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Full Name of Author — Nom complet de l'auteur

Frances Louise Leggett

Date of Birth — Date de naissance July 8; 1949	Country of Birth — Lieu de naissance Canada

Permanent Address — Résidence fixe

#610 90405 Saskatchewan Drive
Edmonton Alberta

Title of Thesis — Titre de la thèse

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Mouthpart Development in Embryos of *Macrosteles fascifrons* Stål (Hemiptera: Cicadellidae)

by

© Frances Louise Leggett

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Doctor of Philosophy

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(SIGNED) Frances Leggett

PERMANENT ADDRESS:

#610 10405 - Saskatchewan Dr.
Edmonton Alberta

DATED April 7 1983

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Mouthpart Development in Embryos of *Macrosteles fascifrons* Stål (Homoptera: Cicadellidae) submitted by Frances Louise Leggett in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

B. S. Heming

Supervisor

Da Craig

Ross Hodgetts

David D. Cass

A. R. Forbes

External Examiner

Date January 14, 1983

To Dr. Joan F. Bronskill

Abstract

Development of the piercing and sucking mouthparts of the leafhopper, *Macrosteles fascifrons* (Homoptera: Cicadellidae) was followed.

The external mouthpart structures include an anterior fronto-clypeus and labrum, lateral mandibular and maxillary plates, and mandibular and maxillary stylets and a posterior labium. Internally, the clypeo-labrum has two sets of cibarial and one set of epipharyngeal dilators. The mandibular and maxillary stylets are enclosed distally in a common membranous sheath and proximally in separate sheaths. Each mandible has a cuticular guide that articulates with an apodemal process of the head capsule and 4 sets of retractors and 3 sets of protractors. Each maxillae has a lever that articulates with the outer process of the hypopharyngeal wing and has 2 sets of retractors and 1 set of protractors. The two maxillary stylets fit together mesially by a series of grooves and ridges to form salivary and food canals. The hypopharynx is a median lobe extending dorsally into the head capsule as a pair of sclerotized, hypopharyngeal wings. Salivary dilators and labial retractors and protractors originate along the sclerotized rods of the wings. The main lobe of the hypopharynx forms the floor of the cibarium and the roof of the salivary syringe. The syringe consists of a cylinder, piston, and afferent and efferent ducts. The three-segmented labium has four sets of intrinsic muscles and a wishbone-shaped apodeme projecting dorsally on which originate the labial protractors.

Development of the mouthparts was followed through a series of stages using % total development time (TDT).

At 20% TDT, ectoderm of the germ band evaginates to form appendage anlagen, first in the thorax then proceeding cephalad and caudad. Except for the labrum, all mouthpart structures begin as paired evaginations.

At 25% TDT, the maxillary appendages subdivide longitudinally to form inner and outer lobes. Each outer lobe forms the maxillary plate and each inner lobe, the lacinial stylet. Small protuberances visible in front of the mandibular segment are remnants of the intercalary appendages.

From 30-45% TDT, the mandibular, maxillary and labial appendages elongate and the sternal region of the intercalary, mandibular, maxillary and labial segments becomes dome-shaped and begins to form the hypopharynx. At the end of this stage, the

clypeo-labrum has a double-fold and cibarial myoblasts and cranial retractor myoblasts of the stylets are apparent.

At 45% TDT, the embryo rotates clockwise 180 degrees on its longitudinal axis. As this occurs, the clypeo-labrum unfolds caudally and the other appendages shift cephalad and dorsally. At the end of rotation, the first embryonic cuticle is present, neural processes are found in the stylets and myoblasts of the maxillary protractors are differentiating.

The embryo now undergoes katatrepsis and moves back out onto the surface of the yolk so that the head again lies at the anterior end of the egg. By the end of this stage, most myoblasts are differentiating. AT 60% TDT, the ectoderm of the genal region on each side of the head, posterior to the antenna and lateral to the maxillary plate, evaginates to form the mandibular plate and its myoblasts differentiate within it.

By 70% TDT, cells of the stylet anlagen and other mouthpart structures assume the form of their respective coadaptations and act as templates for secretion of larval cuticle. From 70% to 85% TDT, cells of the stylet anlagen retract, leaving behind the stylet cuticle and forming the larval retort organs. Each maxillary lever forms from a diverticulum evaginated from its sheath and is thus maxillary in origin. The mandibular lever is secreted by epidermal cells of the mandibular plate and is therefore genal in origin. Just prior to hatching, the cuticle of the stylets and posterior structures of the mouthparts sclerotize.

The salivary glands develop by paired invagination of lateral sternal ectoderm of the labial segment. Cells of these tubular invaginations undergo mitosis and increase their number until after katatrepsis. The cells then differentiate into 5 acinar types with various types of inclusions. This differentiation includes an increase in RER, golgi and mitochondria and a corresponding decrease in free ribosomes.

Development of the mouthparts of *M. fascifrons* confirms that the maxillary plate is maxillary in origin, the mandibular plate, genal and that mouthpart development is similar to that of heteropterans and thysanopterans, which supports Hamilton's (1981) theory on the evolution of the hemipteran cranium.

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Table of Contents

List of Tables

List of Figures

1. General Introduction

1.1 Introduction

Hemipterans, including the two suborders Homoptera and Heteroptera, pierce host tissue with long tapering stylets and use their strong sucking pumps to suck fluids from their hosts. They and their sister group, Thysanoptera, belong to the cohort Condylognatha characterized by mandibles and maxillae modified for feeding by piercing and sucking (Boudreaux, 1979; Kristensen, 1981; Hennig, 1981).

In 1938, J.W. Evans speculated on evolution within Homoptera, and introduced an evolutionary perspective to the study of the hemipteran head. Over the next 43 years, Snodgrass (1938), Evans (1938, 1946), Heslop-Harrison (1956), Duporte (1962), Parsons (1964, 1973), Puchkova (1970) and Hamilton (1981) theorized about evolution of the hemipteroid cranium. Parsons' (1973) review of existing theories emphasized the divergent opinions existing.

All authors relied on morphological and/or embryological evidence. Morphological study generated numerous interpretations and controversies: Snodgrass (1921) felt that

> "Our only safe guide to morphology is comparative embryology-- when we are sure we have all facts on the case."

and Parsons (1964) that

> "... any attempt to discuss hemipteran cephalic development is hampered by our lack of knowledge of the ontogeny and phylogeny of this group."

In conjunction with morphological and paleontological evidence, embryological observations can help to clarify homologies. Previous research on hemipteran mouthpart development is scarce and contradictory (Heymons, 1899; Muir and Kershaw, 1911a, 1911b, 1912; Pesson, 1944; Newcomer, 1948; Singh, 1971) and has generated numerous theories on how Hemiptera evolved.

Early morphological studies on Hemiptera noted that their piercing and sucking mouthparts differed considerably from the biting and chewing mouthparts of less specialized insects. Intrigued by these differences, early morphologists and embryologists began to speculate on homologies of the mouthpart structures in hemipterans.

By the late 1800's, morphologists had homologized the stylets with the mandibles and maxillae of biting and chewing insects and the sheath or rostrum with the labium (Packard, 1874). J.B. Smith (1892), however, homologized them respectively with the stipites and laciniae of the maxillae and the labium with the maxillary galeae. Marlatt (1895) supported earlier workers but felt Smith's work was valuable in

> "... having called attention to certain features of the hemipterous mouth which had not been previously noted, namely, the mandibular sclerite and maxillary sclerite"

Over the next 90 years, many papers were written on the origin and homology of these sclerites.

Heymons (1899) described embryogenesis in several hemipterans. His study supported the homologies expressed by earlier workers. He showed that the stylets formed from anlagen homologous to those forming the mandibles and maxillae of biting and chewing insects and that each maxillary plate developed from the outer lobe of a maxillary anlage.

Although basic homologies of the mouthparts were established by the early 1900's, other controversy had developed. Meek (1903), in his study on the periodical cicada, *Cicada septemdecim* Fabr., emphasized some of the problems that continued to plague morphologists and embryologists for years.

> "Such questions as " what part of the typical maxillae do the setae represent, what has become of the maxillary and labial palpi and what parts of the second maxillae have fused to form the labium?" are yet unanswered."

Other problems included the origin of the mandibular (loral) plates, maxillary plates, stylet levers and sheaths, and salivary syringe and the homology of the median cranial sclerite. The following discussion looks at the principal components of hemipteran mouthparts: the clypeo-labrum, mandibular and maxillary stylets, stylet sheaths and levers, mandibular plates, maxillary plates, hypopharynx, salivary syringe, labium and sutures, and discusses various opinions on their homology.

1.2 Clypeo-labrum

The central sclerite that dominates the head of hemipterans is called various names. It is usually divided into 3 sclerites although this varies and some hemipterans have only 2 sclerites (Evans, 1975).

Marlatt (1895) called the anterior sclerite, the clypeus, and the posterior two, the labrum but his terms never gained acceptance. Since then, four different systems have been used to name these sclerites. Heymons (1899) labelled them frons, clypeus and labrum and this system is still used by many workers (Meek, 1903; Snodgrass, 1921; Muir, 1926; Myers, 1928; Matsuda, 1965; Hamilton, 1981). Muir and Kershaw (1911a, 1911b, 1912) and Cogan (1916) called the sclerites clypeus, labrum and epipharynx. This system has not been accepted because the epipharynx is defined as

> "a median lobe sometimes present on the posterior (or ventral) surface of the labrum or clypeus" (Snodgrass, 1935).

Snodgrass (1927) revised his earlier opinion and labelled the main sclerite, postclypeus; the next, anteclypeus; and the apical projection, labrum. He reasoned that, because the cibarium represented the 'mouth' and not the pharynx, the muscles associated with the cibarium were cibarial dilators and not pharyngeal dilators. Since cibarial dilators are known to originate on the clypeus and not the frons, the plate was the clypeus (Snodgrass, 1927).

Evans (1938, 1946) felt that the large median sclerite often resulted from fusion of frons and clypeus and called it the fronto-clypeus. The amount of fusion varies from group to group and in some species the frons is a separate plate (Evans, 1938, 1975). Although, this is the most universally accepted method (Duporte, 1962; Parsons, 1964, 1974; Puchkova, 1970; Singh, 1971), two recent morphologists (Matsuda, 1965; Hamilton, 1981) favour Heymons' (1899) system.

1.3 Mandibular and Maxillary Stylets

When the stylets of Hemiptera were recognized to be homologous with the mandibles and maxillae of biting and chewing insects, embryologists began to study how cuticular stylets developed from cellular anlagen.

Weber (1930) described how the stylets of pysllids form before a moult. Each stylet forms from cells that lie like a finger of a glove in the upper cavity of the stylet. These cells evert posteriorly before a moult into the main atrial cavity, elongate and secrete the new stylet. Later the cells invert into the body of the new stylet and form the stylet cavity.

Pesson (1944) considered Weber's (1930) scheme improbable and found the stylets to develop differently in coccids. The cells of each stylet anlage elongate back into the head and coil concentrically. These cells secrete the cuticle of the new stylet and later retract into the head to form the larval retort organ. Pesson (1944) found that the coadaptations of the stylets formed after the cells retracted.

Newcomer (1948) and Singh (1971) described another variation in *Oncopeltus fasciatus* and *Oxyrhachis tarandus*, respectively. The anlagen cells elongate back into the head and coil like those of coccids. The cuticle of the stylet is deposited by a hyaline area found on the anterior face of the anlage cells; these cells then disintegrate except for a small number which form the retort organ. Stylet coadaptations form after hatching (Newcomer, 1948).

Questions arising from these studies are: '1. do all the cells of the stylet anlagen secrete the stylet, 2. do the cells of the anlage retract to form the retort organ or do they disintegrate, and 3. when do stylet coadaptations form – before or after hatching?'.

Many hemipterans have innervated stylets (Pinet, 1963; Forbes, 1966; Parrish, 1967; Cobben, 1978). Some, such as *M. fascifrons* have dendrites in both stylets (Forbes and Raine, 1973) while others have dendrites only in the mandibles (Forbes, 1966; *Myzus persicae*). Cobben (1978) provided a list of which stylets are innervated in members of many heteropteran families. When and how hemipteran stylets are innervated during embryogenesis has never been studied.

1.4 Stylet sheaths and levers

Few studies have described formation of stylet levers and sheaths. Although Muir and Kershaw (1912) first called the mandibular levers 'mandibular pillars', Muir (1931) later referred to them as levers and described them as arising from 'a sclerotization of the membranous wall of the genal suture'. Snodgrass (1938) considered the levers to be 'lateral extensions of the mandibular bases' while Parsons (1964) thought they formed from the 'apposed mandibular and genal walls'.

Maxillary levers have been described as a 'sclerotization of the membranous wall of the maxillary sutures' by Muir (1931), as being formed by the walls of the atrial cavity (Parsons, 1964) and as part of the maxillary stipites (Hamilton, 1981).

Embryological evidence on development of levers is lacking. Pesson (1944) found both levers to form from the subgenal region of the head while Newcomer (1948) saw the mandibular lever as being secreted by the wall of the mandibular stylet sac and the maxillary lever by a diverticulum extending out from the maxillary sheath.

Parsons (1964) described formation of the stylet sheaths during evolution of the hemipteran head. Development of the sheaths is followed only briefly in existing embryological studies and deals mostly with formation of the common sheath and not the separate stylet sheaths (Pesson, 1944; Newcomer, 1948; Singh, 1971).

1.5 Mandibular plates

The mandibular or loral plate, a crescent-shaped sclerite lateral to the postclypeus on each side of the head, has generated many ideas as to its origin. Smith (1892) thought it was the mandible, but was shown to be wrong by Marlatt (1895) and others (Heymons, 1899; Meek, 1903). Muir and Kershaw (1911b) described the plates as 'lateral developments of the clypeal region' but Muir (1931) later revised his opinion and considered them to be genal. In 1938, Snodgrass hypothesized that the mandibular plates were lateral expansions of the hypopharynx. In the same year, Spooner (1938) and Evans (1938) concluded that they were lateral extensions of the clypeus. Heslop-Harrison (1956) and Singh (1971) considered the plates to be mandibular, forming from an outpouching of each mandibular anlage. Puchkova (1970) and Hamilton (1981) described the lorae as being genal.

In 1974, Parsons reviewed the three main theories; clypeal, hypopharyngeal and genal-subgenal, noted the lack of conclusive evidence for any of the hypotheses but favoured the second because of its simplicity. This question has yet to be answered.

1.6 Maxillary plates

Homology of the maxillae and maxillary plates is generally accepted. Early embryological studies (Heymons, 1899; Muir and Kershaw, 1911b, 1912) showed each maxillary anlage subdividing into two lobes, the inner lobe forming the stylet and the outer lobe, the plate. Morphologists homologized the stylet with the lacinia and the plate with the stipes or fused cardo and stipes (Muir and Kershaw, 1912; Snodgrass, 1927; Duporte, 1962; Heming, 1980; Hamilton, 1981).

Parsons (1964), using Pesson's (1944) embryological work as evidence, described a series of stages leading to the evolution of the hemipteran cranium. A major premise in her hypothesis was that the maxillary plate was parietal (genal) in origin and not formed from the maxillary anlage. She concluded this because Pesson never found the maxillary anlagen of coccids to subdivide into inner and outer lobes. Puchkova (1970) also considered the plate to be genal. Newcomer's study (1948) on *O. fasciatus* showed subdivision of the maxillae, but neither Parsons (1964) or Puchkova (1970) acknowledged this. Hamilton (1981) accepted Newcomer's (1948) and the early embryological studies (Heymons, 1899; Muir and Kershaw 1911b, 1912) and homologized the maxillary plates with the stipites of biting and chewing insects.

1.7 Hypopharynx and Salivary syringe

The ventral, internal median lobe of hemipterans was first described as being homologous with the hypopharynx of biting and chewing insects by Marlatt (1895). The homology of the structures now called hypopharyngeal wings remained unknown for some time. They were thought to be 'pharyngeal struts' (Muir and Kershaw, 1911a, b), tentorial structures (Cogan, 1916), or maxillary apodemes (Muir, 1926). Snodgrass (1927) pointed out that at least portions of these plates were hypopharyngeal and were 'special developments in Hemiptera' (Snodgrass, 1938). He homologized the free apical lobe with the lingua (Snodgrass, 1938). There is little recent speculation on the subject.

Each embryological study dealing with hemipteran mouthpart development has described different segment venters as contributing to formation of the hypopharynx and salivary syringe. The hypopharynx has been considered to be formed from the venters of the mandibular and maxillary segments (Pesson, 1944), the intercalary and mandibular segments (Newcomer, 1948) and the antennal, mandibular and, in part, maxillary segments (Singh, 1971).

The syringe has been considered to form from the venter between the maxillary and labial segments (Pesson, 1944) and that of the first maxillary segment (Newcomer, 1948). Parsons (1963) reviewed previous hypotheses on the origin of the syringe and developed her own. She felt Snodgrass (1938) and Muir and Kershaw (1912) to be partially correct, in that the syringe was a modified salivarium (Snodgrass, 1938) and part of the salivary duct (Muir and Kershaw, 1912). Other than Pesson's (1944) hypothetical scheme for development of the salivary syringe and Newcomer's (1948) brief description, formation of this structure is poorly understood.

1.8 Labium

The labium or second maxillae of hemipterans does not resemble that of biting and chewing insects. It is a three- ,or a four-segmented sheath, enclosing the stylets and has no apparent palpi, glossae, or paraglossae.

Few researchers have attempted to homologize its parts. Heymons (1899) thought the first segment was the postmentum, the second, the prementum and the last two segments, the endite lobes. Crampton (1921) homologized the three segments with the mentum, palpigers and fused palpi and Matsuda (1965) thought the first two segments were homologous with the prementum and that the last two were modified palpi.

1.9 Sutures

The sutures of the head have had various names assigned to them, depending on how the homology of the plates is interpreted. Muir (1911), Muir (1926) and Snodgrass (1927) were the earliest morphologists to apply names to them. Later, Parsons (1964), Matsuda (1965) and Hamilton (1981) renamed them according to their own views on their homologies.

1.10 Thesis Objectives

I undertook this study of mouthpart embryogenesis *M. fascifrons* to resolve some of the conflicting embryological information and to gather developmental evidence which might help explain how the hemipteran cranium and mouthparts evolved.

During this study I considered the following questions:

1. What is the evolutionary origin of the maxillary and mandibular plates?
2. How do the stylets develop?
3. When and how are the stylets innervated?
4. When do mouthpart coadaptations form?
5. When and how do the levers form?
6. Are the levers appendicular?
7. What sternal regions contribute to formation of the hypopharynx?
8. How does the salivary syringe form?
9. How do the salivary glands develop?
10. What is the ultrastructure of the larval glands?
11. What does all this tell us about the evolution of the hemipteran cranium?

2. Materials and Methods

2.1 Animals

The insect used in this study was *Macrosteles fascifrons* (Stål), the six-spotted or aster leafhopper, an important vector of Aster Yellows. This disease is caused by a mycoplasma-like agent and infects many economically important plants. Beirne (1952) and others believed this taxon to comprise a species complex, as there is much morphological variation among members of geographically isolated populations. For practical reasons, I treat it as one species. The complex is distributed from Mexico to Alaska, occuring in both wet and dry habitats and from sea level to 2,898 m (Beirne, 1952). Adults range in length from 2.0 to 5.1 mm, with females being larger than males. They are greenish to light brown and often, on the vertex of the head, have six distinctive black spots that are responsible for the common name of this insect.

2.2 Rearing

A stock culture was started with adults supplied by Dr. Hiruki, Dept. of Plant Science, University of Alberta. A cage measuring 50 cm by 35 cm and covered on three sides with fine mesh screening was fitted with a sliding glass panel at the front. Caged insects were maintained in a growth chamber, under a 16 hr. light, 8 hr. dark regime and a temperature ranging from 24-25C during the day to 18-19C at night. Humidity was kept above 50%. Temperature and relative humidity regimes were those used by Swenson (1971) and Hagel and Landis (1967).

Adults were also reared in the laboratory on an artificial diet developed by Hou and Brooks (1975). The recipe used was modified as set out by Hou (1976) (see Table 1).

Small cages were made to house the insects as they fed. Bottoms were removed from 4x6 cm glass jars and a hole was cut in the lid of each and fitted with screening (Fig. 1). One half millilitre of diet was sandwiched between two layers of parafilm and these were stretched over the open bottom of the cage. A thin layer of vacuum grease was smeared around the edge of the jar between the two parafilm layers to prevent leakage. Caged insects were kept in a large glass container with relative humidity

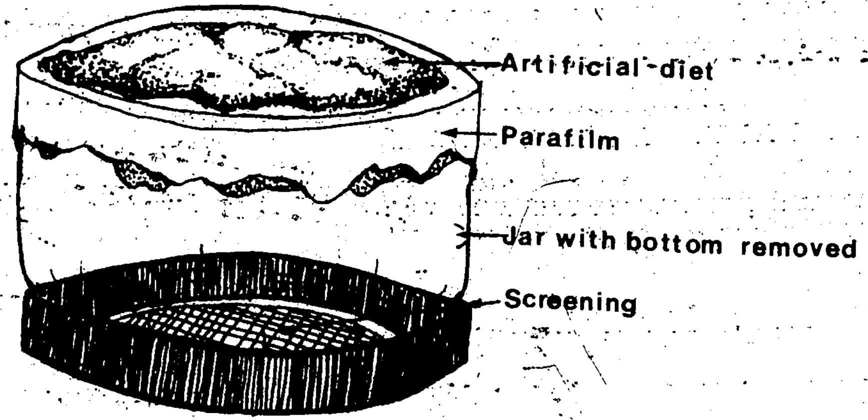
Table 1.

Composition of modified diet for the Aster Leafhopper (Hou, 1976)

I. Amino acids (5x stock)	**mg/100 ml**
L-alanine	20
L-arginine HCl	40
L-asparagine	60
L-aspartic acid	20
L-cysteine (free base)	10
L-glutamic acid	40
L-glutamine (commercial)	120
Glycine	4
L-histidine (free base)	8
DL-homoserine	160
L-methionine	20
L-proline	20
L-serine	20
L-tyrosine	4
L-valine	40
II. B-vitamins and Lipogenic factors (20x stock)	
Biotin	0.05
Calcium pantothenate	2.50
Folic acid	0.25
Nicotinic acid	5.00
Pyrodoxine HCl	1.25
Thiamine HCl	1.25
Choline chloride	25.00
i-Inositol (meso)	25.00
III. Trace metals	
$CuCl_2.2H_2O$	0.051
$FeCl_3.6H_2O$	0.534
$MnCl_2.4H_2O$	0.100
$CaCl_2$	0.4444
Zn-sequesterene	0.160
IV. Others	
Na citrate (50x stock)	10.0
$MgSO_4.7H_2O$	250.0
KH_2PO_4	250.0
Sucrose	3000.0
V. L-ascorbic acid	100.0
VI. Cholesterol dispersion	
Cholesterol S.C.W.	2.5
Lecithin (vegetable)	2.5
Tween 80	5.0

Fig. 1. Artificial diet cage used to feed *Macrosteles fascifrons* adults

scale = 1 cm


Artificial-diet
Parafilm
Jar with bottom removed
Screening

1

maintained above 50%, using a 40% KOH solution and a temperature and light regime the same as that of the growth chamber. Leafhoppers fed readily and after three days females began to lay eggs into the medium through the parafilm. Thus, eggs could be easily collected every day and the time they were laid noted. Eggs were removed from the medium, washed in distilled water, placed in 70% ethanol for 30 sec., rinsed in distilled water and incubated on Whatmann filter paper at 25C.

2.3 Scanning Electron Microscopy

Embryos were prepared for Scanning electron microscopy (SEM) using techniques developed by Zalokar and Erk (1971) and Turner and Mahowald (1975) for *Drosophila* embryos. This technique was used because it provided better resolution of external structures than whole mounts.

Eggs were dechorionated by placing them in 1.0% sodium hypochlorite for 5 min. After dechorionation, eggs were washed four times in distilled water and immersed in a 1:1 mixture of heptane/25% gluteraldehyde in 0.1M collidine buffer plus 0.2M sucrose at pH 7.4. Embryos were then removed, air dried slightly and fixed in trialdehyde fixative (Kalt and Tandler, 1971) in 0.1M collidine buffer plus 0.2M sucrose for 5 to 15 min.. Using a fine tungsten needle, the vitelline membrane was removed from each egg, and the embryo and yolk teased apart. The embryo was fixed overnight (16 hrs.) in trialdehyde. The next day, embryos were washed with buffer for 90 min. (changing the buffer every 15 min.) post-fixed in 1% OsO_4 in 0.1M collidine buffer for 2-4 hrs. and washed in distilled water. Some embryos were critically point-dried using CO_2 with acidified 2,2-Dimethoxypropane as the transition fluid (Muller and Jacks, 1975). Others were freeze-dried from 10% ethanol. Dried embryos were mounted on stubs on inverted v-shaped pieces of cardboard, coated with gold and viewed in the Cambridge Stereoscan 150 electron microscope at 10 kV.

2.4 Light Microscopy

Whole mounts of larvae, prepared using Heming's (1969) technique for thrips, allowed mouthparts and associated muscles to be studied with polarized light.

Living embryos placed in paraffin oil were observed with a compound microscope and used to determine stage of embryogenesis.

Development of internal structures associated with the mouthparts was followed by studying 5 um sections of embryos. Embryos were dechorionated, washed four times in distilled water and fixed as described by Zalokar and Erk (1971). Chorions were removed and the embryos were fixed overnight (16 hrs.) in their respective fixatives. The next day, they were dehydrated, stained with eosin in 95% ethanol, left overnight (16 hrs.) in 1% celloidan in methyl benzoate (Pantin, 1960), embedded in paraffin (m.p. 56–57C) and sectioned at 5um. Sections were stained using Gomori's Trichrome as outlined by Humason (1967, 1979). Substitution of aniline blue recommended in Humason (1979) gave better definition of nervous tissue.

Sections of adults, larvae and embryos were stained to determine the distribution of mucopolysaccharides and proteins in their salivary glands. Methods used were: 1. for mucopolysaccharides, Bauer–Feulgen, Best's Carmine, Mucicarmine, PAS reaction, Diastase digestion, Alcian Blue (Steedman), Alcian Blue (CEC), Alcian Blue–PAS and Aldehyde Fuchsin–Alcian Blue, and 2. for proteins, Ninhydrin, Millon reaction, Performic acid–Alcian Blue, Arginine and DMAB–nitrite (Bancroft, 1975).

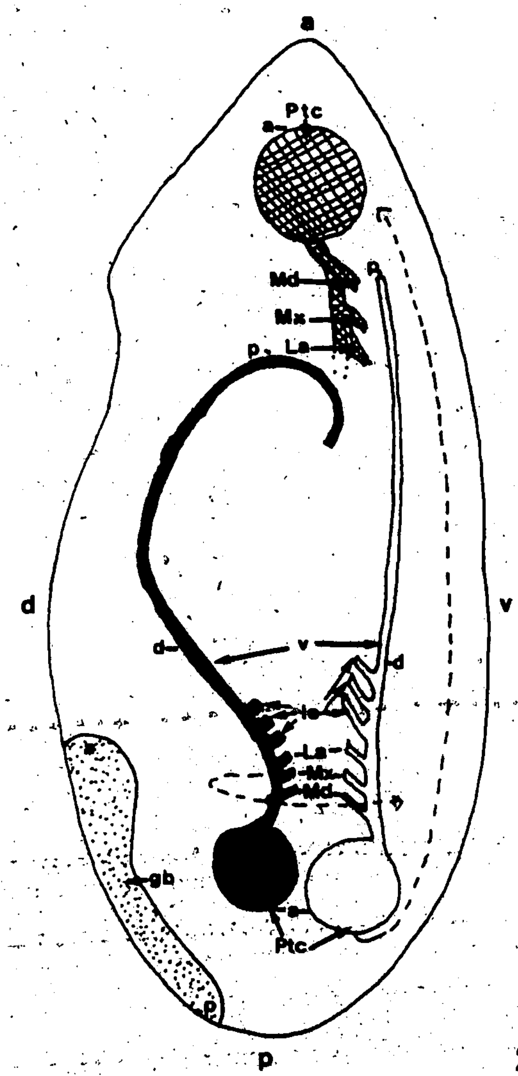
2.5 Transmission Electron Microscopy

Some embryos were fixed for transmission electron microscopy (TEM) using the procedure outlined for SEM. This allowed structures beyond the resolving power of the light microscope to be studied.

Following fixation with OsO_4, the specimens were washed in buffer (0.1M collidine, pH 7.4) stained overnight (16 hrs.) in 1% uranyl acetate at 60C (Hyatt, 1981), infiltrated with resin, Spurr (Spurr, 1969) or Epon (Hyatt, 1981) and embedded. Blocks were sectioned with a diamond knife on a Reichert LKB ultramicrotome and resulting sections were mounted on slot grids and viewed with a Phillips EM 200.

Fig. 2. Orientation of embryo inside egg: before anatrepsis ▨ , before longitudinal rotation ■ , after longitudinal rotation □ , and after katatrepsis ▪ .
scale = 40 um

Abbreviations; anterior (a), dorsal (d), germ band (gb), labium (La), legs (le), mandible (Md), maxilla (Mx), posterior (p), protocephalon (Ptc), ventral (v).



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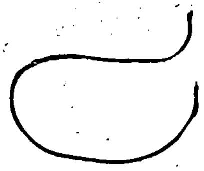
2.6 Orientation of Embryos

M. fascifrons females lay their eggs in host plants with the posterior end towards the ground and the egg's dorsum facing away from the midrib. Figure 2 illustrates the orientation of the embryo during early embryogenesis (before anatrepsis), just before katatrepsis and after katatrepis, as if the egg were embedded in the plant.

In the illustrations, orientation of the embryo and sections is with anterior, top; ventral, right; dorsal, left; and posterior, bottom. The axes are noted on the figure when such orientation was impossible.



3. Staging

3.1 Introduction

Researchers have used several methods to indicate the ages of insect embryos. Usually age is given in hours from oviposition. Others have used descriptive stages since embryos of some insects, for various reasons, do not lend themselves to use of this method. Bentley et al. (1979) quantitatively staged embryos of *Schistocerca nitens* by dividing embryogenesis into equal periods which were percentages of total development time. Although embryos of the same species may develop at different rates at a particular temperature, it has been found that characteristic events occur during characteristic percentages of total development time (TDT) (Edwards and Chen, 1979).

Embryos of *M.fascifrons* are difficult to stage using the hourly method. Observations of females fed on an artificial diet indicate they lay from 0 to 11 eggs per day (N=12; x= 3.97 ± s.d. 0.54 eggs/ female/ day) at irregularly-spaced intervals. Total development time of embryos varies, from 231 to 265 hours at 25C, (N=17; x = 243 ± s.d. 11 hrs.). I use Bentley et al.'s (1979) method to time embryogenesis in *M. fascifrons*.

3.2 Staging

Seventeen eggs whose laying time was known were monitored closely until they hatched. Although these embryos developed at different rates at 25C, characteristic events occurred in them at the same percent of total development time (TDT). From these eggs, the following stages using 5% TDT intervals were established. A summary of these events is presented in Table 2 and in Figs. 5-20.

3.2.1 0% TDT

A freshly laid egg is translucent, quite pliable and contains a symbiont ball (sb) at its posterior pole (Fig. 5). Eggs are oblong and measure 0.99 ± s.d. 0.07 mm x 0.23 ± s.d. 0.02 mm (N=20). They are ventrally (v) convex and dorsally (d) slightly concave (Fig. 3). An eclosion line (ec) extends posteriorly along the dorsal side of the egg, one third of

Table 2

Characteristics of % development stages

Stage	Description
0%	Egg translucent and pliable; symbiont ball visible at posterior pole
5%	Egg translucent and pliable; cleavage energids form
10%	Blastoderm forms; germ band condenses on eggs dorsal side; anatrepis occurs
15%	Immersed germ band; symbiont ball at posterior end of germ band; yolk cleavage
20%	S-shaped germ band; head lobes separate from yolk surface
25%	Early segmentation; appendage anlagen evaginate; thoracic appendages first
30%	Late segmentation; clypeo-labrum visible above stomodaeum; maxillary anlagen subdivide
35%	Egg opaque and turgid; increases in diameter; appendage growth
40%	Abdomen straightens; eye pigmentation begins
45%	180° Longitudinal rotation of embryo; clypeo-labrum unfolds caudally; mouthpart appendages shift cephalad and dorsally
50%	Katatrepsis; mycetomes, thorax and abdomen yellow; 1° embryonic cuticle visible
55%	Provisional dorsal closure; yolk flows into dorsal cavity; serosal plug forms dorsal organ; 1° cuticle apolysis; 2° embryonic cuticle being deposited
60%	Embryo pale yellow; pretarsi form; epidermis replaces amnion as dorsal body wall
65%	Embryo darker yellow; trochanter, femur and tibia form
70%	Tarsi form; contractions visible in abdomen
75%	Dorsal vessel beats irregularly; 2° embryonic cuticle apolyses; larval cuticle being deposited
80%	Eye fully pigmented; inner ommatidia darker; muscle contractions visible throughout embryo
85%	Eyes dark red; stylets' cellular matrices retract
90%	Antennal annuli dark in clypeal region; body movements visible
95%	Antennal annuli and anal setae dark; yolk completely resorbed
100%	Embryo hatches

Fig. 3 and 4. Scanning Electron micrograph of *Macrosteles fascifrons'* egg

Fig. 3. Egg

scale = 50 um

Fig. 4. Eclosion line on external surface of egg.

scale = 20 um

Abbreviations; dorsal (d), ventral (v), anterior (a), posterior (p), eclosion line (ec).

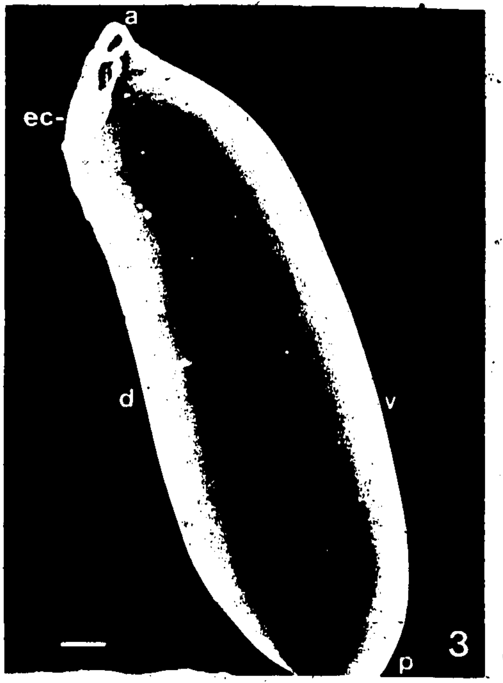


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Fig. 5. 0% Zygote Formation

Fig. 6. 5% Cleavage

Fig. 7. 10% Blastoderm Formation

Fig. 8. 13% Germ Band Formation

Fig. 9. 15% Anatrepsis

Fig. 10. 20% Immersed Germ Band

Fig. 11. 25% Segmentation

Fig. 12. 30% Appendage Formation

Fig. 13. 35% Growth

Fig. 14. 40% Growth

Fig. 15. 45% Longitudinal Rotation

Fig. 16. 52% Katatrepsis

Fig. 17. 55% Provisional Dorsal Closure

Fig. 18. 60% Dorsal Closure

Fig. 19. 65-80% Early Prolarva

Fig. 20. 85-100% Late Prolarva

scale= 50 um

Abbreviations; amnion (am), amniotic pore (ap), antenna (A), blastoderm (b), caudal end (ca), cleavage energid (ce), clypeo-labrum (C-L), dorsal organ (do), eye (e), femur (f), germ band (gb), hypopharynx (H), intercalary segment (In), labium (La), legs (le), mandible (Md), maxilla (Mx), outer maxillary lobe (Mxp), mycetome (my), pretarsi (pr), protocephalon (Ptc), serosal plug (sp), stomodaeum (st), symbiont ball (sb), tarsi (ta), tibia (ti), zygote nucleus (zn).

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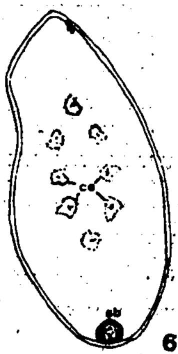

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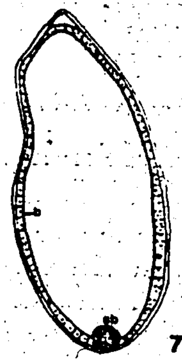

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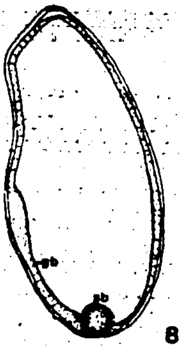

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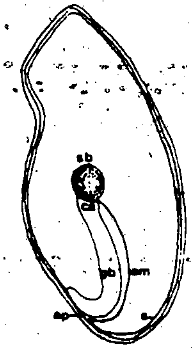

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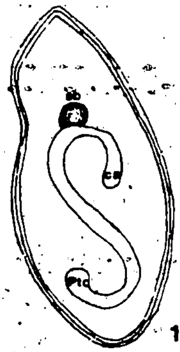

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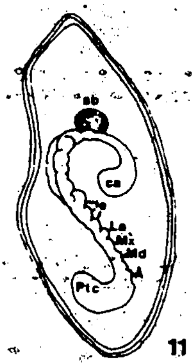

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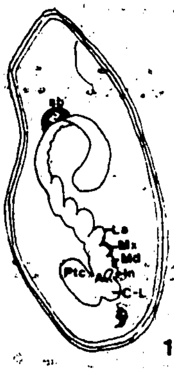

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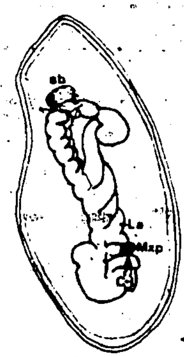

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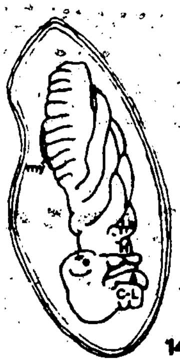

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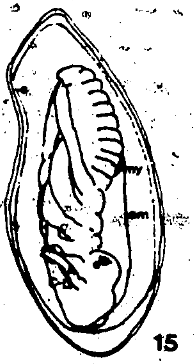

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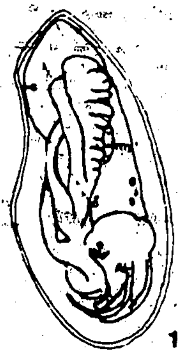

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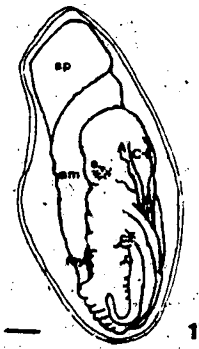

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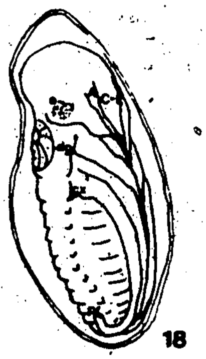

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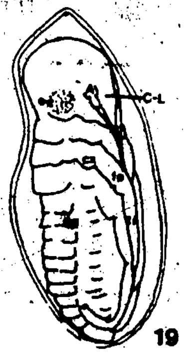

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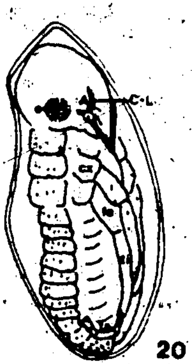

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egg length, and is the only sculpturing found on the chorion (Fig. 4).

The egg is fertilized as it passes the opening of the spermathecal duct. Immediately before or soon after oviposition, female and male pronuclei fuse to form the zygote nucleus (zn) (Fig. 5). As the egg passes down the oviduct, its principal axes are the same as those of the mother. Ovipositing *M. fascifrons* females lay eggs posterior end first, indicating that the egg is not tumbled in the oviduct.

3.2.2 5% TDT

Externally, the egg is the same as at 0% development and contains yolk droplets of various sizes.

Internally, the zygote nucleus and its accompanying cytoplasm divide to form two daughter nuclei surrounded by cytoplasm, each called a cleavage energid (ce) (Fig. 6). These divide synchronously at first to form more energids and as they divide they move toward the periphery of the egg. Eventually, they enter a thin layer of periplasm at the egg's periphery. It is unknown when synchrony is lost. Throughout this stage, the symbiont ball (sb) remains at the posterior pole of the egg (Fig. 6).

3.2.3 10% TDT

Blastoderm (b) formation (Fig. 7), occuring at 10 to 12% TDT is visible in living eggs as thick cytoplasmic bands extending ventrally and dorsally over the surface of the yolk. As time passes, these bands thicken posteriorly and regress anteriorly. The ventral band condenses further towards the egg's dorsal side to form a germ band (gb) at about 13 to 14% TDT (Fig. 8). The germ band, a thickened layer of cells on the dorsal side of the egg, lies with its posterior end against the symbiont ball (sb) (Fig. 8). Its anterior region is thicker and constitutes the head lobes or protocephalon (Ptc).

3.2.4 15% TDT

The egg is still translucent and pliable but the symbiont ball is no longer visible at its posterior pole. Dorsally, about 0.1 mm above the egg's posterior pole, is a tuck in the yolk, the amniotic pore (ap) where, during anatrepsis, the germ band (gb) invaginates posteriorly into the yolk. When the egg is viewed in water with a compound microscope, the band can be seen to bend towards the egg's anterior pole with the symbiont ball at its caudal end (ca) (Fig. 9). As the band moves into the center of the egg, the yolk separates into blocks, due to yolk cleavage in the posterior two thirds of the egg. The head lobes of the germ band remain in contact with the egg's surface at the end of anatrepsis. These are visible on the egg's postero-dorsal side as two clear bands angling outward from each other toward the anterior pole. The ventral side of the germ band faces the egg's venter. Anatrepsis takes about two hours at 25C during which time the amnion (am) and serosa (s) form. The serosa surrounds the yolk and the amnion arises from the margins of the embryo and encloses the amniotic cavity. Both form by stretching of cells at the anterior and posterior ends of the germ band as it invaginates.

3.2.5 20% TDT

The germ band now lengthens within the yolk and its caudal end begins to flex ventrally towards the posterior pole of the egg to accommodate this increased length (Fig. 10). The symbiont ball remains at the point of caudal flexure. Head lobes separate from the yolk's surface and the amniotic pore closes, completely immersing the embryo in the yolk.

3.2.6 25% TDT

On completion of caudal flexure, the germ band is S-shaped. Paired appendages form by evagination of ectoderm and appear as small protuberances from the margins of the band (Figs. 11 and 21).

Scanning electron micrographs (SEM) of embryos at this stage of development show that the thoracic appendages (le) form first, followed by the labial (La), maxillary (Mx), mandibular (Md), antennal (A) appendages and clypeo-labrum (C-L), in that order (Fig. 21). At this stage, the clypeo-labrum is barely visible. Abdominal appendages appear at the same time as gnathal appendages.

Fig. 21 to 24. SEM of *M. fascifrons'* embryos. Lateral aspects of developing head

Fig. 21. 25% TDT: Appendage Formation

scale = 20 um

Fig. 22. 30% TDT: Division of maxillary anlagen

scale = 20 um

Fig. 23. 35% TDT: Organogenesis

scale = 20 um

Fig. 24. 40% TDT: Organogenesis: eye pigmentation begins

scale = 20 um

Abbreviations; antenna (A), clypeo-labrum (C-L), eye (e), hypopharynx (H), intercalary segment (In), labium (La), mandible (Md), maxilla (Mx), neural groove (ng), outer maxillary lobe (Mxp), protocephalon (Ptc), stomodaeum (st).

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3.2.7 30% TDT

Appendage anlagen are more pronounced, the clypeo-labrum protrudes below the head and the head lobes (Ptc) flex dorsally and caudally (Figs. 12 and 22).

SEMs of 30% TDT embryos (Fig. 22) show intercalary appendage anlagen (In) to be present, the antennae (A) growing laterally and the maxillary appendages dividing into inner (Mx) and outer lobes (Mxp) (Fig. 22). A mid-ventral neural groove (ng) extends from the mandibular segment caudally (Fig. 22).

3.2.8 35% TDT

The egg increases both in diameter and length by 0.05 mm and becomes opaque and turgid. Embryonic appendages are well developed and the clypeo-labrum (C-L) has flexed antero-dorsally with a double fold (Fig. 23). Head lobes flex caudally and dorsally and abdominal flexure is still present (Fig. 13).

Light microscopy shows organ systems such as the stomodaeum and salivary glands to begin development at this time. The outer lobes of the maxillary appendages (Mxp), as seen with SEM, are short and conical (Fig. 23). The inner maxillary lobes are elongate; the labial appendages (La) have begun to move mesially; the compound eyes (e) are developing and the neural groove disappears (Fig. 23).

3.2.9 40% TDT

The abdomen has straightened but the embryo's venter still faces that of the egg (Fig. 14). Eye (e) pigment arises posteriorly first and then spreads anteriorly in an 180° arc.

In embryos viewed by SEM, the labial appendages (La) have met mesially and have fused proximally (Fig. 24). The sternal region of labial, maxillary, mandibular and perhaps intercalary segments has become dome-shaped and later develops into the hypopharynx (H, Fig. 24). With fusion of the labial appendages, the salivary invaginations coalesce to form a common salivary duct. Formation of the proctodaeum begins.

3.2.10 45% TDT

The egg is as at 35% TDT externally. Compound eyes (e) are bright red, indicating that the embryo is about to begin 180° longitudinal rotation. Viewed from the egg's posterior pole, rotation is clockwise and is such that the embryo's ventral side ends up facing the egg's dorsal side (Fig. 15). Rotation is easily followed by observing movement of the eye. The clypeo-labrum (C-L) unfolds caudally, pushing the antennae (A) caudally as well (Fig. 25). When rotation ceases, the clypeo-labrum is completely straight with the antennae wrapped underneath. At its distal end, the clypeo-labrum forms a small flap which becomes the actual labrum (L).

Light microscopy shows the remaining mouthpart appendages to shift cephalad and dorsally. The outer maxillary lobes remain external, forming part of the mouthcone. Mandibular and maxillary stylet bases are now internal. The hypopharynx is conical and its distal end points caudally. Annuli begin to form on the surface of the antennae and the first embryonic cuticle is deposited.

3.2.11 50% TDT

Yellow pigment becomes visible in the embryo's mycetomes (my) (Fig. 16); two structures on either side of the abdomen which house symbionts. Slightly later, pigment appears in the sides of the thorax and abdomen, and the yolk boundary extends diagonally across the head, bisecting the clypeus.

In the brain region the head swells, expanding towards the egg's dorsal side. The head continues to expand and deflate until it breaks the amnio-serosal fusion. Meanwhile, the yolk on the egg's ventral side is forced toward the anterior pole by the contracting serosa (s) (Fig. 16). The serosa pulls the head posteriorly, then ventrally. Over the next two hours, the embryo moves out of the yolk towards the egg's anterior pole along its ventral side (Fig. 16). Katatrepsis ends when the abdomen reaches the posterior pole of the egg (Fig. 17). The amnion (am) now closes the dorsum of the embryo as the provisional dorsal closure.

Fig. 25 to 28. SEM of *M. fascifrons'* embryos

Fig. 25. 45% TDT: Longitudinal rotation. Lateral aspect of head.

scale = 50 um

Fig. 26. 55% TDT: Provisional dorsal closure, showing serosal plug.

scale = 50 um

Fig. 27. 55% TDT: Pleuropodia during provisional dorsal closure.

scale = 20 um

Fig. 28. 65% TDT to 80% TDT: Early Prolarva. Lateral aspect of head.

scale = 20 um

Abbreviations; amnion (am), antenna (A), clypeus (C), eye (e), labium (La), labrum (L), mandible (Md), maxilla (Mx), outer maxillary lobe (Mxp), pleuropodia (pl), serosal plug (sp).

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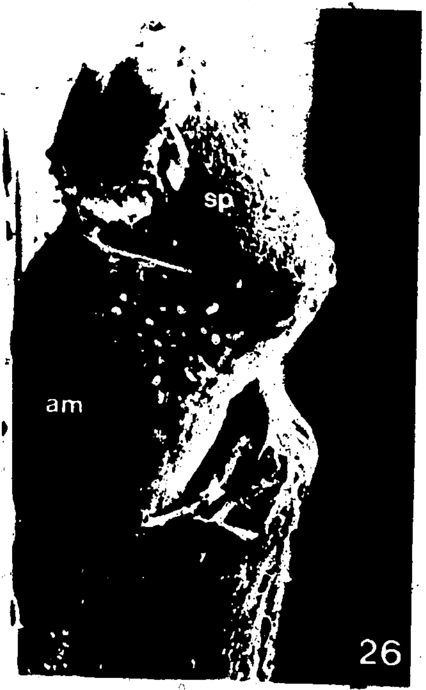

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3.2.12 55% TDT

The embryo, now lying with its head at the egg's anterior pole and its venter facing the egg's ventral side (Fig. 17), is pale yellow. It's mycetomes (my) are dark yellow and its eyes more heavily pigmented. The contracting serosa forms a serosal plug (sp) above the head that is continuous with the amnion (am) closing the dorsal surface of embryo (Fig. 26). Yolk within the serosal plug flows posteriorly into the dorsal yolk cavity above the embryo, leaving an empty serosal sac which is later drawn into the body as the secondary dorsal organ (do, Fig. 18). Provisional dorsal closure is completed in 10–11 hrs. when the secondary dorsal organ (do) forms.

Pleuropodia (pl) on the first abdominal segment shrink and are pulled into the body as peg-like structures (Fig. 27). Only the coxae (cx) are distinguishable in the legs (Fig. 17).

3.2.13 60% TDT

The embryo is still pale yellow and has grown to fill the egg completely (Fig. 18). Its eyes are larger and more deeply pigmented, pretarsi (pr) are forming and the epidermis is growing dorsally on either side to enclose the yolk. Dorsal closure is complete when the epidermis replaces the amnion as the dorsal body wall and when the secondary dorsal organ (do) is being resorbed.

Study of whole mounts show the stomodaeum to extend to the metathorax, and the proctodaeum to the second abdominal segment. Yolk is present in both thorax and abdomen but the ventral nerve cord has not yet contracted anteriorly.

3.2.14 65% TDT

The eyes (e) continue to darken and the body of the embryo attains the dark yellow colour of a freshly hatched larva. Legs have differentiated into femur (fe) and tibia (ti) (Fig. 19), but tarsi are not yet present. Yolk extends within the embryo from the mesothorax to the abdomen, the stomodaeum and proctodaeum are well developed, the midgut is forming and the antennae extend caudally to the abdomen. The ventral nerve cord begins to contract anteriorly but its posterior end is still in segment four of the abdomen.

3.2.15 70% TDT

As the midgut epithelium engulfs the yolk, there are contractions in the abdomen. Yolk is present in the metathorax and abdomen. Central ommatidia in the compound eyes are darker red than peripheral ones and tarsal segments (ta) are forming. The ventral nerve cord continues to contract anteriorly but its posterior end is still present in the abdomen.

3.2.16 75% TDT

The dorsal vessel is beating irregularly and yolk is present in the lower metathorax. The secondary embryonic cuticle has apolysed (Fig. 28) and the ventral nerve cord extends posteriorly to the first abdominal segment.

3.2.17 80% TDT

Body contractions are readily visible, the embryo is bright yellow and its eyes are completely pigmented, although peripheral ommatidia are a lighter red than central ones. Only the abdomen contains yolk and the nerve cord is entirely within the thorax.

3.2.18 85% TDT

Eyes (e) are dark red, the stylets' cellular matrices have retracted into the head and yolk, very reduced, is present only in a few abdominal segments (Fig. 20).

3.2.19 90% TDT

Body movements are noticible, and antennal annuli are beginning to sclerotize in the region of the clypeus. Cellular matrices of the stylets have retracted within the head to form the retort organs which, in future larval stages, will secrete the stylets during each moult. Most yolk is resorbed.

3.2.20 95% TDT

Annuli of the antennae and anal setae are beginning to sclerotize and the embryo begins hatching movements. This can be seen as a circular motion in the eyes. All yolk is resorbed and stylets are completely sclerotized.

3.2.21 100% TDT

The head of the late prolarva expands towards the anterior pole of the egg as the insect takes in air. As the larva pushes upwards, it breaks the vitelline membrane with the top and back of its head, and the chorion splits down the eclosion line. It wiggles its way out of the serosal cuticle and sloughs off the second embryonic cuticle. The stylets are placed in the groove in the anterior face of the labium and their coadaptations engage. The newly emerged first instar larva is bright yellow but soon darkens to greyish yellow.

3.3 Discussion

The percent development system of aging embryos allows direct comparison of embryonic development in different insects. Unfortunately, few authors have used this method and, due to lack of information, few studies can be readily adapted to it.

This system provides a good means of comparing closely related insects. It eliminates problems in comparing results of studies using stages of embryogenesis and those using hours. Insects which are ovoviviparous, or viviparous, or those which lay eggs at various developmental stages do not lend themselves to use of this method. However, embryos of most insects can be compared.

Table 3 compares embryogenesis in eggs of *Schistocerca nitens* (Bentley et al., 1979), *Acheta domesticus* (Edwards and Chen, 1979), and *M. fascifrons* and illustrates differences which can exist between insects in occurrence of events. For example, anatrepsis takes place earlier in *A.domesticus* (10%) than in either *S. nitens* or *M. fascifrons* (15%). Katatrepsis, on the other hand takes place earlier in *S.nitens* (45–50%) than in the other two.

A few authors have discussed the significance of such variation in embryogenesis. Johannsen and Butt (1941) compared embryogenesis of representatives of different insects groups. They examined stages of development, compared various

Table 3

Comparison of embryogenesis in 3 species of insects using Quantitative Staging[1]

Stage	**% of Total development time**		
	Macrosteles fascifrons	*Schistocerca nitens*[1]	*Acheta domesticus*[2]
Cleavage	0–5%	0–5%	0–6%
Blastoderm formation	10–12%	10%	6.5%
Germ band formation	13–15%	15%	9%
Anatrepsis	15%	15–20%	10%
Immersed germ band	20–25%	20–25%	
Appendage formation	25–30%	25–30%	11–19%
Organogenesis	35–45%[3]	35–45%[3]	20–52%[3]
Longitudinal rotation	45–50%[6]	65–75%	
Katatrepsis	50–55%[4]	45–50%[4]	53–55%
Provisional dorsal closure	55–60%	50–55%	57–60%[6]
Dorsal Closure	60–65%	55–60%[6]	60–63%
Early Prolarva	65–80%[5]	65–75%	64–76%[4]
Late Prolarva	80–100%	75–100%[5]	76–100%[5]

1 Bentley et al., 1979
2 Edwards and Chen, 1979
3 deposition 1° of cuticle
4 deposition 2° of cuticle
5 deposition 3° of cuticle
6 eye pigmentation begins

events such as development of the amnion and serosa and the midgut epithelium and described what they felt was the evolutionary sequence of these strategies.

Anderson (1973) compared development in various arthropods and annelids and speculated on the evolution of the phyla using these comparisons. His study supported Manton's (1973) hypothesis that the Arthropoda are polyphyletic.

Ando (1955) compared eye development and ommatidia number in Odonata. His findings showed a relationship between eye development in Zygoptera and that of paurometabolous insects and in Anisoptera and holometabolous insects. He found that comparison of ommatidia number in species of the group indicated that some species are more specialized than previously thought and that this could be related to their life styles.

Cobben (1968) examined embryonic sequences in many Heteroptera from an evolutionary standpoint and constructed a phylogeny based on the variation. He considered such sequences as

> "degree of visible development of the 'pregerm'; location of of the blastopore; growth; orientation, transformation in shape and displacement (mostly clockwise rotations) of the germ band, embryo and prolarva."

Studies of homopteran embryogenesis also show variations in events such as eye pigmentation, extent and timing of longitudinal rotation, and timing of katatrepsis and anatrepsis.

Eye pigmentation occurs just prior to rotation in the cicadellid embryos *M. fascifrons* and *Euscelis plebejus* (Sander, 1959) and in a membracid *Oxyrhachis tarandus* (Singh, 1971) but in the fulgorids, *Siphanta acuta* (Muir and Kershaw, 1912) and *Pyrilla perpusilla* (Sander, 1956), eyes do not pigment until after katatrepsis. Cobben (1968) found variation in time of eye pigmentation in heteropterans: Saldids are the only group in which the eye pigments before katatrepsis. He did not comment on the significance of this variation. In Homoptera, eye pigmentation begins before katatrepsis in representatives of more evolved families (Cicadellidae and Membracidae) and after in more primitive species (Fulgoroidea). However, until more species of Homoptera are studied conclusions can not be made about the evolutionary significance of this.

Other differences exist in homopteran embryogenesis: *M. fascifrons* embryos rotate longitudinally 180° just before katatrepsis while those of *P. perspusilla, S. acuta,* and *E. plebejus* do so during katatrepsis. In fact, *P. perpusilla* embryos rotate 90° at this time and another 90° later. Singh (1971) did not mention whether or not embryos of *O. tarandus* rotate longitudinally. Cobben felt that, in heteropterans, a complete 180° rotation before katatrepsis was primitive. In homopterans studied, this event is quite variable. Unlike heteropterans, more primitive species have a 90° rotation and the more evolved *M. fascifrons* a complete 180° rotation before katatrepsis.

Another variable characteristic is extent and time of immersion of the germ band. Cobben (1968) felt that the primitive state was "immersion with head lobes not detached from the serosa" although he pointed out that there is little direct evidence. In all homopteran embryos studied, germ bands become completely immersed. Recently, Fletcher and Anderson (1980) studied a fulgorid, *Scolypopa australis*, in which the head lobes separate from the serosa much earlier than in other homopterans studied and which is thus more like that of Orthoptera. They felt this represented a specialization within hemipterans.

The need for more extensive study of homopterans is readily evident from the above comparisons. Additional and more thorough studies are needed before enough developmental information is available to use in studying the phylogeny of Homoptera.

4. Cephalic Skeletomusculature in First Instar Larvae of *Macrosteles fascifrons*

4.1 Introduction

Leafhoppers (Homoptera: Cicadellidae) have piercing and sucking mouthparts that they use to suck fluids out of plants. They are opisthognathous with a postero-ventrally pointing mouthcone formed by an anterior clypeo-labrum, lateral maxillary and mandibular plates and a posterior labium enclosing paired mandibular and maxillary stylets, a cibarial pump, salivary syringe and hypopharynx.

The skeletomusculature and sensilla of the mouthparts are well studied in representatives of many families of Hemiptera. However, there are only a few studies on cicadellids and most lack detail.

Spooner (1938) studied head capsules of many hemipterans. He described the extent and location of the frons, vertex, clypeus, tentorium and mandibular and maxillary levers. Using these characters, he constructed a phylogeny of Homoptera. He considered the Fulgoroidea to be the most primitive group, with two subfamilies of Cercopidae giving rise to the other families of Homoptera. He also discussed the origin of the loral or mandibular plates and concluded that they were derived from the 'paraclypeal areas' of the head capsule. These are

> "portions of the clypeus cut off by progressive development of a suture extending from each proximal corner of the anteclypeus." (Spooner, 1938).

For many years, J.W. Evans studied leafhopper systematics (1932-1975), using external head structure as one character to separate members of various groups into superfamilies and families. In 1946, he described the basic head structure of leafhoppers and in particular that of *Putoniessa nigra*. He presented a scheme for the evolution of the hemipteran cranium in which the mandibular lobes originated from the clypeus. He (Evans, 1938) and Spooner (1938) independently arrived at this conclusion. In the third paper of the series (1946), he provided a key to the subfamilies and tribes of the Jassidae using head structure and other external body structures (wing venation, thoracic structure). He also divided the Jassidae into two lines, Ulopides and Macropides and discussed which subfamilies he considered to be more primitive or evolved in each. In 1975, Evans discussed primitive and specialized head characteristics in cicadelloids, comparing them with those of members of other superfamilies of auchenorrhynchous Homoptera.

Kramer (1950) compared cephalic, thoracic and abdominal skeletomusculature of a representative species from each family or superfamily of auchenorrhynchous Homoptera. He discussed previous views on the phylogeny of the group and concluded from his study that fulgorids were the most primitive, that cercopids, cicadellids and membracids were closely related and that the cicadids were more closely related to the latter taxa (Kramer, 1950).

Recently, two papers treated cephalic skeletomusculature in homopterans: Rieger (1976) and Singh (1971). Rieger dealt mostly with Heteroptera but presented a summary of previous studies on Sternorrhyncha and Cicadidae. He then compared homopterans with heteropterans and developed a ground plan for Heteroptera from this comparison.

Singh (1971) described the cephalic skeletomusculature of representatives of all families of Homoptera. His work provided a good comparison of mouthpart structure of the groups but he did not speculate on relationships.

Only six studies treat cephalic skeletomusculature of specific leafhoppers: Evans (1946) on *Putoniessa nigra* ; Willis (1948) on *Typhlocyba ulmi*, Quadri (1949) on two species of *Idiocerus*, Kramer (1950) on *Aulacizes irrorata* , Arora and Singh (1962) on *Idiocerus atkinsoni* and Singh (1971) on *Kolla mimica*. Others described specific details such as stylet innervation (Forbes and Raine, 1973 and Backus and Mclean, 1982), structure of the salivary syringe (Raine and Forbes, 1971) and sensilla of the [illegible]cibarium (Backus and Mclean, 1982) of *M. fascifrons*, stylet structure of *Eupteryx melissae* (Pollard, 1972) and sensilla on the maxillary plate of leafhoppers (Evans, 1973). Other than Evans (1973) and recently (Backus and Mclean, 1982), there are no papers on sensilla of cicadellid crania and mouthparts, although these are available for other Hemiptera (Wensler, 1977; Tjallingii, 1978 ; *Brevicoryne brassicae*).

I describe here cephalic skeltomusculature in first instar larvae of *M. fascifrons*. Larval mouthparts are similiar to those of adults except that placement and number of sensilla differ and only adults have ocelli.

4.2 Observations

4.2.1 External Head Structures

The head of *M. fascifrons* is opisthognathous with the labium and other mouthparts pointing postero-ventrally. However, in this study, I define the axes of the insect as if it were feeding (Fig. 29), the vertex (Ve) dorsal, labium (La) posterior and ventral, clypeo-labrum (Fc, Ac, L) anterior and neck region posterior.

Externally, the head consists of sclerotized plates bounded by sutures. The clypeo-labrum is anterior and consists of a dorsal, convex, fronto-clypeus (Fc), medial anteclypeus (Ac) and small ventral labrum (L) (Fig 30). Posteriorly, the labrum forms an apical ring, open medially, through which the stylets pass. Mandibular plates (Mdp) lie adjacent to the anteclypeus and lateral to them are the maxillary plates (Mxp) (Fig 30). The three-segmented labium (La) closes the apex of the mouthcone and bears a medial anterior groove into which the mandibular and maxillary stylets fit. Antennae (A) are inserted medial to the eyes (e) and lateral to the fronto-clypeus (Fig. 30).

Terms used by morphologists to name sutures are diverse and confusing so I use those of Matsuda (1965) and Parsons (1974), as they seem more consistent. The fronto-clypeus (Fc) is bounded laterally and dorsally by the fronto-clypeal sutures (fcs). The transclypeal suture (tcs) divides the fronto-clypeus (Fc) and anteclypeus (Ac) (Fig. 30) (Parsons, 1974) but this is poorly developed in first instar larvae as they are not heavily sclerotized. The clypeal sutures (cs) (Matsuda, 1965) separate the mandibular plates (Mdp) from the anteclypeus (Ac) (Fig 30), and the intergnathal sutures or genal sutures (gs) (Matsuda, 1965), the maxillary plates (Mxp) from the mandibular plates (Mdp). The labrum (L) is separated from the anteclypeus (Ac) by a fold (Fig. 30, arrow).

4.2.2 Internal Structure

4.2.2.1 Clypeo-labrum

The clypeo-labrum along with the hypopharynx (H) forms the food pump or cibarium (Cib). The roof of the food pump is formed by the inner anterior wall of the anteclypeus, the epipharynx (Epi) and its floor by the anterior wall of the hypopharynx (H). Cibarial dilators (cib.d. 1, cib.d.2) insert on apodemes arising from the roof of the

Fig. 29–30. SEM of head of *M. fascifrons*

Fig. 29. Cast skin of fourth instar larva

scale= 100 um

Fig. 30. Adult

scale= 100 um

Abbreviations; anteclypeus (Ac), antenna (A), clypeal suture (cs), eye (e), flagellum (f), fronto–clypeal suture (fcs), fronto–clypeus (Fc), labium (La), labrum (L), genal suture (gs), mandibular plate (Mdp), maxillary plate (Mxp), pedicel (p), scape (sc), socket (so), stylets (sty), transclypeal suture (tcs), vertex (Ve).


Ve
Fc
29

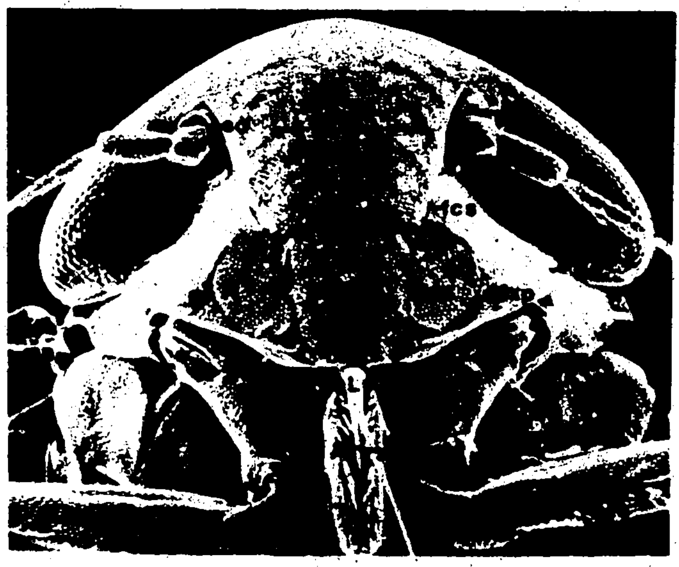
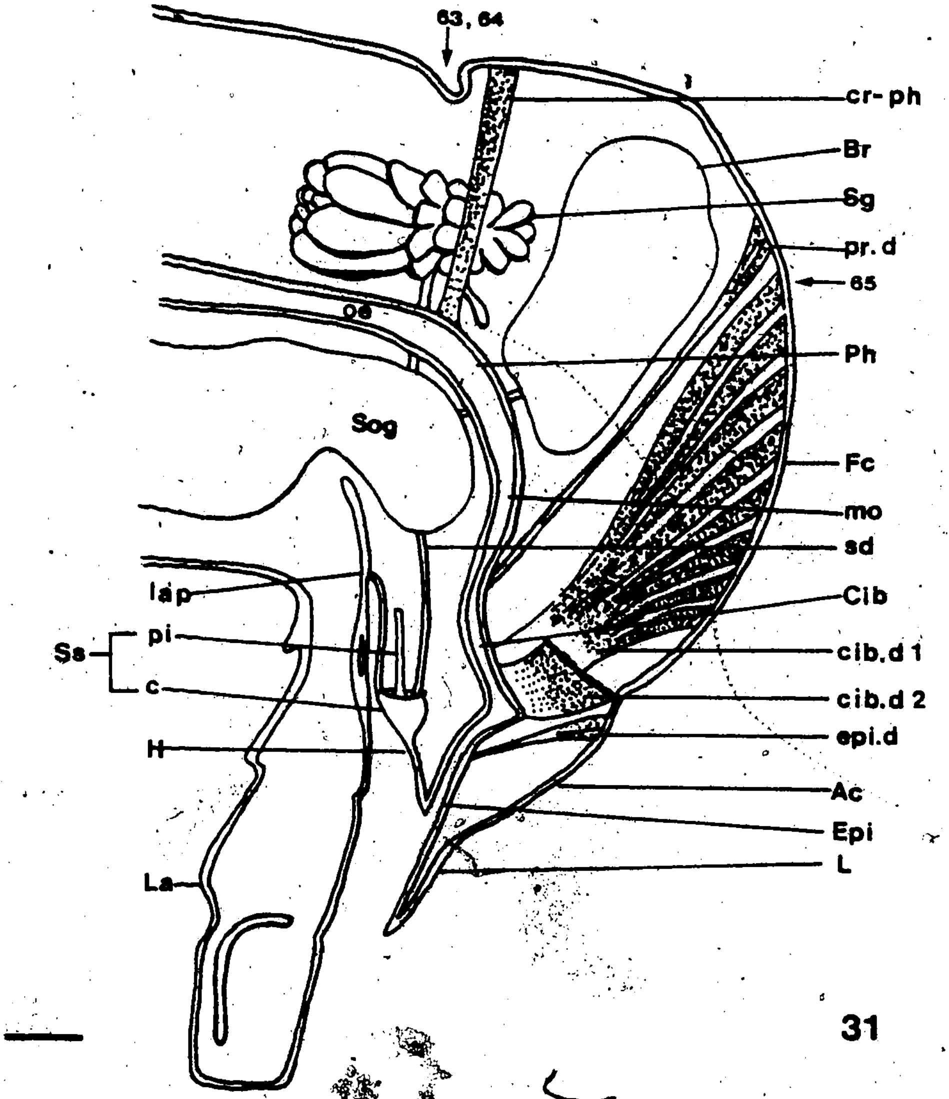

Mcs
L

Fig. 31. Longitudinal section through adult head
scale=20 um

Abbreviations; anteclypeus (Ac), brain (Br), cibarial dilators (cib.d 1, cib.d 2), cibarium (Cib), cranio-pharyngeal dilator (cr-ph) cylinder (c), epipharyngeal dilators (epi.d), epipharynx (Epi), frontoclypeus (Fc), hypopharynx (H), labial apodeme (lap), labium (La), labrum (L), mouth (mo), oesophagus (oe), pharynx (Ph), piston tendon (pi), praepharyngeal dilator (pr.d), salivary duct (sd), salivary gland (Sg), salivary syringe (Ss), sub-oesophageal ganglion (Sog).


63, 64
cr- ph
Br
Sg
pr. d
65
oe
Ph
Sog
Fc
mo
sd
lap
Cib
Ss
pi
c
cib.d 1
cib.d 2
epi.d
H
Ac
Epi
L
La

31

pump (Fig. 31). Origin, insertion and function of the clypeal muscles are listed in Table 5.

Sensilla on the fronto-clypeus and anteclypeus are socketed hairs (sh) (Fig. 32) and additionally, on the fronto-clypeus, campaniform sensilla (cs) (Fig. 33). An adult leafhopper has similar but more numerous sensilla and has two campaniform sensilla at the junction between anteclypeus and labrum (Fig. 35). Recently, Backus and McLean (1982) have described '20 precibarial sensilla' found associated with the epipharynx and hypopharynx; some of these are seen dorsally in Fig. 36 (s). Similar sense organs in aphids are gustatory (Wensler, 1969) and Backus and McLean (1982) feel these precibarial sensilla are also. Functions of other sensilla on the clypeus are unknown.

4.2.2.2 Antennae

Each antenna of *M. fascifrons* consists of scape (sc), pedicel (p) and flagellum (f) (Fig. 37). The antennal socket has a dorsal, overhanging margin and is membranous ventrally. The scape inserts into the membranous region and articulates with the margin of the socket via a ventral antennifer (antf) (Fig. 38). The cigar-shaped pedicel fits into the scape's distal end (Fig. 39) and the tapering flagellum into the pedicel's distal end (Fig. 40).

Muscles moving the antenna are found within the scape (intrinsic) or are inserted into the base of the scape and originate from the dorsal tentorial arm. These are illustrated in Figs. 41 and 42 and listed in Tables 4 and 5.

Antennal sensilla change from instar to instar, so I describe here only those of first instars (Fig. 39-42). The scape (Fig. 39) bears three sensilla: two socketed hairs (sh) ventro-medially near the junction of scape and socket and a campaniform sensillum (cs) on its dorsal distal surface. The pedicel (Fig. 40) has socketed sensilla (sh) on its surface, a peg sensillum (ps) near its insertion in the scape, three hairs on its surface and a distal ventral campaniform sensillum (cs). The flagellum (Fig. 37, 42) has one socketed hair (sh) on each of its second, third and fourth annuli, the one on the fourth segment being dorsal and the others ventral. The fifth annulus bears a campaniform sensillum on its dorsal surface.

Table 4

Head Muscles of *Macrosteles fascifrons*

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1 Musculus levator scapi primus– sc.l1
2 M. depressor scapi primus– sc.d1
3 M. levator scapi secundus– sc.l2
4 M. depressor scapi secundus– sc.d2
5 M. levator scapi tertius– sc.l3
6 M. depressor scapi tertius– sc.d3
7 M. extensor scapo–pedicellaris lateralis– a.ex
8 M. flexor scapo–pedicellaris medialis– a.f
9 M. levator scapo–pedicellaris lateralis– a.l
10 M. depressor scapo–pedicellaris medialis– a.dp
11 M. dilator cibarii primus– cib.d1
12 M. dilator cibarii secundus– cib.d2
13 M. dilator ephipharyngealis– epi.d
14 M. retractor setae mandibularis primus– md.r1
15 M. retractor setae mandibularis secundus– md.r2
16 M. retractor setae mandibularis tertius– md.r3
17 M. retractor setae mandibularis quartius– md.r4
18 M. protractor setae mandibularis primus– md.p1
19 M. protractor setae mandibularis secundus– md.p2
20 M. protractor setae mandibularis tertius– md.p3
21 M. retractor setae maxillaris primus– mx.r1
22 M. retractor setae maxillaris secundus– mx.r2
23 M. protractor setae maxillaris– mx.p
24 M. retractor pistilli– sal.d
25 M. dilator praepharyngealis– pr.d
26 M. dilator pharyngealis dorsalis– ph.dD
27 M. dilator pharyngealis lateralis– ph.dL
28 M. dilator pharyngealis–tentorio lateralis– t–ph
29 M. dilator cranio–pharyngealis– cr–ph
30 M. retractor labii primus– la.r1
31 M. retractor labii secundus– la.r2
32 M. protractor labii primus– la.p1
33 M. protractor labii secundus– la.p2
34 M. protractor labii tertius– la.p3
35 M. protractor labii quartius– la.p4
36 M. depressor labii– la.dp1
37 M. transversalis labii primus– la.t1
38 M. depressor labii– la.dp2
39 M. transversalis labii secundus– la.t2

Table 5

Head Muscles of *Macrosteles fascifrons*

Structure	Muscle	Origin	Insertion	No. of Fibers	Function
(A) Antenna	1	anteriorly on dorsal tentorium near cranium	dorso-lateral base of scape	(1)	levator of scape
	2	posteriorly on dorsal tentorium	ventro-lateral base of scape	(1)	depressor of scape
	3	antero-medially on dorsal tentorium	dorso-lateral base of scape	(4)	levator of scape
	4	postero-medially on dorsal tentorium	ventro-lateral base of scape	(4)	depressor of scape
	5	anteriorly on anterior tentorium	dorso-lateral base of scape	(1)	levator of scape
	6	posteriorly on anterior tentorium	ventro-lateral base of scape	(1)	depressor of scape
	7	dorso-lateral base of scape	postero-lateral base of pedicel	(1)	extensor of antenna
	8	dorso-medial base of scape	postero-medial base of pedicel	(1)	flexor of antenna
	9	dorso-medially on scape	postero-lateral base of pedicel	(4)	levator of antenna
	10	ventro-medial base of scape	postero-medial base of pedicel	(4)	depressor of antenna
(B) Postclypeus	11	postclypeal wall	tendons of roof of cibarium	(8)	dilators of cibarium
(C) Anteclypeus	12	anteclypeus below transclypeal suture	tendons of roof of cibarium	(8)	dilators of cibarium
	13	anteclypeus below muscle 12	tendon of epipharynx	(2)	dilator of epipharynx
(D) Mandibles	14	cranium ventral to antenna	anterior wall of stylet base	(2)	retractor of mandible
	15	posterior vertex of cranium	apodemal process from stylet	(1)	retractor of mandible
	16	antero-lateral process of hypopharyngeal wing	posterior wall of stylet base	(2)	retractor of mandible
	17	antero-lateral process of hypopharyngeal wing	postero-lateral base of mandibular guide	(1)	retractor of mandible
	→ 18	antero-dorsal wall of mandibular plate	postero-dorsally at junction of guide and mandibular apodeme	(3)	protractor of mandible
	19	medial-ventral wall of mandibular plate	anteriorly on stylet base ventral to retractors	(3)	protractor of mandible
	20	antero-ventral wall of mandibular plate	antero-laterally on mandiblular guide	(2)	protractor of mandible

cont. next page

Table 5 cont.

Structure	Muscle	Origin	Insertion	No. of Fibers	Function
(E) Maxillae	21	posterior vertex of head	postero-laterally on stylet base	(6)	retractor of maxilla
	22	posterior vertex of head	anteriorly on apodeme from stylet base	(1)	retractor of maxilla
	23	ventral wall of maxillary plate	antero-laterally on stylet base	(10)	protractor of maxilla
(F) Hypopharynx	24	antero-medial process of hypopharyngeal wing	piston of salivary syringe	(8)	dilator of salivary syringe
(G) Praepharynx	25	dorso-medially on postclypeus	posterior tendon of cibarium	(1)	dilator of cibarium
(H) Pharynx	26	dorso-laterally on postclypeus	antero-dorsally on pharynx	(1)	dilator of pharynx
	27	dorso-laterally postclypeus	antero-laterally on pharynx	(2)	dilator of pharynx
	28	laterally on posterior tentorium	lateral walls of pharynx	(3)	dilator of pharynx
	29	posteriorly on cranium	dorsal wall of pharynx	(1)	dilator of pharynx
(I) Labium	30	postero-laterally on hypopharyngeal wing	antero-laterally on lip of segment 1	(1)	retractor of labium
	31	ventro-laterally on hypopharyngeal wing	postero-medially on lip of segment 1	(1)	retractor of labium
	32	distally on hypopharyngeal wing	antero-apical tip of labial apodeme	(4)	protractor of labium
Segment 1	33	postero-laterally on tip of labial apodeme	posteriorly on base of segment 1	(1)	protractor of segment 1
	34	medially on labial apodeme	posteriorly on base of segment 1	(1)	protractor of segment 1
	35	distally on labial apodeme	posteriorly on base of segment 1	(7)	protractor of segment 1
Segment 2	36	proximo-laterally on segment 2	medial on labial groove	(6)	depressor of segment 2
	37	postero-medial on segment 2	medial on labial groove	(2)	closes labial groove
	38	postero-medial on segment 2	antero-lateral on segment 2	(1)	depressor of segment 2
	39	postero-medial on distal base of segment 2	medial on labial groove	(1)	closes labial groove

Fig. 32–36. SEM of fronto–clypeus and labrum of first instar larva and adult.

Fig. 32. Fronto–clypeus of first instar larva.

scale= 10 um

Fig. 33. Campaniform sensillum found on fronto–clypeus of first instar larva

scale= 1 um

Fig. 34. Socketed–hair sensillum found on fronto–clypeus of first instar larva

scale= 1 um

Fig. 35. Junction between anteclypeus and labrum of adult showing campaniform sensilla.

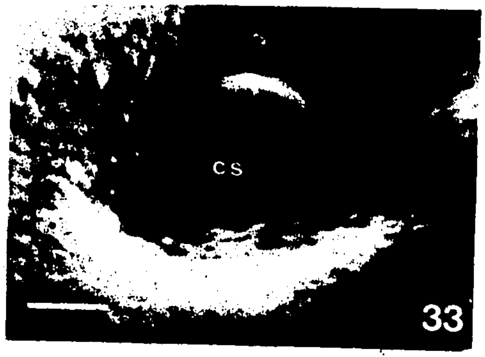
scale= 5 um

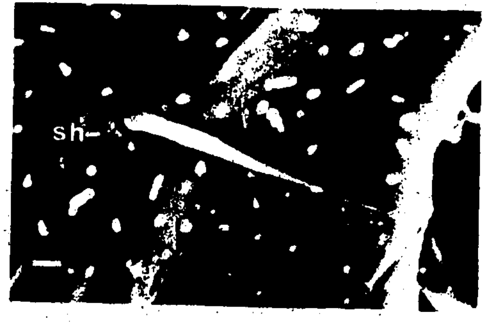
Fig. 36. Epipharynx

scale= 5 um

Abbreviations; anteclypeus (Ac), campaniform sensillum (cs), ephipharyngeal tendons (epit), labrum (L), mandibular plate (Mdp), maxillary plate (Mxp), socketed–hair sensillum (sh) sensillum (s).


cs
Fc
Mdp
Mxp
sh
L
32


cs
33


sh


Ac
cs
35

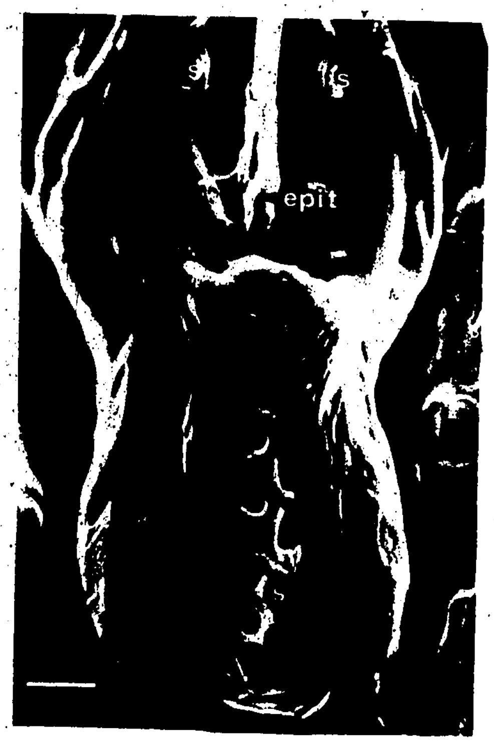

fs
epit

Fig. 37–40. SEM of antenna of first instar larva

Fig. 37. Antenna

scale= 10 um

Fig. 38. Antennifer

scale= 10 um

Fig. 39. Scape

scale= 10 um

Fig. 40. Pedicel

scale= 10 um

Abbreviations; antennifer (antf), campaniform sensillum (cs), flagellum (f), ledge (ld), pedicel (p), peg sensillum (ps), scape (sc), socket (so), socketed-hair sensillum (sh).


so
b
37


so
antf


sc
cs
p


p

Fig. 41–42. Antennal muscles

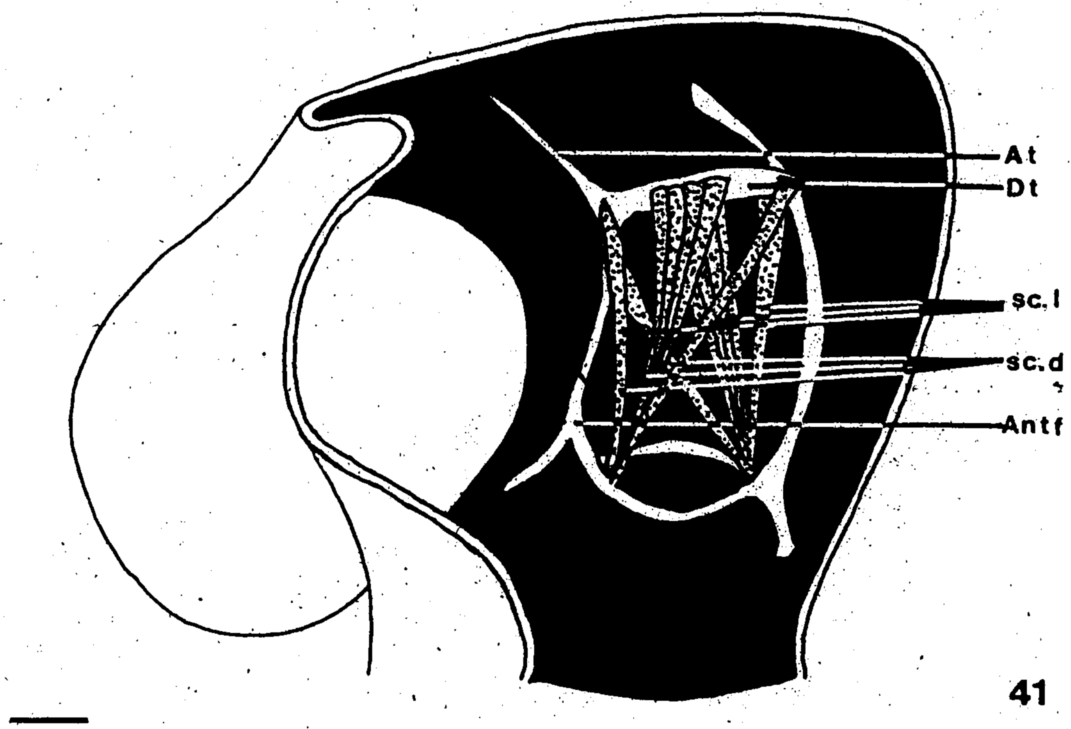
Fig. 41. Scape muscles

scale= 30 um

Fig. 42. Pedicel muscles

scale= 25 um

Abbreviations; antennal depressor (a.dp) antennal extensor (a.ex), antennal flexor (a.fl), anterior tentorial arm (At), antennifer (antf), dorsal tentorial arm (Dt), flagellum (f), pedicel (p), scape (sc), depressor of scape (sc.d), levator of scape (sc.l).



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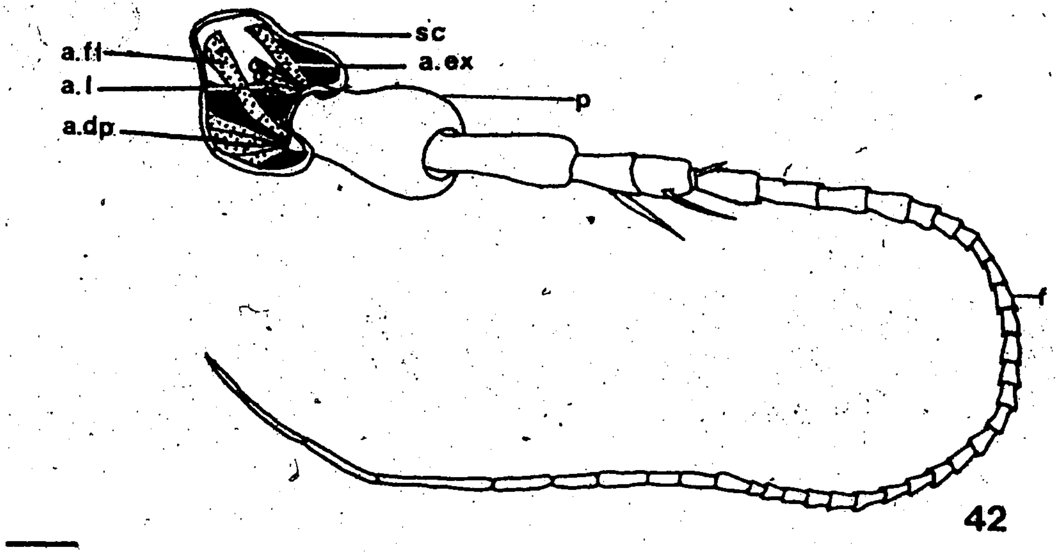
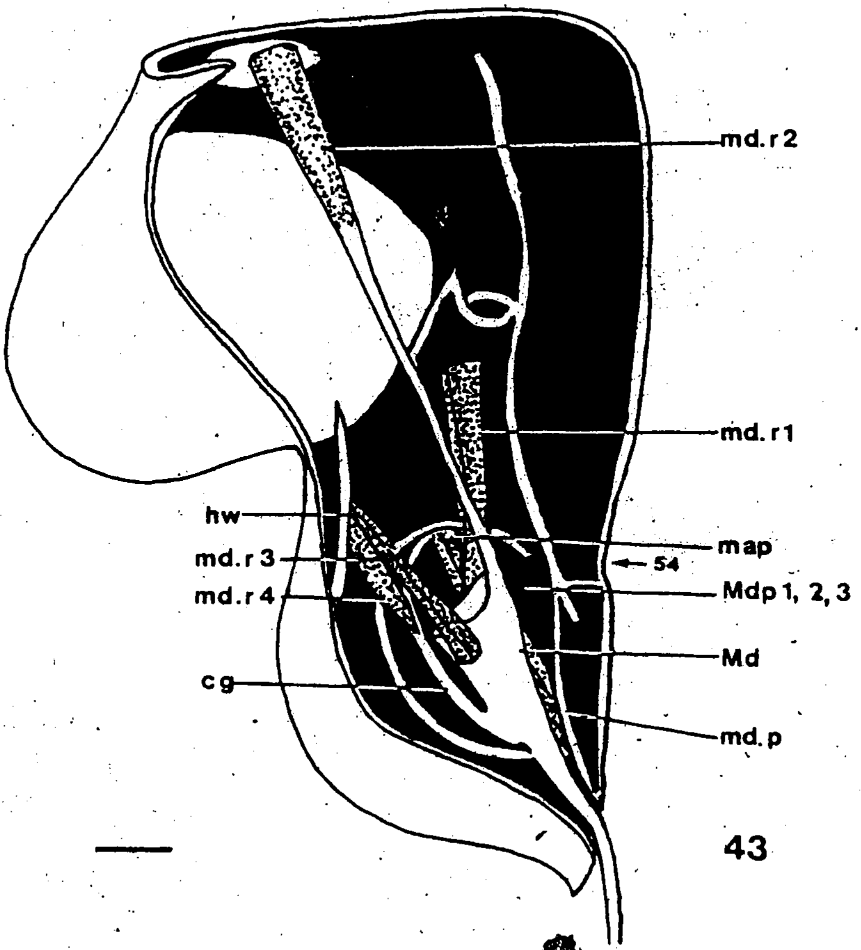


42

Fig. 43. Mandibular muscles

scale= 40 um

Abbreviations; cuticular guide (cg), hypopharyngeal wing (hw), mandibular plate (Mdp), mandibular apodeme (map), Mandible (Md), mandibular protractors 1,2,3 (md.p 1,2,3), mandibular retractors, (md.r 1, md.r2, md.r3, md.r4).



43

Fig. 44–46. SEM of mandible and hypopharyngeal wings

Fig. 44. Mandibular tip

scale= 1 um

Fig. 45. Mandible and cuticular guide (=mandibular lever)

scale= 20 um

Fig. 46. Cast skin of late instar larva showing relationship of stylets and hypopharyngeal wings

scale= 20 um

Abbreviations; cuticular guide (cg), hypopharyngeal wing (hw), fronto-clypeus (Fc), labial apodeme (lap), labium (La), mandible (Md), maxilla (Mx), maxillary lever (mxl), maxillary plate (Mxp), maxillary pore sensilla (mxps), sheath (sth).


44


cg
sth


Mx
hw
sth
mxp
Md
cg
Mxp
La

4.2.2.3 Mandibles

The mandibles (Md) are tubular cuticular stylets, funnel-shaped proximally (Fig. 43) and tapering distally to serrated ends (Fig. 44). They are located anterior to the maxillae and each has a cuticular guide (cg) (=mandibular lever) (Figs. 43, 45, 46) that articulates with an apodemal process (map) arising from the mandibular plate (Fig. 43). Each process is ensheathed in a membranous sac that merges distally with the maxillary sheath.

Pollard (1968) has shown that larvae and adults of *Eupteryx melissae* (Homoptera: Cicadelidae) use their mandibles to puncture the leaf and then to anchor themselves while they feed. Observations of *M. fascifrons* feeding through a membrane on an artificial diet show them to feed in the same manner.

Protractor (md.p) and retractor (md.r1, md.r2, md.r3, md.r4) muscles move the mandibles; their origins, insertions and functions are listed in Table 5 and illustrated in (Fig. 43, 54, 56).

Each mandible contains three sensory dendrites (Forbes and Raine, 1973; Backus and Mclean, 1982). Backus and Mclean (1982) provide ultrastructural evidence to suggest that these are proprioceptive mechanosensilla. The mandibular plates of first instars do not bear sensilla on their outer faces, but in later larval instars and adults they have socketed hairs.

4.2.2.4 Maxillae

The maxillae (Mx) are located posterior to the mandibles and anterior to the labium (Fig. 46). They are tubular, funnel-shaped stylets tapering distally and fitting together mesially to each other by a system of interlocking grooves and ridges (Fig. 47, 49, 53, 55). The left stylet contains the salivary canal (sc) and the two apposed stylets form the food canal (fdc) (Fig. 49, 55) between them. A maxillary lever (mxl) extends from the funnel of each maxilla to articulate with the hypopharyngeal wing (hw) (Fig. 46, 48, 56). The maxilla and hypopharyngeal wing of each side are each enclosed proximally within a membranous sheath (sth) and distally share a common sheath with the mandibles (Fig. 46). Associated with the maxillae are the maxillary plates (Mxp). Each of these fuses postero-medially with the lateral arm of a hypopharyngeal wing.

The maxillary stylets are the main penetrating organs of leafhoppers (Pollard, 1968). Interlocked stylets have properties that allow them to bend and let one stylet

Fig. 47-52. SEM of maxilla and associated structures

Fig. 47. Mandibular and maxillary stylets
scale= 10 um

Fig. 48. Maxilla, lever and hypopharyngeal wing
scale= 10 um

Fig. 49. Transverse section (by hand) of mandibular and maxillary stylets showing food and salivary canals
scale= 2 um

Fig. 50. Maxillary pore sensilla
scale= 2 um

Fig. 51. Internal structure of maxillary pore sensilla
scale= 2 um

Fig. 52. Sensillar structure found on maxillary plate of adult
scale= 2 um

Abbreviations; food canal (fdc), hypopharyngeal wing (hw), mandible (Md), maxilla (Mx), maxillary lever (mxl), salivary canal (sc), sensillum (s), sheath (sth).


Mx
mxl
hv
hv
sth
48

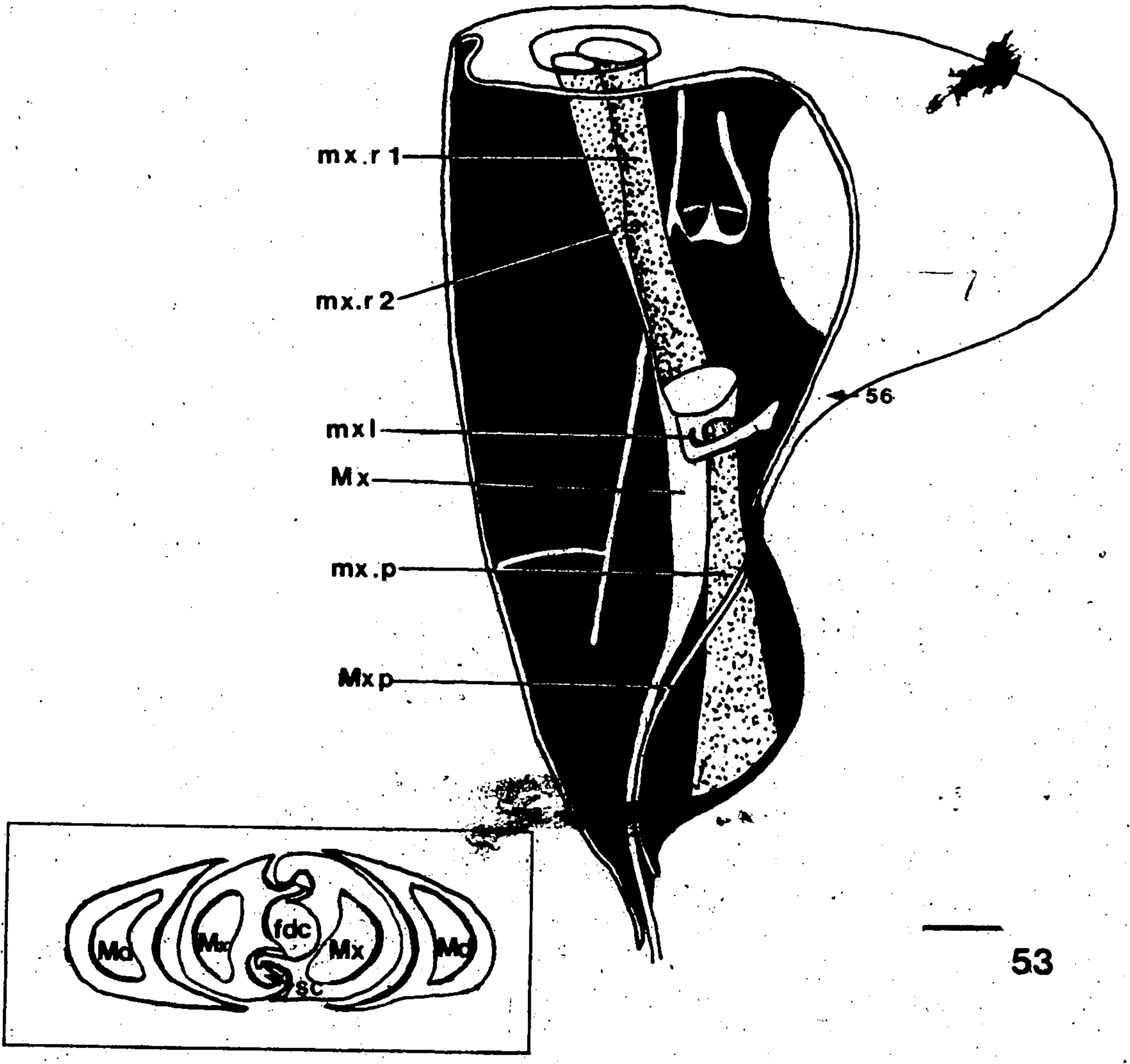

Mx
sc
49

Fig. 53. Maxilla and associated muscles

Inset transverse section of mandibular and maxillary stylets

scale= 40 um

Abbreviations; food canal (fdc), maxilla (Mx), maxillary lever (mxl) maxillary plate (Mxp), protractors of maxilla (mx.p), retractors of maxilla (mx.r 1, mx.r2), salivary canal (sc).



53

Fig. 54–57. Cross sections of head structures

Fig. 54. Mandible

scale= 10 um

Fig. 55. Mandibular and maxillary stylets

scale= 5 um

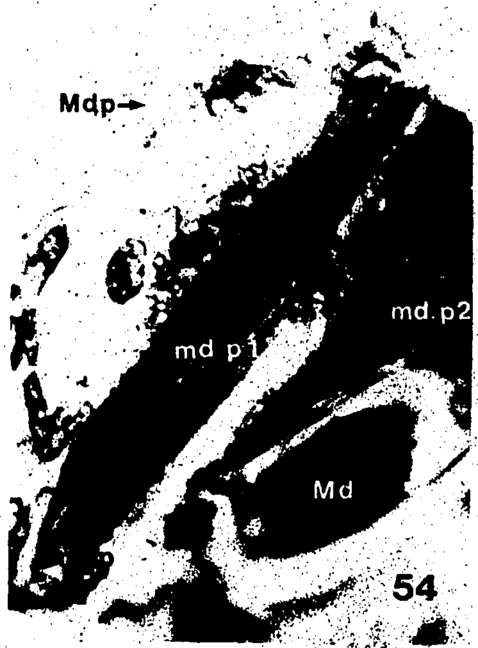
Fig. 56. Maxilla and mandible

scale= 10 um

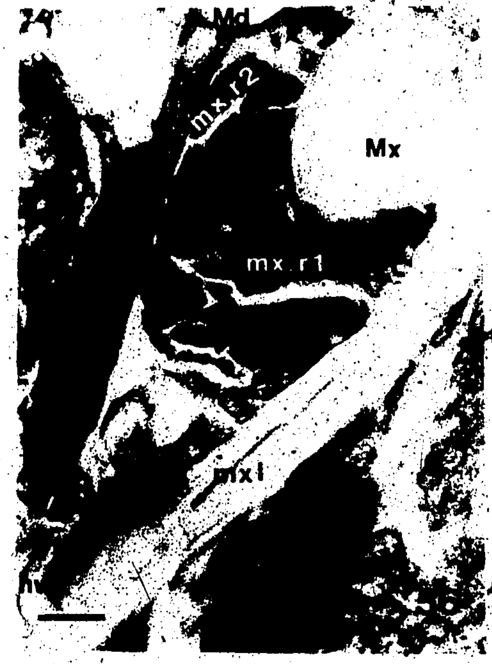
Fig. 57 Hypopharyngeal wing and posterior tentorium

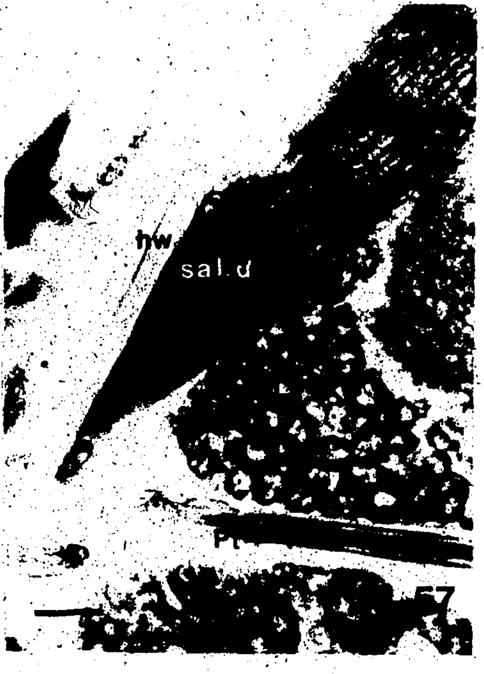
scale= 10 um

Abbreviations; anteclypeus (Ac), food canal (fdc), hypopharyngeal wing (hw), ganglion (g), labium (La), mandibular plate (Mdp), mandibular apodeme (map), Mandible (Md), mandibular protractors (md.p 1, md.p2), mandibular retractors (md.r3, md.r4), maxilla (Mx), maxillary lever (mxl), posterior tentorium (Pt), retractors of maxilla (mx.r 1, mx.r2), salivary canal (sc), dilators of salivary syringe (sal.d).


Mdp
md.p2
md p1
Md
54


Md
dc


Md
mx.r2
Mx
mx.r1
mxl


hw
sal.d
Pt
57

slide ahead of the other when the insect feeds. Muscles moving the maxillae are listed in Table 5 and illustrated in Figure 53 and 56.

Each maxilla contains 5 sensory dendrites (Forbes and Raine, 1973; Backus and McLean, 1982) that extend the length of the stylet and a shorter sixth dendrite that ends at its base (Backus and McLean, 1982). Recent ultrastructural studies by Backus and McLean (1982) support the theory that " sensilla in both the maxillae and mandibles detect direction and torque of the stylets, but dendrites in the maxillae alone detect tension."

On the lateral edge of each maxillary plate is a pore (mxps) containing sensilla (Fig. 50). These are contained within an invaginated, barrel-shaped structure (Figs.45, 51) that Evans (1973) believes to be the remnant of the maxillary palpus. In adults, there are socketed hairs on the outer face of each maxillary plate and other sensilla (Fig. 52) whose function is unknown. A socketed hair is found in all instars, ventral to the antennae and lateral to the clypeus

4.2.2.5 Hypopharynx, Salivary Syringe and Salivary Glands

The hypopharynx (H), a conical lobe posterior to the clypeus, forms the floor of the food pump (Cib) and houses the salivary syringe (Ss) (Figs. 31, 58). Dorso-laterally, it is extended on either side as hypopharyngeal wings (hw), two sclerotized rods joined by a membranous region (Fig. 58). The salivary syringe consists of a cuticular cylinder (c), piston (pi) and afferent (afd) and efferent (efd) ducts (Figs. 31, 59, 62, 63, 68). The efferent duct is continuous distally with the salivary canal (sc) between the maxillae and has a small flap valve (Fig. 63) that help control the flow of salivary secretions out of it. A single afferent duct runs dorsally and branches, with each branch leading to a pair of salivary glands in the prothorax (Fig. 64).

The salivary syringe has one set of muscles, the dilators of the salivarium (sal.d), originating on the inner rod of the hypopharyngeal wings and inserting into the piston (Table 5, Fig. 68).

The hypopharynx bears two campaniform sensilla on the top (Backus and McLean, 1982).

Dobroscky (1931) described the salivary glands of *M. fascifrons*. They are paired structures consisting of a tubular accessory gland, a group of pinnately arranged acini followed by another group of acini having various types of inclusions (Fig. 65). The

Fig. 58–61. SEM of head structures

Fig. 58. Hypopharyngeal wings

scale= 5 um

Fig. 59. Salivary syringe

scale= 5 um

Fig. 60. Labial apodeme

scale= 5 um

Fig. 61. Apex of labium showing sensilla and tip of maxillary stylets

scale= 5 um

Abbreviations: afferent duct (afd), cylinder (c), hypopharyngeal wings (hw), labial apodeme (lap), labial groove (lag), labium (La), piston tendon (pi), sensilla (s), stylets (sty).


pi
afd

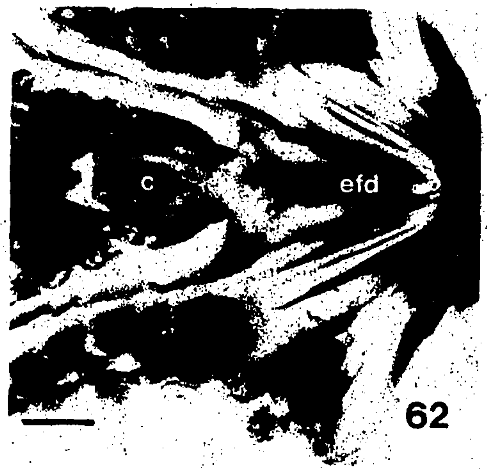

lap
La


La
lag
sty
61

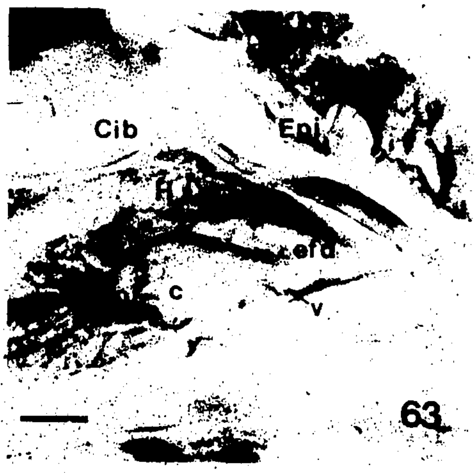
Fig. 62-67. Sections of hypopharyngeal and labial structures

Fig. 62. Frontal section of salivary syringe
scale= 10 um
Fig. 63. Saggital section of salivary syringe
scale= 10 um
Fig. 64. Salivary duct, frontal section
scale= 10 um
Fig. 65. Salivary gland, frontal section
scale= 50 um
Fig. 66. Labial apodeme and muscles, frontal section
scale= 10 um
Fig. 67. Labial apodeme and muscles, frontal section
scale= 10 um

Abbreviations; acini (1-5) (A 1-5), anteclypeus (Ac), common salivary duct (csd), cibarium (Cib), cylinder (c), efferent duct (efd), epipharynx (Epi), hypopharynx (H), labial apodeme (lap), labial depressor (la.dp.1), labial protractor (la.p), labrum (L), piston tendon (pi), salivary duct (sd), salivary syringe valve (v).

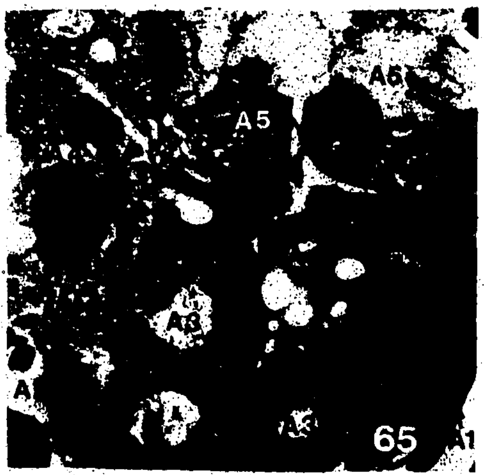


62

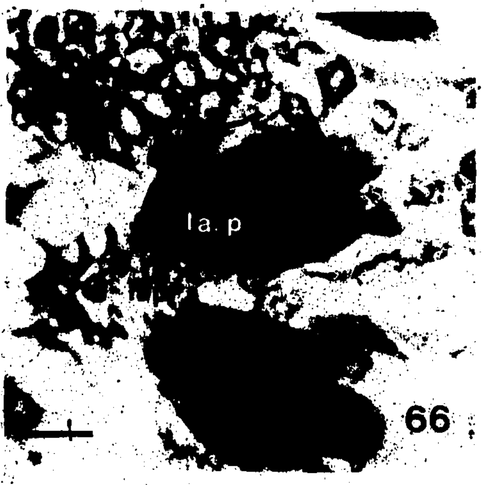


63

64



65

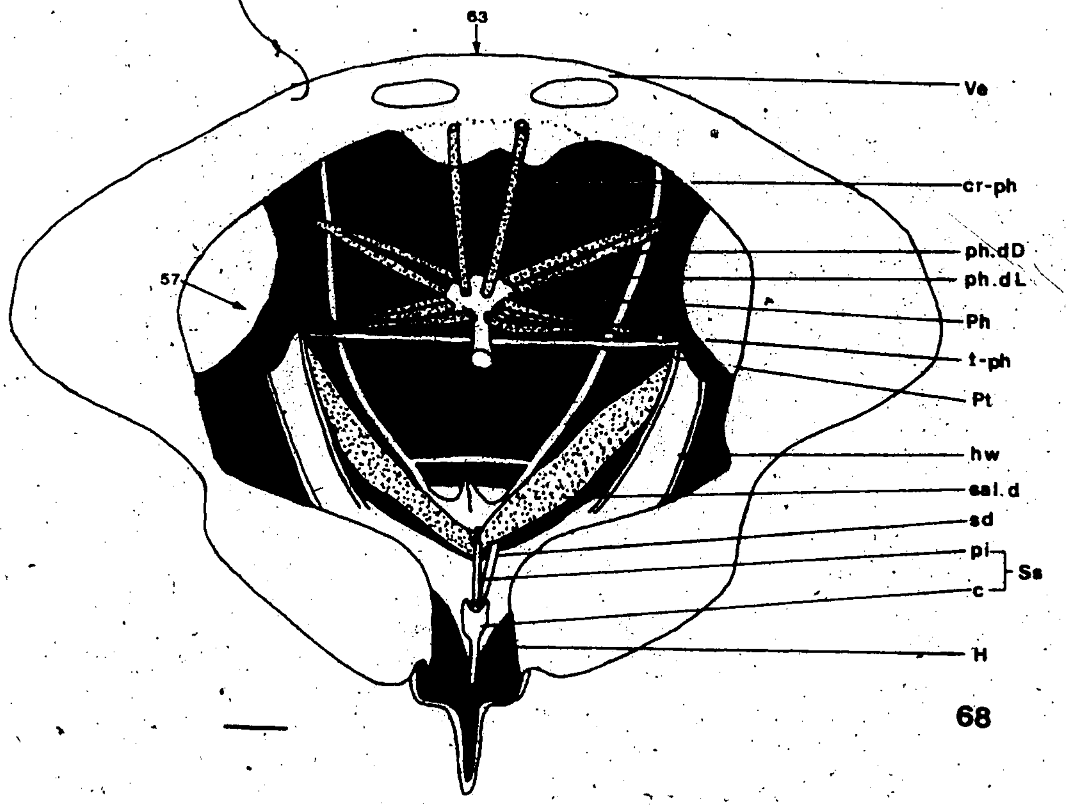


66

67

Fig. 68. Pharyngeal and salivary syringe musculature
scale= 40 um

Abbreviations; cylinder (c), cranio-pharyngeal dilator muscle (cr-ph), hypopharyngeal wings (hw), hypopharynx (H), pharyngeal dilators (ph.dD, ph.dL), pharynx (Ph), piston tendon (pi), posterior tentorium (Pt), salivary dilators (sal.d), salivary duct (sd), salivary syringe (Ss), tentorio-pharyngeal dilator (t-ph), vertex (Ve).



68

actual function of each acinus and its inclusion is unknown.

4.2.2.6 Labium

A three-segmented labium lies posterior to the other mouthparts with the maxillary and mandibular stylets fitting into its medial anterior groove (Figs. 30, 61). An anterior labial apodeme (lap) originates on the first segment and projects dorsally with its apex lying between the connectives of the suboesphageal and prothoracic ganglia (Figs. 31, 46, 60, 66, 67, 69, 70). The labium attaches to the cervical membrane laterally and posteriorly, to the maxillary plates anteriorly and to the hypopharyngeal wings by two ligaments running from its dorsal anterior edge (Fig. 46).

Labial muscles occur in the first two segments, attached to the apodeme and to the proximal base of segment 1 (Fig. 66, 67, 69-75); these are listed in Table 5.

Numerous sensilla occur on the three segments of the labium whose function has not been studied in cicadellids. Distally, on the apex of the third segment on each side are eight sensilla (Fig. 61). In aphids, these are mechanosensory (Tjallingii, 1978) but in the heteropteran *Lygus lineolaris* (Hatfield and Frazier, 1980), they are chemosensory.

4.2.2.7 Tentorium

The tentorium of *M. fascifrons* is similar to that of other cicadellids. The posterior tentorial bar (Pt) runs from one lateral edge of the hypopharyngeal wing (hw) to the other (Fig. 68). The dorsal (Dt) and anterior tentorial arms (At) are not joined to the posterior tentorium and are [illegible] dorsally in the head capsule. The ventral end of the anterior arm attaches to the antennifer (antf) and then extends dorsally to the cranium (Fig. 41). Midway, the [illegible] [illegible] branches off and extends anteriorly to the head capsule, ventral to the oc[illegible] [illegible]. The antennal muscles originate on this arm and insert ventrally and dorsally on the base of the scape. Two muscles also originate on the anterior arm near its junction with the dorsal arm.

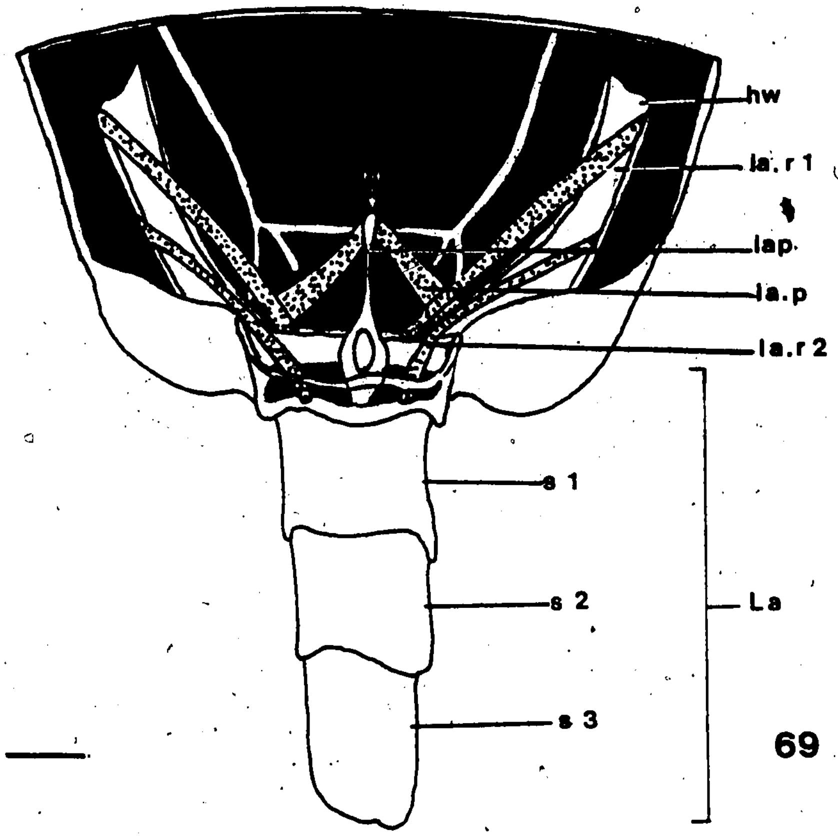
4.2.2.8 Cibarium, Pharynx and Oesophagus

Food is sucked up through the food canal between the maxillary stylets into what Snodgrass (1937) calls 'the functional mouth' by the cibarial pump and from there into the cibarium (Fig. 31, Cib). Next it passes through the "'true mouth', the inner opening of the pump, into the pharynx" (Snodgrass, 1938) and into the oesphagus that leads to the

Fig. 69. Retractor and protractor labial musculature

scale= 40 um

Abbreviations; hypopharyngeal wings (hw), labial apodeme (lap), labial protractor (la.p), labial retractors (la.r.1, la.r2), labium (La), segments 1–3 (s1, s2, s3).

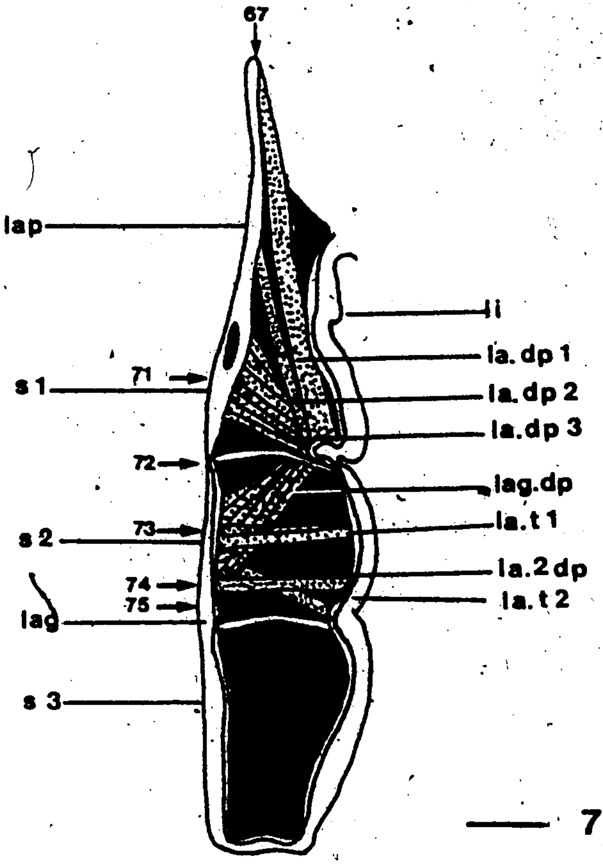


69

Fig. 70. Labial musculature

scale= 40 um

Abbreviations; labial apodeme (lap), labial groove (lag), labial depressors (la.dp1, la.dp2 la.dp3), labial depressor of segment 2 (la.2dp), labial groove depressor (lag.dp), labial transverse muscles (la.t1 la.t2), lip of segment 1 (li), segments 1–3 (s1, s2, s3).


67
lap
li
la. dp 1
s 1
71
la. dp 2
la. dp 3
72
lag.dp
la. t 1
73
s 2
la. 2 dp
74
75
la. t 2
lag
s 3

70

Fig. 71–75. Labial musculature (transverse sections)
scale= 10 um

Abbreviations; labial groove (lag), labial depressors (la.dp1, la.dp2 la.dp3), labial depressor of segment 2 (la.2dp), labial groove depressor (lag.dp), labial transverse muscles (la.t1 la.t2).


la dp 1
la dp 2
la


lag
lag dp

72


lag dp
lag
la t1

73


lag dp
la t2
lag

74


2dp
lag

midgut. Muscles associated with the pharynx (Ph) and praepharynx are listed in Table 5 and illustrated in Figures 31 and 68.

4.2.3 Discussion

It is difficult to compare cephalic structure and musculature between known homopterans because existing studies are incomplete and often incorrect. The suborder is large and diverse and comparison among species could provide insight into their evolutionary relationships.

Table 6 compares selected cephalic structures and muscles in six species of leafhoppers and in representatives of other homopteran families. Most of the latter examples are taken from Singh (1971).

Generally, mouthpart structure in homopterans is very similar. All have mandibular and maxillary stylets, a clypeo-labrum and a labium. Differences arise in modifications of these structures. For example, in auchenorryhnchous Homoptera, there is a tendency for the tentorium and number of ocelli to be reduced. Some sternorrhynchans have a crumen, a membranous sac used to house their long stylets, in the absence of a long labium (Pysllidae, Coccidae). Extent of the loro-maxillary sutures varies in the taxon and the transclypeal suture can be present or absent (Table 6). The mandibular lever can be triangular, quadrangular, rectangular, rod-like or absent (Table 6). The labial apodeme is present in all auchenorrhynchous homopterans but is absent in members of Aphidoidea, Psylloidea, and Coccoidea. The number of retractor and protractor muscles associated with the stylets is also variable (Table 6) although the number of maxillary muscles tends to be more constant.

It is evident that differences do exist not only between families but within families (Table 6). Many of these differences could be correlated with feeding habits. However, until there are more thorough analyses, including studies of feeding behavior, it is difficult to determine if there are any evolutionary trends in the cephalic structure of homopterans.

Rieger (1976) studied the heteropteran *Ochterus marginatus* and speculated on the evolutionary relationships of the suborder Heteroptera. He then looked at representative Sternorrhyncha and Cicadina, using the trends he observed in homopterans

Table 6

Comparison of cephalic skeletomusculature of known adult homopterans.

Taxon	Tr. clyp. Suture	Tentorium fusion	Tentorium post.	Tentorium ant.	Tentorium dors.	Mandible lever	Mandible retr.	Mandible protr.	Maxilla lever	Maxilla retr.	Maxilla protr.	Labium apod.	Labium crumen	# of Ocelli
FULGOROIDEA														
Melichara quadrata[1]	–	+	+	+	+	3g	3	2	r	1	1	+	–	var
Scolops pungens[2]	–	–	+	–	–	+	1	1	+	1	1	+	–	2
CICADIDAE														
Tibicina septendecim[2]	+	+	s	+	+	r4g	1	2	r	3	2	+	–	3
Melampsalta sp.[3]	+	+	+	+	+	4g	1	1	?	1	1	+	–	3
Platypleura octogutatata[1]	+	+	+	+	+	3g	4	3	r,c	2	2	+	–	3
CICADELLIDAE														
Typhlocyba ulmi[4]	–	–	s	–	–	r	1	1	r	2	1	+	–	0
Putoniessa nigra[5]	+	–	s	?	?	r	3	1	r	1	1	+	–	2
Kolla mimica[1]	+	–	s	+	+	r	3	2	r,c	1	2	+	–	2
Idiocerus atkinsoni[6]	+	–	s	+	+	r	4	3	r,tv	1	2	+	–	2
Aulacizes irrorata[2]	–	–	s	tnd	+	r	2	1	+	1	2	+	–	2
Macrosteles fascifrons[7]	+	–	s	+	+	r	4	3	r,b	2	1	+	–	2
CERCOPIDAE														
Ptyelus nebulosus[1]	–	+	+	+	+	3g	3	2	r,c	2	2	+	–	2
Lepyronia quadrangularis[1]	–	–	+	+	+	+	1	1	+	2	2	+	–	2
MEMBRACIDAE														
Oxyrhachis tarandus[1]	+	–	+	+	+	3g	3	2	r,c	1	2	+	–	2
Ceresa bulba[2]	+	–	!	–	+	+	3	1	+	1	2	+	–	2
APHIDOIDEA														
Macrosiphum rosaeiformis[1]	+	+	a	+	–	r	1	2	+	1	2	–	–	3
COCCIODEA														
Perissopneumon tectonae[1]	–	+	a,b	+	–	sh,b	2	2	+	1	1	–	+	0?
ALEUROIDOIDEA														
Aleurolobus barodensis[1]	–	+	a	+	–	c	2	2	s	1	2	+	–	2
PSYLLOIDEA														
Diaphorina citri[1]	–	+	a	+	–	co	1	1	r,s	1	2	–	+	3
Psylla mali[8]	–	+	a	+	–	–	2	2	r	2	2	–	+	2

+ = present; – = absent; var = variable; r = rod–like; s = straight; c = curved; sh = short; b = broad; co = conical; tv = transverse; a = arched; 3g = triangular; 4g = quadrangular; r4g = rectangular; tnd = tendon; *– nos refer to no.of sets of muscles; [1] Singh, 1971; [2] Kramer, 1950; [3] Myers, 1928; [4] Willis, 1948; [5] Evans, 1938; [6] Arora and Singh, 1962; [7] this study; [8] Grove, 1918.

to develop a ground plan for Heteroptera.

Rieger described displacement ~~of~~ the maxillary lever, from a more primitive articulation with the head capsule to an articulation with the hypopharyngeal wing, to its absence in some heteropterans. In *M. fascifrons*, the maxillary lever articulates with the hypopharyngeal wing, supporting Evans' (1947) belief that this is a more specialized leafhopper.

Rieger also compared the number of mandibular protractors and retractors and the shape of the mandibular lever. Unfortunately, he based his conclusions only on sternorrhynchous homopterans and on members of one family of auchenorrhynchans. This resulted in some incorrect conclusions. For example, he stated that homopterans have only one mandibular protractor muscle and always a rod-like mandibular lever. Table 6 lists data from other studies which contradict this statement.

Hamilton (1981) used head structure to reconstruct a phylogeny of the Homoptera. He used loss of tentorium, loss of median ocellus and extent and presence of mandibular sutures to separate families. Table 6 illustrates some of these trends; for example, membracids and cicadellids are considered to be more highly evolved since they have no median ocellus and a reduced tentorium.

It might be more valid to compare head structure within families than within Homoptera as a whole. Evans (1947), in his classification of the leafhoppers, heavily weighted external head structure in determining primitive and more derived groups. Results of previous studies show that differences do exist in limits of sutures, extent of plates, presence or absence of tentorium and attachment and number of muscles. Some of these differences no doubt correlate with changes in feeding habit associated with adaptive radiation in leafhoppers.

There are only six studies of adult cephalic skeletomusculature in species representing a range of primitive to derived leafhoppers. *Typhlocyba ulmi*, according to Evans (1947), is near the base of the Jasssoid stem although not ancestral. *Kolla mimica* and *Putoniessa nigra* are more central. *Idiocerus atkinsoni* (Arora and Singh, 1962), represents a more specialized grade of development and *Aulacizes irrorata* (Kramer, 1950) and *M. fascifrons* are both at "the culmination of development" (Evans, 1947) in the taxa Ulopides and Macropsides respectively.

Comparison of these leafhoppers (Table 6) shows that differences do exist. One characteristic is the presence or absence of the dorsal and anterior tentorial arms. Absence is considered by most authorities to be a more advanced characteristic. However, *T. ulmi*, at the base of the Jassoid stem (Evans, 1947), apparently has no dorsal or anterior tentorial arms. This could be an incorrect observation or perhaps the mesophyll feeding of *T. ulmi* is less demanding – a strong footing for stylet muscles being unnecessary. *T. ulmi* also has a smaller number of mandibular muscles.

The number of mandibular retractor and protractor muscles appears to increase as leafhoppers become more specialized. *M. fascifrons* and *I. atkinsoni* have four sets of retractor muscles and *A. irrorata* has two; all are more specialized leafhoppers. *T. ulmi*, a primitive leafhopper, has only one set.

These few studies indicate trends and do not allow any conclusions to be made. More complete stud[illegible]presentatives of a variety of primitive to highly specialized leafhoppers is req[illegible] understand the evolution of their cephalic skeletomusculature.

5. Mouthpart Development in Embryos of *Macrosteles fascifrons* (Stål)

5.1 Introduction

In this chapter, I describe mouthpart embryogenesis in *Macrosteles fascifrons* (Stål) (Hemiptera: Cicadellidae). Hemipteran mouthparts are very different from those of most exopterygotes and their development is of great interest to morphologists and to those studying their evolution .

Homoptera, a large hemimetabolan suborder (Evans, 1963), is generally divided into 2 groups, the Sternorrhyncha and Auchenorrhyncha, but there is some question as to the validity of this division (for a discussion of this see Scudder (1979) and Hennig (1981)). The Sternorrhyncha include aphids, coccids, aleurodids and pysllids and the Auchenorrhyncha, fulgorids, cicadids, cercopids, cicadellids, and membracids. There are more embryological studies (Table 7) on sternorrhynchans than on auchenorrhynchans (Table 7). This is likely due to the unusual life cycles, development and economic importance of sternorrhynchans (Scudder, 1979).

Mouthpart embryogenesis in homopterans has been described by Muir and Kershaw (1912) in a fulgorid, by Pesson (1944) in several coccids, and by Singh (1971) in a membracid (see Table 7 for species names). In heteropterans, the sister group of Homoptera (Hennig, 1981), mouthpart development has been studied by Muir and Kershaw (1911) and Newcomer (1948) (Table 7).

In the introduction, I pointed out that there is still controversy over the homology of some structures of the hemipteran head. Since homology of mouthparts is used in discussing the evolution of the hemipteran cranium (Snodgrass, 1938; Evans 1946; Heslop-Harrison, 1956; Duporte, 1962; Parsons, 1964; Puchkova, 1970; and Hamilton, 1981), it is important that such homologies be correct. In addition to morphological studies, embryological studies are used to establish homologies. Unfortunately, as discussed in the introduction, they have often created more confusion than clarification.

In this chapter, I describe mouthpart embryogenesis in *M. fascifrons*, discuss homologies of the various parts, and address the questions posed in chapter 1. I first describe mouthpart development as it proceeds through a series of stages encompassing varying percentages of total development time (TDT) and then describe, in detail, the

Table 7

Species used in embryological studies of Hemiptera.

Higher Taxon	Species	Author
Homoptera		
Auchenorrhyncha		
Fulgoroidea	*Siphanta acuta*	Muir and Kershaw 1912
	Pyrilla perpusilla	Sanders 1956
	Scolypapa australis	Fletcher and Anderson 1980
Cicadidae	*Cicada septemdecim*	Heymons 1899
Cicadellidae	*Euscelis plebejus*	Sanders 1959
Membracidae	*Oxyrhachis tarandus*	Singh 1971, 1981
Sternorrhyncha		
Aphididae	*Chaitophorus populi*	Witlaczil 1884
	Aphis sambuci	Witlaczil 1884
	Aphis pelargonii	Will 1883
	Melanoxanthus salicis	Tannreuther 1907
	Melanoxanthus salicicola	Tannreuther 1907
	Lachnus rosae	Bömel and Jancke 1942
	Aphis pomi	Bömel and Jancke 1942
Coccidae	*Pseudococcus medanieli*	Shinji 1919
	Lecniodiopsis pruinosa	Shinji 1919
	Icerya purchasi	Shinji 1919
	Pseudococcus adlonidun	Pesson 1944
	Pulvinaria mesembryanthemi	Pesson 1944
	Aspidiotus ostreaeformis	Pesson 1944
Aleurodidae	*Trialeurodes vaporariorum*	Weber 1935
Psyllidae	*Psylla buxi*	Wilcke 1941
Heteroptera		
Naucoridae	*Naucoris cimicoides*	Heymons 1899
Notonectidae	*Notonecta glauca*	Heymons 1899
Nepidae	*Nepa cinerea*	Heymons 1899
Cimicidae	*Cimex dissimilis*	Heymons 1899
Reduviidae	*Pristhesancus papuensis*	Muir and Kershaw 1911
	Rhodnius prolixus	Mellanby 1935, 1936
Pyrrhocoridae	*Pyrrhocoris apterus*	Seidel 1924
	Pyrrhocoris apterus	Mantolin 1973
Lygaeidae	*Oncopeltus fasciatus*	Newcomer 1948
	Oncopeltus fasciatus	Butt 1949
most families	representative species	Cobben 1968
Gerridae	Gerris paludum insularis	Mori 1969, 1976

development of specific parts.

5.2 Observations

5.2.1 General Development of Mouthpart Appendages

During anatrepsis, the germ band, lying on the postero-dorsal surface of the egg invaginates posterior end first into the yolk (Fig. 9). Once it immerses in the yolk, it elongates and its caudal end flexes ventrally toward the egg's posterior pole (Fig 10, 76).

Over the next 5% of TDT the ectoderm evaginates segmentally to form paired appendage anlagen, beginning in the first thoracic segment and progressing cephalad and caudad (Figs. 76, 77). The stomodaeum (Figs. 77, 78) invaginates behind the clypeo-labral evagination (C-L) and the mesoderm (me) segments and forms coelomic sacs within the base of each appendage (Fig. 79). The head lobes (Ptc) begin to flex medially and caudally (Fig. 77).

From 30-45% TDT, the evaginated anlagen lengthen by mitosis in their cells, change shape, and shift position and organ rudiments such as the stomodaeum, salivary glands, nerve cord, fat body and proctodaeum begin to develop.

At 30% TDT, the clypeo-labrum (C-L) is a single lobe in front of the stomodael invagination (st) and the antennae (A) are beginning to grow medially behind the clypeo-labrum (Fig. 80). Behind the stomodaeum and in front of the elongating mandibular anlagen (Md), intercalary appendage rudiments are visible (Fig. 80, In). The maxillary anlagen subdivide longitudinally to form inner and outer lobes (Fig. 81, 82) and the labial appendages (La) elongate (Fig. 81). Lateral ectoderm of the intercalary, maxillary and labial venters invaginates medial to the appendages to form the anterior tentorium (Fig. 168), posterior tentorium (Fig. 171) and salivary glands (Fig. 83), respectively.

As growth proceeds, the appendage anlagen lengthen and the antennae (A) cross ventrally behind the clypeo-labrum, obscuring the stomodaeum and mandibles (Fig 84). The clypeo-labrum develops a double-fold (Figs. 85, 86) and the mandibular and inner maxillary anlagen grow medially over the venters of their segments, their distal ends meeting mid ventrally (Fig. 84, 87, 88). The outer maxillary lobes (Mxp) become conical and maintain this shape and size for the rest of embryogenesis (Figs. 84, 87). The distal

Fig. 76–79 Segmentation and Appendage Formation– 20–25% TDT

Fig. 76 Ventro-lateral aspect of evaginating appendage anlagen

scale= 50 um

Fig. 77 Evaginating appendage anlagen, parasagittal section

scale= 10 um

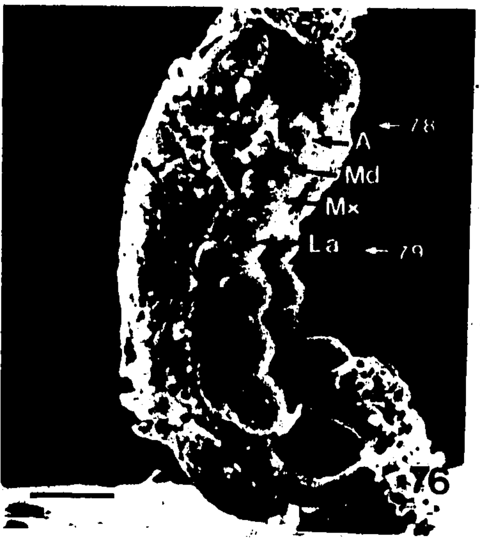
Fig. 78 Stomodael invagination, parasagittal section

scale= 10 um

Fig. 79 Mesoderm within appendage anlagen, parasagittal section

scale= 10 um

Abbreviations; antenna (A), clypeo-labrum (C-L), ectoderm (ec), intercalary segment (In), labium (La), mandible (Md), maxilla (Mx), mesoderm (me), protocephalon (Ptc), stomodeum (st).


← 78
A
Md
Mx
La
← 79
76


77


78


79

Fig. 80–83 Growth at 30% TDT

Fig. 80 *M. fascifrons'* embryo, ventro–lateral aspect of head

scale= 20 um

Fig. 81 *M. fascifrons'* embryo, ventro–lateral aspect of head

scale= 20 um

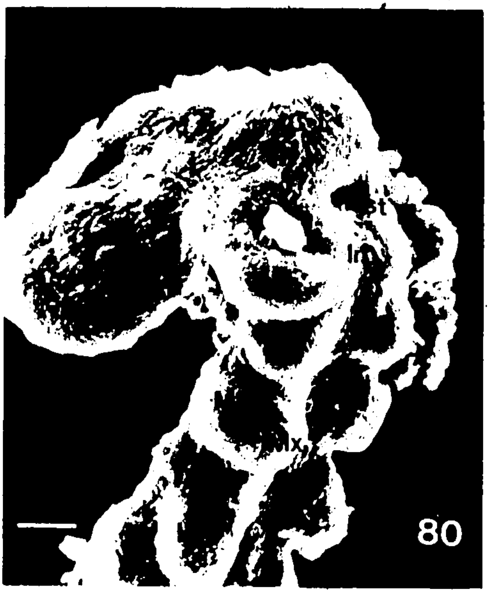
Fig. 82 Maxillary appendage anlage subdividing, transverse section

scale= 10 um

Fig. 83 Salivary gland invagination, transverse section

scale= 10 um

Abbreviations; antenna (A), clypeo–labrum (C–L), intercalary segment (In), labium (La), mandible (Md), maxilla (Mx), maxillary plate (Mxp), salivary gland primordium (Sg), stomodaeum (st).



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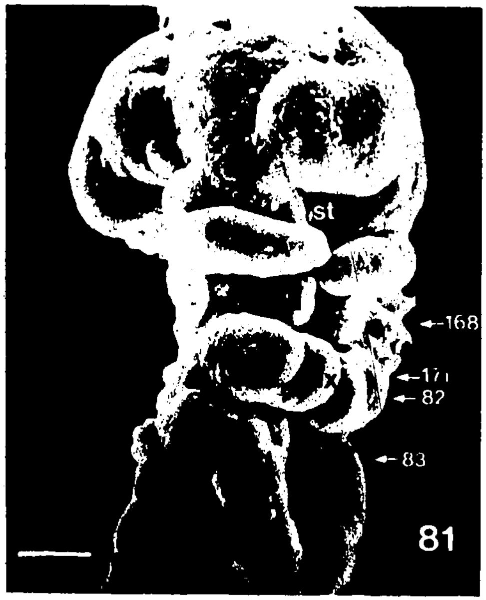

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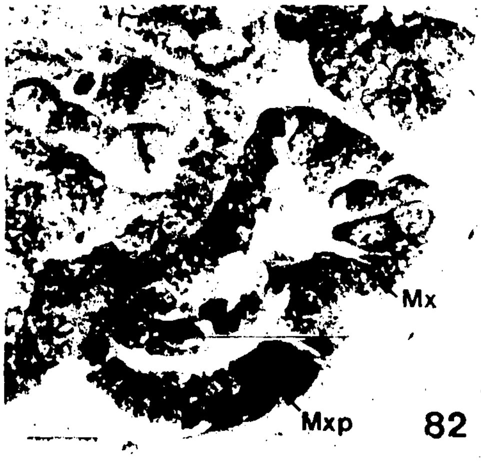


82

Fig. 84-89 Growth at 35-45% TDT

Fig. 84 Ventral aspect of *M. fascifrons'* embryo at 35% TDT

scale= 25 um

Fig. 85 Clypeo-labrum, lateral aspect

scale= 25 um

Fig. 86 Clypeo-labrum, transverse section

scale= 25 um

Fig. 87 Ventral aspect of *M. fascifrons'* embryo at 40% TDT

scale= 25 um

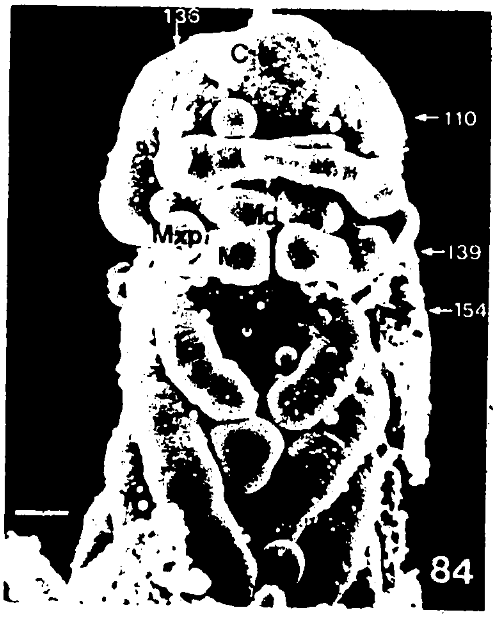
Fig. 88 Hypopharynx, transverse section

scale= 10 um

Fig. 89 Primary cuticle, (TEM)

scale= 1 um

Abbreviations; antenna (A), clypeo-labrum (C-L), hypopharynx (H), labium (La), labrum (L), mandible (Md), maxilla (Mx), maxillary plate (Mxp).



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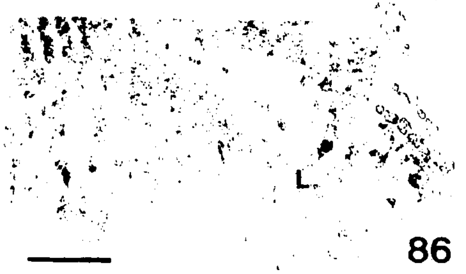

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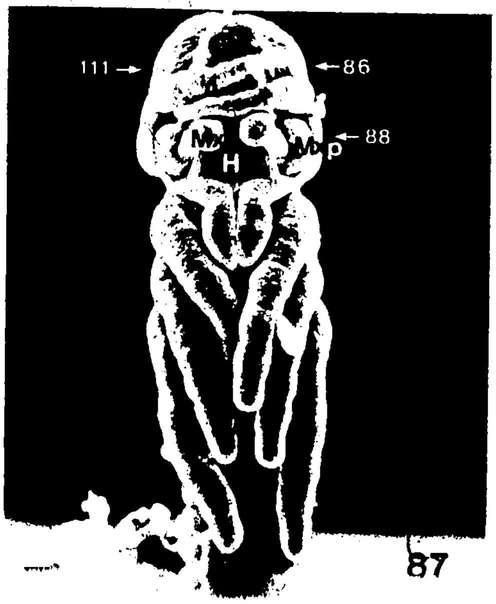

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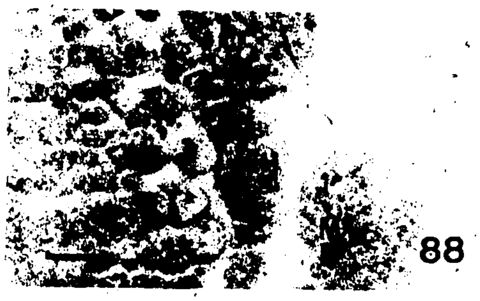


88

89

ends of the labial appendages (La) begin to move medially towards the midline of the embryo (Fig. 84).

Cell division continues, and the epidermis begins to secrete the first embryonic cuticle (Fig. 89).

At 40% TDT the embryo shortens, eliminating its caudal flexure (Fig. 87). The maxillary and mandibular stylet anlagen are longer and the labial appendages fuse medially over the midline of the embryo to form the labium (Fig. 87). The sternal region between the mouthpart anlagen which eventually forms the hypopharynx (H) becomes dome-shaped (Fig 88). Myoblasts of the cibarial dilators and maxillary protractor muscles aggregate at the bases of these appendages. Cell division in most appendages ceases by the end of this stage.

As the embryo begins to rotate 180° on its longitudinal axis (45% TDT), the labrum straightens caudally and the bases of the other mouthpart appendages shift anteriorly into the head so that their distal ends point caudally (Figs. 90). At the end of rotation, the clypeo-labrum is completely extended and at its tip a finger-like projection, the labrum (L), is evident (Fig. 93). The antennae point caudally although their tips still cross beneath the labrum (Fig. 93). Both the clypeo-labrum and maxillary lobes (Mxp) cover the bases of the stylet anlagen to form the beginnings of the rostrum. As the bases of the mandibles, maxillae and labium shift cephalad, the hypopharynx (H) becomes conical (Fig. 91), and ectodermal cells of the labial sternal region invaginate to form a rosette of cells that later secretes the salivary syringe (Ss) (Fig. 91). The hypopharyngeal wings (hw) form as the postero-lateral sides of the hypopharynx invaginate dorsally towards the bases of the maxillary stylet anlagen and the posterior tentorium (Fig. 92).

Myoblasts of the antennal extensors and flexors, mandibular and maxillary retractors (Fig. 94), dilators of the salivary syringe, and labial and pharyngeal muscles become apparent.

Below each antenna, ectodermal cells invaginate. These later secrete the cuticle of the antennifer. The posterior tentorial invaginations fuse medially and dorsally between the maxillary and mandibular segments (Fig. 172) and the anterior tentorial anlagen shift to a position adjacent to the antennae (Fig. 169). The labial apodeme (lap) invaginates (Fig. 95) and primary embryonic cuticle (1° cut) is deposited as a thin

Fig. 90–95 Longitudinal Rotation

Fig. 90 Unfolding clypeo–labrum, ventral aspect

scale= 50 um

Fig. 91 Hypopharynx and salivary syringe, median saggital section

scale= 10 um

Fig. 92 Stylets and hypopharyngeal wing, transverse section

scale= 10 um

Fig. 93 Embryo at the end of longitudinal rotation, ventral aspect

scale= 50 um

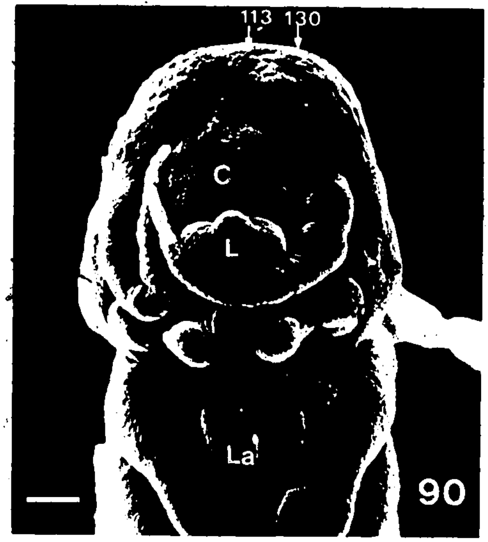
Fig. 94 Mandibular retractor myoblasts, transverse section

scale= 10 um

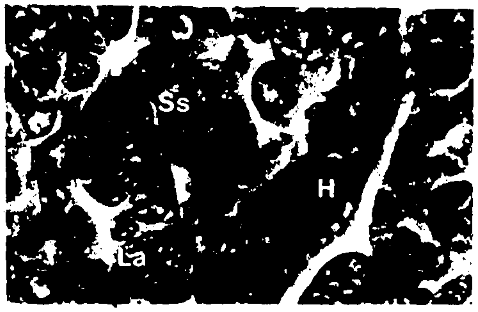
Fig. 95 Labial apodeme, transverse section

scale= 10 um

Abbreviations; anteclypeus (Ac), antenna (A), clypeus (C), eye (e), hypopharynx (H), hypopharyngeal wings (hw), labial apodeme (lap), labium (La), labrum (L), mandible (Md), mandibular retractor myoblasts (primus) (md.rm1), maxilla (Mx), maxillary plate (Mxp), salivary syringe (Ss).

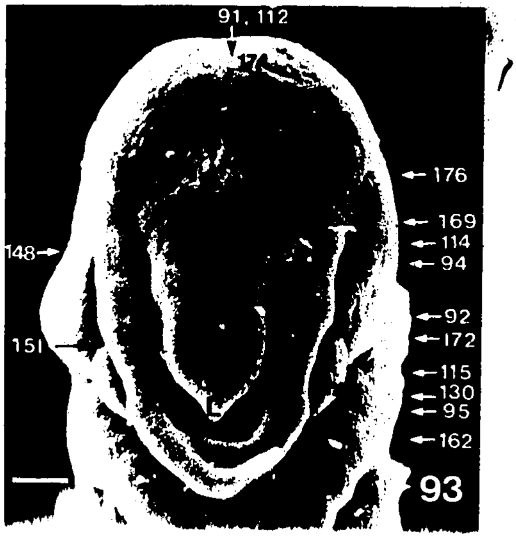

113
130
C
L
La

90


Ss
H
La


L
Mx
Md
nw
A

92


91, 112
176
169
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92
172
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115
130
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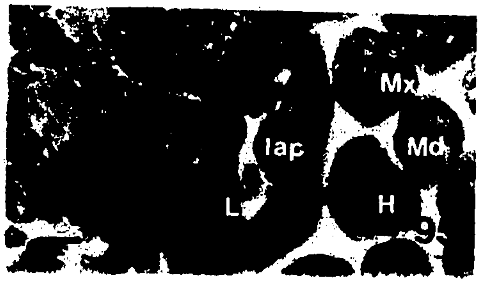
162

93


A
md

94


Mx
lap
Md
L
H
9

epicuticular layer (Fig. 184).

Following rotation, the embryo begins to undergo katatrepsis (Fig. 96). The primary embryonic cuticle (1° cut) apolyses and the epidermis begins to lay down the second embryonic cuticle (2° cut) (Fig. 185). During provisional dorsal closure (55% TDT) (Fig. 97), the mandibular (=loral) plates (Mdp) arise as paired ventral folds of the genal region of the head behind the antennae and anterior to the hypopharynx and maxillary lobes (Fig. 99, Mdp).

During dorsal closure (55% TDT) (Fig. 98), the epidermis expands to replace the amnion as the dorsal body wall and the dorsal organ (do) (Fig. 98) is resorbed. Cells of the epipharyngeal wall of the clypeus secrete the cuticle of the cibarial apodemes and the elastic cuticle of the roof of the cibarium (Fig. 100, rf).

By 65% TDT, the bases of the stylet anlagen reach the dorsal surface of the embryo and their ends begin to curve caudad (Figs. 101, 102). The upper (u), anterior layer of cells within each styligenous organ becomes thick while the lower (lo), caudal layer attenuates (Fig. 101, 102). Cells of the thicker upper surface of each anlage deposit the cuticle of the stylet (Fig. 102).

Myoblasts of most muscles are present at their points of insertion but no differentiation is yet visible within them (Fig. 101).

Between 70 and 75% TDT, the labial ectodermal cells of the hypopharynx form a template of the salivary syringe and begin to secrete the cuticle of the cylinder (c) and piston (pi) (Fig. 103). Maxillary levers evaginate from stylet sheath epithelium (sth) of mesial cells of the maxillary plate drawn in during invagination of stylet bases (Fig. 105). Proximally, separate sheaths (sth) enclose each stylet, but distally, all stylets share a common sheath (Fig. 104). Deposition of the sheath material begins at the same time as that of larval cuticle. Longitudinal grooves form medially at the distal ends of the hypopharynx and labium and a mandibular apodeme invaginates from the antero-dorsal angle of each mandibular plate.

From 75–80% TDT (Fig. 106), the muscles of the head differentiate. Striations are at first weakly visible but develop fully by 80% TDT (Fig. 107). Cells of the stylet anlagen retract deeply into the head, to form the larval retort organs (ro) which later secrete the cuticle of the larval stylets (Fig. 108). Stylet anlagen cells assume the shape

Fig. 96–100 Development at 52%– 60% TDT

Fig. 96 Katatrepsis, lateral aspect

scale= 50 um

Fig. 97 Provisional dorsal closure, lateral aspect

scale= 50 um

Fig. 98 Dorsal closure, parasagittal section

scale= 50 um

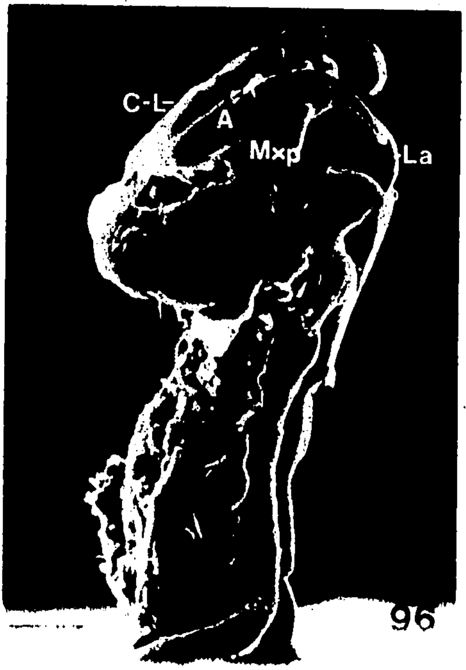
Fig. 99 Mandibular plate and myoblasts, transverse section

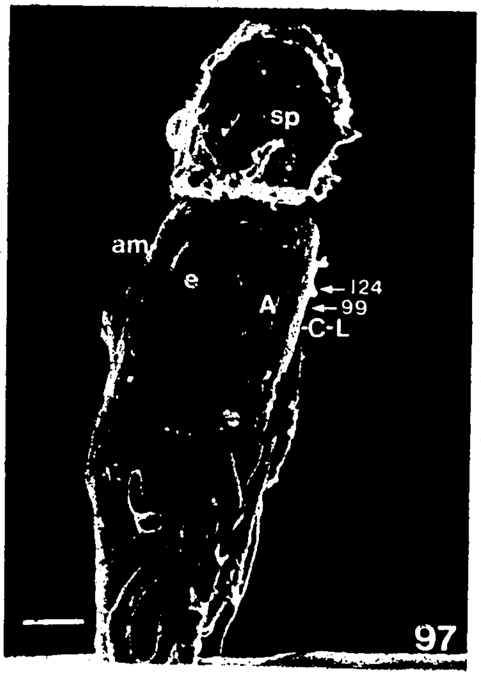
scale= 10 um

Fig. 100 Mandibular plate and roof of cibarium, transverse section

scale= 10 um

Abbreviations; amnion (am), antenna (A), clypeo–labrum (C–L), dorsal organ (do), eye (e), labium (La), labrum (L), Mandibular plate (Mdp), mandibular protractor myoblasts (md.pm), Maxillary plate (Mxp). roof of cibarium (rf), serosal plug (sp).


C-L
A
Mxp
La
96


sp
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A
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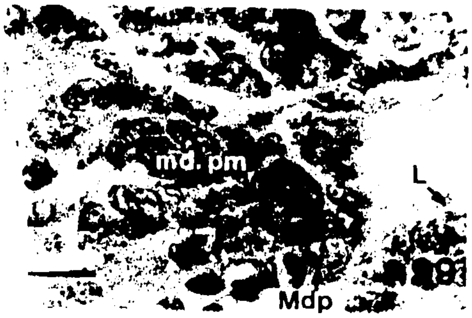
←99
C-L
97


do
La
98


md. pm
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Mdp
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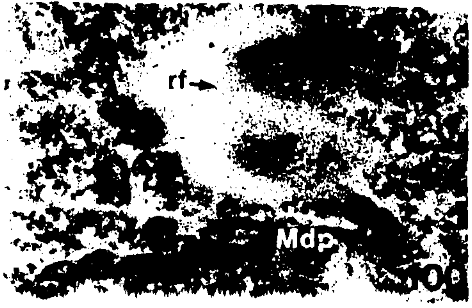

rf
Mdp
00

Fig. 101–105 Development at 65%–75% TDT

Fig. 101 Stylet anlagen, sagittal section

scale= 10 um

Fig. 102 Invaginating maxillary stylet anlage, sagittal section

scale= 10 um

Fig. 103 Hypopharynx and salivary syringe, median sagittal section

scale= 10 um

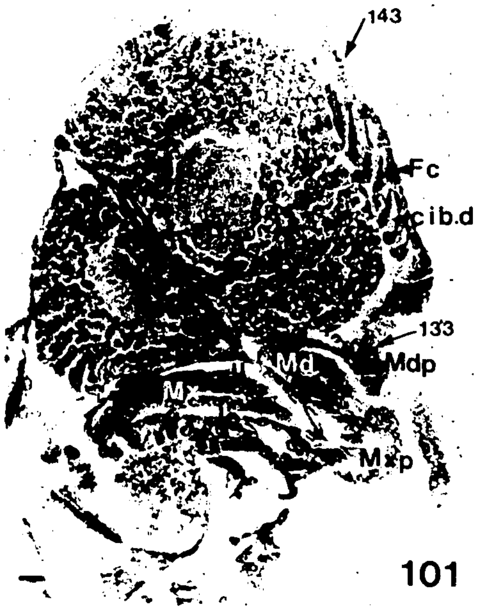
Fig. 104 Stylet bases and sheaths, parasagittal section

scale= 10 um

Fig. 105 Hypopharyngeal wing and maxillary lever, sagittal section

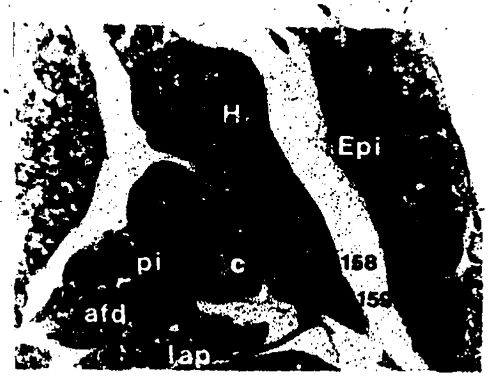
scale= 10 um

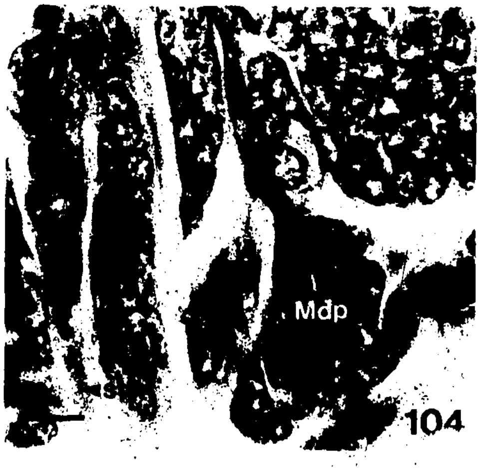
Abbreviations; afferent salivary duct (afd), antenna (A), cibarial dilators (cib.d), cylinder of salivary syringe (c), epipharynx (Epi), fronto–clypeus (Fc), hypopharynx (H), hypopharyngeal wings (hw), labial apodeme (lap), labial retractor 2 (la.r2), lower cells of stylet anlage (lo), mandible (Md), mandibular plate (Mdp), mandibular retractor 3,4 (md.r3,4), maxilla (Mx), maxillary lever (mxl), maxillary plate (Mxp), piston of salivary syringe (pi), stylet cuticle (stc), stylet sheath cells (sth), stylet cranial retractors (str), upper cells of stylet anlage (u).


143
Fc
cib.d
133
Mdp
Md
u
Mx
Mxp

101


sth
stc
Mx
lc
u


H
Epi
pi
c
158
15
afd
lap


Mdp

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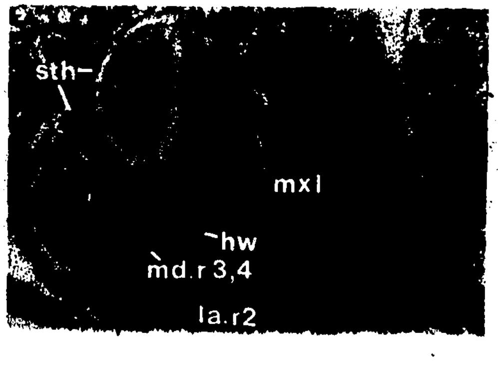

sth
mxl
hw
md.r 3,4
la.r2

Fig. 106-109 Late Embryo

Fig. 106 Late embryo, ventral aspect. The larval cuticle is hidden under persisting secondary embryonic cuticle

scale= 50 um

Fig. 107 Maxillary cranial retractor muscles exhibiting cross striations, transverse section

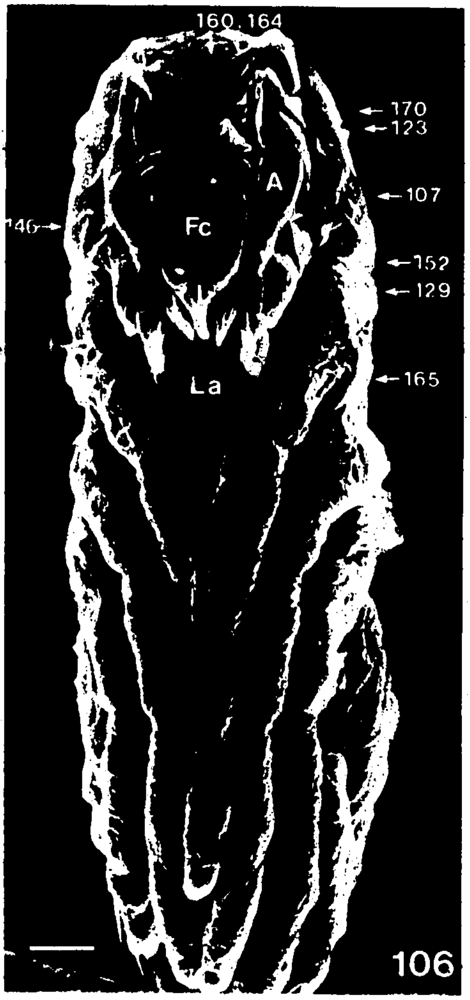
scale= 10 um

Fig. 108 Formation of maxillary retort organ, sagittal section

scale= 10 um

Fig. 109 Maxillary stylet anlage and formation of coadaptations, TEM section
scale= .2 um

Abbreviations; antenna (A), coadaptations (co), 2° cuticle (2° cut), fronto-clypeus (Fc), labium (La), labrum (L), maxilla (Mx), maxillary retractors (mx.r), retort organ (ro).



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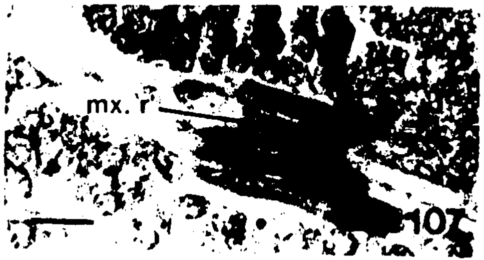

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10

10

of stylet coadaptations (co) and deposit cuticle over these (Fig. 109). By 80% TDT, all three labial segments (Fig. 164) are present and cells of the mandibular apodeme have secreted its cuticle (Fig. 150).

The larva prepares for hatching. Most structures are fully differentiated and sclerotization of larval cuticle has begun.

Although deposition of larval cuticle is complete, it is hidden under the second embryonic cuticle (2° cut) until the latter is sloughed off at hatching (Fig. 106). All muscles are fully differentiated and some have begun to contract rhythmically with commencement of hatching behaviour.

By 85% TDT, cells of the stylet anlagen have retracted completely to the bases of their stylets leaving behind the cuticular stylets themselves which sclerotize just before hatching. Mandibular and maxillary levers have formed and their cuticle has been deposited but not sclerotized. Just prior to hatching the mandibular apodemes, stylets, lower portions of the hypopharyngeal wings and external cuticular structures sclerotize (=preharden), with additional sclerotization occuring just after hatching (not illustrated).

5.2.2 Details of Mouthpart development

5.2.2.1 Clypeo-Labrum

The clypeo-labrum (C-L) evaginates last as a single lobe in front of the stomodaeal invagination (Figs. 76, 80, 81). By 35% TDT, cells at the base of the evagination, close to the head are undergoing mitosis (Fig. 110). Growth results in its apex being pushed ventrally and a fold of cells forming behind it (Fig. 85). Myoblasts of the first cibarial dilators (cib.d) are visible just prior to longitudinal rotation of the embryo (Fig. 111).

By 35-40% TDT small groups of epidermal cells have invaginated in the outer lobe of the clypeo-labrum (Fig. 112, 2 arrows) to form epipharyngeal sense organs. Internally on the epipharyngeal base of the clypeo-labrum, additional epidermal cells invaginate simultaneously and later develop into the cibarial tendons (Fig. 112, 1 arrow). Similar groups of cells invaginate from the outer surface of the clypeus to form the socketed sensilla of the larval clypeus. All sensilla associated with the clypeo-labrum are innervated from the frontal ganglion.

Fig. 110–114 Development of the clypeo–labrum

Fig. 110 Clypeo–labral base, transverse section. Arrows indicate dividing cells.
scale= 10 um

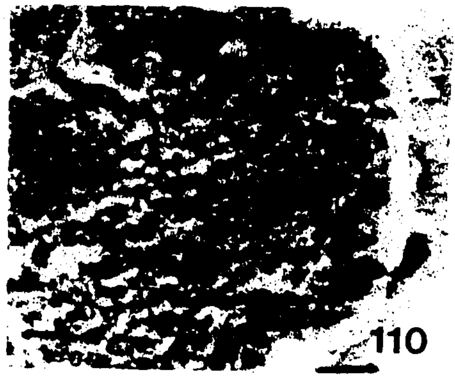
Fig. 111 Myoblasts of cibarial dilators, transverse section
scale= 10 um

Fig. 112 Cibarial tendon cells (one arrow) and epipharyngeal sensillar cells (two arrows), median sagittal section
scale= 10 um

Fig. 113 Pharyngeal myoblasts (arrow) and frontal–clypeal boundary, sagittal section
scale= 10 um

Fig. 114 Fusion of clypeus and genal region of head, transverse section
scale= 10 um

Abbreviations; antenna (A), cibarial dilator myoblasts (cib.dm), clypeo–labrum (C–L), clypeus (C), gena (ge), hypopharynx (H), labrum (L).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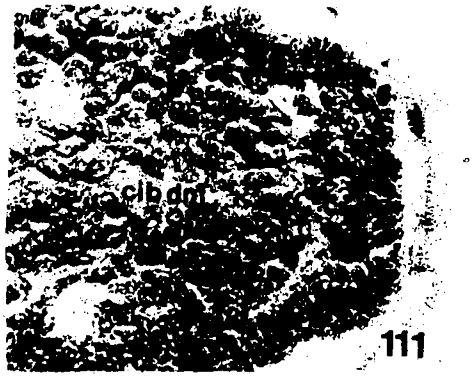

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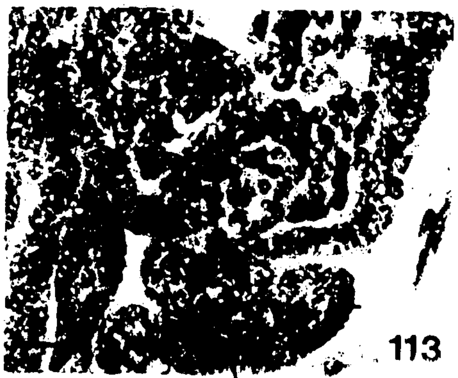
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During longitudinal rotation, the clypeo-labrum unfolds caudally and the bases of the other appendages shift cephalad (Figs. 90, 113). How this is accomplished is unknown; however, there is some evidence to suggest that the outer epidermis may contract in the clypeo-labral region and pull the anterior part of the head anteriorly and ventrally. Before rotation, retractor myoblasts of the mandibles and maxillae contact the dorsal ectoderm directly above the stylets. As rotation occurs, these muscles shift anteriorly as do the stylet bases. After the clypeo-labrum (C-L) unfolds, demarcation between the frons and clypeus is visible as a thickening of cells at the anterior end of the unfolding anlage (Fig. 113). Praepharyngeal myoblasts also appear to originate from here (arrow in Fig. 113). Antero-laterally the sides of the clypeus fuse with the sides of the head below the antennae (Fig. 114).

By the end of longitudinal rotation, the myoblasts of all muscles associated with the clypeo-labrum are present and the tube of cells that later secretes the epipharyngeal apodeme (epit) has invaginated below the two proximal epipharyngeal sensilla (Fig. 115).

Between 50-60% TDT, the clypeus and frons fuse and expand anteriorly (compare Fig. 93 and 97). This may result from condensation of dorsal cells of the head during dorsal closure or from expansion of cibarial myoblasts within. Internally, the lateral walls of the hypopharynx (H) and epipharynx (Epi) fuse to form the cibarial chamber (Cib), typical of hemipterans. At the base of the epipharyngeal surface of the clypeus, invaginated epidermal cells, 5-8 deep, secrete the cuticle of the cibarial dilator apodemes (Figs. 116, 117, 118, cib.t).

By 65% TDT, the labrum (L) is finger-like and extends posteriorly to the proximal part of the labium. Near the cibarial roof the epipharynx invaginates anteriorly and ventrally (Fig. 116). Posterior to this, invaginated ectodermal cells form the epipharyngeal sensilla (epi.s) (Fig. 119).

By 70% TDT the clypeo-labrum resembles that of the first instar larva and epidermal cells along the roof of the cibarium have secreted a cuticular flap that acts as a cibarial valve(v) (Fig.116). The cells, dorsal to these, secrete the cuticular roof of the cibarium (Fig. 100 and 116).

Just prior to hatching, the proximal end of the labrum folds under the apex of the anteclypeus, forming the labral fold (Fig. 120, lf). The transclypeal suture forms after

Fig. 115–120 Development of the clypeo–labrum

Fig. 115 Epipharyngeal tendon anlage, transverse section

scale= 10 um

Fig. 116 Cibarial tendons and valve, sagittal section

scale= 10 um

Fig. 117 Cibarial tendons, (TEM) transverse section

scale= 2 um

Fig. 118 Cibarial tendons, (TEM) transverse section

scale= .5 um

Fig. 119 Epipharyngeal sensilla, (TEM) transverse section

scale= .5 um

Fig. 120 Formation of labral fold, ventral aspect (SEM)

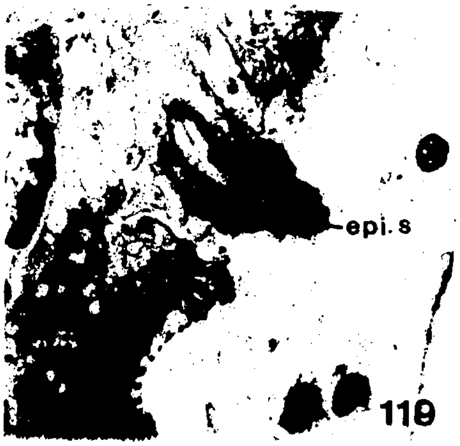
scale= 25 um

Abbreviations; antenna (A), epipharyngeal sensilla (epi.s), epipharyngeal tendon anlage (epit), cibarial tendons (cib.t), cibarial valve (v), fronto–clypeus (Fc), hypopharynx (H), labral fold (lf), labrum (L), maxillary plate (Mxp), salivary gland (Sg), stylets (st)


Sg
H
15


H
V
117
19
L
116


b


epi. s
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0

hatching.

5.2.2.2 Antennae

Antennae (A) evaginate from ectoderm on either side of the stomodael invagination (Figs. 80, 81). Subsequently they elongate rapidly and cross each other behind the clypeo-labrum (C-L) and over the opening of the stomodaeum (Fig. 81). By 35% TDT the scape segments, and slightly later the pedicels have appeared (Fig. 121).

As the clypeo-labrum straightens during revolution, it pushes the antennae caudally but their ends remain wrapped behind the labrum (L) (Figs. 90, 93). The movements of katatrepsis pulls them straight (Fig. 96). Mitosis continues in the antennal bases until 55% TDT, at which time they have reached their larval length (Fig. 122).

Intrinsic muscles of the scape (sc) and the extensor and flexor myoblasts of the antennae arise at the end of longitudinal rotation and, by 70% TDT, have reached their points of insertion (Fig. 123). Beneath the antennae invaginations form that differentiate into the antennifers (Fig. 124, antf).

Cells forming the antennal sensilla have invaginated by 45% TDT and neurites (it is unknown if they are axonal or dendritic) are found in the proximal region of the scape. Distal to this, cilia-like structures (nine double filaments) are found surrounded by dark patches that may be developing scolopale rods (Chapman, 1975) (Figs. 125). By katatrepsis the neurites are more completely developed and Fig. 126 illustrates the variety of structures found in the antenna. Both antennae are innervated from the deutocerebrum of the brain which forms from neuroblasts of the antennal segment.

5.2.2.3 Intercalary segment

The intercalary segment (In) appears briefly as two swellings behind the stomodaeum (Figs. 80, 127). Its neuromeres become the tritocerebrum of the brain and its ectoderm contributes to formation ofthe anterior wall of the hypopharynx (Fig. 128). By 45% TDT, epidermal cells of the intercalary segment have invaginated (Fig. 128), and later form two campaniform sensilla (cs) in the hypopharynx (H) (Fig. 129). These are innervated by nerves from the tritocerebrum which forms from neuroblasts of the intercalary segment.

Fig. 121–126 Development of the antennae

Fig. 121 Beginning of antennal segmentation, SEM of lateral aspect

scale= 25 um

Fig. 122 Mitosis in antennal base at 55% TDT, parasagittal section

scale= 10 um

Fig. 123 Muscle formation in scape (antennal depressor), sagittal section

scale= 10 um

Fig. 124 Antennifer, transverse section

scale= 10 um

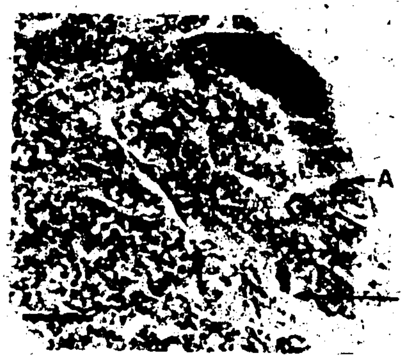
Fig. 125 Transverse section of antenna, (TEM) through pedicel

scale= 1 um

Fig. 126 Transverse section of antenna, (TEM) through pedicel

scale= 1 um

Abbreviations; antenna (A), antennal depressor myoblasts (a.dpm), antennifer (antf), clypeo-labrum (C-L), eye (e), flagellum (f), maxillary plate (Mxp), cells undergoing mitosis (mit), pedicel (p), scape (sc).



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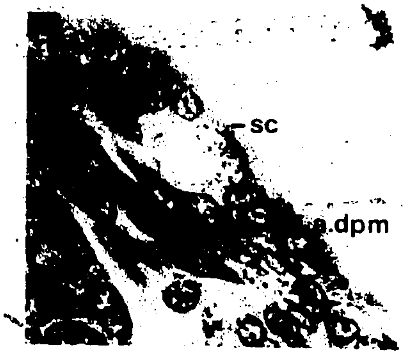

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Fig. 127–129 Development of the intercalary segment

Fig. 127 Intercalary segment, ventral aspect

scale= 20 um

Fig. 128 Ectodermal cells that develop into hypopharyngeal sensilla, median sagittal section

scale= 10 um

Fig. 129 Hypopharyngeal campaniform sensilla, transverse section

scale= 10 um

Abbreviations; antenna (A), campaniform sensilla (cs), clypeo–labrum (C–L), hypopharynx (H), intercalary segment (In), labium (La), mandible (Md), maxilla (Mx), protocephalon (Ptc), stomodeum (st).

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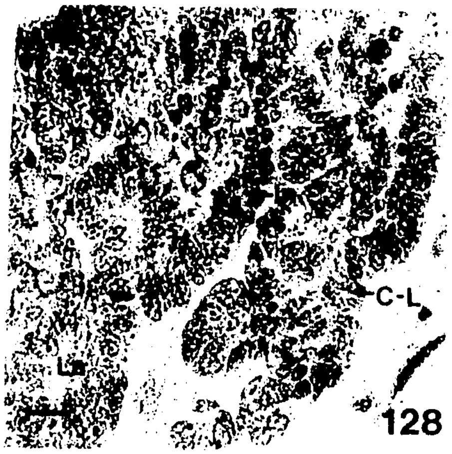

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5.2.2.4 Mandibular and Maxillary Stylets, Stylet Levers and Stylet Sheaths

Stylets. – The mandibles (Md) and maxillae (Mx) develop as paired ectodermal outgrowths behind the intercalary segment (In) (Fig. 76). The mandibular appendages lie anterior to the maxillae and never subdivide (Fig. 80). The latter subdivide into inner and outer lobes, the inner lobe (Mx) forming the stylet and the outer lobe (Mxp), the maxillary plate (Fig. 81).

The stylets elongate postero–medially during growth until their distal ends meet along the midline of the embryo (Fig. 84). By 35% TDT, they have become innervated by nerves from their respective neuromeres which later coalesce to form part of the suboesophageal ganglion.

During rotation, the stylet bases shift cephalad and their distal ends point caudally and become tapered (Fig. 130). By 65% TDT, the bases of the stylet anlagen have invaginated into the head capsule, and curve caudally (Fig. 101). The anterior, upper layer (u) of each primordium is thick and its posterior layer (lo) attenuated (Fig. 101, 102). Later the upper cells secrete the cuticle of the larval stylet. As development proceeds, cells of the stylet anlagen invaginate deeper into the head and begin to form the larval retort organ (Fig. 108, ro). Still later the cells retract still farther into the head, pulling back from the ventral surface of the embryo and leaving behind the cuticle of the stylets. As the cells retract, they assume the shape of their stylet coadaptations and deposit c[illegible]le over this template (Figs 109, 133, 134).

By 45% TDT, neurites are found centrally in the stylet anlagen (Figs, 131, 132). Since it is difficult to find the cell body, I was unable to tell if the developing structures illustrated in Fig. 132 were axons or dendrites. Distal to these (Fig. 132), ciliary structures of nine microtubule doublets were found in both the maxillary and mandibular stylet anlagen. Sections of the stylet bases show that the cell bodies are not located there (not illustrated). Serial sections of anlagen will likely show that the cell bodies are centrally located in stylet anlagen before the cells begin to retract. As the cells retract, they pull with them the sensory axons and cell bodies to the base of the stylets, leaving the dendrites (d) (Fig. 134) behind in the cuticular stylets. the dendrites (d) (Fig. 134). Figure 134 shows the mandibular stylet and cilia–like structures of the dendrites surrounded by dark patches that may be developing scolopale rods. Each mandibular

Fig. 130–135 Development of mandibular and maxillary stylets

Fig. 130 Invaginating stylets during longitudinal rotation, sagittal section

scale= 20 um

Fig. 131 Mandibular and maxillary stylets, transverse TEM section

scale= 2 um

Fig. 132 Central cell in maxillary stylet (arrow in 131), tranverse TEM section, showing sensory neurites

scale= 1 um

Fig. 133 Mandibular stylet and developing coadaptations, transverse TEM section

scale= 2 um

Fig. 134 Mandibular stylet and sensory dendrites (arrows), transverse TEM section

scale= 1 um

Fig. 135 First instar larval stylets (arrows point to dendrites), transverse TEM section

scale= 2 um

Abbreviations; coadaptations (co), food canal (fdc), mandible (Md), maxilla (Mx), neurites (ne), salivary canal (sc), stylet sheath (sth).


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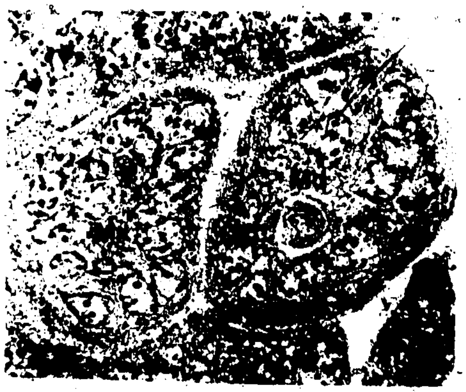


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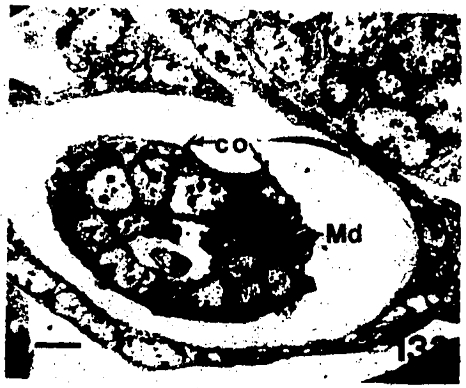
co
Md
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Md

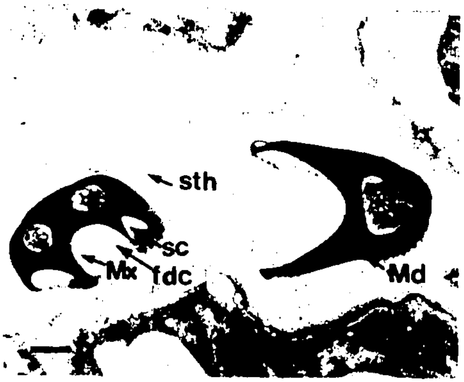
sth
sc
Mx
fdc
Md

Fig. 136–139 Stylet muscles

Fig. 136 Mandibular and maxillary cranial retractors, sagittal section

scale= 10 um

Fig. 137 Mandibular–genal retractors, transverse section

scale= 10 um

Fig. 138 Mandibular–hypopharyngeal retractors, transverse section

scale= 10 um

Fig. 139 Maxillary protractors, transverse section

scale= 10 um

Abbreviations; cranial retractor myoblasts (cr.rm), hypopharyngeal wing (hw), insertion (i), mandibles (Md), mandibular retractor 1 myoblasts (md.rm1), mandibular retractor 3,4 myoblasts (md.rm3,4), maxilla (Mx), maxillary protractor myoblasts (mx.pm), origin (o).

7

137

139

stylet has three dendrites, and each maxillary stylet, five (Fig. 135) Their structure was described by Forbes and Raine (1970) and Backus and McLean (1982).

The cranial retractor myoblasts (my) of the mandibles and maxillae appear early in development and by 40% TDT are situated at their points of insertion (i) on their stylet bases (Fig. 136). Mandibular retractor muscles (md.rm1) originating beneath the antennae are present by 45% TDT (Fig. 137) and those (md.rm3,4) originating on the hypopharyngeal wings (hw) slightly later (Fig. 138). The latter do not associate with their points of insertion until much later, around 85% TDT. Protractor muscles of the maxillae (mx.pm) develop early, at 40% TDT (Fig. 139), while mandibular protractors (md.pm) are not visible until 55% TDT when the mandibular plate forms (Mdp) (Fig. 99).

Stylet sheaths. — As each stylet anlage base invaginates, it pulls in surrounding ectodermal tissue that then forms at least a portion of its stylet sheath (sth) (Fig. 140). In addition, to separate sheaths proximally (Fig. 143), the stylets have a common distal sheath secreted by cells of adjacent head structures (Fig. 142). The mandibular sheath is genal, hypopharyngeal and maxillary in origin (Fig. 141). The maxillary sheath forms from the cells of the hypopharynx and maxillary plate (Fig. 141).

Cells secreting the common sheath are present by 45% TDT, after the stylet bases have invaginated into the head and external head structures have descended to enclose them (Fig. 142). At this time, the anlagen are surrounded by cells of the clypeo-labrum (C-L), maxillary plate (Mxp), and internally, by the hypopharynx (H) (Fig. 114). The separate sheaths form as cells of the stylet anlagen invaginate more deeply into the head (Fig. 143) and pull with them the surrounding ectoderm (Fig. 140). Each mandible pulls in ectodermal tissue from its sternum which is hypopharyngeal and each maxilla draws in ectoderm from the hypopharynx and maxillary plate. Later the ventral, lateral portion of the mandibular sheath forms from cells of the mandibular plate after it has descended between the labrum and maxillary plate. These cells begin to secrete sheath cuticle around 65% TDT at the same time as epidermal cells elsewhere secrete larval cuticle (Fig. 105).

Stylet Levers. — The mandibular lever (cg) and apodeme (map) develop from the mandibular plate (Mdp) (Fig. 150). The apodemal invagination develops by late 70% TDT and its cuticle is secreted by 80% TDT (Fig. 146, 150). The apodeme forms from a

Fig. 140-147 Development of stylet sheaths and levers

Fig. 140 Invaginating maxillary stylet and sheath, sagittal section

scale= 10 um

Fig. 141 Relationship of mandibular plate, maxillary plate and hypopharynx, frontal section

scale= 10 um

Fig. 142 Common stylet sheaths, frontal section.

scale= 10 um

Fig. 143 Separate stylet sheaths, frontal section

scale= 10 um

Fig. 144 Mandibular lever formation, frontal section

scale= 5 um

Fig. 145 Mandibular lever formation, frontal section

scale= 5 um

Fig. 146 Mandibular apodeme formation, transverse section

scale= 10 um

Fig. 147 Maxillary apodeme and lever, frontal section

scale= 10 um

Abbreviations; antenna (A), apodeme (ap), clypeo-labrum (C-L), cuticular guide (cg), hypopharynx (H), labrum (L), mandible (Md), mandibular apodeme (map), mandibular protractors (md.p), mandibular plate (Mdp), maxilla (Mx), maxillary lever (mxl), maxillary plate (Mxp), stylet sheath (sth).

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tubular invagination of the ectoderm in the antero-dorsal part of the mandibular plate (Fig. 146, 150). Ectodermal cells invaginate first medially and then posteriorly.

Cells of the mandibular plate (Mdp) secrete the cuticle of the lever (=cuticular guide) (cg) late in embryogenesis (Fig. 144, 145). These cells lie posterior to the distal tip of the mandibular apodeme and next to the ventro-medial cells of the maxillary plate. By 90% TDT, these cells have secreted a bar of cuticle that articulates anteriorly with the mandibular apodeme but is connected with the stylet by a cuticular bridge just before hatching (Fig. 145). Cells secreting the cuticle joining stylet and lever are medial cells of the mandibular plate that lie next to the free stylet (Fig. 144, 145). Lever cuticle does not sclerotize until the larva hatches.

The maxillary lever (mxl) forms within a diverticulum that evaginates from the wall of its sheath (Fig. 105). This evagination emanates from the postero-medial portion of the sheath and grows laterally toward the side of the head and the outermost bar of the hypopharyngeal wing (hw) (Fig. 147). By 90% TDT, the cells of the diverticulum begin to secrete the cuticle of the lever (Fig. 147) and this sclerotizes after the larva hatches.

5.2.2.5 Mandibular Plate

The mandibular plates (Mdp) and their myoblasts (md.pm) are not visible until 55% TDT (Figs. 99, 100). Ectoderm of the genal region of the head, dorsal to the antennae, evaginates, grows postero-ventrally (Fig. 104) and eventually fuses distally with the inner dorsal wall of the hypopharynx (Fig. 149). Prior to formation of the plate, (45% TDT), mesodermal protractor myoblasts (md rm) of the mandible appear to lie posterior to the antennae (Fig. 148).

As the plate and its myoblasts develop, some myoblasts lying next to the hypopharynx (H) attach themselves to its upper lateral wall and on differentiating appear to originate on it (Fig. 149, 150).

5.2.2.6 Maxillary Plate

A maxillary plate (Mxp) develops from the outer lobe of each maxillary anlage by its longitudinal division at 25% TDT (Figs. 80, 81). By 35% TDT, the plate is cone-shaped and remains this way for the rest of development (Figs.23, 24, 25).

Fig. 148-153 Development of the mandibular and maxillary plates

Fig. 148 Presumptive mesodermal cells forming mandibular retractor myoblasts, transverse section

scale= 10 um

Fig. 149 Mandibular protractors, frontal section

scale= 10 um

Fig. 150 Mandibular plate and apodemal invagination, transverse section

scale= 10 um

Fig. 151 Maxillary plate sensillum, frontal section

scale= 10 um

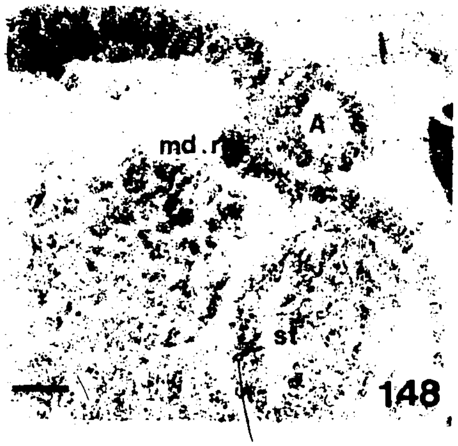
Fig. 152 Maxillary plate sensillum, sagittal section

scale= 5 um

Fig. 153 Maxillary plate sensillum, sagittal TEM section

scale= 2 um

Abbreviations; antenna (A), basal body (bb), cell body (cb), cibarium (cib), cibarial dilators 1 (cib.d1), cilium (ci), dendrite (d) epipharynx (Epi), eye (e), hypopharynx (H), mandibular apodeme (map), mandibular myoblasts (md.rm), mandibular protractors (md.p), mandibular plate (Mdp), maxillary plate (Mxp), maxillary pore sensilla (mxps), maxillary protractor myoblasts (mx.pm), sheath cells (sh).



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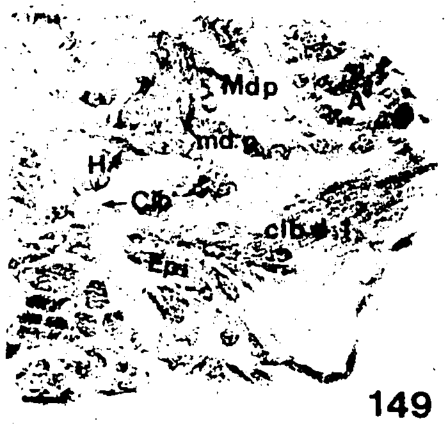

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Initially the maxillary plates are joined only to the stylets anlagen, but as development proceeds the head lobes move ventrally and caudally and come to lie next to them (Fig. 93). Following katatrepsis and invagination of the maxillary stylets into the head, the plates and anlagen separate and the outer lobes fuse with the genal region of the head (Figs. 96, 97, 101).

By 40% TDT, a sensillar structure (mxps) that may be a remnant of the palpus (Evans, 1973) begins to form on the outer wall of each plate (Fig. 151). A group of epidermal cells invaginate near the anterior margin of the lobe and by 60% TDT, the sensillar hairs and their dendrites have formed (Figs. 152, 153). By 70% TDT, surrounding cells have secreted the cuticle of the barrel-shaped structure that contains the sensilla (Figs. 45, 51).

Protractor myoblasts (mx.pm) of the maxillae form by 40% TDT (Figs. 139, 151) and reach their point of insertion on the stylet bases by 60% TDT.

5.2.2.7 Hypopharynx and Salivary syringe

The hypopharynx (H) forms from sterna of the intercalary [(In)], mandibular [(Md)] and maxillary [(Mx)] segments (Fig. 155). It houses the salivary syringe (Ss) which develops from the venter of the labial segment [(La)]. During growth, the neural groove (Fig. 80) disappears and the sternal region (H) between the mouthpart appendages becomes dome-shaped (40% TDT) (Figs. 87, 154). Ectoderm (H) between the mandibles and maxillae becomes conical (Fig. 88) while that between the labial appendages invaginates dorsally as the embryo rotates longitudinally (Fig. 155). In the intercalary segment [(In)] two groups of ectodermal cells invaginate (Fig. 155), that later form the campaniform sensilla (cs) of the hypopharynx (Fig. 129).

As the embryo rotates and the clypeo-labrum (C-L) unfolds posteriorly, the distal end of the hypopharynx (Mx) shifts cephalad and becomes more conical (Fig. 155). The intercalary sternum [(In)] forms the anterior part of the hypopharynx and the mandibular [(Md)] and maxillary [(Mx)] sterna, its apex (Fig. 155).

When the labial appendages (La) fuse mesially at 40% TDT their bases invaginate dorsally (Fig. 87). At 45% TDT, the labial sternum (La) shifts cephalad and comes to lie dorsal to the free maxillary (Mx) portion of the hypopharynx (Fig. 155). Its anterior ectodermal cells then withdraw and thicken (Fig. 155). Posterior to these cells, the

Fig. 154–157 Development of the hypopharynx and salivary syringe

Fig. 154 Labial sternum, transverse section

scale= 10 um

Fig. 155 Invaginating ectodermal cells that form the salivary syringe, parasagittal section

scale= 10 um

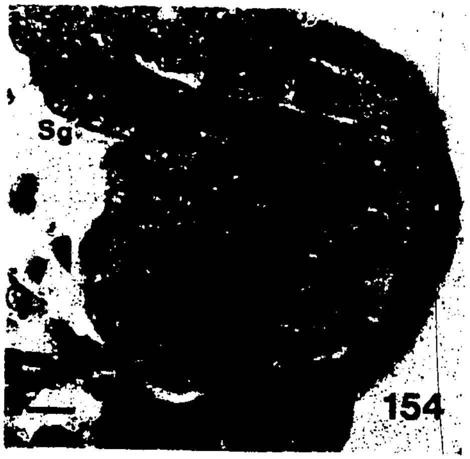
Fig. 156 Hypopharynx and salivary syringe, median sagittal section

scale= 10 um

Fig. 157 Salivary syringe and salivary dilators, frontal section

scale= 5 um

Abbreviations; afferent salivary duct (afd), campaniform sensilla, (cs), cylinder of salivary syringe (c), efferent salivary duct (efd), hypopharynx (H), intercalary sternite [(In)], labial apodeme (lap), labium (La), Labial sternite [(La)], mandibular sternite [(Md)], maxillary sternite [(Mx)], piston of salivary syringe (pi), salivary dilators (sal.d), salivary duct (sd), salivary gland (sg), salivary syringe (Ss).


Sg
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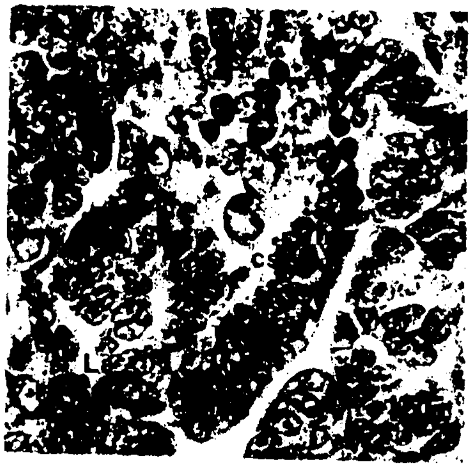
c
L


pi
afd
efd
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sal.d
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ectoderm invaginates to form the labial apodeme (lap) (Fig. 95, 156).

Folowing katatrepsis, the distal tip of the hypopharynx becomes tapered. Cells secreting the syringe invaginate dorsally to leave a cylinder-shaped structure (c) (Figs. 156-159). Cells surrounding this cavity secrete the cuticle of the salivary syringe cylinder (c) while a more posterior group of cells that invaginates dorsally in the form of a tube secretes the cuticle of the piston (pi) (Figs. 156-159). Posterior to both, the common salivary duct (afd) formed when the labial appendages fused, opens into the cavity of the salivary syringe as the afferent duct (Fig. 156). Ventrally and posteriorly, a flange of cells also of labial origin forms the base of the cylinder and the efferent duct (efd) of the syringe (Fig 156). The syringe is completely formed by 80% TDT (Fig. 160), although its cuticle does not sclerotize until the larva hatches. Myoblasts of the salivary dilators (sal.d) are present by 50% TDT and reach their point of insertion by 60% TDT (Fig 157).

The hypopharyngeal wings (hw) form at 45% TDT (Fig. 92), as two wing-like invaginations that later develop into templates for secretion of cuticle of the larval wings (Fig. 161).

A ventral groove running medially along the anterior surface of the hypopharynx and acting as a guide for the stylets forms between 70 and 75% TDT and its cuticle is secreted and sclerotized by 95% TDT (not illustrated).

5.2.2.8 Labium

Labial anlagen (La) are the first to evaginate after the legs (Fig. 76). Subsequently, they elongate and, as the embryo condenses, shift mesially and fuse on the embryo's midline (Fig. 87). This fusion also forms the common salivary duct (Fig. 156, afd). By the end of longitudinal rotation, labial myoblasts (my) are present (Fig. 162) and the labial apodeme (lap) has begun to invaginate (Fig. 95). By 70% TDT, the labial lip (li) and the anterior segment of the labium (s 1) has formed (Fig. 163). The lip originates from ectoderm posterior and anterior to the labial base as it invaginates dorsally (Fig. 163). The labium is completely segmented by 80% TDT (Fig. 164) and slightly later the labial groove (lag) forms along its entire length (Fig. 165). Just before hatching, epidermis of the posterior labial segments forms four sclerites, two small Y-shaped sclerites at the distal tip of the labium (Fig. 166) and two hooked-shaped ones at the proximal end of segment

Fig. 158–161 Development of the hypopharynx and salivary syringe

Fig. 158 Formation of the cylinder of the salivary syringe, transverse TEM section

scale= 2 um

Fig. 159 Formation of the cylinder and piston of the salivary syringe, transverse TEM section

scale= 2 um

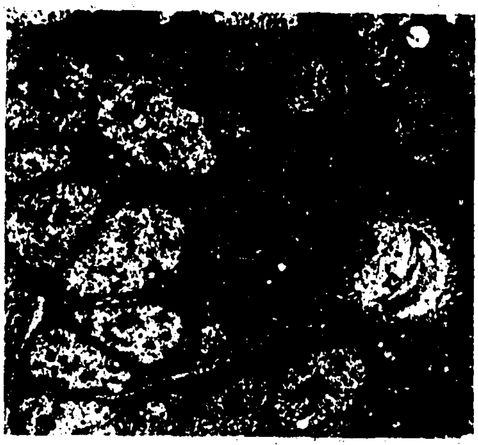
Fig. 160 Median sagittal section of the salivary syringe and hypopharynx

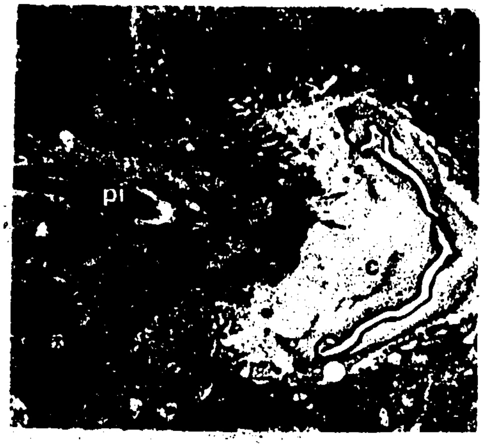
scale= 10 um

Fig. 161 Hypopharyngeal wing, frontal section

scale= 10 um

Abbreviations; campaniform sensilla (cs), cylinder of salivary syringe (c), hypopharyngeal wing (hw), piston of salivary syringe (pi).




pi
c


c
p
cs
1


hw
16

Fig. 162-167 Development of the labium

Fig. 162 Labial myoblasts, transverse section

scale= 10 um

Fig. 163 Formation of labial lip and segment 1, median sagittal section

scale= 10 um

Fig. 164 Labium at 80% TDT, median sagittal section

scale= 10 um

Fig. 165 Labial groove, transverse section

scale= 10 um

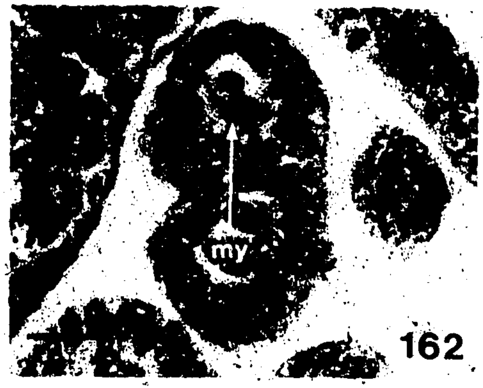
Fig. 166 Y-shaped sclerites (arrows), frontal section

scale= 10 um

Fig. 167 Hooked-shaped sclerites (arrows), frontal section

scale= 10 um

Abbreviations; myoblasts (my), labial groove (lag), labium (La), lip of labium (li), labial segments 1,2,3, (s1, s2, s3).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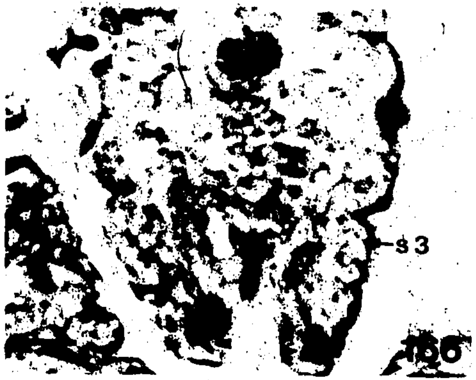
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167

Fig. 168–173 Development of the tentorium

Fig. 168 Anterior tentorial invagination, transverse section

scale= 10 um

Fig. 169 Anterior tentorium, transverse section

scale= 10 um

Fig. 170 Dorsal tentorium, transverse section

scale= 10 um

Fig. 171 Posterior tentorial invagination, transverse section

scale= 10 um

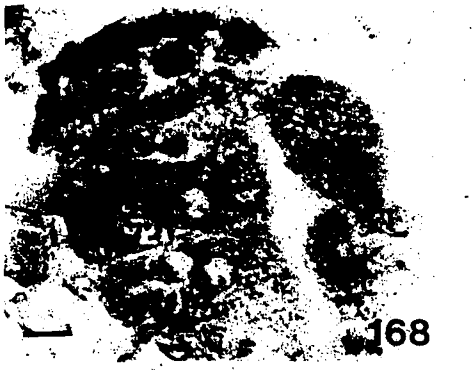
Fig. 172 Fusion of posterior tentorial invaginations, transverse section

scale= 10 um

Fig. 173 Posterior tentorium, transverse section

scale= 10 um

Abbreviations: antenna (A), anterior tentorium (At), dorsal tentorium (Dt), eye (e), mandible (Md), maxilla (Mx), myoblasts (my), pharynx (Ph), posterior tentorium (Pt).



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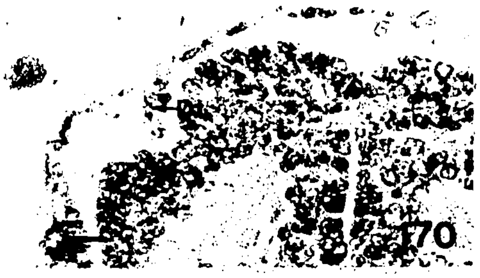

170

172

73

three (Fig. 167).

5.2.2.9 Tentorium

The anterior tentorium (At) forms from a pair of ectodermal invaginations between the intercalary and mandibular segments (Fig. 168). As the embryo rotates and the appendages shift cephalad, the two tubes do also and, by 45% TDT, lie next to the antennae (A) (Fig. 169). Later in development, anterior tentorial cells evaginate laterally to form the dorsal tentorial arms (Dt) (Fig. 170) that extend to the head capsule and are the point of origin of the extrinsic muscles of the antennae. The cells secrete cuticle into the lumina of the tubes by 95% TDT and this sclerotizes after the larva hatches.

The posterior tentorium (Pt) in embryos of *M. fascifrons* forms from a pair of ectodermal invaginations on either side of the maxillary sternum (Fig. 171). During growth, these invaginations lengthen towards the dorsum of the embryo and their tips fuse by the end of longitudinal rotation (Fig. 172). Cuticle of the tentorium secreted into the lumina by the cells of these invaginations sclerotize after hatching (Fig. 173).

5.2.2.10 Cibarium, Pharynx, Oesophagus

The pharynx (Ph) and oesophagus (Oes) form from the stomodaeal invagination (st) (Fig. 78). The stomodaeum forms at segmentation and is an invagination of the germ band behind the clypeo–labrum (C–L) and above the intercalary segment (In) (Figs. 80, 81). During early embryogenesis, it is a short tube that extends up to the dorsal wall of the embryo (Fig. 174). Following dorsal closure, it becomes convoluted and anterior midgut rudiment cells at its distal end expand around the yolk to form the midgut, along with posterior midgut rudiment cells at the anterior end of the proctodeum (arrow in Fig. 175).

Pharyngeal myoblasts (Ph.m) are first visible at their points of origin at 40% TDT (arrow in Fig. 113) and attach to their points of insertion by 45% TDT (Fig. 176).

The cibarium (Cib), or sucking pump, forms through fusion of the epipharyngeal walls of the clypeus (Epi) and the sides of the hypopharynx (H) (Fig. 177). After the clypeo–labrum unfolds (Fig. 93), the two structures lie apposed to one another and by the time of katatrepsis fuse to enclose a sucking chamber operated by strong cibarial dilator muscles (cib. d) (Fig. 177).

Fig. 174–177 Development of the cibarium, pharynx and oesphagus

Fig. 174 Stomodaeal invagination, median sagittal section

scale= 50 um

Fig. 175 Cibarium, pharynx, and oesphagus, median sagittal section

scale= 50 um

Fig. 176 Pharyngeal myoblasts, transverse section

scale= 10 um

Fig. 177 Formation of cibarium, frontal section

scale= 10 um

Abbreviations; antenna (A), cibarial dilators (cib.d), cibarium (Cib), clypeus (C), epipharynx (Epi), hypopharynx (H), labrum (L), mandibular plate (Mdp), oesophagus (oes), pharyngeal myoblasts (Ph.m), pharynx (Ph), stomodeaum (st).

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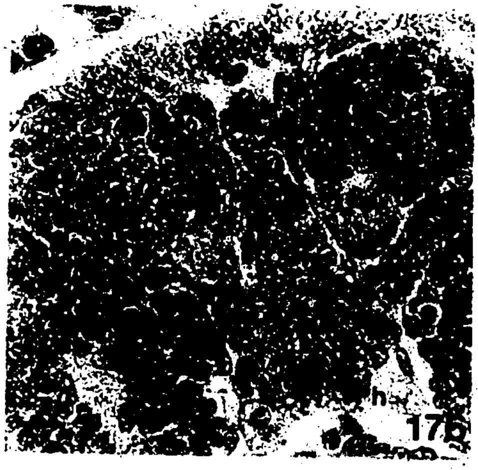

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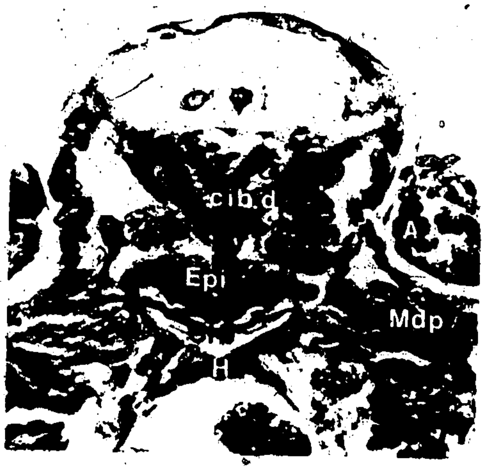


Fig. 178–183 Muscle development

Fig. 178 Maxillary protract[illegible] myoblasts, transverse section

scale= 10 um

Fig. 179 Salivary dilator muscles attachment at point of insertion, transverse section

scale= 1 um

Fig. 180 Tendons (arrowhead) at point of origin of maxillary retractor myoblasts, parasagittal section

scale= 10 um

Fig. 181 Condensing pharyngeal myoblasts, sagittal section

scale= 10 um

Fig. 182 Cross striations (arrow) appearing at 80% TDT, transverse section

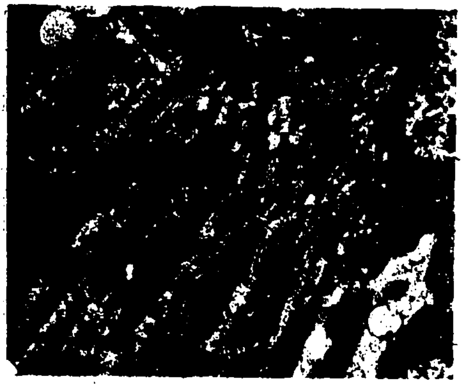
scale= 10 um

Fig. 183 Muscles at 75–80% TDT, transverse TEM section

scale= 1 um

Abbreviations; mandible (Md), mandibular apodeme (map), mandibular protractors (md.p), maxilla (Mx), maxillary protaractor myoblasts (mx.pm), pharyngeal dilators (Ph.d), pharynx (Ph), salivary dilators (sal.d).


mx
179




180


Ph.d
Ph
18


map
Md
md.p
182


18

Fig. 184–189 Electron micrographs of sections showing cuticle formation

Fig. 184 Formation of primary cuticle (cuticulin) on epidermal microvilli, transverse section

scale= .5 um

Fig. 185 Apolysis of primary cuticle and formation of cuticulin of secondary cuticle, transverse section

scale= .5 um

Fig. 186 55% TDT formation of procuticle of secondary cuticle, transverse section

scale= 1 um

Fig. 187 60–65% TDT plaques of larval cuticulin forming at apices of microvilli, transverse section

scale= 1 um

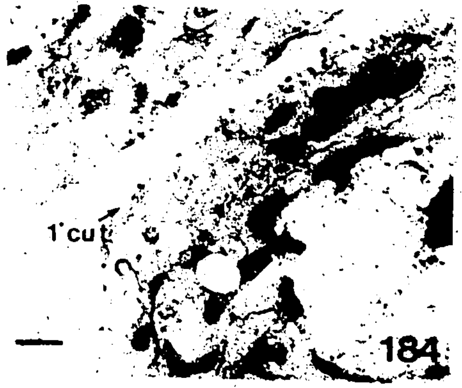
Fig. 188 70% TDT, larval cuticulin layer complete, transverse section

scale= 1 um

Fig. 189 Cuticle of a just hatched first instar larva, transverse section

scale= 1 um

Abbreviations; primary cuticle (1° cut), secondary cuticle (2° cut), larval or tertiary cuticle (3° cut).



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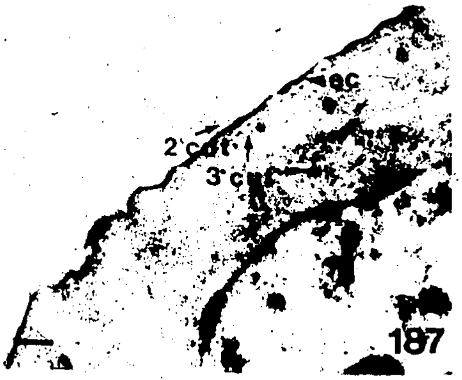

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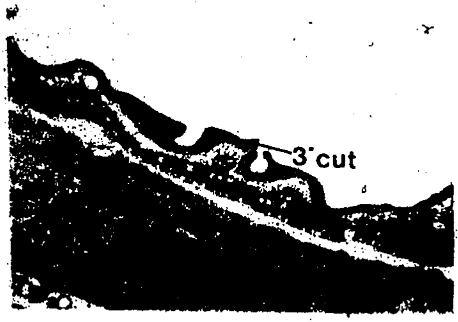

5.2.2.11 Muscle Development

Muscle development in insects is reviewed by Finlayson (1975) and I have found development in embryos of *M. fascifrons* to follow her description.

Between 35–45% TDT, spindle-shaped myoblasts first form (Fig. 178). Some such as those of the mandibular protractors, appear later because of later development of the mandibular plates (Figs. 99, 100). These myoblasts accumulate in the appropriate sites in the embryo, align themselves and elongate, attaching first to the epidermis at their points of origin. They continue to elongate, eventually reaching their points of insertion (Fig. 179), where some appear to attach to the plasma membranes of epidermal cells by tendon-like structures (arrow in Fig. 180). As development proceeds, these structures contract, pulling the thickened muscle fibers to the epidermal surface by 90% TDT (not illustrated). The fibers condense by 70% TDT (Figs. 181, 183) and exhibit cross striations, as viewed in light microscopy, by 80% TDT (Fig. 182).

Some cephalic muscles insert on tendons or apodemes, such as the mandibular and maxillary retractors and the cibarial dilators. The former form within invaginations of stylet sheath epidermis (Figs. 145, 147) and the latter within invaginated epidermal cells at the base of the clypeo-labrum (Figs. 117, 118).

5.2.2.12 Cuticle Formation

During embryogenesis, three cuticles form. The first embryonic cuticle (1° cut) begins to be deposited at 40% TDT (Fig. 89) and is continuous by 45% TDT (Fig. 184). This layer is very thin and is probably equivalent to the cuticulin layer described by Locke (1974). Epidermal cells form microvilli and secrete plaques of cuticulin (Locke, 1974) at their tips (Fig. 89). These coalesce and form the cuticulin layer of the epicuticle (Fig. 184). At katatrepsis (Fig. 185), this layer apolyses and the epidermal cells begin to secrete the second embryonic cuticle (2° cut) (Fig. 185). The first cuticle has completely disappeared by 55% TDT (Fig. 186) and the second embryonic cuticle has formed (Figs 187, 188). This cuticle appears to consist of the cuticulin layer, the inner epicuticle layer and at least some of the procuticular layer (Fig. 188). Beneath all of these the epidermal cells secrete the ecdysial membrane (Figs. 187, 188). After apolysis of the secondary embryonic cuticle the epidermal cells begin to secrete the third or larval cuticle (3° cut) (65% TDT) (Fig. 187) and by 70% TDT the cuticulin layer is formed (Fig. 188). The remaining layers are secreted (Locke, 1974) during the next 35% TDT and the larval cuticle (Fig. 189) is completely formed just prior to hatching.

5.3 Discussion

In the introduction, I stated that there is much controversy concerning homologies of hemipteran mouthparts. Table 8 lists the structures and varying interpretations of the five principal studies on hemipteran mouthpart embryogenesis.

The main controversy concerns the identity of the maxillary and mandibular plates. Heymons (1899) and Muir and Kershaw (1912) considered the maxillary plates to be maxillary, but Pesson (1944) attributed them to "replis primordiaux" from "regions pleurales des segments gnathaux". Pesson felt that earlier researchers had misinterpreted their work because they relied too heavily on whole mounts. Later, Newcomer (1948) and Singh (1970) described the plates as forming from an "outpouching" of the outer walls of the maxillary stylet anlagen.

SEM micrographs of *M. fascifrons* embryos show that maxillary appendages divide into inner and outer lobes with the outer lobes subsequently forming the maxillary plates (Figs. 81, 82). Since there is no well defined boundary between this plate and the genal region of the head above, it is hard to tell if the lobe contributes entirely to the plate or if it is a composite structure. This can be solved by looking at heads of less specialized leafhoppers in which plate boundaries are more clearly marked. Pesson's interpretation may have resulted from his failure to examine whole mounts of his embryos or, as Parsons (1973) commented

> "Pesson's (1944) embryological descriptions would have been more convincing if they had been more fully illustrated and if he had studied a more typical type of homopteran. In Coccoidea, a specialized, lateral "replis primordiaux" develops prior to the mandibular and maxillary lobes, and conceals them.".

Heming (1980) found, in embryos of *Haplothrips verbasci* (Thysanoptera) that the maxillae subdivide into inner and outer lobes and concluded that the plate was maxillary in origin. My study confirms his hypothesis and shows that in homopterous insects as well, the maxillary lobe is maxillary in origin and homologous with the stipes of biting and chewing insects and that the maxillary stylet is homologous with the lacinia (Heming, 1980).

TABLE 8

Comparison of homologies and development of selected mouthpart structures in Hemiptera

	Heymons (1899)	Muir & Kershaw (1912)	Pesson (1944)	Newcomer (1948)	Singh (1971)
Maxilla	homologous with lacinia	homologous with galea+lacinia	does not homologize	does not homologize	does not homologize
Max. Lever	—	—	subgenal suture	diverticulum of max. stylet sac	develops after hatching
Max. Sheath	—	—	—	surface ectoderm	hypopharyngeal, mandibular and maxillary plates
Max. Plate	homologous with galea + palp	homologous with cardo + stipes	pleural parts of labial and maxillary segments	outpouching of ectodermal wall of first maxilla	outgrowth of maxillary appendage
Mand. Lever	—	—	sugenal suture	wall of mandibular stylet sac	develop after hatching
Mand. Sheath	—	—	—	surface ectoderm	hypopharyngeal, mandibular and maxillary plates
Mand. Plate	derived from mandibular segment	clypeal in origin	pleural-portions of tritocerebral and mandibular segs.	surface of intercalary and mandibular segs.	'stumpy outgrowth' of mandibular appendage
Co-adaptations	—	—	form after retraction of stylets as they sclerotize	aquired at hatching	—
Hypopharynx	sternal area of gnathal segments	—	mandibular and maxillary segments	mandibular and intercalary segments	—
Salivary Syringe	homologous with salivary duct	modified portion of salivary duct	1st and 2d maxillae	venter of 1st and 2d maxillary segs.	—

The mandibular plate has been hypothesized to be hypopharyngeal, clypeal or genal in origin (Parsons, 1974). Embryological evidence for any of these origins is scarce. Muir and Kershaw (1912) thought the plates arose from fusion of the mandibular and pharyngeal sulci but later attributed them to the clypeus. A hypopharyngeal origin is not supported by any embryological evidence (Parsons, 1973) but the genal, sub-genal theory has some support from Pesson's (1944) work. Recently, Singh (1970) described the mandibular plates as being formed from an outgrowth of each mandibular appendage and therefore to be mandibular in origin.

Difficulty in interpreting the origin of these plates arises because they are hidden from view in whole mounts by the antennae (Fig. 106). Sections examined by light microscopy are, at times, difficult to interpret because of close juxtaposition of parts. In embryos of *M. fascifrons*, the plates arise as ectodermal outgrowths of the head behind the antennae (Figs. 99, 100). During provisional dorsal closure, they are separate from the hypopharynx, but as they lengthen caudally they associate closely with either side of the hypopharynx (H) (Fig. 149). Later, some of the protractor muscle myoblasts attach to the lateral wall of the hypopharynx giving the impression that the two are joined (Fig. 149).

Parsons' (1974) criticism of the genal sub-genal theory is that

> "It does not explain the position of the loromaxillary cleft in such Homoptera as the Cicadidae. The sequence diagrammed in Fig. 8 would produce a head in which the mandibular plates would be broadly continuous with the dorso-lateral part of the head capsule and thus appear to be ventral extensions of the gena. This is the condition in Coccoidea... and in Heteroptera
> In many Homoptera, however, the mandibular plate is separated from the genal region by the loromaxillary cleft ... whose dorsal end (C) lies on, or immediately lateral to, the edge of the postclypeus.".

If one looks at first instar larvae of *M. fascifrons*, the loromaxillary cleft is not complete and the mandibular plate appears to be a ventral extension of the gena. These clefts are secondary strenghthenings, forming partially from fusion between the mandibular and maxillary lobes and with a later extension of this cleft to the clypeal boundary.

The stylets are homologous with the mandibles and maxillary laciniae of biting and chewing insects and their manner of formation is generally accepted. Some small details vary. Newcomer (1948), for example, stated that cells of the stylet degenerate after their cuticle is secreted and that their coadaptations do not form until after hatching, while Pesson believed that coadaptations formed earlier, after retraction of the stylet anlagen by

> " ou bien que la paroi atriale de l'organ retortiform , placee en regard de la face sculptee du stylet ... a exece sur celui-ci un role morphogenetique inducteur.".

Pesson (1944) also found that the cells of each stylet anlage retracted into the head to form a retort organ, leaving the secreted stylet behind.

This stage of stylet ontogeny is easy to observe in embryos *M. fascifrons* because these insects have short stylets which do not coil in the head but curve, slightly at their proximal ends (Fig. 101). TEM provides the resolution necessary to study formation of coadaptations. In the early prolarva, as the cells of each stylet anlage retract, the surface of its upper layer of cells assumes the shape of the coadaptation (co) and secretes larval cuticle over this template (Figs. 109, 133, 134).

All stylets are innervated and nerves can be seen entering their anlagen as soon as neuropile appears in ganglia of the CNS. Pioneer neurons may grow proximally from the tips of the appendages early in their development (Bate, 1976) but these have not been observed. As the cells retract, they carry with them the sensory cell bodies and their dendrites of these cells elongate progressively.

As the bases of the stylet anlagen invaginate into the head, they pull with them surrounding ectoderm to form the stylet sheaths (Fig. 140). Maxillary primordia pull in ectoderm from the inner walls of the maxillary lobes and that of the lateral sternum that forms the hypopharynx (H) (Figs. 141, 142). The sheath is, therefore, both maxillary and hypopharyngeal in origin. The mandibular sheath is also composite in origin. Distally, each mandibular plate (genal in origin) grows down in front of a mandibular stylet and its inner wall forms the outer wall of the sheath (Fig. 101). The inner wall of the sheath is hypopharyngeal and, posteriorly, it is maxillary since it arises from the inner wall of the maxillary plate (Mxp) (Fig. 141).

Lever cuticle is deposited by sheath epithelial cells. Cells of each maxillary sheath evaginate as a diverticulum which grows out and contacts the hypopharyngeal wing (hw) (Fig. 147). Cells of each mandibular lobe invaginate mesially and posteriorly to form a tube in which cuticle of the mandibular apodeme is later secreted (Fig. 182). Postero-lateral cells of the mandibular plate secrete the cuticle of the mandibular lever

(=cuticular guide) that later articulates with the posterior end of the mandibular apodeme (map) (Figs. 144; 145). The distal end of each mandibular lever subsequently articulates with that of the apodeme. Comparison of my observations on levers and sheaths with those of others is difficult since previous studies are unclear.

The hypopharynx is also composite in origin, but there are differing views as to what segments contribute to its formation. Newcomer (1948) considered the intercalary and mandibular venters to form the hypopharynx while Pesson thought it came from the mandibular and maxillary segments. In embryos of *M. fascifrons* the intercalary, mandibular, and maxillary segments form the hypopharynx (H) (Fig. 155).

The labial sternum invaginates cephalad behind the hypopharynx and some of its cells pull back from the surface to form a cavity (Fig. 155). Some of these cells form a tube and secrete the cuticle of the piston, while those surrounding the cavity, secrete the cylinder of the salivary syringe (Fig. 156). Heymons (1899) and Muir and Kershaw (1912) believed the salivary syringe to be a modified expansion of the salivary duct and Newcomer (1948) and Pesson (1944), a derivative of the first and second maxillary sterna.

I conclude that the maxillary plate of the hemipteran head is maxillary in origin, and the mandibular or loral plate, genal. The mandibular lever and apodeme are also genal while both the mandibular and maxillary sheaths are composite. Stylet coadaptations form as secretion of larval cuticle begins and styligenous cells later retract into the head. The hypopharynx forms from sternal regions of the intercalary, mandibular and maxillary segments and the salivary syringe from the labial sternum. This information will be used later in discussing the evolution of the hemipteroid head.

6. Salivary Gland Embryogenesis

6.1 Introduction

Cicadellids and other homopterans have complex, paired salivary glands, each consisting of an accessory gland and a principal gland (Miles 1972). The principal gland contains a species specific number of acini. In hemipterans, acini are lobes of the salivary gland that are single cells grouped around a common salivary duct. In other insects, these lobules may have more than one cell. Each type of acinus produces and secretes different substances that have different functions. These include: salivary enzymes to digest plant cell walls, cement to anchor the tip of the labium to the substrate during feeding, sheath material that envelops the stylets while the insect feeds, and lubricants for the stylet fasicle (Miles, 1972).

Miles (1972) reviewed salivary secretion in Hemiptera and discussed the structure, function and evolution of the salivary system. Most studies emphasize salivary gland structure, the role of salivary secretions in insect feeding and the effect they have on hosts. The glands are also a site of plant virus and mycoplasma replication in species that are vectors of plant diseases (Miles, 1972).

Salivary gland development has been little studied in Hemiptera or in Hemimetabola but several papers treat that of holometabolous insects, mostly of larval glands in various Diptera (Berridge et al., 1976, Simoes et al., 1977 and Eeken, 1977).

In this chapter, I describe larval salivary gland structure, ultrastructure and embryogenesis in *M. fascifrons*.

6.2 Observations

6.2.1 Larval Structure

Dobroscky (1931) described the salivary glands of *M.fascifrons* at the light microscope level. The following description incorporates her findings with mine and describes the ultrastructure of each acinus.

Each gland consists of an accesory gland (ac) and a principal gland (pg) (Fig. 190). The principal gland has an upper lobe of pinnately arranged cells that Dobroscky classified as acini Type 5 and a lower lobe containing several acinar types having characteristic inclusions (Figs. 31, 191). The common salivary duct (sd) enters the gland at the junction of these two groups of cells (Fig. 190).

The accessory gland is tubular and extends from the serous (Type 5) acini up into the head (Fig. 190). It consists of a duct which joins the main duct in the serous gland and ends in a bulb of four cells (Figs. 190). Duct cells have few mitochondria, numerous vacuoles (v) containing sparse granular material, dark irregular inclusions, and numerous vesicles (Fig. 192).

There are seven pinnately arranged serous cells of acini Type 5 (Dobroscky, 1931) (Figs. 190, 191, 193). The upper cells have very little cytoplasm and stain light pink with Gomori's trichome; the lower cells stain light to dark blue (Fig. 191). The lower cells contain large irregularly shaped vacuoles and round, mottled inclusions (Figs. 193, 195, in). Their dense cytoplasm contains free ribosomes (r), rough endoplasmic reticulum (RER), and a few mitochondria (m) (Fig. 195). All cells open into ducts (1 arrow) which join the common salivary duct (2 arrows) (Fig. 193). Duct cell nuclei (nu) are small and ovoid and the cytoplasm of the cells contains numerous mitochondria, disorganized arrays of microtubules (mt) and microvilli (mv) and a principal duct (pd) lined with cuticle (Fig. 194).

The four types of acini in the lower lobes (Fig. 190) all have characteristic types of inclusions and two nuclei per cell (Figs. 191–201).

Each Type 1 acinus has six cells arranged in a rosette near the posterior end of the salivary gland (Figs. 190, 191). These are long and thin and have round, small nuclei staining blue with Gomori's trichome. Their inclusions are strongly PAS positive and negative results from tests with diastase indicate that these are neutral mucopolysaccharides and not glycogen. In TEM sections, the inclusions (in) are small and round and have a grey, mottled appearance (Figs. 196, 197). Cell cytoplasm contains large amounts of RER, some mitochondria, and free ribosomes (Fig. 197).

There are six large Type 2 acinar cells that are packed with brilliantly red-staining inclusions and bluish cytoplasm (Fig. 191). The two centrally located nuclei (nu) of each cell are large and round (Figs. 191, 198). Histochemical staining indicates that inclusions

Fig. 190 Adult salivary gland

scale= 20um

Abbreviations; accessory gland (ac), acini 1,2,3,4,5, (Ty 1,2,3,4,5), principal gland (pg), salivary duct (sd).

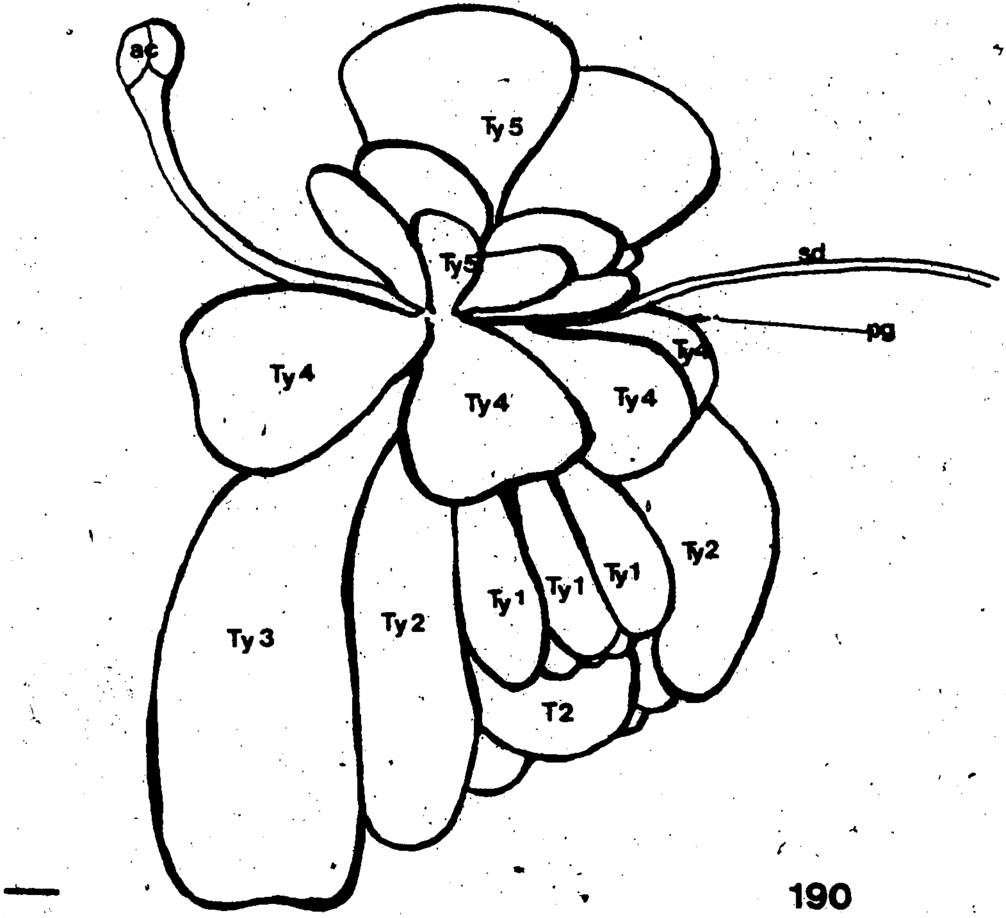

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Fig. 191-195 Larval salivary gland

Fig. 191 Frontal section of adult gland

scale= 50um

Fig. 192 Salivary gland duct cells and inclusions, transverse TEM section

scale= .5 um

Fig. 193 Acini type 5 and inclusions, transverse TEM section

scale= 5 um

Fig. 194 Acini type 5 inclusions, transverse TEM section

scale= .5 um

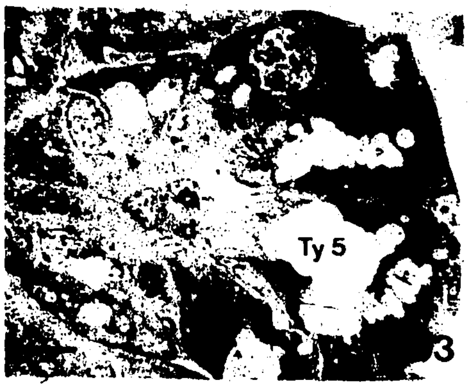
Fig. 195 Salivary duct, transverse TEM section

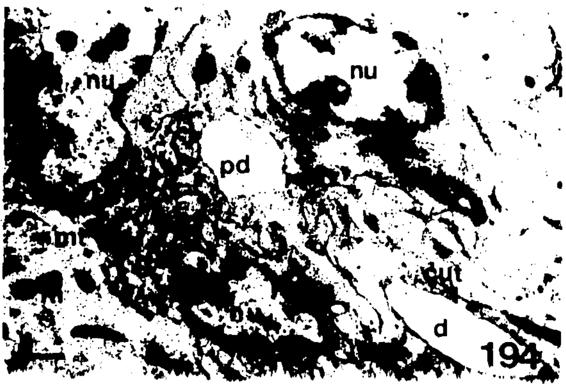
scale= .5 um

Abbreviations; acini type 1-5 (Ty 1-5), brain (Br), cuticle (cut), duct (d), inclusions (in) microtubules (mt), mitochondria (m), nucleus (nu), rough endoplasmic reticulum (RER).


Ty4
Ty


m
v
v
v
m
192


Ty 5
3


nu
nu
pd
bm
b
dut
d
194

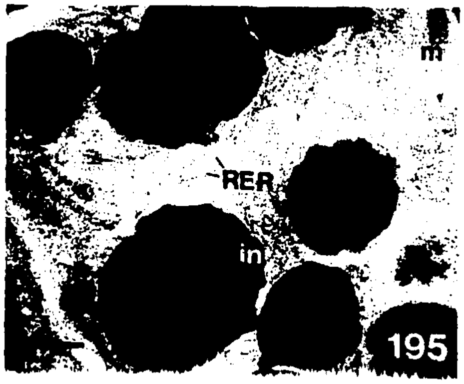

m
RER
in
195

Fig. 196–201 Larval salivary gland, TEM's

Fig. 196 Type 1 and type 2 acini, transverse section

scale= 5 um

Fig. 197 Type 1 acini and inclusions, transverse section

scale= .5 um

Fig. 198 Type 3 and type 2 acini, transverse section

scale= 5 um

Fig. 199 Type 2 acini and inclusions, transverse section

scale= .5 um

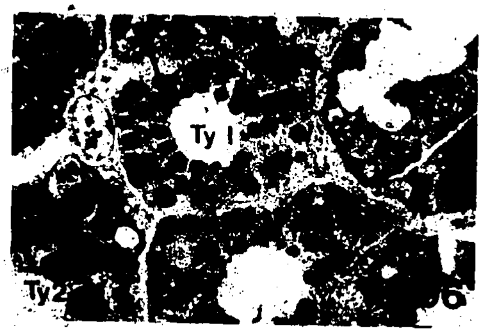
Fig. 200 Type 3 acini and inclusions, transverse section

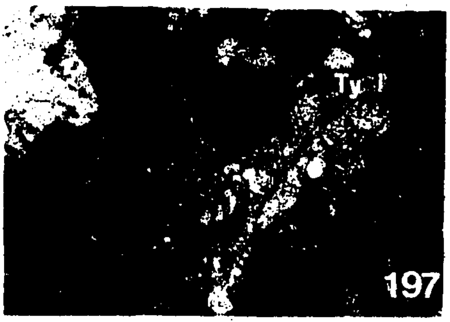
scale= .5 um

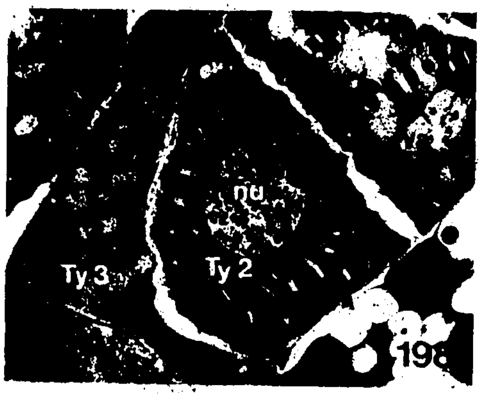
Fig. 201 Type 4 acini and inclusions, transverse section

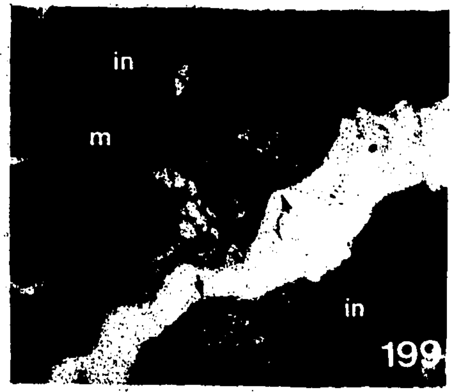
scale= .5 um

Abbreviations; acini type 1, 2, 3, 4 (Ty 1, Ty 2, Ty 3, Ty 4), inclusions (in), mitochondria (m), nucleus (nu), rough endoplasmic reticulum (RER), vesicular endoplasmic reticulum (VER).


Ty I
Ty2
196


Ty I
197


nu
Ty 3
Ty 2
198


in
m
in
199


m
RER
Ty3
in
in
200

of these cells may be proteinaceous, but because of test unreliability it is impossible to confirm this. Ultrastructurally, the inclusions are round, electron-dense and vary in size (Figs. 198, 199). Cell cytoplasm contains vacuoles (v) with flocculent inclusions, sparse mitochondria?(m), and parallel arrays of RER, some closely associated with the plasma membrane (arrow in Fig. 199), others interspersed throughout the cell (Fig. 199). Many of the mitochondria are situated close to inclusions (Fig. 199).

There are two Type 3 acinar cells (Fig. 190), one larger than the other and both with light blue cytoplasm, two large nuclei and irregularly shaped inclusions (Figs. 191,?198, 200). The material in the inclusions tests positive for carboxylated mucosubstances with Alcian Blue CEC (0.06M) and Aldehyde Fuchsin-Alcian Blue. The results of these tests vary and are only a rough indication of what the inclusion might be. TEM shows irregularly shaped inclusions of varying size containing a granular, greyish substance (Fig. 198 and 200). There are numerous small mitochondria, short strands of RER, free ribosomes and some golgi (Fig. 200).

Four broad flat cells that are Type 4 acini (Fig. 190) lie in front of the previous acini posterior to Type 5 'serous' (Dobroscky, 1931) acini (Figs. 190; 191). Stained with Gomori's trichome, these are purplish blue, uneven in texture, and their two nuclei are large and round (Fig. 191).

No postive reaction was found in their cytoplasm for mucopolysaccharides or proteins. Ultrastucturally, their inclusions are large, irregular and grey with an internal honeycomb structure (Fig. 201). Also present are a few round, more darkly staining inclusions (not illustrated). The cytoplasm contains many mitochondria, and short strands of RER, some vesicular (Fig. 201).

6.2.2 Salivary Gland Embryogenesis

Salivary gland development progresses through formation, proliferation, and differentiation.

After evagination of appendages, lateral ectoderm on either side of the labial sternum invaginates dorsally to form the two presumptive salivary glands (Sg) (Fig. 202). Each invagination elongates towards the dorsal surface as a hollow tube (Fig. 202).

Fig. 202-207 Salivary gland embryogenesis

Fig. 202 Salivary gland at 30% TDT, low power TEM section
scale= 5 um

Fig. 203 TEM of salivary gland cells, transverse section
scale= .5 um

Fig. 204 Salivary gland at 35% TDT, sagittal section
scale= 10 um

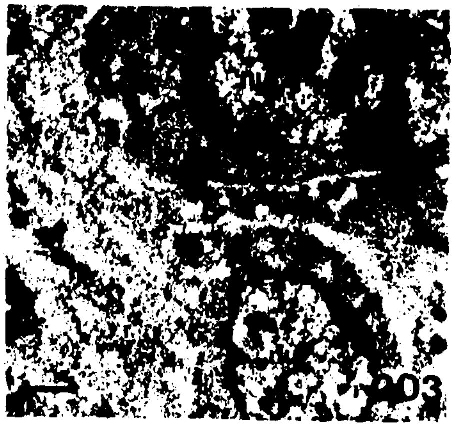
Fig. 205 Salivary gland at 45% TDT, sagittal section
scale= 10 um

Fig. 206 TEM of salivary gland at 45% TDT, transverse section
scale= .5 um

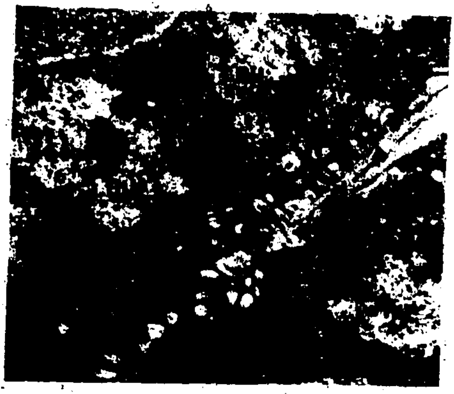
Fig. 207 TEM of salivary gland cell at 45% TDT, transverse section
scale= .5 um

Abbreviations; anterior lobe (al), duct (d), mitochondria (m), nucleus (nu), posterior lobe (pl), ribosomes (r), salivary gland (Sg), smooth endoplasmic reticulum (SER).


d
sg


203


d



TEM show the duct cells (d) expanding into a sac (Fig. 202). Density of cell cytoplasm varies with position in the primodium, apical cells (arrow) appearing darker than proximal cells (2 arrows) adjacent to the duct. Nuclei vary in size, although those of the duct are smaller. Gland cells form microvilli at their apices, and secrete their product into a secondary duct which enters the main duct (Fig. 202). The microvilli form dense plaques at their tips and mitochondria of varying size and shape are dispersed throughout the cytoplasm of the cells. There are many free ribosomes, little ER and poorly defined cell membranes (arrow) (Fig. 203).

Next, the cells of each primodium proliferate. At first, each gland (Sg) appears as a bulbous group of cells at the apex of its duct (d) (Fig. 204). By 40% TDT, the ducts of each gland primodium fuse medially to form a common salivary duct. Gland cells in each anlage then divide into three groups: the accessory, anterior (al) and posterior lobes (pl) of the principal gland (Fig. 205).

Gland nuclei by 45% TDT are of varying size, those of the posterior lobe being larger (Fig. 205). The amount of cytoplasm increases in each cell and separation of cells into acini begins (Fig. 205). Cells of each acinus have two irregularly shaped nuclei and there are many free ribosomes, a few mitochondria and some smooth endoplasmic reticulum (SER) (Fig. 206). Plaques of cuticle form at the tips of duct cell microvilli (Fig. 207).

At the end of katatrepsis, mitosis ceases and differentiation of gland acini begins (Fig. 209 and 210). By 60% TDT, accessory lobe cells (ac) form a tube (Fig. 208). Internally, apical microvilli with plaques of cuticle at their tips (arrow) project into the lumen of the accessory lobe cells and vesicles (ve) with inclusions are visible within the duct (Fig. 211). Mitochondria (m), are located close to the microvillar border (Fig. 211) and the nuclei of the cells are irregularly shaped (not illustrated). Vacuoles (va) containing granular inclusions are present in the cytoplasm of the acinar cells and there are many free ribosomes, some smooth ER (SER) and golgi (g) (Fig. 212, 213). The gland is irregular in shape and a flocculent material surrounds it, probably a precursor of the basement membrane (Fig. 210, arrow).

At this time, ultrastructure of cells of the anterior and posterior lobes is similar. Cell nuclei are irregularly shaped and larger than those of accessory and duct cells (Fig.

Fig. 208–213 Salivary gland embryogensis

Fig. 208 Accessory gland, transverse section

scale= 5 um

Fig. 209 Salivary gland 55% TDT, transverse section

scale= 5 um

Fig. 210 TEM of salivary gland at 55% TDT, transverse section

scale= 2 um

Fig. 211 TEM of salivary duct cells at 55% TDT beginning to secrete cuticulin at the tips of their apical microvilli

scale= .5 um

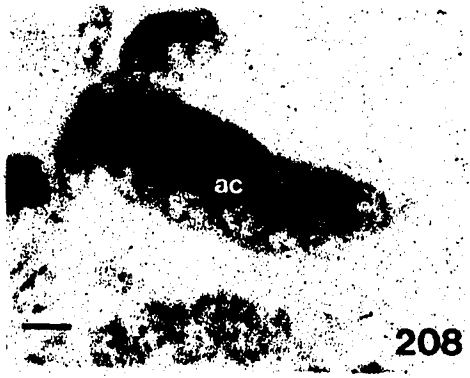
Fig. 212 TEM of salivary gland cell cytoplasm

scale= .5 um

Fig. 213 TEM of salivary gland cell cytoplasm

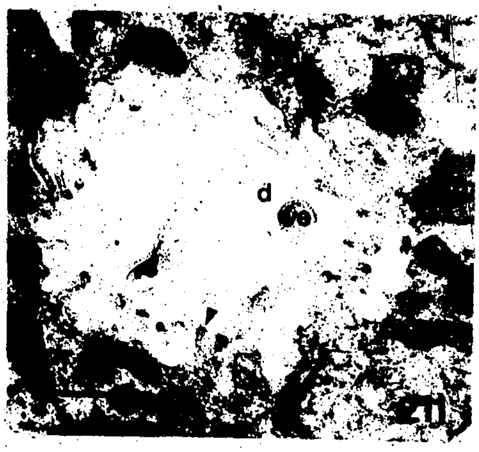
scale= .5 um

Abbreviations; accessory gland (ac), acini (a), duct (d), mitochondria (m), nucleus (nu), principal gland (pg), riboeomes (r), smooth endoplasmic reticulum (SER).


ac
208


a
209


ng
d
210


d
ve
211


nu
SER
213

210). The cytoplasm of the cells contains few mitochondria, free ribosomes (r), some smooth ER and occasional lipoid droplets (lp). The cells abut on duct cells that bear apical microvilli secreting cuticle into the lumen of the duct. Cytoplasm of the duct cells is complex and contains many mitochondria, RER, golgi (g) and microtubules (Fig. 211).

By 70% TDT, salivary gland nuclei reach their final size, anterior lobe cells assume a pinnate configuration and the posterior acini elongate (Fig. 214). Inclusions are not visible under the light microscope at this stage.

The first inclusions to be stained by Gomori's trichome appear at 75% TDT as green globules in Type 2 acini (Fig. 215, arrow). Type 3 acini, the largest cells in the insect's body, continue to lengthen.

At this stage, TEM studies of accessory gland cells show round, electron dense droplets to be present in their cytoplasm and numerous mitochondria along the apical microvillar border (Fig. 216). There is an increase in RER, additional vacuoles and fewer free ribosomes (not illustrated). Salivary duct cells are lined with cuticle and in their cytoplasm are numerous mitochondria, long strands of ER and vesicles (not illustrated). In the acinar cytoplasm, there are more mitochondria that often appear in groups, long strands of ER, some free ribosomes and a few lipoid droplets (Fig. 217, 218).

By 80% TDT, each Type 3 acinus is long and its structure resembles that of the larva (Fig. 220). Type 2 acinar inclusions stain both red and green with Gomori's trichome and are more numerous than earlier. Type 1 acini are PAS positive as is the accessory gland and parts of the common salivary duct. Slightly later, inclusions in Type 2 acini stain red and pack each cell. Ultrastructurally, Type 2 acinar cells have RER formed in parallel arrays next to plasma membranes (Fig. 221, arrow), and shorter strands throughout the cytoplasm (Fig. 221). There are also numerous mitochondria, round, electron-dense inclusions of various sizes, and groups of vesicles in the cytoplasm (Fig. 222). In other acinar cells inclusions are being packaged by the golgi (Fig. 222, 223). Cells of the common salivary duct surround a cuticle-lined lumen, and their cytoplasm contains numerous, free ribosomes, and mitochondria. Duct cell membranes are deeply infolded (Fig. 224).

During the last 10% TDT, gland acini assume the staining properties of the larval salivary glands and inclusions appear in Types 3, 4, and 5 acinar cells. Just before

Fig. 214-219 Salivary gland embryogenesis

Fig. 214 Salivary gland of Early prolarva

scale= 10 um

Fig. 215 Salivary gland at 75% TDT showing developing inclusions

scale= 10 um

Fig. 216 TEM of accessory gland

scale= .5 um

Fig. 217 TEM of acinar cells

scale= 1 um

Fig. 218 TEM of acinar cells

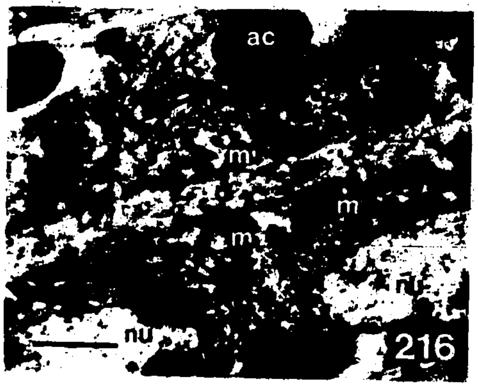
scale= .5 um

Fig. 219 TEM of acinar cells

scale= .5 um

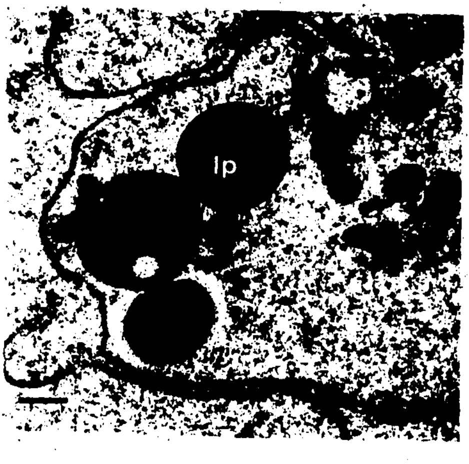
Abbreviations; accessory gland (ac), acini 1-5 (Ty 1-5), duct (d), mitochondria (m), nucleus (nu), ribosomes (r), rough endoplasmic reticulum (RER) smooth endoplasmic reticulum (SER), vesicular endoplasmic reticulum (VER).

164



216

217



219

Fig. 220–224 Salivary gland embryogenesis

Fig. 220 Late prolarva salivary gland

scale= 20 um

Fig. 221 Type 2 acini

scale= .5 um

Fig. 222 Type 2 acini

scale= .5 um

Fig. 223 Developing inclusions in acini

scale= .5 um

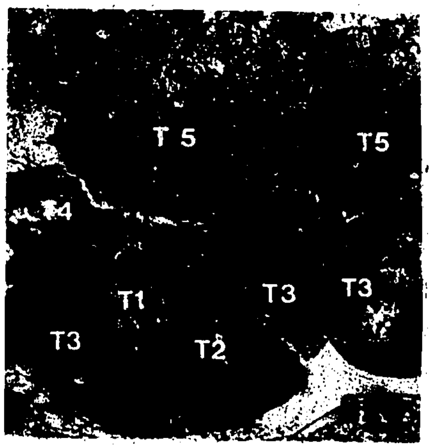
Fig. 224 Salivary gland duct cells

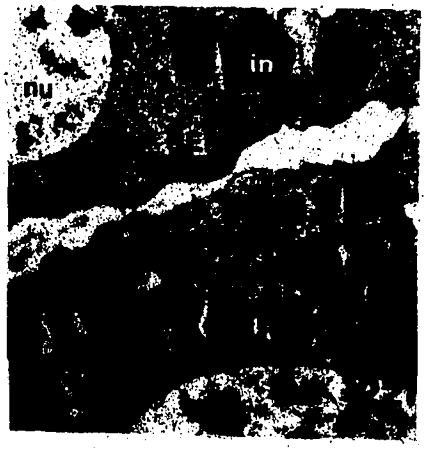
scale= .5 um

Fig. 225 Salivary gland duct cells

scale= .5 um

Abbreviations; acini 1–5 (Ty 1–5), developing inclusions (din), duct (d), golgi (g), inclusions (in), mitochondria (m), nucleus (nu), ribosomes (r), rough endoplasmic reticulum (RER), smooth endoplasmic reticulum (SER).





222

225

hatching, the upper anterior lobe cells become vacuolate and the gland resembles that of the first instar larva (Fig. 220).

6.3 Discussion

6.3.1 Larval Structure

Comparing the ultrastructure of larval and adult glands in hompterans is difficult because only those of *Myzus persicae* have been examined (Moericke and Wolftharth-Botterman, 1960a, b). Below I consider secretions and probable functions of gland acini.

Salivary secretions in hemipterans have been characterized by histochemical and biochemical tests (Miles, 1960). The latter provide reliable evidence of what is present in hemipteran saliva. Histochemical techniques are less reliable and localization of the various secretions is difficult.

Most hemipterans produce two salivary components: sheath material and watery saliva (Miles, 1959). Although not all bugs secrete salivary sheaths, *M. fascifrons* does as it feeds. Sheath material is primarily proteinaceous and contains about 10% phospholipid. Conjugated carbohydrate and oxidizing enzymes are secreted with it. Watery saliva contains mucoprotein and various enzymes (Miles, 1960). The number of enzymes present varies and has not been determined for *M.fascifrons*. Saliva of *Empoasca fabae* has amylase, oligosaccharases and a protéinase (Berlin and Hibbs, 1963) and that of *M. fascifrons* may be similiar.

By studying the histochemical properties and ultrastructure of acini and their inclusions, it is possible to speculate on their role in salivary secretion.

Inclusions of Type 1 acini stain strongly with PAS. Because the granules were shown not to be glycogen, they may be either neutral mucopolysaccharide, or lipoprotein. If lipoprotein, they could contribute to formation of sheath material. If neutral mucopolysaccharide they could combine with proteinaceous inclusions to form the mucoprotein of watery saliva. Because the pH of sheath material is close to neutral, and that of watery saliva alkaline and because the pH of the principal gland, and its Type 1 acini is close to neutral, its inclusions are probably neutral polysaccharides. Positive staining for tryptophan suggests that Type 2 acini have proteinaceous inclusions, and that their secretions contribute to formation of the salivary sheath. Miles (1960), showed that salivary sheath material contains a trace of tryptophan.

Type 3 acini appear to stain for carboxylated mucosubstances but their role is unknown.

Types 4 and 5 acini do not stain positively for proteins or mucopolysaccharides. Occurrence of vesicular and short stranded RER in the cytoplasm of Type 4 acini could indicate that the inclusions are enzymes that are either the hydrolyzing enzymes found in watery saliva or the oxidizing enzymes of the sheath material of this insect (Dailey and Crang, 1978). Dobroscky (1931) suggested that Type 5 acini produce a watery secretion. TEM and histochemical examination of the glandular inclusions in *M. fascifrons* do not give any indication of their role. Furthur histochemical and biochemical study is required to determine the nature of these inclusions.

Duct cells contain numerous mitochondria and microtubules, the former providing energy to move secretions, the latter functioning in transport of materials through cells (Threadgold, 1976).

6.3.2 Embryogenesis

There is little detailed information on salivary gland development in hemimetabolous insects. Existing studies merely summarize their origin from labial ectoderm. Detailed studies on postembryonic development of salivary glands in Diptera do exist but these glands are tubular, not acinar as in *M. fascifrons*.

Undifferentiatied salivary gland cells in *M. fascifrons* contain free ribosomes, sparse mitochondria, and a few lipoid droplets. They originate by lateral invagination of labial sternal ectoderm and proliferate to yield the cells present in the larval glands. During cellular proliferation, the principal need of the cells is for structural proteins produced on polyribosomes (Fawcett, 1981). Mitochondria and lipids may provide the energy source required for protein synthesis (Fawcett, 1981).

Proliferation ceases and differentiation begins after katatrepsis. Cells of the primordia become more complex, the number of golgi and mitochondria increases, and some ER appears. Blebbing of the nuclear membrane apparently forms ER, golgi and plasma membrane material (Threadgold, 1976). Polyribosomes, though less numerous, are still present and presumably continue to produce structural proteins as the cells continue to develop (Fawcett, 1981). Additional mitochondria and lipid droplets provide more energy for synthesis of organelles and secretion products (Fawcett, 1981). Later, the golgi package the secretory products (Figs. 222, 223).

By the early prolarva, the salivary gland duct has a cuticular intima, and its cells contain many mitochondria in close association with their microvillar luminal border; their basal membrane is involuted with more RER. Mitochondria that provide energy and microtubules that transport materials in the cell form subapically.

At this stage, accessory gland cells contain more numerous mitochondria, and RER, involved in formation of secretory droplets, occurs in these cells.

Principal gland acinar cells of the early prolarva do not actively synthesize secretory products, but produce organelles that later are involved in synthesis. In their cytoplasm, there are long strands of RER, additional mitochondria and golgi. In the late prolarva, gland acini begin to secrete their products and their cells contain long strands of RER forming parallel arrays, or short strands or vesicles, depending on type of secretion.

7. General Discussion

7.1 Introduction

It is accepted that hemipterans, with their piercing and sucking mouthparts, evolved from a biting and chewing ancestor (Evans, 1938; Parsons, 1964; Hamilton, 1981). This involved major modifications of existing, and development of new, mouthpart structures.

A discussion of hemipteran mouthpart evolution must consider changes in the following structures: 1. clypeo–labrum; 2. mandibular and maxillary stylets, and their levers and stylet sacs; 3. mandibular plates; 4. maxillary plates; 5. labium; 6. tentorium; 7. cibarium; 8. hypopharynx and salivary syringe and a development of entognathy.

In the following discussion, I deal with each of the above, discuss the theories on their evolution, and look at existing embryological evidence applicable to these theories.

7.2 Clypeo-labrum

Homology of the large median sclerite in the heads of hemipteroids is a much–debated issue. Various names are used for this sclerite (usually divided into 3) and these are discussed in Chapter 7. The system used most is that of Snodgrass (1927, 1935), who called them (from base to apex) postclypeus, anteclypeus and labrum.

The problem of homologizing this sclerite is apparent if head capsules of hemipterans and biting and chewing insects are compared (compare Fig. 30 and Fig. 226). Is the bulging sclerite [illegible] frons (Matsuda, 1965; Hamilton, 1981), an enlarged clypeus (Snodgrass, [illegible]) a clypeus joined with a reduced frons (Evans, 1946; Du[illegible], 1962; Parsons, 1964; Puchkova, 1970)? Singh (1971) discussed the various interpretations quite thoroughly, so I will only summarize some major points.

Snodgrass (1935) defined the clypeus as

> "the facial area of the cranium just above the labrum usually separated from the frons by an epistomal suture and sometimes divided into an anteclypeus and postclypeus."

This definition does not cover all possibilities and he used additional characters such as muscle insertions and the position of the anterior tentorial pits to help define the clypeus.

Fig. 226 Head of orthopteran insect
(after Snodgrass, 1935)

Abbreviations; clypeus (Clp), frons (Fr), labrum (Lm), mandible (Md).

According to Snodgrass (1935), muscles originating on the 'clypeus' are cibarial dilators because their insertions are on the cibarium. The food pump is the cibarium, since it lies anterior to the frontal ganglion which marks the beginning of the pharynx.

Evans (1938), Duporte (1956), Parsons (1964) and Puchkova (1970) called the median sclerite the fronto-clypeus but Evans (1946) gave no morphological evidence for considering this plate a union of the frons and clypeus. He did postulate that the whole structure might represent

> "the primitive prostomium, and the epistomial suture is a secondary fold which developed in the first place as a direct result of the acquisition of the anterior articulations of the mandibles.".

In hemipterans, he felt the structure resulted from a

> "backwards development of the clypeus which is accompanied by a reduction in the size of the frons... a direct result of the backward pressure of the dilator muscles of the sucking pump, together with those of the mandibular-tentorial protractor muscle.".

Duporte (1962) disagreed with Snodgrass' use of muscle origins and position of the anterior tentorial pits to delineate between frons and clypeus. He pointed out that muscles can shift their points of origin and that the anterior tentorial pits do not always lie on the fronto-clypeal suture. He described examples of the pits moving their position, but stated that

> "apart from these, their position seems to be fixed. They do therefore, mark the position of the fronto-clypeal suture, not because they lie in it, but because a line drawn through them, or through their ventral ends if they are vertically elongated, marks the boundary between the frons and clypeus, and can be used to identify these regions on the face in the absence of a suture.".

He then used this criterion to identify the limits of the frons and clypeus in the cicada, and concluded "the plate, therefore, is a fronto-clypeus in which the frons is greatly shortened while the postclypeus is elongated.".

Parsons (1964) followed Duporte (1962) and called the median sclerite the fronto-clypeus. Puchkova (1970) also adopted this term, though her reasons were not clearly stated. All three felt that during hemipteran evolution, the clypeus elongated and the frons became reduced (Duporte, 1962; Parsons, 1964; Puchkova, 1970). Singh (1971) favoured the view that this sclerite is the fronto-clypeus, but did not give reasons.

Matsuda (1965) considered the median sclerite to be the frons. He believed that since the plate is not pre-oral, it cannot be clypeal. He concluded that Snodgrass' criteria are not reliable, and that

> "in the absence of absolutely reliable criteria, the distinctions between the pre-oral clypeus and post-oral frons in higher insects is often merely 'hypothetical'.".

Hamilton (1981) agreed with Matsuda and considered the median sclerite to be the frons. He felt that the cibarial muscles were not homologous with the clypeal dilators [illegible] the epipharynx (as did Snodgrass, 1927, and Matsuda, 1965) but "are more similar to the 'fronto-pharyngeal muscles' of Micropterygidae". During hemipteroid (this includes the Psocoptera, Pthiraptera, Thysanoptera and Hemiptera) evolution, these muscles enlarged and shifted their insertions to the mouth and resulted in an enlarged frons to accomodate these muscles (Hamilton, 1981).

Embryonic development of the clypeo-labral region may provide some insight into the homology of this sclerite. The clypeo-labrum of insects develops either as a bilobed or single-lobed structure above the stomodeum (Folsom, 1900; Rempel and Church, 1971; Counce, 1972). In the Acercarida, it is not consistently bilobed or single lobed. It develops as a bilobed structure in embryos of *Pristhesancus papuensis* (Heteroptera: Reduviidae) (Muir and Kershaw, 1911b), *Oncopeltus fasciatus* (Heteroptera: Lygaeidae) (Newcomer, 1948), and *Oxyrhachis tarandus* (Homoptera: Membracidae) (Singh, 1971), and is single-lobed in those of *Liposcelis divergens* (Psocoptera: Liposcelidae) (Goss, 1953), *Haplothrips verbasci* (Thysanoptera: Phlaeothripidae) (Heming, 1980), *Siphanta acuta* (Homoptera: Fulgoroidea) (Muir and Kershaw, 1912), and *Macrosteles fascifrons* (Homoptera: Cicadellidae). If the clypeo-labrum is bilobed, it eventually coalesces into a single structure which unfolds caudally during development to form the frontal sclerite.

In more primitive insects, the median sclerite develops in a manner similar to that described by Folsom (1900) for the collembolan *Anurida maritima*:

> "the labrum (really clypeo-labrum) is a median hemispherical papilla...at no period does it give evidence of a paired origin...at stage 5 the labrum is decidedly longer. The basal part represents the clypeus.".

He reviewed the development of this structure in other insects and arthropods; and concluded;

> "among insects then, the labrum and clypeus develop from a median evagination between the procephalic lobes.".

It appears, therefore that the median evagination should properly be called the clypeo-labrum as indicated by Folsom (1900), while the frons is part of the head capsule.

In acercaridans, the more anterior part of the median lobe forms a large bulging sclerite (Newcomer, 1948; Goss, 1953; Heming, 1980). In embryos of *M. fascifrons,* this lobe also forms the median sclerite (Figs. 80, 81, 84, 85, 90, 93) and the labrum itself grows out as a finger-like projection after the lobe has unfolded caudally (Figs. 93, 106). At this stage, the unfolded lobe covers the other mouthpart appendages, and its antero-dorsal limits are still visible (Figs. 106, 120). The area above the creases of the unfolded clypeo-labrum is probably the frons.

Following katatrepsis, the creases are no longer visible and the clypeus and frons have merged during blastokinetic movements. The sclerite, therefore, is, as Duporte (1962), Parsons (1964), Evans (1946) and Puchkova (1970) presumed, the fronto-clypeus. The remaining structures of this sclerite, if they develop at all, do not form until just before (labral fold) or after hatching (transclypeal suture).

7.3 Mandibular and Maxillary Stylets, Stylet Levers and Stylet Sheaths

Stylets. – The stylets of hemipterans have been homologized with the mandibles and maxillae of biting and chewing insects since the 1800s. Early embryological studies by Heymons (1899) and Muir and Kershaw (1911b, 1912) clearly showed the mandibular and maxillary anlagen of hemipterans to resemble, in their early stages, similar anlagen in embryos of biting and chewing insects. Some researchers pointed out that the maxillary stylet is homologous with the lacinial pick of psocopterans, and that the Psocoptera, Pthiraptera, Thysanoptera and Hemiptera are closely related (Heslop-Harrison, 1956; Heming, 1980; Hamilton, 1981).

Stylet development appears to be similar throughout the Hemiptera. There are some reported differences (Pesson, 1944; Newcomer, 1948) which may result from differences in interpretation due to resolving power of the techniques used or may be real.

The stylets begin as paired evaginations of the surface ectoderm of the germ band (Heymons, 1899). The buds, or anlagen, elongate, sink back into the head, and eventually coil a number of times in embryos of some species (Pesson, 1944; Newcomer, 1948); in other embryos they simply curve caudad (Singh, 1971; *M. fascifrons*).

Pesson (1944) and Newcomer (1948), studying embryos of coccids and *O. fasciatus* respectively, described stylet development in detail. According to Pesson (1944), epidermal cells of the stylet anlagen secrete the cuticle of the stylet and then retract to form the retort organ, leaving a central cavity in each stylet. Newcomer (1948) viewed the process slightly differently. He described an area "on the external surface of the setae...which becomes homogenous and hyaline in texture.". This region is the "forerunner of the bristle" and differentiation proceeds from the tip proximally with anlagen cells disintegrating as this occurs. Singh (1971) found stylet primordia in embryos of the membracid *O. tarandus* to follow a similar developmental path. Pesson (1944) described the stylet coadaptations forming in coccids after retraction of epidermal cells from stylet cuticle while Newcomer (1948) felt that they do not form in *O. fasciatus* until the larva hatches.

In *M. fascifrons* embryos, stylet anlagen cells also secrete the cuticle of the stylets. In fact, the cells actually secrete three successive cuticles, the last being the larval cuticle. As in coccids (Pesson, 1944), the cells retract to form the retort organs of the first instar larva, leaving behind unsclerotized cuticle. I have not observed disintegrating cells in the stylet anlagen as development proceeds. TEM studies show coadaptations to form as anlagen cells retract. The surface of the anlagen cells act as a mold, taking on the shape of the stylet, with the cuticle subsequently being deposited around this. Pinet (1970) observed the same thing when following formation of stylet coadaptations during metamorphosis in *Rhodnius prolixus*. TEM studies of developing stylets in other hemipterans will probably show the coadaptations to form in a similar manner.

Either the mandibular or both mandibular and maxillary stylets are innervated in hemipterans (Forbes, 1966; Forbes and Raine, 1973; Cobben, 1978). In *M. fascifrons*, both stylets are innervated (Forbes and Raine, 1973). In anlagen, before elongation, the cell bodies and axons of their sensory neurons are found at their tips. As the anlagen cells elongate and retract, the cell bodies and axons of these neurons pull back with them, trailing their lengthening dendrites behind them in the pre-cuticular stylet.

In thysanopterans, development of the stylets is slightly different:

> the cuticle of each stylet is secreted about the surface of an elongate cytoplasmic matrix extending caudad from a single mass of trichogen-like secretory cells.". (Heming, 1980)

Heming (1980) felt that this different type of formation may be due to "the relatively small size and shortness of the stylets in the larvae of this species of thrips.".

Goss (1953) did not describe development of the psocopteran lacinial forks, so it is impossible to compare their development with those of other acercaridans.

Stylet sacs. – Stylet sacs, or stylet sheaths, are new structures arising during the evolution of the hemipteran cranium. They are membranous, and wrap the stylets and their bases internally. Distally, both stylets are enclosed in a common sheath, while proximally each has a separate sheath.

Snodgrass (1938) and Parsons (1964) were the only morphologists to discuss the evolution of sheaths.

Snodgrass (1938) described them as "special developments in Hemiptera, since they are correlated with the invagination of the mandibular and maxillary bases and with the presence of a salivary ejection apparatus.".

Parsons (1964) dealt more extensively with their formation, describing their evolution through a series of stages. In Stage 3, a V-shaped cavity forms between the lamina maxillaris and the hypopharynx (Parsons, 1964). During Stage 4, fusion of the various parts takes place; "the atrial cavity dorsally divides into separate sacs and ventrally it remains a common one"; and "the atrial walls become very closely applied to the body of the stylets,...these parts of the sacs are membranous.". Part of the sacs are sclerotized, the parts of the hypopharyngeal wings which form "the medial walls of the maxillary sacs" (Parsons, 1964).

Only a few embryological studies deal with formation of the sacs. Mellanby (1936) called them "pocket-like invaginations", and described each stylet as having its own pocket and a common pocket. In *O. fasciatus* embryos, the common sac is formed as the stylet anlagen invaginate into the head, pulling with them the attached epidermis

(Newcomer, 1948). Internally they branch to form separate stylet sacs. Newcomer did not discuss the segmental origin of the sacs.

Pesson (1944) described similar events in coccid embryos. The stylets invaginate into the head forming their separate sacs, while distally they remain in a common sac.

In thrips (Heming, 1980), the mandibular sheath is formed by walls of the labrum and maxillary stipes. The maxillary sheath develops from labral, hypopharyngeal, stipital and labial cells.

Singh (1971) described the common sheath in embryos of *O. tarandus* as being formed from the hypopharyngeal wing and an extension of the maxillary plate. The invaginating stylets form the separate sacs, but Singh (1971) did not mention from which segments they come.

In *M. fascifrons* embryos, as the sides of the head capsule descend ventrally to cover the mandibular and maxillary bases, and as the stylet bases and hypopharnyx shift cephalad into the head, the stylet sheaths arise. The stylets bases sinking back into the head, pull with them surrounding ectoderm from their pleural and sternal regions to form their separate sacs. The common sheath results as ventral margins of the head capsule descend ventrally and as the hypopharynx shifts cephalad. With juxtaposition of these parts and secretion by the epidermal cells of cuticular membrane, the sheaths form.

Stylet levers. – The evolution of thin, piercing stylets within the head capsule resulted in the loss of articulation of the mandibles and maxillae with the head capsule and the leverage this provided during feeding. New structures, the levers, evolved to provide the necessary leverage although not all hemipterans have levers. Rieger (1976) felt that they were lost during evolution of such species and that their role was transferred to other structures. Cobben (1978) believed that some heteropterans did not require levers due to their feeding habits.

Snodgrass (1938), Parsons (1964) and Hamilton (1981) have discussed the formation and evolution of levers.

Snodgrass (1938), in his discussion of the mandibular plate, also described formation of the mandibular lever. He did not call them levers, but 'mandibular protractor arms', and described them as:

"proximal extensions of the lateral walls of the mandibular bases, and

> represent the same areas of the mandibles as those of biting insects on which the hypopharyngeal muscles are attached" (Snodgrass, 1938)

This tied in with his hypothesis that the mandibular or loral plate is an expanded portion of the hypopharynx.

Parsons (1964) agreed with Snodgrass that the mandibular plate was hypopharyngeal. She hypothesized that the levers formed from a fold lying between the lamina maxillaris (=maxillary plate) and hypopharynx. Since she considered the lamina maxillaris to be genal, the lever was therefore 'sub-genal' in origin. The cavity between the lamina maxillaris and hypopharynx Parsons called the atrial cavity. The maxillary lever is formed from walls of this cavity towards its distal end. She considered both levers to be secondary, non-appendicular structures.

Hamilton (1981) described the mandibular plate as being genal and the mandibular lever, or 'pillar', also as genal, and therefore non-appendicular. He cited Newcomer's (1948) work with *O. fasciatus* embryos as providing evidence for this but did not show how it did so. According to Hamilton (1981), the maxillary lever is appendicular since it is formed from a diverticulum of the setal sac, which is stipital in origin.

Embryologically, three studies describe formation of levers in hemipterans (Pesson, 1944; Newcomer, 1948; Singh, 1971), and one in thysanopterans (Heming, 1980).

Pesson (1944) concluded from his study of coccids that

> "les leviers articulaires des stylets sont des formations secondaires, pouvant etre considerees comme des pleurites. L'apophyse dorso-ventrale...est comparable, par ses rapports anatomiques, a la suture subgenale, des autres Pterygotes.".

Parsons (1964) used this evidence to support her hypotheses on the origin of the levers.

Newcomer (1948) described formation of the levers in *O. fasciatus* embryos differently:

> "The mandibular lever is secreted by the walls of the mandibular setal sac after hatching...[while] the maxillary lever is elaborated by a special diverticulum of the maxillary setal sac.".

Heming (1980) found in thrips embryos that the levers are secreted "from the walls of their respective sheaths". Therefore, the mandibular lever is labral and the maxillary lever stipital. The mandibular lever is thus non-appendicular and the maxillary, appendicular in accord with Hamilton's (1981) hypothesis.

Singh (1971) did not describe lever formation in *O. tarandus* embryos since they develop after hatching.

In embryos of *M. fascifrons*, lever development is as described by Newcomer (1948) for those of *O. fasciatus*, except that in the latter the cells secrete precuticular material which likely sclerotizes as the insect hatches, while in the former the levers are fully formed. In *M. fascifrons*, the mandibular lever is genal in origin, and the maxillary lever is, as in thrips, stipital.

The absence of the mandibular plate in thrips accounts for the difference in origin of the mandibular lever in thrips and hemipterans. In each, the structure nearest the mandible (mandibular plate in Hemiptera, and labrum in Thysanoptera) contributes to the formation of the lever.

The difference between coccids and other hemipterans may be real or due to misinterpretation by Pesson (1944) of the origin of the two external plates and therefore of the levers.

7.4 Mandibular Plates

The mandibular and maxillary plates are the most controversial structures of the hemipteran head. While origin of the maxillary plate is fairly well agreed upon, the origin of the mandibular plate is still unclear, and has generated much discussion (Snodgrass, 1938; Pesson, 1944; Parsons, 1964, 1974; Puchkova, 1970; Hamilton, 1981).

The plates have been described as clypeal (Evans, 1938; Spooner, 1938), hypopharyngeal (Snodgrass, 1938; Duporte, 1962; Parsons 1964, 1974), mandibular (Heslop-Harrison, 1956; Singh, 1971), or genal (Puchkova, 1970; Hamilton, 1981). Parsons (1974) provided a comprehensive review of the various theories and evaluated each. She favored the hypopharyngeal theory since, according to her, it is the simplest, although she also agreed that the genal-subgenal theory had good support. In the most recent paper on the subject, Hamilton (1981) favored the genal theory, although his evidence is not made entirely clear.

Embryological studies have not helped a great deal in solving this controversy. The antennae of the embryo tend to obscure the area in question, and due to the juxtaposition of parts, interpretation of histological studies is difficult.

Authors of the main studies (Muir and Kershaw, 1911b, 1912; Pesson, 1944; Newcomer, 1948; Singh, 1971) came to different conclusions.

Muir and Kershaw (1911b) found that the plates did not belong to the mandibular segment but were "lateral developments of the clypeal region". Pesson (1944) described them as forming from "replis primordiaux" which "semblent correspondie aux regions pleurals des segments gnathaux". Newcomer (1948) thought they were of dual origin: part from the head surface and part from the mandibular and maxillary segments. Singh (1971) described them as forming from an "outpouching of the ectodermal wall of the mandibular appendage at its latero-basal portion" and therefore of mandibular origin.

In embryos of *M. fascifrons*, I have never observed mandibular anlagen subdividing or forming an 'outpouching'. This is readily evident by observing 40–45% TDT embryos by SEM (Figs. 24, 25, 84). Sections show that the plate develops as a ventral growth o[illegible]ead capsule from the gena (Figs. 99, 100). By comparing Singh's (1971) microgr[illegible]with mine of *M. fascifrons*, I conclude that the plate forms the same way in both embryos.

The mandibular plate in *M. fascifrons* is genal in origin, in agreement with the hypotheses of Puchkova (1970) and Hamilton (1981). I believe that if sectioned material of other hemipterans is reevaluated and SEM studies done, that the plate would prove to be genal in origin in these as well.

7.5 Maxillary Plate

The origin of the maxillary plate was, at one time, also controversial. However, it is now generally accepted that it is at least partially maxillary in origin.

Heymons (1899), Muir and Kershaw (1911b, 1912) and Newcomer (1948) all described the subdivision of each maxillary appendage into inner and outer lobes early in embryogenesis. Pesson (1944) disputed this, stating that this observation was an artifact and that the plate was formed from pleura of the gnathal segment. Parsons (1964) accepted Pesson's view and used it to substantiate her hypothesis on the evolution of the hemipteran cranium. Puchkova (1970) also thought the maxillary plate to be genal.

Heming's (1980) recent study on embryos of thrips, and my own on *M. fascifrons* confirm earlier workers' opinion that the maxillary appendages subdivide. In *M. fascifrons*, the outer lobe merges with the gena and the limits of the maxillary portion are obscured. Its upper region may be the point were the maxillary pore sensilla develop. Singh (1971) described the plate as forming as an outpouching of each appendage, but it is likely that SEM study would reveal that these anlagen develop as in *M. fascifrons* embryos.

7.6 Hypopharynx and Salivary Pump

Evolution of a piercing and sucking feeding mechanism necessitated the reshaping of the salivarium into a pumping device to deliver saliva into the salivary canal of the apposed maxillary stylets.

Muir and Kershaw (1911b) described the salivary pump as forming from the common afferent duct and Snodgrass (1938) as the modified salivarium of biting and chewing insects.

Parsons (1963), describing its evolution, felt that its anterior walls were hypopharyngeal and its posterior wall formed from the base of the prementum. In Stages 1 and 2, the salivarium remained like that of biting and chewing insects. However, by Stage 3, its sides had fused laterally. The common salivary duct formed the afferent orifice of the pump, and the efferent duct formed secondarily from a fold in the hypopharynx in front of the pump. In embryos of *M. fascifrons* the salivary pump forms from an invagination of surface ectoderm on the venter of the labial segment. A rosette of cells retreats from the surface and secretes the cuticle of the syringe and piston of the salivary syringe. As with the stylets, the cells assume the shape of the cylinder and piston, and then secrete cuticle.

Embryological evidence supports Parsons' hypothesis, except for differences in interpretation of which segments contribute to its formation. According to Parsons (1963) the piston is formed from the hypopharynx. In embryos of *O. fasciatus*, Newcomer (1948) stated that the salivary pump forms from "an invagination upon the combined venters of the intercalary, mandibular and first maxillary segments near the level of the first maxillae.", while the hypopharynx forms from the venter of the mandibular and intercalary segments. Singh (1971) reported the hypopharynx of *O. tarandus* embryos to form from the the venters of the antennal, mandibular and part of the maxillary segments. The salivary pump develops from an invagination on the venter of the maxillary and labial segments.

In embryos of *M. fascifrons*, the anterior part of the hypopharynx, including the free lobe, forms from the venters of the intercalary and mandibular segments.

7.7 Labium

The labium or rostrum of hemipterans is homologous with the fused second maxillae of biting and chewing insects. During evolution of the group, it has become considerably simplified compared to that of other insects. It is difficult to homologize the segments of the hemipteran labium with those of the labium of more specialized insects. It develops from two anlagen behind the first maxillae, which elongate and fuse mesially during subsequent development, to only superficially resemble the labium of biting and chewing insects. Only a few morphologists (Matsuda, 1965) and embryologists (Heymons, 1899) have attempted to homologize the labial segments. According to Heymons (1899),

> "die Stammglieder durften wahrscheinlich die beiden Basalglieder (7. und 2. Glied) des Labiums gebildet haben, welche wahrscheinlich dem Submentum und Mentum an der Unterlippe anderer Insekten entsprechen. Aus den Laden sind dagegen die beiden distalen. Endglieder des Rhynchotenlabiums hervorgegangen, welche sich mit der Subgalea und den untereinander verwachsenen Laden vergleichen lassen durften.".

Matsuda (1965) felt that the first segment was premental and that the distal ones represented the fused labial palpi. He admitted that there was no evidence for this other than comparison of labia with representatives of such groups as the Siphonaptera and Diptera.

Singh (1971) accepted Heymons' views. Singh described four segments, while most workers have decribed three. Apparently, he considered the lip of the 'first' segment of other workers to be the base of segment one, and the rest of the 'first' segment to be segment two.

In thrips, palpi are still present on the final segment of the labium (Heming, 1978). If it is assumed that the palpi became reduced and ultimately lost, rather than enlarged and fused (as Matsuda (1965) believed), then the ultimate segment of the labium of thrips and homopterans may be considered homologous. It may represent the fused glossae and paraglossae (Heming, 1978). The segments of a 3-segmented labium would thus be homologous with the prementum and postmentum of other insects, as Heymons (1899) stated, although his terminology differed.

This is pure speculation and, unless an intermediate stage is found between the hemipteran and thysanopteran conditions, it must remain so.

7.8 Tentorium

The hemipteran tentorium is often absent or reduced. It is completely absent in all known Heteroptera, but varies in form in known Homoptera, in which members of more advanced families have a reduced tentorium. Puchkova (1970) felt that this resulted from loss of the gnawing function of the mouthparts.

Matsuda (1965) discussed the evolution of the insect tentorium, and Singh (1971) and Hamilton (1981), emphasized the amount of variation that exists.

The anterior tentorial pits are used to delineate the level of the mouth (Parsons, 1964) and the position of the frons and clypeus (Snodgrass, 1935; Duporte, 1962). Duporte (1962) disagreed with Snodgrass' use of the pits to mark the beginning of the epistomal suture, pointing out that their position was not constant. Duporte felt that as the large frontal plate enlarged during the course of evolutionary change, the position of the anterior tentorial pits migrated dorsally. As homopterans evolved, the tentorium was reduced and the anterior arms lost their connections with the posterior tentorium (Hamilton, 1981). The anterior and dorsal tentoria were displaced dorsally, and muscles normally attached to them attached to the head capsule.

In *M. fascifrons*, a more derived cicadellid (Evans, 1947), the tentorium consists of a transverse bar or posterior tentorium, and separate anterior tentorial arms, from each of which extends a dorsal arm.

The posterior tentorial bar runs from the lateral edge of one hypopharyngeal wing to the other, and is a point of attachment for some of the pharyngeal muscles. The anterior and dorsal arms are displaced dorsally and the ventral tip of each anterior arm articulates with the tip of the antennifer. The extrinsic antennal muscles still originate on the dorsal arms, but the origins of the mandibular retractors have shifted to the cranium ventrad of the antennae.

7.9 Cibarium

A new structure highly characteristic of hemipteroids is the powerful sucking, or food, pump. In more primitive insects, the cibarium opens to the exterior anterior to the 'true mouth', and is considered the 'functional mouth' (Snodgrass, 1935). In sucking insects, it is closed off laterally on either side, forming a closed cavity that functions as a sucking pump.

Snodgrass (1938) and Parsons (1964) described formation of the pump during evolution similarly. The hypopharynx and epipharynx become closely opposed to each other and join on either side. The hypopharynx forms the floor of the pump, and Snodgrass (1938) and Parsons (1964) considered it to be homologous to the sitophore of other insects. The epipharynx forms the roof of the pump and inserted into it are powerful muscles dilating the pump. Greater development of these muscles resulted in development of an enlarged clypeus.

Parsons (1964) described formation of the pump during evolution as occurring through a series of stages. In Stage 1, the clypeus enlarges, and in Stage 2, the hypopharynx expands on either side to form the mandibular plates. Later, in Stage 3, the cibarium closes off laterally on either side by union of the epipharyngeal and anterior mandibular (hypopharyngeal) walls. The sucking pump that is formed is closed proximally, but ventrally is only apposed, with the tip of the hypopharynx forming a free lobe.

Hamilton (1981) agreed with Snodgrass (1927) and Parsons (1964), but considered the cibarial muscles to be fronto-pharyngeal muscles whose insertions had descended onto the epipharyngeal ridge. Thus, according to him, the first stage in formation of the pump was enlargement of the frons, not clypeus. During the third stage, the sucking pump is formed by invagination of the cibarium. Presumably this resulted in lateral fusion of the epipharynx and hypopharynx, although he did not state this.

Embryological evidence supports the hypotheses of Snodgrass (1927) and Parsons (1964). The clypeo-labrum which begins as a lobe above the stomodeum unfolds caudally and the other appendages shift cephalad. After the mandibular or loral plates form, the lateral walls of the hypopharynx and epipharynx fuse to form the sucking pump (Pesson, 1944; Newcomer, 1948; Singh, 1971; *M. fascifrons*).

7.10 Entognathy

Parsons (1964) considered hemipterans to be entognathous because their principal mouthpart structures are concealed by the rest of the head. Parsons hypothesized that development of entognathy began in Stage 2 with development of the 'parietal lobes' and hence concealment of stylet bases. In Stage 4, the condition is consolidated by fusion of the parietal lobes and hypopharyngeal walls, to close the atrial cavity (Parsons, 1964).

Hamilton (1981) described formation of the opisthognathous mouthcone as "a reduction in size of the preoral structures: the labrum, labium and stylets.".

During embryogenesis, development of entognathy (opisthognathy) occurs in most hemipterans around the time of katatrepsis. The clypeo-labrum unfolds caudally, the stylet bases elongate and sink into the head, and the maxillary lobes and decending genal lobes form the outer plates (Pesson, 1944; Newcomer, 1948; Singh, 1971; *M. fascifrons*). The outer plates fuse to each other to form the sides of the mouthcone and internally fuse to the hypopharynx to form the cibarium and stylet sacs. Similar events, except for formation of mandibular plates, occur in thrips embryos (Heming, 1980).

7.11 Conclusion: Evolution of the Hemipteran Head

The development and alteration of the structures discussed above that occured during evolution resulted in the development of the very specialized piercing and sucking mouthparts of hemipteroid insects.

As was pointed out by Heming (1980)

> "comparison of gnathal development in embryos of investigated species of Psocoptera (Goss, 1953) Phthiraptera (Scholzel, 1937, Young, 1953), Thysanoptera, Homoptera, (Pesson, '44; Leggett, in preparation), and Heteroptera; (Newcomer, '48) provides support for current ideas on evolutionary relationships of these taxa and suggests ways in which their

diverse mouthparts might have evolved ".

He then provided a summary of events which may have occurred during evolution of the various kinds of hemipteran mouthparts.

Hamilton (1981) used comparison of head structure of representative species of these groups and results of previous embryological studies to propose a hypothetical series of stages which led to the evolution of the hemipteran head. He felt that his hypothesis " greatly reduces the supposed evolutionary gap between mandibulate and rhynchotan head structures" and was a more simplified explanation of what actually occurred. He was concerned primarily with external head structures and considered the formation of stylet sacs, cibarium and salivarium only superficially. While more accurate than previous theories, it is at times too simplified. Although, Parsons' (1964) theory is the most complete it is unfortunately inaccurate due to her reliance on Pesson's (1944) embryological data It is also weak because she did not relate her stages to evolutionary relationships existing within the Condylognathida.

Other scientists have speculated on the evolution of the hemipteran cranium, but their hypotheses are less detailed than either Parsons'(1964) or Hamilton's (1981). Table 9 summarizes existing theories.

I feel that a combination of existing theories would provide a more complete hypothesis on how the hemipteran mouthparts and cranium evolved. I developed my ideas by comparing adult and larval head structures and embryonic development of representatives of the various groups and from homologies that I found in my study of mouthpart embryogenesis in *M. fascifrons*.

As with any hypothesis assumptions had to be made. Unless it was readily obvious that the data of a study were incorrect, I had to assume that existing studies and reviews were correct. Another limitation was the lack of information on mouthpart structures of key acercaridans, especially the psocids. It was also difficult to construct the ground plan of an ancestral head when there is so little information or agreement on what are the primitive taxa in each order of Acercarida. Finally, more information is required on mouthpart embryogenesis in representative Psocodida.

The ancestor of the Acercaridans probably had a primitive pterygote body plan similar to that of modern Blattodea. Comparison of the muscles of primitive pterygotes with those of the least specialized extant acercaridans, the psocids, shows the blattods

TABLE 9. Comparison of theories on evolution of the Hemipteran cranium. A=ancestor; ant.=anterior; *afp*=anterior tentorial pits; *C*=clypeus; *Cib*=cibarium; *epi*=epstomium; *H*=hypopharynx; *La*=labium; *Md*=mandible; *Mx*=maxilla; *pl*=parietal lobe=lamina maxillaris; post.=posterior. Numbers in bold-face indicate hypothetical stages from which groups below it are derived.

EVANS 1938	PARSONS 1964	PUCHKOVA 1970	HEMING 1980	HAMILTON 1981
A=primitive pterygote similar to Mecoptera larva with pair ocelli near post.corners *C* *C* partly subdivided **1a**.*Md*-stylets with only ant.articulation; *atp* on inner corner of *C* **2a**.epistomal suture & antennal ledges shifted post. **b**.backward development of *C*; reduced frons **c**.*Md* abductors and adductors become pro- & retractors **3a**.epistomal suture disappears **b**.*C*-lobes elongate, cut off frons at base by backward extension of *C* **c**.transverse suture appears associated with *C* **d**.*C*-lobes attach to sides of *H* **4a**.transverse suture completely separates ante- & postclypeus **b**.*C* fuses with ant. margins of genae **c**.loss of epistomal suture **d**.postfrontal and frontal sutures lose separate identity	A=primitive pterygote similar to Machilidae **1a**.lateral part cranium descends to level of *atp* **b**.*C*-labral region elongates **c**.frons small; frontogenal sulcus short **d**.subgenal sulcus pronounced **e**.*Md* & *Mx* stylet-like, constricted at base **2a**.genal & postgenal regions descend ventrally (*pl*) **b**.ant.-lateral walls of *H* expand between *pl* & *C* (lora) **c**.cavity between *H* & *pl* holds stylet bases **3a**.*Cib* & salivarium closed laterally **b**.salivary pump forms from union of ant. & post.walls salivarium **4a**.atrial cavity closes laterally; cavity partly subdivides **b**.levers form from endoskeletal walls **c**.atrial cavity reduced; retained only around stylet bases **Homoptera**-tentorium may be reduced **Hemiptera**-head capsule closes posteriorly -tentorium lost	A=mandibulate insect **a**.formation of cluster of mouth appendages **b**.formation of sharp stylets **c**.stylets elongate **d**.*Md* & *Mx* reduced and fused with remains of *H* and gena **e**.*Md* lose gnawing function leading to reduced tentorium **f**.*epi* surface & *H* fuse to form cibarium **g**.caudad displacement of acral complex **h**.*C* enlarges, fuses with frons **i**.*Md*-plates form from genal lobes	A=biting-chewing insect with galeae fused to stipes; laciniae invaginate **Psocoptera, Amblycerans** -like ancestor, but with specialized *H* **Ischocerans** -*Mx*-palpi suppressed -*Mx* and labrum fuse **Rynchoptherines** -head produced into a snout -*Md* terminal, turned outward **Anoplurans** -*H* & labium form trophic sacs & stylets **A of Thrips + Hemiptera** **a**.small paired *Md* **b**.short lacinial style **c**.weak cibarial pump **d**.palpi prominent **A of Thysanoptera** **a**.right *Md* degenerates **b**.left *Md* adapted for punching **c**.labrum encloses lacinial fascicle **d**.laciniae with food canal only **A of Hemiptera** **a**.*Md* & *Mx* stylets form **b***La* enclosed stylets **c**.palpi lost **d**.cibarial & salivary pumps develop **e**.loral lobes form	**1a**.fronto-pharyngeal muscles enlarge, shift to mouth region **b**.frons enlarges **c**.*Mx*-lobes divide to produce lacinial lobes connected to stipes only at base **Psocoptera** -formation of "mortar and pestle" apparatus **2a**.labral, labial apices narrow; *Md*, *Mx* reduced to stylets **b**.stylet bases invaginate **c**.stylet levers form **d**.*H* develops wing-like invaginations **e**.palpi reduced **Thysanoptera** -asymmetric mouthparts **3a**.labium forms rostrum **b**.palpi lost **c**.*Cib*-pump forms from invagination of *Cib* **d**.labrum reduced **e**.stylet levers attain articulating joints **Homoptera** -enlarged foramen magnum -enlarged loral sutures **Hemiptera** -develop. of gular area -Y-shaped or triangular "genal pillars" -frons reduced

to be most similar (Matsuda, 1965).

A major modification occurring in the head of this first stage hemipteroid was the development of a long, thin lacinia only loosely connected to the stipes. The function of this lacinia would be limited to assisting in the scooping of food forward into the cibarium and an alternate, more effective method to transport food to the cibarium would have to develop. The simplest means of accomplishing this was through development of a stronger pump with stronger cibarial muscles. Initially, this pump was weakly developed since other mouthparts still provided the principal means for transporting food to the cibarium. As the cibarial muscles enlarged, the clypeus expanded dorsally to accomodate them and the frons became reduced. Evidence presented earlier supports the hypothesis that the pump muscles are cibarial and not fronto-pharyngeal as Hamilton (1981) described. Such development of the cibarium into a sucking pump is credible as Snodgrass (1952) described the cibarium of *Periplaneta americana* acting as a sucking pump during drinking (p.301).

The role of the hypopharynx would alter as a sucking pump developed, and it and its associated sclerites and muscles would become reduced. The posterior lingual sclerites of the cockroach, *P. americana* unite proximally around the salivary duct and form a fulcrum that aids in movement of the hypopharynx (Snodgrass, 1952). As the functional role of the hypopharynx is reduced the need for such a fulcrum is lost. This resulted in the two united arms of the lingual sclerites separating to form two apodemal arms – the hypopharyngeal wings. In *P. americana*, the anterior sclerite or hypopharyngeal suspensoria has two sets of arms: the oral and the mandibular arms (Snodgrass, 1952). The mandibular arms act as points of insertion for the mandibular muscles and for muscles operating the salivarium. The mandibular arms appear to have been lost during evolution although what precipitated this loss is unclear. As the mandibular arms were lost, their associated muscles were either lost or attached to different structures.

Such might have been the mouthparts of the stem species of the Psocodida and Condylgnathida. Members of the latter lineage specialized more extensively.

Changes described above continued during the evolution of each lineage. The lacinia detached completely from the stipes and remained connected to it only by a set of muscles as in the heads of modern psocids. The cibarium and clypeus develops furthur and the cibarial muscles simultaneously enlarged. As the need for their sensory role was reduced (perhaps by development of replacement sensilla on the labial apex), the labial palpi become reduced . The lingual sclerites of the hypopharynx developed into ovoid structures with apodemal arms on which the muscles of the salivarium originated. These muscles previously originated on the mandibular arms which are no longer found in psocodidan insects. A number of new structures developed as well. The epipharyngeal wall of the cibarium and the hypopharynx develop into a 'mortar and pestle' apparatus which in psocids is thought to grind food (Matsuda, 1965). The epipharynx developed a ridge which fitted into a groove on the sitophore of the hypopharynx as in modern psocids. The labium also developed a groove that, along with the apposed hypopharynx formed the salivarium.

From this psocodidan ancestor, a number of additional modifications led to development of psocopteran insects and to a pthirapteran ancestor.

The mouthparts of Psocoptera result from only minor changes to the ground plan of the stem species. The lacinia of psocopterans apparently acts as a support for the insect to brace itself as the mandibles scrape the food into the cibarium (Matsuda, 1965). The galeae, no longer playing a role in feeding, are either reduced or lost. The clypeus and cibarial muscles are enlarged presumably to suck up the material the mandibles scrape into the cibarial cavity. The strongly developed mortar and pestle apparatus grinds the detritus and fungus which the insects eat. The muscles of psocopterans resemble those of blattods for the most part (Matsuda, 1965) with certain muscles being lost if their associated structures are lost or reduced.

The major change in pthirapterans is the development of a prognathous head whose development Matsuda (1965) felt was a result of the insects becoming ectoparasitic and therefore more dorso-ventrally flattened. Symmons (1952) invisioned prognathy as evolving either by elongation of the neck region or by extension of the postgenal region of the head and she felt that both might have played a role.

The development of prognathy led to a number of other changes. The mandibles though still biting and chewing now had a horizontal swing. The clypeus became dorsal and the labrum rotated such that it became more ventral. The tentorium was reduced and ocelli lost. Such changes resulted in an insect closely ressembling the modern amblycerans.

Furthur reduction of a number of structures and increased development of the cranial sclerites led to the appearence of the anoplurans. Although ischnocerans are usually placed in the Mallophaga, Boudreaux (1979) felt that this was an artificial grouping and that they are more closely related to anoplurans. I have adopted his scheme.

The main steps which led to development of the stem species of Anoplura were a shift in the mandibles to articulate on a vertical axis and continued reduction of the tentorium and maxillary palpi. Both these changes reflect change in feeding habits of these insects.

In ischnocerans, there was increased development of the mortar and pestle apparatus and development of a new structure, the 'pulvinus' considered to be an enlargement of the clypeo-labral suture.

The lipognathean group has two suborders, Rhynchophthirina and Siphunculata. Members of these lineages evolved from an anopluran ancestor by continued reduction of certain structures, by fusion of others and by modification of the head sclerites to form a snout.

Rhynchopthirines developed a long snout, through prolongation of the clypeus, the mandibles inserting at the tip of this structure (Weber and Wenk, 1969). Ferris (1931) felt that this snout was an adaptation to feeding on elephants. Fusion of other structures such as the galeae and stipites very likely resulted from lengthening of the head.

Lice of the Siphunculata represent an example of extreme reduction and modification of head structures for ectoparasitic life. The tentorium is completely absent and both the mandibles and maxillae are reduced. The hypopharynx and labium have elongated to form long thin stylets and parts of the labium have invaginated to form a trophic sac in which these stylets are lodged. These changes reflect the assumption of a blood-sucking mode of life. Mouthpart structures and phylogeny in these taxa need to be studied more fully (Kim and Ludwig, 1978).

The stem species of the Condylgnathida gave rise to lineages whose members began to exploit the internal fluids of plants and, in doing so, whose mouthparts were modified in a manner different from those of pscodidans.

Major changes were increased development of the clypeus, reduction of the frons and hypopharynx, evolution of the mandibles and maxillary lacinia into stylet-like structures, and anterior-posterior flattening of the head.

A principal change was the modification of the mandibles into thin stylets. Initially, they may have maintained their original articulations with the head capsule but as they became progressively thinner and longer they lost all articulation with the sides of the head capsule.

At this stage of evolution the clypeus was still weakly developed. The labrum was reduced as its role in food intake was reduced due to development of the sucking cibarial chamber. The hypopharynx ceased to move relative to the other mouthparts and, as a result its sclerites become reduced. The apodemal arms of the lingual sclerites remained as they provide points of origin for the salivary dilators. The hypopharyngeal suspensoria were reduced and frontal muscles normally attaching to the oral arm transfer to the prepharynx. The labrum, glossae, paraglossae and labial palpi also became smaller.

Such an insect may have used its mandibles to lacerate plant tissue, injecting its saliva to liquify its food material, and then using its cibarial pump to suck this fluid into its stomach.

When the mandibles lost their articulation with the head capsule, their bases became internal and the external sclerites of the head came together and fused.

In the stem thysanopterans, the stipites fused with the labrum and labium and pointed rostrum resulted (Heming 1978, 1980). The mandible required a point of articulation with the head capsule and this developed from a thickening at the base of the labro-stipital suture. This fusion of plates and the hypopharynx and its fulturae, (remnants of the lingula sclerites), contributed to formation of the stylet-sheaths. These sheaths, new structures found only in hemipteroid insects, evolved directly as a result of the internalization of the stylet bases and the fusion of the external sclerites. In addition, the lateral, epipharyngeal walls of the labrum fused with the anterior wall of the hypopharynx to form a closed, elastic cibarium. Another modification that occurred was the loss of the right mandible which is found in the embryo but which is lost before katatrepsis (Heming, 1980). Because of the way the mouthcone developed the stylets were pushed together, distally. In thysanopterans, the lacinal stylets coadapt to each other to form the food canal, the proximal end of which opens near the cibarial chamber (Heming, 1978). These insects are true fluid feeders although their mouthparts are not as highly developed as in hemipterans.

Hemipteran insects evolved from a condylognathidan ancestor in a slightly different manner. As with thrips, the bases of both sets of stylets become internal. In hemipterans, however, the stipites did not fuse with the labrum anterolaterally. Instead, the genal area next to the clypeus descended between the stipites and labrum to form the mandibular or loral plates, with a mandibular lever forming between the maxillary–genal sulci on each side. The stylets sheaths of hemipterans resulted from the juxtaposition of genae, stipites and hypopharyngeal wings and by internalization of the stylet bases. The labrum in homopterans was reduced still further to a small triangular flap, (in some heteropterans, however, it is relatively much larger). Both maxillary and labial palpi were suppressed or lost and the paraglossa and glossa fused. Although homologies of the hemipteran labium are unknown, I support Heymons'(1899) view that the first segment is the postmentum, the second, the prementum and the last the fused glossae and paraglossae. The labium developed an anterior longitudinal groove which encircles the stylets as apposed to the thysanopteran situation in which the labrum guides the stylets (Heming, 1978).

Homopterans are generally less specialized than heteropterans although there was a tendency for reduction of the tentorium and enlargement of the clypeus and cibarial muscles as the taxon evolved (Evans, 1975 and Hamilton, 1981) Heteropterans developed a gular area by extending the neck region, but the tentorium in these insects was lost completely and the labium developed an additional segment for a total of four (Parsons, 1964).

These I believe are some of the stages that led to formation of the piercing and sucking mouthparts of hemipteroid insects. The changes that occurred were, as Hamilton (1981) perceived not that complicated and were structural responses to changes in food preferences of these insects. Perhaps, the insects fed in litter then exploited the newly evolved leafy plants, where some continued to bite and chew and others began to pierce and suck.

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