

GILBERT

Embryological

Studies on Hemiptera

1. Development and Morphology
of the Mouth Parts

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EMBRYOLOGICAL STUDIES ON HEMIPTERA
1. Development and Morphology of the Mouth Parts

BY

JOHN PHILO GILBERT, A. B., 1905

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John Philo Gilbert, A.B.,

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OF Master of Arts.

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EMBRYOLOGICAL STUDIES ON HEMIPTERA.

1. Development and Morphology of the Mouth-Parts.

by

John Philo Gilbert.

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INTRODUCTION.

The morphology of the mouth-parts of Hemiptera has long been a subject of dispute among zoologists. Nearly all the investigators who have studied the morphology of the Hemipterous mouth-parts have neglected to study the development of these organs. Organs so highly specialized as these, however, cannot be understood unless studied in the egg and nymph as well as in the imago.

This thesis was undertaken in the hope that embryology might throw some light on disputed points relating to the structure and morphology of the hemipteran mouth-parts. The common squash bug, Anasa tristis, was selected for study because this insect is a representative species and because the material is most available.

The present studies were made under the supervision of Dr. J. W. Folsom to whom I am most grateful for encouragement and advice.

MATERIALS.

Some of the more important observations made in collecting materials for this thesis are included here for the information and guidance of those who desire to make further investigations on Anasa tristis.

Eggs for this work were obtained in two ways: first, by collecting from the food plants; second, by keeping pairs of adults under observation in captivity. By searching the lower surfaces of squash and pumpkin leaves, large numbers of eggs were easily obtained. The exact age of these eggs, however, was not known. (Females cease oviposition when slightly jarred or when the light strikes them suddenly). To avoid uncertainty as to the age of the eggs used, about one hundred pairs of adult insects were placed in a bell-jar in a sunny window, and given fresh squash and pumpkin leaves every six hours. In forty-eight hours not an egg had appeared, so about seventy-five pairs of the insects were placed on a small squash vine in the garden. A box open at the bottom and covered above with wire screen served to keep the insects in captivity. In an hour, one female was depositing eggs and during six hours, fifteen clusters were laid on the leaves. The twenty-five pairs left in the bell-jar for several days deposited but few eggs. Evidently the insects preferred the plant surrounded by the box. The box, however, prevented the observation of egg-laying on the under side of the leaf.

A. tristis is most active on sunny days and rests near the base of the plant, partially sheltered by leaves and clods. The box darkened the plant too much, however, and the insects collected on the wire screen instead of about the plant. A bag made of mosquito netting and left open at both ends met all difficulties admirably. By slipping this over a running vine and tying the ends loosely, the insects were put under nearly natural conditions. This bag could be raised without disturbing oviposition, and one could readily make observations and remove clusters of eggs. All eggs were rejected unless I knew their age to within fifteen minutes. By continuing these observations for seven weeks I obtained a large number of eggs of known age. The leaves bearing these eggs were kept under a bell-jar to prevent excessive wilting. Eggs adhere so firmly to the leaves that they are not dislodged by the operations of killing and fixing. From five to ten eggs at a time were thus removed and placed in hot corrosive sublimate--acetic acid killing fluid. This consisted of a saturated solution of mercuric chloride in 35 per cent. alcohol with 2 per cent of glacial acetic acid. Eggs were left in the killing fluid for two hours, and then transferred to 60 per cent. alcohol for six hours. They were then left in 80 per cent. alcohol for six hours and finally preserved in 95 per cent. alcohol. Several series, complete from deposition to hatching, were obtained, the intervals between successive stages being never greater than two hours.

Material can be collected from the middle of June until late Fall. The first squash bugs appeared on the vines June 15 and the bugs were numerous June 21. Eggs were found June 18 and

were fairly abundant June 23. They hatch in from nine to twelve days. I found no exception to this rule, though Chittenden ('99) places the period at from eight to thirteen days. Clusters of eggs were on the vines August 15, and oviposition undoubtedly continues much later than that date. On November 4, after the vines were dead, A. tristis was found in very large numbers on partially ripened, unpicked squashes and pumpkins. These insects, together with Diabrotica vittata, were literally eating to the center of the fruit. At this time no eggs were found and there were no nymphs of the first and second stages, though all other stages were abundant. The third instar,* however, was not so abundant as the fourth and fifth. The instars are from six to eight days in length, excepting the first, which has a length of about five days. Chittenden ('99) places this period at three days, a period which is too short, so far as my own observations go. Granting the maximum time for each stage, the eggs which produced nymphs of the third stage November 4 were deposited as late as the first of October.

Length of stages.

Egg	-----	9 to 12 days.
1st Instar	-----	4 to 6 days.
2nd "	-----	6 to 8 days.
3d "	-----	<u>6 to 8 days.</u>
Total		25 to 34 days.

* The term "instar," suggested by Fischer and recommended by Sharp, is here adopted for the sake of convenience.

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A careful search November 16 revealed no third instar. No dead nymphs could be found, either, so that the third instar must have changed to the fourth or fifth within this period. Material can thus be collected until the middle of October if food is abundant, as it was in this instance. The most rational conclusion is that the collector will find two broods from which to gather material provided the food supply holds out during the Fall months.

METHODS.

By far the greater portion of the work was done under a Greenough's Binocular Microscope. Eggs less than seventy-five hours old were stained in toto and decolorized with 5 per cent. acid alcohol until the germ band could be distinctly seen in the yolk mass. The yolk could then be removed easily. At the age of about seventy-five hours the appendages take on a bright red color, which deepens and extends as development proceeds. Such germ bands can be isolated without artificial staining, though staining is essential for the proper differentiation of parts. Later stages were often partially dissected in order to facilitate staining. After removing the chorion and embedding in hard paraffine, serial sections were made with a Minot-Zimmermann microtome. Sections of earlier stages were cut to a thickness of 10μ , while those of nymphs and adults were in most cases as thick as $16\frac{2}{3}\mu$ or 20μ . Sections were affixed to the slide with Mayer's albumen fixative, and then stained with Grenacher's borax-carmin, orange G, Delafield's haematoxylin or safranin. Carmine and orange G were particularly serviceable both for sections and

for in toto preparations. Aniline green was found to be an excellent stain for chitin.

Dissections were made in glycerine. Temporary preparations were left in glycerine, and permanent mounts were made in Canada balsam. Objects were examined both by transmitted and by reflected light. When tissues were too hard or too brittle, treatment with boiling water removed the difficulty. Adults and nymphs were collected late in the season when they had assembled in large numbers on such fruit as remained in the patch. These insects were killed and then preserved in 95 percent. alcohol.

Outlines and proportions for all the drawings were obtained by the use of the Abbe' camera lucida.

THE EGG.

When deposited, eggs may be light in color but are usually dark red or brown. Light colored eggs usually, but not always, turn darker on exposure to light.

The egg is roughly triangular in cross section, with the dorsal side flattened somewhat at the place of attachment to the leaf. The other two sides are strongly rounded. The dimensions are as follows: longitudinal axis 1.70 mm., transverse axis 1.18 mm. and dorso-ventral axis 2.25 mm. These dimensions vary but slightly in different eggs. Before oviposition the dorsal surface of the egg is somewhat concave, but as development continues this fills out until the egg is nearly circular, in all instances in which it is not pressed firmly against the leaf at oviposition. When eggs rest lightly on the tips of leaf-hairs, as they fre-

quently do, the cross section is almost circular. But usually, after breaking down the leaf-hair by a slow forward and backward movement of the plates of the ovipositor, the female presses the egg firmly against the leaf surface. When thus attached there is more or less flattening of the dorsal surface of the egg. A small amount of a mucilaginous secretion fastens the egg to the leaf. The leaf-hairs frequently adhere to this substance, and some writers, as Chittenden ('99) have mistaken this hardened secretion and the portions of the leaf adhering to it for a protuberance, or "nipple," belonging to the egg itself. There is not, however, the slightest indication of any thickening, extra curvature, or other modification of the chorion at the place of attachment.

Near the anterior pole of the egg is a lid, which is removed when the nymph emerges. The lid, ventral in position, is delimited by a light colored border, even at the time of oviposition. The chorion is marked off into very regular hexagonal areas. Just beneath the chorion is the delicate vitelline membrane.

From 9 A.M. to 1 P.M. I found to be the usual time for oviposition and eggs are seldom laid at any other time. The female usually selects an angle between the veins on the under side of the leaf, turns her head toward the edge of the leaf, and places her eggs in rows, in a rather compact mass. The egg is placed with the ventral surface downward, when leaves are in their normal position. Nymphs emerge head first, after loosening the lid and pushing it off.

All the eggs of a cluster have the same hatching period, with but little variation. It takes the female from one to two

hours to deposit a cluster of eggs, and the interval between the appearance of the first and the last nymphs from the same cluster is seldom greater than three hours. The blastoderm becomes evident when the egg is about twelve hours old, and segmentation is in process at thirty hours (Plate I, Figure 1). The primitive band is of the invaginated type, occupying a superficial position near the ventral surface of the egg. The major portion of the band always remains near the ventral surface, but the posterior segments and the antennae extend around beyond their respective poles of the egg. The protocerebrum and deutocerebrum can be distinguished easily from other segments when the eggs are thirty hours old, but the remaining segments are very similar to each other. (Plate I, Figures 1 and 2). The germ band consists of twenty segments, six of which are cephalic, three thoracic, and eleven abdominal. The protocerebrum appears at approximately twenty-one hours as a pair of large lobes, and the deutocerebrum, bearing the antennae, appears at about the same time. The thoracic segments develop faster than the remaining ones (Plate I, Figures 1 and 2 th.). There is a rather gradual diminution in size from the metathoracic segment (Plate I, Figure 1, th. 3) forward to the tritocerebral segment (Plate I, Figure 1, tr.). Within a few hours after the appearance of the protocerebrum the fundamentals of appendages appear and the difference between the segments becomes more apparent. The labrum appears also at this time, or when the egg is about forty hours old. When it is fifty hours old, the inequality of development in different regions shows very prominently.

Rudimentary abdominal appendages first appear when the germ

band is about thirty-five hours old. Fifteen hours later these appendages stand out rather conspicuously on the first eight abdominal segments (Plate 2, Figure 3, ab.,ap.). They are less distinct on the ninth and tenth segments, and are difficult to detect, although present, on the last segment. These rudimentary appendages become more prominent on all the segments and reach their maximum development when the egg is about seventy hours old (Plate 2, Figure 4, ab.,ap.). They are then slowly resorbed, but persist, however, until revolution occurs, when they disappear.

When about seventy-five hours old, the fundaments of the compound eyes appear at the outer border of each protocerebral lobe, and at ninety hours they become conspicuous.

Previous to its revolution the germ band lies near the ventral surface of the egg with the head at the posterior pole of the egg and the appendages pointing toward the dorsal surface (Plate 3, Figure 7). Just before revolution, the appendages change position so that their tips point toward the median ventral line. When the egg is about one hundred hours old the caudal portion of the germ band moves rapidly toward the posterior pole of the egg (Plate 3, Figure 8). The head quickly migrates to the anterior pole (Plate 4, Figure 1) where it remains until the nymph emerges. This figure corresponds with that of *Pyrrhocoris apterus*, Karawajeff ('93) (Plate 2, Figure 46). Very soon after revolution the legs, which now point toward the median ventral line, elongate, cross the median line and interdigitate. The abdominal portion of the germ band now grows up the sides of the egg and closes over at the median dorsal line of the egg, thus enclosing the yolk mass within the abdominal walls. The organs

remain in the above described position until emergence. The process of revolution is a very rapid one, and requires but two or three hours for its completion. The three figures referred to above, (Plate 3, Figures 7 and 8, and Plate 4, Figure 9), represent eggs from the same cluster, a fact which indicates how rapidly migration proceeds during the process of revolution.

ANTENNAE.

The antennae are the first appendages to appear, and they are visible when the egg is twenty-five hours old. The antennal fundamentals arise as evaginations of the deutocerebrum. When viewed externally they appear to be posterior to the labrum, but sections prove that the labrum has its origin posterior to the bases of the antennae. The fundamentals show a slight constriction when thirty-one hours old (Plate 1, Figure 2.). Growth occurs throughout the entire appendages, but it is most rapid, however, in the apical region. The segmentation of the antenna begins at the base and proceeds toward the apex, until at length the four segments are formed. Soon after its formation the fourth segment becomes larger than the remaining three segments. Previous to revolution, the antennae point forward with tips curving inward so as to meet in front of the head. After revolution they point caudad and are paramedian in position, one on each side of the labium. During the period when the egg is from seventy to ninety hours old the forward migration of the antennae occurs. They are post-oral in origin, but this forward movement, together with a backward migration of the labrum and the oral region,



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leaves the bases of the antennae anterior to the stomodaeum and to the compound eyes. At the time of emergence, the antennae are clothed rather sparsely with stout setae. The fourth segment has, in addition, numerous fine setae. The segments are sub-^{e}}elliptical and nearly uniform in size when the insect emerges. During the nymphal stages, however, the second and third antennal segments become more slender. The joint between the third and fourth segments is of special interest in that it presents a very short, but distinct, sub-segment in the antennae of the adult insect. The sub-segment is not found in any stage of the nymph, but the fifth instar has an elongated third joint preliminary to the formation of this sub-segment. The structure is apparently of great service in giving freedom of motion to the outer, or tactile, segment. Such freedom of motion is possible in the nymph without this provision, since the antennae are not heavily chitinized, but this special structure is essential to the hard unyielding antennae of the adult insect.

LABRUM AND CLYPEUS.

The labrum arises as an evagination of the anterior part of the tritocerebrum, and first appears when the egg is from thirty-five to forty hours old. It has its origin posterior to the antennae, but protrudes forward between their bases during the early stages of its development (Plate 2, Figures 3 and 6 lr.). When about fifty-five hours old the anterior border of the labrum is almost a straight line, with a slight median indentation (Plate 2, Figure 5 lr.). This indentation may have led to the erroneous

conclusion of some authors that the labrum is a paired organ. Careful examination, however, proves that the labrum is not a paired organ, but a single median evagination, as found by various other authors. The labrum (Plate 2, Figures 3 and 5, lr.), corresponds, in every important detail, with the labrum of the mandibulate type- compare my figures with those of Calopteryx, Brandt (Plate 1, Figure 11, v.), Forficula, Heymous, (Plate 1, Figure 9, ab), and Oëcanthus, Ayers (Plate 18, Figure 15). When it is seventy-five hours old, the labrum begins a rapid elongation; and, at the same time, it begins the migration which eventually leaves it situated between the bases of the antennae and somewhat posterior to them. The migration is accompanied by a change in direction, so that the organ points caudad.

The first evidence of oral invagination appears just when migration begins. A distinct stomodaeum is formed by the time revolution occurs, and the cells surrounding this opening are closely connected with the ventral surface of the labrum. At the base of the labral fundament, an enlargement appears which from its situation, may be termed the epipharynx. The stomodaeum lengthens and develops until it extends far back through the thorax to the stomach. Just after revolution the clypeus appears as an enlarged thickened area at the base of the labrum (Plate 4, Figure 10, cl.). This area is separated from the labrum by a distinct groove within twelve hours after revolution. While this groove is forming, the sides of the clypeus grow forward and side-ward for some distance and thus form an elongate, rather narrow piece on each side of the base of the labrum. These pieces occupy the same relative positions in the adult insect as the areas in the Cicada head which Smith ('92), Marlatt ('92⁵), and Meek

('03), term the "mandibular sclerite." Any one investigating A. tristis from the purely anatomical standpoint, as these three investigators have done with Cicada, might easily fall into the error of calling these areas "mandibular sclerites." The more trustworthy embryological studies, however, show the true origin to be from the clypeus. This fact suggests the possibility that the "mandibular sclerite" of Cicada may not have its origin in the mandibular segment. At any rate, it is certain that there is no "mandibular sclerite" in A. tristis. The labrum, before emergence, becomes transversely and deeply grooved on the dorsal surface, and these grooves persist in the adult insect. The labrum is hinged to the clypeus by an articulation which allows considerable freedom of motion. The labrum is slender and pointed, and extends in a depression down to the middle of the second segment of the labium. Into this depression the labrum fits very closely, when in its normal position. On its ventral surface, the labrum is deeply grooved, to admit the mandibular and maxillary setae. At the base of the labrum this groove is completely closed by heavily chitinized walls which hold the setae securely within the base of the groove (Plate 5, Figure 1, lr.). The groove gradually becomes shallow until at the tip of the labrum there is only a shallow furrow for the setae (Plate 5, Figure 2, lr.). For about one half the distance from base to tip of the labrum, the setae lie entirely within the labral groove (Plate 5, Figure 3, li.gr.). At the middle of the labrum, the labium and the labrum share about equally in surrounding the setae, while near the tip of the labrum the setae lie almost entirely within the labial groove. It is easily to be seen that the labrum acts mechanically in bending the setae into position. It thus plays a

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very important part in guiding and supporting the setae in their movements within the labial groove.

INTERCALARY SEGMENT.

When the egg is thirty hours old, the intercalary segment is well developed (Plate I, Figure 1, tr.) and it is almost as large as the mandibular segment (Plate I, Figure 1, md.).

The intercalary segment gives rise to the labrum. Soon after the formation of the labrum, however, the intercalary segment becomes so modified and so united with other segments of the head that it can no longer be distinguished as a separate segment.

MANDIBLES.

The fundamentals of the mandibles appear when the egg is about thirty-five hours old, and ten or fifteen hours later they are quite conspicuous (Plate 2, Figures 3 and 5, md.). Until the egg of A. tristis is about fifty hours old, the germ band resembles that of Orthoptera and Odonata so closely that it would be impossible to say whether the fundamentals of the mouth parts will develop into the suctorial or the mandibulate type. This ^bpart, in connection with the other well known evidence, may be taken to indicate that the suctorial type originated from a mandibulate type. The mandibular fundamentals, like those of the maxillae and the labium, are evaginations of the germ band. During revolution, the ventral portion of the germ band where the mouth parts are attached grows rapidly anterior to the mandibular fundamentals and is partially resorbed posterior to the labial fundamentals. Not all of the germ band takes part in this extra development, so that the

mouth parts, which are at first at right angles to the germ band, become parallel to it. When revolution is completed the bases of the mandibles withdraw into the head. The process of revolution, together with the withdrawal into the head, bends the basal portion of the mandible, so that it curves ventrad, leaving little or no direct connection with the top of the head. The tips of the mandibles retain their position, but the bases rapidly retreat within the head, growing rather close to the side walls of the head. The bases of the mandibles soon lose their connection with the group of cells from the germ band, and the curvature increases as growth proceeds until the bases are distinctly coiled.

By the time the egg is about one-hundred-forty hours old the mandibles extend to the posterior part of the head. Yet this backward growth does not cease then, but continues until the base of the mandible reaches the metathorax (Plate 5, Figure 14, md.).

Here the base of the organ remains coiled up until emergence.

While the mandible is elongating, a muscular sheath forms around it near the tip, (Plate 5, Figure 15, mu.s). The muscular fibres connected with this sheath are attached to the sides and top of the head. The mandibles first enter the labral groove during the process of emergence. To do this, they slip down through the muscular sheath, uncoil, leave the thorax completely, and move forward until the knob-like structure at the base of the organ reaches the sheath (Plate 6, Figure 16, k.). This change of position is a very rapid one and is certainly brought about by the movement of the muscles when the insect struggles out of the shell. A very large number of specimens just ready to emerge were dissected and in these the mandibular setae were always coiled in the

thorax. Large numbers of nymphs were dissected just after emergence--some even before the legs were entirely unfolded, but the setae had moved down into the labral and labial grooves and their bases were always forward within the head, or at the muscular sheath. If a nymph just ready to emerge is dissected, the setae may be easily slipped back and forth through this sheath, by a little skillful manipulation. Figure 15, Plate 5, and Figure 16, Plate 6 represent dissections from the same cluster of eggs-- Figure 15 is from a specimen just ready to emerge and Figure 16 is from a nymph barely out of the shell. The position of the base of the mandible relative to the sheath, shows how far the setae migrate in the brief period of a few minutes. Certainly the setae travel a distance equal to the length of the labium, for they never enter the beak before emergence, and they are always thrust down the entire length of the labium immediately after leaving the shell. This description of the mandibular setae and their migration into the beak applies equally well to the maxillary setae, for the mandibles and maxillae act together in all these changes and movements.

Immediately after revolution, each mandibular fundament presents a very shallow groove, extending along the inner surface of the fundament for the entire length of the organ. This groove deepens and its borders close over and unite. This process leaves a hollow tube of ectodermal cells entirely inclosed within the fundament. These cells secrete the chitinous substance which forms the mandibular setae. Figure 17, Plate 6, although representing the maxillary fundament, will illustrate equally well the development of the mandibles, since the fundaments of the mandibles

and maxillae develop in essentially the same way (Plate 6, Figure 18). Owing to their mode of formation, the mandibles contain a central cavity which is closed, however, at the base and at the tip of the organ.

The mandibular setae are very small as compared with the mandibular fundaments, and the fundaments become smaller as the cells differentiate and assist in forming the chitinous setae. This shrinkage leaves the clear wall of the fundament more or less wrinkled, but entirely enclosing the seta. The seta ruptures this wall at its tip while the insect emerges, after which the clear wall completely disappears. The enlarged basal portion of the mandibles and maxillae (Plate 6, Figure 16) disappears as the nymph develops and the basal portion of the seta becomes slightly larger than the remaining chitinous part.

In the nymph and the adult, the brown chitinous mandibles are situated laterad of the maxillae and are held closely to the latter by a neatly fitting articulation (Plate 7, Figure 19, md. a.). This joint permits of a free lengthwise movement of the mandibles, independently of the maxillae, but does not permit, however, any lateral movement. An examination of these joints (Plate 7, Figure 19) will make clear the cause of the difficulty experienced in an attempt to separate the setae. The labral groove holds the setae firmly where they leave the head, and the tube formed by the labrum and the labium supports them and helps to prevent the separation of the long slender setae. The mandibles are uniform in structure throughout most of their length, but the tip presents several distinct barbs (Plate 7, Figure 20) which doubtless serve to hold the mandibles in the tissues of the

food plant. Just above these barbs there is a piece projecting anteriorly on each edge of the mandible (Plate 7, Figure 20, md. p.) which probably serves to prevent the organ from entering too far into the tissues. Just above this plate, the ventral edge is serrate for a short distance (Plate 7, Figure 20, md.se.). The dorsal edge is joined to the maxilla of the same side, but is thin and extended, and near the tip, has grooves running from the center of the organ downward and toward the dorsal border. Extending to the dorsal border, these grooves give it a slightly serrated appearance also. This modified tip of the mandible is not joined to the maxillae, as is the remainder of the mandible, but it is held to them only by the grooved labium. When drawn out of the labium the lower ends of the mandibles become free from the maxillae and usually curve outward to some extent. This free portion is concave on the inner surface, thus allowing a passage way for the fluids to and from the maxillary tubes. It is important to note that only a part of the mandibular fundament takes part in the formation of the mandibular seta. The finished mandible is, consequently, homologous with only a part of that of the mandibulate type.

MAXILLAE.

The maxillae retreat into the head, coil up in the thorax ^{or} from the setae by invagination along the entire fundament, and migrate into the beak exactly as was described in the case of the mandibles. There are important differences, however, which de-

serve special attention.

The maxillae are situated posterior to the mandibles, and like the latter, are attached to the walls of the head by means of muscles. A distinct maxillary palpus appears laterally at the base of the maxillary fundament when the egg is seventy-five hours old, and this palpus is prominent when revolution occurs (Plate 7, Figure 21, mx.p.). The palpus enters the head with the maxillary fundament. When the egg is one-hundred-and-forty hours old, this palpus is still found near the tip of the maxillary fundament, but has undergone considerable modification (Plate 6, Figure 17, mx.p.). Modification continues until the maxillary palpi form pointed chitinous pieces which fit closely into a V shaped cavity at the base of the labrum (Plate 8, Figure 22, mx.p.). There is thus formed a very hard chitinous bridge, consisting of the two modified palpi pressed closely together. The upper surfaces of the palpi slope toward the median plane of the body thus forming a trough or groove in which the setae move at the point where they enter the labral groove.

Within the beak, the maxillae are the inner pair of setae (Plate 8, Figure 23 mx.). They are larger than the mandibles, but the walls of the maxillae are not quite so heavy as those of the mandibles. Like the mandibles, the maxillae develop as a closed tube, the lateral walls of which grow together in such a way as to divide the lumen of the tube into two canals--one dorsal and the other ventral (Plate 8, Figure 23, lu.). The inner face of each maxilla bears two grooves such that when the maxillae are brought together, two open tubes are formed. The dorsal tube is the larger and is confluent with the ph^orynx at the base of the

tube. The distal end of the tube opens on the side of the maxillae a little above their tips, (Plate 8, Figure 24, f c o). The opening is guarded by a broad flattened piece which is fastened below but is free above, and stands out a little from the opening (Plate 8, Figure 24, vX). The ventral tube which is smaller in caliber, connects with the "Wanzenspritze" and opens at the distal end in much the same manner as the larger canal (Plate 8, Figure 24, s c o). This canal, however, opens a little nearer the tips of the maxillae than does the food canal. The apices ~~tips~~ of the maxillae are very sharp and can readily pierce the food plant.

The tongue and groove articulations holding the maxillae together are very perfectly made and are somewhat complicated (Plate 8, Figure 24, mx.a). These joints hold so perfectly that it is almost impossible to separate the maxillae without thrusting a needle between their bases back within the head of the insect. The maxillary setae may be moved lengthwise and alternately with perfect ease. The joints are so perfectly fitted that they are doubtless air tight, especially where the walls of the labrum press upon the setae. In this manner the tubes are perfectly adapted to their offices of conveying the plant juices brought up by suction and the saliva forced down by pressure. Indeed, this pressure required to force the saliva into the tissues of the food plant, makes this perfect union of the maxillae a necessity. Otherwise, the pressure would doubtless separate the setae, and thus destroy the tube. The edges of the maxillae are smooth throughout and there are no teeth or barbs near the tip such as are found on the mandibles. Only a part of the maxillary fundament is involved in the formation of the finished

maxilla, thus, as with the mandibles, the maxillary seta is homologous with only a part of the maxilla of the mandibulate type.

LABIUM.

The labial segment is larger than the other segments which give rise to mouth parts, even when the egg is only thirty hours old (Plate 1, Figure 1, li). When the egg is fifty hours old the labial fundaments are prominent and are considerably longer than the fundaments of the mandibles and the maxillae. The fundaments of the labium continue to develop more rapidly than those of the mandibles and maxillae and by the time revolution occurs they are fully three times as long as the maxillary and mandibular fundaments. Immediately after revolution the labial fundaments begin to unite at the base (Plate 9, Figure 25 li). This union of the fundaments proceeds from the base until they are completely united. Figure 10, li, Plate 4 is from a specimen killed a few hours after revolution, and presents the halves of the labium almost completely united. About this time, also, the segmentation of the labium begins (Plate 9, Figure 26, li). The hypophorynx appears at the base of the labium a few hours after revolution (Plate 9, Figure 26, hy).

Just previous to revolution, labial palpi are found laterad of the main labial fundament (Plate 9, Figure 27, li p). After revolution these palpi disappear during the expansion of the basal walls of the labial fundament to form the lower surface of the head. Figure 26, li p, Plate 9 presents traces of the palpi, which are now very much less distinct than they were before revo-

lution, and the palpi become still less distinct as development proceeds.

The labium is by far the most conspicuous of the mouth parts in the adult insect. It is four-jointed and lies, when at rest, on the median ventral line of the body. The labium reaches to the bases of the hind coxae. The groove on the dorsal side of the labium is broad and shallow at the base and thus permits the labrum to lie partially within the trough so formed. Below the tip of the labrum, which reaches to the middle of the second labial joint, the groove deepens and completely envelops the setae. Near the tip one edge of the labium overlaps the other, and the inner surface bears a chitinous projection (Plate 9, Figure 28, li ch), which is doubtless concerned in some way with the operations of the setae in piercing the food plant. This chitinous projection is found only near the tip of the organ. The labial groove is not formed as soon as the labial fundamentals unite, but it is formed only a short time before the insect emerges. It forms along the dorsal line of union of the labial fundamentals, but not until the labium has become a single organ. The apex of the labium is covered with specialized setae which are, doubtless, organs of touch. Their position and nature make it impossible to thrust the labium into the food-plant. The simple setae covering the labium and pointing downward would also prevent this organ from entering the tissues. The extreme tip of the labium, however, is so modified that it might spread out slightly, so as to press the inner surface of the labium firmly against the leaf and form a narrow disk around the organ to protect the plant juices from exposure while the setae are in action. Such a procedure,

though lacking confirmation by observation, seems probable from the structure of the beak. Each segment of the labium has a distinct set of muscles which move it upon the preceding segment. These muscles have their origin dorsally at the distal end of the segment and their insertion on the ventral side of the following segment a little behind its distal end. Chitinous tendons assist in the attachment of these muscular fibers. Figure 29, li r, Plate 10 represents the basal segment of the labium and shows a muscle which bends the organ toward the body. The basal segment also bears a muscle (Plate 10, Figure 29, li e) which doubtless acts in opposition to the muscle just mentioned.

Since the labial fundaments in their entirety form the labium of A. tristis, this organ can probably be homologized with that of the mandibulate type. The necessary embryological studies of the mandibulate labium, however, have not been made, and without these studies, an attempted comparison would doubtless lead to error.

PHARYNX.

The stomodaeal invagination forms the pharynx and the aesophagus, as usual. Soon after revolution, the outlines of the chitinous walls and muscles of the pharynx may be detected beneath the labrum and the clypeus. A cross section of the pharynx (Plate 10, Figure 30) best illustrates the structure of this organ. A chitinous frame-work (Plate 10, Figure 30 f), with muscular fibres between its walls, serves as a base for the chitinous floor of the canal (Plate 10, Figure 30, Vf1). This lower wall of the

canal is broadly U shaped and is very heavily chitinized and rigid. To the ends of this piece a thinner chitinous piece (Plate 10, Figure 30, dl) is attached. This plate, when in its normal position, follows the outline of the U shaped floor. The upper piece, however, has a series of strong tendons attached to the middle of the cross section, and by means of these it may be drawn away from the floor and the canal thus be opened (Plate 11, Figure 31, o). This movement may be readily produced by the strong pharyngeal muscles attached to the tendon (Plate 10, Figure 30, pm). Such an action, by producing a partial vacuum, doubtless brings the food through the beak and into the pharynx.

A smaller chitinous tube connects the pharynx with the dorsal maxillary tube. This is accomplished by means of a fine chitinous tube which enters the maxillary tube at the point where the two maxillae unite. The connection between the maxillary tube and the pharynx is a very delicate one, but it serves perfectly to form a passageway from the tips of the maxillae to the pharynx when suction begins. Figure 32, Plate 11 illustrates how the chitinous tube from the pharynx and that from the "Wanzenspritze" run side by side just before entering and connecting with their respective maxillary tubes. It will thus be seen that the pharynx forms a suction pump of considerable power. When the upper, or thinner chitinous wall of the pharynx is lifted so as to form a $\frac{a}{v} \frac{u}{\phi} \frac{c}{\chi}$, it is placed under considerable tension. When the muscles which lift it retract, the elasticity of the chitinⁱⁿ forces the piece downward to its original position and this forces the food back into the ^oaesophagus. When the ends of this upper piece are broken loose they immediately take the position shown in Plate

msent

11, Figure 33. This is sufficient proof of the elasticity of the piece and of the fact that elasticity tends to throw the cross section of the piece into circular form. If the ends of an elastic piece shaped like that shown in Plate 11, Figure 33 should be pulled apart and downward for a distance the tendency of the central portion (Plate 11, Figure 33 c) would be to move downward. This is exactly the condition of the upper wall of the pharynx. The chitinous upper wall tends to coil up, but the edges are securely attached to the edges of the lower wall. The central portion to which the tendons are attached thus moves downward to the lower wall and closes the cavity as soon as the muscles relax.

The pharyngeal muscles are attached to the dorsal wall of the head, and they are arranged in pairs (Plate 10, Figure 30, pm). I found no valves in the pharynx, but these are not necessary, however, for its operations. A rythmic motion of the pharyngeal muscles would accomplish the same result as would valves. The anterior muscles probably contract first and then are followed in turn by the posterior muscles. These muscles doubtless relax in the same order as they contract. Such action would make valves wholly unnecessary, and yet the pharynx would be an effective suction pump.

WANZENSPRITZE.

The hypopharynx, which appears very soon after revolution (Plate 9, Figure 26, hy) gives rise to the "Wanzenspritze" (Plate 12, Figure 34). This remarkable organ is situated near the ventral wall of the head. It has heavily chitinized walls forming a

distinct chamber (Plate 12, Figures 34 and 35, ch). This chamber is provided with inlet and outlet tubes. The inlet tube or salivary duct, (Plate 12, Figure 35, st) leads from the salivary glands, empties on the ventral side of the chamber and is provided with a valve to close the opening (Plate 12, Figure 35, iv). This duct divides into two branches a very short distance from the chamber, one branch leading to each of the salivary glands. These glands are located in the dorsal portion of the metathorax, and are rather large, crow-foot shaped organs (Plate 12, Figure 36). Meek ('03) finds the salivary glands of Cicada "in the rear and upper part of the head," certainly a different location to what I find in A. tristis. The salivary reservoir mentioned by some authors is not found in connection with the salivary ducts. These ducts are glandular in structure, long, slender, and are practically free from convolution. The opening for the passage of the saliva is of uniform size throughout the entire length of the ducts (Plate 12, Figure 37, od).

The outlet tube, leading from the dorsal side of the chamber is also provided with a valve (Plate 12, Figure 35, ov), but this structure is not so strong as the valve to the inlet tube. The outlet valve doubtless serves to prevent the saliva from returning to the chamber of the "Wanzenspritze" when the piston is drawn back to allow the saliva to flow into the partial vacuum thus formed. This outlet tube leads to the ventral tube of the maxillae. In order to reach the point where the maxillae unite, the tube runs very close to the pharyngeal tube previously mentioned (Plate 11, Figure 32). The connection between the outlet tube and the ventral maxillary tube is like the pharyngeal con-

nection, made by a fine, chitinous, closely-fitting tube extending down and uniting with the maxillary tube.

A heavily chitinized dark brown piston (Plate 12, Figures 34 and 35 pn) works in the chamber of the "Wanzenspritze." This piston is hollowed at its anterior extremity and appears as though this might be a provision for spreading the end of the organ if it should be thrust forward against the anterior walls of the chamber. The piston is drawn backward by a strong chitinous tendon (Plate 12, Figures 34 and 35, tp). The walls of the chamber appear concave at its posterior end where they unite with the tendon of the piston (Plate 12, Figure 35 co). No doubt this wall is made convex when the strong "pump muscles" attached to the tendon contract and draw the piston back. The chitinous walls thus drawn out of their normal position are doubtless placed under considerable tension. When the muscles relax this elastic piece throws the piston forward into its original position. When the piston is drawn back, the chamber is enlarged and a partial vacuum is produced. This permits the entrance of the saliva from the salivary ducts and glands and the chamber fills with this fluid. When the saliva is needed, the muscles relax and the chitinous walls throw the piston forward. This movement closes the inlet valve and forces the saliva through the outlet tube and ventral tube of the maxilla to the lower maxillary opening where it comes into contact with the food plant. Meek demonstrated this chitinous elasticity in the "Wanzenspritze" of Cicada, and the same principle doubtless underlies the working of this organ in A. tristis and other Hemiptera.

From the anterior portion of the "Wanzenspritze" two chi-

tinous arms extend backward, one on either side of the chamber. These arms are broad, and the muscles which control the piston are attached to their posterior portions (Plate 12, Figure 34,a). There is no attachment of these muscles to the head walls, but only to these arms and the tendon which controls the piston.

The development of the "Wanzenspritze" from the hypopharynx may be traced by dissections, beginning with eggs one hundred hours old and running to those about two hundred hours old.

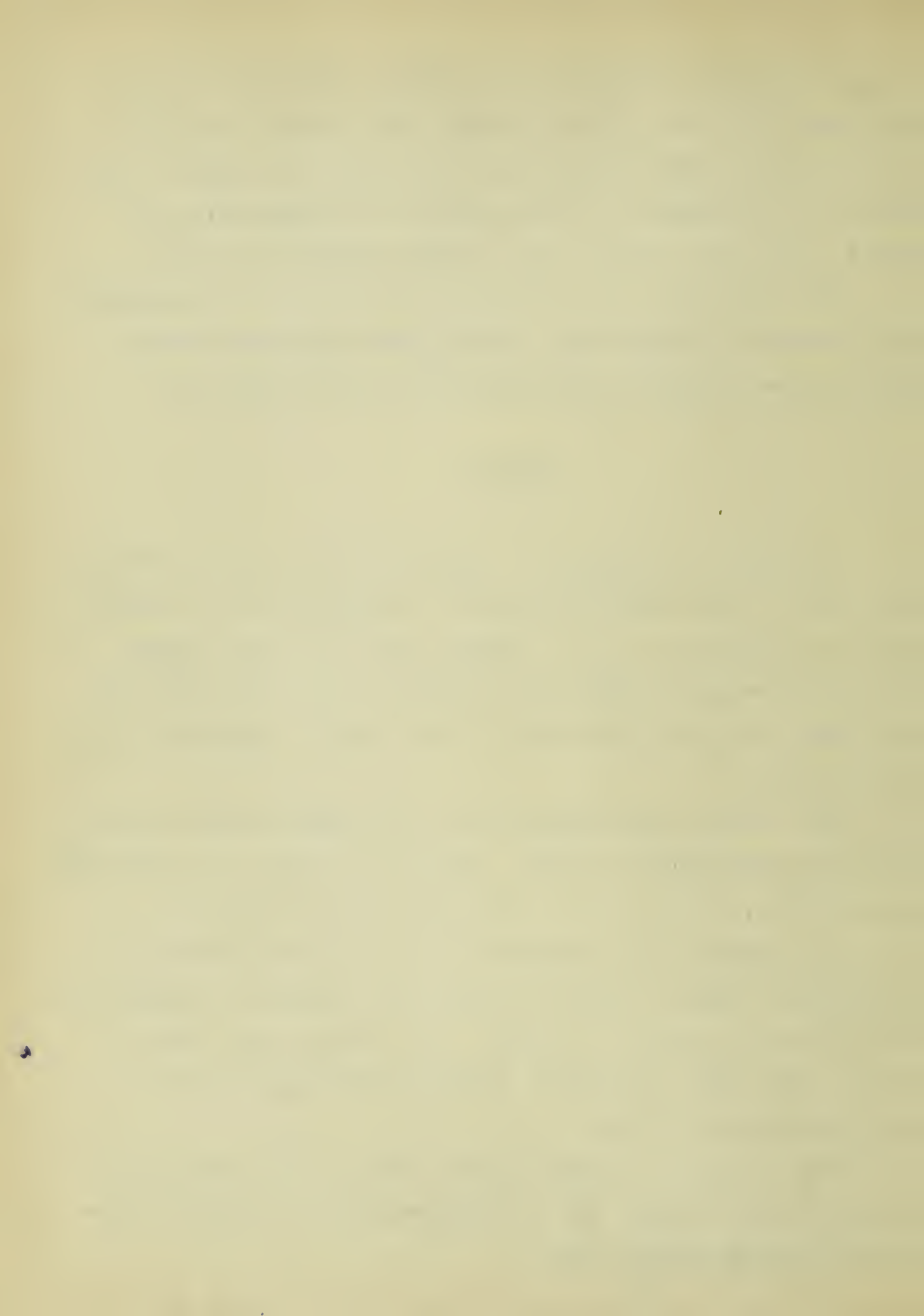
SUMMARY.

The head of A. tristis is composed of six primary somites. The first of these segments bears the compound eyes, the second bears the antennae, while the third gives rise to the labrum. The fourth segment produces the mandibular setae, the fifth the maxillary setae, and the sixth, or last segment, forms the labium, or beak.

The antennae are evaginations of the deutocerebrum and are the first appendages to appear. They are post-oral in origin and, by migration, become pre-oral just previous to revolution.

The labrum is an evagination of the tritocerebrum and is not a paired organ. The oral invagination appears at the base of the labrum just before revolution. The clypeus takes part in forming the sides of the head, while the labrum is grooved to hold and guide the setae.

The intercalary segment appears early as the equivalent of other primary segments, but it disappears before distinct intercalary appendages are formed.



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The mandibular seta is formed by invagination along one side of the mandibular fundament, but only a part of the comparatively large fundament is involved in forming the seta. The fundaments extend to the metathorax, where they coil up until emergence. At this time, the finished mandibular organ migrates quickly into the beak and its base reaches the muscular sheath of the mandible within the head, where it remains. To this base the muscles become firmly attached. The mandibles fit closely around the maxillae, are barbed at the tips, and serve to tear the plant tissues so that the juices may be obtained readily.

In regard to their formation, situation, and migration, the maxillary setae are like those of the mandible. The maxillary fundaments, however, bear palpi, which ^{firmly} form a bridge consisting of two chitinous pieces, over which the setae pass as they enter the labral groove. The maxillary setae are twice grooved; thus, when brought together in their normal positions, they form two canals. One of these canals conveys saliva from the "Wanzenspritze" to the food plant, and the other canal conveys fluid from the plant to the pharynx. The maxillae are so completely joined together that they may move on each other longitudinally, but they permit no lateral motion. The apices of these setae are very sharp and readily pierce the food plant.

The four-jointed labium is formed just after revolution by the union of the paired fundaments of the labial segment. These fundaments bear palpi, which disappear as the bases of the fundaments enter into the formation of the lower head walls. The labial groove forms shortly before emergence. It is broad and shallow near the base of the organ, but for most of its length, completely envelops the setae. It acts as a mechanical support

and guide for the mandibles and the maxillae, and takes no part in piercing the plant tissues.

The tubular pharynx is made up of a thick chitinous U-shaped lamella, and a thinner elastic chitinous lamella which, when in its normal position, follows the outline of the ventral lamella. The upper elastic lamella is moved by means of a series of strong muscles attached to the dorsal wall of the head. The contraction of these muscles produces a partial vacuum. The organ thus becomes a suction pump. The pharynx is connected with the anterior maxillary canal, and the food is consequently pumped up this canal and into the pharynx. A rythmic motion of the upper wall of the pharynx forces the food into the aesophagus.

The "Wanzenspritze" is formed from the hypopharynx. The organ is essentially a force pump which supplies the setae with saliva. The "Wanzenspritze" is provided with inlet and outlet valves which open and close as the piston works back and forth in the chamber. The piston is drawn back by the strong "pump muscles" and it is thrown forward by the elasticity of the chitinous walls of the organ.

HISTORICAL.

The structure of hemipterous mouth-parts has been discussed by a number of authors, chief among which are Geise ('83), Wedde ('85), Leon ('87), Smith ('92), Marlatt ('92), Karawaj^eff ('93) and Meek ('03). Geise and Wedde each discussed the pharynx and the "Wanzenspritze" at some length. Geise speaks of the Pharynx in Corixa ~~Hydrocoris~~ as having many cutting and grinding processes,

while Wedde refers to that of Pyrrhocoris apterus as being "a simple unmodified tube." In A. tristis the inner walls of the pharynx are smooth throughout. The tube, however, is much modified as shown in the previous description and in Figure 30, Plate 10. Leon found the maxillary palpus to have disappeared in Pen-tatoma. He found vestigial labial palpi on one of the Tingitidae. In A. tristis the maxillary palpi are functional, but serve a purpose very different, indeed, from the usual function of these organs. This fact suggests that embryological studies might reveal these palpi similarly modified in other Hemiptera. The disappearance of the labial palpi has been previously described. Leon's conclusion that the labium is composed of submentum, mentum, glossae, and paraglossae is certainly premature since given, without the corresponding embryological data on the mandibulate labium.

With preconceived ideas as to what the parts of the hemipterous mouth represent, Smith ('92), allowed himself to propose homologies which he calls "revolutionary," and which any one making embryological investigations must certainly call "imaginary." He pronounces the so-called "mandibular sclerite" the true mandible, yet it is doubtful if this sclerite had its origin in the mandibular fundament. He says that the maxillae are represented by two setae, yet in A. tristis one pair of these setae comes directly from the mandibular fundaments and the other pair from the maxillary fundaments. He represents the labium as a part of the maxillae, also; yet in A. tristis it may be traced from the labial fundaments through every stage to that of the finished beak. Marlatt justly criticises Smith for his "erroneous conception," but Marlatt himself falls into the error of saying that the labium is

not a paired organ but is a simple one. My own figures of A. tristis show how this organ originates from paired fundamentals.

Smith, Marlatt, and Meek have investigated the mouth-parts of Cicada. Marlatt and Meek are probably correct in most of their conclusions, but they both reach, from purely anatomical data, conclusions which need the additional evidence to be furnished by embryological studies. Valuable as anatomical studies are, they have led a number of authors to the most irrational conclusions concerning the homologies of the mouth-parts of insects. Until anatomical evidence is tested and confirmed by embryological evidence, much error will continue to be published on this subject. Embryological methods are laborious and slow, but they are essential as supplementary to anatomical data, if we are to discover the truth in regard to many of the disputed points in the morphology of the insectean mouth-parts.

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EXPLANATION OF PLATES.

ABBREVIATIONS.

- a----- arms which support the muscles of the "Wanzenspritze."
 ab-----abdominal segments.
 ab ap--abdominal appendages.
 an----- antennae.
 ap----- anterior pole of egg.
 ba----- barbs.
 c----- center of dorsal pharyngeal wall.
 c e----compound eyes.
 ch----- chamber.
 cl----- clypeus.
 co----- posterior end of chamber.
 dl----- dorsal elastic lamella of pharynx.
 f----- frame supporting pharynx.
 f c----food canal.
 fco--- outer opening of food canal.
 g----- ganglion cells.
 hy----- hypopharynx.
 iv----- inlet valve.
 k----- knob at base of setae at time of emergence.
 l----- legs.
 li----- labium.
 lich---chitinous projection in labial groove.
 lie--- extensor of labium.
 ligr---labial groove.
 li p-- labial palpus.
 li r-- flexor of labium.
 lr----- labrum.

lu---- lumen of setae.
 m----- muscle.
 md---- mandible.
 md a-- mandibular articulation.
 md p-- projecting piece on mandible.
 md se- serration on mandible.
 mu s-- muscular sheath of setae.
 mx---- maxillae.
 mx a-- maxillary articulation.
 mx p---maxillary palpus.
 o----- pharyngeal opening.
 od---- opening of salivary duct.
 ov---- outlet valve.
 p----- pharynx.
 pl---- protocerebral lobes.
 pm---- pharyngeal muscles.
 pn---- piston.
 pp---- posterior pole of egg.
 sc---- salivary canal of maxillae.
 sco--- opening of salivary canal.
 se --- serosa.
 sm---- muscles of "Wanzenspritze."
 st---- tubes to salivary glands.
 th---- thorax.
 tp---- tendon of piston.
 tr---- tritocerebral segment.
 v----- valve closing opening to food canal.
 vl---- ventral lamella of pharynx.
 w----- "Wanzenspritze."
 y----- yolk.

PLATE I.

Fig. 1. Ventral aspect of the primary head segments and thoracic segments of a germ band. Egg thirty hours old. X 125.

Fig. 2. Oblique aspect of the same regions of the germ band shown in Fig. 1. Egg about thirty-one hours old. X 125.

PLATE II.

Fig. 3. Ventral aspect of germ band when the egg is fifty hours old. X 78.

Fig. 4. Lateral aspect of first four abdominal segments just previous to emergence, showing abdominal appendages. X 125.

Fig. 5. Head segments of germ band from egg fifty-five hours old. X 78.

Fig. 6. Relative positions of labrum and antennae at seventy-seven hours old. X 125.

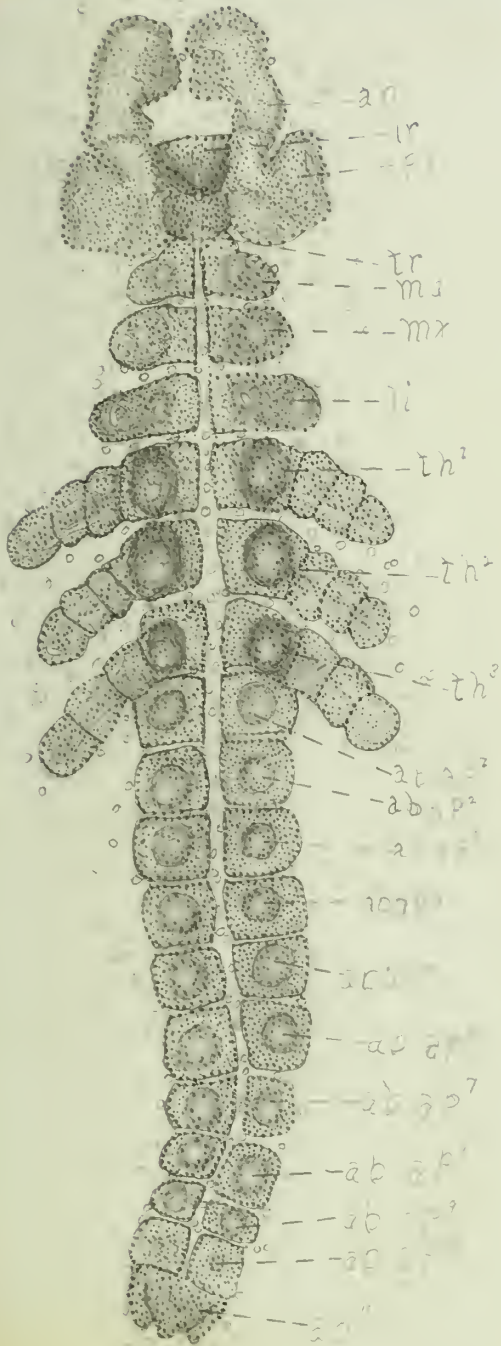


Fig. 3.

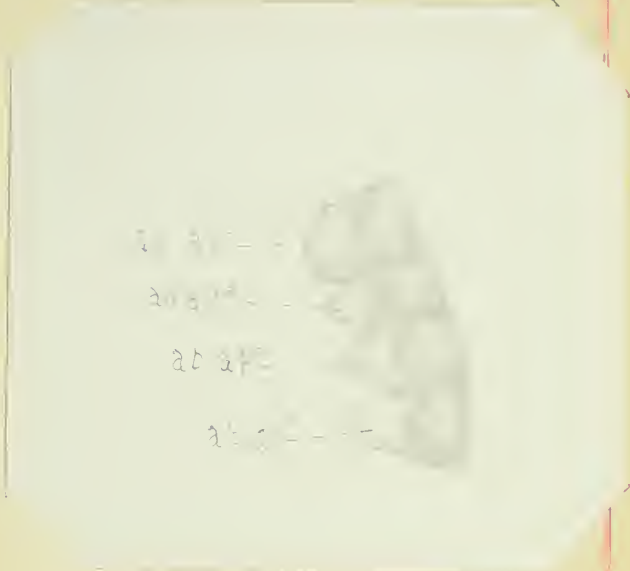


Fig. 4.



Fig. 5.



Fig. 6.

PLATE III.

- Fig. 7. Paramedian section from egg 100 hours old. Right aspect. Revolution beginning. X 98.
- Fig. 8. Paramedian section from same set of eggs as Fig. 7. Left aspect. In process of revolution. X 98.

PLATE III.



Fig. 7.



Fig. 8.

PLATE IV.

- Fig. 9. Paramedian section from egg of same set as Fig. 7.
Right aspect. Revolution nearing completion. X 98.
- Fig. 10. Frontal aspect of head a few hours after revolution. X 125.

PLATE IV.

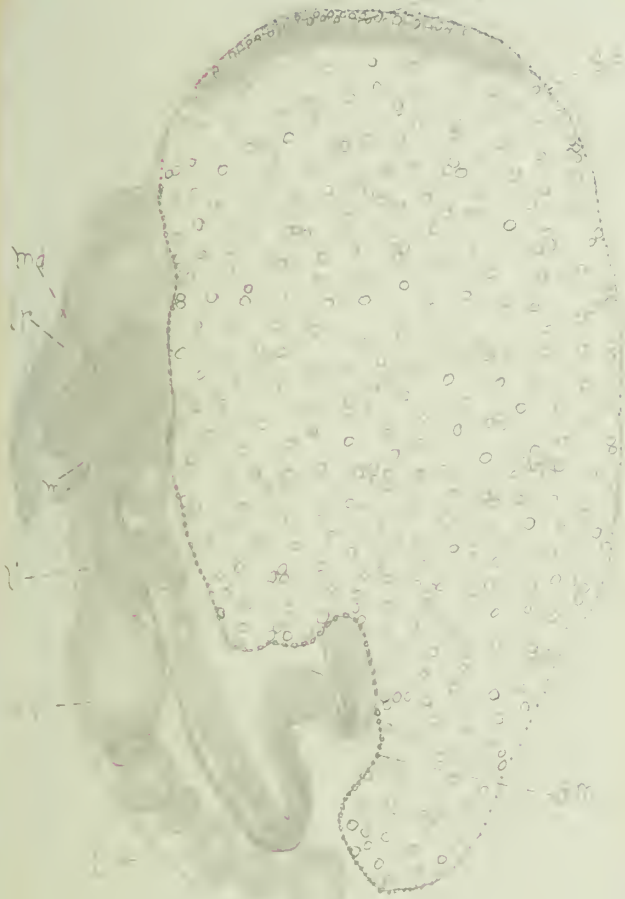


Fig. 9.



Fig. 10.

PLATE V.

- Fig. 11. Outlines of cross section through base of beak and labrum of nymph. X 98.
- Fig. 12. Outlines of cross section through middle of labrum of same nymph as ⁱⁿ Fig. 11. X 98.
- Fig. 13. Outlines of cross section near tip of labrum of same nymph as ⁱⁿ Fig. 11. X 98.
- Fig. 14. Mandiblar and maxillary fundamentals coiled in meta-thorax previous to emergence. X 52.
- Fig. 15. Position of muscular sheaths on setae immediately before emergence. X 98.

PLATE V.



Fig. 11.



Fig. 14.

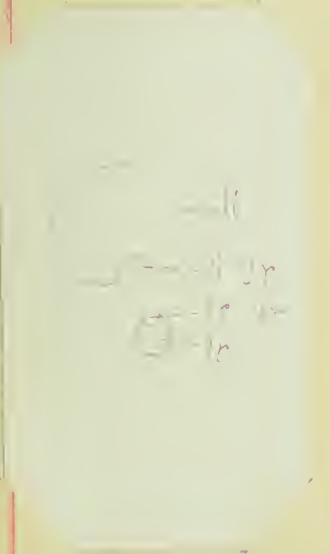


Fig. 12.

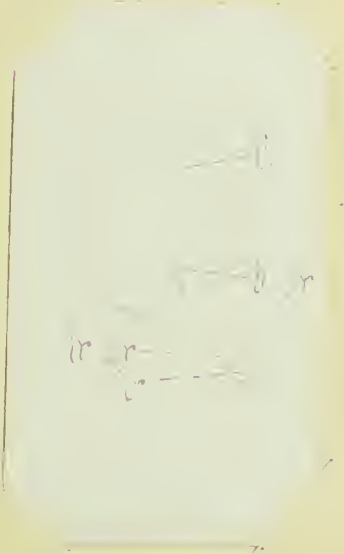


Fig. 13.



Fig. 15.

PLATE VI.

Fig. 16. Position of muscular sheath on seta immediately after emergence. Figures 15 and 16 are drawn from specimens from the same set of eggs. X 125.

Fig. 17. Maxillary fundament with palpus and groove. From egg about 140hours old. X 125.

Fig. 18. Cross section of mandible. X 650.

PLATE VI.



Fig. 16.



Fig. 17.



Fig. 18.

PLATE VII.

- Fig. 19. Cross section of setae in normal position. Nymph.
First segment. X 1350.
- Fig. 20. Lateral aspect of tip of mandible. X 1350.
- Fig. 21. Maxillary fundament at time of revolution. X 650.



Fig. 19.



Fig. 20.



Fig. 21.

PLATE VIII.

Fig. 22. Median sagittal section of head of nymph. Relative positions of pharynx, Wanzenspritze, labrum, and maxillary palpus. X 52.

Fig. 23. Cross section of setae in normal position. Nymph. Third segment of same specimen as Fig. 19. X 1350.

Fig. 24. Tips of maxillae, one seta raised. Nymph. X 1350.

PLATE VIII.



Fig. 22.

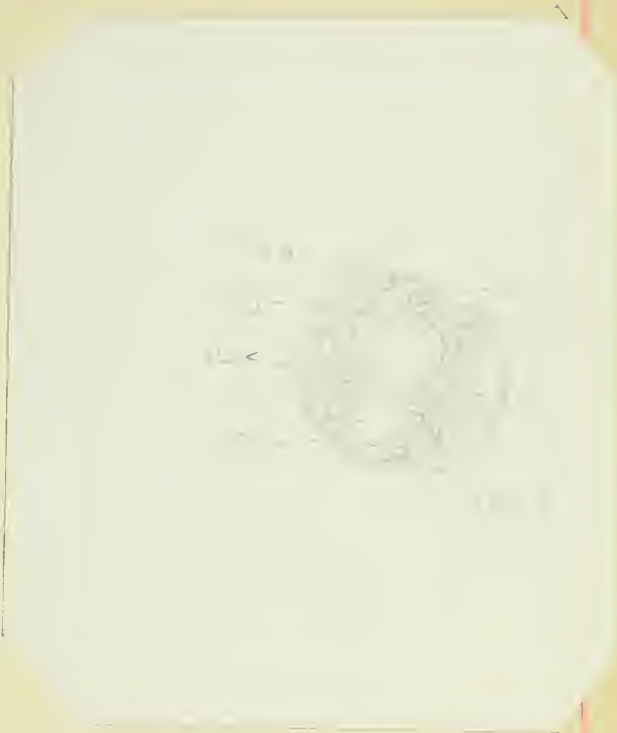


Fig. 23.



Fig. 24.

PLATE IX.

Fig. 25. Labial fundaments. Egg 102 hours old. X 98.

Fig. 26. Labium and hypopharynx. Egg 115 hours old. X 98.

Fig. 27. Labial fundament and palpus. Just before revolution. X 125.

Fig. 28. Cross section of labium near tip.

PLATE IX.



Fig. 25.



Fig. 26.



Fig. 27.



Fig. 28.

PLATE X.

Fig. 29. Sagittal section through base of labium. X 98.

Fig. 30. Cross section of pharynx. X 52.

PLATE X.



Fig. 29.



Fig. 30.

PLATE XI.

Fig. 31. Cross section of open pharynx. X 650.

Fig. 32. Lateral aspect of pharynx and "Wanzenspritze."

Tubes leading to union of maxillae. X 180.

Fig. 33. Cross section of dorsal lamella of pharynx with
edges free from ventral lamella. X 650.

PLATE XI.



Fig. 31.



Fig. 32.



Fig. 33.

PLATE XII.

Fig. 34. "Wanzenspritze." X 98.

Fig. 35. Sagittal section through chamber and piston of
"Wanzenspritze." X 1350.

Fig. 36. Salivary gland. X 125.

Fig. 37. Cross section of tube leading from salivary
glands. X 1350.



Fig. 34.



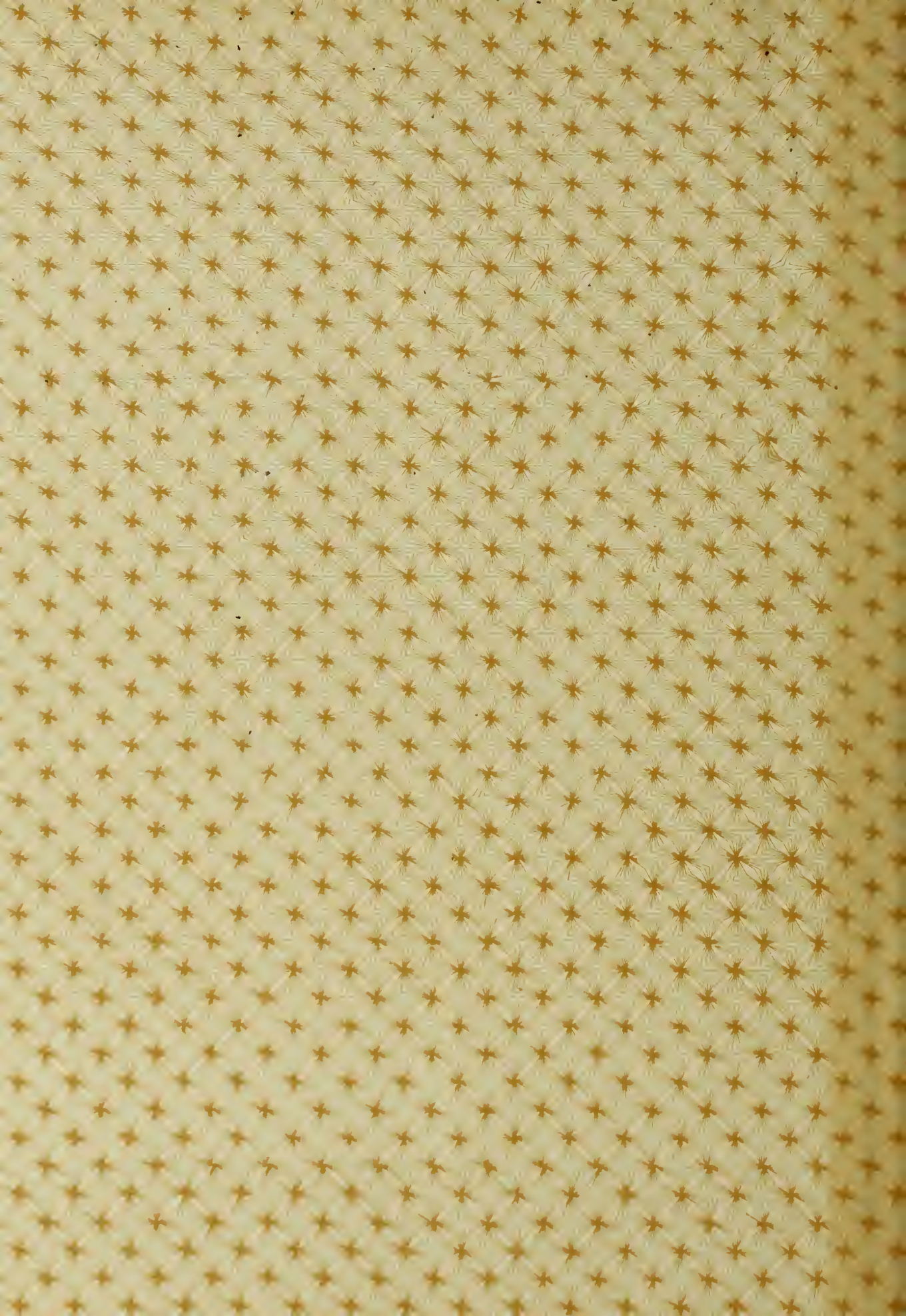
Fig. 35.



Fig. 36.

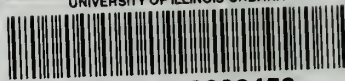


Fig. 37





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