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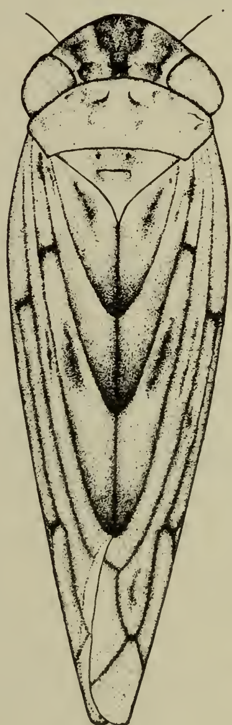
Studies on the Morphology of the Beet Leafhopper

Eutettix tenellus (Baker)

G. F. KNOWLTON



A dark form of the beet leafhopper,
Eutettix tenellus (Baker)
(x 29)

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STUDIES ON THE MORPHOLOGY OF THE BEET LEAFHOPPER[1]

Eutettix tenellus (Baker)

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INTRODUCTION

The beet leafhopper, *Eutettix tenellus* (Baker), is one of the most serious insect pests of western North America. Its chief importance is as a vector of the plant disease curly-top, which it transmits to beets, tomatoes, beans, melons, and many other agricultural plants. The virus apparently is introduced into the plant during the process of feeding, and is responsible for the frequent and often enormous losses to the sugar-beet growers and sugar manufacturers of the west. Apparently, the virus multiplies and remains active in the body of a leafhopper for some time, making it possible for the insect, after once feeding on a curly-top plant, to transmit the disease for a period of several weeks or even months. This study was undertaken to obtain information regarding certain of the internal organs. The writer also entertains the hope that a discussion, together with illustrations of the structures, might be of assistance to workers interested in a study of the internal structures to determine, if possible, the region or regions in which the virus is carried while in the body of the insect. Especial emphasis has been placed on the digestive tract and its accessory glands, as they appear to be the organs most closely associated with disease transmission.

GENERAL EXTERNAL MORPHOLOGY

The body of the beet leafhopper is small, slender, and tapers posteriorly (Fig. 2). The widest point of the body when the wings are normally at rest is in the region immediately behind the metathorax.

[1]The writer wishes to thank Dr. H. J. Pack, Station Entomologist, for suggestions and criticisms of this paper, and Dr. R. E. Snodgrass of the U. S. Bureau of Entomology for reading and making suggestions on the manuscript. Work on this project is carried on in cooperation with the U. S. Bureau of Entomology, (Dr. Walter Carter in charge) and with the Idaho Agricultural Experiment Station.

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In the females the length to the tip of the wings is about 3.5 mm.; it is slightly shorter in the males. The abdomen does not extend to the end of the wings and in the males is somewhat shorter than that in the females. Mature individuals are always winged. Wing rudiments are noticeable in the third nymphal instar. Reddish, brownish, or blackish saddle-like markings ordinarily occur on nymphs after the second or third molt. Adults vary in color from creamy-white to greenish, or possess brownish to blackish markings on front wings, head, pronotum, and scutellum. The sclerites of the abdomen are blackish to black with lighter colored margins. The color pattern of *tenellus* is subject to considerable variation.

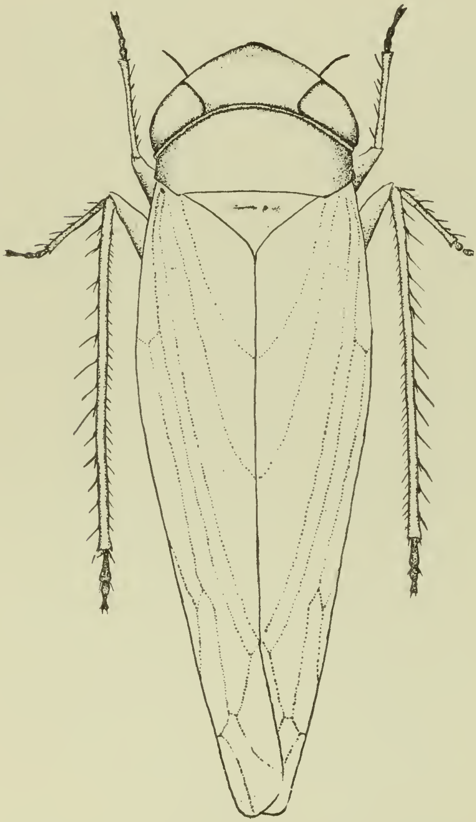

FIG. 1.—A light-colored form of the beet leafhopper, *Eutettix tenellus* (Baker) (x 30)

Head.—The head (Figs. 2,3) is a short and rather rigid capsule, with a short sloping vertex, rounded in front, about one-fourth longer at center than against the eyes, and with a short coronal suture. Head broadly joined to thorax, permitting little if any movement. Compound eyes prominent, moderately large and cover the dorso-lateral surfaces of the head. The two ocelli (Fig. 3) are small and situated on the margin of the vertex between and near to the compound eyes. Antennae (Fig. 4) setaceous or awl-like, with two distinct basal segments, and with a small bristle arising from the thickened basal part of the distal structure, which tapers gradually to a thin portion at its apex. The antennae are situated on the front of the head, between the eyes and in depressions. The labium arises on the underside and from the back of the head. The mouthparts are composed of the labium (Fig. 5), or sucking tube, a dorsally-grooved sheath which is fused along its ventral margin and approximated or somewhat fused along the dorsal groove. A groove in the labium contains the stylet-like bristles, or mandibles and maxillae, which pierce the plant tissues.

The anterior, outer pair arising in the head are the mandibles; back of these lie the maxillae. A pair of grooves in the approximated maxillae provide both a tubular opening to carry the saliva down into the plant and another groove leading to the mouth cavity, which serves for an opening through which to suck out the plant juices from the host. Inside the labium and next to the labial groove, the mandibles and maxillae lie compactly together. The apex of the labium is armed with a number of sensory setae, which may aid in locating a place to start feeding. The labium ordinarily does not penetrate the plant tissue, but the mandibles and maxillae do. Apparently, it is during the feeding process and contact through the sucking mouthparts that the virus of curly-top is transmitted to beets, squash, tomatoes, and other susceptible plants.

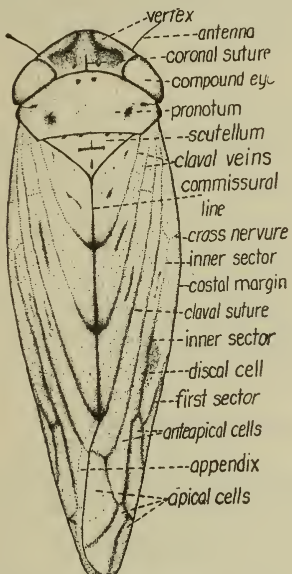

FIG. 2.—A moderately dark form of the beet leafhopper, *Eutettix tenellus* (Baker) (x 23)

Thorax.—This is the second or middle region of the insect's body, specialized for locomotion. The three pairs of legs and the two pairs of wings are attached to this portion of the body; the large mass of nerve tissue is also housed here. The thorax, especially the meso- and meta-thoracic divisions, is highly developed and encased in a sturdy sclerotized sheath. Several phragmas or infoldings of the thoracic wall occur, giving added surface for the attachment of muscles.

The prothorax bears the first pair of legs, is covered above by the pronotum, and is smaller than the following divisions. Immediately behind the pronotum is the triangular scuttellum. The meso- and meta-thoracic segments each bear a pair of wings attached to the upper part of the pleural, and lateral parts of the tergal segments. These are attached at the base by thinly sclerotized flexible connections, or membranes, permitting free movement in flight. The wings are hollow, 2-layered

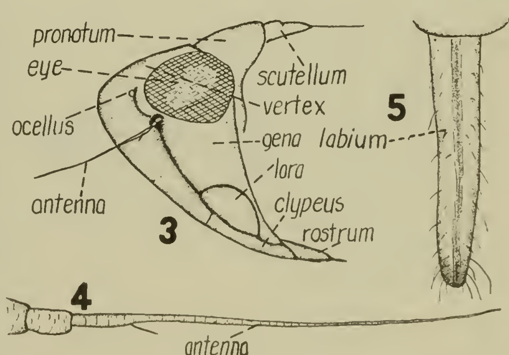

FIG. 3.—Lateral view of head of mature imago
FIG. 4.—Antenna, much enlarged
FIG. 5.—Labium of *Eutettix tenellus*

outgrowths from the body wall, continuous with the cuticula of the thorax. The margin of the thorax surrounding the wing bases is quite heavily sclerotized. The forewings (Figs. 1, 2) are uniformly sclerotized and held roof-like over the thorax and abdomen; they cover the second pair of membranous meta-thoracic wings. The front wings (Fig. 6)

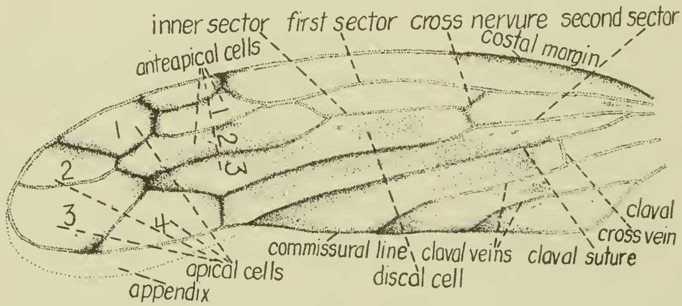

FIG. 6.—Front wing of *Eutettix tenellus* (Baker) with veins and cells labeled

are moderately broad, rounded at the apex, closely folded, and exceed the abdomen in length. Often they have dusky pigmented areas over part of the surface. One cross nervure is present between the first and second sectors; the inner branch of the first sector forks on the disc of the corium; the inner sector is twice-forked, forming three ante-apical cells.

Two thoracic spiracles are present on each side of the thorax.

The coxae of the legs are attached between the pleura and the sternum, and support the well-developed legs which are adapted for jumping. The hind pair of tibia is equipped with two rows of spines, one on each margin. The tarsi are 3-jointed and armed with claws. Coxa and trochanter are short, while the femur, tibia, and tarsus are elongate, being longest in the meta-thoracic legs.

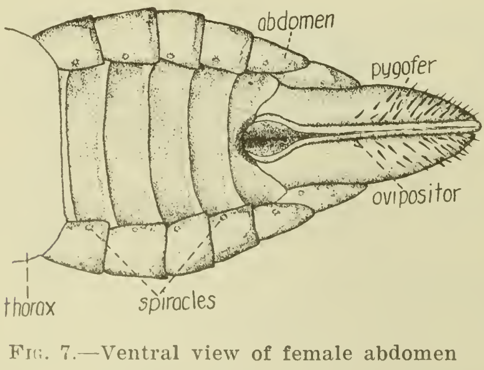

FIG. 7.—Ventral view of female abdomen

Abdomen.—The abdomen (Fig. 7) is distinct and extends backward from its juncture with the meta-thorax, to which it is broadly joined anteriorly, and tapers toward the caudal end, especially in the females. The anus opens on the last segment. The orifice of the male reproductive organs is on the ninth segment; the reproductive opening of the female is on the eighth. The external genitalia of the male and female beet leaf-hoppers are distinctive. The ovipositor of the female is long and reaches to or extends slightly beyond the tip of the abdomen. The spiracles (Fig. 7) open in a row along each side of the abdomen on the ventral surface of the body, lying near the lower margins of the tergal sclerites, where these approach the sternal plates, and near the line of juncture with the longitudinal intersegmental membrane.

STRUCTURE OF THE BODY WALL

The sclerotized exo-skeleton of the beet leafhopper is well-developed, giving plenty of strength and rigidity for active muscular activity, with lightness in weight, permitting rapid movements and a quick getaway from the resting position.

The body wall (Fig. 8) consists of the following layers:

1. The *cuticula* is in general the sclerotized portion of the body wall, and its infoldings, composed of a sheet of chitin. This may be divided into an outer, hard layer, the primary cuticula, and an inner, thicker layer, the secondary cuticula, which is softer. In sectioning entire insects these two layers sometimes become separated. The cuticula forms the covering over the outside of the body and in addition the hard parts of the inside of the body. The cuticula differs greatly in thickness in different parts of the body wall. The sclerites in most regions of the body are well-chitinized. The sutures may be grooves only and not movable, or they may be thinly sclerotized, more or less membraneous articulations. In the head and thorax, most of the connections between the sclerites are rigid, or fused. In the abdomen, most of the sutures are flexible.

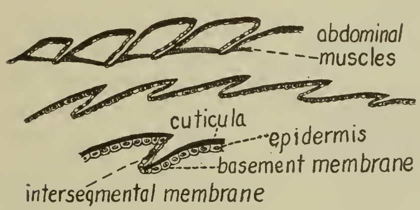

FIG. 8.—Sections of the body wall through the abdomen

In *tenellus*, most of the body is smooth, but cuticular appendages, in the form of hairs, occur on the end of the abdomen, and on the tip of the rostrum, as well as in a few other places; small pits or imbrications occur over much of the body wall.

Most of the muscles of the body are attached to the external cuticula, or its infoldings, the apodemes. These vary greatly in size and shape. The infoldings of the thorax, to which the dorsal longitudinal muscles are attached, are well-developed and conspicuous.

2. The *epidermis* consists of a single layer of cuboid or flattened cells. In nymphs and younger adults, the cell walls are usually distinct. In older adults, and in many parts of the body of younger-winged forms, the boundaries of the cell walls are lost, often the nucleated hypodermal layer forms a syncytium, the cell walls not being distinguishable. The hypodermis cells secrete the chitin and the basement membrane, lying on either side of it.

3. The *basement membrane* is a thin, almost structureless membrane, secreted by the hypodermal cells, and covering the inner surface of the hypodermis. It is interrupted in places by insertion of nerves and muscles.

STRUCTURE OF THE HEAD

The homologies of the head plates in Hemiptera and Homoptera are still offering a difficult problem to morphologists. The dorsal surface (Fig. 2) of the head of *tenellus* is broad and rather short; the face is flattened and slopes backward.

The posterior surface of the head is broadly joined to the prothorax by the neck or cervix; a fairly large opening exists between the head and thorax, the occipital foramen or foramen magnum. The dorsal and lateral area of the head surrounding this opening is the occipital area. The true ventral part of the head is that lying between the bases of the mouthparts. Part of the mouthparts lie outside of the head, including the distal ends of the labium, mandibles, and maxillae. The head contains the brain, the mouth, pharynx, pharyngeal muscles, a part of the oesophagus, the basal portion of the mandibles, maxillae, and their muscles, a small amount of adipose tissue, the tentorium, and some other structures.

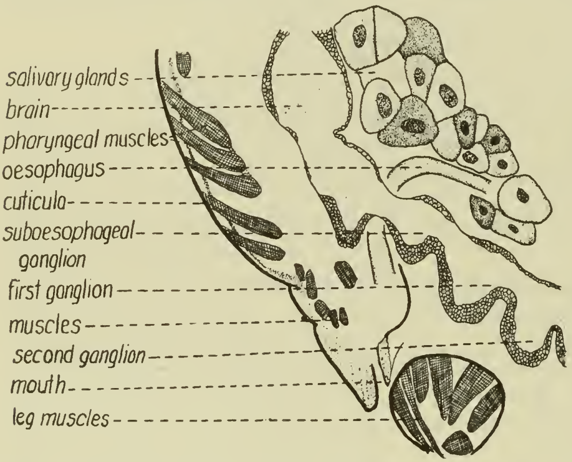

Fig. 9.—Longitudinal section through lower part of head and pro-thorax, seen from the left

The mouthparts are made up of the stylet-like mandibles and maxillae, the hypopharnyx, and the fused labium, which forms the rostrum and is a sheath containing the mandibles and maxillae. The hypopharynx lies just back of the mouth, forming part of the floor of the mouth, behind. The mouth (Fig. 9) is a short tube leading from the tubular opening of the maxillae into the pharynx. The walls of the mouth are thickly chitinized. The pharynx is most heavily chitinized on its posterior side. The pharynx is apparently capable of considerable distension; at rest the two walls lie next to each other, almost closing the lumen of this chamber. The pharynx is operated by the powerful pharyngeal muscles (Figs. 9, 10), which are arranged in two rows on each side of the median line of the head and extending down to the pharynx, at an angle from the head. The anterior wall of the pharynx is flexible, compared to its opposite more heavily chitinized wall. Contraction of the dilator muscles opens the bulb, creates a partial vacuum and draws up the plant juices, when the insect is feeding. Relaxation of the pharyngeal muscles allows the chamber to spring back to the closed position. Most of these muscles arise from what Snodgrass (1927) considers the large post-clypeal sclerite. No valves are found at either end of the pharynx, which becomes smaller and changes to oesophagus as it passes between the short, thickened circum-oesophageal commissures. The pump and pharynx seem to be the same structure in *tenellus*, although the walls of the organ are not muscular, at least in the lower, more expanded part. The food channel, which begins in the small tubular opening through the interlocked maxillae, is a closed tube, continuing on into the mid-intestine. The mandibles and maxillae are capable of some movement, produced by the protractor and retractor muscles in the head, which aid in forcing these structures into the plant tissues. Ordinarily, the labium is not inserted into the plant but rests against it during feeding, while the maxillae particularly may invade the tissues for some distance. The labium may be partially retracted into the head.

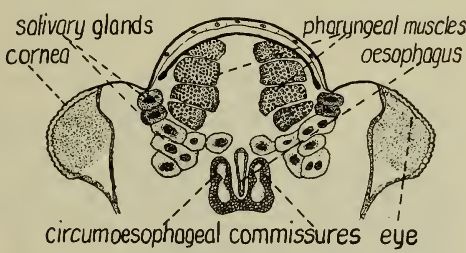

FIG. 10.—Longitudinal section through lower part of head, seen from above

Most of the head cavity in *tenellus* is taken up with the brain, pharyngeal muscles, bases of the mandibles and maxillae and their muscles. Little room is left for salivary glands to lie in the head, although a small portion of these glands may lie in the capsule just back of the brain and next to the circum-oesophageal commissures.

STRUCTURE OF THE THORACIC SEGMENTS

The process of walking and the leg structures of the leafhopper are primarily concerned with the sternal and lower pleural parts of the thorax. The development of wings and their function as flight organs are more largely connected with the upper pleural and tergal regions, with part of the sternal regions being used for the attachment of the tergo-sternal muscles.

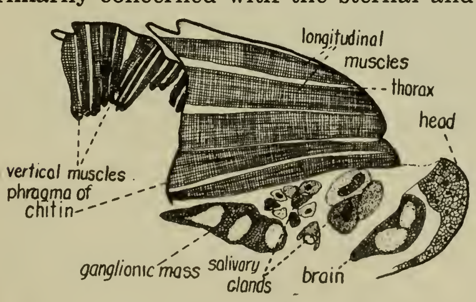

FIG. 11.—Longitudinal section through head and thorax, showing longitudinal dorsal muscles lying in the left side of the mesothorax

Flight in the beet leafhopper is produced by an alternation, or change in the shape of the comparatively rigid thorax, by the alternate movements of the indirect wing muscles. Only a few small muscles attach more directly to the wings, but the indirect wing muscles are composed of heavy masses of muscles. The indirect wing muscles include the longitudinal, or dorsal longitudinal muscles, and the vertical, or tergo-sternal, muscles. In addition the meso-thorax is equipped with a set of modified coxal muscles and a few other small muscles. The meso- and meta-thoracic segments are supplied with a much greater mass of muscular tissue than the prothorax, which segment is lacking the function of flight, and the well-developed structures connected with this type of locomotion.

The meso-thorax has a well-developed anterior and a posterior phragma; there is a posterior meta-thoracic phragma for the attachment of the longitudinal dorsal muscles. When the dorsal longitudinal muscles (Fig. 11) contract they cause the tergum to bend upward in a gradual curve, which gives the down-stroke to the wings.

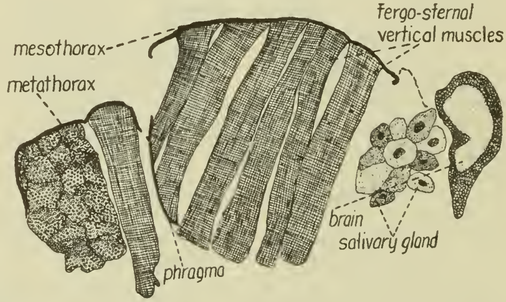

FIG. 12.—Longitudinal section lateral to that in Figure 11, showing the tergo-sternal muscles in the meso-thorax

The pleura of the meso- and meta-thoracic segments support the bases of the wings (Fig. 13), and with their rigidity give resistance to the downward pull of the tergo-sternal (Fig. 12) and tergo-coxal muscles (Fig. 13). The meso-thoracic coxal muscles attach to plates beneath the base of the wing and comprise the basalar and subalar muscles.

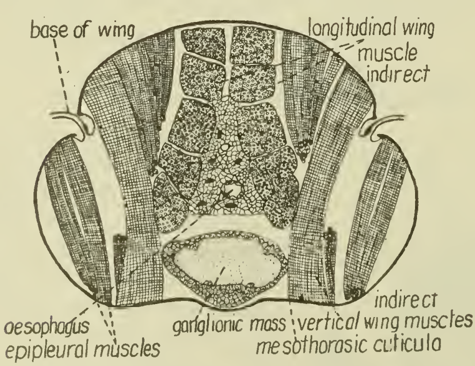

FIG. 13.—Cross-section of meso-thorax through the bases of the wings, showing the longitudinal and vertical indirect wing muscles and the epipleural muscles

The indirect wing muscles include the tergal muscles and the tergo-sternal muscles, which are primarily responsible for the movements which depress and elevate the wings through changing the shape of the thorax. These are heavy, well-developed muscles in *tenellus*. The longitudinal dorsal muscles are thick and powerful, shortening the thorax and depressing the wings. These muscles attach primarily to the well-developed phragmata. The oblique dorsal muscles apparently are the wing elevators.

The epipleural muscles, or basalar and subalar coxal muscles (Fig. 13), are well-developed in the meso-thoracic segment and are not attached directly to the wings but near the basal part. The basalar muscle is attached near the anterior margin of the wing base. The epipleural and third axillary muscles have more direct action upon the wings and may be considered as direct wing muscles, but are attached near and not directly to the basal part of the wing. The basalar muscle has a direct action on the wing, being attached near its anterior margin. The epipleural and third axillary muscles have more direct action upon the wings and may be considered as direct wing muscles, in contrast to the more distantly attached longitudinal dorsal muscles and the tergo-sternal muscles.

The wings in the nymphs are external growths of the body wall, consisting of the cuticula, hypodermis, basement membrane and possessing a lumen into which the liquids of the body cavity are able to enter and bathe the tissues. The adult wings are 2-layered, reinforced by trachea, and practically a lifeless structure. The adult wing is held roof-like over the abdomen when at rest but can quickly be extended laterally and develop rapid up-and-down motions with a slight amount of rotation.

STRUCTURE OF THE ABDOMEN

The abdomen of *Eutettix tenellus* is the third primary division of the body, and although broadly joined to the thorax it is not difficult to draw a line separating the two regions. The abdomen lacks external supporting structures, but in the case of females possesses a well-developed ovipositor. The main function of the abdomen is to hold and to protect the greater part of the digestive tract, the reproductive organs, the heart, the large fat body, and other organs of the region. The cuticla of the abdomen is not so strongly sclerotized as is that in most parts of the head and thorax.

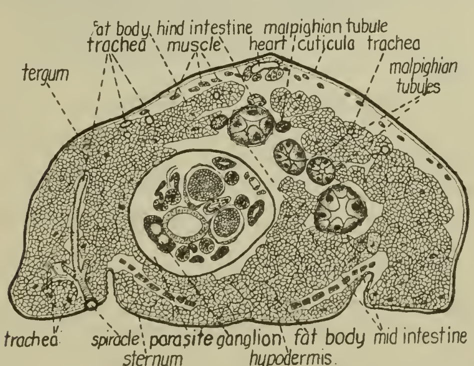

FIG. 14.—Cross-section through the abdomen of *Eutettix tenellus*, and through an internal parasite it contained

The abdomen consists of ten segments, the caudal segments being modified in connection with the reproductive functions and being somewhat retracted or telescoped. The plates forming the dorsal and lateral walls are the terga, and the ventral plates are the sterna. The ovipositor is composed of plates arising from the eighth and ninth sterna. The tergal and sternal plates are connected by an articular membrane, which is weakly chitinized and allows considerable extension or retraction of the segments. The posterior margin of each tergite or sternite overlaps the succeeding sternite or tergite externally, Thus, the anterior edge of most segments acts as part of the lining of the abdomen, while the caudal part of the segment is more of a supporting flap, overlapping the succeeding segment.

Rather frequently an internal parasite is found lying within the abdomen of a leafhopper.

MUSCLES

The muscles in the beet leafhopper are all striated, including the muscles surrounding the digestive tract.

Muscles in *tenellus* are very numerous and may or may not be grouped together. With the chitinous exo-skeleton affording such a great amount of surface for the attachment of muscles, the number in the abdomen (Fig. 16) alone is considerable. Even where great masses of muscle occur, as in the longitudinal tergal and the tergo-sternal muscles of the thorax, the muscles are not well bound together with connective tissue, as in vertebrate muscles, but are rather easily separated into many muscle fibers. Each muscle fiber is really a compound cell, having a number of nuclei. A section through the thoracic muscles (Fig. 15) will show an enormous number of nuclei in the muscle masses constituting the indirect wing muscles, as well as a supply of tracheal elements to aid in carrying oxygen to these well-developed structures.

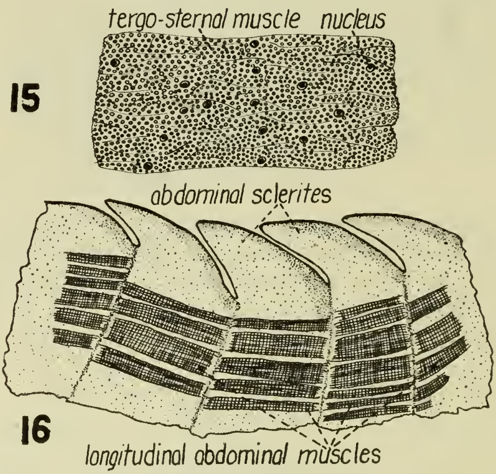

FIG. 15.—Cross-section through a tergo-sternal muscle, greatly enlarged
FIG. 16.—Longitudinal abdominal muscles

The muscles are attached to, or through, the hypodermis by chitinized tendon-like structures which do not stain darkly, as do the muscles. A bundle of muscle fibers usually has a common tendon-like connection with the body wall or internal ridges, the infoldings of the body wall.

Muscles occur in various parts of the body and produce the movement of flight, hopping, walking, movement of antennae, mouth parts, and sucking of the sap; they also assist with breathing movements of the abdomen and have a connection with digestion in the digestive tract. Muscles are responsible for practically all movements in the body of the leafhopper.

A great number of muscles (Fig. 16) are attached to the terga and sterna, of the abdomen, producing abdominal movements. If all muscles contract at once, the abdomen is telescoped. If the ventral muscles are contracted, the abdomen bends downward. Movement upward, downward, and laterad is possible, depending on the muscles used.

THE ALIMENTARY CANAL

The alimentary canal of the beet leafhopper consists of a closed tube, running from the mouth to the anus. There may be some justification for considering the maxillary canal as a part of this tract, although this lies principally outside of the body proper.

The digestive tract (Fig. 17), according to its origin, is divided into three parts. From the anterior invagination of the body wall, or stomodeum, is derived the fore-intestine, and from the rear invagination, or proctodeum, develops the hind-intestine. Between the fore- and hind-intestines is the stomach, or mid-intestine which, when the opening between them is completed, gives one continuous tube running from mouth to anus. In *tenellus*, this forms a rather simple, slightly coiled tube. The mid-intestine is longer and somewhat larger than either the fore- or the hind-intestine.

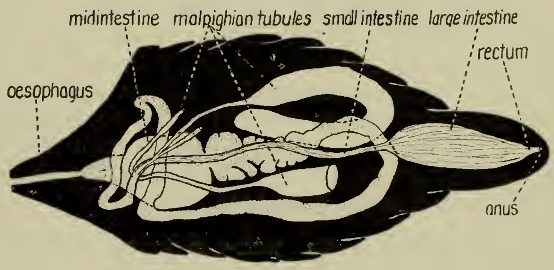

FIG. 17.—Diagrammatic view of digestive tract and parts of malpighian tubules, lying in the thorax and abdomen

The fore- and hind-intestines, being invaginations of the body wall, are continuous with it at the extremities and afford strong attachments. In addition to the support received by its attachments, the digestive tube is supported by a large fat body (Fig. 14), which forms a sheath for this tube throughout much of its length. Tracheae also assist in supporting the digestive tract, as do a few suspensory muscles attached to dorsal parts of the body wall.

GROSS ANATOMY OF THE TUBE

Fore-intestine.—The gross parts of the fore-intestine include the mouth, pharynx, oesophagus, and oesophageal valve. (1) The mouth carries the liquid food material from the maxillary duct into the pump of the pharynx. (2) The pharynx is provided with powerful muscles attached principally to its anterior central portion and the front of the head, making this a sucking organ, or pump, and comprising the principal part of the region of the fore-intestine lying in the head. The pharynx becomes smaller as it passes between the very much shortened circum-oesophageal commissures (Fig. 10), and emerges from these as the oesophagus. (3) The oesophagus (Figs. 18, 19) is a tubular organ, serving as a throat tube. Crop and gizzard are lacking, and the oesophagus runs almost directly backward from its bend at the juncture with the upper portion of the pharynx, to the place where it joins with the mid-intestine. It is of rather uniform thickness throughout. (4) The oesophageal valve (Figs. 18, 20, 21), or cardiac valve, is derived principally from the fore-intestine. The lips of the valve are more or less symmetrical, well-developed, pointed directly backward, and lying (Fig. 17) in the meta-thorax.

Mid-intestine.—The mid-intestine, or stomach, consists of a single tube, which forms a large, open sack, distended and somewhat folded at the anterior end, but tapers off and runs backward, and into a tubular, somewhat smaller portion; this makes a loop forward, a loop or two penetrating the meta-thoracic cavity, and finally bends backward and joins the hind-intestine. The anterior distended end of the mid-intestine arises approximately at the middle of the meta-thoracic segment, lying in the cavity between the heavy muscles. The structure of the stomach is very similar throughout, although often the epithelial cells may be small or almost lacking in the extreme anterior end, following its juncture with the oesophageal valve. The anterior end of the stomach, when distended with liquid food, may take up a very large part of the anterior end of the abdomen; the wall of such a sack is ordinarily quite thin.

Hind-intestine.—No well-developed pyloric valve is found in *tenellus*. The region of the mid-intestine joining the hind-intestine (1) is not distinct; it may be a mixture of the tissues of the two. This region lies just preceding the place where the malpighian tubules join the hind-intestine (Figs. 17, 26). Two tubules fuse before joining the hind-intestine (Fig. 26) making three ducts from the malpighian tubes, instead of four, which join the small intestine (2). (3) The first part of the hind-intestine is small (Fig. 17), and runs posteriorly for some distance before enlarging. (4) The abrupt change from small intestine to large intestine would constitute a poorly developed intestinal valve (Fig. 24). (5) The tube now becomes distended, forming a thin-walled, sac-like large intestine (Figs. 24, 25). (6) This tapers off, forming a narrow, thicker-walled rectum, and ending at the external opening, (7) or anus, on the last segment of the abdomen. The hind-intestine is but slightly longer than the abdomen, running almost directly backward to the anus, from its origin near the juncture of thorax and abdomen. Sometimes it seems to arise just within the posterior edge of the meta-thorax, but in some cases it arises at the anterior end of the abdomen. The diameter of the small intestine is less than that of the tubular part of the mid-intestine.

HISTOLOGY OF THE FORE-INTESTINE

The fore-intestine, in general, is composed of the following layers: (1) The intima (Fig. 19) or cuticula of chitin. This layer is thin throughout the length of the oesophagus, extremely thin over the oesophageal valve (Fig. 18), and thicker in the mouth (Fig. 9) and parts of the pharynx. The posterior wall of the lower part of the pharynx is heavily chitinized, but the chitin on the anterior part of the pump is not so heavy and more flexible. The chitin in the upper part of the pharynx becomes thinner and grades off into that of the oesophagus. (2) The stomodeal epithelium (Figs. 18, 19) of hypodermal

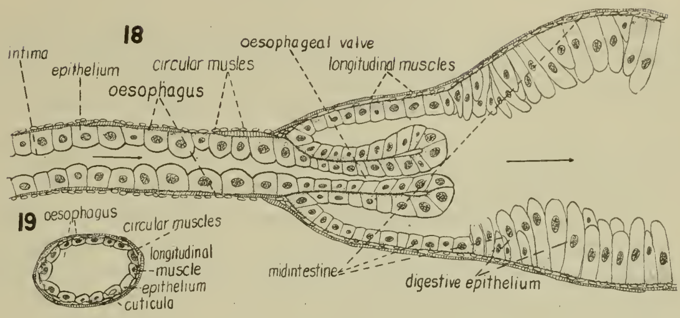

FIG 18.—Longitudinal section through oesophageal valve, showing posterior end of oesophagus and its junction with the mid-intestine

FIG. 19.—Cross-section through the oesophagus

cells is well-developed in the oesophagus and oesophageal valve. The cells are flattened or cuboid in shape in the oesophagus, somewhat tapering outward to columnar shape at the end of the oesophageal valve, but very thin and much reduced in the area of the mouth and pharyngeal pump. In the oesophagus and oesophageal valve, the cell walls are usually distinct (Fig. 18), but in some specimens, part or all of the cell walls in the oesophagus are not distinguishable (Fig. 21) and the hypodermis forms a syncytium. (3) The basement membrane is thin and often difficult to distinguish. It lies between the hypodermis and the muscle layers. (4) The longitudinal muscles lie next to the basement membrane (Fig. 19), in strands, and do not form a continuous layer. (5) The circular muscles (Fig. 18) form an outer layer, lying closer together than the longitudinal muscles. These last two layers are not well-developed around the mouth and pharyngeal pump, but are distinguishable in the oesophagus.

The oesophageal valve (Fig. 18) consists of a fold of the fore-intestine which extends down into the mid-intestine, folds back upon itself outwardly, and returns as the outer layer of the valve to join the mid-intestine at its upper edge. Outside the wall, the circular muscles are better developed in this place and possibly act as a sphincter to close this valve.

HISTOLOGY OF THE MID-INTESTINE

The stomach or mid-intestine of the beet leafhopper consists of the following layers: (1) Digestive epithelium of endodermal cells. This may consist of rather flattened pavement epithelium following the osophageal valve. These may be almost lacking in the beginning of the large, anterior end of the stomach (Fig. 20) and often in the greater part of the open, sac-like end of this intestine. Columnar cells usually follow which grade off into fairly large cuboid cells with well-developed nuclei in the smaller tubular portion of the stomach (Fig. 20), which comprises the greater part of the length of the mid-intestine. No cuticula covers the digestive epithelium. The epithelium of the stomach usually stains darker than the thick portion of the malpighian tubes, when stained with iron haemotoxylin and eosin. (2) The basement membrane, secreted by the digestive epithelium, is visible and in contact with the layer of (3) circular muscles which surround it. These circular muscles are numerous, forming a coat around the outside of the digestive epithelium and basement membrane. (4) There is a partial coat of longitudinal muscles (Fig. 22) outside of the layer of circular muscles. These two layers of muscles are reversed in position in the region of the oesophageal valve and are in opposite order in the mid-intestine to that occurring in the oesophagus. The limits of the mid-intestine are marked anteriorly by the oesophageal valve (Fig. 20) and posteriorly by the malpighian tubules (Fig. 17). No thickening of the muscular layer is evident at the junction of the mid- and hind-intestines, to form a pyloric valve. The posterior end of the stomach apparently is quite widely open where it changes to the narrower hind-intestine.

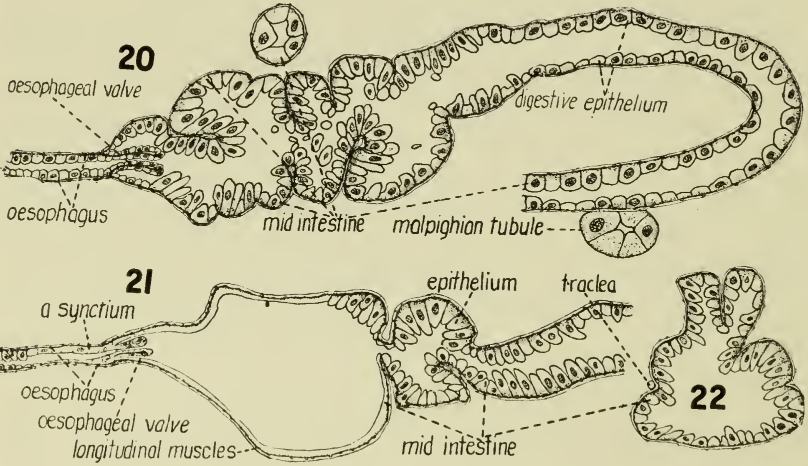

FIG. 20.—Composite section through oesophagus and much of the mid-intestine, showing folded walls and well-developed cells in anterior end of stomach.
FIG. 21.—Section through anterior end of distended mid-intestine, showing large sac-like portion almost devoid of well-developed epithelial cells.
FIG. 22.—Cross-section through folded anterior end of mid-intestine

HISTOLOGY OF THE HIND-INTESTINE

The layers of the hind-intestine include: (1) The intima or cuticula of chitin, which is thin, especially in the thin-walled large intestine. This is continuous with the external chitin of the body covering, but so thin in most of this intestine that it is possible that some absorption of food may take place through it. (2) The proctodeal epithelium or hypodermis varies in the three parts of the intestine. In the small intestine (Fig. 24) the cell walls are sometimes distinguishable, and the pavement epithelium is fairly thick. In the sac-like large intestine

(Fig. 25) this layer is a syncytium, nucleated but usually with no distinguishable cell walls. Occasionally the cell walls are distinguishable, especially in the fore part of the large intestine. In the rectum the epithelial layer is fairly thick and the cell walls may or may not be distinct. (3) The basement membrane is thin and more or less structureless. (4) A layer of circular muscles (Fig. 23) lies next to the basement membrane and composes a fairly continuous layer, usually closer together than the outer longitudinal layer. These muscle layers can sometimes be well shown in sections of the thin-walled large intestine. (5) The longitudinal muscles are fairly numerous, lying along the outside of the inner, circular muscle coat. Apparently, the outer layer of circular muscles, present in some insects, is absent here. The intestinal valve, lying between the small and large intestines, is distinguished by an abrupt change from the thick-walled, small intestine to the thin-walled large intestine. The muscles are not well enough developed at this point to make this function as a very efficient valve. The rectum is small but rather thick-walled and runs toward its posterior end, finally joining the body wall and forming the anus. The rectum possesses a small lumen, surrounded by rather large cuboid to somewhat columnar epithelial cells.

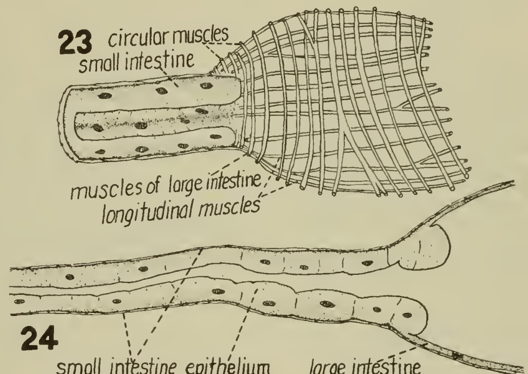

FIG. 23.—Longitudinal section through posterior end of small intestine, showing muscles, only, of adjoining large intestine.

FIG. 24.—Longitudinal section through posterior end of small hind-intestine, and its junction with the thin-walled large intestine

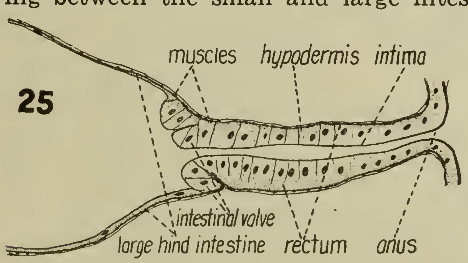

FIG. 25.—Longitudinal section through posterior end of large intestine, rectum, and anus

THE SALIVARY GLANDS

The salivary glands (Fig. 9) are composed of large cells, frequently with two nuclei, and staining with some variation in intensity. These salivary glands are fairly large and lie back of the head, principally in the thorax. Here they occur just back of the brain, on the sides of the short circum-oesophageal commissures, and above the fore part of the large ganglionic mass. The ducts from the salivary glands fuse, and open at the tip of the hypopharynx, and just between the bases of the maxillary bristles, making a contact with the salivary duct in the maxilla.

In view of the fact that curly-top is apparently transmitted through the process of feeding, the salivary glands naturally fall under suspicion as being possible reservoirs for the storage or incubation of the virus causing the curly-top disease of sugar-beets.

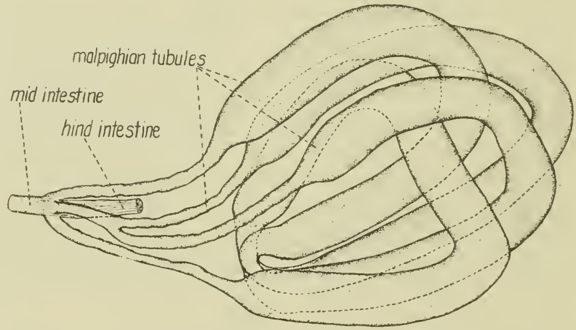

FIG. 26.—Malpighian tubules and their juncture with the hind intestine

THE MALPIGHIAN TUBULES

In common with other leafhoppers, *Eutettix tenellus* possesses four well-developed malpighian tubules (Fig. 26). These structures may be divided into a proximal, small, tubular portion, which runs forward and attaches to the anterior end of the hind-intestine, and a larger, glandular portion, which runs backward, and then turns and runs forward again. There appears to be a joining or fusing of these tubes, where the distal ends approach each other, becoming slightly smaller and making a short connection.

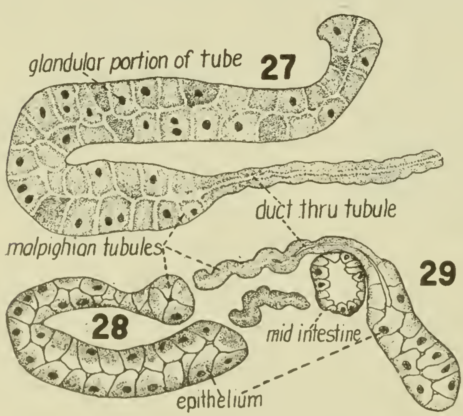

FIG. 27.—Longitudinal section through one malpighian tubule, showing thick glandular tube and small portion of tubule running forward to join the hind-intestine

FIG. 28.—Section of thick portion of malpighian tubule

FIG. 29.—Section through malpighian tubule, showing the junction of the large tube with its small tubule

The small, anterior connectives run forward from their junction with the thick, glandular portion of the tubes and approach the anterior end of the hind-intestine. Externally, these small tubes are uneven along the margins, where the cells bulge out at the sides. Two of these tubules fuse, forming a single connective, while the other two tubes remain free. Thus, the four tubules join the fore end of the small hind intestine with only three connectives.

These small, proximal connectives appear to carry the fluid from the large, distal portions of the malpighian tubules and are provided with an open tubular cavity (Fig. 29). The small anterior portion of the tubules is made up of somewhat flattened and darker staining cells than those composing the thick, glandular posterior portion.

The glandular portion of the tubules is large (Fig. 27), thick, and somewhat coiled, running posteriorly, and then returning anteriorly again. The cells of this portion of the tube are large and of rather fine texture. When stained, one or two nuclei are conspicuous in each cell. The inner margins of the cell are usually stained somewhat lighter than the center and outer portions. The lumen of this tube is not so large in proportion to the size of the tube as the lumen in the anterior tubules running forward and connecting with the hind-intestine.

Apparently the tubules are covered throughout their length with a coat of connective tissue.

THE NERVOUS SYSTEM

The nervous system (Fig. 30) in the beet leafhopper is especially well-developed and highly specialized. This is a particularly important system, as upon it depends the coordination of movements and functions of the body.

The nervous system consists of a brain, a central nerve trunk (Figs. 30, 33) ventrally located, and a number of peripheral branches. The functional unit is the neuron or nerve cell, with connectives.

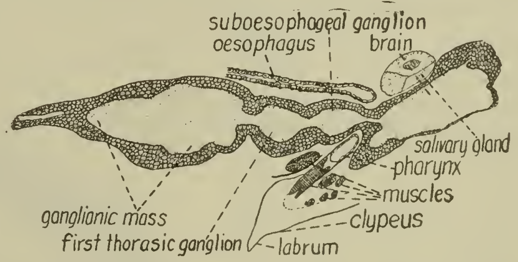

Fig. 30.—Longitudinal section through central nervous system, showing internal fibrillar mass and outside covering of nucleated cells

In the central trunk, the ganglia of the abdomen and thorax have become very largely fused (Fig. 30), forming a large thoracic ganglionic mass. This multiple or compound ganglion gives rise to a number of branches. The entire trunk from the brain to the tapered posterior end in the meta-thorax is somewhat of a shortened, compact mass with a single opening through which the oesophagus passes.

The brain (Fig. 32) lies in the head, and takes up the space between the eyes with lateral extensions downward, the shape of dorsoventral sections in some regions of the brain resembling, in general, the shape of the head (Fig. 31). The brain is connected to the suboesophageal ganglion by the two short, rather thickened circumoesophageal commissures. Before running backward to join the midintestine, the upper part of the pharynx comes up to this opening and becomes the oesophagus as it passes between these two commissures.

The three parts of the brain can be distinguished in *tenellus* rather easily. The proto-cerebral lobes (Fig. 32) are well-developed, and to them are attached the two well-developed optic lobes of the compound eyes and the small nerves running to the two ocelli. The deuto-cerebrum lies back of the proto-cerebral lobes, and consists of two smaller lobes lying above and in front of the circum-oesophageal commissures. From it arise the antennal nerves. Sections cut below the deuto-cerebrum pass throughout the third division of the brain, the trito-cerebrum (Fig. 33).

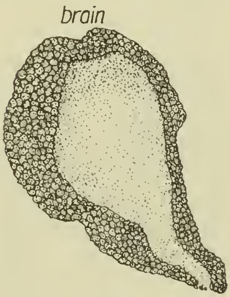

FIG. 31. — Longitudinal section through brain, viewed from the left side

In structure, the brain consists of an outer layer, consisting of a great number of small cells with large, dark-staining nuclei. Inside this layer lies the mass of the brain, which is fibrillar in structure. The brain, suboesophageal ganglion, and the ganglionic mass are histologically very much the same. The thickness of the nucleated layer seems to vary in thickness in the different regions.

The suboesophageal ganglion (Fig. 9) lies back of and below the mass of the brain, to which it is attached by the circum-oesophageal commissures (Fig. 10) and from which it is partially separated by the opening through which the oesophagus passes. From this lower head ganglion arise the nerves running to the mouth parts of the last three head divisions — mandibles, maxillae, and labium.

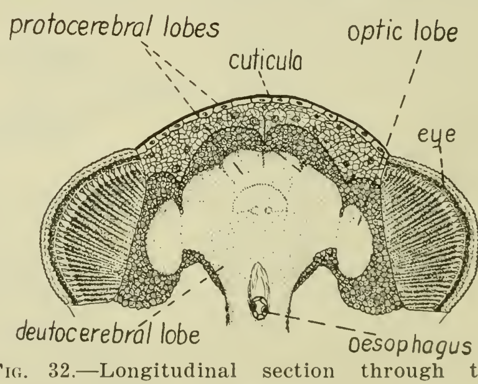

FIG. 32.—Longitudinal section through the head, viewing brain and eyes from above

To the posterior portion of the suboesophageal ganglion is connected the first thoracic ganglion. Only depressions and constrictions separate these two ganglia, which do not differ greatly in size from each other.

Following the first thoracic ganglion lies the rather large ganglionic mass. Sections through this and slight constrictions indicate its compound nature, but it is difficult to see exactly how many ganglia it represents. The second ganglion may be distinguished through a ventral constriction which follows it.

The thoracic ganglia have evidently fused with the abdominal ganglia, which have moved forward. The ganglionic mass (Fig. 33) lies principally in the pro- and meso-thorax, tapering off after entering the meta-thorax. Large nerves run backward, and a number of other nerves are given off from this nerve mass. The ganglionic mass hardly passes beyond the coxae of the meta-thoracic segment in *tenellus*. The posterior part of the ganglionic mass is tapering and somewhat arrowhead in shape, the point of the arrow being toward the abdomen.

THE COMPOUND EYES

The compound eyes of the beet leafhopper (Fig. 34) are large; each eye is composed of a great number of facets with a corresponding number of ommatidia. The facets of the compound eyes are relatively small. Each ommatidium is complete in itself and is a visual unit, possessing a nerve ending, or nerve fiber. The outer surface of the eye, or cornea, is divided into about 1300 smaller areas, or facets, each of which has its corneal lense. Under each lense is the corresponding ommatidium, or visual unit. The surface of the eye appears something like a honeycomb, the shape of the facets being something between round and 6-sided but not so decidedly 6-sided as in many larger insects.

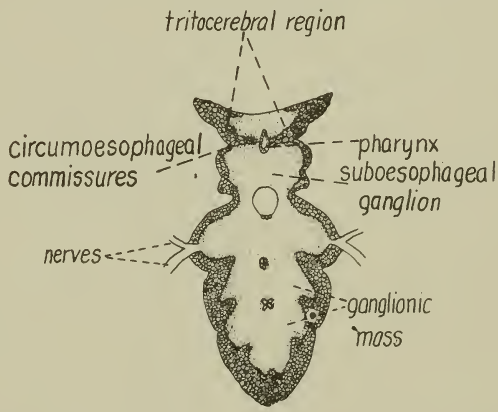

Fig. 33.—Longitudinal section through lower portion of brain and the ensuing mass of the central nervous system, as seen from above

The ommatidia are long and slender, converging inwardly, to where they join the basement membrane at the ends of the lateral portion of the optic lobes of the brain. The ommatidia are modified and highly specialized hypodermal cells. The pigment sheath around each ommatidium is dark in thin sections giving the eye a dark appearance, and black in thicker sections. This pigment is usually so thick that the cell nuclei are hidden. Under each corneal lens is a transparent cone-like structure, the crystalline cone, with the acute angle pointing inwardly. Ordinarily the visual cells and rhabdom are difficult to distinguish because of the dark coloring of the pigment cells. The basement membrane, at the inner end of the ommatidia is easily distinguished, stains dark, and is fairly thick. Nerve fibers penetrate this membrane to enter the ends

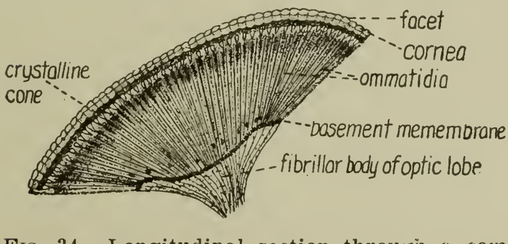

Fig. 34.—Longitudinal section through a compound eye, showing its connection with the optic lobe

of the ommatidia. The optic lobes are fairly thick where they join the basement membrane of the compound eye, with the outer fibrillar body. The optic lobes run to the brain, joining the proto-cerebrum.

THE FAT BODY

The fat body (Figs. 14, 35) in *tenellus* is a large tissue taking up a considerable part of the space in the abdominal cavity. A tissue found in certain regions of the thoracic and head cavities appears to be part of this fat body.

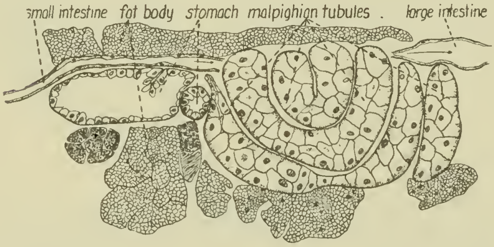

FIG. 35.—Longitudinal section through portions of the fat body, mid- and hind-intestine, and malpighian tubules

The fat body very largely supports the digestive tract, malpighian tubes and lies very closely around them throughout most of their length. It is pierced by many trachea and tracheal branches. Aside from functions connected with storage of food or excretion, this tissue is of considerable importance as a supporting tissue for the other body organs.

The fat body is composed of large, vacuolated, irregular shaped cells. The nuclei are of moderate size, compared with the large size of many of the cells. In the sections, the material of the cells resembles a net work.

The fat body in a freshly killed *tenellus* is yellowish-white to greenish-white.

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