n.* labial nerve ; *md. n.* mandibular nerve ; *mx. n.* and *mx. n. 1-4*, maxillary nerve and its branches ; *n. f.* nerve ; fibre ; *p. m.* palpal muscle of the labium ; *pr. m.* premental muscle ; *rao.* retractores angulorum oris ; *s. f.* sense-fibre ; *s. o.* receptor organ ; *s. o. g.* sub-oesophageal ganglion ; *sg. f. g.* sub-galear flexor of galea ; *sg. f. p.* segmental flexor muscles of the palpus ; *st. f. sg.* stipital flexor of sub-galea ; *st. p.* stipital muscle of the palpus ; *sus. sk.* suspensorial skeleton ; *v. f. mx.* ventral flexor of maxilla.

determining whether a muscle acts as an extensor or as a flexor. These muscles may be described as :—

1. *Dorsal* (*anterior*) *flexor of the maxilla.*—This muscle (*d.f.mx.*) takes its origin partly from the lateral rim of the foramen magnum, and partly from the posterior arm of the tentorium, and is inserted on the dorsal (anterior) apodeme of the cardo.

2. *Ventral* (*posterior*) *flexor of the maxilla.*—This muscle (*v.f.mx.*) also arises from the posterior arm of the tentorium and is inserted on the ventral apodeme of the cardo. It is situated mesially to the dorsal flexor.

3. *Extensor of the maxilla.*—This muscle (*e.mx.*) arises from the lateral wall of the cranium and is inserted on the longest apodeme of the cardo which begins from a place in between the dorsal and the ventral apodemes described above and extends outwards as shown in text-figure 2.

4. *Extensor of the lacinia.*—The fibres of this muscle also take their origin partly from the posterior arm of tentorium and partly from the rim of the foramen magnum. It is inserted on a long process arising from the outer angle of the base of the lacinia. Contraction of this muscle can serve only for the deflexion of the lacinia and not for its flexion. This muscle has not been named as an extensor before. Bauer (1910) calls this muscle as a superior flexor of the maxilla in *Dytiscus marginalis* (Coleoptera), but in his sketch, he does not show any definite proximal boundary of the lacinia and has probably not appreciated the distinct insertion of the muscle on the lacinia. Snodgrass (1935) does not mention any muscle with an extensor function associated with lacinia. He describes only a flexor muscle of the lacinia inserted on the mesial angle of the base of the lacinia. No such flexor muscle is present in *Coccinella septempunctata*, nor has any such muscle been described by Bauer in *Dytiscus*. Das (1937) describes only flexor (cranial and stipital) muscles of the lacinia and defines these muscles, like Snodgrass, as those having their insertion on the inner base of the lacinia, although in his sketches of *Rhagium*, *Tenebroides* (fig. 28)[1], and *Agriotes* (fig. 31), all three belonging to the order Coleoptera, he definitely shows that these muscles are inserted on the outer edges of the base of the lacinia. It appears, therefore, that the point of insertion of the lacinial muscle is not constant and that the muscle serves as a flexor or an extensor according as the insertion is near the inner or near the outer angle of the lacinia.

5. *Flexor of the sub-galea.*—This muscle (*sg.f.*), arises from the ventrolateral rim of the foramen magnum and is inserted on the proximal corner of the sub-galea, *i.e.*, the ventro-mesial sclerite of the stipital region. Neither Snodgrass nor Das describes any muscle of this designation. Bauer (1910) describes a similar muscle under the name of anterior flexor of maxilla but he has studied this muscle as imperfectly as the extensor of lacinia described above. As already described, the anterior (dorsal) flexor of maxilla is inserted on the apodeme of the cardo in Coccinellid beetles.

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[1] These figures refer to Das's diagrams.

(*b*) *The intrinsic muscles of the maxilla.*—The intrinsic musculature consists of :—

1. Sub-galear flexor of galea (*sg.f.g.*).
2. Stipital flexor of sub-galea (*st.f.sg.*).
3. Stipital muscle of palpus (*st.p.*).
4. Proximal segmental flexor of the palpus (*sg.f.p.*).
5. Distal segmental flexor of palpus (*sg.f.p.*).

1. *Sub-galear flexor of the galea.*—This muscle originates from the mesial margin of the sub-galea and runs distally to be inserted on to the base of the distal segment of the galea. This muscle has, in every case, been described to take its origin from the stipes proper, although Das (1937) has, most probably through inadvertence, wrongly named it as the cranial flexor of galea. As the sub-galea is distinctly separate from the stipes proper in Coccinellids, I have named the muscle as *sub-galear flexor of galea.*

2. *Stipital flexor of the sub-galea.*—This muscle takes its origin from two separate places, *i.e.*, along the small lengths of the mesial margins of both the anterior (dorsal) and posterior (ventral) walls of the stipes. The two sheets of muscle-fibres from the two margins converge towards each other and are inserted along the mesial margin of the sub-galea. A muscle of this nature has not been described before. It may be suspected that it might be the stipital flexor of the lacinia which has been mistaken for the flexor of sub-galea but I have definitely ascertained by repeated dissections and serial sections that the insertion is on the sub-galea and not on the lacinia which lies near by.

No muscular connection between the sub-galea and the stipes has been recorded before and the sub-galea has therefore been regarded as a secondary differentiation from the stipes. Snodgrass writes, " in some insects the area of the stipes supporting the galea is differentiated as a distinct lobe called the sub-galea, but the base of the true galea is to be determined by the point of attachment of its muscle." The presence of the stipital flexor of the sub-galea in these insects is very significant, as it renders the homology of the sub-galea an open question. If the musculature is at all a reliable criterion, the sub-galea should be regarded as a separate entity from the stipes.

3. *Stipital muscle of the maxillary palpus.*—This is a fairly strong muscle with its insertion along the proximal rim of the basal segment of the palpus. This muscle combines in itself both the levator and the depressor muscles described in other insects, the distinction between the two being difficult to make out, both at the origin as well as at the insertion. There is no doubt that the various movements of the palpus are possible by the contraction of some fibres and the relaxation of others.

4. *Proximal segmental flexor of the palpus.*—The fibres of this muscle arise from the second segment of the palpus and converge to be inserted on the third segment.

5. *Distal segmental flexor of the palpus.*—This muscle is an exact replica of the proximal segmental flexor, originating from the third segment and inserted on the fourth, *i.e.*, the last segment of the palpus.

MUSCLES OF THE LABIUM.

There are no *extrinsic muscles* in the labium of these insects. The *intrinsic musculature* consists of:—

1. Muscles of the pre-mentum (*pr.m.*).
2. Muscles of the palpi (*p.m.*).

1. *The muscle of the pre-mentum.*—These muscles originate from a median pointed fragma on the base of the sub-mentum and are inserted along the ventral rim of the base of the pre-mentum. Careful observation reveals a grouping of these fibres into four sets lying at the same level. This grouping probably represents two pairs of muscles which have been named by Das as median and lateral muscles of the pre-mentum in insect larvae. The contraction of these muscles serves to retract the pre-mentum, the retraction being made possible on account of the wide membrane between the pre-mentum and the mentum.

2. *The muscles of the palpi.*—These muscles originate from the proximal sclerotised rods of the pre-mentum and run above the pre-mental muscles to be inserted on the bases of the palpi. The action of these muscles like that of the palpal muscles of the maxillae is to give various movements to the palpi.

MUSCLES OF THE HYPOPHARYNX.

The hypopharynx proper has no muscles but mention may be made of a pair of muscles (text-fig. 2, *rao.*) which arise from the dorsal wall of the cranium and are inserted on what has been described by Snodgrass as the oral branches of the suspensorial sclerites of the hypopharynx. A mention of these muscles at this place is justified on the ground that the contraction of these muscles raises the floor not only of the buccal cavity (post-oral) but also of the cibarium (pre-oral).

THE NERVE-SUPPLY OF THE MOUTH-PARTS.

A survey of the available literature shows that the nerve-supply of the insect mouth-parts has not been adequately studied. So far little effort has been made to homologise or even to name the various branches of the appendicular nerves of the insect head. Our knowledge of insect neurology being so deficient, hardly anything can be stated at present about the value of nerve-supply in determining the morphological relations of the mouth-parts. But this much is clear that much study is needed to fill up this gap in our knowledge of insect anatomy.

All the mouth-parts, except the labrum, receive their nerve-supply from the infra-oesophageal ganglion, the various nerves supplying the mouth-parts being (1) *labral nerve,* (2) *mandibular nerve,* (3) *maxillary nerve,* and (4) *labial nerve,* all of which are paired.

1. *Labral nerve.*—This nerve arises in common with the frontal nerve-connective from the tritocerebrum, the common stem being known as the labro-frontal nerve (text-fig. 1, *lbr.f.*). The labro-frontal nerve soon divides into its two components. The labral nerve, as shown in

text-fig. 1, gives off various minute branches to the roof of the cibarium before entering the labrum proper where it branches profusely.

2. *Mandibular nerve.*—The mandibular nerve (text-fig. 1, *md.n.*) arises from the infra-oesophageal ganglion near the circum-oesophageal connectives. About half-way between the brain and the mandible, the nerve gives off a branch the *ramus muscularis proximalis* (*md.n.1*), to the mandibular muscles. This branch of the mandibular nerve soon divides into two sub-branches, one of which (*md.n.2*) innervates the adductor and the other (*md.n.3*) the abductor muscle of the mandible. After giving off this branch, the mandibular nerve passes over the tendon of the adductor muscle and enters the cavity of the mandible wherein it divides into several branches innervating the entire body of the mandible (*md.n.4*). There is also a second branch supplying the muscles (*md.n.5*) which may be called the *ramus muscularis distalis.* It arises from the mandibular nerve after the latter enters the body of the mandible. It comes out of the mandible and reaches almost the origin of the mandibular muscles where it divides to innervate both the adductor and abductor muscles.

3. *Maxillary nerve.*—The maxillary nerve is the stoutest nerve (text-fig. 2, *mx.n.*) in the head-capsule and arises antero-laterally from the infra-oesophageal ganglion. At a little distance from its origin, it gives off a comparatively slender branch, the *ramus muscularis* (*mx.n.1*). This branch soon gives off a long but fine sub-branch to the extensor of the maxilla and then passes through the muscle-complex arising from the tentorium and the rim of the foramen magnum (*i.e.*, the dorsal and ventral flexors of the maxillae, the extensor of lacinia and the flexor of sub-galea). The branch to the extensor of the maxilla also gives minute branches to the glands in the region of the eye and the antenna as shown in text-fig. 2. There is a triangle formed by nerves in this region (*n.t.*). After giving off the ramus muscularis, the maxillary nerve (*mx.n.2*), enters the cavity of the maxilla as the most prominent nerve, passes through the stipital flexor of the sub-galea and reaches the level of the distal end of the stipital region. Here it gives off a branch to the galea (*mx.n.3*) and turns away into the maxillary palpus wherein (*mx.n.4*) it passes on through various muscles till it reaches the last segment of the palpus where its fibres spread out to form a prominent cone-shaped receptor organ (*s.o.*). The branch entering the galea also ends into a number of sense-cells situated in the distal segment of the galea. The maxillary nerve, during its course, gives off very minute branches to the various muscles within the maxilla through which it passes.

4. *Labial nerve.*—The labial nerve arises (text-fig. 2, *l.b.n.*) from the infra-oesophageal ganglion mesially to the maxillary nerve and passes over and along the labial muscles supplying them with very minute branches at the level of the mentum. On reaching the base of the labial palp, the labial nerve, after giving off very minute branches to the ligula, enters the labial palp and continues to its last segment to supply the sense-cells lodged therein.

Shortly after its origin, the labial nerve also gives off a small branch to the labial glands.

RECEPTOR ORGANS ON THE MOUTH-PARTS.

As referred to above, the chief centres at which the receptor-cells have accumulated on the mouth-parts are the distalmost segments of (1) the maxillary palpus, (2) the galea, and (3) the labial palpus (text-fig. 2).

Morphologically the sense-cells at all these centres are alike. They are fusiform in shape, and are supplied at their proximal ends with fine nerve-fibres (*n.f.*) while their distal ends are continued into still finer sensory fibres (*s.f.*). The receptor-cells of the maxillary palpus are, however, smaller than those of the galea. The receptor-cells in the maxillary palpus, in fact, are so small and so compactly crowded in spindle-shaped groups that their separate identity is made out with difficulty. Next to the eyes, the receptororgan of the maxillary palpus, is by far the most highly developed receptor organ in the head of these beetles. As shown in text-figure 2, it looks like a beautiful cone-shaped bouquet filling almost the whole of the distalmost segment of the palpus.

The sense-fibres in the galea enter the bases of long fine bristles, those in the maxillary palpus end at the bases of minute hollow pegs[1] whereas those in the labial palpus the sense-fibres end on a very thin chitinous surface although there are a few minute hollow pegs also present at the extremity.

The recognition[2] of these receptor organs is important as it fills up the gap left by McIndoo (1916) in his study of olfactory organs in Coleoptera. McIndoo searched for these organs in several parts of the body of Coleoptera (including Coccinellids) but omitted the mouth-parts where the sense-organs are best developed, at least in the Coccinellidae, although he suspected their presence on these parts.

In his experiments on *Epilachna borealis* in which he tested as to which parts of the body are affected by odor stimuli; McIndoo records, " They were extremely quiet and when tested they generally moved away slowly. They often vibrated the antennae and *mouth-parts*[3] and sometimes the legs." About the reaction of the same beetles after removal of antennae, McIndoo records " When tested with odors, most of them worked the *mouth-parts* ; some moved away, a few vibrated one or more legs and some failed to respond." These observations clearly show that the mouth-parts are probably most sensitive in these beetles.

COMPARISON OF MOUTH-PARTS IN CARNIVOROUS AND HERBIVOROUS COCCINELLIDS.

Besides those of *Coccinella septempunctata,* the mouth-parts of six other species have been examined and sketched (text-figs. 3-6), two of these species are herbivorous, and four are carnivorous. This comparative study reveals the following significant differences which are probably

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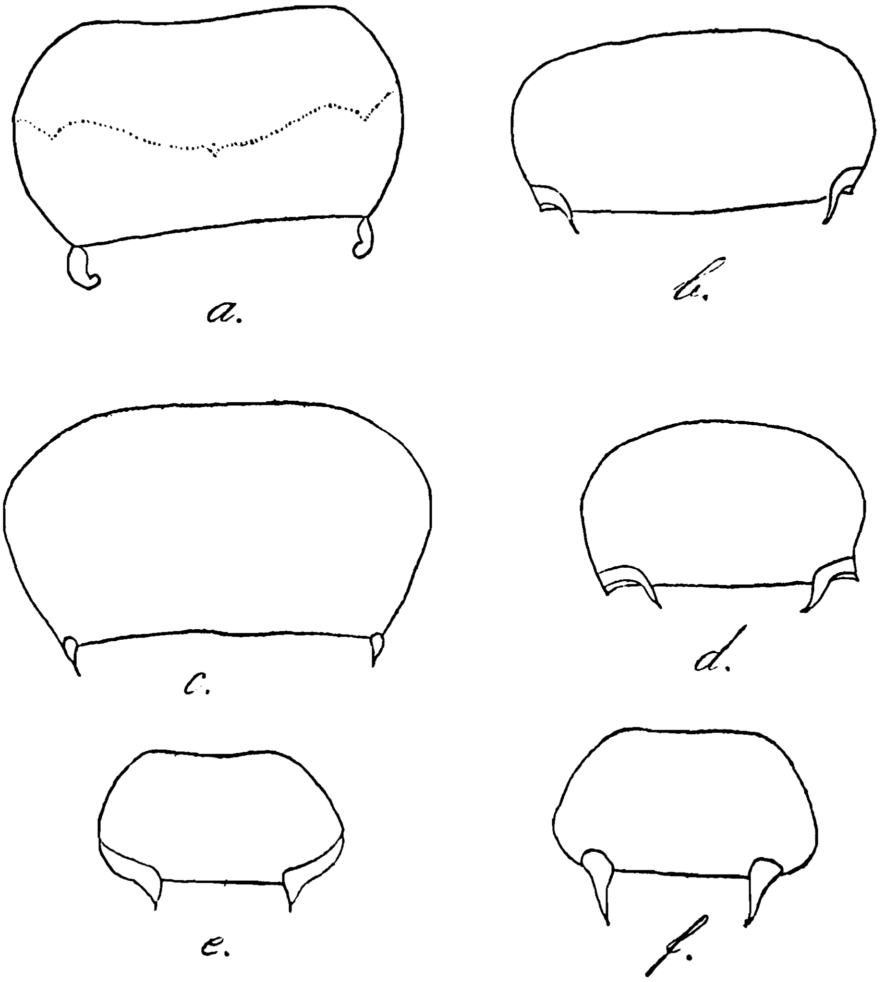
[1] These pegs are too small to be shown in the text-figure.

[2] Sense-organs have already been described on the palpi at least in *Dytiscus.*

[3] The italics are mine.

correlated with differences in feeding habits (carnivorous or herbivorous) of these beetles.

1. *Labrum.*—As text-fig. 3 brings out sufficiently the specific differences, a detailed account is hardly necessary.

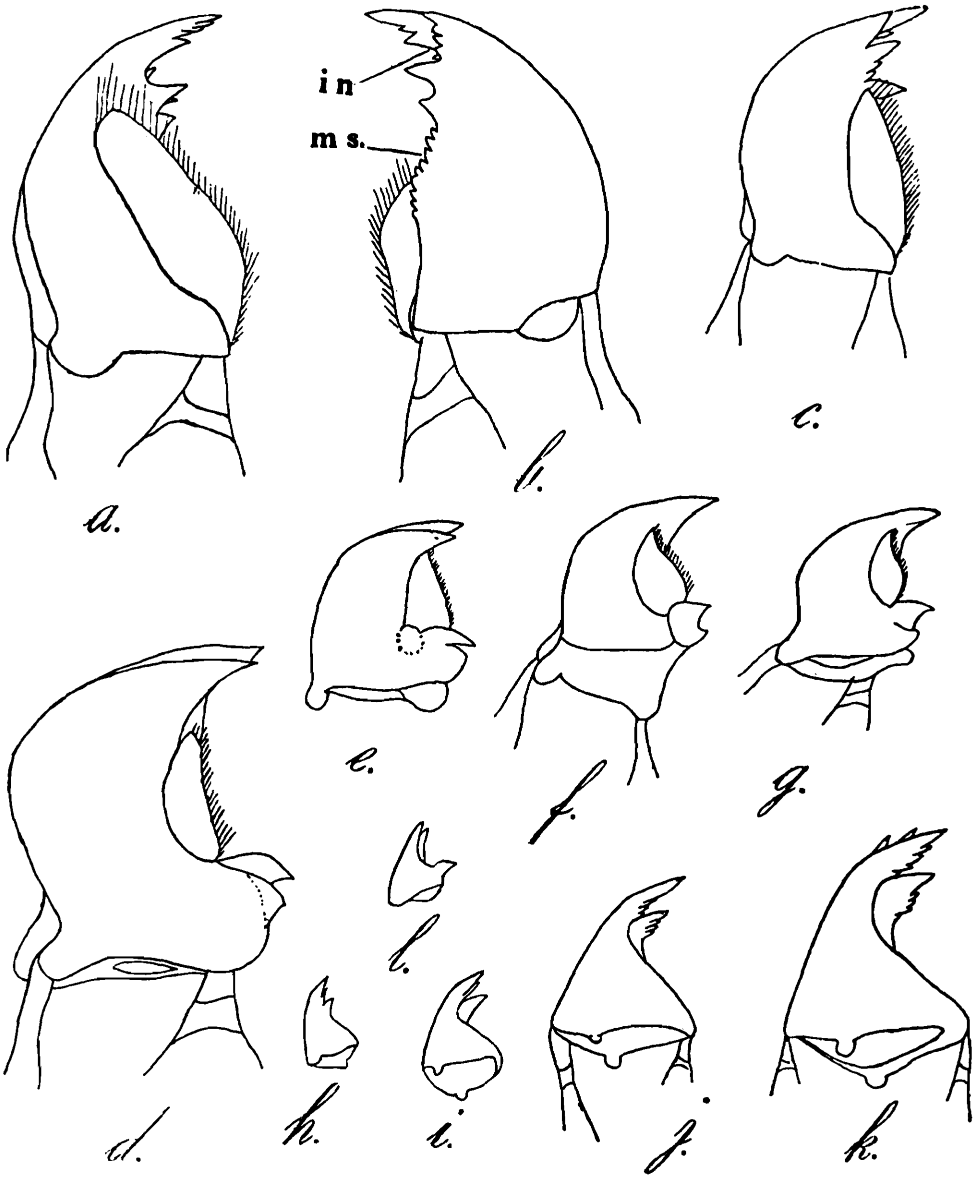


TEXT-FIG. 3.—Labrum of Coccinellids.

a. Epilachna indica; *b. E. vigintioctopunctata*; *c. Synia melanaria*; *d. Chilomenes sexmaculata*; *e. Chilocorus nigritus*; *f. Brumus suturalis.*

2. *Mandibles.*—The mandibles (text-fig. 4) show the most important and constant differences between carnivorous and herbivorous Coccinellids—differences which are probably more or less constant throughout the whole order Coleoptera. This, however, is not unexpected since mandibles are mechanically the most important of the mouth-parts. The mandibles of the herbivorous genus *Epilachna* (*E. indica* text-fig. 4, *a*, *b*), and *E. vigintioctopunctata* (text-fig. 4, *c*) are characteristically differentiated into (*a*) distal *incisor portion* (*in.*) meant for scraping the epidermis of the leaves on which these beetles feed, and (*b*) the proximal *molar area* (*m.s.*) where the scrapings are masticated. The incisor portion is provided with a large number of teeth of various sizes, whereas the molar surface is rather uniformly tuberculated with masticatory teeth. The mandibles of the carnivorous species examined are essentially similar to those of *C. septempunctata* with a strong bifid incisor portion and two pointed basal teeth, the molar area being entirely smooth, with no masticatory teeth. The mandibles of *Brumus suturalis* (text-fig.

4, *g*) and *Chilocorus nigritus* (text-fig. 4, *f*) are not even bifid at their distal extremity. The mandibles of the larval stages of *E. indica* (text-figs. 4, *h-k*) and of the first instar larva of *Chilomenes sexmaculata* (text-fig. 4, *l*) have also been examined. As shown in the sketches, the mandibles of the earlier instars of *E. indica* have simple incisor portions showing greater resemblance to those of carnivorous Coccinellids. This fact combined with the observation that the first instar larvae of *E. indica* show a carnivorous tendency in eating up the unhatched eggs of their own parents[1], throws some light on the ancestry of the herbivorous Coccinellids which have probably descended from carnivorous forms.



TEXT-FIG. 4.—Mandibles of Coccinellids.

a. Epilachna indica (ventral or posterior view); *b. E. indica* (dorsal or anterior view; *in.* incisor portion; *m. s.* masticatory (molar) portion, *c. E. vigintioctopunctata* (ventral view); *d. Synia melanaria* (ventral view); *e. Chilomenes sexmaculata* (ventral view); *f. Chilocorus nigritus* (ventral view); *g. Brumus suturalis* (ventral view); *h. E. indica* (1st instar); *i. E. indica* (2nd instar); *j. E. indica* (3rd instar); *k. E. indica* (4th instar); *l. Chilomenes* sp. (1st instar).

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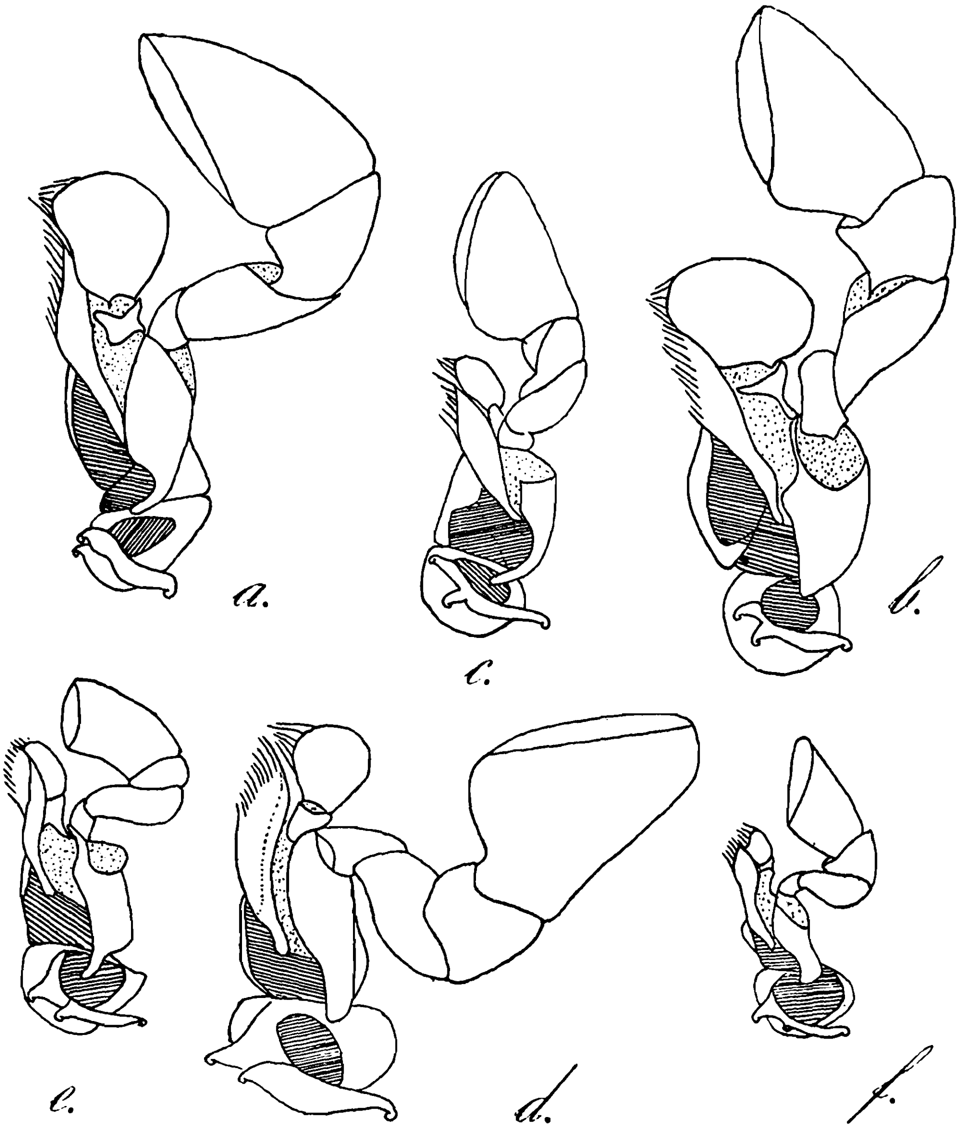
[1] Pradhan, S., *Proc. Ind. Sc. Cong.*, (1936).

Maxillae.—The chief visible difference in the chitinous structure of the maxillae (text-fig. 5) lies in the galea which is comparatively much larger in species of *Epilachna* (text-fig. 5, *a, b*) than in the carnivorous forms. The study of the nerve-supply indicates that this structure is chiefly sensory in function. It may be conjectured that as the *Epilachna* beetles remain scraping the epidermis, the galeae are in constant contact with the leaf-surface and serve, on account of their sensory nature, to guard against scraping that portion of the epidermis on which some harmful substance may be lying. Thus the galea may have become better developed in the herbivorous forms.

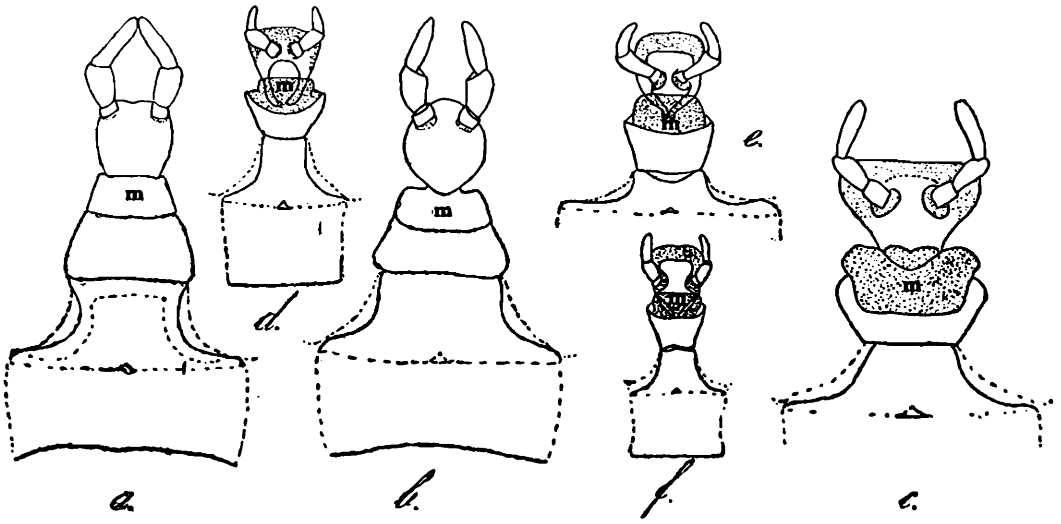


Text-fig. 5.—Maxillae of Coccinellids, (dorsal or anterior view).
a. Epilachna indica; *b. E. vigintioctopunctata*; *c. Chilomenes sexmaculata*; *d. Synia melanaria*; *e. Chilocorus nigritus*; *f. Brumus suturalis.*

Labium.—The study of the labium (text fig. 6) shows two important differences between the carnivorous and herbivorous Coccinellids :—

1. The pre-labium in carnivorous forms (text-fig. 6, *c-f*) is comparatively larger and more expanded than in the herbivorous genus *Epilachna* (text-fig. 6, *a, b*) as is clear from the diagrams. I am not able to explain this difference on the basis of their dietetic deviation.

2. The membranous connection (*m*) between the pre- and the post-labium which allows the pre-labium to be inflected upwards in carnivorous forms has become fairly strengthened in herbivorous forms in which the pre-labium is not inflected upwards. This difference is probably correlated with the mode of feeding in this way : *Epilachna* remains continuously scraping the epidermis with its mouth-parts almost at right angles to the leaf-surface while the carnivorous Coccinellids pick up their prey and suck its juice while keeping the prey raised above the surface. The pre-labium, thus, has to be often inflected upwards in carnivorous forms, a need for which seldom arises in the herbivorous *Epilachna.*



TEXT-FIG. 6.—Labium.

a. Epilachna indica ; *b. E. vigintioctopunctata* ; *c. Synia melanaria* ; *d. Chilomenes sexmaculata* ; *e. Chilocorus nigritus* ; *f. Brumus suturalis* ; *m.* membrane between mentum and sub-mentum.

SUMMARY.

This paper embodies :—

1. A description of the chitinous structures of the mouth-parts of *C. septempunctata.*
2. A description of both the extrinsic and intrinsic musculature of the mouth-parts of the same species, with the function of the muscles in each case.
3. A description of the nervous supply of the mouth-parts of the same species.
4. A comparison of the chitinous structures of the mouth-parts in seven species of Coccinellidae.
5. A short description of the sense-organs situated on the mouth-parts.

These studies have brought to light some facts of morphological importance. Thus, for example, the muscles of the designations *Extensor of Lacinia, Cranial Flexor of Sub-galea,* and *Stipital Flexor of Sub-galea* do not exist in literature, the first two being recorded but differently interpreted, while the last one not being recorded at all.

The study of nervous supply has revealed prominent aggregations of sensory cells in the labial and maxillary palpi and the galea. These sense-organs appear to be olfactory in nature. Thus, these findings fill up the gap left by McIndoo (1916) in his study of olfactory sense-organs in several parts of the body of Coleoptera. McIndoo searched for these organs in several parts of the body of Coleoptera (including Coccinellidae) but omitted to examine the mouth-parts where they are best developed in Coccinellidae at least.

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