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COMPARATIVE STUDY OF MOUTH PARTS OF REPRESENTATIVE HEMIPTERA-HOMOPTERA

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F. H. Butt

The members of the order Hemiptera, commonly known as the true bugs, and their close relatives, the members of the order Homoptera, among which are aphids, leafhoppers, and others, constitute a group of insects of great economic importance to man. Some of them cause widespread damage to vegetation through the withdrawal of heavy amounts of plant juices; others spread causative organisms of plant diseases; and some attack man and domestic animals, causing irritation and great economic loss. They all have piercing and sucking mouth parts that act as efficient hypodermic syringes. The mechanism that operates these mouth parts, the methods of penetration of plant or animal tissues, and the withdrawal of food from these tissues have long been subjects of interest to entomologists and much work has been done in those fields. This memoir is the result of comparative studies of the food pump and of the mouth parts and their muscle attachments in several representative species of the Homoptera and the Hemiptera, to determine wherein the mouth parts of the two orders are similar and wherein they differ in their methods of operation.

Tibicina septendecim (L.), the seventeen-year Cicada (Plate II, A), and the nymph of *Cephisus siccifolius* (Walker), a South American member of the family Cercopidae (Plate I, C) were used as representatives of the Homoptera. *Benacus griseus* (Say) (Plate I, A), and *Notonecta* sp. (Plate I, B), were used to represent the aquatic Hemiptera; *Oncopeltus fasciatus* (Dallas), the milkweed bug, (Plate I, E), and *Acrosternum hilare* (Say) a stinkbug (Plate I, D) represent the terrestrial plant-feeding forms.

The author is indebted to R. E. Snodgrass of the United States Bureau of Entomology and Plant Quarantine for his suggestions, which have been helpful in the conduct of the investigations leading to this memoir, and for the use of his illustration of the mandibles of the roach (Plate VIII, B).

THE HEAD

The head of Cicada is triangular in outline with eyes at the outer corners and the mouth parts suspended from the lower point. The most prominent feature of the head is a convex bulge between the compound eyes with horizontal corrugations on its surface marking the attachment of powerful muscles within (Plate II, A). This bulge is the postclypeus (Pclp). Beneath the postclypeus is the anteclypeus (Aclp) and attached to its distal margin is the small labrum (Lm) which is applied closely to the base of the labium. The labium (Lb) itself is elongate, grooved on its anterior surface to contain the bristles constituting the feeding apparatus, and suspended freely from the membrane posterior to the maxillary plates.

Bounding the lower lateral edges of the postclypeus are two plates, the lora (Lo), or mandibular plates, and laterad of these the maxillary plates (Mx) continuous with the cranial wall. They merge into the genae beneath

the eyes. The antennae are close to the epistomal sutures and project from beneath overhanging bulges mesad of the compound eyes.

The cephalic aspect of Cephisus shows the same characteristics as Cicada (Plate I, C). The clypeus is divided into the enormous postclypeus (Pclp) and distally the smaller anteclypeus (Aclp). Attached to the distal end of the anteclypeus is the small pointed labrum (Lm) covering the base of the trough in the labium (Lb). Laterad of the post- and anteclypeus on each side are the exposed loral plates (Lo) and beneath them the maxillary plates (Mx). Cephisus is included mainly to show the musculature of the labium more clearly than Cicada does.

In Notonecta the eyes are enlarged and the area between them, the clypeus, extends across the top of the head where it merges into the front (Plate I, B). There are no frontal sutures or ocelli.

The maxillary plates are partially covered by the extension of the clypeal wall of the head. Laterally two oval sclerites (Mx) of the maxillary segment are visible but the median lobes to which the maxillary protractors are attached lie below the lora adjacent to the hypopharynx. The clypeus extends to a line on the front of the head along the lower extremity of the maxilla. At this point is the clypeo-labral suture, and below it lies the labrum, a triangular flap that covers the trough and part of the basal segment of the labium.

Specializations found in the head of Benacus are likewise due to the enlargement of the eyes in adaptation to aquatic life (Plate I, A). But the clypeus is divided into postclypeus fused with the front (Pclp + Fr) and anteclypeus or tylus (Aclp). The lateral areas of the postclypeus extend downward between the eyes alongside the tylus.

The maxillary plates (Mx) are greatly altered by enlargement of the eyes and are pushed distally until they form flap-like covers for the sides of the basal segment of the labium. These flaps nearly meet in front along the median line overlapping the anteclypeus or tylus (Aclp) for a short distance. The labrum (Lm) is a long striated lobe attached to the lower extremity of the anteclypeus. It forms a cover for the bristle trough in the labium (Lb). The antennae are pushed to the caudal surface of the head where they have become embedded in cavities immediately beneath each eye. If the surface of an eye is removed the inner surface of one of these cavities appears as a dome-like protuberance (Plate IV, A, Y), just above the antennal fossa.

The heads of the milkweed bug, *Oncopeltus fasciatus*, (Plate I, E) and of *Acrosternum* (Plate I, D) are typical of the terrestrial forms of the Hemiptera. From the dorsal side of the head, the anteclypeus (Aclp) appears as a narrow, well defined median sclerite marked off from the jugum (Ju) on each side by deep clefts (Plate I, E, D). The cranium is unbroken dorsally by other sutures than these. Caudad of the anteclypeus are two ocelli, mesad of the compound eyes. Between the ocelli are the fused postclypeus and frons (Pclp + Fr).

The beak arises at the anterior point of the head (Plate VI, B) and is curved back beneath the thorax when not in use. The anteclypeus merges into the long pointed labrum, or upper lip, (Lm), which helps to hold the bristles within the trough of the beak. Below and in front of the antennal base is the maxillary plate (Mx). The suture (s) between the jugum and maxillary plate is a constant feature and is always well marked in the forms

studied. Below the maxillary plate is the narrow buccula (Buc). On the lower surface of the head extending back from the antenna is a suture (Ocs), not always distinct, which marks off the gula plate (Gu).

The hypopharynx is a median lobe protruding from the lower surface of the head between the mandibular plates, concealed by the anteclypeus and labrum in the Cicada, by the unbroken front surface of the head in Notonecta, and by the anteclypeus in other Hemiptera. The upper surface of the hypopharynx is grooved narrowly toward the tip to form the floor of the tube that carries food to the sucking pump. This groove runs into a median basin-like enlargement forming the floor of the sucking pump, which is well sclerotized and braced to withstand the suction resulting from the action of the dilator muscles of the pump. The hypopharynx (Hphy) and the floor of the food pump (Flpmp) are clearly seen when the anteclypeus is cut away in Oncopeltus (Plate VIII, I) or in Acrosternum (Plate VIII, H). A mid-sagittal section through the head of Cicada (Plate II, B) or of Cephisus (Plate III, A) shows that the food duct on the upper surface of the hypopharynx runs vertically into the pump in these insects.

THE SYRINGE AND THE HYPOPHARYNGEAL WINGS

In more generalized insects, at the point where the ventral or posterior wall of the hypopharynx (figure 1) becomes the dorsal or anterior wall of the labium, a pocket forms, called the salivarium (Slv), into which the salivary ducts empty. On its dorsal wall is inserted a pair of dorsal salivary muscles (1s), which originate either on the suspensory sclerites (Hs) of the hypopharynx or on the lateral walls of the hypopharynx when these are absent. On its ventral wall are inserted the salivary muscles of the labium (2s and 3s). In the Orthoptera the dorsal wall of the salivarium is somewhat concave (Snodgrass, 1935). In both the Homoptera and Hemiptera this concave surface is modified into a closed tube which delivers the salivary juices to the tip of the hypopharynx and from there into the salivary canal in the bristle bundle (Plate VI, C, Duct). The salivarium of the Orthoptera has become modified in the Homoptera and Hemiptera into a pump, the salivary syringe, that is equipped with a piston and valves to control the direction of flow of the salivary liquid (Plate II, B; Plate III, A; Plate VI, A, D; Syr).

The lower lateral surfaces of the hypopharynx in Homoptera and Hemiptera are extended back into the head as two divergent trough-like plates or wings (Plate IV, A, D, Hphyw; Plate V, C, Hphyw). To the under side of these the dorsal salivary muscles of the salivarium, now greatly enlarged into the dilator muscles of the syringe (Plate IV, D, dlsyr), are fastened. The salivary muscles from the labium have disappeared. Plate IV, D shows the relationship of the syringe to the backward flaring wings of the hypopharynx in Notonecta. The hypopharynx has been cut away for this figure to show the salivary pump (Syr). The posterior extremities of the wings are narrowly extended for the origin of the dilator muscles (dlsyr). In Cicada and in Cephisus the wings remain broad and flat and are united closely with the posterior tentorial arm (Plate II, F, Tnt). In Oncopeltus they show considerable modifications; they extend back into the head as in Cicada and Notonecta, but beyond the point where the maxillary lever is located they become membranous, are deeply folded, and are attached to the ventral head

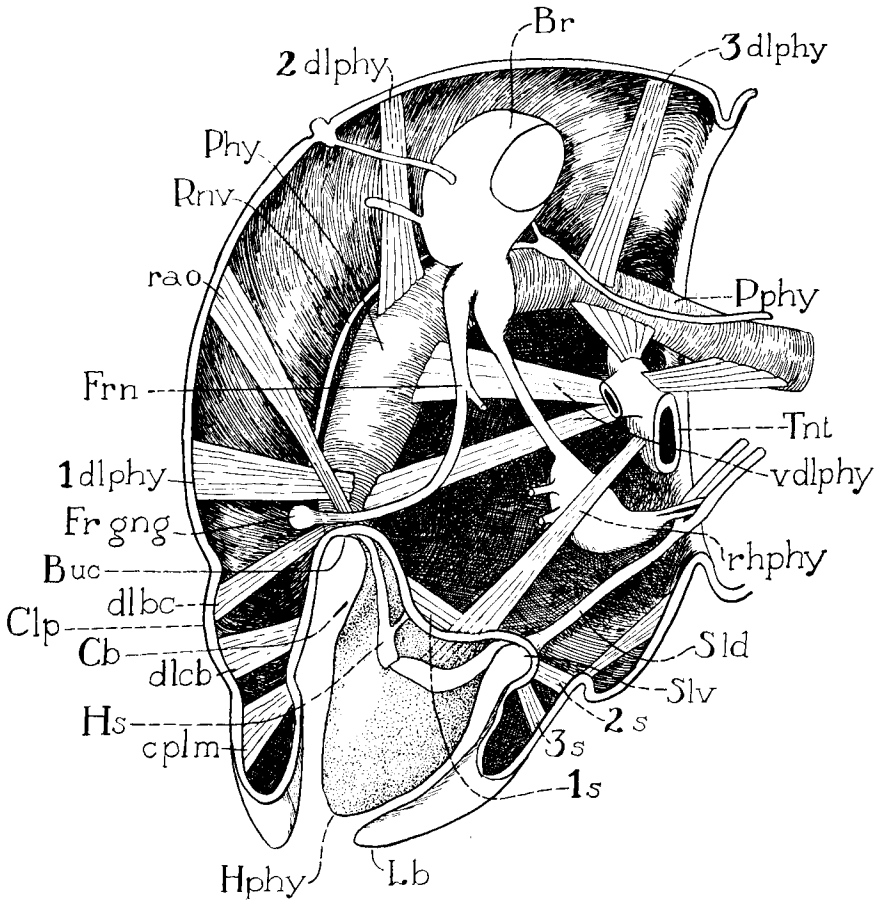


FIGURE 1. SAGITTAL SECTION OF GENERALIZED INSECT HEAD TO THE LEFT OF THE MEDIAN LINE

wall (Plate VII, B, D; Hphyw) by means of fibers resembling tonofibrillae. As a consequence of this modification the origins of the dilators of the syringe (dlsyr) have migrated to the ventral lateral surfaces of the head.

Other muscles originating on the hypopharyngeal wings are the first adductors (add 1) of the labium in Notonecta (Plate V, C, D) and in Oncopeltus (Plate VI, A). Short fibers (fi) extend from the upper inner surface of the wings (Hphyw) to the under surface of the food pump floor (Flpmp) in these insects (Plate V, C, D, and Plate VI, D, E). These fibers hold the floor of the food pump firm against the pull of the pump muscles.

THE LORA

If the labrum and the anteclypeus of Cicada are lifted up to expose the hypopharynx (Hphy) (figure 2), the loral plates (Lo) are seen to be continuous with the upper surface of the hypopharynx and the pump (Snodgrass, 1938). In Notonecta the loral surfaces are enclosed entirely within the head and can be seen only when the front surface of the head capsule has been removed (Plate IV, B, Lo).

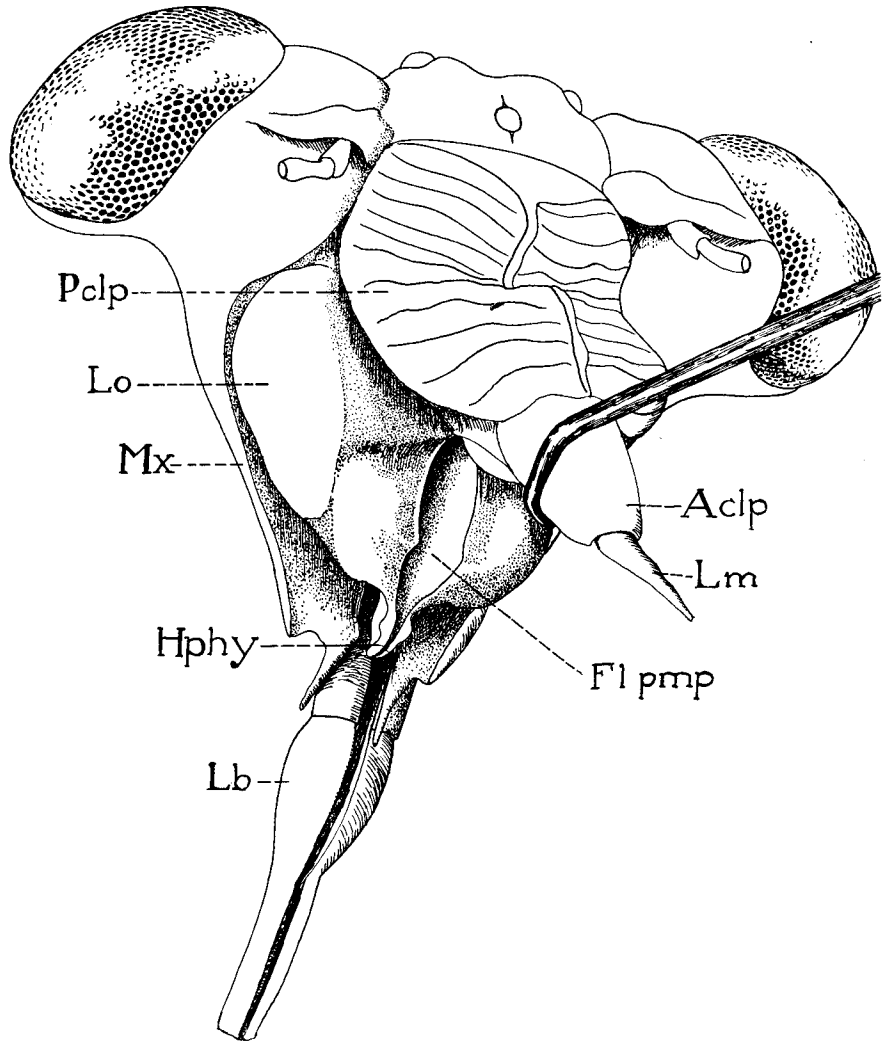


FIGURE 2. CEPHALIC ASPECT OF CICADA WITH LABRUM AND ANTECLYPEUS LIFTED TO SHOW HYPOPHARYNX AND FLOOR OF FOOD PUMP

In Benacus (Plate I, A), Oncopeltus (Plate I, E), Acrosternum (Plate I, D), and other Heteroptera the lora are modified in a different way. In these forms the postclypeus (Pclp) fuses with the front (Fr) of the head but the anteclypeus (Aclp), or tylus, remains distinct. The lora (Lo) are not flat plates, but form vertical walls continuous with the upper surface of the hypopharynx inside the head (Plate VI, D). The anteclypeus (Aclp) fits

tightly in the groove between the loral plates (Lo) so as to form a lid for the food pump.

THE FOOD PUMP

The cibarium (Cb) of the generalized insect is a space just in front of the opening into the stomodaeum enclosed anteriorly by the epipharyngeal surface of the clypeus (figure 1, and Plate VIII, B). Its floor is the slightly concave upper surface of the hypopharynx; it is flanked by the hypopharyngeal suspensorial sclerites (Hs). The cibarium is compressed by the contraction of the retractor muscles of the mouth angles (rao) which help to force the food into the buccal region of the stomodaeum (Buc).

Behind the buccal region is the pharynx (Phy), which crosses over the tentorium. The pharynx usually appears as an enlarged portion of the stomodaeum, and may be divided into the anterior pharynx (Phy), that portion in front of the cerebral nerve connectives, and the posterior pharynx (Pphy), which lies above the tentorial bar (Tnt). The dorsal dilators (dlphy) of the pharynx arise on the head wall before and behind the brain and the lateral and ventral dilators (vdlphy) arise on the tentorium.

Just behind the dilators of the cibarium (dlcb) is a pair of muscles also arising on the clypeus and inserted on the upper surface of the buccal region (Buc). These are the dilators buccales (dlbc) of Snodgrass. Behind them and separating them from the muscles of the pharynx is the frontal ganglion (Fr gng). The frontal ganglion and the frontal connectives (Frn) always form a loop enclosing the dilators of the pharynx and the retractors of the mouth angles (rao).

The food pump of Cicada evidently represents the cibarial region of the more generalized insects (Snodgrass, 1935). As has already been pointed out, its floor (figure 2, Flpmp) is the basin on the upper surface of the hypopharynx (Hphy); the cover, which is flexible and acts as a diaphragm, is the epipharyngeal surface of the anteclypeus. The dilator muscles (dlcb) of the pump originate on the corrugated walls of the postclypeus (Pclp) that form such a striking feature of the head (Plate II, A, B).

While the functional mouth of Cicada is represented by the tube leading from the deep cleft (Duct) between the anteclypeus and the hypopharynx, the true mouth (Mth) is the posterior opening of the pump into the stomodaeum. The stomodaeum extends upward from the inner mouth and enlarges into a small sac resting on the transverse bar of the tentorium (Plate II, B, C, Phy). This sac, according to Snodgrass (1935), is the true pharynx since the frontal ganglion (not shown in figures of Cicada) lies on its anterior end. The walls of the pharynx are muscular and the organ is provided with dilator muscles (dlphy) arising on the postocular region of the head and on the tentorium (Plate II, C). The pharynx is also provided with dilator muscles originating immediately behind the dilators of the food pump (Plate II, B, dlphy). These dilator muscles are not large and their origin is separate from that of the more cephalic pump muscles, but in some members of the Hemiptera these two masses of muscles are difficult to distinguish and one must rely on the position of the frontal nerve and ganglion to distinguish them. Probably the pharynx in Cicada takes little part in the pumping of the liquid food into the alimentary canal, but in other forms the pharynx is more highly developed.

In Cephisus (Plate III, A) the food pump is similar to that of Cicada. The dilators of the pharynx (dlphy) however, are more highly developed and fan out along the forepart of the pharynx as they do in Notonecta (Plate V, B). The dilator muscles that arise on the back of the head and on the tentorium are similar to those of Cicada.

In Notonecta the food pump is similar to that already described (Plate V, B). The cibarial dilators (dlcb) arise on the front of the head and are inserted on the epipharyngeal cover of the pump (Pmp). The floor of the pump is sclerotized heavily at its anterior end. Underneath, the pump floor (Flpmp) is held firmly against the pull of the powerful cibarial muscles by muscle fibers (fi) extending from the hypopharyngeal wings (Hphyw) to the pump floor (Plate V, D). These fibers undoubtedly are present in Cicada and Cephisus although they were not observed. The dilator muscles of the pharynx (dlphy) are compressed in a small opening between the frontal nerve (Frn) and the brain, but they fan out along the upper surface of the pharynx (Plate V, B).

In Oncopeltus the muscles of the food pump are divided into two masses (Plate VI, A). The smaller anterior group (dlcb) is entirely within the anteclypeus and probably corresponds to the dilators of the cibarium in the generalized insect. The larger group (dlbc) originating on the front and inserted anteriorly on the pump, partly within the anteclypeus, would then correspond to the dilators of the buccal cavity (dlbc) of the generalized insect (figure 1).

The pharynx is elongated in Oncopeltus and the dilators (dlphy) are relatively much larger than in Notonecta and spread out over an extensive length of the pharynx (Plate VI, A). Near their point of insertion these muscles are separated longitudinally into two parts by a broad thin band of muscles (lm phy), extending from a point just back of the dilator of the buccal cavity (dlbc) to a point beneath the brain (Br). In cross section this muscle (lm phy) appears larger than any of the vertical muscles near it (Plate VII, D). Its function appears to be to collapse the walls of the pharynx when tension is relaxed in the vertical dilators. While the pharyngeal pump is much more extensive in this insect than in Notonecta or Cicada, there are no fibers on the ventral walls of the pharynx to hold it firm against the pull of the dilators in this region. The pharynx undoubtedly aids in the pumping of the food, but probably, through the closing action of the longitudinal muscle, it also acts as a valve to prevent the regurgitation of food when the anterior food pump is in action.

THE LABIUM OF CICADA AND CEPHISUS

Material suitable for preparing serial sections of the labium of Cicada was lacking; therefore, histological sections of the labium of Cephisus were prepared to show the arrangements of the muscles. Dissections made of the Cephisus labium indicate that, with the exception of the transverse muscle in the second segment (Plate III, D, trans 2), which is lacking in Cicada, the musculature of the two insects is the same. In the following description of the muscles, both insects will be considered together.

The labium (Lb) of Cicada is a long slender organ consisting of three segments, with its anterior surface deeply grooved to accommodate the mandibular and maxillary bristles (Plate II, A, B, C). It is not firmly

attached to the head capsule as in the Hemiptera but is suspended from the neck membrane back of the maxillary segment and is provided with two sets of cranial muscles to control its movements (Plate II, F). A process (P), for the attachment of these muscles, extends into the head from the upper surface.

The muscles of the labium are as follows:

1. The protractors of the labium (plb) originating on the sclerotized edge of the head capsule and inserted on the ends of the labial process (P) (Plate II, C, F).

2. The retractors of the labium (rlb), originating on the head wall beneath the end of the tentorium (Tnt); fanning out at the other end to attach to the membrane at the base of the labium (Plate II, F).

3. The first adductor (add 1); origin on under side of labial process (P); insertion on ridge between first and second segment (Plate II, B; Plate III, A, D; and in cross section of labium of Cephisus, Plate III, C).

4. Paired transverse muscles of bristle groove (trans 1); origin laterally on walls of second segment; insertion on back of bristle groove (Plate II, B; Plate III, A, D, and E).

5. Retractors of terminal segment (r ter s); origin caudally on walls of the second segment; insertion on apodemes laterally placed on the ridge between the second and third segments (Plate II, B; Plate III, A, D, E, and F).

6. Transverse muscles of the second segment (trans 2); origin on the rear surface of the labial wall in Cephisus; insertion on the bristle trough, not present in Cicada (Plate III, A, D, and F).

7. Transverse fibers in third segment (trans 3); extending between rear wall of the labium to the bristle groove (Plate III, D, G).

8. Transverse fibers in all segments extending from front walls of the labium to the lateral walls of the groove (dlg). These fibers are found in all insects dissected for this study, but are poorly developed in Notonecta (Plate III, C, E, F, G). Kemper (1932) describes them in Cimex, but calls them the transverse muscle bundle (trans).

THE LABIUM OF NOTONECTA

In Notonecta the labium, consisting of four segments, articulates with the head capsule instead of the membrane of the neck region. Caudally the head capsule forms a collar-like, heavily sclerotized area that merges ventrally into a median plate between the two maxillary sclerites; this plate is known as the gula or hypostomal bridge (Gu; Plate IV, C; Plate V, A). At its ventro-lateral corners this plate invaginates and is continuous with the upper surface of the first labial segment (Plate IV, C, D, Lb seg 1), which is in turn continuous with the ventro-lateral hypopharyngeal wing plates (Hphyw). The labium is separated posteriorly from the gula or hypostomal bridge by a deeply infolded, flexible joint that extends to the sides of the labium, but not in front (Plate V, C). The front surface is continuously sclerotized but elasticity of this area allows the labium to swing in a vertical longitudinal plane.

The whole structure in the middle of the head, consisting of the gula or hypostomal bridge (Gu; Plate V, C) and the wings of the hypopharynx

(Hphyw), forms a rigid support for the mouth parts, the beak, the food and salivary pumps, and a point of attachment for the muscles that operate these movable parts of the head.

The muscles of the labium are as follows:

1. First adductors of the labium (add 1); a pair of muscle bundles having their origins on the inner surfaces of the hypopharyngeal wings; insertions on the ridge between the first and second segments (Plate V, B, C, D, and F).

2. Second adductors of the labium (add 2); a pair of muscle bundles originating laterally on the upper front surface of the first segment; inserted on lateral conjunctiva between the first and second segments, the posterior fibers on a dorsally extending apodeme (Plate V, C, D, and F).

3. The median transverse muscles of the bristle trough (m trans); a median muscle bundle originating on the upper anterior surface of an apodeme extending inward from the floor of the groove between first and second segments; insertion on floor of groove in first segment (Plate V, B).

4. Third adductors of labium (add 3); a median bundle arising on lower surface of apodeme (Ap) inserted on conjunctiva between second and third segments (Plate V, B, C, D, and F).

5. First transverse muscles of bristle trough (trans 1); a pair of muscles arising laterally on front surfaces of second segment; inserted on median ridge of bristle trough in second and third segments (Plate V, C, D, and E).

6. Retractors of terminal segment (r ter s); a pair of bundles arising laterally on walls of third segment and on dorsal extensions of ridge between second and third segments (Plate V, C, D, and E); inserted on ridge between third and fourth segments.

7. Second transverse muscles of bristle trough (trans 2): a single group of muscles arising on median ventral surface of third segment converging and inserted on bristle trough (Plate V, B, C, and D).

8. Fibers in terminal segment to support bristle trough (not shown in plates; trans 3).

9. Transverse fibers from front wall of labium to side walls of trough (dlg). Rudimentary in Notonecta.

A study of these muscles reveals that there are no abductor muscles in Notonecta. Probably the labium is used mostly in a vertical position, which requires not much movement from its normal resting position. From the large size of the cavities within the labium it seems that blood pressure might aid in extending the labium.

THE LABIUM OF ONCOPELTUS

The labium of Oncopeltus is a long slender structure attached to the front of the head, and when not in use is carried close to the under side of the head and thorax with its tip extending back between the legs. It is very mobile and can be swung from the resting position forward until its axis lies almost in the same plane as that of the insect's body.

Of the four insects studied, Oncopeltus has the most highly developed musculature for the labium. The muscles are as follows:

1. The first adductors of the labium (add 1): a pair of slender muscles arising on inner walls of the hypopharyngeal wings (Hphyw) inserted on

conjunctiva between first and second segments, (Plate VI, and Plate VII, A). These correspond to muscles that are similar in Notonecta, but not present in Cicada or in Cephisus.

2. The first abductors (abd 1) : a pair of muscles originating on the front wall of the first segment toward its base; inserted laterally on the ridge between the first and second segments (Plate VI, A, and Plate VII, A).

3. The second adductors (add 2) : a single large muscle mass originating on front surface of first segment on inner wall of trough; inserted in two parts on same apodemes as add 1 (Plate VI, A, and Plate VII, A).

4. The third adductor muscle (add 3) : a single muscle bundle originating on the trough for a considerable distance in the second segment; inserted on apodeme from the ridge on rear surface between the second and third segments (Plate VI, A, and Plate VII, C).

5. First transverse muscles of the trough (trans 1) : a pair arising laterally in the third segment and slanting downward to attach to the bristle trough. There are five fibers in each set (Plate VI, A, and Plate VII, E).

6. Median transverse muscles of the third segment (trans 1 a) : a series of muscles originating medially on back wall; nearly all horizontal; inserted on trough (Plate VI, A).

7. Paired retractors of the terminal segment (r ter s). They arise laterally, three fibers on extreme outer portion of the front surface; the others, a much larger group, on the rear wall adjacent to the median line (not distinctly shown in figures) ; inserted on ridge between third and fourth segments on each side (Plate VI, A, and Plate VII, E).

8. Second transverse muscles of third segment (trans 2) : a median group of muscles appearing as a continuation of the first transverse muscle group but heavier and two-layered, arising on back wall running horizontally to the trough (Plate VI, A, and Plate VII, F).

9. Transverse fibers in fourth segment to support trough (trans 3; Plate VI, A, and Plate VII, G).

10. Transverse fibers from front walls of labium to side walls of trough (dlg) ; well developed in Oncopeltus throughout length of trough (Plate VII, A, C, E, F, and G).

The musculature of the terminal segment of all four insects is similar; it consists of the transverse fibers at the back of the bristle groove (trans 3) and the transverse fibers originating on the front walls of the labium, inserted on the lateral walls of the groove (dlg). The next segment is also similar in three of the insects, and but for one muscle, also in Cicada. In Cicada the second transverse muscle of the second segment (trans 2) is missing but is present in the others. The retractor of the terminal segment in Cephisus (r ter s) varies slightly in the position of its origin and is more highly developed in Oncopeltus but is similar in position and function in all the forms studied and in Cimex as described by Kemper. The first adductor (add 1), situated in the first segment in Cicada and Cephisus of the Homoptera, is similar in function to the same muscle in the second segment of the Hemiptera but in origin it differs in the two orders.

The greatest difference between the two groups of insects is in the attachment of the labium to the head, and the different muscular arrangement in the base of the labium. The labium of Cicada and Cephisus arises from the neck membrane behind the maxillary segment and its flexibility or mobility

is due to this position. It is controlled by protractor (plb) muscles and retractor (rlb) muscles within the head. The labium of Notonecta or Oncopeltus, consisting of four segments, is attached to the front of the head capsule, its mobility depending entirely on the flexibility of the membrane between segments.

Kemper (1932) states that the abductors and adductors of the Cimex labium arise on the clypeus. This is not true in more primitive insects, and is not like the arrangement of the same muscles in Hemiptera, as found by the writer. The suture (s) between the jugum (Ju) and the maxillary lobes (Mx) in these insects extends backward on the side of the head to the base of the antennae (Plate VI, B). In this same region the anteclypeus (Aclp), or tylus, lies in the trough between the loral surfaces (Lo) of the head, closing tightly the food canal on the upper surface of the hypopharynx (Plate VI, D). Plate VI, C, represents a cross section posterior to the point where the first adductor muscles of the labium enter the head; these muscles originate upon the lower lateral walls of the mouth cavity ahead of point y. For any muscles of the labium to originate on the clypeus or any other dorsal area of the head near this region is obviously impossible.

To bring out more clearly the relationships and dissimilarities that exist between the muscles of the labium, they are classified in the table on page 14, together with the muscles of Cimex, as given by Kemper (1932).

THE MANDIBLE AND MAXILLA OF CICADA

Both the mandibular and maxillary bristles of Cicada arise from the walls of the bristle pouches. They are enlarged at their proximal ends and both are forked; the branches of the mandible are longer than those of the maxilla.

The enlarged base of the mandibular bristle lies inside the bristle pouch just under the overlying edge of the loral plate (Lo, Plate II, D). It is forked, one arm (ra) proceeding dorsally along the inner walls of the pouch, giving attachment to the first retractor muscles (1 rmd) that arise on the dorsal wall of the head; the other arm (pa) extends dorsally at the bottom of the groove between the lorum and the maxillary plate, its upper end articulating with the posterior lateral margin of the lorum (Lo) (Snodgrass, 1938). The protractor muscles (pmd) of the mandible originate on the inner face of the lorum (Lo) and are inserted on a wide, thin apodemal inflection along this protractor arm (not shown in Plate II, D).

The maxillary lever in Cicada is joined to the maxillary bristle by a flexible joint allowing considerable freedom of action in the lever, while the protractor arm of the mandible is a rigid part of the base of the bristle to which the protractor muscles are attached. The flexible joint lies at point X (Plate II, E). It is evident, therefore, that the maxilla can be protruded farther than the mandible.

The inner end of the maxillary bristle serves as a point of attachment for retractor muscles (Plate II, E, rmx), which originate on the dorsal walls of the head. A large protractor (2 pmx) originating ventrally on the inner face of the maxillary plate (Mx) is inserted on the end of the bristle. The lever (Lvr) of the maxilla is a modification of the wall of the bristle pouch and extends from the bristle to the posterior edge of the maxillary plate (Plate II, E, Mx). Apparently this lever serves as a contrivance to hold the maxilla in line as the bristle moves in and out in the Hemiptera,

LABIAL MUSCLES

HOMOPTERA			HEMIPTERA			
Cicada	Cephisus		Notonecta	Oncopeltus	Cimex	
Protractor (plb)	Protractor	*First segment*				
Retractor (rlb)	Retractor					
add 1 (origin and insertion differ in Hemiptera but function same)	add 1		add 1	add 1	add 2 (origin on clypeus similar to that of add 1 of Oncopeltus)	
			add 2	add 2 (not the same as in Notonecta)	add 1 (similar to add 2 of Oncopeltus)	
		First segment	No add 3 as in Cimex	No add 3 as in Cimex	add 3 (not the same as in Notoncta)	
			No abd 1	abd 1	abd 1	
			No abd 2	No abd 2	abd 2	
			m trans	No m trans	No m trans	
			No add 4	No add 4	add 4	
		Second segment	add 3 (origin differs from that of Oncopeltus)	add 3 (origin differs from that of Notonecta)	add 5	
trans 1	trans 1		trans 1	trans 1	trans 1	
No trans 1 a	No trans 1 a	*Second segment*	No trans 1 a	trans 1 a	No trans 1 a	
r ter s	r ter s	*Third segment*	r ter s	r ter s	add 6	
No trans 2	trans 2		trans 2	trans 2	trans 2	
trans 3	trans 3	*Third segment*	trans 3	trans 3	trans 3	
dlg	dlg	*Fourth segment*	dlg	dlg	trans	

but in Cicada it also serves as a point of insertion for a heavy protractor muscle (1 pmx), which originates on the lower maxillary plate with the first protractor, and for a fine retractor muscle (tm) which originates on the tentorium.

THE MANDIBLE AND MAXILLA OF HEMIPTERA

The mandibular bristle of Notonecta consists of a modification of the mesal wall of the mandibular sac. On its inner end is inserted the retractor muscle, (Plate VIII, D, rmd), the origin of which is on the back of the head at the edge of the foramen magnum beneath the eye. There is only one protractor (mdh), its origin being on the inner face of the lorum, its insertion on the mandibular process (Mdpr).

The mandibular process (Mdpr) is one of the most important landmarks of the inner head skeleton. It is found in all members of the Hemiptera thus far studied, and is constant in position. The outward invagination marking the inward projecting process is always just mesad and in front of the antennal fossa and in Notonecta and Benacus slightly below this point (Plate IV, A, B; Mdpr).

In Oncopeltus removal of the upper surface of the jugum will reveal the mandible and its muscles in place inside the head (Plate VIII, I, Md). The large antennal base crowds the point of invagination of the mandibular process (Mdpr) forward. The process is enlarged to form the point of insertion for the fan-like hypopharyngeal transverse protractors of the mandible (mdh). These muscles originate on the vertical walls of the food trough (Plate VIII, I, Lo; and Plate VI, D, Lo), which correspond to the lora of Cicada and the lateral extension of the upper surface of the hypopharynx in Notonecta (Plate VIII, A, Lo).

In most of the Hemiptera the inner edge of the mandibular sac (Plate VIII, I) is sclerotized to form a strong bar (Lvr) connecting the process (Mdpr) with the bristle (Md). This is the lever of the mandible. In Notonecta the lever (Lvr) is not heavily sclerotized and thus not so highly developed as in Oncopeltus and Acrosternum, (Plate VIII, D). In the latter insects the lever is highly developed and is bent at a sharp angle near its middle (Plate VIII, I), so that its inner half lies parallel to and on top of the mandibular bristle (Md). Plate VIII, K, shows the process (Mdpr) and lever (Lvr) of Acrosternum after muscles have been removed. The lever has been lifted by a needle to show the fold in the sac (Md sac) that begins at this bend of the lever (Lvr).

In Oncopeltus as in Notonecta the hypopharyngeal-mandibular muscle is the only mandibular protractor present. In Acrosternum there is a second protractor of the mandible (Plate VIII, H, J; pmd) inserted on the outer half of the lever and arising in the anterior extremity of the lobe, the top surface of which is the jugum (Plate I, D, Ju; and Plate VIII, H, Ju). The point of insertion of this group of muscles (pmd) on the lever (Lvr) is revealed if the hypopharyngeal-mandibular protractor muscles are removed (Plate VIII, J).

Snodgrass (1938) says, "In the Hemiptera both the primary articulations of the mandible on the subgenal margin of the cranium have been suppressed to give freedom of movement to the mandibular base; the articulation with the lorum represents the mesal point of contact between the mandibular base

and the base of the hypopharynx. The retractor muscle of the hemipterous mandible (Plate VIII, A, rmd) arising on the vertex is evidently the adductor muscle of the biting jaw (Plate VIII, B, admd); in Cicada the primitive cranial abductor appears to be represented by a second retractor muscle (Plate II, D, rmd) arising on the gena and inserted laterally on the mandibular base. The reduction in size of the mandibular bases in Hemiptera has exposed the lateral parts of the hypopharynx on the sides of the head, and the retraction of the mandibles has converted the primitively hypopharyngeal adductor muscles of the mandibles (Plate VIII, B, mdh) into protractor muscles (Plate II, D, pmd)." (Snodgrass here does not use "Hemiptera" in the restricted sense, but includes as well the members of the Homoptera.)

Snodgrass's diagram of the mandible and hypopharynx of the roach has been included here for comparison with the same structures in Notonecta. The same relations described for Cicada exist in Notonecta. In Notonecta the hypopharyngeal muscle of the mandibles (Plate VIII, A, mdh) retains its transverse position in the head. Its origin is on the inner surface of the loral plate (Lo), an expansion of the upper surface of the hypopharynx (Hphy). Its insertion is on the mandibular process (Mdpr). Retraction of the mandible in the head has caused the hypopharyngeal muscle to act as a protractor of the bristle. It works *against* the retractor muscle in Notonecta, instead of *with* it as in the roach.

A difference between Notonecta and Cicada should be pointed out. In Cicada the hypopharyngeal muscle is inserted directly on the protractor arm of the mandible. In Notonecta this muscle acts upon the mandibular process (Plate VIII, A, D; Mdpr), which is connected with the mandible itself by the lever (Lvr). The lever is a sclerotized bar lying in the inner wall of the mandibular bristle sac and is connected to the mandible by a flexible joint. The structure of the mandible, lever, and mandibular process is similar in all members of the Hemiptera studied and constitutes a fundamental difference between the mandible of this group and the mandible of Cicada.

Beneath and mesad of the mandible of Notonecta lies the maxilla formed as a heavily sclerotized rod in the membrane of the bristle pouch. The maxilla is less complex than the mandible. It has a single retractor bundle of muscles (rmx) originating on the inner wall of the head capsule at the edge of the foramen adjacent to the mandibular retractor (Plate VIII, C) and inserted on the mesal edge of the maxillary bristle.

The maxillary segment of the head consists of two parts: the maxillary plate (Plate IV, B, Mx), the external sclerotized plate beneath the eye, and a fleshy lobe, probably the galea, not visible because it is covered by the lower part of the clypeal region of the head and by the labrum. The protractor muscles (pmx) have their origins on the lower surface of the fleshy lobe (Plate VIII, C); the edge of the lobe is apparently reinforced by a sclerotized margin extending from the external plate to take the pull of the muscles. No maxillary lever is present in Notonecta.

Dissections of Oncopeltus made to expose the maxilla reveal it as a sclerotized bristle which broadens at its inner end (Plate VIII, G, Mx). The maxillary sac is expanded inwardly to accommodate a curved transverse bar; this is the lever (Lvr) in the membrane of the upper surface of the sac, articulating with the inner side of the maxillary bristle and

extending to the head wall at a point beneath and slightly caudad of the compound eye. The lever is bowed and can best be seen from the under side as shown in Plate VIII, G. The protractor muscle (pmx) originates on the end of the maxillary segment and is inserted on the broad base of the bristle. It is encircled by the lever on the under side. The retractors (rmx) are inserted on the inner end of the bristle and extend to the edge of the foramen magnum laterad of the mandibular muscles. The arrangement of the maxilla is similar in Acrosternum; and, except for the more elaborate musculature, it is similar in Cicada (Plate II, E). The lever (Lvr) of Oncopeltus at its outer end is joined to the head wall by a series of fibers (fi) extending from the epidermal layer of the maxillary sac to the epidermal layer of the head capsule (Plate VII, B). These fibers probably correspond to tonofibrillae. The inner vertical wall of the sac is formed from the wing of the hypopharynx (Hphyw). At the line along which the wing approaches the lower surface of the head and where the sac (Mx sac) bends outward under the lever, another series of fibers (fi) connects the head wall with the sac.

Back of the lever, the walls of the sac (Plate VII, D, Hphyw) become membranous and highly convoluted and the muscles of the salivary syringe (dlsyr), which in Cicada, Cephisus, and Notonecta are attached to the under side of the hypopharyngeal wings (Plate II, F, dlsyr; Plate IV, C, and D dlsyr), have migrated upon the head capsule.

At the posterior end of the food pump in Oncopeltus (Plate VI, E) a cross section shows that from here forward the hypopharyngeal wings (Hphyw) are joined to the floor of the food pump (Pmp) by fibers (fi) that support the pump by opposing the pull of the pump muscles (dlbc). A section taken through the antennal base (Plate VI, D) indicates that the mandibular and maxillary sacs have merged into the bristle sac (B sac) in front of the compound eyes and behind the base of the antennae.

The maxillary protractors (pmx) each divide into three bundles near the region where they attach to the wall of the head (Plate VI, D). The inner maxillary protractor bundle (a) originates on the wall of the bristle pouch. The lower bundle (b) (Plate VI, C) fastens to the wall of the maxillary lobe toward its tip on the lower side, and the upper lateral bundle (c) has its origin dorsally in the maxillary lobe toward its anterior extremity (Plate VI, C).

The mandibular and maxillary bristles are hollow, seta-like organs. Outside the bristle sac and within the trough of the labium the mandibles (Md) are on the outside of the bristle bundle (Plate VIII, E, F,), acting as guides for the maxillae (Mx) within. The mandibles are flanged on their upper surface in Notonecta, the flange overlying the maxilla on the side facing the opening in the labial trough. Near the proximal end of the mandible, where it lies under the labrum, the mesal margin of the flange is ridged (Plate VII, F, r). The ridge on each mandible runs in a slot on the inner surface of the labrum (Plate V, F, r). Evidently these grooves are effective in forcing the mandibles and maxillae together beyond the point of the hypopharynx. In Oncopeltus the flange and ridge are not present and the bristles are forced into a compact bundle in a different way. The labrum (Lm) of Oncopeltus is grooved on its lower surface and fits tightly around the bristle bund

(Plate VII, A). Evidently the labral groove forces the mandibles (Md) and maxillae (Mx) together beyond the end of the hypopharynx.

In Notonecta the bristle bundle (Bb) is flattened and apparently unable to turn in the labial groove (Plate V, E). In Oncopeltus the bristle bundle is nearly cylindrical and can turn in the labial groove. Serial sections of the labium with the bristle bundle in place show the axis of the bristle bundle to be different in each section. Possibly this indicates that the bristles have a twisting motion, like that of a drill, as they penetrate the plant tissue (Plate VII, A, C, E, F, and G; Md, Mx).

SUMMARY

In Cicada and Cephisus, the clypeus is divided into postclypeus and anteclypeus; the loral plates are exposed at the sides of the clypeus. In Notonecta the entire clypeus is fused with the front; the loral plates lie inside the head and are entirely covered. In Benacus, Oncopeltus, and Acrosternum, the postclypeus is fused with the front; the anteclypeus or tylus is narrow and lies in a trough between the vertical loral plates.

The lower-lateral surfaces of the hypopharynx are extended into the head as two divergent trough-like plates. In Cicada and Cephisus a tentorium is present and these plates rest on the under surface of the tentorium and appear to be united closely with it. The dilator muscles of the salivary syringe are attached to their under surfaces.

In other forms studied no tentorium is present. The wings of the hypopharynx extend backward in Notonecta and give support to the inner ends of the salivary retractor muscles. In Oncopeltus the hypopharyngeal wings are greatly modified. They become membranous caudally and are attached to the head wall along their lower edges. The origins of the salivary-pump retractors are on the head capsule instead of the wings.

The food pump of Cicada represents the cibarial region of generalized insects. The functional mouth is a tube leading from the cleft between the anteclypeus and the hypopharynx. The true mouth is the posterior opening of the food pump into the pharynx which lies above the tentorial bar.

The muscles of the food pump are the dilators of the cibarium, a large mass arising in the large clypeal bulge on the front of the head. Behind these are the pharyngeal dilators. Cephisus and Notonecta are similar. In Notonecta and Oncopeltus the frontal nerve and ganglion lie between these two masses. The pharyngeal dilators reach their greatest development in Oncopeltus, where they fan out on the upper surface of the pharynx in two parts, with a longitudinal muscle lying between.

The three-segmented labium of Cicada and of Cephisus is attached to the neck membrane. The four-segmented labium of the Hemiptera studied arises from the head capsule at its anterior end. The protractor and retractor muscles of the labium of Cicada and of Cephisus originate on the posterior edge of the head capsule under the end of the tentorium. These muscles do not exist in the Hemiptera; the adductor muscles and abductors, when present, originate on the hypopharyngeal wings. The muscles of the terminal labial segment and of the next-to-the-last segment in Cicada and in Cephisus are similar to the muscles in the same segments in the Hemiptera studied. Other muscles in the labium differ in the two groups of insects except that

the first adductor in Cicada and Cephisus is similar in function to the first adductor in Notonecta and Oncopeltus.

The mandibles and maxillae of the Homoptera and Hemiptera arise from the walls of the bristle pouches. The protractor muscles of the mandibles in Cicada are attached directly to the protractor arm and arise on the loral plates. In Notonecta and other Hemiptera studied they arise on the loral plates, but are inserted on the mandibular process, a constant feature in the Hemiptera. The process is joined by a lever to the mandible. In Acrosternum an additional set of protractor muscles is attached directly to this lever.

The maxillary bristle of Cicada is equipped with a lever attaching to the head capsule behind the eye, as are the maxillary bristles of Oncopeltus and Acrosternum. No maxillary lever is present in Notonecta.

REFERENCES

CRAMPTON, G. C.

1921. The sclerites of the head, and the mouthparts of certain immature and adult insects. Ent. Soc. Amer. Ann. **14**: 65–110.

KEMPER, HEINRICH

1932. Beiträge zur Biologie der Bettwanze (Cimex lectularius L.) III. Über den Mechanismus des Stechsaugaktes. Ztschr. Morph. u. Ökol. Tiere **24**: 491–518.

MUIR, F., and KERSHAW, J. C.

1912. The development of the mouthparts in the Homoptera, with observations on the embryo of *Siphanta*. Psyche **19**: 77–89.

SNODGRASS, R. E.

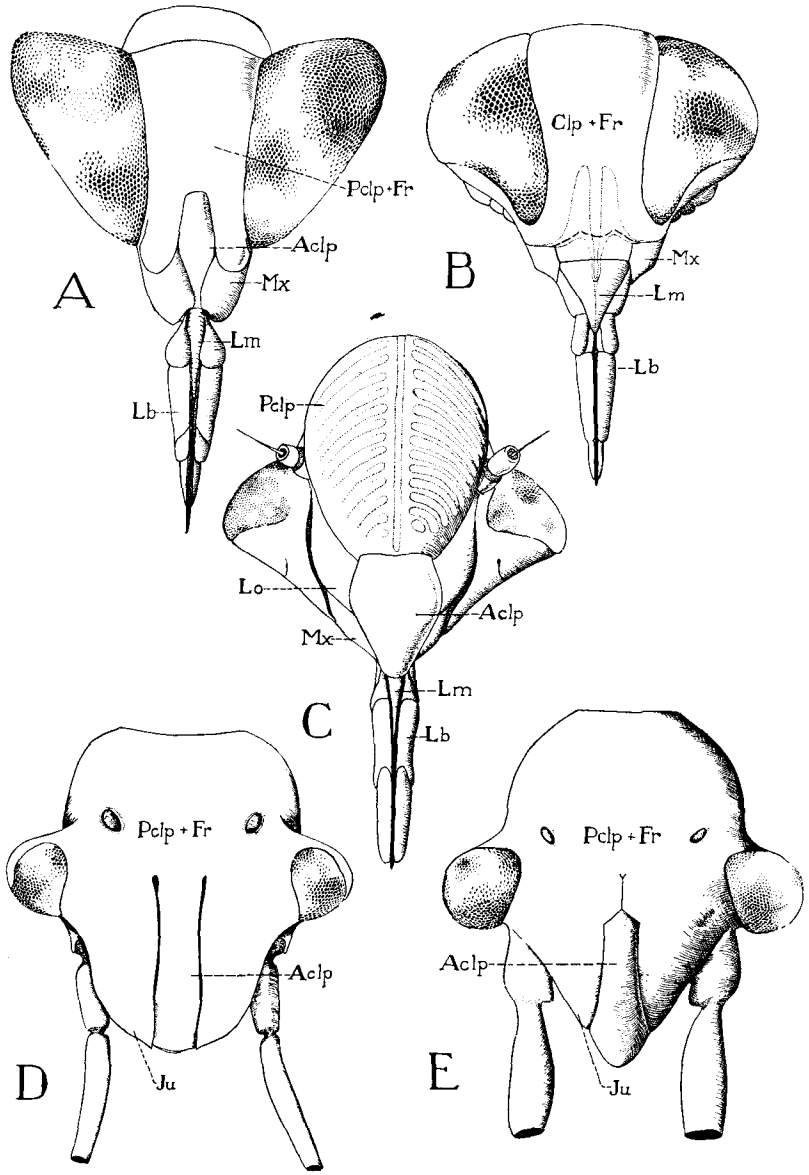
1921. The mouth parts of the cicada. Ent. Soc. Wash. Proc. **23**: 1–15.
1927. The head and mouth parts of the cicada. Ent. Soc. Wash. Proc. **29**: 1–16.
1935. Principles of insect morphology. 666 pages.
1938. The loral plates and the hypopharynx of Hemiptera. Ent. Soc. Wash. Proc. **40**: 228–236.

WEBER, HERMANN

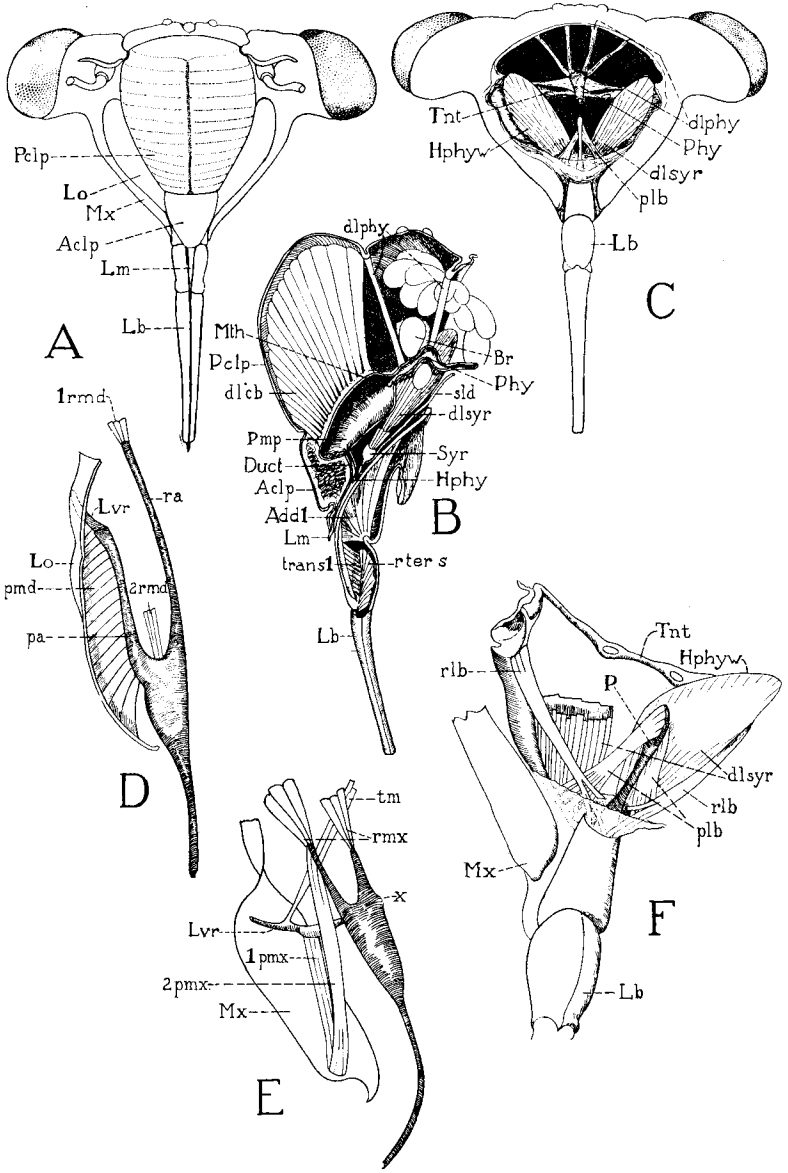
1929. Kopf und Thorax von Psylla mali Schmidb (Hemiptera-Homoptera). Ztschr. Morph. u. Ökol. Tiere **14**: 59–165.
1930. Biologie der Hemipteren. 543 pages.
1933. Lehrbuch der Entomologie. 726 pages.

ABBREVIATIONS

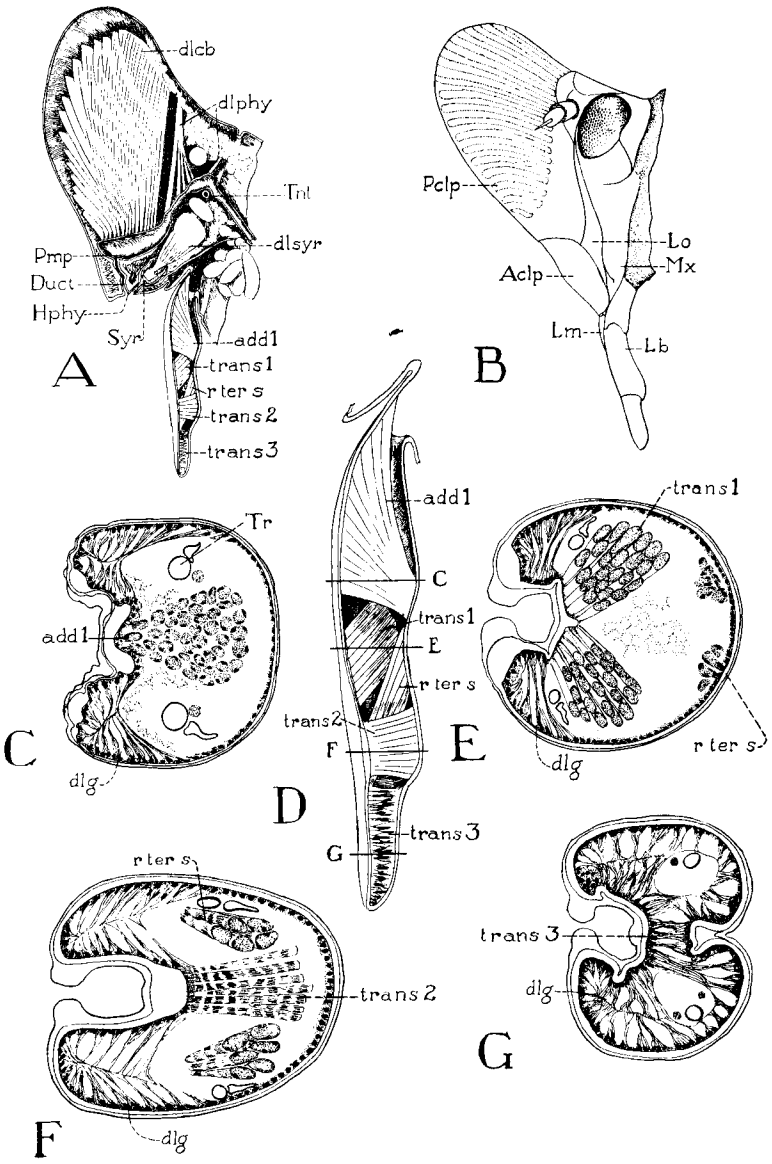
abd = abductor muscle
abmd = abductor of mandible
Aclp = anteclypeus
add = adductor
admd = adductor of mandible
Ant = antenna
antm = antennal muscle
Ap = apodeme
At = anterior tentorial arm
Bb = bristle bundle
B sac = bristle sac
Br = brain
Buc = buccula, or buccal cavity
Cb = cibarium
Clp = clypeus
cplm = compressor of labrum
dlbc = dilator of buccales
dlcb = dilator of cibarium
dlg = transverse dilators of the groove
dlphy = dilator of pharynx
dlsyr = dilator of syringe
Fd = food duct
fi = muscle fibers
Flpmp = floor of pump
Fr = frons
Fr gng = frontal ganglion
Frn = frontal nerve
g = groove in labium of Notonecta
Gu = gula
Hphy = hypopharynx
Hphyw = hypopharyngeal wings
Hs = hypopharyngeal suspensorium
Ju = jugum
Lb = labium
Lb seg 1 = first labial segment
Lm = labrum
lm phy = longitudinal muscle of pharynx
Lo = lora
Lvr = lever
m trans = median transverse muscle
Md = mandible
Md b = mandibular bristle
mdh = hypopharyngeal-mandibular muscle
Mdpr = mandibular process
Md sac = mandibular sac
Mth = mouth
Mx = maxilla
Mx sac = maxillary sac
Ocs = occipital suture
Oes = oesophagus
Op n = optic nerve
P = process of labium
pa = protractor arm
Pclp = postclypeus
Phy = pharynx
plb = protractor of labium
pmd = protractor of mandible
Pmp = food pump
pmx = protractor of maxilla
Pphy = posterior pharynx
r = ridge on upper surface of mandible
ra = retractor arm
rao = retractors of mouth angle
rhphy = retractor of hypopharynx
rlb = retractor of labium
rmd = retractor of mandible
rmx = retractor of maxilla
Rnv = recurrent nerve
r ter s = retractor of terminal segment
s = suture
1s = dorsal salivary muscle
2s, 3s = salivary muscles of the labium
Sld = salivary duct
Slv = salivarium
Sm = salivary meatus
Stom = stomodaeum
Syr = syringe (salivary)
tm = tentorial retractor muscle of maxilla
Tnt = tentorium
Tr = trachea
trans = transverse muscle
vdlphy = ventral dilators of pharynx
Y = dome-like protuberance in eye of Benacus



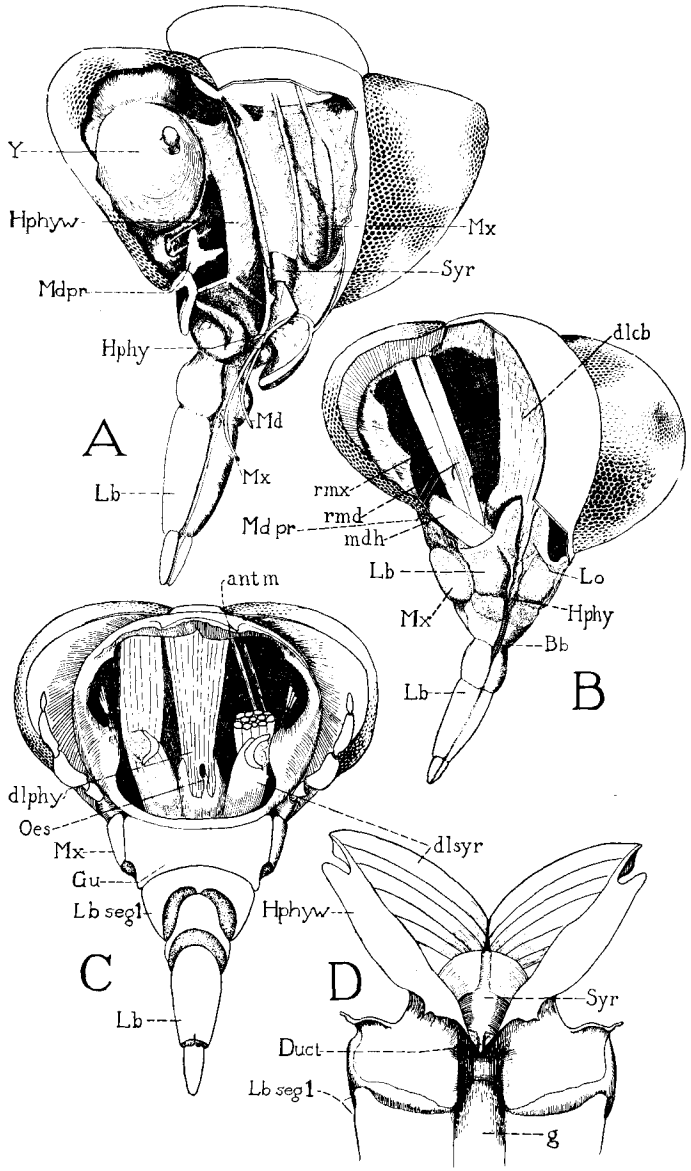
A. Cephalic aspect of *Benacus griseus.*
B. Cephalic aspect of *Notonecta* sp.
C. Cephalic aspect of *Cephisus siccifolius* nymph.
D. Dorsal aspect of head of *Acrosternum hilare,* a stinkbug.
E. Dorsal aspect of head of *Oncopeltus fasciatus,* the milkweed bug.



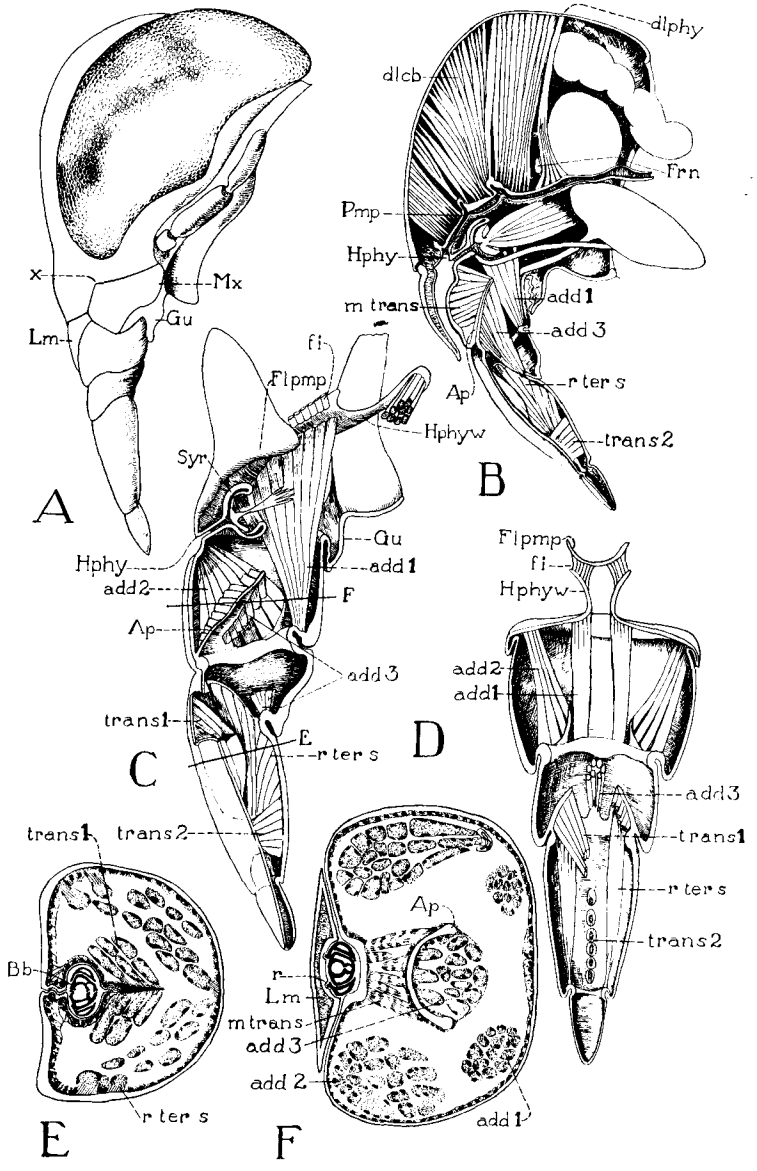
A. Cephalic aspect of *Tibicina septendecim*, the seventeen-year Cicada.
B. Median sagittal section of head of Cicada.
C. Caudal aspect of head of Cicada.
D. Mandible and its muscles, of Cicada.
E. Maxilla and its muscles, of Cicada.
F. Base of labium of Cicada with its muscles.



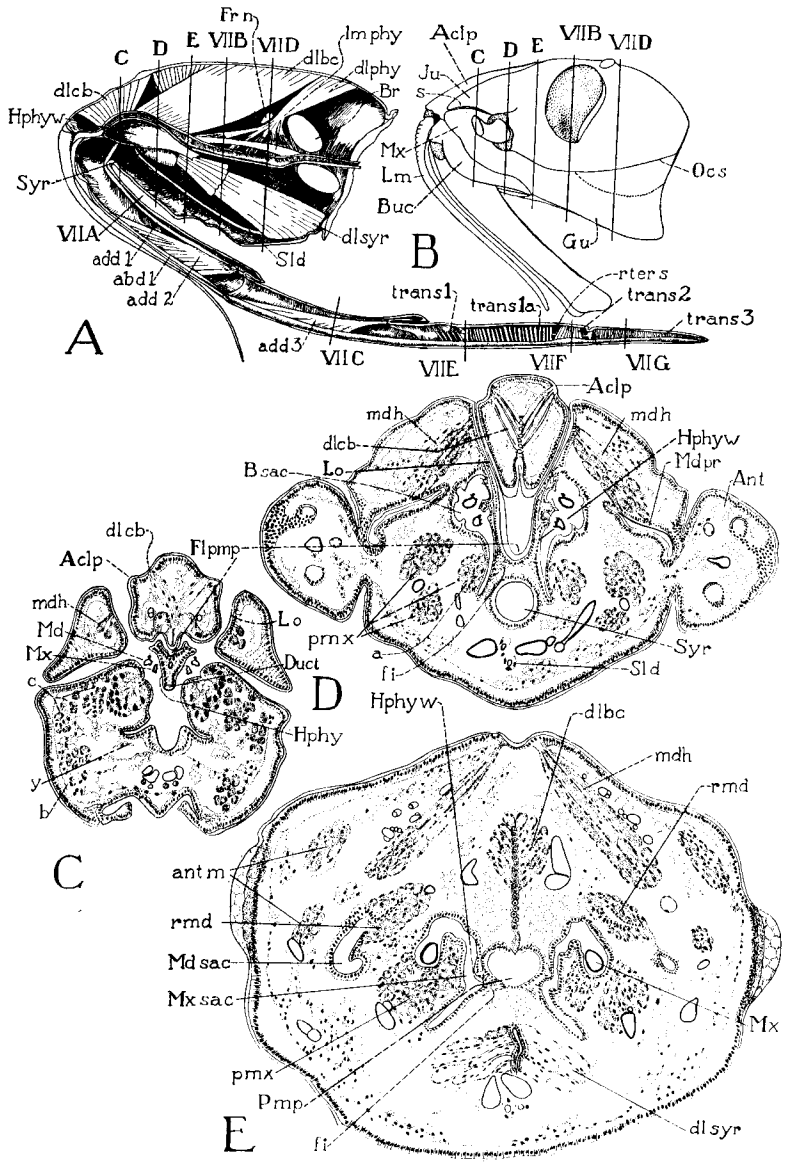
A. Median sagittal section of head of *Cephisus siccifolius.*
B. Lateral aspect of head of Cephisus.
C. Cross section of basal segment of labium of Cephisus.
D. Median sagittal section of labium of Cephisus.
E. Cross section of labium of Cephisus through the second segment.
F. Cross section of labium of Cephisus through distal portion of second segment.
G. Cross section through terminal labial segment of Cephisus.



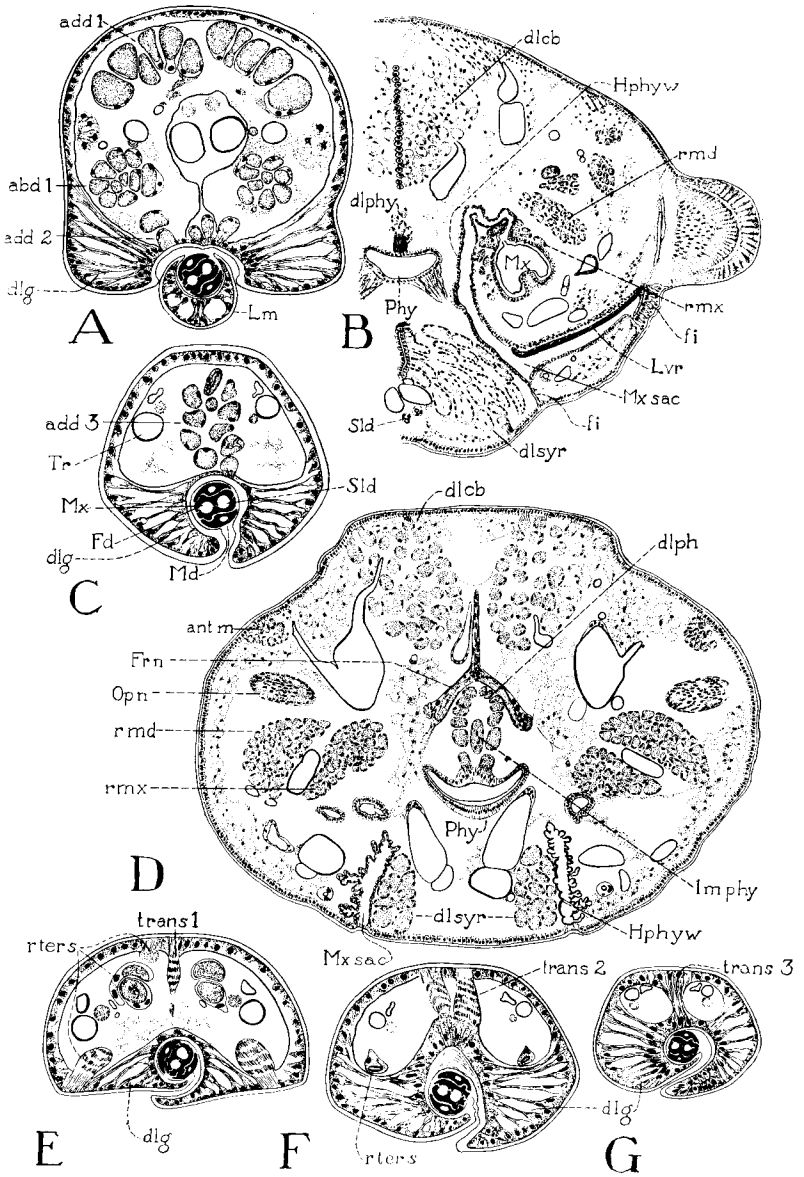
A. Head of *Benacus griseus* with part of head and eye cut away to show hypopharyngeal wings.
B. Head of Notonecta with part of head and eye cut away to show food pump, mouth parts, and their muscles.
C. Caudal aspect of head of Notonecta.
D. Hypopharyngeal wings and salivary syringe of Notonecta.



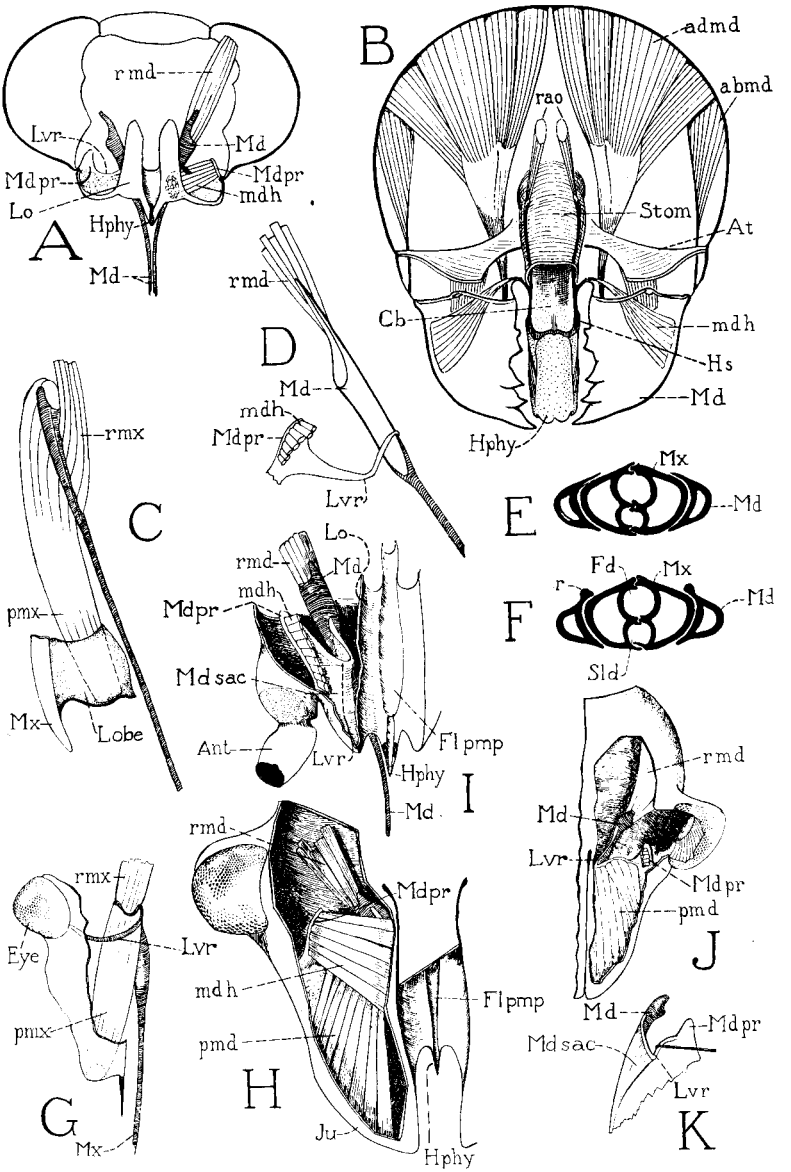
A. Lateral aspect of head of *Notonecta* sp.
B. Median sagittal section of head.
C. Median sagittal section of labium.
D. Frontal section through labium.
E. Cross section through third labial segment.
F. Cross section through basal labial segment.



A. Median sagittal section through head and labium of *Oncopeltus fasciatus.*
B. Lateral aspect of head.
C. Cross section of head in front of antenna.
D. Cross section of head through antennal base.
E. Cross section of head between antenna and eyes.



A. Cross section of labium through basal segment (Plate VI, A).
B. Cross section of head through eyes (Plate VI, A, B).
C. Cross section of labium through second segment (Plate VI, A).
D. Cross section through head behind eye (Plate VI, A, B).
E. Cross section of labium through third segment (Plate VI, A).
F. Cross section of labium through distal portion of third segment (Plate VI, A).
G. Cross section of labium through fourth segment (Plate VI, A).



A. Diagram of Notonecta showing mandibles and hypopharynx.
B. Diagram of roach showing mandibles and hypopharynx.
C. Maxilla of Notonecta.
D. Mandible of Notonecta.
E. Cross section of bristle bundle of Notonecta beyond end of labrum.
F. Cross section of bristle bundle in region of labrum.
G. Maxilla of Oncopeltus.
H. Head of Acrosternum dissected to show mandibular muscles and hypopharynx.
I. Head of Oncopeltus dissected to show mandible and hypopharynx.
J. Head of Acrosternum dissected to show protractors of mandible inserted on lever.
K. Mandible of Acrosternum dissected to show lever and mandibular sac.