THE ANATOMY, HISTOLOGY, AND CYTOLOGY OF THE GREENBUG, SCHIZAPHIS GRAMINUM (RONDANI), IN RELATION TO FACTORS RESPONSIBLE FOR RESISTANCE IN BARLEY AND WHEAT

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PREFACE

Recent trends in applied research have increased the interest of physiologists and toxicologists in the internal morphology of insect pests, particularly the Homoptera. The realization of the devastating effects on different crops by aphids and their capacity to build up a huge population in a short period has been challenging in present times. Due to their small size, they seem to be the only important group of insects which have failed to receive attention pertaining to such studies.

In connection with studies to determine the nature of resistance in barley and wheat to the greenbug, Schizaphis graminum (Rondani), it was found that there was very little available information on the internal morphology of this aphid. This information becomes essential before the overall research program on the nature of resistance in barley and wheat can be completed.

Thus the present work embodies information on the anatomy, histology, and cytology of the greenbug. Each chapter of the thesis represents an original research paper written in the style of entomological journals to which it will be presented for publication.

I wish to take this opportunity of recording my deep sense of gratitude to my major adviser, Dr. Harvey L. Chada, Professor of Entomology, Oklahoma State University and Investigations Leader, Grain and Forage Research Branch, Entomology Research Division, U. S. Department of Agriculture, and Sponsoring Scientist of PL 480 programme on sorghum and millet insects, executed in India, for his competent guidance, unstinting help, invaluable suggestions and providing all possible facilities throughout the course of this work.

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TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

Plate Page

INTRODUCTION

Though aphids are considered as one of the most important pests to our agricultural crops, very little is known about the exact nature of damage they do to plants. During the preceding years spectacular success was obtained in their control by the application of newer types of insecticides. But it proved to be a very expensive way of controlling aphids, since they are capable of multiplying to enormous numbers parthenogenetically within a short period of time, which requires repeated application of insecticides. Furthermore, the development of resistance to insecticides has been reported in quite a number of insects. This state of affairs diverted the attention towards the production of resistant varieties of crop plants by modern plant breeding methods. Concerted efforts for a number of years led to the development of wheat and barley varieties resistant to the greenbug, Schizaphis graminum (Rondani). The resistant wheat, Dickinson Selection 28A, maintained resistance and was used as the source of resistant germ plasm in breeding for resistance, until recently, when its resistance was lost due to the appearance of a new biotype of Schizaphis graminum. The repercussions on account of this loss stimulated interest in the investigation of factors responsible for the resistance and susceptibility in wheat and barley plants to the greenbug.

Determination of factors such as these necessitates thorough knowledge of the external and internal morphology, feeding habits, nutritional requirements and ecological and physiological responses of the greenbug. Except for its taxonomic determination, very little work has been done on other aspects. Practically no information is available on the anatomy, histology and cytology or the nutritional requirements of the greenbug.

Hence, the present work was undertaken to obtain information about the structure of mouth parts, stylet penetration and suction of food material from plant tissues, form and structure of salivary glands, the act of salivation, nature of damage to leaf tissues by salivary secretion, role of different regions of alimentary tract concerning the physiology of secretion, assimilation and excretion, the process of excretion in relation to continuous feeding and the details of the nervous system.

MOUTH PARTS AND FEEDING MECHANISM

The mechanism of feeding in aphids has attracted attention of quite a large number of workers. A fairly large volume of literature exists on the mode of feeding of different species of aphids, but there is much less on the greenbug, Schizaphis graminum (Rond.). Important references on other aphids include that of Davidson (1923) who made biological studies of Aphis rumicis Linn. He mentions that the food of this aphid is the cell sap derived from various cells, especially the vascular bundles. The phloem is particularly sought after, but other tissues, such as the cortex and mesophyll of the leaf, may also be tapped for nourishment. Horsfall (1923) published on the effect of feeding punctures made by certain aphids in plant tissues. Smith (1926) made a comparative study of the feeding methods of certain Hemiptera and stated that aphids usually penetrate intercellularly, but Macrosiphum solanifolii Ashm. often has an intracellular stylet tract. Tate (1937) worked on a number of aphids with regard to the mode of penetration of stylets and the formation of the stylet sheath. He is of the opinion that the penetration is effected intercellularly and the stylets generally try to reach the phloem tissues. Roberts (1940), in Myzus persicae (Sulz.), Myzus circumflexus Buckt., and Macrosiphum gei Koch., found that the penetration of stylets is both

intercellular and intracellular, and the aphids mostly feed on phloem tissues. Chatters and Schlehuber (1951) reported the feeding mechanism of Toxoptera graminum (Rond.) on Hordeum (barley), Avena (oat), and Triticum (wheat) and found that the stylets are specifically directed to reach the phloem tissues. They further mention that the injection of saliva, and not the uptake of food, is the main cause of tissue damage. Balch (1952) found the wooly aphid, Adelges piceae (Ratz.), feeding on parenchymatous tissues. Bradley (1956) while studying the effects of the stylet penetration mentions that sometimes the stylets remained motionless in a cell and the aphid appeared to be feeding. If the tip of the proboscis was observed during this time, a variation caused by a pumping-like action within the proboscis could be seen. This was probably the pharyngeal pump at work, and when this vibration continued for 3 minutes, the cell became plasmolyzed. Mittler (1957) noticed the uptake of phloem sap by Tuberolachnus salignus (Gmelin), where the stylets passed inter- and intracellularly through the cortical tissues of S. fragilis stems, and ended in newly differentiated phloem sieve tubes lying adjacent to the cambium. Miles (1958), from his experiments on the chemoreception internal to the stylet food canal of Oncopeltus fasciatus (Dallas) and Dindymus versicolor H. Sch., arrived at the conclusion that these bugs secrete saliva on the substrate before feeding. The saliva is then drawn up the stylet food canal where it is brought in contact with gustatory sensillae. Both species could discriminate between different liquids sucked up into the

canal. Bradley, Sylvester, and Wade (1962) examined the stylet movement of Myzus persicae and reported that the movements most easily seen were rapid alternate oscillations at the stylet tips and a back and forth swinging of the entire stylets as they enter a cell. Amputation of both mandibles resulted in the maxillae alone making the swinging movements. Bradley (1962) reported that the amputated mandibles revealed conspicuous dark breaks in their central duct. At those places where the breaks occurred the duct was empty, otherwise, it was filled with a translucent material which when pulled out was found to be in the form of a thread-like structure. The sensitivity of the mandibles to chemicals suggests that they have nerves, and this thread-like structure appears to be the nerve fiber. An overall picture of the types of penetration of stylets and the feeding sites within the host plants has been given in a resume by Auclair (1963). McLean (1964) attempted to relate the depth of stylet penetration in Acyrthosiphon pisum (Harris) and Myzus persicae to the transmission efficiency of viruses by noting the length of probing time and measuring the length of stylets penetrated. McLean and Kinsey (1964) developed a technique for recording aphid feeding and salivation. They noted that when the aphid probes into the substrate and the stylets get filled with saliva or substrate liquid, an electric circuit is completed which records on the oscilloscope. The more liquid the aphid ingests or salivates, the higher the voltage is recorded. Production of stylet sheath was found related to changes in voltage recorded on the chart, but it became

apparent with further experimentation that the salivary sheath was of low electrical conductivity. In most instances, however, strong increase in voltage occurred during sheath production, but this obviously was not related to the secretion of sheath material. It appeared as though another material was being secreted or that the liquid substrate was being ingested. McLean and Kinsey (1965) while studying salivation and ingestion of aphids, feeding on artificial diets by electrically recorded curves, found that many aphids began secreting salivary sheaths as soon as the stylets entered the sucrose substrate. Distinct diverticulaein the form of bulges were noticed as the sheath was extended. Close observation of the formation of these diverticulae showed that the aphid secreted a small amount of sheath and then expanded a portion into a bulge. Kinsey and McLean (1967) further gave evidence that when the stylets of Acyrthosiphon pisum penetrate through a membrane into a sucrose solution, a salivary secretion flowing from the stylets produces an encompassing sheath within which the stylets occupy a central canal which is open.

With the exception of the reports by Chatters and Schlehuber (1951), there was little published information on the greenbug, Schizaphis graminum (Rond.), with respect to stylet movement, musculature of the mouth parts, mode of feeding, and feeding sites in plant parts. They did this work on what is now designated as biotype A. Researchers at Oklahoma State University developed wheats, barleys, and oats with resistance to this biotype. However, during the past

several years all wheats became susceptible to the greenbugs currently infesting small grains in the Southwest. Since there are no morphological differences between biotype A and the greenbugs currently infesting small grains, but the plants react differently to their feeding, the latter has been designated biotype B. These designations will be used throughout the text. The studies on mouth parts and feeding mechanism will involve both biotypes A and B.

During the summer of 1968, very heavy, damaging aphid infestations occurred in grain sorghums throughout the southwestern United States. Taxonomists have identified it as another biotype of Schizaphis graminum on the basis of available descriptions and taxonomic keys. However, it differs ecologically, morphologically, and physiologically from biotypes A and B, and it is now called biotype C. While some study by the author has been made on the mouth parts and feeding of this aphid, these data will not be included here. It is felt that further study will show this aphid to be something other than a biotype of S. graminum.

Materials and Methods

Both greenbug biotypes A and B which had been feeding continuously on susceptible Rogers barley plants for more than 48 hours were killed in such a way that death was instantaneous, and the greenbugs could not remove their stylets from the plant tissues. Various methods have been used for this purpose by different workers. Mittler

(1957) anaesthetized aphids by means of a gentle stream of carbon dioxide gas. Sorin (1966) paralyzed feeding aphids with ethyl ether gas before putting them in the fixative. Schaefers (1967) first immobilized the aphids with carbon dioxide and then placed them in F.A.A. solution. In the present study, portions of leaves with a number of feeding greenbugs were placed directly into Carnoy's fixative. An increase in the proportion of chloroform and acetic acid in making Carnoy's solution was found to produce better results. The proportions used were: ethyl alcohol 100% - 6 parts; chloroform - 4 parts; and acetic acid - 2 parts. The fixative in its changed ratio was found to be very effective, and almost 99% of the aphids were killed with the stylets intact in the leaf tissues. The aphids thus killed were fixed for 6 hours in Carnoy's solution and transferred directly to absolute alcohol, cleared in xylol, and embedded in paraffin. Both longitudinal and transverse sections were cut at 15 micron thickness. In order to shorten the whole lengthy process, cutting of sections after fixation was also tried by freeze-drying technique. No success was achieved, because while freezing the material, proper orientation could not be obtained, and hence this method was abandoned. Combinations of stains employed were Delafield's haematoxylin - acid fuchsin, Ehrlich's haematoxylin - eosin and safranin O - fast green. Best results were obtained by double staining with safranin O and fast green.

For making a study of the working of stylets, the musculature attached to it, and the inner details of the head, the specimens were

dissected in Ringer's fluid and examined. Stained whole mounts were prepared by staining the specimens with acid fuchsin, dehydrating in different grades of ethyl alcohol, and keeping in turpentine oil overnight. Turpentine oil dissolved the fat bodies completely and rendered the muscles quite distinct. Finally, the specimens were placed in clove oil for one hour and mounted in Canada balsam.

For electron microscope study of the stylets, the heads were cut off and placed in a fixative consisting of veronal acetate buffer - 5.0 ml.; 0.1 N hydrochloric acid - 5.0 ml.; deionized water - 12.5 ml.; and glutaraldehyde - 2.5 ml. The pH of the fixative can be adjusted to 7.2 or 7.4 with 0.1 N sodium hydroxide (NaOH), if necessary. The material was fixed for 3 - 4 hours at 4°C. Tissues suspended in glutaraldehyde fixative drops were subjected to osmium tetroxide vapors for one-half hour. Then the fixative was removed and the tissues were transferred directly to 25% ethyl alcohol. The dehydrating series of ethyl alcohols used were 25, 50, 70, 85, 95, and 100%. The specimen was kept in 25% ethyl alcohol for 30 minutes with one change after 15 minutes, in 100% ethyl alcohol for 45 minutes with two changes after every 15 minutes, and in the rest of the dehydrating series for 15 minutes in each. Next the material was transferred to embedding medium, consisting of methyl methacrylate (10 gms), butyl methacrylate (40 gms) and benzoyl peroxide (0.5 gm), for one hour. Fresh embedding medium was replaced after one hour, and the material was kept for 2 1/2 hours at 4°C. Finally, the material was placed in the capsules filled

with the embedding medium and properly oriented. The capsules could also be kept at room temperature. Blocks were trimmed and sections of 600 angstrons thickness were mounted on grids and examined under the electron microscope.

Results and Discussion

The mouth parts and mechanism of feeding have been described in other aphids by different workers. Earlier reports, as cited previously, in other aphids indicate that the maxillary stylets contain two longitudinal grooves running parallel throughout the entire length, and simply by close apposition form two canals which lead to the extremity of the stylets. The larger canal serves as the suction canal and is connected with the suction pump formed by the pharynx of the alimentary canal. The smaller canal is the salivary channel through which the saliva from the salivary glands is injected into the plant tissues. The salivary canal is connected with the salivary pump situated just below the salivary meatus.

In the greenbug, the mouth parts essentially consist of two mandibular and two maxillary stylets. The latter lie internal to the mandibular stylets and after emergence from the head become so closely apposed to each other as to appear a single piece. No salivary pump exists in the greenbug. The salivary meatus is formed by the fusion of the ducts from the four pairs of salivary glands. The details of the salivary meatus will be discussed in the chapter on salivary glands.

The mandibular and maxillary stylets originate from the ring-like piece of tentorium (Fig. 3, R) located close to the clypeal region of the head. Four protractor muscles arise from the inner wall of the clypeus (Figs. 1 & 3, PM), each of which is inserted at the base of each stylet. The contraction of these muscles brings about extension of the stylets outside the labium but since they seem to be weak muscles, their extending force alone would be quite insufficient to affect any piercing action into the plant tissues. It, therefore, looks obvious that for effecting any puncture in the plant tissue, a downward pressure of the head is essential. The contraction of the protractor muscles accompanied by the downward pressure of the head will then result in full extension and effective penetration of the stylets. On each of the two tentorial rings just at the place of origin of mandible and maxilla, two strong muscles, one on mandible and the other on maxilla, are inserted (Figs. 1 & 3, SM, N). They are the retractors of mandibles and maxilla, and by their size and thickness appear to be powerful muscles. These four retractor muscles originate from the tentorial bar in the proximity of the vertex (Fig. 3, TB) in two distinct groups and immediately before their insertion at the base of the stylets, bifurcate to form separate retractor muscles for each mandible and maxilla. The contraction of these retractors exerts a pulling-in-action on the stylets and effects in the immediate withdrawal of the stylets from the plant tissues without visible movement of the head. The mandibles, besides having protractor and retractor muscles, also possess four other

muscles, two of which are inserted on each mandible (Figs. 1 & 3, RM). These muscles take their origin from the wall of the clypeus adjacent to the protractor muscles. They are probably the rotator muscles whose alternate contractions will bring about a rotating movement of the mandibles enabling them to perform drilling action while penetrating the plant tissues. The rotator muscles also appear to be responsible for any sideways movement by the mandibular stylets. These muscles are not present on the bases of maxillae.

Snodgrass (1935) mentions that the aphids which have no protractor mechanism for the labium, often have much difficulty in extracting the mouth bristles. But from the present studies it is evident that so far as the retraction of stylets is concerned, the labium plays little part since the stylets themselves have strong retractor muscles. Heriot (1934) is of the opinion that the main function of the stylet muscles is to control the direction of the tip of the stylets in order that a larger area could be explored and a selective feeding could be possible. His observations, thus, imply that the tactile sense organs are associated with the stylets and there should be a nerve supply to these tactile sense organs. The association of nerves with mandibles has already been shown by Forbes (1966) in green peach aphid and has also been found in the present study on greenbug, but the other assumption that the main function of the stylet muscles is to serve as directing agents, does not appear to be in conformity with the observations in the greenbug since it does not explain other vital movements performed by the

stylets.

Davidson (1913, 1914) and Auclair (1963) have described the presence of a central duct running longitudinally throughout the entire length of each mandible. Recent electron microscope studies on the mandibles of Myzus persicae by Forbes (1966) have given sufficient evidence of the presence of nerve inside the duct of each mandible. The existence of the nerve inside the mandibular duct establishes the fact that the mandibles not only act as piercing organs but also serve the primary function of detection of a suitable site for feeding.

The electronmicrophotograph of the mandibles of the greenbug (Fig. 5, F) also clearly manifests the presence of a central duct and the nerve inside it (Fig. 5, N). The anterior and posterior end of each mandible has a head-like form and the body bulges in the middle where the duct is contained (Fig. 5, H). The duct runs throughout the length of the mandible and ends up blindly shortly before the distal tip. The sections show that the proximal region of the mandibular duct is not wholly occupied by the nerve and always some space is left inside, whereas towards the distal part, almost the whole space of the duct is occupied by the nervous tissue. This may suggest that the mandibular ducts are probably not only meant for the retention of nerves but may also be imparting flexibility to the mandibular stylets on account of the hollow space within them.

Bradley (1952) while reporting about the transmission of a strain of henbane mosaic virus by Myzus persicae, mentions that the stylets

consist of two pointed mandibles and a pair of maxillae. The maxillae appear to be permanently fused. The mandibles lie on either side of the maxillae and are capable of independent movement. The fused maxillae form two ducts, a dorsal larger one through which the insect's food passes and a much smaller ventral duct through which the saliva is ejected. In the greenbug, though, the maxillae always remain closely apposed to each other but no such fusion of their distal ends is present. Electron microscope studies (Fig. 5) of the stylets of the greenbug clearly show that the right and left maxillae differ in their width and also in the arrangement of their grooves. The left maxilla is shorter and about two thirds of the width of right maxilla. Both maxillae have projections, named here as condyles, on their inner surfaces and with the accompanying grooves, they form a ball and socket-like arrangement which makes their disengagement rather impossible. The right maxilla has 4 grooves and 5 condylar projections on its inner surface while the left maxilla is provided with 3 grooves and 3 condylar projections. The first anterior groove in the right maxilla (Fig. 5, RG1) is small and acts as a socket for the reception of the first condyle of left maxilla (Fig. 5, LC1). The first condyle of right maxilla (Fig. 5, RC1) fits in the first groove (Fig. 5, LG1) of the left maxilla. The second grooves of the right and left maxillae (Fig. 5, RG2 & LG2) are the largest and together form the food canal. The food canal is 0.12 micron in diameter. The third circular groove on the right maxilla (Fig. 5, RG3) is quite deep and the condyles third and

fourth (Fig. 5, RC3 & RC4) converge a little to form a seat for the placement of a small second condyle of the left maxilla (Fig. 5, LC2), which closes this third concavity of the right maxilla and makes it act as a duct for the flow of the salivary fluid. The salivary channel measures 0.05 micron in diameter. The fourth condyle of right maxilla (Fig. 5, RC4) fits into the third groove of the left maxilla (Fig. 5, LG3) and the third condyle of the left maxilla (Fig. 5, LC3) fits into the fourth groove of the right maxilla (Fig. 5, RG4). The fifth condyle of right maxilla caps over the posterior end of the left maxilla. This ball and socket-like arrangement of the two maxillae suggests that the disengagement of both is not possible unless the condyles are damaged but they can slide up and down against each other. This arrangement further throws light as to how the stylets are able to change their course inside the plant tissues, and direct their tips to bend in the way it is required. The up and down movement of the maxillae is brought about by the retractor muscles.

The mandibular stylets lie closely appressed to the maxillary stylets but sometimes separate from them when the stylets are withdrawn from the plant tissues. The stylets after emergence from the hypognathus head, are always encased inside the anterior part of the labium in a longitudinal groove. The labium arises just behind the oral aperture, and is in the form of a tubular structure containing a groove on its inner roof at the distal end. This labial groove (Fig. 4, La) keeps the stylets in position and whether functioning or not, the

stylets always lie in the labial groove. At the time of feeding the labium is much shortened in its length as it is pressed by the downward pressure of the head. The basal portion of the labium is, in fact, withdrawn in a postero-anterior direction. The farther the stylets are inserted into the plant tissues, the more the labium is retracted. The ventral posteriorly directed position of the labium (Fig. 1, L) together with the forward movement of the head, allow the maximum penetration of the stylets. The insertion of the stylets in the plant tissues is always at an angle less than the right angle to the feeding surface.

In the living greenbugs when the stylets were freed from the labial grooves, the mandibles automatically parted and a lateral and vertical movement of the stylets was noticed. The stylets were partly withdrawn within the head, the labium was straightened forward and with a slight upward tilt of the head, the greenbug was again able to put back the stylets in the labial groove. This clearly indicates that the labial groove is responsible for keeping the stylets in position and essential for proper functioning. The stylets kept within the labial groove are only able to perform an up and down sliding movement without bringing about any movement on the part of the labium, while the sideways movement of the stylets is effected by the movement of the labium.

Bradley (1952) mentions that during the feeding punctures, Myzus persicae appears to push with its head causing the proboscis to shorten like a telescope and the stylets are forced into the leaf.

The advancing stylets appear to be assisted by a drilling action of the mandibles vibrating back and forth. The observations made on greenbug confirm Weber's (1923) conclusions as to how the stylets penetrate. The mandibles apparently function to penetrate by being protracted and sliding along the surface apposed to the maxillae. The swinging movements of the mandibles being caused by the rotator muscles.

It may be mentioned here that the stylets and the musculature attached to them, were studied in both greenbug biotypes, but in both cases the structures were identical.

Mode of feeding on host plant - According to the feeding behavior of different aphids and the mode of penetration of stylets into the plant tissues, Davidson (1923) and Tate (1937) have categorized them in three different types: first, those in which the stylets follow a course leading to vascular bundles passing intercellularly through the cortex; second, where the stylets pass intracellularly through the cortex and do not go to the vascular bundles; and third, the stylets leading to the vascular bundles and passing intracellularly through the cortex. Auclair (1963) mentions that variation in the mode of penetration of stylets may occur within a single species. Sorin (1966) worked on 40 species of aphids and found that the stylets are inserted into the epidermis both intercellularly and intracellularly or sometimes through stomata, but intercellular penetration is effected in the majority of them. The stylets usually reach phloem, especially sieve tubes, but in a few cases reach xylem bundle sheaths and also palisade

parenchyma. Schaefers (1967) reported that penetration of the plant tissue most frequently occurred near a vein. In nearly every instance the tissue was initially entered between the epidermal cells. The selection of the site may be passively related to the depressions occurring at the intercellular junctions.

Biotype B - A detailed study of the feeding behavior of greenbug biotype B indicated that the penetration of stylets was effected both intracellularly and intercellularly, but in a majority of the sections an intracellular penetration was noticed. The stylets were always found to have penetrated the leaf tissues in a straight course (Figs. 4, 6-9), and in most cases there was no indication of the stylets going to the vascular bundles. Only in a very few cases the penetration was made into the vascular bundles, but even in such cases the stylets had taken a straight course (Fig. 10). This indicates that biotype B feeds mostly on the sap of the parenchymatous tissues. In no case were the stylets found to have punctured the mid-rib of the leaf. The sections of the aphids on the leaf were cut by selecting various combinations of sitting postures of earlier instars and of adults, but in almost all of them the same condition of stylet penetration was found. As a result of this feeding behavior only the parenchymatous cells of the leaves showed much damage, whereas the vascular bundles were noticed to be intact in such cases (Fig. 11). The greatest injury done to the leaf is chlorosis of most of the chloroplast cells containing chlorophyll due to injection of saliva (Fig. 4, S). The plasmolyzed cell contents are

sucked by the aphid through the food canal. The straight nature of the salivary sheaths (Figs. 12 & 13, SH) noticed inside the palisade parenchyma are further proof of the straight penetration of the stylets going to the parenchyma. Thus the present observations indicate that the initial penetration of stylets is made by ejecting the salivary fluid in the region of the epidermal cells (Fig. 4, S), which breaks down the cells and enables the stylets to penetrate deeper. When the saliva comes in contact with the cell contents, there is marked plasmolysis of the cell, and usually the protoplasm gets concentrated towards the region of contact (Fig. 4). The contents of the cell become disorganized, the nucleus swells considerably and eventually becomes a deeply staining homogeneous mass of irregular shape. In extreme cases the cytoplasm becomes disintegrated and ultimately the cell wall ruptures. The introduction of saliva not only brings about the breakdown of cells at that point, but the adjacent cells are also affected resulting in the formation of large vacuolar spaces in the parenchyma (Figs. 10 & 11, Va).

McLean and Kinsey (1967) electronically recorded the waveforms of the probing behavior of pea aphids, Acyrthosiphon pisum, and found a distinctive curve pattern when the stylets contacted phloem sieve elements. They could determine that the pea aphids ingest fluids from the subepidermis, mesophyll parenchyma, phloem parenchyma, companion cells, phloem sieve elements, and xylem. Lowe (1967) while working on the feeding behavior of Aphis fabae Scop.,

Myzus persicae, and Myzus ornatus Laing, found that the probes of adult Aphis fabae were always directed to the phloem in the veins while the probes of young larvae, in a number of cases, ended in the mesophyll tissues. This indicated that the young larvae of Aphis fabae are also capable of feeding in the spongy mesophyll. He further mentioned that 70% of the deep probes of adult and larval Myzus ornatus passed into the spongy mesophyll only. These probes terminated well away from the vascular bundles and there was no indication of them being directed towards the vascular bundles. It seems, therefore, that Myzus ornatus is able to feed from alternative food sources in the bean leaf, one being the phloem, the other the spongy mesophyll, and that the mesophyll is the preferred food source in this species.

Results of similar nature having been obtained in the case of greenbug biotype B, evidently prove that this biotype has a definite preference for the mesophyll parenchyma as the food source.

Biotype A - Studies made on biotype A confirm the original observations of Chatters and Schlehuber (1951). The stylets were always found to have entered intercellularly and continued their passage into the tissues in the same manner. As a result of intercellular penetration they followed a sinuous course and ultimately reached the vascular bundles in every case (Figs. 14 - 16). In a few sections it was noticed that the stylets followed a round-about path along the xylem vessels in order to reach the phloem (Figs. 14 & 15). The salivary sheaths exhibited curved patterns and always ended in the phloem tissues

(Fig. 17, SH). The branched nature of the salivary sheaths as reported by Chatters and Schlehuber could not be detected in any of the preparations. Sorin (1966) mentioned that the salivary sheaths are usually developed more distinctly within than between the cell walls and are formed even in the air between the tip of the rostrum and the surface of plant epidermis or between leaf sheath and stem when the aphid feeds on the stem through the sheath. But in all the sections of this biotype, the salivary sheaths were noticed only within the plant tissues and intercellular in disposition. Weatherly, Peel and Hill (1959), from the stylets of Tuberolachnus salignus, and Hill (1962), from the stylets of Longistigma caryae (Harris), obtained the exuding plant sap by using the technique of Kennedy and Mittler (1953). After biochemically analyzing the fluid, they reached the same conclusions, which had already been reported by other workers based on the histological observations, that these aphids tapped the phloem sieve tube elements.

The present studies on biotype A and those of Chatters and Schlehuber on the same biotype, give a definite indication that it feeds in the phloem tissues.

Hence it will be pertinent enough to conclude that the mesophyll parenchyma is the food source of biotype B and phloem sieve tubes and phloem parenchyma are the feeding sites of biotype A.

SALIVARY GLAND SYSTEM

Glands associated with the intake of food are generally present among insects although they are wanting in many of the Coleoptera. In most insects the salivary glands are morphologically the labial glands but in such cases where they have taken up some other function, the mandibular and maxillary glands perform the salivary function. Among Hemiptera and Homoptera, the labial as well as the mandibular and maxillary glands, are involved in the process of salivary secretion, and some authors call them by the collective name, the salivary glands. Though salivary glands and the salivary pump of many Hemipterous insects have been studied because of their importance, either in transmitting virus infection to plants or being a major pest to the crops, the studies on the anatomy of these glands and that of salivary pump in the case of Homoptera are almost lacking.

The feeding of the greenbug is marked by the appearance of small yellow patches on the wheat or barley leaves which is also indicative of the injury done to the plants. Chatters and Schlehuber (1951) point out that maximum injury is done to the plants, not by removal of sap, but by the introduction of saliva which seems to be toxic to plants. In other words, this would mean that a greenbug-resistant plant is able to tolerate the toxicity of salivary secretion. This may be

accomplished either by producing chemicals which neutralize the toxic effect or by developing some anatomical structures which arrest the secretion, keeping it localized in that area without affecting the adjacent tissues, the plant getting rid of the salivary secretion by some physiological process at a later stage.

Hence the importance of salivary secretion and morphology of salivary system is all the more enhanced when studies pertaining to factors for plant resistance and susceptibility are taken up. A study of such vital importance has received little attention so far. Most of the work was on Hemiptera. Since there is close similarity between phytophagous Hemiptera and Homoptera, mention of the work on Hemiptera will also be made here.

Negi (1934) studied the alimentary canal and salivary glands of the adult female lac insect. He found the salivary glands in the form of a bunch of grapes situated in close proximity to the ventral ganglion. Breakey (1936) described the salivary system of Anasa tristis (DeGeer) as consisting of main glands, accessory glands and salivary syringe. He called the principal glands the main glands and described them to be composed of six lobes, while the accessory glands as merely the continuation of the salivary ducts. The salivary pump consisting of a chitinous tissue provided with a heavily sclerotized pyriform piston and operated by a large pair of dilator muscles. Elson (1937) divided the order Hemiptera into five groups based on the feeding habits of the bugs, viz: phytosuccivorous types, predatory types, algophagous,

mycetophagous, and haematophagous. He further stated that the principal glands consist of numerous finger-like lobes variable in size and number. The accessory glands are elongated and tube-like, except in Capsidae where the distal end is bulbous. Hood (1937) worked on the digestive system of plant sucking Oncopeltus fasciatus (Dallas) and gave a brief reference to the structure of salivary glands as consisting of 4 lobes and a tubular convoluted accessory gland. Baptist (1941) studied the anatomy and physiology of the salivary glands of a large number of Hemipterous bugs and described the details of their histology and different forms. Woolley (1949) mentioned that the salivary glands of the boxelder bug consist of primary and accessory glands. The primary salivary glands are large and four lobed, whereas the accessory glands are in the form of thin coiled filaments. Southwood (1955) states that the structure of salivary glands depends more on the taxonomic relationship of the species than on feeding habits or on the nature of secretions and proposed the use of salivary gland structure for classification. Adams and McAllan (1958) found the enzyme pectinase in the saliva of 23 species of apterous aphids but not in the alate forms. They contend that even forms of the same species are distinct animals among which manifold and perhaps important physiological differences occur. Bronskill, Salkeld, and Friend (1958) described the structure and secretion of salivary glands of the bug, Oncopeltus fasciatus. Their study indicated that various lobes of the salivary glands contained different digestive enzymes. Miles (1959) reported

that in both Oncopeltus fasciatus and Dysdercus fasciatus Sign., two types of saliva are ejected. One, the sheath material which coagulates rapidly and forms a lining to the path of stylets when the insect feeds on natural food material, and the second, a watery and water soluble saliva which is secreted and sucked back again both on the surfaces of the substrates and within them. He suggested that once feeding has begun, the secretion of watery saliva is inhibited by the flow of liquids up the food canal. The stylet activity is decreased by the presence of acceptable substances in these liquids, but cessation of the inhibition can be brought about by sensory adaptation. The secretion of the sheath-material is elicited by the resistance to the passage of the stylets, but the rate of flow is uncontrolled and only a limited amount can be secreted continuously. Nuorteva and Laurema (1961) attempted to investigate the effect of diet on the amino acids in the haemolymph and salivary glands of Heteroptera. They found that d-valine occurring in the diet is of no value to the bug, whereas l-valine present in the diet is one of the most essential amino acids for the body of the bug. The d-valine amino acid is transferred from the haemolymph to the salivary glands which indicates that salivary glands also function as excretory organs and are able to eliminate some toxic substances from the haemolymph. He further mentioned that the elimination of toxic substances by this route instead of through the malpighian tubules may be of biological significance in Heteroptera, because toxic

materials in the salivary secretions may alter the physiological condition of the host plant in a direction in which its suitability as food for insect increases. Jacob and Jurand (1963) made electron microscope studies of the large cells of the anterior portion of larval salivary glands of the sciarid, Bradysia mycorum Frey and found that the supranuclear region of the cells is primarily concerned with the production and condensation of the secretory material. The apical end of these cells is bound by a brush border. He related the different morphological features of the basal cytoplasm of the cells to different functional steps involved in the mechanism of secretion. Miles (1965), while working on the salivary physiology of plant bugs, stated that the morphology of the salivary glands of aphids appears to be quite simple, because the cells of the main lobe empty independently by minute canals into the common duct and perhaps represent a number of separate lobes, such as are found in Jassoidea and Fulgoroidea. There are no sac-like reservoirs for the secretions and the identification of the final secretory products of the cells remains open to doubt. He further added that the accessory gland of Homoptera in general is not fully comparable with that of Heteroptera, since it does not seem to be a source of polyphenol oxidase in Homoptera, whereas it is the chief source of this enzyme in Heteroptera.

Materials and Methods

Adult aphids, both alate and apterous, were dissected in Ringer's fluid and the anatomy was studied. It was found that it was easier to study fresh specimens than the preserved ones, since the salivary glands in fresh aphids took much deeper methylene blue stain. Immediately after dissection the Ringer's fluid was drained off, and the dissected specimens were kept for 10 minutes in the methylene blue solution of 1:1000 strength. The glands get differentially stained during this period and then the methylene blue stain was replaced by normal saline. By this method the principal and accessory glands could be clearly noticed, but the mandibular and maxillary glands were exclusively studied by cutting thin serial sections.

For histological preparations, the material was fixed in Bouin's and Carnoy's fluids. Longitudinal, transverse, and cross sections were stained in combinations of Delafield haematoxylin--eosin, and safranin O--fast green. Sections were cut both on freezing and rotary microtomes.

In studying the cellular details of the salivary glands, double staining with Heidenhain's haematoxylin and orange G proved to be most successful. Attempts were made to obtain different secretory phases of the principal glands by fixing them at varying intervals of time after the commencement of feeding, but no successful results could be obtained and hence it was abandoned.

Aoyama's silver nitrate method for the demonstration of nerve endings was employed, but it did not give satisfactory results as the whole gland darkened so much by silver impregnation that it was impossible to detect the nerve endings. Best differentiation was obtained when a dissecting dish with white wax was used, and dissected specimen was covered with .5% acetocarmine stain for 5 minutes.

Results and Discussion

The salivary gland complex in Schizaphis graminum (Rond.) consist of a pair of principal glands, one pair of accessory glands, one pair of mandibular glands and one pair of maxillary glands. They are closely associated with the central nervous system and exhibit a pattern which differs from that of the phytophagous Hemiptera. No evidence of the existence of salivary pump could be found which, at least in Hemiptera, forms quite an elaborate structure.

Principal glands - The principal glands are located in the prothoracic region closely applied to the lateral sides of the posterior portion of suboesophageal ganglion and the anterior region of the thoracic ganglionic mass (Fig. 18, pg). In fresh dissections they appear as two white sac-like structures with the posterior region looking more dense and the anterior part as slightly membranous. During staining with acetocarmine, only the posterior half is deeply stained and the anterior region takes very little stain. Due to this light staining of the anterior part, the nervous plexus present on the anterior end is clearly

differentiated. A short nerve arising from the posterior portion of suboesophageal ganglion goes to form a cap-like innervation on the posterior end. The whole principal gland is surrounded by a network of minute tracheal branches which keep it bound to the ganglionic mass. From the anterior region of each principal gland a duct originates on the ventro-lateral aspect and extends down to the base of maxillae. The place from where this duct emerges is known as hilus (Fig. 21, h). Just at the point of emergence of this duct another duct from the accessory gland joins it and forms the salivary duct (Fig. 21, sd). The salivary duct of both sides, as they run down, combine to form a common salivary duct at the base of the maxillary stylets. No innervation of the salivary duct or of the common duct by any nerve or the formation of a nerve plexus on them could be noticed. The common salivary duct just after its formation runs for a short distance parallel and close to the cibarial chamber and opens next to it (Figs. 32 & 33).

The transverse and longitudinal sections of the principal glands, stained with safranin O and fast green, and with Heidenhain's haematoxylin, distinctly showed that the gland is divided into two different regions, an anterior membranous part and a posterior glandular portion (Figs. 19 & 20). The shape, size, and nature of the cells of these two regions are completely different and their staining reactions also differ. The wall of the anterior region appears to be quite elastic, because in some cases (Fig. 22) this region is found swollen, while in others it is present in a collapsed state.

The posterior region of the glands consists of closely packed large glandular cells with almost round nuclei (Fig. 19, 20 & 22). In some cells often two nuclei are noticed. The nuclei contain two or more nucleoli, and the chromatin is uniformly distributed (Fig. 19, ch). The glandular cells are so large that the lumen of the gland in this portion is completely obliterated (Fig. 20). Minute globules of secretions emerge from these cells, which after escaping into the lumen, combine to form larger globules (Fig. 19, sm). In the interior of the cells, both in the subnuclear and supranuclear regions, the cytoplasm is occupied by vacuoles containing granular secretory material. Some workers, while describing the cytology of the principal glands in Hemiptera, have called these secretory granules the zymogen granules. The posterior glandular region is provided with intercellular spaces (Fig. 22, is) which converge and open into the anterior lumen of the gland (Fig. 23, L). This suggests that the anterior region of the principal gland is specifically meant for the collection of the secretory material and acts as a reservoir.

The anterior portion of the principal gland giving light staining reactions, consists of columnar cells which are rather flattened and not so large as those of the posterior region. These cells are not so compact, and on account of their small size a fairly large lumen is found in this region. When the lumen of the anterior region is filled with the secretion of the posterior glandular cells, it presents a swollen appearance and in sections with swollen anterior part, the exact

shape and size of the columnar cells becomes difficult to discern. The cells are in general small and flattened. Their nuclei are small and irregular in shape containing normally more than two nucleoli. In no case were two nuclei noticed in any cell of the anterior region like that observed in the posterior part. The chromatin material inside the nuclei is more concentrated in the central region than in the peripheral part.

The structure of the principal glands in the developing embryos (Figs. 24 & 25) shows that the cells of the anterior region are initially large and like those of the posterior region, but as the development proceeds, these cells become smaller and flattened. It is characteristic to note that the staining reaction of these cells is different from the early stage of their development, which points to the fact that probably from the earliest stages of their development they are set apart from those of the posterior ones in their nature and are destined for a different function in the future. From the present studies it appears most probable that the anterior region of the principal gland is meant for storage of secretory material discharged from the glandular cells of the posterior region. The swollen and collapsed conditions and the membranous appearance of the wall are further evidence for this possible function of the anterior region of the gland. At the same time, it will be erroneous to call this region purely a receptacle or a reservoir meant only for the storage, since it might be possible that this region might also be secreting a different type of secretion with

different function. A detailed histochemical study is needed to ascertain the exact nature of the cells of this region.

The present study does not include the investigation into the nature of the secretion from principal glands of the greenbug, but this study is planned to be taken up at a later date. However, from the researches of other workers on phytophagous Hemiptera and a few aphids, it is apparent that no definite conclusions have so far been reached. Miles (1959) reported that in Aphis craccivora Koch two types of saliva are secreted, a watery saliva and the other a viscid secretion which forms the stylet sheath. Salkeld (1960) made histochemical studies on secretions in the principal glands of Oncopeltus fasciatus and found that each lobe of the trilobed principal gland contained a chemically different secreted product. The secretion of the anterior lobe was composed of glyco-protein and neutral mucopolysaccharide. The secretion of the lateral lobe was mainly proteinaceous, while that of the posterior lobe appeared to be a mucoprotein. He further suggested that the secretion of the anterior lobe may form the stylet sheath, whereas the secretions of the lateral and posterior lobes more likely have a digestive function. Miles (1964) made histochemical studies on the salivary glands of insects belonging to different families of Hemiptera and Homoptera. His tests revealed that in Macrosiphum euphorbiae (Thomas) and Aphis lutescens Monell (Aphis nerii B. de F.), the posterior region of the principal gland is the site of phenolase activity. A phenolase is secreted by the cells which brings

about the oxidation of diphenols that occur in the salivary glands of all the Hemiptera and Homoptera. Miles (1967) again reported that dihydroxyphenylalanine is the substrate for the salivary polyphenol oxidase and phenylalanine is the precursor. His chromatographic experiments of the haemolymph showed that free tryptophan and phenylalanine are the normal constituents.

Accessory glands - In the greenbug, the principal gland on either side is provided with an accessory gland (Fig. 26, Ac) located in the posterior part of the head. A short duct arises from each accessory gland which runs to the posterior side to meet the duct of the principal gland just at the hilus (Fig. 26, d). The accessory gland presents a very small rounded whitish appearance and is not easily detectible due to the mass of fat bodies around it. It is surrounded with a network of tracheal branches and is supplied with a nerve from the anterior region of the suboesophageal ganglion. No nerve plexus is formed by this nerve on the accessory gland like that observed in the case of principal gland. The transverse sections of the gland (Fig. 27, Ac) show that it consists of four large cubical cells each containing a round nucleus in the center. The lumen of the gland is considerably reduced on account of the large size of these glandular cells. The cytoplasm of the cells is densely packed with large secretion granules and very few vacuoles are noticed. Breakey (1936), in Anasa tristis, and Bronskill, Salkeld and Friend (1958), in Oncopeltus fasciatus, reported the presence of an intimal lining over the inner border of the cells of the accessory

gland and its duct. But no such intimal lining is found either in the accessory glands or their ducts in the greenbug. The ducts of the accessory gland of the greenbug contain a uniform lumen, and the wall is composed of thin flattened cells, theinner margins of which exhibit a striated appearance.

The salivary duct, which is formed by the union of the ducts from the accessory and principal glands, also has a wide lumen and its walls are made up of thin flattened cells. There is no trace of the chitinous intimal lining covering these cells. Baptist (1941) suggested that the accessory gland and its duct in Hemiptera should be considered as purely a development of the salivary duct. But, in the present case the morphological and histological differences between the accessory gland, its duct, and the salivary duct are so great that it is doubtful if any homology exists.

The exact fuction of the accessory glands or the type of secretion they produce is still unknown. According to Baptist (1941) the accessory glands of Hemiptera produce a watery secretion. The experiments of Miles and Helliwell (1961) showed that an oxidase, other than cytochrome oxidase, is present in the salivary ducts of Aphanus sordidus Fabr. They further state that the presence of a similar enzyme in both the accessory glands and the salivary duct is a complicating feature, since either or both parts of the glandular system could provide the oxidase in the watery saliva and an enzyme which could oxidize the sheath precursors. Possibly both parts are functionally similar and the accessory gland should be considered as purely a

development of the salivary duct. But Miles (1965) contradicts this previous view and states that the accessory glands of Homoptera in general can not be fully compared with that of Hemiptera, since it does not seem to be a source of polyphenol oxidase in Homoptera, whereas it is the chief source of the enzyme in Hemiptera.

Maxillary glands - According to Snodgrass (1935) the maxillary glands are present in Protura, Collembola, Hemiptera, Homoptera, Neuroptera, Trichoptera, Hymenoptera, and larval Coleoptera. Among Hemipterous insects these have been described as cephalic glands, or as lubricating glands. The glands are multicellular and may be either tubular or acinous. They develop as invaginations of the integument and are always associated with the maxillae, opening either directly into the preoral cavity or outside the preoral cavity on either side of the head at the base of the proboscis.

In the case of the greenbug the maxillary glands (Fig. 28, mx) lie on the lateral side of the head in close proximity to the maxillary sclerites. They are comma-shaped structures with the anterior part glandular. A duct from each gland runs down uniting midway to form a common maxillary duct (Fig. 32 & 33, K) which joins the common manibular duct (Figs. 32 & 33, J) immediately before opening at the base of the maxillary stylets next to the common salivary duct.

Sorin (1966) found that in Aphis craccivora this common maxillary duct joins the common mandibular duct and also the salivary duct before opening at the base of the maxillary stylets. The junction of

the union of these three ducts, he called the salivary meatus. But in the greenbug the union of the common maxillary duct was found only with the common mandibular duct and not with the salivary duct.

The outer side of the comma-shaped maxillary gland is occupied by a collecting duct (Fig. 28, cd) which runs throughout the entire length of the gland, and the glandular part (Fig. 28, z) presents a vacuolated appearance. In thick longitudinal sections, which give a complete view of the maxillary glands, the collecting duct on the outside and the vacuolated glandular portion on the inside are distinctly noticed (Fig. 28). The transverse sections of the maxillary glands (Fig. 29) show the gland cells arranged peripherally and the central portion occupied by a mass of connective tissue. The peripheral glandular cells are so compacted that the cellular boundaries are hardly distinguishable. The nuclei are fairly large, some oval, while others are of irregular shape. They always occupy the basal regions of the cells. A single large nucleolus is present at the one end of the nucleus and the dense chromatin granules are evenly distributed. Very minute intercellular spaces are faintly discernible which converge towards the collecting duct and are probably responsible for bringing the secretion of the glandular cells into the collecting duct.

Linder (1956) reported that the maxillary glands of Oncopeltus fasciatus are composed of two types of cells, the large peripheral cells within which the secretion is formed, and the centrally located smaller cells surrounding a system of inter- and intracellular chitinous

ductules. But in the maxillary glands of the greenbug no such mass of central cells exists and no intracellular spaces are present. However, the intercellular spaces are present, but they are not chitinous in nature, since nowhere in the gland or in the collecting duct is such a chitinous lining found. Linder (1956) did not give details about the nature of the smaller cells of the center nor did he assign any function to them, although about peripheral cells he has clearly mentioned that they form secretion. His histochemical studies indicated that the peripheral cells of the maxillary gland produce a proteinaceous secretion which might be a mucoprotein or neutral mucopolysaccharide.

Mandibular glands - The mandibular glands (Fig. 30, mn) are in the form of two elbowed structures, the free ends of the elbows pointing towards the posterior side of the body. They are located immediately behind the maxillary glands and beneath the suboesophageal ganglion. Comparatively, they are much smaller than the maxillary glands. The elbowed part is the main glandular portion whose proximal end continues down in the form of a duct and meets its counterpart from the other side and forms the common mandibular duct. The common mandibular duct runs towards the stylets, and as it descends down it joins the common maxillary duct (Figs. 32 & 33, J). No collecting duct like that observed in the case of maxillary gland is present here. The transverse sections of the mandibular gland (Fig. 31) show six large columnar glandular cells occupying the major portion of the gland and very small lumen in the center. The cells are bound externally by a

basement membrane and a thin structureless connective tissue layer. Each cell contains a large round nucleus situated in the center and the boundaries of the cells are clearly marked. The nucleolus occupies a central disposition inside the nucleus, and the chromatin granules are evenly distributed. Around the nucleus of each cell, a vacuolar space containing numerous secretory granules is present (Fig. 31). No intimal lining over the cells is found, and the free ends of the cells do not appear to possess a striated border. The wall of the mandibular duct is lined with thin flattened cubical cells. No muscular layers have been noticed surrounding either the mandibular or maxillary glands or their ducts.

The nature of the secretion of the mandibular glands of aphids, or even of Hemiptera, is still not clear, although some suggestions here and there have been made. Linder (1956) is of the view that the mandibular glands of Oncopeltus fasciatus secrete a lubricant material for the stylets, whereas Sorin (1966) reported that the mandibular and maxillary glands secrete a highly viscous fluid which is used for stylet sheath formation.

Mechanism of salivary secretion - In phytophagous Hemiptera the expulsion of salivary secretion is effected by the salivary pump. The common duct from the principal and accessory glands, and the common duct formed by the union of maxillary and mandibular glands, unite to form a salivary meatus which is connected with the salivary pump. The salivary pump consists of chitinous tissue provided with a heavy

sclerotized pyriform piston, and it is operated by a pair of dilator muscles. Sorin (1966), while describing the suction mechanism of plant juice by aphids, only mentioned that the salivary pump is polygonal in shape in cross section. He did not give any structural details of the salivary pump nor did his drawings show the pump clearly.

In the present studies on the salivary glands of the greenbug, no salivary meatus or the salivary pump is present, since no union between the two common ducts, one coming from the principal and accessory glands and the other from the maxillary and mandibular glands, could be noticed (Figs. 32 & 33). Both these common ducts run adjacent to each other and open into the salivary channel of the maxillary stylets at the same point. In transverse serial sections, also, no such polygonal structure with chitinous lining could be detected. Thus, in the absence of the salivary pump and the muscular layers on the glands or their ducts, it appears possible that the expulsion of the salivary fluid is brought about only by the pressure of the haemolymph upon the walls of the glands and their ducts.

Salivary sheath - With regard to the chemical nature of the salivary sheath of Homoptera and the glands responsible for the secretion of this material, very little information is available. Miles (1965) demonstrated that granules with sulphydryl group were present throughout the salivary glands of Myzus periscae (Sulz.) and Aphis craccivora, but these were concentrated in the main cells of principal glands rather than in the accessory gland cells. According to him no other

structures in the head capsule showed any marked content of sulphydryl groups which are the characteristics of the sheath material and are the sheath precursors. Sorin (1966) claims that the sheath material of aphids is secreted by the maxillary and mandibular glands.

The sheath material of phytophagous Hemiptera is considered by some to be precipitated from plant cells by the action of insect saliva, since the salivary sheath contains calcium pectate, callose, and tanin. But Miles (1960) after performing histochemical tests on the sheath material of Oncopeltus fasciatus, arrived at the conclusion that it contained lipoprotein, tryptophan, and was rich in tyrosine. It contained no chitin and carbohydrates, whereas the watery saliva contained mucoprotein.

So far as the function of salivary sheath is concerned, various views have been put forward but none appears convincing. Sukhov (1944) claimed that the sheath secreted by Myzus persicae is never open at the end and that it acts as a filter which prevents viruses from entering the insect. But Miles (1959) found that Oncopeltus fasciatus and Dysdercus fasciatus absorb materials from the open end of the sheath or beyond it. Mittler (1957) pointed out that the stylet sheath is not meant for the support of the stylets, since the sheath is soft enough and allows the stylets to break through during branching of the tract. The function of the stylet sheath as a means of support to stylets is discounted by the observations made by Miles (1959) that Oncopeltus fasciatus can penetrate peanut tissue and guide the stylets in agar gel

without the aid of a stylet sheath. According to Miles, the most convincing hypothesis of the function of the stylet sheath has been given by Mittler (1957) that the stylet sheath of aphids prevents the sap from exuding round the stylets to the exterior. But this suggestion also does not seem to be so conclusive, since it is known that as the saliva is injected into the plant tissue, not only the cells of contact are dissolved, but it brings about cell lysis of quite a number of adjacent cells, also. Hence, the sap can exude from any part adjacent to the salivary sheath.

From the present studies made on the feeding mechanism of Schizaphis graminum, it appears probable that the salivary sheath might act as a means for preventing the plugging of the ultramicroscopic openings of the salivary and food canals, and allowing only that part of the liquid food to pass which can safely be conducted through the food canal.

DIGESTIVE SYSTEM

It is surprising that very little attention has been given to the internal morphology of aphids, although a vast amount of work has been done on its various other aspects, such as mode of feeding, composition of honey dew, artificial diet, etc. Only a few accounts of some earlier workers are available on the gut of aphids giving descriptions of the general structure of the different regions and the presence or absence of the malpighian tubules. Davidson (1913, 1914) reported on the biology, mouth parts and the suction mechanism of the woolly apple aphid, Eriosoma lanigerum (Hausmann) (Schizoneura lanigera Hausmann). Knowlton (1925) studied the digestive tract of Longistigma caryae (Harris) and gave a brief account of the histology and structure of the filter chamber. Miller (1932) worked on the digestive epithelium of Macrosiphum sanborni Gillette and described the histological details of the mid-gut. Pelton (1938) gave details on the alimentary canal of Prociphilus tessellatus (Fitch). Smith (1939) performed his studies on Macrosiphum solanifolii (Ashmead) and described the digestive system.

Since aphids cause considerable damage to crops by sucking the plant sap or by feeding on the plant tissues, the study of the digestive system becomes the foremost requisite for further research. Since no

work in this regard has been done so far on the greenbug, Schizaphis graminum (Rond.), this study was undertaken to obtain data on morphological, histological and cytological details of the alimentary canal and on the suction mechanism.

Materials and Methods

The greenbugs were reared on barley plants in a controlled environment growth chamber. Only mature alate and apterous greenbugs were selected for dissections and sectioning. Dissections were performed in Ringer's solution. Various parts in situ were studied after staining with Borax carmine and also sometimes with neutral red (0.1%). For studying the histology of the gut, aphids were fixed in Bouin's fluid, Carl's solution, Zenker's fluid and Carnoy's fixative. Best results were obtained with Carnoy's solution. The legs of the aphids were removed in order to allow complete penetration of the fixative. Serial transverse and longitudinal sections were cut at 6 microns. In the study of the suction pump, longitudinal and cross sections were cut at 10 microns, since it was found that slightly thicker sections yielded better pictures of the structure. Histological sections were stained with Ehrlich's haematoxylin and eosin. The sections were cut with both freezing and rotary microtomes.

For cytological preparations living aphids were dropped directly into the fixative, and after one hour the legs were removed. Fixation in Helly's fluid was found to be superior to other fixatives tried, and

the staining of sections was done with Heidenhain's haematoxylin and orange G. Paraffin sections were brought down to water and kept in a 3% solution of ferric ammonium sulphate for 45 minutes, washed with distilled water and then stained in Heidenhain's haematoxylin for 30 minutes. After rapid washing, the sections were cleared in 1.5% solution of ferric ammonium sulphate. When correct differentiation was obtained, the sections were dehydrated in different strengths of ethyl alcohol and counterstained in a 1% orange G in 90% ethyl alcohol solution for 5 minutes. The sections later were differentiated in 90% alcohol, cleared in cedar wood oil and mounted in balsam. Photomicrographs were taken with a Nikon Auto-microflex Camera on Panatomic X 35 mm film.

Results and Discussion

General Structure of the Alimentary Canal - The digestive tract (Fig. 34) forms a coiled tube-like structure occupying the mid-visceral region of the body. It consists of an extremely thin oesophagus extending from the head to the mesothoracic region where it opens into a dilated, bulb-like stomach. The oesophagus has been termed the fore-gut (Roeder 1953), stomodaeum (Snodgrass 1935) or fore-intestine (Knowlton 1925). Various other names have been assigned to this bulb-like structure, such as stomach, mid-gut, mesenteron, mid-intestine or ventriculus. Snodgrass divides the mid-gut of Homoptera into ventriculus I, ventriculus II and ventriculus III, whereas other authors

have called the anterior dilated region, the stomach, and the posterior region, the intestine.

The stomach is broadest at its anterior end. This is commonly referred to as the cardiac end, and it lies in the mesothoracic region. It gradually narrows down to the region of the second abdominal segment. The continuing narrow tubular structure is the intestine. Snodgrass (1935) and Imms (1957) in discussing the alimentary canal of Homoptera designated the region after the origin of the malpighian tubules as the intestine. The mid-gut in that case, consists of an anterior bulb-like portion, ventriculus I and a long posterior thin tubular structure divided into ventriculus II and ventriculus III. But, since no malpighian tubules are present and the filter chamber is lacking in the greenbug, no such demarcation can be made here. Hence, the anterior dilated region of the mid-gut will be referred to here as the stomach, and the posterior tubular part as the intestine.

After its origin in the third abdominal segment, the intestine runs posteriorly, makes a U-turn in the region of the sixth abdominal segment, continues anteriorally to the mesothoracic region where it forms two loops closely applied on the ventral sides of the stomach, and finally descends down dilating into a transparent membranous rectum. This membranous transparent rectum is also sometimes referred as proctodaeum or hind-intestine.

Sucking pump - The anterior-most region of the oesophagus is slightly dilated and is often called the pharynx. The anterior portion of the pharynx is greatly modified and forms the chamber of the suction pump which opens into the food canal of the maxillary stylets. The wall of the suction chamber on the front is infolded, over which strong muscles are inserted (Figs. 35 & 36, S). This whole structure has been termed differently by various authors as pharyngeal pump, suction pump, or cibarial pump.

Snodgrass (1935) in describing the pump chamber of Homoptera mentions that this structure represents the preoral cibarium of the generalized Orthopteroid insect. He states that the posterior part is formed from the proximal part of the hypopharynx, whereas its anterior wall is derived from epipharynx. The functional mouth is formed by the application of the distal surface of the hypopharynx on the epipharyngeal wall of the anteclypeus, and the true mouth is represented where the pump chamber meets the oesophagus. He further suggests that this pump should be called the sucking pump, or cibarial pump, on the basis of its function and not the pharynx or pharyngeal pump. Auclair (1963) called it the cibarial-pharyngeal food pump. Sorin (1966) completely separates the sucking pump from the region of the pharynx. He stated that in cross sections the sucking pump is polygonal and that the pharynx is nearly semicircular in shape. He further stated that the posterior side of sucking pump is much sclerotized while the anterior side is membranous, and that the dilator muscles

arising from the clypeus attach at the center of the anterior side in Myzus persicae (Sulzer).

The transverse sections of the sucking pump of the greenbug exhibit an infolding of the wall on the anterior side (Fig. 36, I), and on either side where the wall bends inwards, the dilator muscles (Fig. 40, P) are inserted. A lateral view of the pump chamber in longitudinal sections shows the series of dilator muscles (Fig. 36, M) attached along this infolding throughout the length of the chamber. The dilator muscles are fairly large and originate in the clypeal region of the head. The wall of the pump at the place of insertion of muscles is thicker in comparison to that of the opposite side.

Davidson (1914), in the case of Eriosoma lanigerum (Hausmann), and Weber (1928) in Aphis fabae Scopoli, described the large dilator muscles inserted along the mid-line of the distal end of the anterior wall of the pump chamber. They found that these muscles are inserted by a long cuticular tendon, while in the proximal region of the pump chamber, the insertion is along either side of the mid-line of anterior wall of pump.

In the greenbug, however, the arrangement of muscle insertion at the distal and proximal ends is the same. The infolding of the wall on the proximal side is not so deep as on the distal end. The contraction of the dilator muscles stretches the infolding of the wall, due to which the space of the lumen is increased and the vacuum so created results in the suction of the liquid food through the food canal.

It appears probable that the extreme thinness of the oesophagus is partly responsible for maintaining the continuous inflow of the liquid food through capillary attraction once the reduced pressure inside the cibarial pump is established. The relaxation of the dilator muscles removes the vacuum and no food can be sucked in.

The concept that the uptake of sap mostly depends upon turgor pressure within the plant cells, as has been shown by Kennedy and Mittler (1953), and the final conclusion of Mittler (1957) that the turgor pressure contributes significantly to sap ingestion by aphids, does not explain how aphids are able to feed on artificial diets alone and produce generations after generations without the existence of turgor pressure. From the present study of the morphological and histological details of the cibarial pump and its elaborate muscular arrangement, it is obvious that the greenbug is capable of sucking the food material on its own. Transverse sections of the cibarial chamber indicate the presence of a prominent layer of circular muscle fibers forming an external investment and an inner thin epithelial layer formed of flattened cells. The intimal lining present over the thin epithelial layer does not exhibit any modifications, although it is comparatively thicker towards the distal end of the chamber and thinner at the proximal end where it continues into the oesophagus.

Oesophagus - The oesophagus (Fig. 37, oes) runs posteriorly after passing through the circumoesophageal connectives to the end of the mesothoracic region where it opens into the dilated stomach. It is

present in the form of an extremely thin tubular structure having a uniform diameter throughout its length, and opens into the stomach by means of a highly developed oesophageal valve. The wall of the oesophagus consists of a very thin layer of circular muscle fibers (Fig. 38, C) and an inner epithelial layer (Fig. 38, E) consisting of flattened cells, apparently without any cellular boundaries but containing oval nuclei occupying central positions. The cytoplasm of the cells has a granular appearance, and the details of the cells are only distinct when stained with Heidenhain's haematoxylin. The longitudinal ridges or folds of the epithelial layer of the oesophagus, as found in some insects, are absent here. The thin layer of intimal lining investing the epithelium is quite smooth, and does not show any particular structure throughout the entire length of the oesophagus.

The well developed oesophageal valve (Figs. 41, V), which is also sometimes known as cardiac valve, consists of two layers of cells (Fig. 39, X & Y), an inner layer and an outer layer. The inner layer is in continuation with the oesophageal epithelial layer and consists of the same type of flattened cells, although they are more prominent in this region. The granular nature of the cytoplasm in these cells is more marked than cells at the distal end, and the fairly large nuclei occupy the major portion of the cells. The outer epithelial layer consists of columnar type cells resembling those of the stomach epithelial cells, but they are smaller in size (Figs. 41 & 42). Weber (1928) stated that the oesophageal valve is enclosed in the stomach epithelium

which folds back around it. Snodgrass (1935) believes that this outer layer of the oesophageal valve is the extension of the oesophageal epithelial layer. The observations made on the greenbug agree with Weber's views.

The intimal lining in the greenbug stops short at the end of the esophageal valve (Fig. 42, In) and is not continued to the outer epithelial layer or does not hang freely, as reported by Forbes (1964) in Myzus persicae. In the case of Aphis fabae, Martini (1958) described the intimal lining of the oesophageal valve as surrounding the end of the valve in the form of a sac-like structure. The latter is filled with secretory material derived from the outer epithelial layer of the valve. Weber (1928) had also referred to this structure and believed that this secretory material provides turgidity to the valve and might also diffuse into the lumen of the stomach and aid in digestion.

The function of the oesophageal valve in Aphis fabae, according to Weber (1928) and Martini (1958), is to prevent the backflow of the liquid food from the stomach into the oesophagus. When the stomach is fully distended the oesophageal valve is closed. Wigglesworth (1965) reported that the cardiac sphincter, or oesophageal valve, which is considered to function in preventing regurgitation from the mid-gut may have this function, but in most insects the invagination is quite unsuited by its structure to act as a valve. The walls are too rigid and are so disposed that the mid-gut contents can not exert pressure on its outer face.

Stomach - The stomach in the greenbug can be divided into an anterior, or cardiac end, and a posterior part. The differentiation in the two regions has been based mainly on the differences in shape, size and the number of columnar cells lining the inner epithelium. The epithelial layer of both regions consist of two types of cells: large columnar cells and small basal cells which are regenerative in function. The cardiac region has the greater number of columnar and regenerative cells. The regenerative cells (Fig. 43, R) are very small, flattened and are situated at the base of the columnar cells. The nuclei are fairly large and oval and occupy the major portion of the cells. The columnar cells are of different shapes and sizes. Some are lobate, some cylindrical and others pyramidal. Also, the shape of nuclei varies greatly (Figs. 44 - 47). Their shape is governed mainly by the secretory phase through which they are passing. The secretory activity appears to be very high in the cardiac region, as evidenced by the different physiological phases of a majority of the cells (Fig. 47). The cross sections show that the secretion is of holocrine type, because a number of cells are observed detached from the epithelial lining along with their nuclei and cytoplasmic contents (Figs. 44 & 45). The cell wall, nucleus and other cytoplasmic contents of the cell disintegrate (Figs. 43 & 46, D), the secretory material is thus liberated in the lumen of the stomach. The regenerative cells form new cells in place of the detached columnar cells (Fig. 46, Q). In the newly formed columnar cells, the secretory granules appear to arise in the basal half or sub-

nuclear region (Fig. 46, SG) from where they migrate to the lumen end, or supra-nuclear portion, and accumulate there. When the supra-nuclear region gets compacted with secretory materials, the nuclei appear to be pushed down. At this stage the concentration of the secretory material immediately below the striated border is readily observed (Fig. 47, SG). After this phase, the cell detaches from the epithelial lining (Fig. 44, F). The detached cell presents a vacuolar appearance, loses its regular boundary and exhibits different patterns (Fig. 45, G). Weber (1928), in Aphis fabae, called these secreting columnar cells active digestive cells, and those which did not show the secreting phases were termed resting digestive cells. He also stated that these resting digestive cells were more numerous in the posterior region of the stomach.

The secretory activity is not so apparent in the posterior region of the stomach (Fig. 48) of the greenbug. Only a very few cells are noticed in the secretory phases, and hence, the columnar cells have a more regular outline. There are fewer cells which are broader and are of pyramidal shape as distinguished from those of the cardiac region. The nuclei are located in the center of the cell, and the granular appearance of the cell is less marked. The striated border (Fig. 48, SB) of the cells is distinct, and properly stained sections show the striated border as a thin clear edge of the cell towards the lumen side. The regenerative cells are also few in number and their shape and size is similar to those of the cardiac region. The posterior end of

the stomach appears to be more concerned with the process of absorption.

A number of investigators have studied the mode of secretion in the mid-gut of insects. In some groups of insects only mecrocrine secretion has been described, while in some both mecrocrine and holocrine secretions occur. In others only holocrine secretion takes place. Gouin (1946) reported holocrine secretion in Chironomidae and Owsley (1946) described it in the family Asilidae. Weber (1928) and Miller (1932) have reported rhythmic secretion in aphids, but they did not indicate the type of secretion. Present studies indicate that only holocrine secretion occurs in the greenbug.

The striated border is present on the lumen surface of the epithelial cells of the mid-gut in almost all insects. Newell and Baxter (1936) reported that in some insects the striated border consists of a cilia-like structure embedded in the cuticle, while in others the cell surface is pierced by minute canals. Roeder (1953) stated that the nature of the striated border is unknown, but the elements of which it is composed lack basal granules. Forbes (1964) performed electron microscope studies of the striated border of Myzus persicae and found it to consist of numerous infoldings of the cell membrane which produce narrow septa or lamellae. Since the details of the striated border were beyond the scope of the present study, it was not worked out in the greenbug.

In the region of the mid-gut, or stomach of the greenbug, the epithelial layer is not internally bound by intimal lining. The peritrophic membrane is also absent in this aphid, as has been reported in some Hemiptera, adult Lepidoptera, and some Diptera which feed only upon fluids. Knowlton (1925) found the peritrophic membrane covering the inner surface of the digestive epithelium in Longistigma caryae, and Pelton (1938) states that the ring of columnar cells in the stomach around the oesophageal valve of Procipilus tessellatus, may be the remains of the cells that secrete the peritrophic membrane. But in the greenbug, the epithelial cells around the oesophageal valve do not present any such marked feature, and it is simply a continuation of the epithelial layer of the stomach. Forbes (1964), likewise, did not find any trace of peritrophic membrane or the presence of a circle of specialized peritrophic cells around the oesophageal valve in Myzus persicae.

The epithelial layer is externally bound by a connective tissue layer (Fig. 45, T) in close association with the basement membrane of the epithelial cells. This investing sheath has been designated as a thick basement membrane by Knowlton (1925) and Snodgrass (1935). Forbes (1964) states that usage of the term basement membrane for the whole sheath by insect morphologists is rather unfortunate, and in order to distinguish it from the generalized basement membrane, he uses the term tunica propria.

Knowlton (1925) described the circular muscle fibers lying underneath as delicate muscles in a discontinuous layer over the length of the mid-intestine and longitudinal muscles scattered irregularly on the outside of the circular muscles. The present observations agree with those of Forbes on Myzus persicae, in the presence of only the circular muscle fibers. Even in the most carefully prepared stained sections the presence of longitudinal muscle fibers could not be observed in the greenbug.

Intestine - The intestinal region of the mid-gut is marked by considerable narrowing of the posterior region of the stomach into a thin, greatly elongated tubular structure forming convolutions as described before. This results in much reduction of the lumen throughout the entire length (Fig. 49) until the intestine passes into the rectum where the lumen is considerably increased. The transverse section of the intestine (Fig. 50) shows three large epithelial cells with oval nuclei centrally disposed and occupying the major portion of the cells. No secretory activity by the epithelial cells was observed in this region of the mid-gut, and probably they have an absorptive function. The striated border of the epithelial cells is more prominent in this region. The basement membrane, connective tissue layer, and the muscular layer are exactly like those of the stomach.

The pyloric valve, marking the posterior end of the mid-gut in a number of other insects, and the malpighian tubules, are completely lacking in the greenbug. The absence of the pyloric valve in some

aphids has been reported by a number of workers: Knowlton (1925) in Longistigma caryae, Smith (1939) in Macrosiphum solanifolii, and Forbes (1964) in Myzus persicae. However, Pelton (1938) states that the pyloric valve in Porciphilus tessellatus consists of a slight constriction and differentiation of cells. He stated that the large irregular cells of the mid-intestine end abruptly and the irregular columnar cells of the hind intestine arise.

Rectum - The most evident mark of transition from the mid-gut to rectum, or hind gut, is the origin of an extremely thin, transparent, expanded, sac-like, long structure (Fig. 34) which opens outside by the anus. Histologically, the transition is marked by the ending of the large columnar cells of the mid-gut, the beginning of the highly flattened epithelial cells with small nuclei (Fig. 51, E), reappearance of a delicate intimal lining, and very prominent nature of the muscular layers. The connective tissue layer, which is found to be quite thick in stomach and intestinal regions (Fig. 50, T), becomes almost indistinct in this region and is bound by a distinct layer of circular muscles and scattered longitudinal muscles outside.

Knowlton (1925), found the hind intestine in Longistigma caryae connected to the anus by a short thick walled region, which he termed the rectum. But in the greenbug, no such modification of the posterior-most region of the hind gut could be observed.

The structure of the wall of rectum, in the greenbug, suggests that it is capable of picking up excretory products from the body cavity for excretion outside through its lumen.

CORNICLE STRUCTURE AND FUNCTION

The presence of cornicles in aphids is a characteristic feature which so fundamentally separates them from the rest of the terrestrial insects. Although the cornicles have been regarded as important traits in taxonomic studies, their exact function is unknown and the type of secretion which comes out of them is still uncertain. The aphid is often noticed with a globule of secretion in the form of a dried ball-like structure fixed at the tip of the cornicles. Earlier workers considered these droplets as honey dew. In later years, however, it was realized that the honey dew was an anal secretion in the form of minute clear, transparent droplets which differ greatly from the cornicle secretion in consistency and color. The cornicle secretion is not ejected so frequently and seems to depend upon certain conditions discussed below.

Witlaczil (1882) appears to be the first worker who performed studies on the anatomy of aphids and said that the honey dew was given out from the cornicles. He further mentioned that the globules so prominently present in the abdomen at the base of the cornicles were of various colors, such as pink, green, yellow, or red, and the coloration of certain species is due to their presence. Buckton (1882) also believed that cornicles were the source of honey dew. He called them

nectaries or honey tubes which yielded honey dew at the call of the ants. Busgen (1891) gave a completely different view after analyzing the cornicle droplets. He considered that the cornicles were the outlets of wax producing glands located in the abdomen of aphids, and that the secretion was utilized for defensive purposes against predacious enemies. Bueno (1907) claimed that the cornicles were the excretory canals of wax-producing glands differentiated in a special manner, the product of which was a means of defense against coccinellids and chrysopids. He noticed that when an ant stroked an aphid with its antennae, a clear drop appeared always at the end of the abdomen, while the cornicles excreted nothing. Gillette (1908) stated that at times waxy drops of white, yellow, brown, red, or the deepest black fluid may usually be seen as they are expelled from the tips of the cornicles, whereas the honey dew drops are formed of colorless and transparent fluid. He pointed out that it might be true that the exudation from the cornicles is somewhat protective, but it is rather difficult to believe that this secretion can be very effectual in defending the aphids from the attacks of their predaceous and parasitic enemies. Theobald (1926) described cornicles as the honey tubes placed on the dorsum of the sixth abdominal segment towards the sides. He regarded them as the terminations of the excretory ducts which pass out clear drops of fluid, but not the copious quantity of the so called honey dew that the aphids have the power of expelling from the anus. Palmer (1952) worked on the taxonomic characters where he described different types of

cornicles found in aphids. His studies were confined only to their external shape, color, and size on which he based the differentiation in genus and species. Leonard (1966) found in one specimen of Aphis sambucifoliae Fitch, a pair of additional cornicles. They were situated on the following abdominal segment nearer to the median line and were cylindrical and narrower, appeared to be less heavily chitinized, and about one-half of the length of the primary cornicles. Edwards (1966) worked on the cornicle secretion and noticed that deflection of the cornicle or a light touch on the aphid's body elicited the release from the cornicle of a fluid composed of lipid droplets in a water vehicle. The lipid droplets coalesced, and when in contact with a solid surface, rapidly crystallized to form hard waxy plaques. A small predator, such as a coccinellid or a syrphid larva receiving such a droplet, was promptly fixed and was unable to extricate itself. He gave reasons for the hardening of the cornicle secretion upon its extrusion that the fluid was in a stable liquid-crystalline state within the body, but changed to the solid crystal phase on contact with an external object. The rapid crystallization on contact with a solid surface like a hair or dust particle, suggests that the liquid wax is in a supercooled state and that the foreign material provides a seeding nucleus for the rapid crystallization. Strong (1967) made observations on the cornicle secretion of Myzus persicae (Sulzer), Acyrthosiphon pisum (Harris) and Chaitophorus Koch sp., and performed its chemical analysis. He mentions that the globules within the body constitute

lipid material emulsified in an aqueous medium. When the external droplet is produced, the globules coalesce and in some unexplained manner become miscible with the aqueous medium. The droplets harden as soon as sufficient water has evaporated to supersaturate the solutes contained therein. This evaporation undoubtedly causes some supercooling of the droplet which aids in the rapid crystallization of the lipid material. His chemical analysis indicated that the cornicle secretion was not composed of wax. The secretion was primarily composed of triglycerides, and myristic acid was the major fatty acid component of these triglycerides.

So far, Hottes (1928) appears to be the only researcher who attempted morphological and histological studies of the cornicle of aphids. Since the external form of cornicles varies in different groups of aphids, they have been recognized as important characters, and thus on the basis of structure, he divides them in to five catagories: procornicular, tuberculate, truncate, cylindrical, and pore-like. He concisely describes the internal structure of each type and finally traces the evolution of cornicles in the family Aphididae. His histological description depicts the idea that in each type a well developed glandular system is present, although he could not find any particular gland associated with his so called gland cells. Hottes claims to have seen nuclei and cytoplasm in the globules of secretion, and hence he called them gland cells containing the secretion, which escape through the opening of the cornicle. In order to give support to this theory he mentioned that the

large amount of waste material given off in the form of honey dew by the aphids indicates that the sap upon which they feed is limited in some elements, probably proteins, which can be obtained in necessary amounts only by taking into the digestive system an excessive amount of the sap which is composed largely of carbohydrates. The sap of plants is known to be a very complex substance, and when these substances are incapable of being assimilated, they are discharged along with these gland cells.

The observations made by Hottes do not present a vivid picture, and the idea conceived by him that the globules are gland cells, does not find any parallel instance in the whole insect group. Since very little information is available on the aphid cornicles and their function, and absolutely no work exists in the case of Schizaphis graminum, it was thought pertinent to investigate them.

Materials and Methods

The anatomical studies of cornicles were made by dissecting fresh specimens of both apterous and alate forms in Ringer's solution. The whole mounts of aphids were prepared in order to study the musculature of cornicles and their general morphological characters. For histological preparations Carnoy's fluid and Bouin's solution were used. Longitudinal and transverse serial sections were cut at 6 microns. The sections were stained with safranin O and fast green.

The cornicle secretion was collected from the greenbugs by artificial means and given to the Biochemistry department for chemical analysis. For the collection of the secretion it was noticed that sometimes a mild touch on the body of the aphid, whether immature or adult, provoked it to raise the cornicles and emit a large globule of secretion which soon dried into a solid ball-like mass. This secretion was collected from the tips of the cornicles. But quite a number of aphids did not respond to this mechanical method of touch, and hence other methods were tried, such as blowing air, stroking the antennae and legs, or even pressing the abdomen gently. The best method turned out to be that of giving low voltage electric shock on the head. The shocks were given at different voltages and cycles per second, and it was found that at 10 volts and 80 cycles per second, the aphid responded best. The first shock at this voltage immediately resulted in the production of secretion from both of the cornicles. After 10 or 15 minutes when the same aphid was tried again, sometimes the secretion from only one cornicle and seldom from both, was obtained, but this second time the size of the secretion globule was always smaller in comparison to the first ones. The secretion could not be obtained a third time even after a lapse of two hours. At the time of giving electric shocks to the feeding aphids, it was noticed that apart from discharging the secretion from the cornicles, they also withdrew their stylets from the plant tissues and did not attempt to feed for quite a long time. Thus, for the collection of the secretion both apterous and

immature forms were given shock only once, and the secretion was picked up from the tips of the cornicles as soon as it was dry. Two petri-dishes containing secretion from about 1200 aphids were given to the Biochemistry department for analysis.

Results and Discussion

The cornicles of Schizaphis graminum (Rond.) are a pair of tube-like structures about. 15 mm long located on the dorsolateral surface of the sixth abdominal segment. Normally, the cornicles remain pointing towards the posterior (Fig. 60), but they are capable of movement along the longitudinal plane of the body and are held erect or slightly pointing towards the anterior at the time of discharge of the secretion (Fig. 63). The distal one-third portion, including the tip, is black, and the proximal two-third part matches the color of the body. The basal portion of the cornicle exhibits transverse wrinkles, and the body wall surrounding the place of the origin appears to be slightly raised. The external aperture of the cornicle is almost circular and the edge of the tip is thrown into many short flanges (Fig. 52, F) which surround this aperture. When viewed dorsally, the center of the aperture is noticed to be occupied by round chitinous valve (Fig. 54) which regulates the opening and closure of the aperture.

The chitinous layer forming the external wall of the cornicle is in continuation with the general integument of the body, but is comparatively thicker and darker in color. The hypodermal layer lying

immediately below the valve is the same as in the rest of the body. Hottes (1928) believed that the external chitinous layer is derived from the ectoderm, and Witlaczil (1882) considered the internal hypodermal layer to be derived from mesoderm of the embryo.

The lumen of the cornicle lies in direct continuation with the haemocoel of the body (Figs. 58 & 62), and is not connected either directly or indirectly with any special gland. This is evidenced by the fact that when the tips of the cornicles containing the valve are removed by cutting, and the body of the aphid is pressed gently, the haemolymph oozes out through them after the extrusion of the globular material which was accumulated at the base of the cornicles in that region of the abdomen. This further suggests that the extrusion of the fluid from the cornicle is wholly dependent upon the valve. The valve of the cornicle (Figs. 53 - 57) is situated at the tip and in dorsal view it appears as a separate chitinous piece. The longitudinal sections of the cornicles show that the chitin to which the valve is fastened extends downwards for a short distance and then bends back upon itself, forming a sort of hinge on one side (Figs. 52 & 55, H). The valve fits against an inwardly projecting portion of the rim or flange of the tip of the cornicle, thus causing the opening to be completely closed. Just below the outer chitinous layer of the valve there are highly elongated cells with oval nuclei. These cells are drawn into muscular fibers farther back and form the so called long and thick muscle of the valve. This longitudinal muscle traverses down into the abdomen and is attached on the

ventro-lateral side of the venter of the 6th abdominal segment opposite the internal opening of the cornicle into the abdomen (Figs. 58 & 59, Lm).

The elongated cells of the valve in other aphids, have been considered by some previous workers to be glandular in function, but Hottes (1928) claimed that although these cells are much larger than the ordinary cells of the hypodermis, they are not so large that any glandular function can be ascribed to them. Besides none of the characteristics of the active glandular cells are exhibited by these cells, and since they differ only in size they are probably modified hypodermal cells. The present studies on greenbug support the contention that their presence in such a place is not without purpose. These cells are the modified hypodermal cells which probably secrete a fluid. Since it is already known that the secretion of the cornicle is sticky and soon dries on exposure to air, there is every possibility of the valve being plugged and that the secretion from these cells might be rendering it free from such sticking. It is true that these cells do not present any features typical of glandular cells, but judging the cells by their mere appearance is no criteria. Their location and possible function are equally important. The present observations on the greenbug are in agreement with those of Hottes that they are hypodermal in origin because, in sections of both adults and nymphs, continuation of the hypodermal layer of the body wall (Fig. 57, Y) beneath the valve is distinctly noticed on one side. Further, there are numerous instances

in the histology of insects where the hypodermal cells have adopted secretory function and are connected with the muscles. Snodgrass (1935) mentioned that the most important mechanical feature of insect organization is the intimate connection between the body wall and the muscles. Yet in their origin, the hypodermis and the muscle tissue are entirely distinct, the first being derived from the ectoderm and the second from mesoderm. The muscle fibers are attached to these cells by fine connective fibrils, the tonofibrillae (Fig. 55, Tn). The tonofibrillae are produced by the transformation of the hypodermal cells at the ends of the muscles into cuticular fibrils that become continuous with the muscle fibrillae. Further, Hottes (1928) does not give any reason for the presence of such hypodermal cells, because as far as only the operation of the valve is concerned, it could have been effectively accomplished by the direct insertion of the muscle fibers over the chitinous wall of the valve. The hypodermal cells would have been quite superfluous. Thus, it appears reasonable enough that these elongated hypodermal cells placed on the inside of the chitinous wall of valve are secretory in function.

Normally the cornicles are found in a relaxed state bent towards the posterior side in a plane approximately parallel to the longitudinal axis of the body (Fig. 60), but at the time of the discharge of the globular material from the abdomen they are always held pointing towards the anterior of the body or vertical to it (Figs. 62 & 63). This shows that in the relaxed state when the cornicles are pointing posteriorly,

their openings remain closed by means of the valves. The contraction of the muscle of the valve not only pulls the valve and opens the aperture of the cornicle but at the same time moves the cornicle about 90 degrees to the anterior side, and the accumulated globular material then escapes to the exterior. The relaxation of the muscle brings about the shifting of the valve to its original position thereby closing the opening and gradually moving the cornicle back to its posterior direction due to release in tension. This backward and forward movement of the cornicle is solely dependent upon the elongated muscle of the valve. It is unable to perform any sideways movement, because no other muscle is present to bring about its lateral movement. Hottes could not observe the proximal insertion of this muscle in his sections but suggested the possibility that either it was inserted at the base of the cornicle or in the abdomen. In the greenbug, the proximal end of this muscle is attached on the inner lateral side of the venter of the 6th abdominal segment (Fig. 59).

Cornicle secretion - The mechanism which forces the globular droplets from within the abdomen to the exterior is not known. Edwards (1966) suggested that the expulsion of the cornicle wax is effected by abdominal turgor pressure. But, it is doubtful if the abdominal turgor is solely responsible for forcing out the fluid, since the production of the droplets is a voluntary affair and not a mechanical one. All the aphid instars produce the secretion from the cornicles. The production

appears to be under direct nervous control, since any stimulus applied on the body results in the erection of the cornicles and ejection of the fluid. The droplets when they emerge (Fig. 62) from the cornicle opening, coalesce to form a large ball of secretion (Fig. 63) which is so commonly noticed attached to the tip of the cornicle of most aphids. In the greenbug this ball of secretion is greenish in color at first, and as it begins to harden it turns slightly blackish. In the case of 50 specimens the average time taken for the hardening of the secretion was ascertained to be 21.1 seconds. It was noticed that when this hardened ball of secretion was kept on water soaked filter paper, the black color dissolved and disappeared, and the globule again became of the original color. But, those collected on dry filter paper maintained their blackish tinge.

The material which is secreted is distinctly visible accumulated within the living aphid in the posterior segments of the abdomen close to the base of the cornicles (Fig. 60, W), in the form of greenish globular material. These droplets appear to originate in the thoracic region (Fig. 61) from where they are pushed posteriorly along the lateral sides of the abdomen and accumulate in the 6th and 7th abdominal segments, with the result that these segments of the body exhibit deeper greenish color than the rest of the body. Hottes (1928) called them regular cells in the form of spheres containing nuclei, vacuolated cytoplasm, and sometimes enclosing a large vacuole. But his presumtion was completely wrong, since he could not realize the nature of

these globules. The greenish granular material which adheres to these globules and is stained deeply by any regular nuclear stains was mistaken for nuclei and it was these structures which led him to think that the globules were gland cells. Edwards (1966) called this globular secretion the cornicle wax and suggested that the cornicle wax arises from cells which may be modified oenocytes. According to him the secretion is stored in large globules enclosed by a membrane, sometimes together with residual cytoplasm and nucleus, sometimes without, which lie in the cornicle stalk and in the haemocoel below the cornicle. But the observations made on the greenbug did not indicate the presence of any such membrane enveloping the globules or the presence of nucleus and cytoplasm, even though various nuclear and cytoplasmic stains were used. They appeared like the normal lipid droplets containing some greenish granular material which always took a heavier stain (Fig. 64). Strong (1967) also did not notice any such membrane and called them only droplets. Strong is of the opinion that the cornicle droplets originate from the dorsolateral area of the abdomen in the area of cornicle attachment, and the globules which form the cornicle droplets must be separated from blood sinuses, because the blood is not extruded along with them. But this separating membrane has never been observed. With regard to the extrusion of haemolymph and blood cells along with the droplets, the observations on greenbug differ somewhat from those of Strong. Very few blood cells could be found in the first globule of secretion emitted from the

cornicles (Figs. 65 & 66). When the aphid was stimulated further, the second mass of secretion was always found to be accompanied with some quantity of haemolymph with blood corpuscles, as is evidenced by the microphotograph of the second discharge of secretion displaying a number of blood cells and greenish yellow lipid plaques having radiating lines (Fig. 67). This indicates that there is no separation of the lipid droplets from the haemolymph by means of a membrane or any such structure. Because the lipid droplets have a higher density than that of the haemolymph, they tend to be attracted to one another. Their accumulation at that place pushes the haemolymph from that area so that normally the area is almost occupied by the lipid droplets, which are the first to be extruded. The reason for the globules accumulating in that area alone and not in other regions of the abdomen can be ascribed to the fact that the anterior region of the body cavity beyond sixth abdominal segment is packed with developing embryos, and there is hardly any space to permit such an accumulation.

The source from which the secretion globules are derived is still unknown. Witlaczil (1882) designated these droplets as sugar cells found in the cornicles and in the vicinity of their base although he recognized that the honey dew was ejected from the anus. Later, he modified his views and regarded these cells as having a urinary function. Busgen (1891) conceived the idea that the cornicle droplets were composed of wax. But Hottes (1928) did not comment either on their chemical nature or on their origin. He mentioned that the spheres

show a somewhat distant resemblance to fat cells from which they may be separated quite easily by their nuclei. Their cytoplasm is more uniformly vacuolated than the cytoplasm of the fat cells and takes a darker stain. Edwards (1966) remarked that these globules are cellular elements which are derived from modified oenocyte cells of haemolymph. But neither in the investigation of Strong (1967) nor in the present studies on the greenbug, could any cellular nature of the globules or the presence of nuclei be detected. If the cornicle secretion arises from the modified oenocyte cells, there does not appear to be any plausible reason for such origin in the absence of any vital function. Further, it would then be difficult to explain the fact that there is no increase in the number of these globules inside the body if the aphid is starved for a few hours. It might look more reasonable that the secretion is a by-product of the sap taken from the plants which is not required by the body.

It is not only when the aphid is attacked by predators or parasites that the secretion is ejected from the cornicles, but it also comes out normally and more frequently during warm weather. The correlation of cornicle secretion with that of temperature was also noticed by Strong (1967) in the case of pea aphids.

Strong (1967) rightly pointed out that if the droplets were wax material, then wax-producing glands, specialized cells, or some other such structure should have been present to produce this material. The histological observations made on the greenbug also did not reveal any

glandular structure at the base of the cornicles or in other parts of the body which could be assigned this function. The globules are present, though of much smaller size, in the region of the meso- and metathorax from where they are pushed posteriorly along the lateral sides of the abdomen towards the base of the cornicles (Fig. 61). These droplets, as they migrate from the anterior to the posterior part of the body, grow larger so that in the region of their accumulation droplets of different sizes are commonly noticed. Thus the region of their origin appears to be that which is accupied by the anterior portion of the mid-gut.

The general misunderstanding that the cornicle secretion is composed of a wax-like substance dates back from the time of Busgen (1891) who was the first man to analyze this substance and declare its waxy nature. Recently Strong (1967) analyzed the cornicle secretion of Myzus persicae and Acyrthosiphon pisum and showed that the droplets were not wax. He found traces of six amino acids in the cornicle droplets of M. persicae, but none in A. pisum. He did not identify these amino acids individually. In his further experiments for lipid constituents, he found 3 triglycerides and a small amount of hydrocarbons.

The biochemical analysis of the cornicle secretion of the green-bug showed the presence of 8 amino acids, of which one could not be identified. In the tests for lipids, triglycerides were found to be the major components. Some phospholipids and traces of long chain hydrocarbons were also present. The different amino acids and the lipid

constituents identified are given in Table 1.

Table 1. Components of cornicle secretion of Schizaphis graminum.

Free Amino Acids	Lipid Isolation
1. Aspartic acid	1. Triglycerides
2. Threonine	2. Phospholipids
3. Serine	3. L. C. Hydrocarbons
4. Glycine	
5. Alanine	
6. Tyrosine	
7. Phenylalanine	
8. Unknown	

The constituents of the cornicle secretion show that some of the free amino acids which are ordinarily considered to be of vital importance for normal growth and other metabolic processes of insect body, are also given out. This suggests that the body of the aphid is already getting the required amount of these important elements, and the excess is discharged. Otherwise, they would not have been metabolically set apart for later elimination from the body. The same holds true for lipid components which are the main elements of insect fats. In view of the feeding habits of aphids it appears most probable that the intake of the plant sap rich in proteins, carbohydrates, and lipids,

is so much that the removal of the excess material becomes equally important. Certain of these sap products must be incapable of being assimilated even though they enter into the blood stream of aphid, and it is probably these products that form the globules which ultimately collect at the base of the cornicle.

Function of cornicle - Various functions like excretion, respiration and defense have been ascribed to the cornicles of aphids. The function of respiration was rejected outright because the cornicles are not connected to any respiratory organs and they can not be compared to the respiratory siphon of some insects. The validity of the theory of defense which has persisted for many years and is held even now by some aphidologists can be questioned very seriously, and the presence of cornicles for the sole purpose of defense would appear inappropriate when considered critically, keeping in view their internal structures, the variation in form they present in different aphids, and the type of secretion produced by them. The cornicles are not in the form of long tubular structures in all aphids. In some, they are very short while in others they are only represented by pores. In such cases the secretion can not be directed towards the predator or parasite. Even the tubular types are only movable in one plane, parallel to the longitudinal axis of the body and are incapable of performing any sideway movement. Further, in other insects whenever we find any tubular chitinous secretory structure serving for defensive purposes, they are always associated with some type of internal glands specifically meant

to produce such a secretion. The constituents of secretion of other insects are almost similar, but in aphids the constituents of cornicle secretion may differ even in the same species depending upon the plant and tissues upon which they are feeding. This is evidenced by the present results of analysis on the greenbug and those of Strong on green peach aphids and pea aphids. The cornicles are mere extensions of body wall and are not connected with any gland whatsoever. Roth and Eisner (1962) worked on the defensive organs of arthropods, particularly the insects, but they have not recognized the defensive nature of cornicles. They stated that defensive secretions are produced by definite glands. Many animals do not discharge their secretions at random but actually aim them towards the source of disturbance. Localized unilateral stimuli will elicit a discharge from only the one gland of the corresponding side. Some cockroaches can control to some extent the direction of discharge from the abdominal glands by turning the abdomen to the right or left or by raising and lowering it. The ability to aim the secretion is clearly an advantage, since it provides for maximum effectiveness with minimum expenditure of secretion.

A case of haemocoelic discharge performing defensive function is found in coccinellid beetles, as reported by Happ and Eisner (1961). According to them, the coccinellid beetles have the peculiar habit of discharging small droplets of blood from one or more points on their legs when they are handled or otherwise molested. They named it reflex bleeding and called it a mechanism of defense against their

enemies. The fact of special interest they noticed was that all the legs do not bleed simultaneously but only a particular leg closest to the stimulus responds. The leg is even sometimes rotated in such a way that its blood-laden joint is brought closest to the point of stimulus. In the case of greenbugs, the haemocoelic discharge, which has been termed here as cornicle excretion, is normally without any trace of blood.

The movement of tubular cornicles forwards and backwards might have led some workers to believe that the secretion is aimed at the source of disturbance, but the idea does not seem to be correct. The construction of the cornicle valve in the greenbug is such that when the cornicle is directed posteriorly, the valve keeps the aperture closed and the valve muscle remains relaxed. At the time of the discharge of the globular material, the valve muscle contracts so that the cornicle tube is pulled anteriorly, and the valve then slides back thus making the aperture open. Edwards (1966) states that when the cornicle valves are opened, the aphid releases the material from the haemocoel. It looks curious that a parallel method of reflex bleeding should exist in coccinellids which are important predators of aphids. If it is supposed that the haemocoelic discharge of coccinellid beetles is comparable to that of aphids, then there should not be any necessity for the separation of the globular material from the blood. The blood as such could have been discharged and performed a defensive function

Strong (1967) plugged the cornicles of Myzus persicae and Acyrthosiphon pisum with silver paint and found that the aphids remained alive for 12.5 days. From this he deduced that if the cornicles were closed it would do no harm to the insect. In other words, he implies that if the cornicles are meant for excretion the aphid would not live that long, and consequently, a defensive function attributed to them would appear more appropriate. But, it is known that in the absence of malpighian tubules, other organs besides alimentary canal, like the salivary glands, (Nuorteva and Laurema 1961) take up the function of excretion and are able to eliminate toxic substance from the haemolymph. Since the process of excretion is not completely withheld by plugging the cornicle opening, no symptoms of immediate fatal injury is likely to be noticed and the effect is bound to be obvious after a prolonged period. At the same time it must be borne in mind that the removal of undesired substances present in the blood by the salivary glands is very limited. In the absence of malpighian tubules, the cornicles and alimentary canal are the only structures present through which the insect can get rid of the heavy amount of these substances. The only difference between the excretion by malpighian tubules and by cornicles that would appear to exist, would be that the former absorb undesirable substances from the haemolymph and pour it into the alimentary canal for expulsion outside of the body while in the latter, a separation of these substances from the haemolymph first occurs by some mechanism and then the material so separated in the

form of globules is directly expelled outside.

Hottes (1928) after performing a detailed study of the structure of cornicles in different aphids, could not assign them any other function except that of excretion. The observations made on the greenbug, too, point the facts only in this direction and appear to be much more convincing than the defensive function.

Thus it can be safely concluded that the cornicle secretion of the greenbug is actually excretory material, and the cornicles are primarily concerned with the process of excretion. The aphid also might be ultilizing this fluid for defensive purposes.

NERVOUS SYSTEM

Recent trends in applied research has increased the interest of physiologists and toxicologists in the morphology of insect nervous systems. Much more has been learned in the past decade about the central, sympathetic and peripheral nervous system than was made known by all earlier studies combined. Major work has been done on Hemiptera, but although Homoptera is a closely related and economically more important group, it has not received such attention. The work on insects, other than aphids, includes that of Bickley (1942) who gave a comparative account of the stomodaeal nervous systems in grasshopper, dragonfly naiad, cicada, green stink bug, wheel bug, green June beetle, wasp, and robberfly. He preferred to call the sympathetic nervous system the stomodaeal nervous system, because the ganglionic centers belonging to this system arise during embryonic development by the ingrowths from the dorsal wall of stomodaeum. Woolley (1949) described the general plan of the central nervous system in Leptocoris trivittatus (Say). He found that the mesothoracic, metathoracic, and all the abdominal ganglia had fused into a single ganglionic mass which was situated in between the pro- and mesothoracic segments. Johansson (1954) experimented on the relationship of nutrition to corpora allata and egg production. He reported that in

Oncopeltus fasciatus (Dallas), nutrition is responsible for the normal development of corpora allata which induces the development of egg. Starvation of the bug hampers the normal growth of corpora allata and leads to no egg production. Rutschky and Stryjak (1955) described the outline of the central nervous system of O. fasciatus and very briefly discussed the sympathetic nervous system. Again Johansson (1957) published a comprehensive description of the various parts of the central and sympathetic nervous systems of O. fasciatus. Wigglesworth (1959, a & b) reported his findings on the peripheral nervous system and central ganglia of Rhodnius prolixus Stal. His work gave the first clear conception of the effect of secretions from neurosecretory cells, commonly known as hormones, on the molting and metamorphosis of an insect. His findings led to intensive research in this field on other insects by various other workers, thus adding to the knowledge of the nervous control on such physiological processes. Schmitt (1962) incorporated the findings of other workers and gave a comparative review of the central nervous systems of Neuroptera, Plecoptera, Orthoptera, Lepidoptera, and Coleoptera. He pointed out that the nerve topography in insects has lagged far behind in comparison to other aspects of morphology due to the difficulty of relating the findings of one group of insects to those on another.

Among aphids, probably the small size has been responsible for lack of enough research in this field. Important contributions, however, include that of Grove (1909) who worked on the anatomy of

Siphonophora rosarum Walk. and described a general plan of the central nervous system. According to him the nervous system of this aphid is greatly condensed due to considerable fusion and elimination of ganglia. The whole nervous system is marked by three prominent ganglionic masses, the supraoesophageal ganglia, suboesophageal ganglia, and the thoracic ganglionic mass. Cazal (1948) described the stomatogastric nervous system, particularly the retrocerebral endocrine glands, in a number of Homoptera. Johnson (1962) reported on the neurosecretion and transport of secretory material from corpora cardiaca and neurosecretory cells of the brains of Aphis fabae Scop. and Drepanosiphum platanoides (Schrank). The secretory material from neurosecretory cells is considered to be released directly into the blood. He has shown that large amounts of secretory material found in aphids appears to leave the corpora cardiaca along the lateral and medial nerves, suggesting thereby that this is probably the main method of release and that the secretory material does not enter the blood at all but is transported directly to the tissues which have to be influenced. He further mentioned that in aphids the presence of neurosecretory material throughout the length of the ventral nerve cord indicates that the neuroendocrine system of insects is rather a more closed system than was thought before. Johnson (1963) contributed to the knowledge of histological studies of neurosecretion in Aphis craccivora Koch, Aphis fabae, Acyrthosiphum pisum (Harris), Pemphigus bursarius Linnaeus and Drepanosiphum platanoides. He concluded that in aphids,

the corpora cardiaca functions as the neurohaemal organ since such organs have not so far been demonstrated in insects. But, in crustaceans it has been shown that the secretory material of the neurosecretory cells is transported along the axons and these axons have been traced to distinct organs termed the neurohaemal organs which are responsible for the release of the neurosecretory substances into the blood.

Absolutely no work exists on the nervous system of Schizaphis graminum (Rond.). Therefore, an investigation pertaining to central and stomatogastric nervous systems, was considered most essential.

Materials and Methods

Adult greenbugs reared in the laboratory on Rogers barley plants with a minimum number of embryos inside were selected for dissections. The general plan of the nervous system and nerve innervation in different parts was examined both in fresh and preserved specimens. Dissections of fresh specimens were always covered with 5% acetic acid solution for 10 minutes in order to bring stiffness to the nerves. The dissections were stained with 1:1000 methylene blue solution and some with aceto-carmine stain. Methylene blue solution was found useful in the study of nerve branching in the abdominal region with the visceral parts intact, while aceto-carmine gave better differentiation in the head and thoracic regions.

Most of the observations were confirmed by serial transverse and

longitudinal sections because of the minute size of the insect. The sections of the embryos were also prepared in order to trace some of the developmental stages of the nervous system. The material for sectioning was fixed in Petrunkevitch's paranitro-phenol solution for 6 hours. The fixative consisted of 60% ethyl alcohol - 96 ml.; nitric acid - 3 ml.; ether - 5 ml.; cupric nitrate - 2 grams; paranitro-phenol - 5 grams; formaldehyde - 26 ml. The specimens were dehydrated with dioxane and cleared in xylol. The paraffin of the sections was dissolved in xylol and then the slides containing sections were placed in 1% protargol solution containing copper filings (4 gms. of metallic copper per 100 ml. of solution) and incubated for 24 hours at 38°C. Next the sections were washed with distilled water and kept for 5-10 minutes in the reducing solution consisting of hydroquinone 1 gram, anhydrous sodium sulphite 5 grams, and 100 ml. of distilled water. After reduction, the sections were thoroughly washed by keeping them for 5 minutes in each of the 3 changes of distilled water. The sections were gold toned by placing the slides in .1% solution of gold chloride for 15 minutes, rinsing in distilled water and keeping for 5 minutes in 5% sodium thiosulphate solution. Finally, the sections were dehydrated in ethyl alcohol series, cleared in xylene, and mounted in Canada balsam.

Results and Discussion

The nervous system of the greenbug is greatly condensed (Fig. 68) and is marked by only a few ganglionic masses present in the head and thoracic regions. The abdominal region is completely devoid of any

ganglionic structure, though the ventral nerve, as in Hemiptera, innervates the first seven segments. The nervous system has been greatly simplified by the elimination of a number of ganglia and the fusion of the existing ones. The simplicity of the nervous system might appear to indicate primitiveness, but, in fact, it is more highly evolved since the primitive segmental arrangement of ganglia is no longer present and the consolidated ganglionic mass controls the whole portion of the body from these centers alone.

Central Nervous System - The central nervous system of the greenbug consists of cerebral ganglia, suboesophageal ganglion, thoracic ganglionic mass, and the ventral nerve cord (Fig. 68). The two cerebral ganglia are completely fused and the suboesophageal ganglion is represented by a single lobe (Fig. 69) although, according to Snodgrass (1935), in other insects during it embryonic development it is formed by the fusion of three pairs of ganglia. The thoracic ganglia of the greenbug, though externally have the appearance of a single mass (Fig. 70, r) are, however, partly separate and have fused only in the middle (Fig. 69, Tg). The abdominal ganglia are represented by a single ganglion (Fig. 69, Ag) which has also fused with the thoracic mass at the posterior end. From the posterior end of the abdominal ganglion, the ventral nerve cord originates and traverses most of the segments of the abdomen.

Cerebral ganglia: The cerebral ganglia or brain of the greenbug occupies about two-third of the space of cranial cavity. Embryologically,

the brain is formed by the fusion of three neuromeres of the embryo, but this coalescence is much less apparent by the external contours in the adult brain. All three parts are distinct in the internal organization of the brain. The dorsal and largest part is the protocerebrum (Fig. 69 & 74, Pr), the middle part which projects slightly to the anterior side is the deutocerebrum (Fig. 74, De), and the third part of conical shape situated on the ventral aspect is the tritocerebrum (Fig. 74, Tr). From the posterior end of the conical tritocerebrum, two short thick branches arise which pass into the suboesophageal ganglion and are known as circumoesophageal connectives (Fig. 69, K). The internal organization of the brain is mainly an association center between the motor neurones of different body parts and the sense organs of the head. It is marked by a dense mass of nerve fibrils running in different directions and a large number of association neurones (Fig. 71, An).

The protecerebrum on its lateral aspect on either side bears prominent optic lobes (Fig. 69, Op) which contain the complex visual centers of the eyes. The optic lobes consist of 3 ganglionic divisions: a distal bulb-shaped part, the lamina ganglionaris; a small middle part, the medulla externa; and the largest proximal part, the medulla interna (Fig. 72). The nerve fibrils of lamina ganglionaris form a chiasma before they enter the medulla externa as do the nerve fibrils of medulla externa when they enter the medulla interna. The medulla interna possesses a larger mass of nerve fibrils than the other two regions. The condensed chiasmatic condition of the fibrils, as noticed in

lamina ganglionaris and medulla externa, is not so clear in this region since fiber tracts adopt different and divergent courses. The medulla interna joins the protocerebrum by means of a large number of nerve fibrils.

In the middle of the two lobes of protocerebrum lies the disk-shaped body, the corpus centrale (Fig. 72, CC). It consists of numerous glomeruli and is considered to be the most important association center of the brain. Fibrils from different parts of the brain converge into it.

On the dorsal and posterior side of the corpus centrale a transverse body the pons cerebralis, or the protocerebral bridge (Fig. 72, PC), is located. This transverse structure appears to merge on either side in the large ganglionic structures, the corpus pedunculatum (Fig. 72, Cp). Pons cerebralis is the association center of the brain. In some insects according to Johansson (1957) it has often been considered as a center for the ocellar stalk.

The corpora pedunculata (Fig. 72, Cp) are the mushroom-shaped bodies situated dorsally on either side of the corpus centrale. Each corpus pedunculatum consists of a broad posterior part, a middle stalk-like structure, and a cap-like slightly expanded terminal part. The cap-like portion is covered with association cells which have nuclei rich in chromatin. These cells commonly known as globuli cells are more dense on the anterior side of the cap than on posterior part. The stalk is mostly formed of the axons of the globuli cells of

the cap which further branch in the broad portion where they establish intercommunication with one another. Snodgrass (1935) mentions that corpora pedunculata constitute the largest and most highly developed association centers in the brain of pterygote insects.

The dorsomedial portion of the brain, lying partly between the two corpora pedunculata, has been designated as pars intercerebralis. In some Hemiptera and other insects, pars intercerebralis is completely surrounded on either side by corpora pedunculata. In the greenbug (Fig. 72, Pl) the cap and stalk portion of corpora pedunculata reach only midway, the anterior part being more broad and free. Lately the pars intercerebralis has assumed great importance since it is in this portion of brain that the glandular neurones have been found. These neurosecretory cells secrete a hormone which plays a vital role in the molting and metamorphosis of the immature stages of insects. In the adult stages of some insects they are concerned with the maturation of gonads. In the greenbug the neurosecretory cells are mostly concentrated in the broader part of pars intercerebralis. They are easily detected as they take much deeper stain.

In the alate females of the greenbug 3 ocelli are present on the head, 2 just at the bases of the antennae while the third occupies a mid-anterior position. These ocelli are borne on ocellar pedicels formed of nerve fibrils from the protocerebrum in the respective spots. The ocelli are completely absent in the apterous forms. The deutocerebrum (Fig. 72, Dc) is the middle part of the brain, and like the

protocerebrum, is a two-lobed structure although externally no such demarcation can be made out. The only nerves given out from this part are the short, stout antennary nerves. Each antennary nerve (Fig. 72, A) arises from the anterior portion of each division of the deutocerebrum and is composed of both sensory and motor fibers contained in a single trunk. The sensory fibers are given out by the various sense organs lodged in the antennae, and the motor fibers supply the muscles of the antennae. The main body of deutocerebrum is composed of loosely scattered nerve fibrils, large number of glomeruli, ganglion cells, and a few association neurones. Johansson (1957) mentioned that in Oncopeltus fasciatus, out of the two parts of deutocerebrum one is a sensory center while the other acts as a motor center. But in the greenbug no such plan appears to exist since each division receives its own sensory fibers and sends out the motor fibers. The arborizations of both motor and sensory nerves are present in each lobe of the deutocerebrum.

The tritocerebrum (Fig. 74, Tr) is the postero-ventral part of the brain which projects posteriorly in the form of two cone-shaped lobes. From these lobes of tritocerebrum two short and stout circumoesophageal connectives run ventrally and posteriorly around the oesophagus and join the suboesophageal ganglion. Just at the point of origin of the circumoesophageal connectives, a transverse commissure connects the two lobes of the tritocerebrum. The only other nerve given out from each lobe of tritocerebrum is to the frontal ganglion, thus

establishing a connection with the stomatogastric nervous system. These nerves enter the frontal ganglion on either side. The nerve fibrils from the deutocerebrum run to the tritocerebrum and form connections with the nerve fibrils forming the circumoesophageal connectives and the transverse commissure. However, the fiber tracts are much less in this region in comparison to other parts of the brain.

Suboesophageal ganglion - The suboesophageal ganglion (Figs. 69 & 74, S) lies immediately below the thin tubular oesophagus, posterior to the brain. It extends from the mid-posterior region of the cranial cavity to the anterior part of the prothoracic segment. The circumoesophageal connectives joining it with the brain are short and thick. A pair of nerves arising from its anterior part run antero-ventrally where they bifurcate and supply the mandibles and maxillae. Another pair innervates the principal salivary glands, the branches of which ramify on the membranous part. The anterior region sends out a nerve to accessory glands on either side. A single nerve goes to the cibarial pump, and a pair arising from the ventral aspect of the suboesophageal ganglion supplies the labium. The nerves contain both motor and sensory fibers. The main mass of suboesophageal ganglion contains a large number of longitudinal fiber tracts. According to Snodgrass (1935) in other insects, these fiber tracts are very important since they contain connective fibers between the sensory centers of the head and the motor centers of the body.

Thoracic ganglionic mass - In the greenbug the posterior part of the suboesophageal ganglion is fused with the anterior portion of the thoracic ganglionic mass. This ganglionic mass is in the form of an oval structure extending from the posterior region of the prothoracic segment to the first abdominal segment. Externally the whole mass appears to be a single structure being encased in a continuous perilemma (Fig. 70, T), but actually it is formed by the fusion of pro-, meso-, and metathoracic ganglia, and a single abdominal ganglion at the posterior end. The abdominal ganglion is also included in the same perilemma (Fig. 69, Ag). The three thoracic ganglia are almost completly fused except on the lateral margins where the divisions can be distinctly noticed in a longitudinal section (Fig. 69, Tg).

During the early embryonic development, the 3 pairs of thoracic ganglia are separate from each other (Fig. 73, Tg) and from the suboesophageal ganglionic pair. In the later stages of development, the suboesophageal pair coalesces (Fig. 75) completely and also fuses posteriorly with the already fused thoracic ganglia. The abdominal ganglion (Fig. 75, Ag) shows up at the posterior end of this thoracic ganglionic mass and the ventral nerve cord arises from it. At this stage the divisions of the thoracic ganglia are only marked on the lateral sides which persist as such in the adult stage.

Four pairs of nerves arise from the thoracic ganglionic mass. The three anterior thoracic pairs supply the legs (Fig. 68), while the fourth pair, emerging from the abdominal ganglion, innervates the

first abdominal segment supplying the spiracles and the abdominal muscles in that segment. A pair of minute visceral nerves are also given off from the abdominal ganglion which supply the alimentary canal in that region.

Ventral nerve cord - The ventral nerve cord (Figs. 68 & 70, VN) originates in the first abdominal segment from the abdominal ganglion. It runs posteriorly to the 7th abdominal segment where it bifurcates and is transformed into a large number of minute branches supplying the reproductive organs, abdominal muscles, and the last pair of spiracles. The innervation of nerves in the abdominal region where the reproductive organs are lodged, appears to be greater than any other segment of the abdomen. In each abdominal segment from the 2nd to 6th, a pair of segmental lateral branches (Fig. 68, Ab) are given off from the ventral nerve cord supplying the respective spiracles and abdominal muscles. Besides, a pair of very small nerves, the visceral branches, emerge in each segment from the ventral nerve cord and supply the trachea and muscles investing the alimentary canal. The segmental lateral branches and the visceral nerves of the first abdominal segment emerge directly from the abdominal ganglion and not from the ventral nerve cord. The ventral nerve cord and its branches of each segment consist of both motor and sensory fibers.

Generally, in other groups of insects the ventral nerve cord consists of double longitudinal trunks running very close and parallel to

each other or sometimes included in the same covering, so that it appears to be a single longitudinal trunk. But, in the greenbug, and probably in other aphids too, according to Grove (1909), the ventral nerve cord is represented by only a single nerve trunk. The transverse sections of the adult ventral nerve cord or its embryonic developmental sequences clearly suggest that it originates as a single longitudinal trunk and is not a derivative of two fused nerves. Grove (1909) reported that in Siphonophora rosarum the ventral nerve cord at its terminal end in the posterior abdominal segment expands into a fairly large ganglion from which nerves are given off to the muscles that control the anal and reproductive apertures. On the contrary, in the greenbug there is no trace of such a posterior abdominal ganglion. The ventral nerve cord at the posterior end in the 7th abdominal segment simply bifurcates and supplies the muscles and the reproductive organs.

Stomatogastric Nervous System - Johnson (1963) made studies on the sympathetic nervous system of a number of aphids and gave a general plan of the system as found in those aphids. The plan of the stomatogastric nervous system in the greenbug is largely in agreement with his observations. The retrocerebral endocrine glands of the greenbug consist of a frontal ganglion, a hypocerebral ganglion, two ganglia forming the corpora cardiaca, and a single corpus allatum (Fig. 74).

The frontal ganglion is a very small nervous mass (Fig. 74, Fg) located almost mid-way between the ascending tubular oesophagus and

the brain. It receives two nerves from the tritocerebral lobes and is connected to the hypocerebral ganglion by a recurrent nerve. The hypocerebral ganglion (Fig. 74, Hp) is approximately of the same size as the frontal ganglion, and is situated above the oesophagus just opposite to the tentorium (Fig. 74, Tm) where the oesophagus turns posteriorly towards the thoracic region. Immediately behind the hypocerebral ganglion and very closely applied to the oesophagus are two ganglia, the corpora cardiaca. The corpora cardiaca (Fig. 74, Cd) are so close to each other that they can easily be mistaken for an unpaired ganglionic mass. Each corpus cardiacum is connected to the hypocerebral ganglion by a very short thin nerve. The corpus allatum (Fig. 74, CA) lies in continuation with the corpora cardiaca and is the biggest of all the three ganglia. The anterior end of the corpus allatum is intimately associated with the corpora cardiaca. The nerve fibrils pass directly into the corpus allatum without being bundled into a nerve. In other insects, in general, the corpora allata are paired structures, but Johnson (1963) found that in all the aphids he studied, the corpus allatum represented a single body. In the greenbug, also, the corpus allatum is unpaired, has intimate association with the corpora cardiaca, and consists of a fairly large number of glandular cells.

The role of corpus allatum and corpus cardiacum has been investigated in quite a number of insect groups, but so far such information is completely lacking in the case of aphids. Judging from the endocrine role in Hemiptera and other adult insects, it seems very probable that

in adult aphids, too, the corpus allatum is in some way responsible for the parthenogenetic development of egg. Based on the studies in the greenbug, it is further suggested that the extrinsic factors like environmental conditions or insufficiency of food might throw a disbalance on the hormonal activity of the endocrine glands which results in the production of alate parthenogenetic female forms.

SUMMARY AND CONCLUSIONS

This study was taken up to investigate the anatomical, histological, and cytological details of the greenbug, Schizaphis graminum (Rondani). The systems worked out include the structure of mouth parts, feeding mechanism, salivary glands, the act of salivation, structure of alimentary canal, the phenomena of digestion and assimilation, cornicle structure and their function, and the nervous system.

The mouth parts consist of 4 stylets, 2 mandibles, and 2 maxillae. The maxillae have an interlocking type of arrangement. The mandibles are provided with nerve extensions contained in the mandibular ducts and perform sensory function as well. The mode of feeding in the two greenbug biotypes differs. In the immature and adult stages of biotype A, the stylets penetrate intercellularly into the plant tissues and are directed to the phloem in a sinuous way in the majority of the cases, whereas, the stylets in the adult and immature forms of biotype B, in a large number of cases, are inserted inter- and intracellularly straight into the mesophyll parenchyma of the leaf. Only in a small percentage the stylets are found entering the phloem tissues of vascular bundles, but the penetration is always straight and not sinuous like biotype A. This indicates that biotype B has a preference for feeding in the mesophyll parenchyma rather than in the phloem tissues.

Consequently, biotype A destroys the phloem tissues, whereas biotype B damages the mesophyll parenchyma.

The salivary gland complex consists of principal, accessory, maxillary and mandibular glands. The principal glands are largest in size and contain a glandular, and a membranous part. The membranous region serves for the storage of secretory material. A salivary meatus or a salivary pump is absent. A common duct from principal and accessory glands and a common duct from maxillary and mandibular glands open separately at the base of the maxillary stylets into the salivary channel. The expulsion of salivary fluid from these glands is probably brought about by the pressure of haemolymph. Studies on the salivary sheath indicate that it functions as a means of protection for the ultramicroscopic openings of the food and salivary channels.

The alimentary canal is devoid of a filter chamber, and the malpighian tubules are absent. The suction pump which is highly developed is operated by a number of strong muscles. The stomach is appreciably dilated, and the digestive activity is mainly confined to the anterior region while the posterior part and the long intestine serve as the assimilating areas. The process of secretion is purely of holocrine type. The rectum is the enlarged transparent portion of alimentary tract. The structure of its walls suggests that it is capable of picking up excretory products from the haemolymph and excreting them outside, thus serving as a further aid to the process of excretion.

The cornicles are hollow tubular extensions of the body wall having their lumen in direct continuation with the haemocoel and not connected to any glandular structure. The outside opening of the cornicle is controlled by a valve which is operated by a very long muscle. Normally the cornicles lie pointing posteriorly and are able to move only in a plane parallel to the longitudinal axis of the body. Studies of cornicles and their secretion indicate that they are excretory in function. The discharge of excretory products by the cornicles directly from the haemocoel to the exterior appears to be a mechanism developed to serve the excretory function normally performed by malpighian tubules in other insects. The analysis of excreted material from the cornicle showed that it was composed of 8 amino acids, triglycerides, phospholipids, and traces of long-chain hydrocarbons.

The central nervous system is greatly condensed and consists of cerebral ganglia, suboesophageal ganglion, thoracic ganglionic mass, and the ventral nerve cord. The cerebral ganglia are divisible into 3 regions, the protocerebrum, deutocerebrum, and tritocerebrum. The protocerebrum is the most important association center of the brain. The deutocerebrum is the middle portion which sends nerves out to antennae. The tritocerebrum forms the postero-ventral part of the brain which projects posteriorly in the form of two cone-shaped lobes. In the greenbug the suboesophageal ganglion assumes great importance since it supplies nerves to the mouth parts, salivary glands, and posteriorly joins the thoracic ganglionic mass. This mass is formed

by the fusion of 3 pairs of thoracic ganglia and an abdominal ganglion. A single ventral nerve cord emerging from the abdominal ganglion extends to the 7th abdominal segment with transverse branches in each segment.

The stomatogastric nervous system consists of a frontal ganglion, a hypocerebral ganglion, two ganglia forming the corpora cardiaca and a single corpus allatum.

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ILLUSTRATIONS

PLATE I

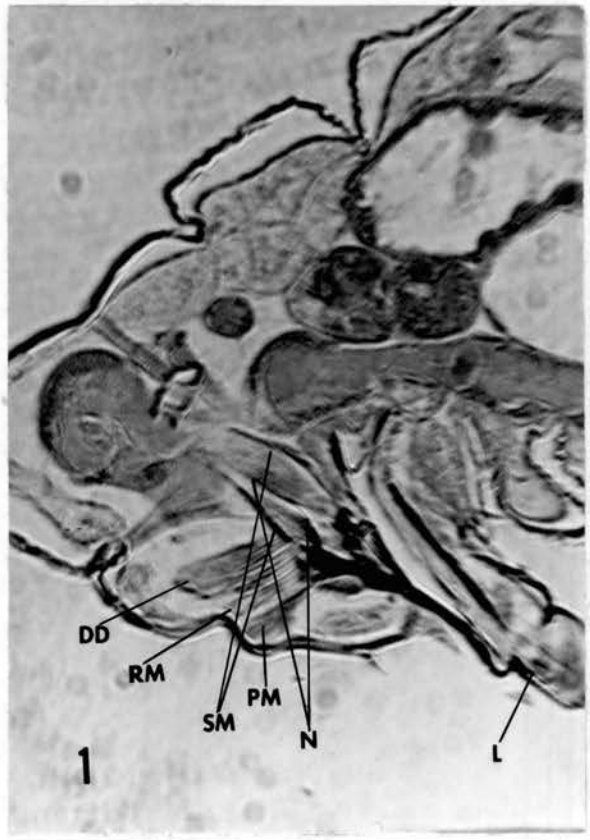
Fig. 1 Photomicrograph of longitudinal section of the greenbug Schizaphis graminum (Rondani) showing musculature of mouth parts. x 3440

Fig. 2 Photomicrograph of longitudinal section of the greenbug showing musculature of cibarial pump and mouth parts. x 3440

Fig. 3 Diagrammatic view of the musculature of mouth parts and cibarial pump.

Fig. 4 Photomicrograph of the penetration of stylets of biotype B in the mesophyll parenchyma of Rogers barley leaf. x 7760

DD, dilator muscles of the distal end of cibarial pump; DP, dilator muscles of the proximal end of cibarial pump; L, labium; La, labial groove; Mn, mandibles; Mx, maxillae; N, retractor muscles of maxillae; PM, protractor muscles of maxillae and mandibles; R, tentorial ring; RM, rotator muscles of mandibles; S, salivary fluid; SM, retractor muscles of mandibles; TB, tentorial bar; W, Joint group of retractor muscles of mandibles and maxillae.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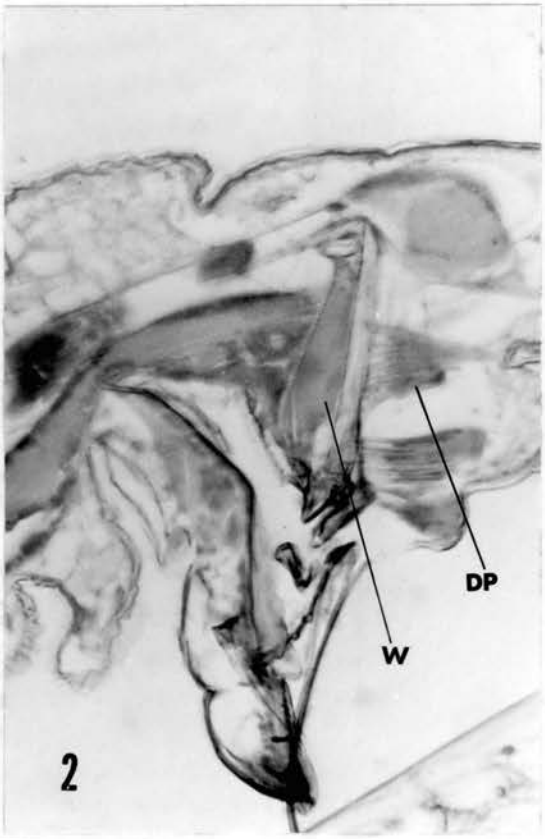
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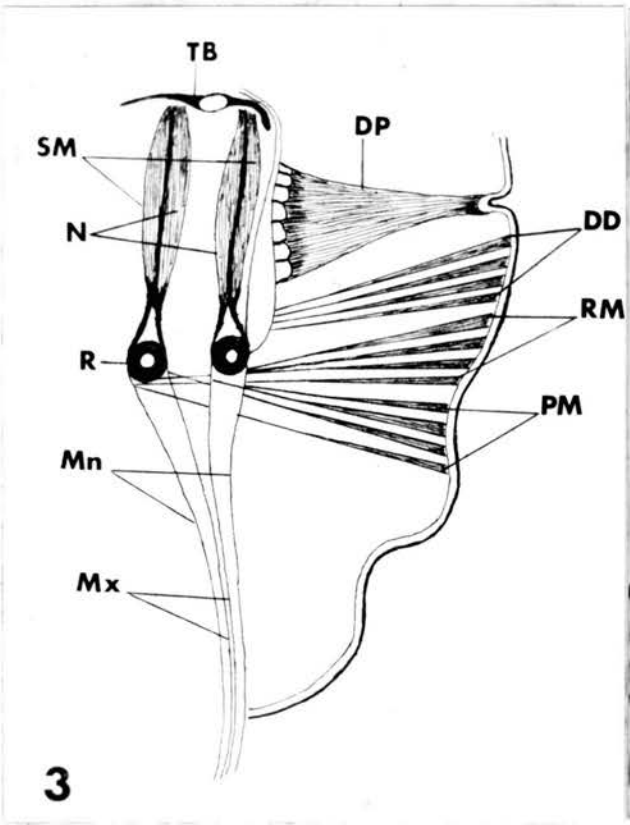
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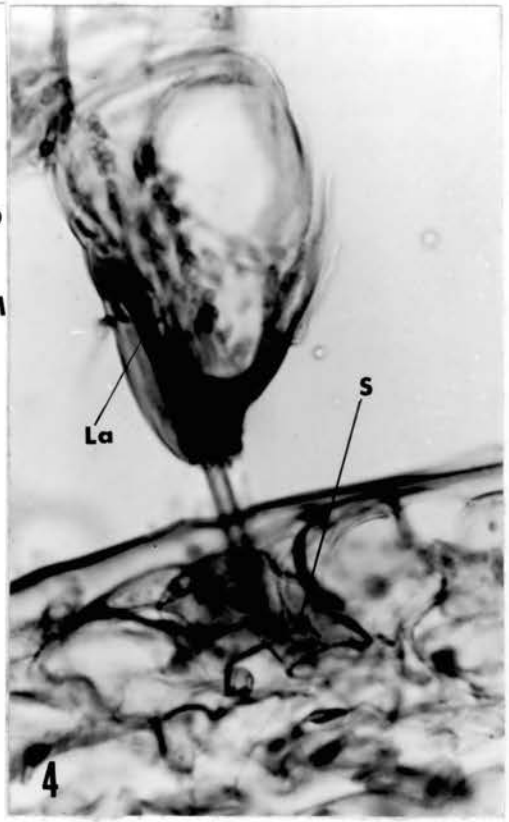
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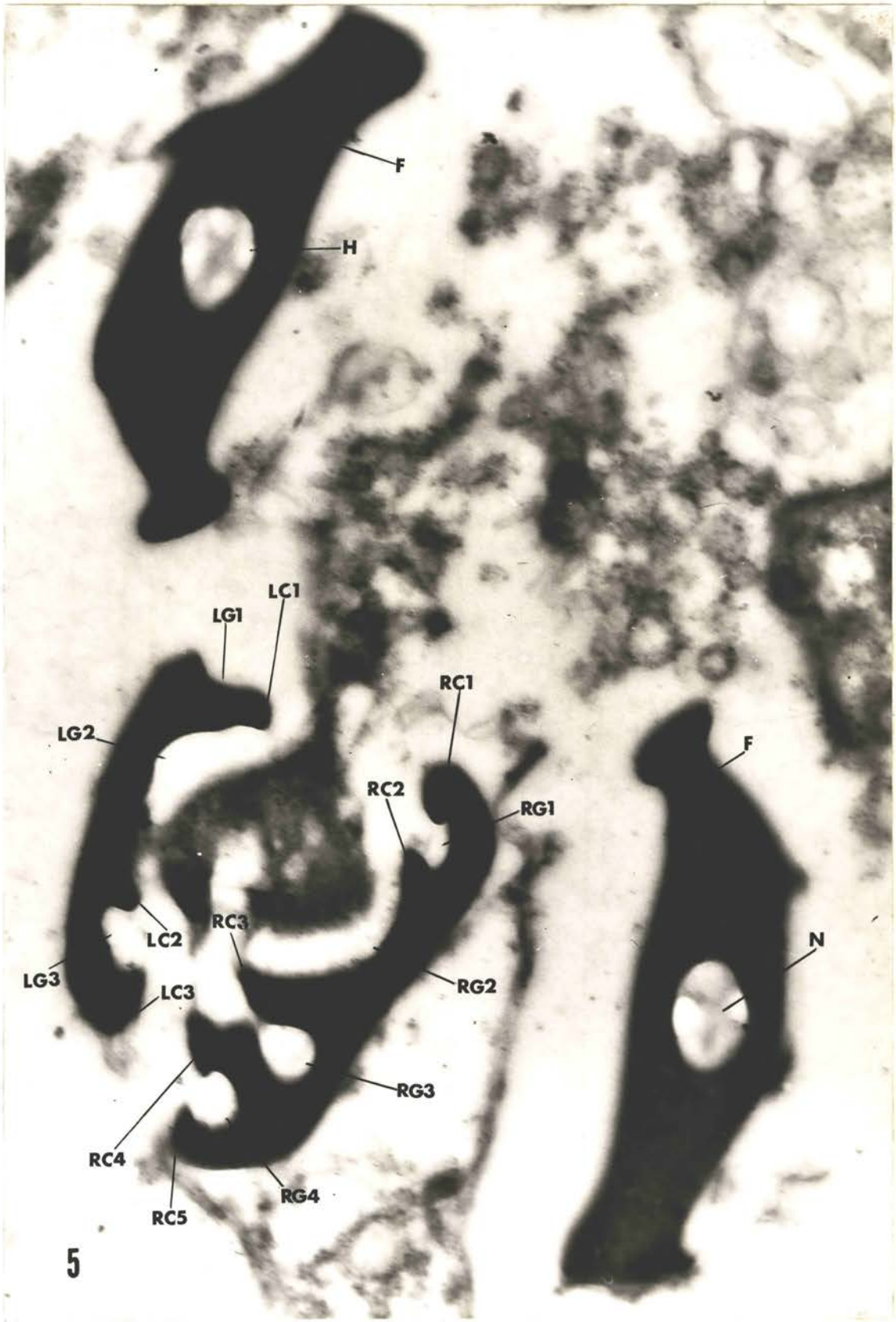
PLATE II

Fig. 5 Electron photomicrograph of the transverse section of stylets of the greenbug. x 41,000

F, mandible; H, mandibular duct; LC2 and LC3, first, second and third condyles of left maxilla; LG1, LG2 and LG3, first, second and third grooves of left maxilla; N, nerve of the mandibular duct; RC1, RC2, RC3, RC4 and RC5, first, second, third, fourth and fifth condyle of right maxilla; RG1, RG2, RG3, RG4 and RG5, first, second, third, fourth and fifth groove of right maxilla.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RC1
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RC2
RG1
LC2
RC3
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LG3
RG2
LC3
RG3
RC4
RG4
RC5
5

PLATE III

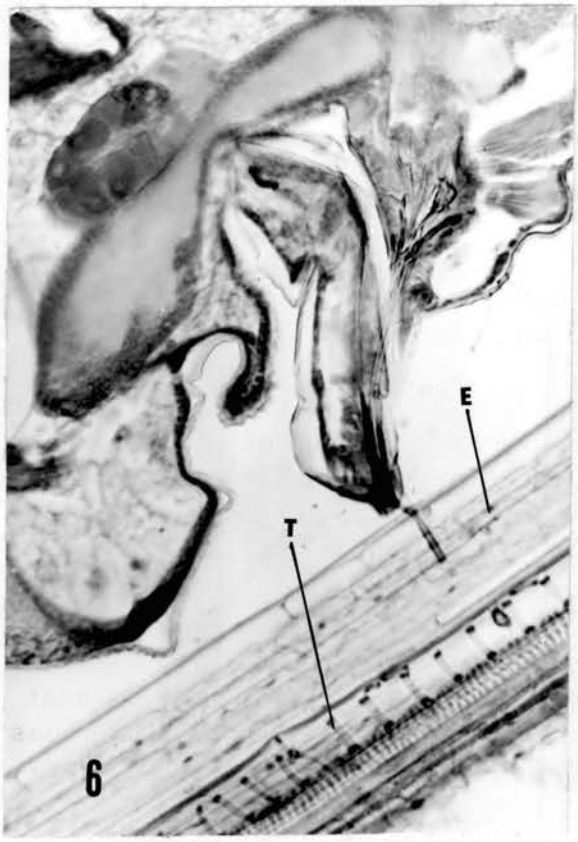
Fig. 6 Photomicrograph of the longitudinal section of Will barley leaf showing the feeding of adult biotype B in the mesophyll parenchyma. x 3440

Fig. 7 Photomicrograph of the longitudinal section of adult biotype B showing feeding on Rogers barley leaf in the mesophyll tissues. x 3440

Fig. 8 Photomicrograph of the longitudinal section of second instar nymph feeding on Rogers barley leaf. x 3440

Fig. 9 Photomicrograph of the transverse section of DS 28A wheat leaf showing adult biotype B feeding in the mesophyll tissues. x 3440

E, mesophyll parenchyma; T, leaf vein in longitudinal section; V, vascular bundle.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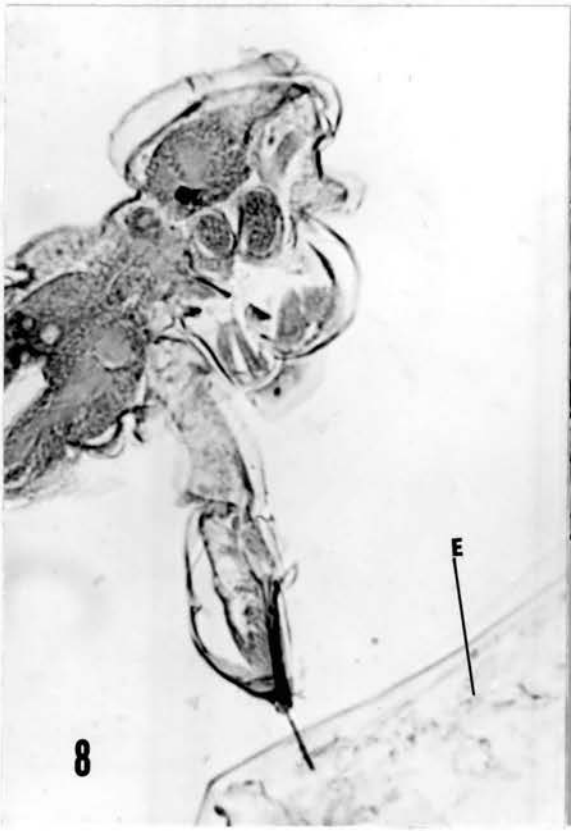
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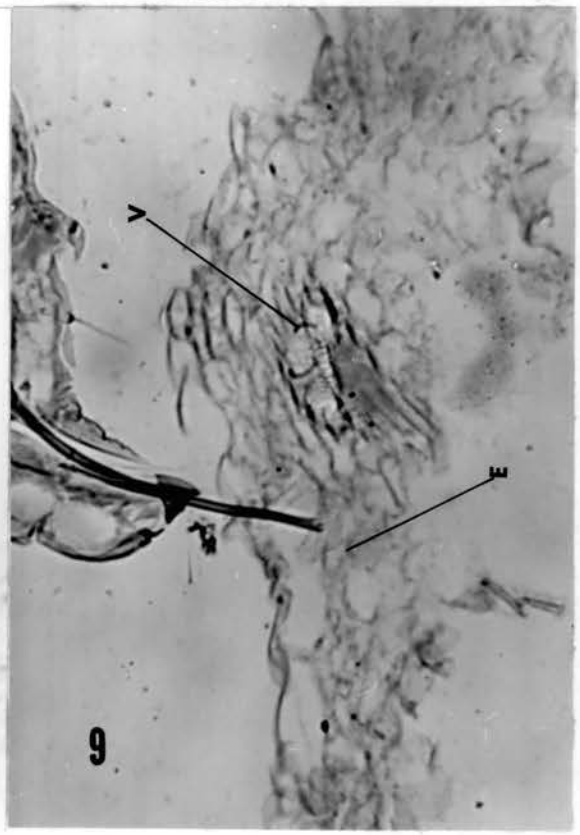
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PLATE IV

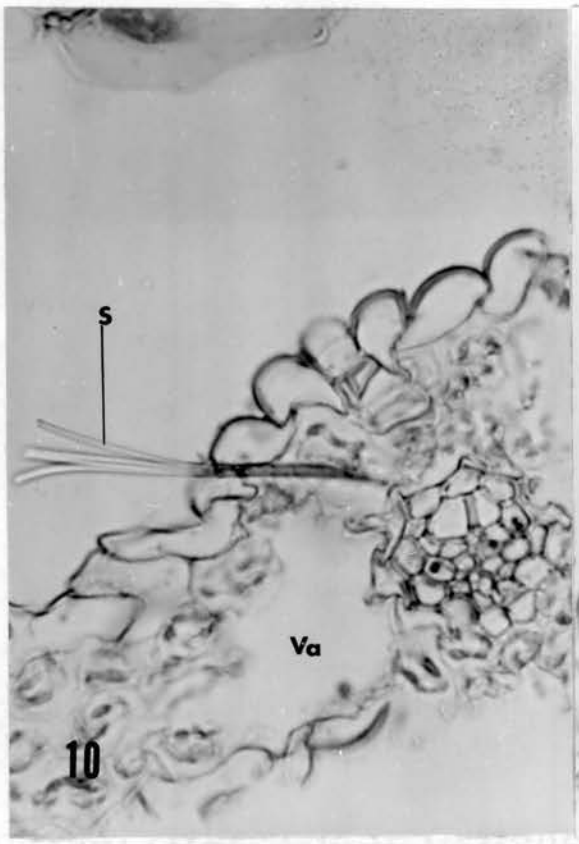
Fig. 10 Photomicrograph of the transverse section of Rogers barley leaf showing straight penetration of stylets of biotype B in the vascular bundle. x 3440

Fig. 11 Photomicrograph of the transverse section of DS 28A wheat leaf showing stylet sheath in the mesophyll tissues. x 3440

Fig. 12 Photomicrograph of straight stylet sheath in the mesophyll parenchyma of Rogers barley leaf. x 7760

Fig. 13 Photomicrograph of the straight stylet sheath in the mesophyll parenchyma of DS 28A wheat leaf. The area stained dark indicates diffusion of salivary fluid in the adjacent tissues. x 7760

E, mesophyll parenchyma; S, stylet; SH, stylet sheath; Va, vacuolar space.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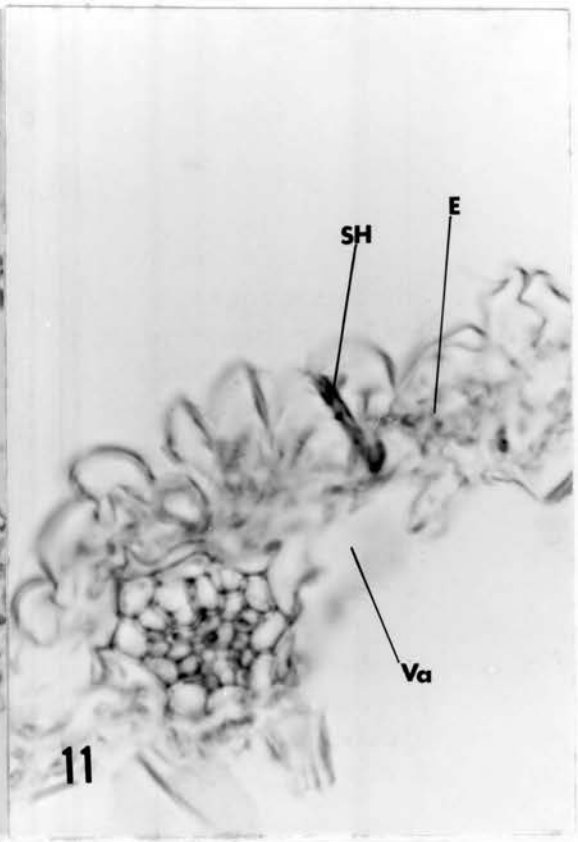
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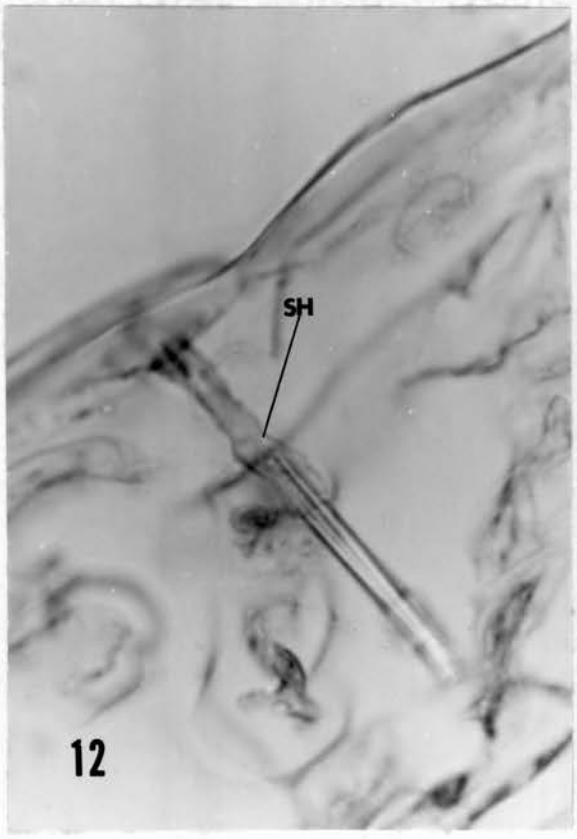
SH
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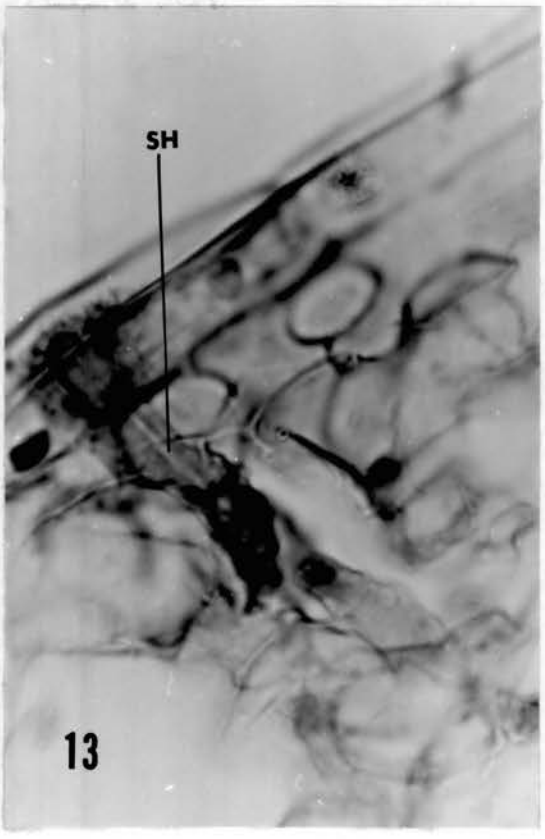

SH
13

PLATE V

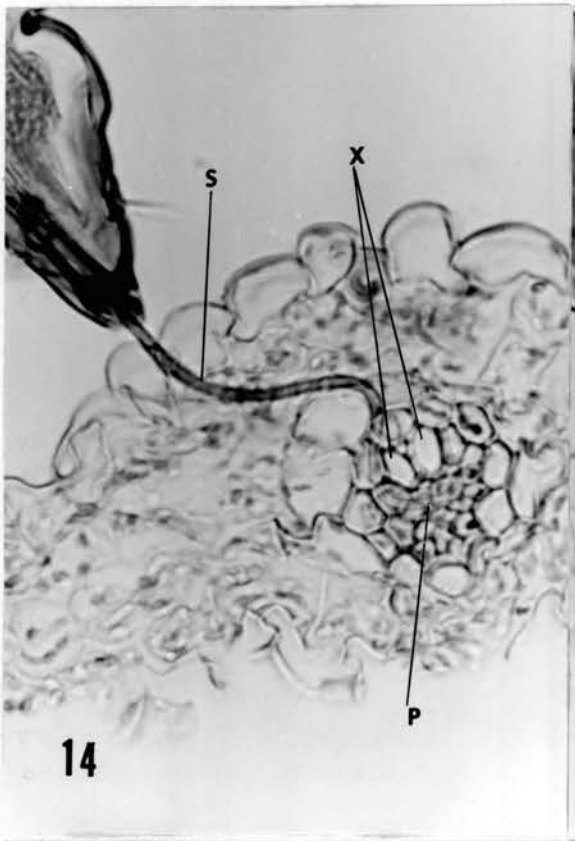
Fig. 14 Photomicrograph of the transverse section of Rogers barley leaf showing stylets of adult biotype A penetrated in the phloem tissues. x 3440

Fig. 15 Photomicrograph of the transverse section of Rogers barley leaf showing curved path of stylets of biotype A, going to phloem tissues. x 3440

Fig. 16 Photomicrograph of the transverse section of Will barley leaf showing stylets of second instar nymph of biotype A, directed towards the vascular bundle. x 3440

Fig. 17 Photomicrograph of the transverse section of Rogers barley leaf showing the stylet sheath and damage to phloem tissues by biotype A. x 3440

P, phloem tissues; S, stylets; SH, stylet sheath; X, xylem vessels.



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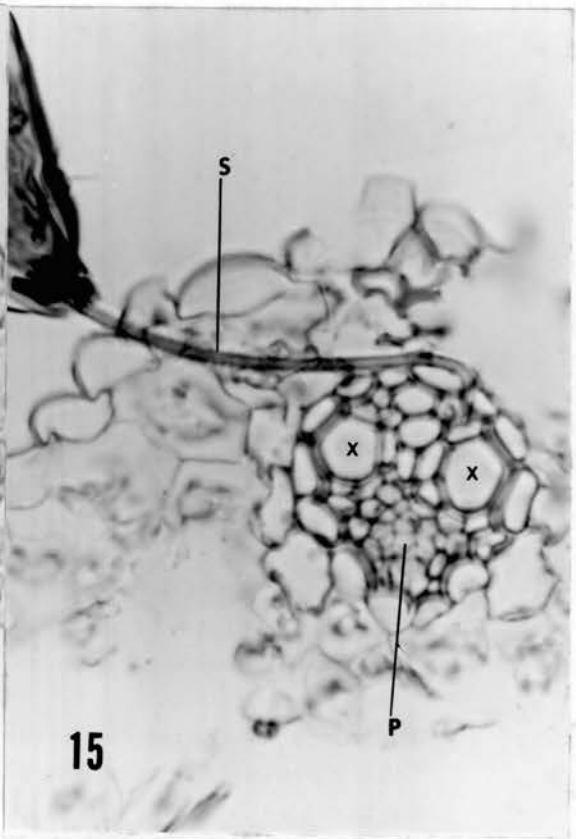

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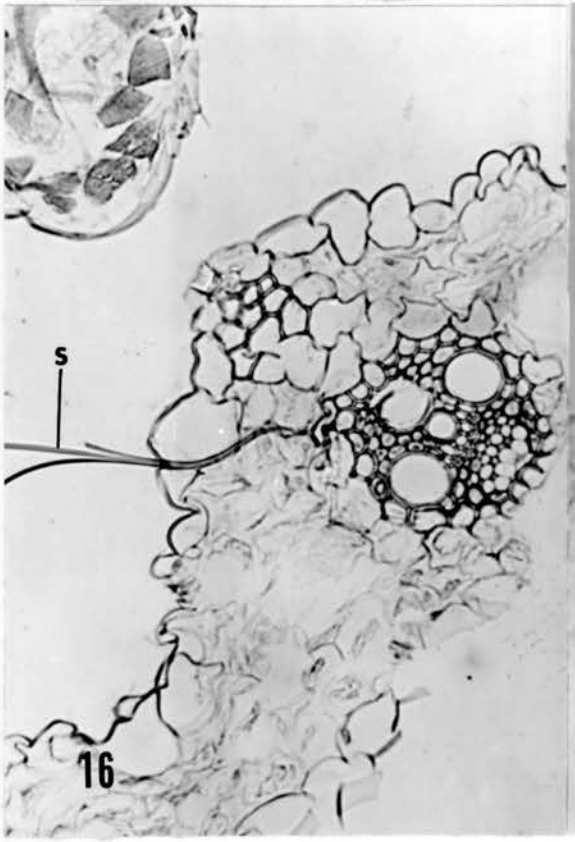

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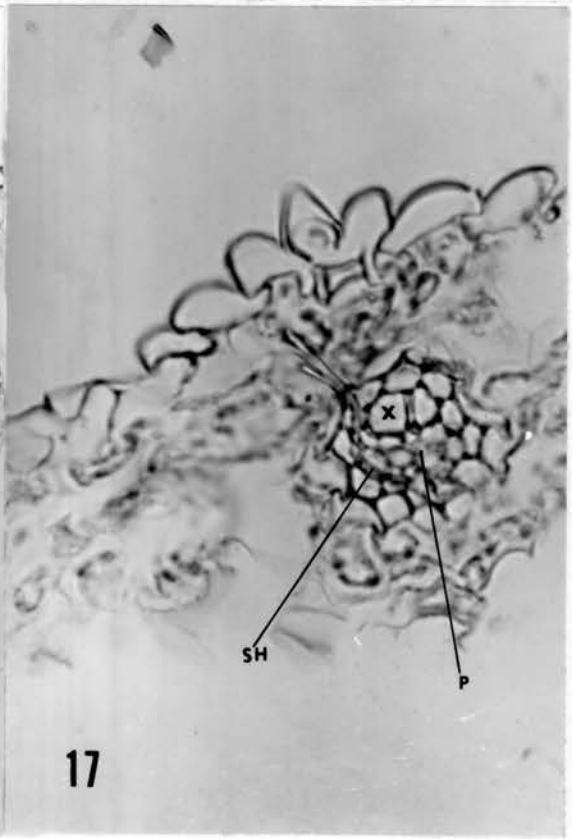

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PLATE VI

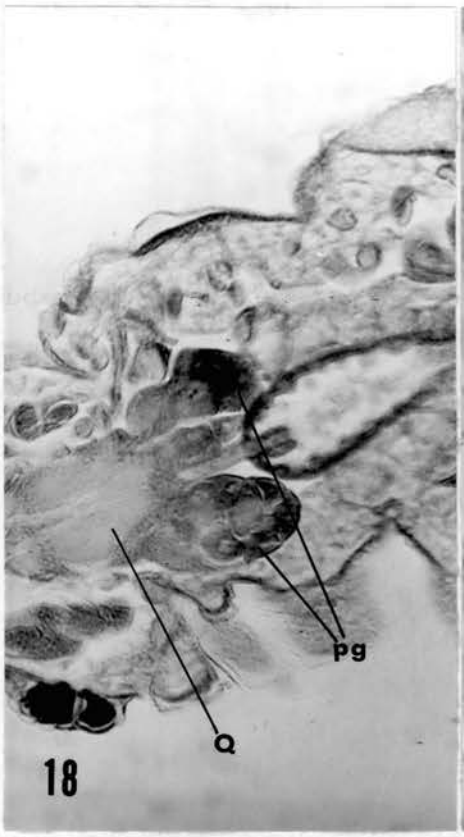
Fig. 18 Photomicrograph of the longitudinal cross section of greenbug showing the disposition of principal glands. x 3440

Fig. 19 Photomicrograph of the cross section of principal glands showing cytological details. x 7760

Fig. 20 Photomicrograph of the longitudinal section of principal gland showing membranous and glandular portions. x 7760

Fig. 21 Photomicrograph of the longitudinal section through the body showing salivary duct. x 2400

ch, chromatin granules; gl, glandular portion; h, hilus; L, lumen; mb, membranous region; n, nucleus; nu, nucleolus; oes, oesophagus; pg, principal gland; Q, suboesophageal ganglion; sd, salivary duct; sm, secretory material; Th, thoracic ganglion.



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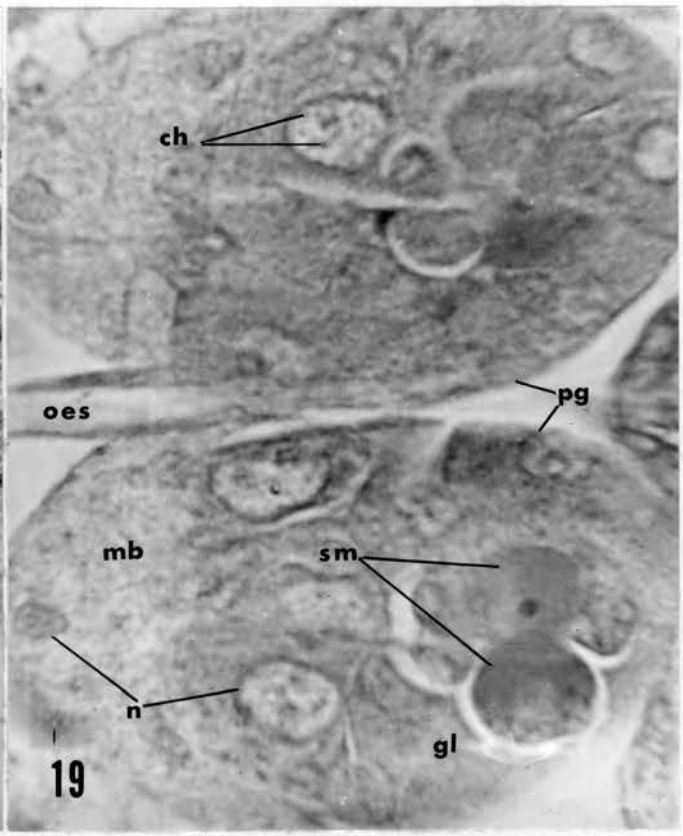

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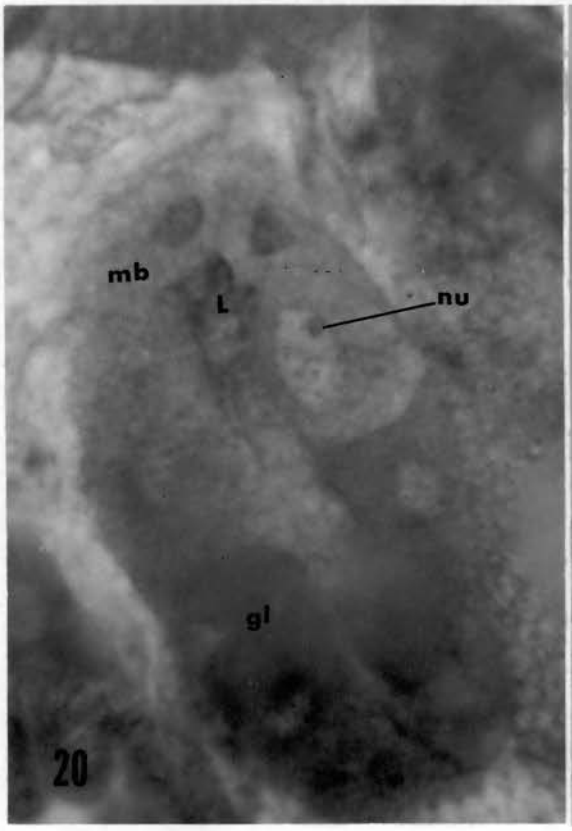

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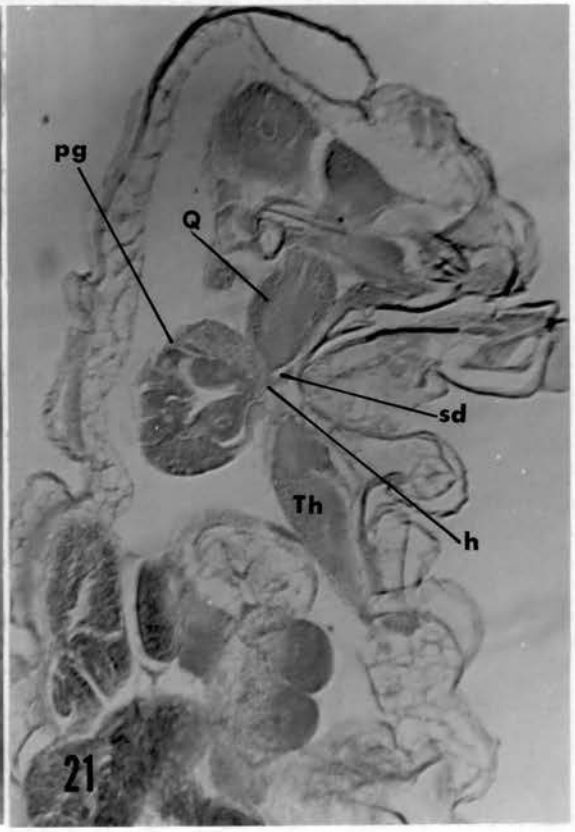


21

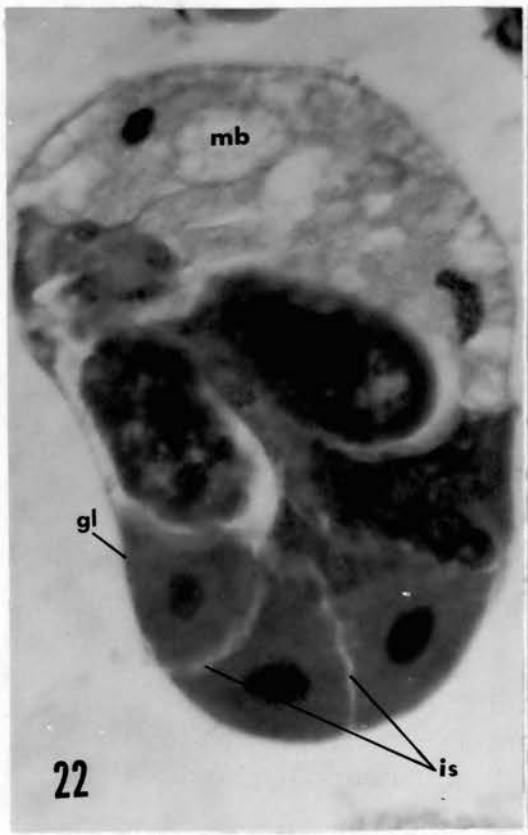
PLATE VII

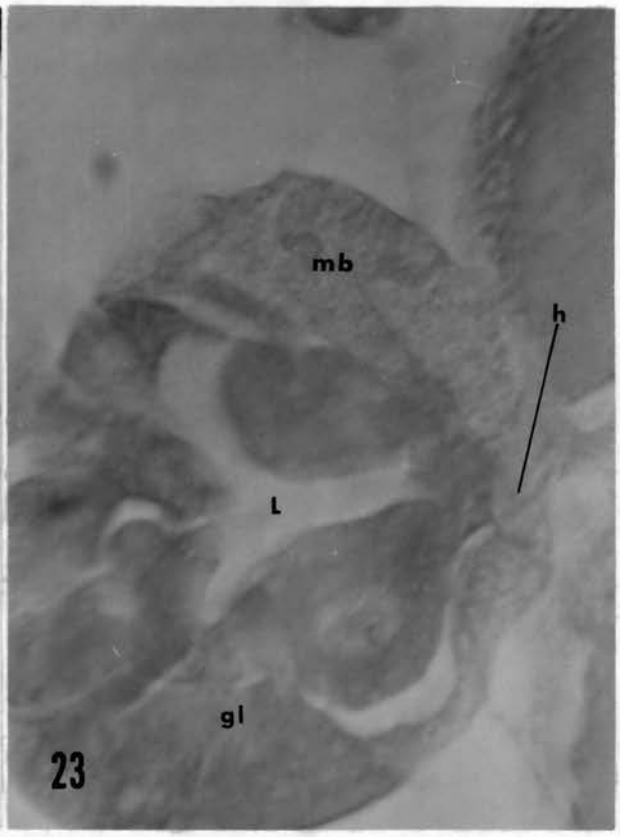
Fig. 22 Photomicrograph of the longitudinal section of principal gland showing swollen membranous portion. x 7760

Fig. 23 Photomicrograph of the longitudinal section of principal gland showing the lumen and converging intercellular spaces. x 7760

Figs. 24 & 25 Photomicrographs of the longitudinal sections of embryos showing the principal glands in the developing stages. x 7760

D, duct of embryonic principal gland; gl, glandular portion of principal gland; h, hilus; is, intercellular spaces; L, lumen; mb, membranous portion of principal gland.


mb
gl
is
22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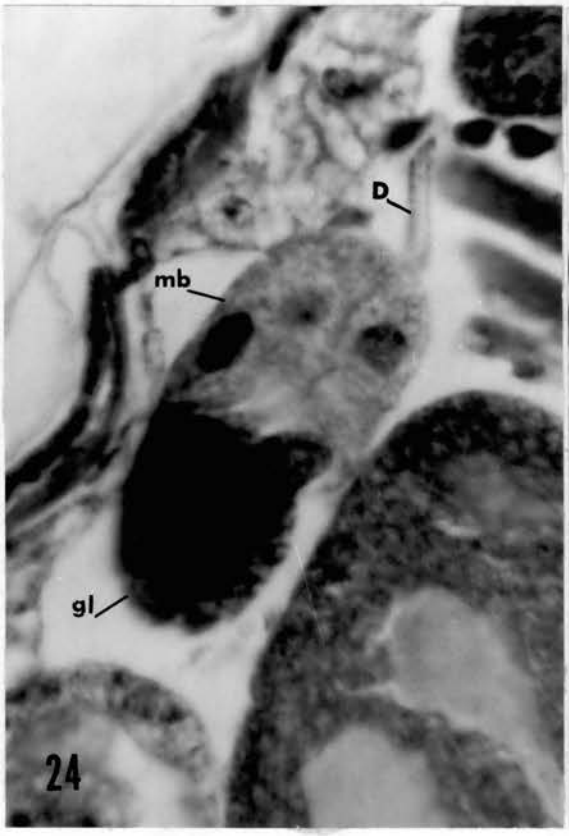
h
L
gl
23


D
mb
gl
24

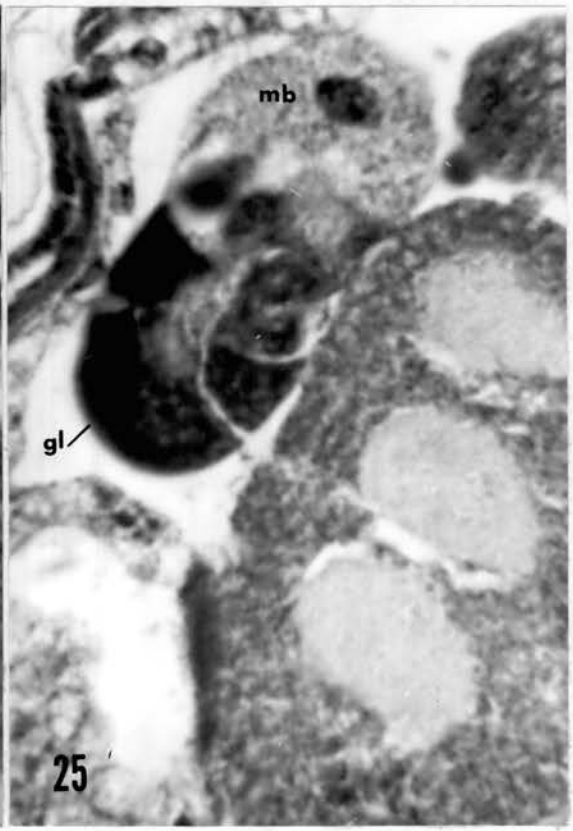

mb
gl
25

PLATE VIII

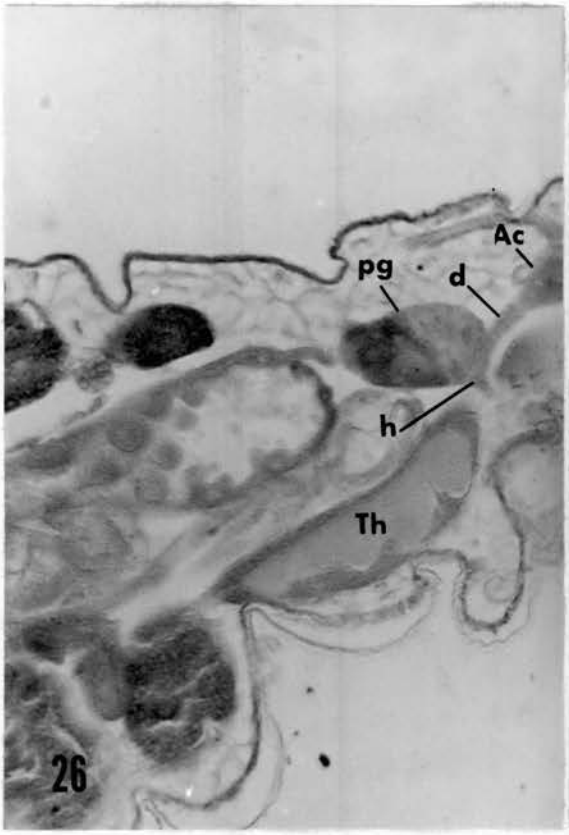
Fig. 26 Photomicrograph of the longitudinal section through body showing the union of ducts from accessory and principal glands. x 3440

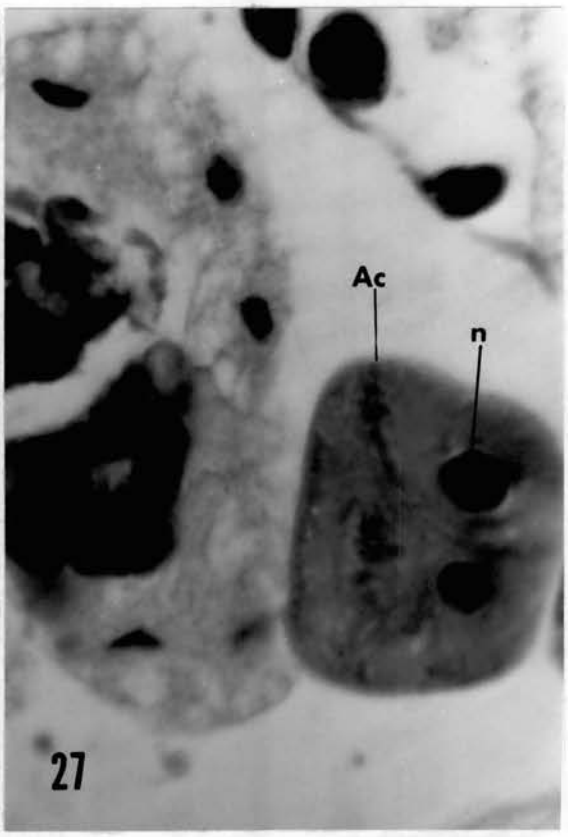
Fig. 27 Photomicrograph of the transverse section of accessory gland. x 7760

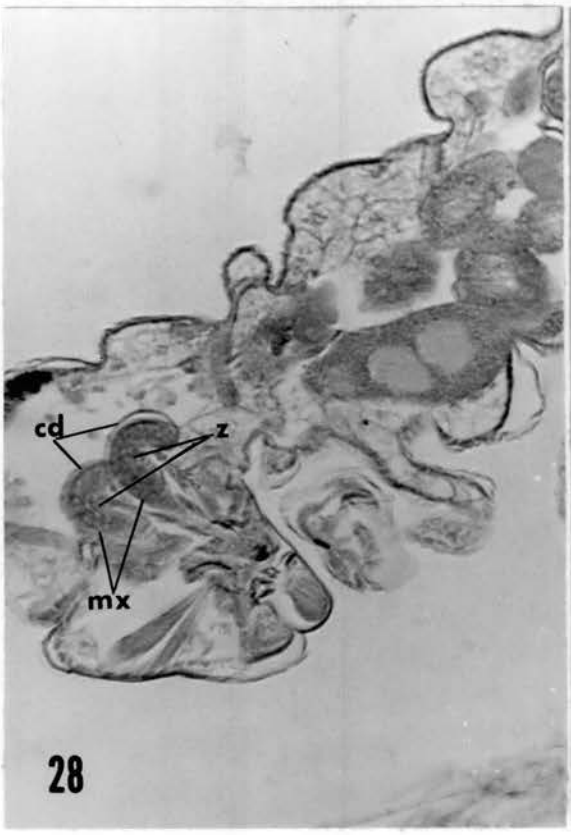
Fig. 28 Photomicrograph of the longitudinal section through head showing maxillary glands. x 3440

Fig. 29 Photomicrograph of the transverse section of maxillary glands. x 7760

Ac, accessory gland; cd, collecting ducts of maxillary glands; d, duct of accessory gland; h, hilus; mx, maxillary glands; n, nucleus; pg, principal gland; Th, thoracic ganglion; z, glandular region of maxillary gland.


Ac
pg
d
h
Th
26


Ac
n
27


cd
z
mx
28

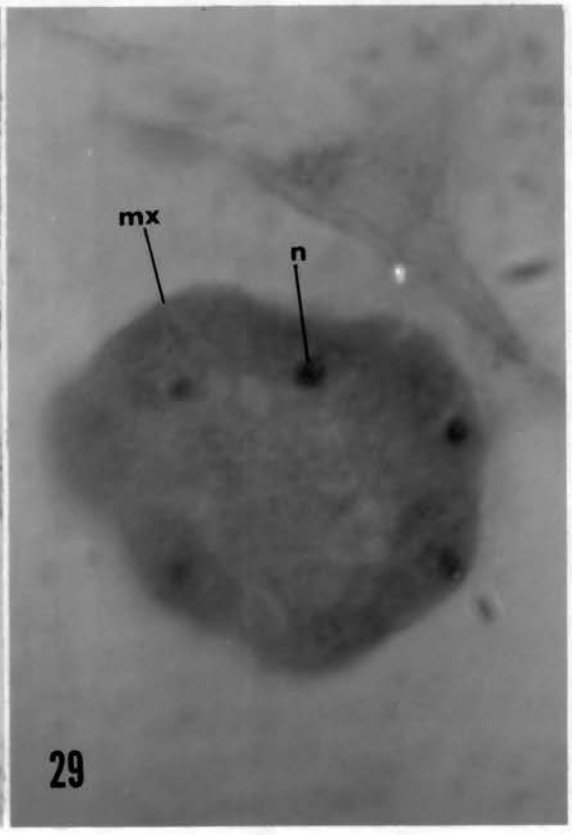

mx
n
29

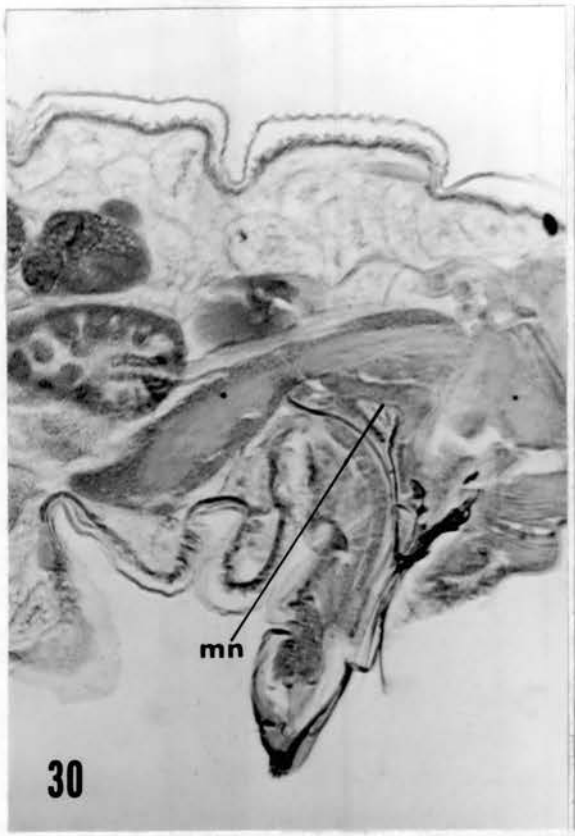
PLATE IX

Fig. 30 Photomicrograph of the longitudinal section through head showing the disposition of mandibular gland. x 800

Fig. 31 Photomicrograph of the transverse section of mandibular gland. x 7760

Figs. 32 & 33 Photomicrographs of the longitudinal sections of head showing the dispositions of common salivary duct, common maxillary duct and common mandibular duct. x 7760

J, common duct from mandibular glands; K, common duct from maxillary glands; mn, mandibular gland; n, nucleus; N, common duct from principal and accessory glands; sg, secretory granules; SP, suction pump; v, vacuolar space.



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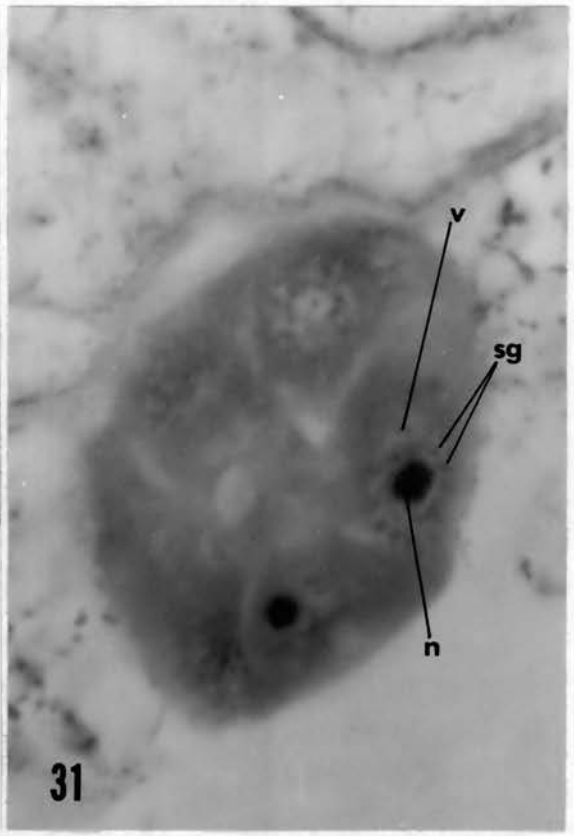

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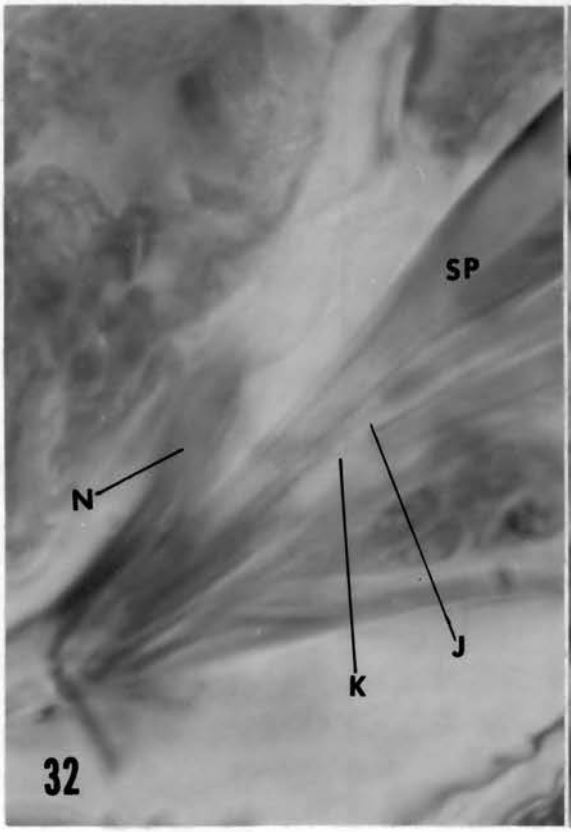

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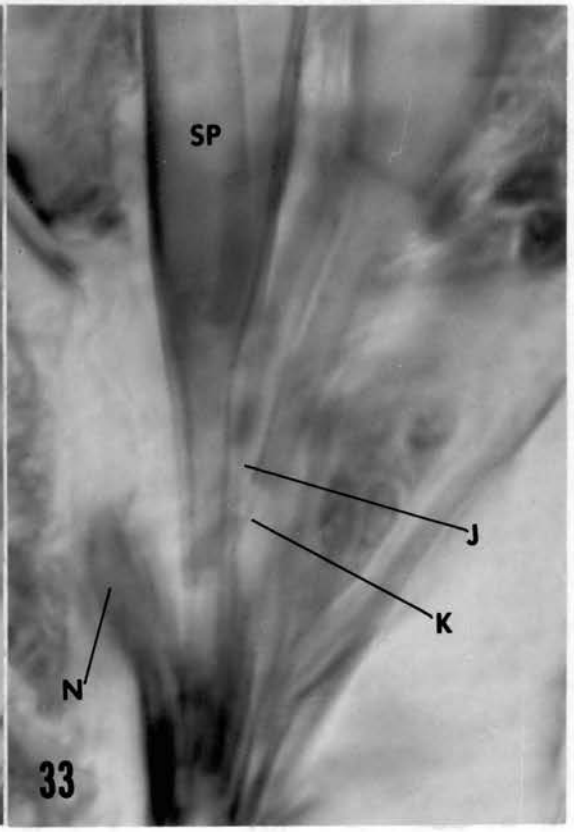

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PLATE X

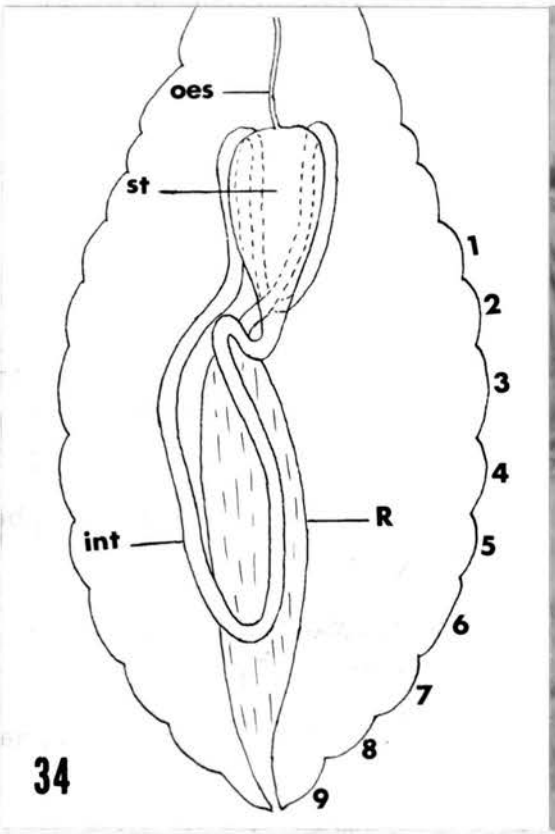
Fig. 34 Diagrammatic dorsal view of the alimentary canal.

Fig. 35 Photomicrograph of the longitudinal section of suction chamber showing the series of muscles inserted on the infolding of its wall. x 7760

Fig. 36 Photomicrograph of the transverse section of suction chamber showing inward folding of wall. x 7760

Fig. 37 Photomicrograph of the longitudinal section through body showing the entire length of oesophagus. x 800

I, infolding of wall; int, intestine; M, muscles; oes, oesophagus; R, rectum; S, suction chamber; St, stomach; V, oesophageal valve.



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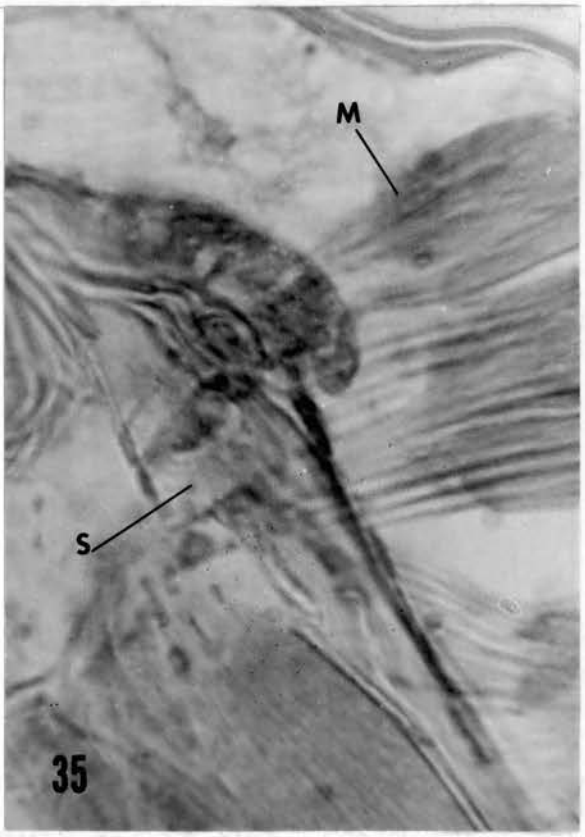

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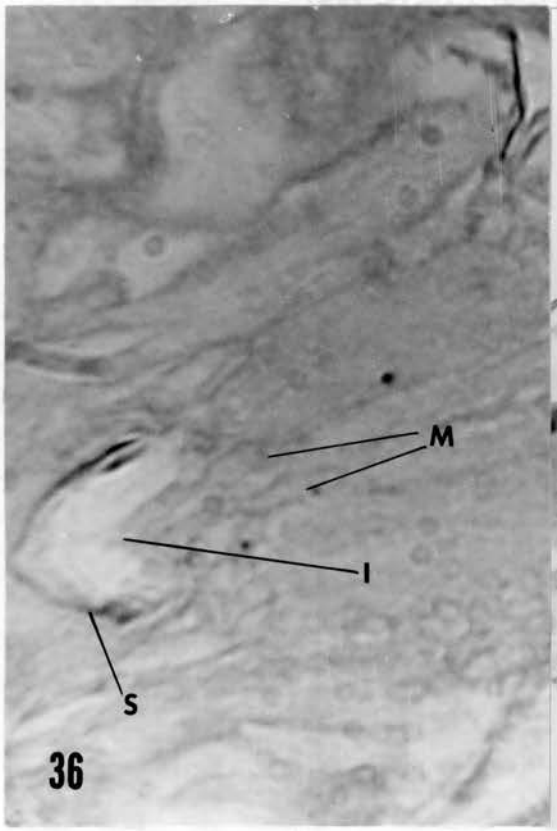

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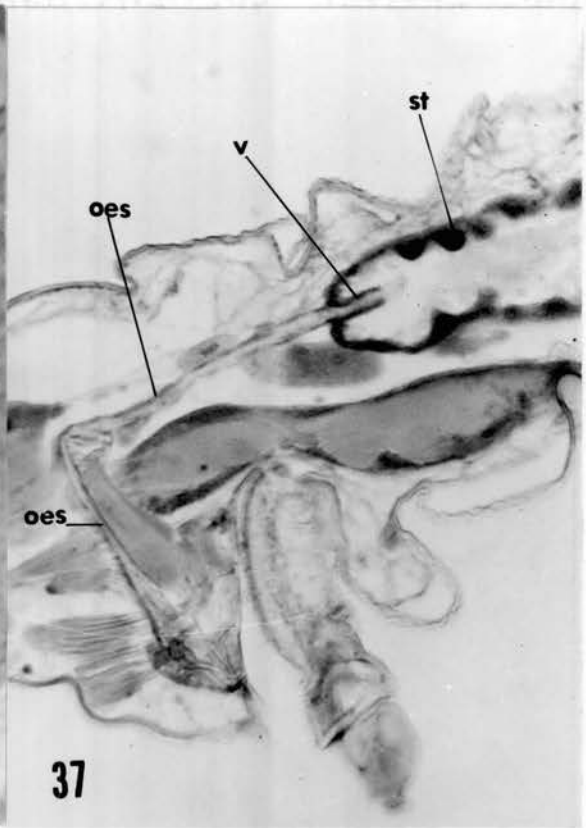

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PLATE XI

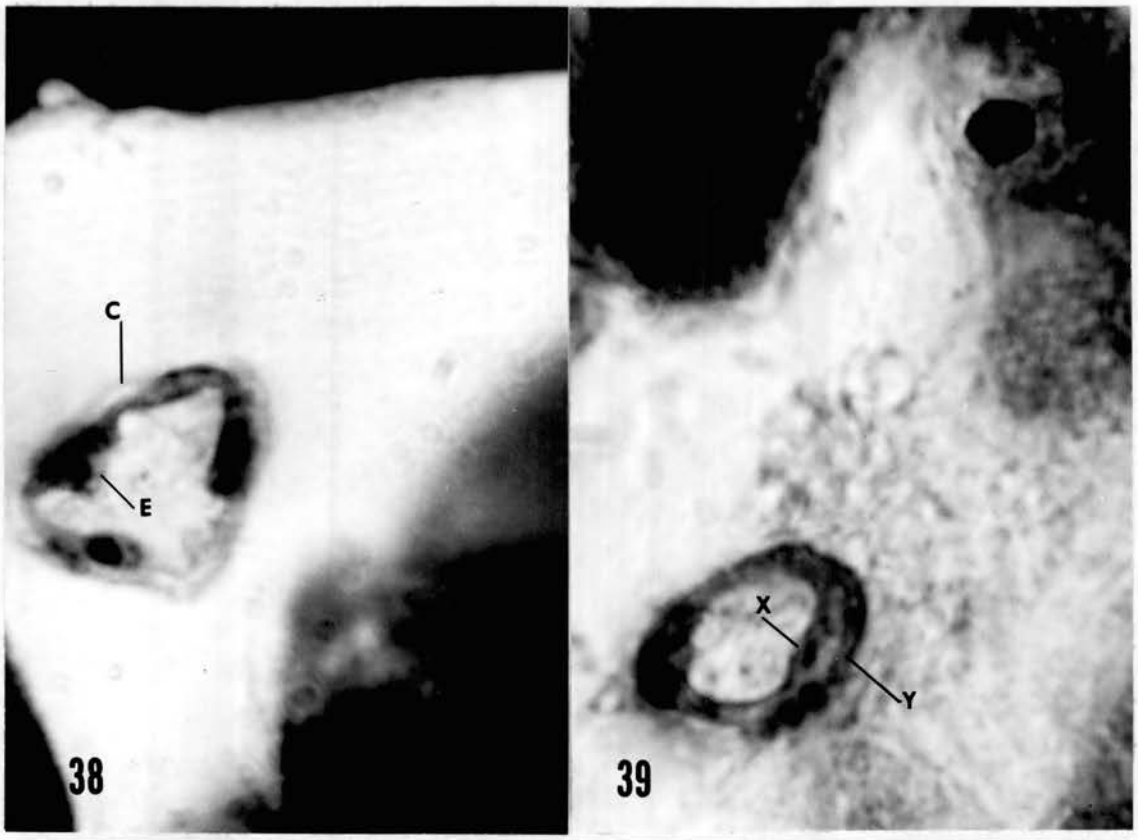
Fig. 38 Photomicrograph of the transverse section of oesophagus. x 7760

Fig. 39 Photomicrograph of the transverse section of oesophageal valve. x 7760

Fig. 40 Photomicrograph of the transverse section of posterior region of suction chamber showing the position of the insertion of muscles. x 3440

Fig. 41 Photomicrograph of the longitudinal section of anterior portion of stomach with oesophageal valve. x 3440

C, circular muscle layer; E, epithelial cell; M, muscle; P, points of muscle insertion; S, suction chamber; St, stomach; V, oesophageal valve; X, oesophageal epithelial layer; Y, stomach epithelial layer.


C
E
38
X
Y
39

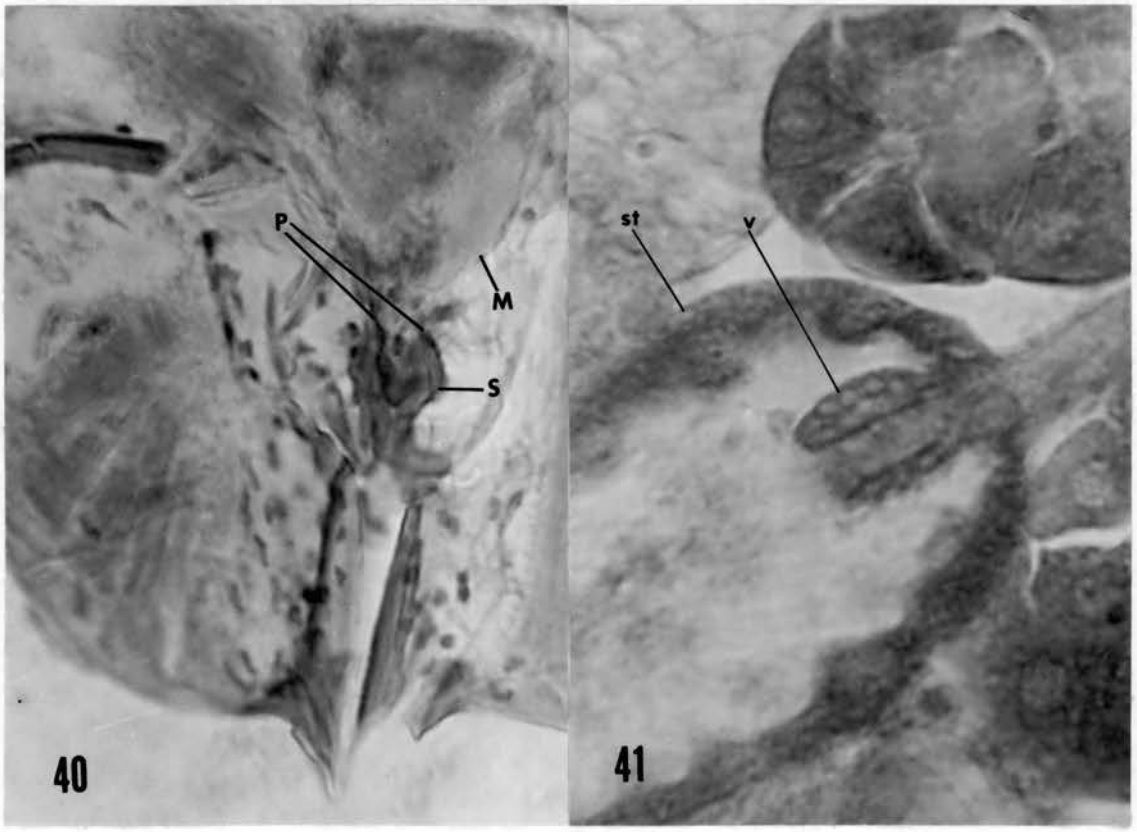
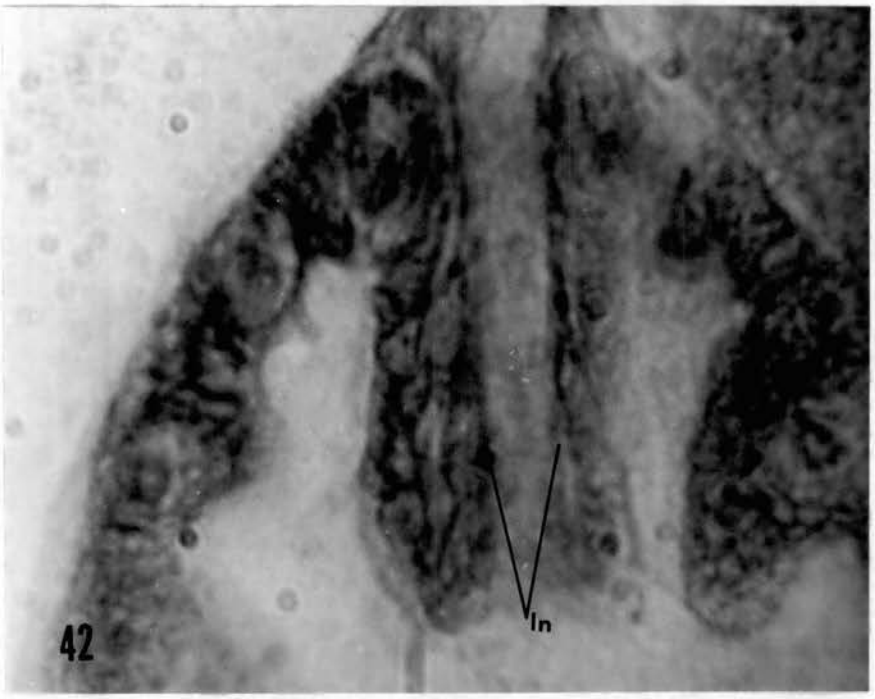

P
M
S
40
st
v
41

PLATE XII

Fig. 42 Photomicrograph of the oesophageal valve. x 7760

Fig. 43 Photomicrograph of the transverse section of stomach showing regenerative cells. x 7760

D, disintegrating columnar cells; In, intimal lining; R, regenerative cells.


In
42

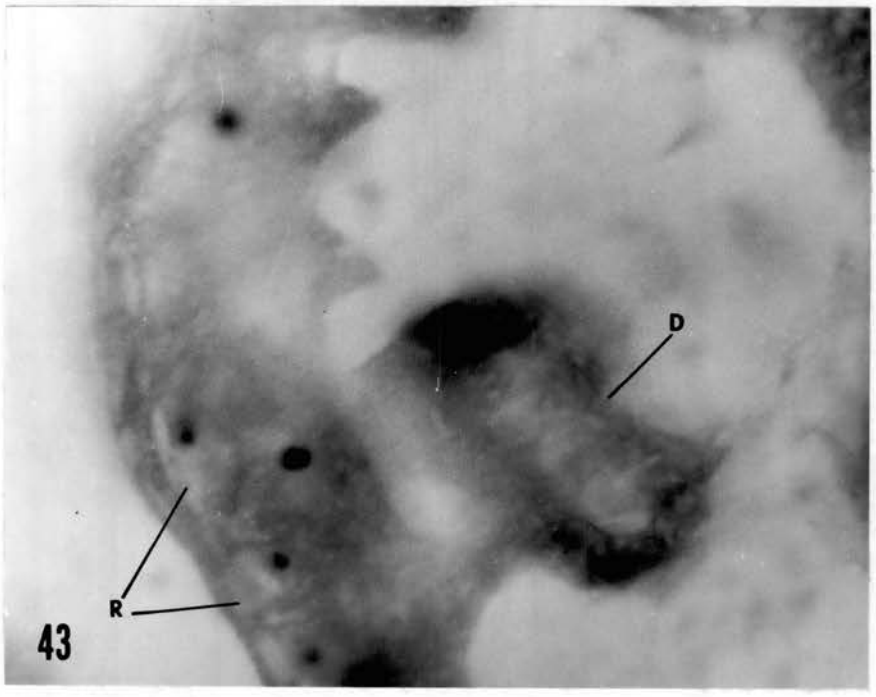

D
R
43

PLATE XIII

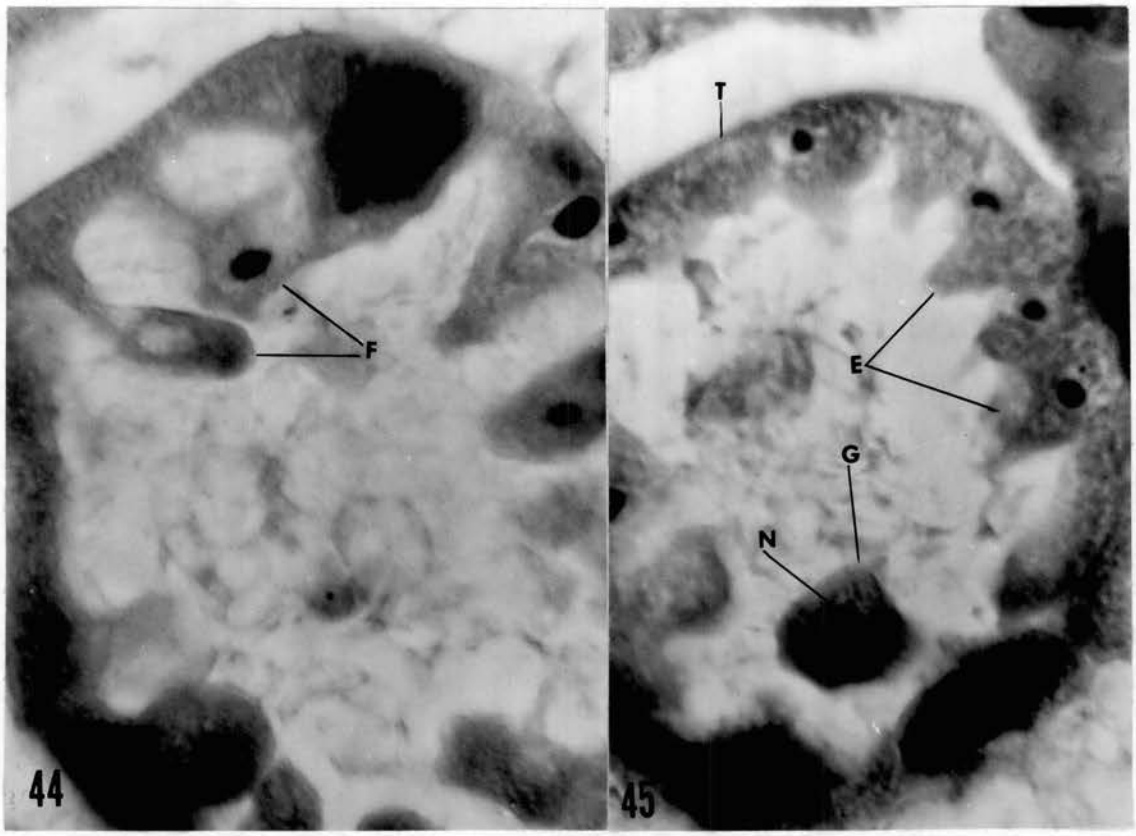
Fig. 44 Photomicrograph of the transverse section of anterior region of stomach showing detaching columnar cells. x 7760

Fig. 45 Photomicrograph of the transverse section of stomach showing newly detached columnar cell with intact nucleus. x 7760

Fig. 46 Photomicrograph of the detached disintegrating columnar cell and the formation of new columnar cell in place of it. x 9700

Fig. 47 Photomicrograph of the transverse section of stomach showing columnar cells in different physiological phases of secretion. x 7760

C, circular muscle layer; D, disintegrating columnar cells; E, columnar epithelial cells not in secretory phase; F, detaching columnar cell; G, detached cell; N, nucleus; Q, newly formed columnar cell; SG, secretory granules; T, connective tissue layer.


F
44
T
E
G
N
45

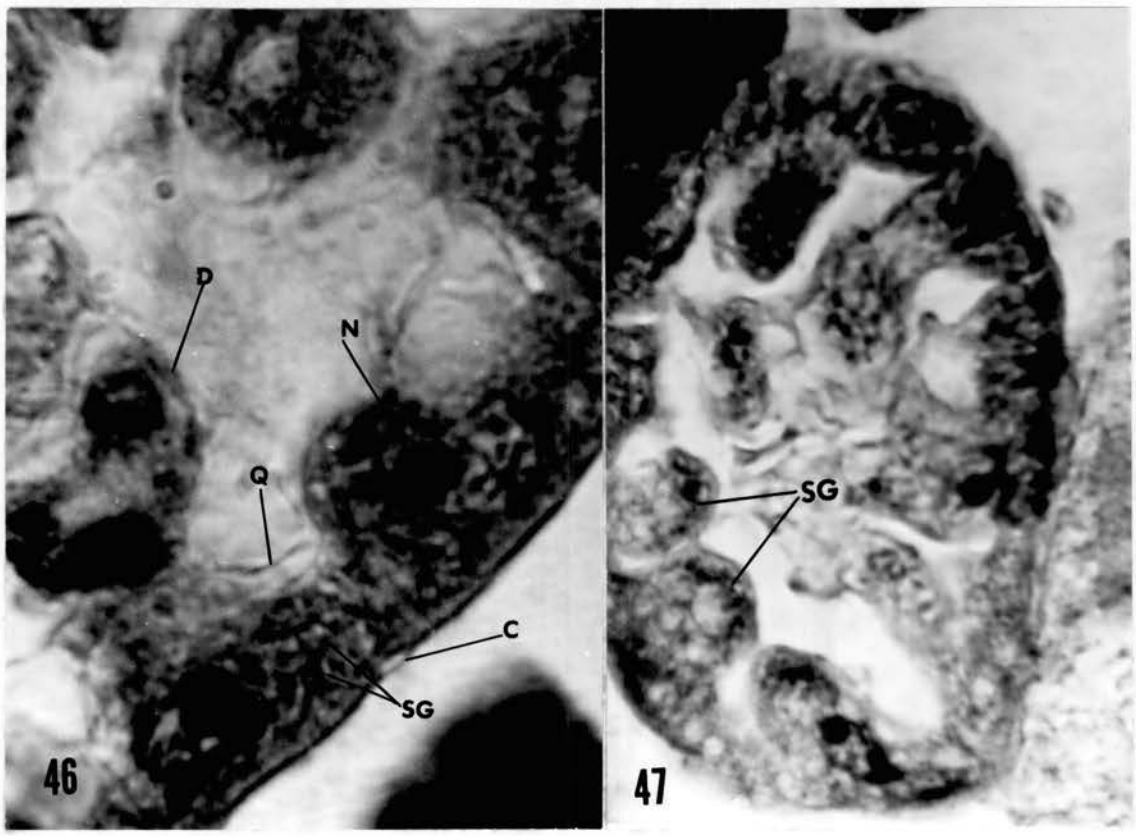

D
N
Q
C
SG
46
SG
47

PLATE XIV

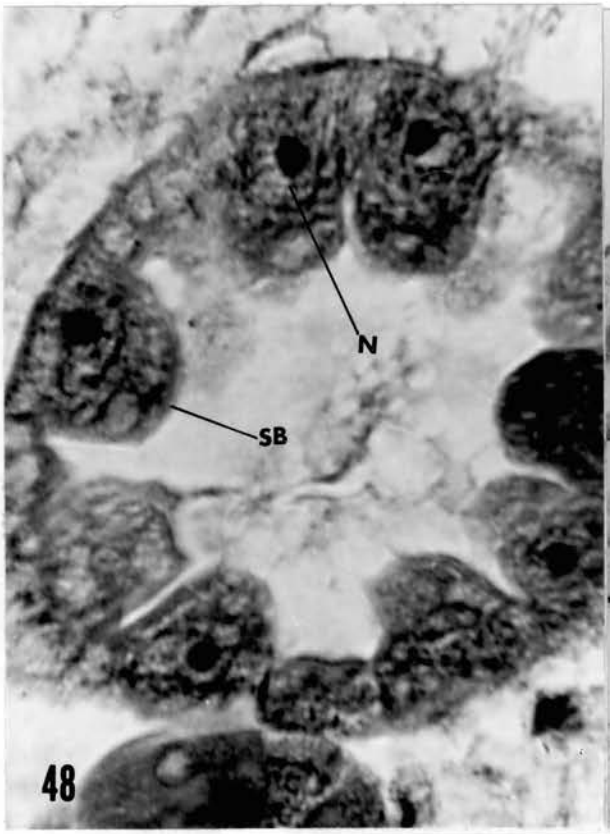
Fig. 48 Photomicrograph of the transverse section of posterior region of stomach with least secretory activity. x 7760

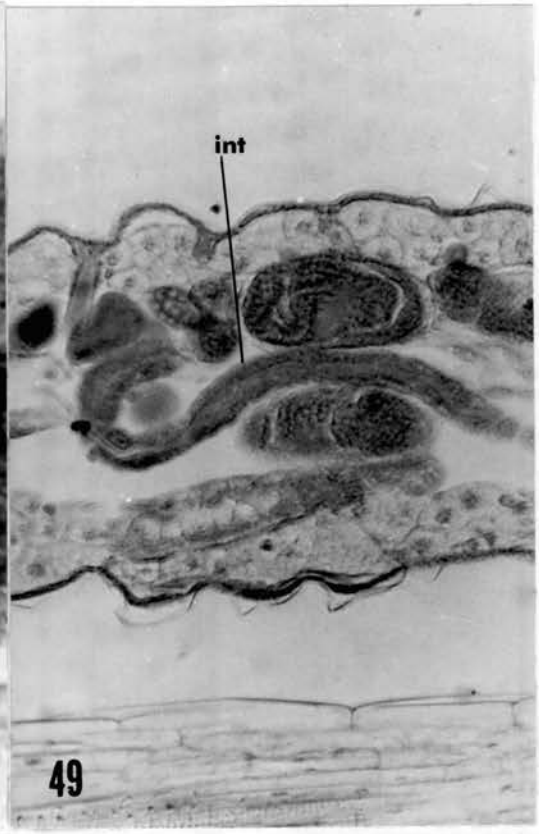
Fig. 49 Photomicrograph of the longitudinal section of body showing a part of intestine. x 800

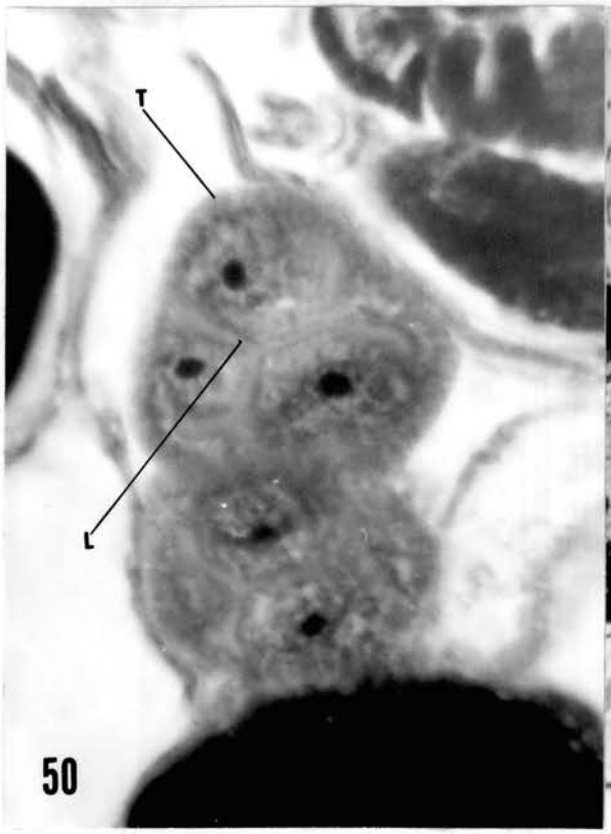
Fig. 50 Photomicrograph of the transverse section of intestine. x 7760

Fig. 51 Photomicrograph of the transverse section of body showing extremely thin wall of rectum with thin flattened epithelial cells. x 3440

E, epithelial cell; H, rectum; int, intestine; L, lumen; N, nucleus; SB, striated border; T, connective tissue layer.


N
SB
48


int
49


T
L
50

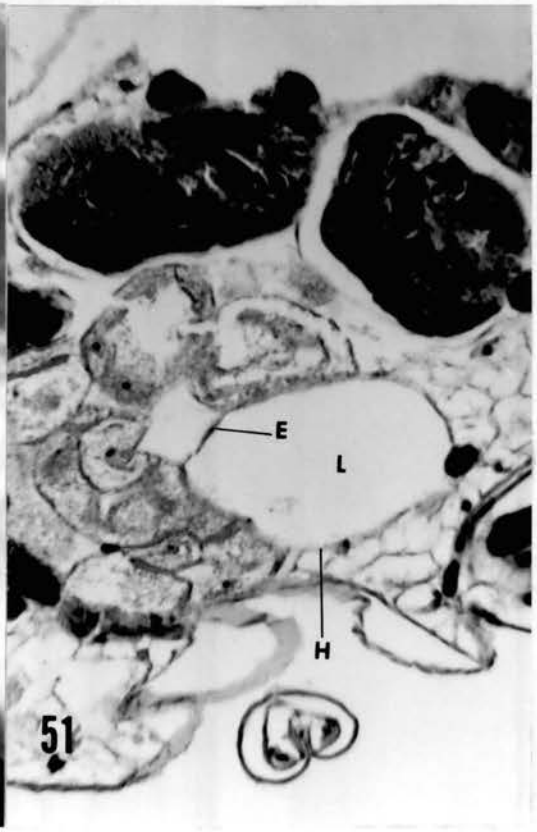

E
L
H
51

PLATE XV

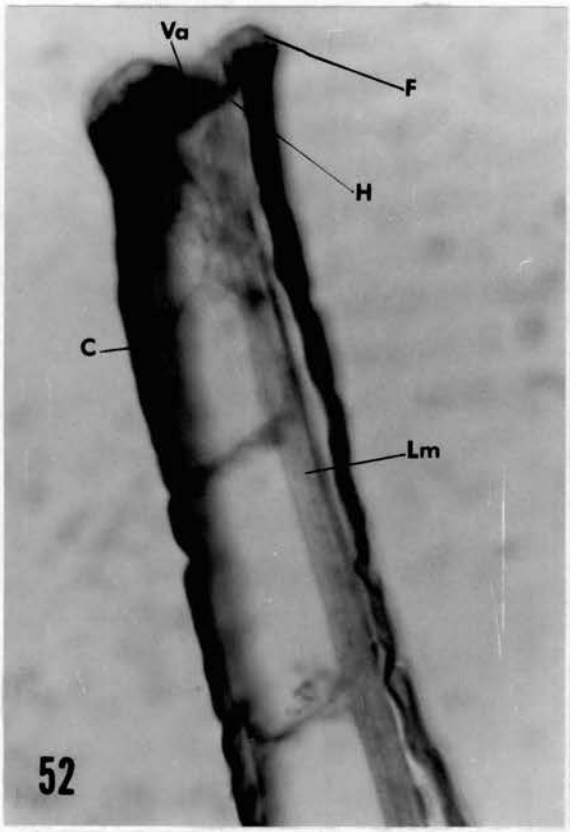
Fig. 52 Photomicrograph of the longitudinal section of cornicle showing longitudinal muscle of the valve. x 3440

Fig. 53 Photomicrograph of the longitudinal section of cornicle with valve shifted to one side thereby opening the aperture. x 3440

Fig. 54 Photomicrograph of the longitudinal section of cornicle showing the exact construction of the valve. x 3440

Fig. 55 Photomicrograph of the longitudinal section of cornicle showing the attachment of valve and the hypodermal elongated cells. x 7760

C, cornicle; F, flange; H, hinge; hec, hypodermal elongated cells; Lm, longitudinal muscle; Tn, tonofibrillae; Va, cornicle valve; W, secretion globule.



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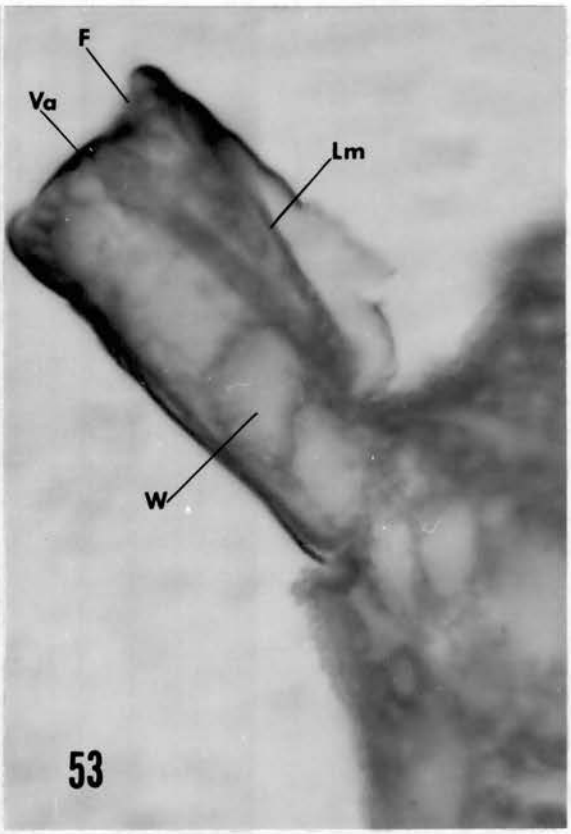

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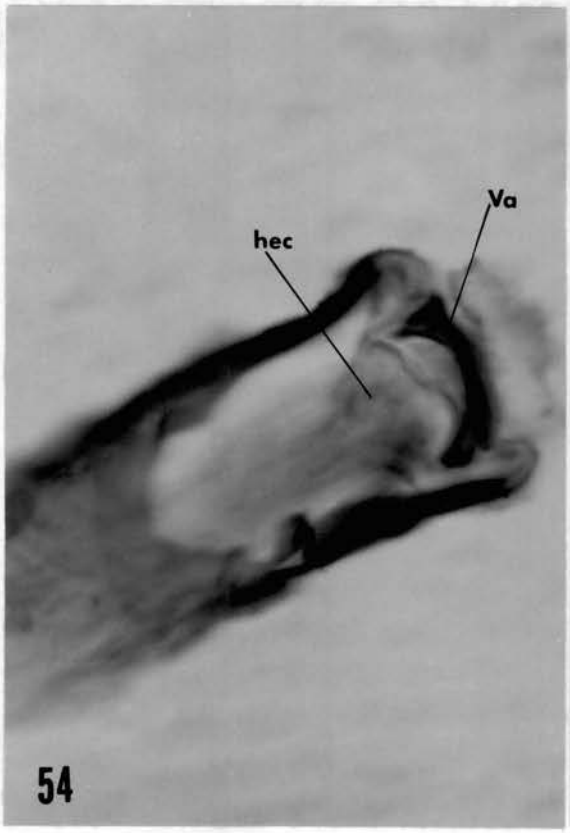

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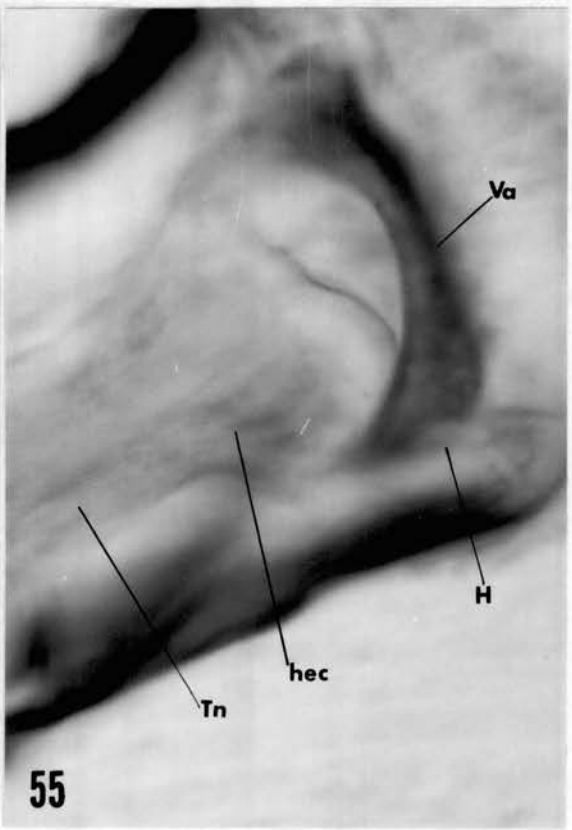

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PLATE XVI

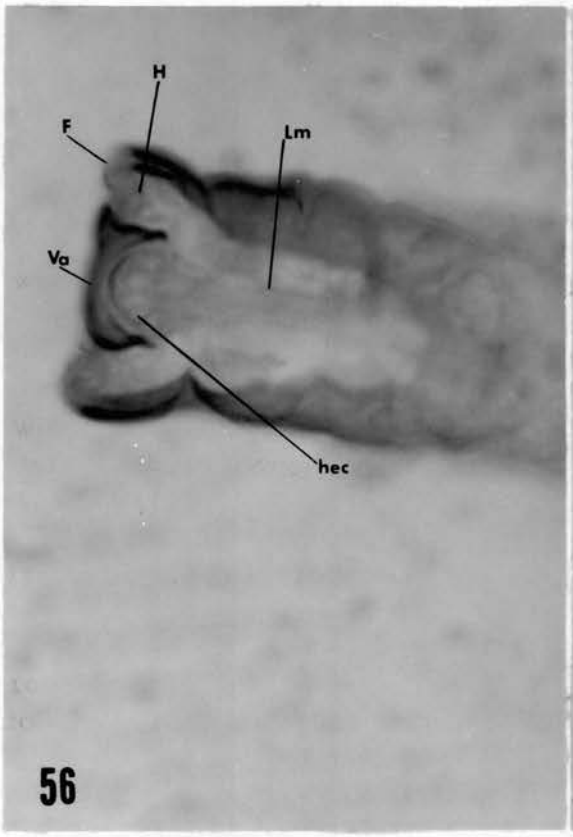
Fig. 56 Photomicrograph of the longitudinal section of cornicle showing the arrangement of hypodermal elongated cells beneath the cornicle valve. x 3440

Fig. 57 Photomicrograph of the longitudinal section of cornicle showing the secretion globules and the general hypodermal layer of the cornicle. x 3440

Fig. 58 Photomicrograph of the longitudinal section of posterior part of body with cornicle. x 800

Fig. 59 Photomicrograph of the stained whole mount of posterior portion of greenbug showing the course of longitudinal muscle of the valve inside the abdomen. x 800

C, cornicle; F, flange; H, hinge; hec, hypodermal elongated cells; Lm, longitudinal muscle; Va, cornicle valve; ven, venter of abdomen; W, secretion globule; Y, general hypodermal layer of cornicle.



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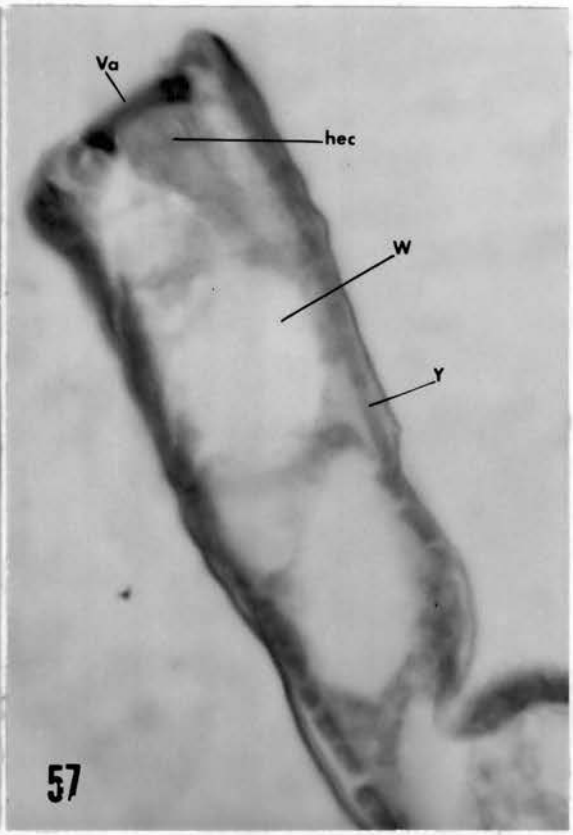

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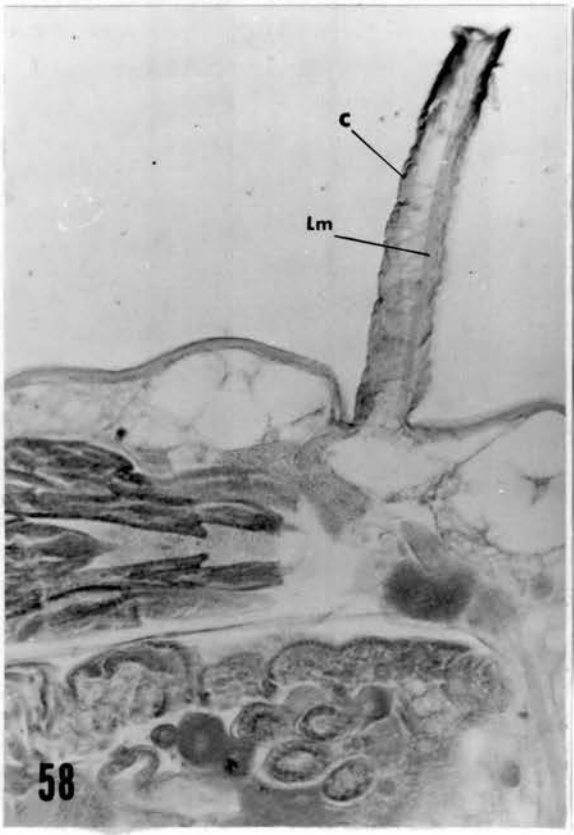

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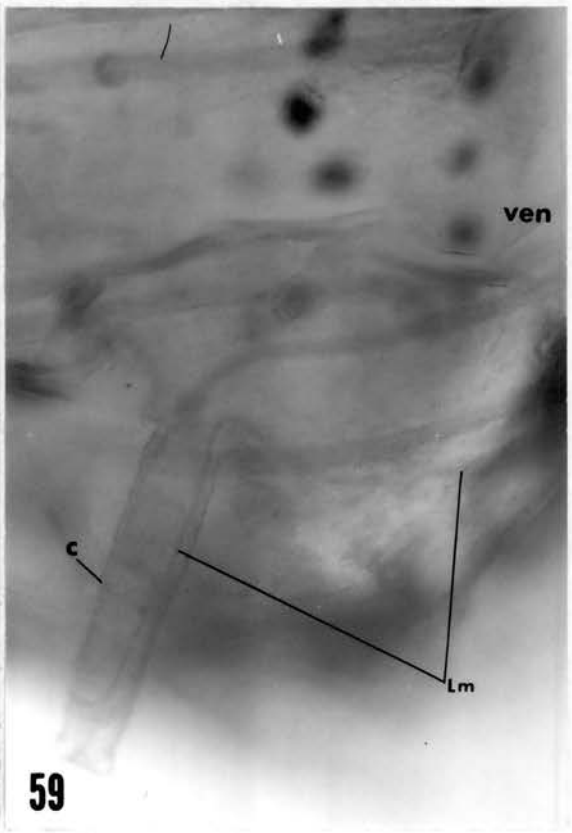


59

PLATE XVII

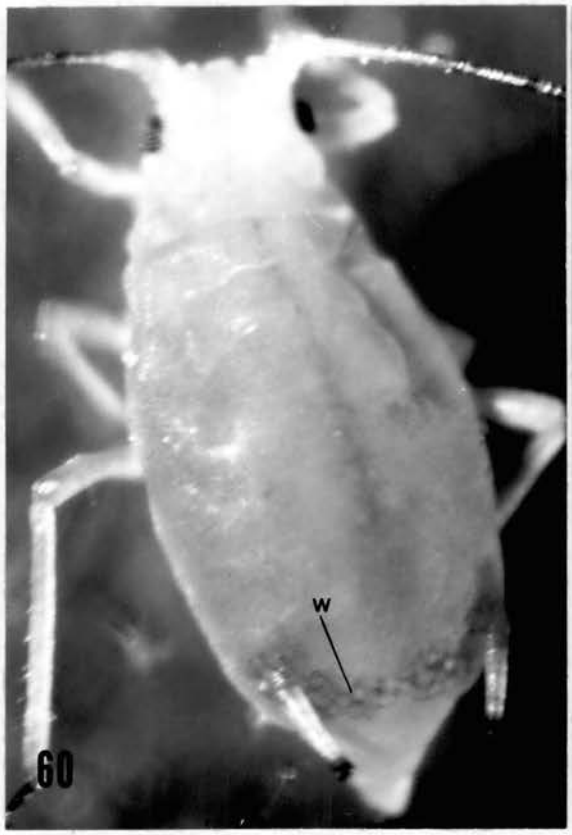
Fig. 60 Photomicrograph of the dorsal view of living greenbug showing the accumulation of secretion globules in the posterior part of the abdomen. x 270

Fig. 61 Photomicrograph of the longitudinal section of lateral part of abdomen showing the secretion globules originating anteriorly, migrating posteriorly and assembling below the cornicles. x 800

Fig. 62 Photomicrograph of the longitudinal section of cornicle showing the secretion globules in the process of being excreted. x 800

Fig. 63 Photomicrograph of the dorsal view of living greenbug with ball-like secretions at the tips of cornicles. Note the disposition of cornicles while discharging the secretion and compare it with the resting position in Fig. 60. x 240

C, cornicle; W, secretion globules.


W
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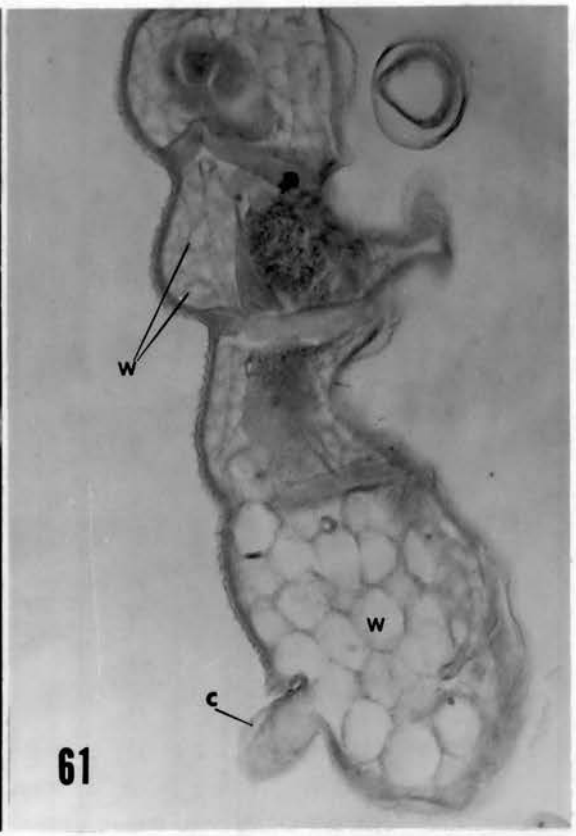

W
W
C
61

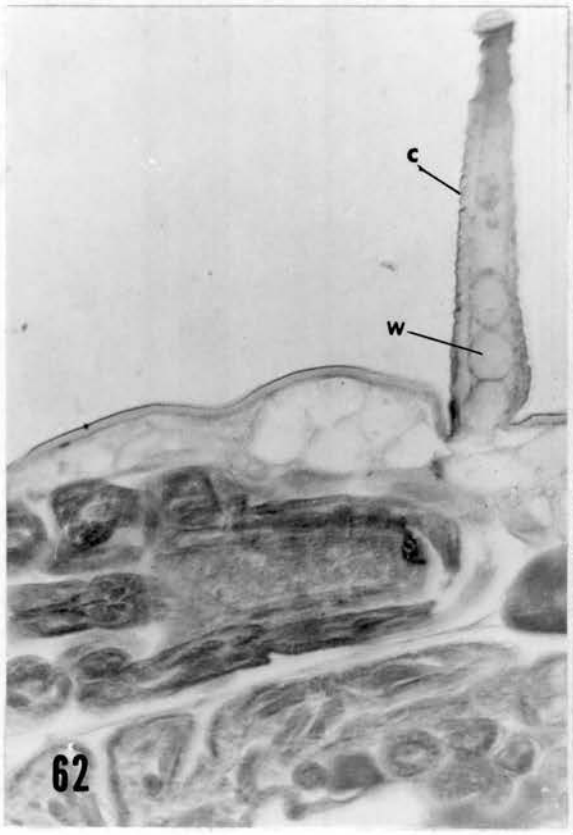

C
W
62

PLATE XVIII

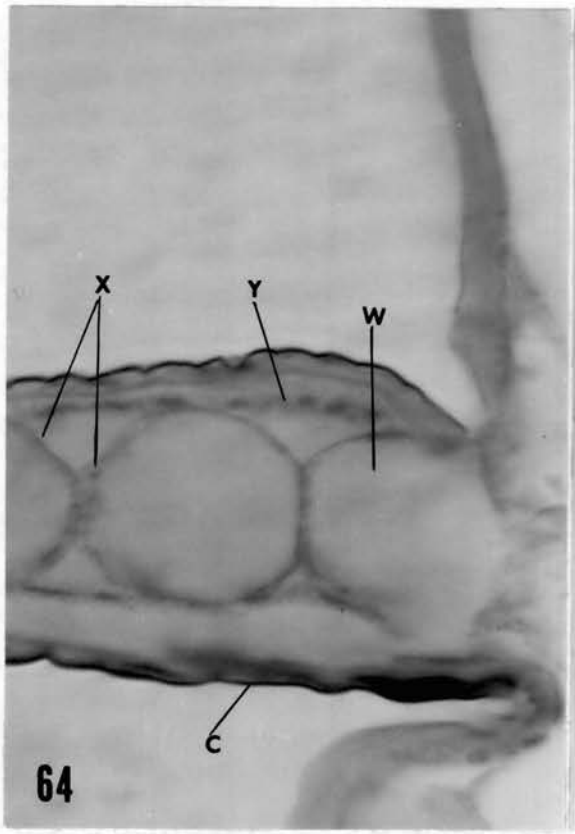
Fig, 64 Photomicrograph of the longitudinal section of cornicle showing the details of secretion globules. x 3440

Fig. 65 Photomicrograph of the first ball of cornicle secretion. x 3440

Fig. 66 Photomicrograph of the smear of first cornicle secretion. x 7760

Fig. 67 Photomicrograph of the smear of second cornicle secretion showing blood corpuscles. x 7760

Bc, blood corpuscles; C, cornicle; Lp, radiating lipid plaques; W, secretion globule; X, greenish granular material; Y, general hypodermal layer of cornicle.



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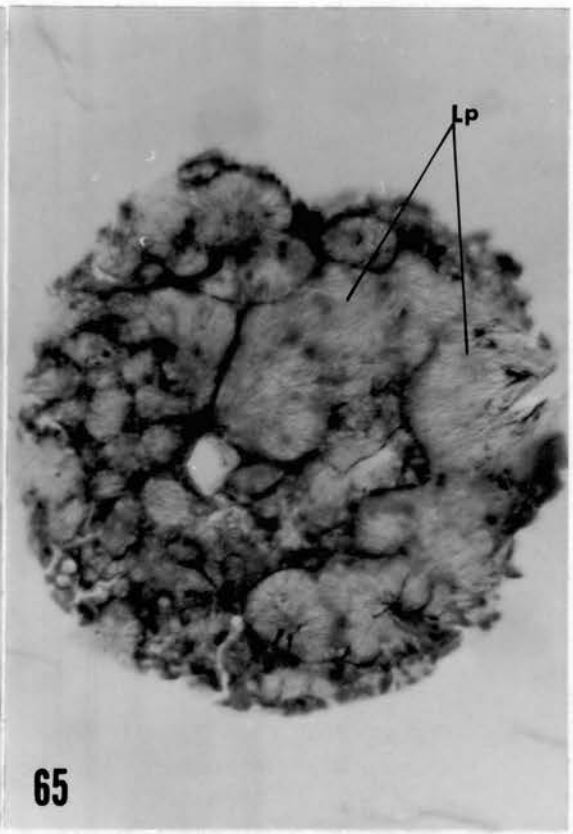

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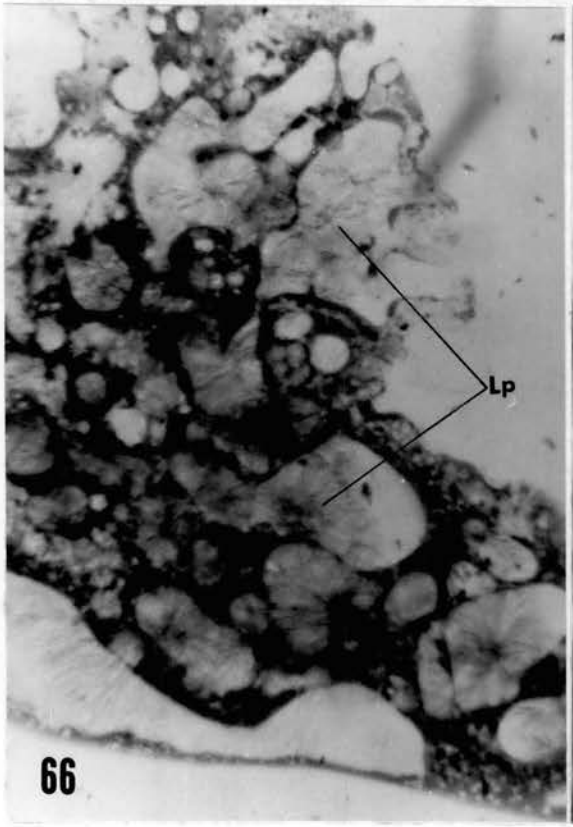

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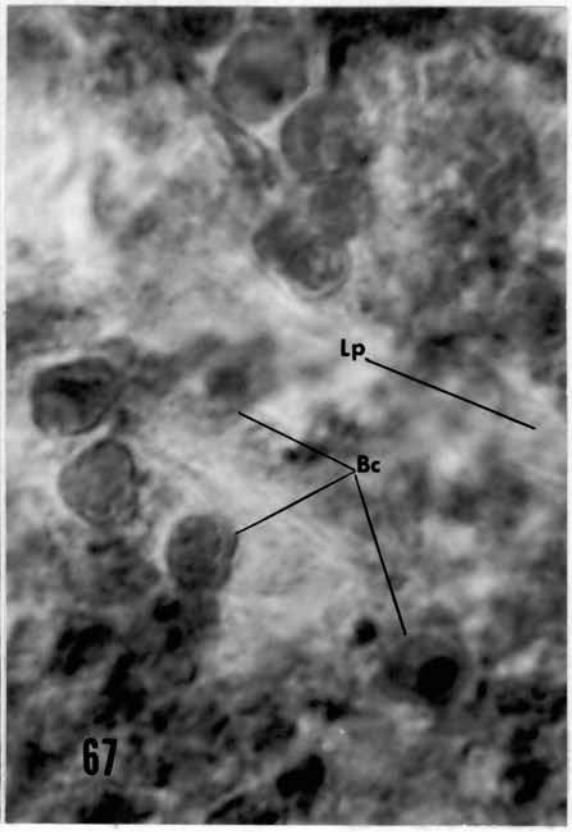

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PLATE XIX

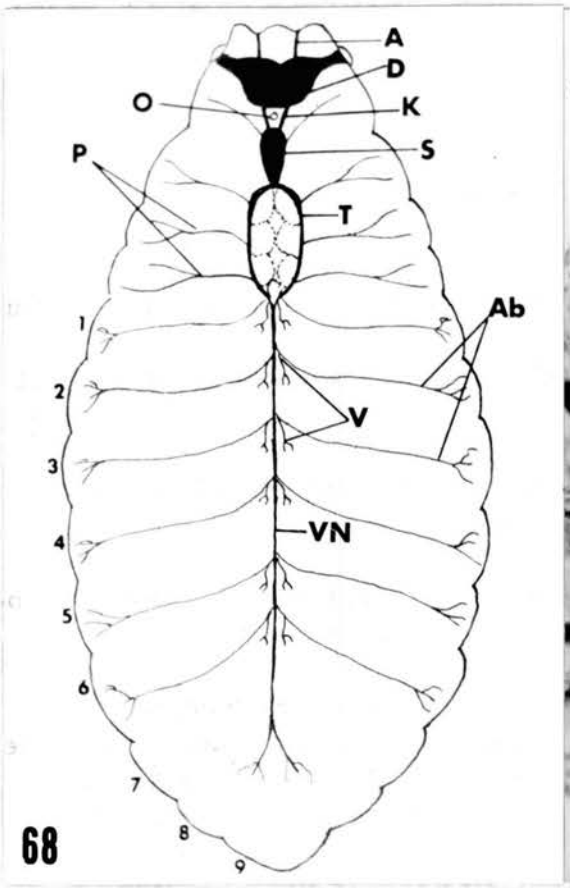
Fig. 68 Diagrammatic view of the central nervous system of greenbug.

Fig. 69 Photomicrograph of the longitudinal cross section of central nervous system. x 800

Fig. 70 Photomicrograph of dissection showing thoracic ganglionic mass and the ventral nerve cord. x 360

Fig. 71 Photomicrograph of a portion of cerebral ganglia showing fiber tracts and a few association neurones. x 7760

A, antennary nerve; Ab, segmental lateral branches of ventral nerve cord; Ag, abdominal ganglion; An, association neurone; D, cerebral ganglia; De, deutocerebrum; Fb, fiber tracts; K, circumoesophageal connective; O, oesophagus; Op, optic lobe; P, thoracic nerves; Pr, protocerebrum; S, suboesophageal ganglion; T, thoracic ganglionic mass; Tg, thoracic ganglia; Tr, tritocerebrum; V, visceral nerves of ventral nerve cord; VN, ventral nerve cord.



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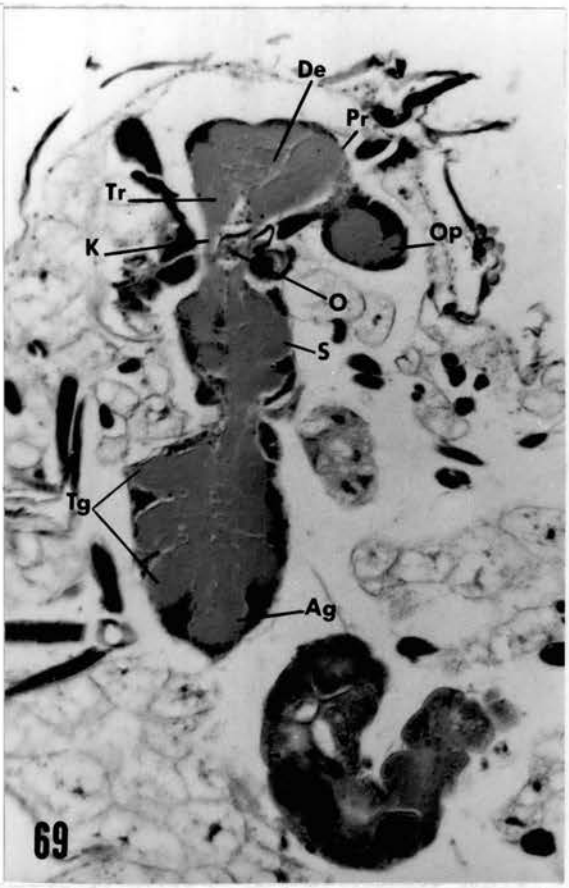

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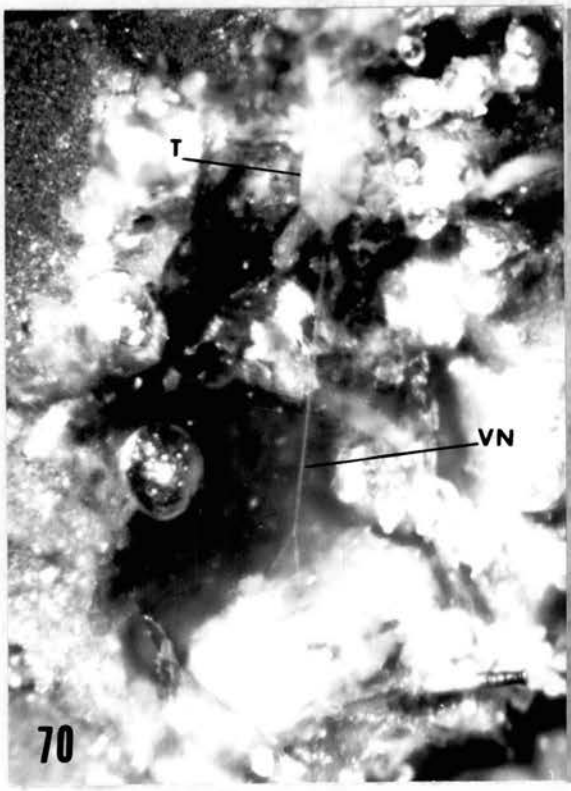

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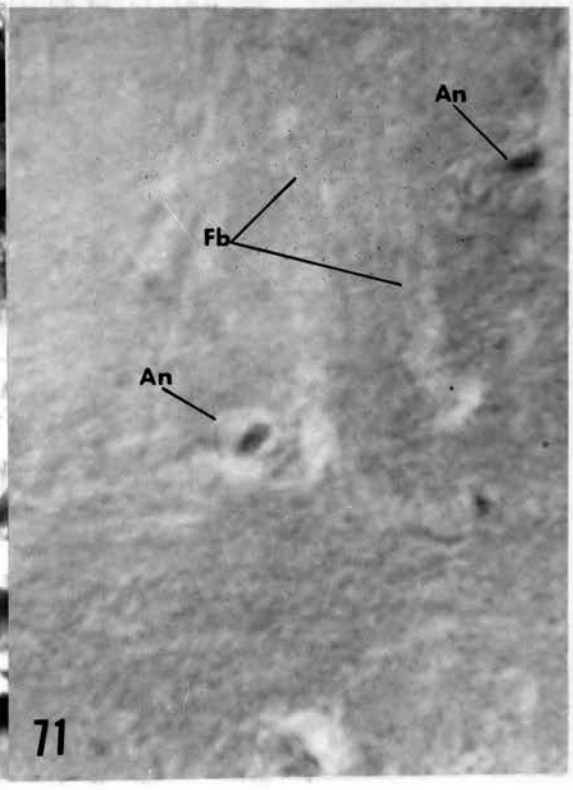

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PLATE XX

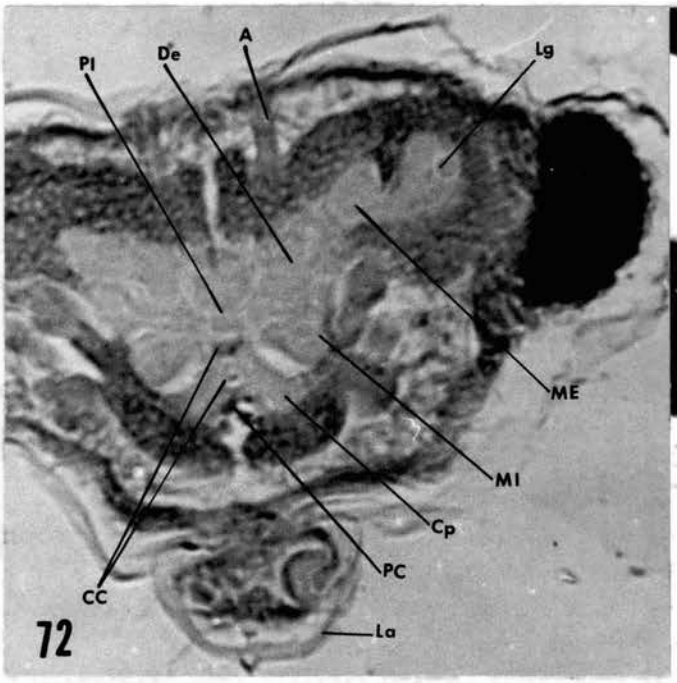
Fig. 72 Photomicrograph of the transverse section of head showing different parts of protocerebrum. x 3440

Fig. 73 Photomicrograph of the longitudinal section of embryo (approximately 48 hours old) showing the formation of suboesophageal ganglion and thoracic ganglionic mass. x 1200

Fig. 74 Photomicrograph of the longitudinal section of head and thorax showing stomatogastric nervous system. x 3440

Fig. 75 Photomicrograph of the longitudinal section of embryo (approximately 60 hours old) showing the fusion of suboesophageal ganglion with the thoracic ganglionic mass and the appearance and fusion of abdominal ganglion with thoracic ganglionic mass. x 1200

A, antennary nerve; Ag, abdominal ganglion; CA, corpus allatum; CC, corpus centrale; Cd, corpora cardiaca; Cp, corpus pedunculatum; De, deutocerebrum; Fg, frontal ganglion; Hp, hypocerebral ganglion; La, labium; Lg, lamina ganglionaris; ME, medulla externa; MI, medulla interna; O, oesophagus; PC, pons cerebralis; PI, pars intercerebralis; Pr, protocerebrum; S, suboesophageal ganglion; T, thoracic ganglionic mass; Tg, thoracic ganglia; Tm, tentorium; Tr, tritocerebrum.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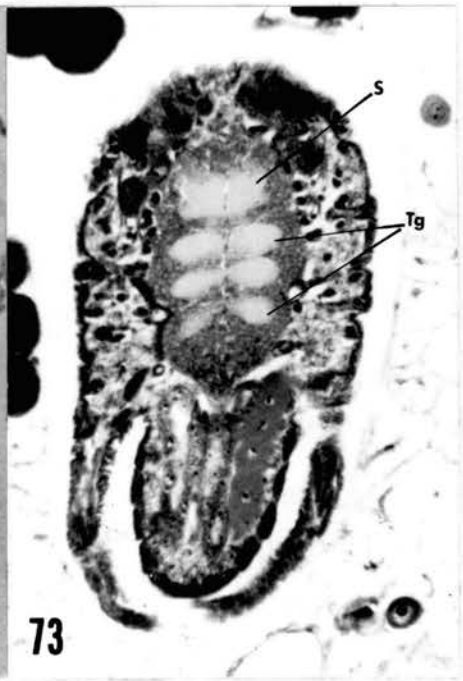
72


S
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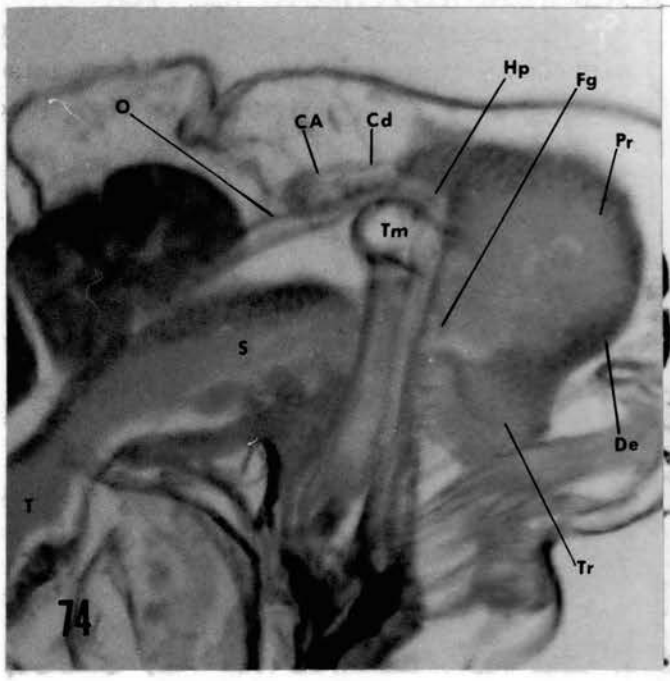
73


Hp
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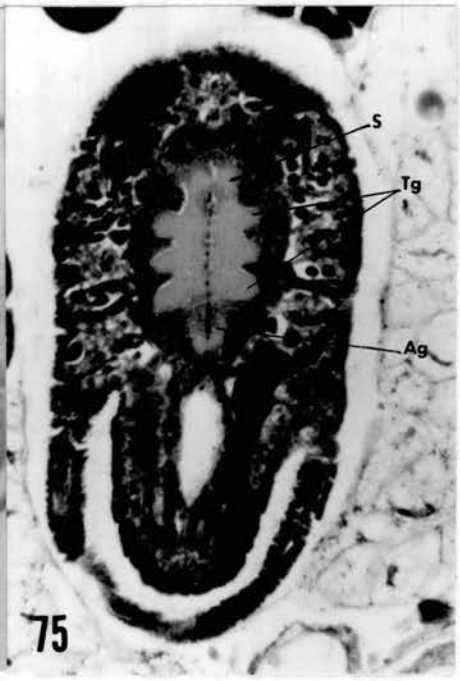
S
Tg
Ag
75

VITA

Prakash Narain Saxena

Candidate for the Degree of

Doctor of Philosophy

Thesis: THE ANATOMY, HISTOLOGY, AND CYTOLOGY OF THE GREENBUG, SCHIZAPHIS GRAMINUM (RONDANI), IN RELATION TO FACTORS RESPONSIBLE FOR RESISTANCE IN BARLEY AND WHEAT.

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