

THE ANATOMY OF PSYLLIA  
MALI, SCHMIDBERGER

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THE ANATOMY OF PSYLLIA MALI, SCHMIDBERGER

By

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partial fulfilment of the requirements for the  
degree of M.Sc.

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( 5 plates )

## TABLE OF CONTENTS.

	Page.
Introduction.....	1
Literature.....	4
Technique.....	6
Acknowledgments.....	8
External Anatomy: Head.....	9
Thorax.....	14
Abdomen.....	21
Internal Anatomy: Digestive system.....	29
Nervous system.....	32
Reproductive system.....	35
Circulatory system.....	43
Tracheal system.....	43
Musculature.....	44
Glands.....	44
Pseudovitellus.....	45
Adipose tissue.....	46
Bibliography.....	47
Explanation of plates.....	50

The Anatomy of Psyllia mali, Schmidberger.

INTRODUCTION.

During the summer of 1920 the writer was engaged in studying the bionomics of the Apple Sucker, Psyllia mali, in Nova Scotia, and, having occasion to make numerous dissections, he was struck by the lack of literature dealing with the anatomy of any members of this family, particularly with regard to the internal organs. Investigation showed many interesting and unusual features in the morphology of the insect and so the entire anatomy was chosen as the subject for this thesis. The field is a wide one, and it has not been found possible to follow out all points in full detail in the time available, with only preserved material with which to work. If there appears to be a hesitancy and uncertainty in describing certain structures, it must be borne in mind that the body of this insect is only 2.5 m.m. long, so that the individual organs and sclerites are in most cases extremely minute, rendering the work of dissection very delicate and trying. The writer hopes to follow up those points which have only been lightly touched upon, extending the field of investigation to related species, with the object of producing a more complete and valuable piece of work.

The Insect:

The Apple Sucker, Psyllia mali, Schmidberger, is a European pest recently introduced into Nova Scotia, probably upon nursery stock. It is confined to a small area of ten or fifteen square miles in the vicinity of Wolfville, N.S., but it is spreading rapidly, and increasing in numbers to an alarming extent in the infested area. It is not known anywhere else on the continent of North America.

The pest hibernates in the egg stage upon the twigs and small branches of the apple; the eggs are minute, orange-yellow, oval bodies appearing like gold-dust scattered over the twigs and lodged in cracks and crevices. Early in spring, when the buds are bursting, the eggs hatch, and the tiny, flattened, oval nymphs creep down into the buds and commence to feed on the sap, sucking it out through their long thread-like proboscis. The five nymphal stages occur on the petioles of leaf and blossom clusters, the nymphs crowding there in such numbers that sixty or more may often be taken from a single cluster. Their presence is readily noted by the appearance of globules of honey dew excreted from the anus, covered by a white waxy powder to prevent the substance from sticking to the insect. On a still day a light breeze will shake down these globules like rain in a badly infested orchard. The feeding of the nymphs when in large numbers results in the wilting and shrivelling of the blossom and leaf clusters.

The adults appear about one month after the eggs hatch, and live in the foliage of the trees throughout the season until the severe frosts of late autumn. During the summer they are pale yellowish-green insects, but as the season advances a marked change takes place, the body color of the females changing to yellow, orange, and finally deep blood red, while the chitinous sclerites take a brown or coal black color with definite markings, producing a very beautiful insect in the latest stages. The male changes less radically, the body color never becoming red, but dusky markings appear on the thorax and abdomen. No dusky markings ever occur upon the wings of either sex.



## LITERATURE.

There are very few published accounts in detail of psyllid anatomy: Witlaczil's paper in 1885, Stough's "Hackberry Psylla" in 1910, Crawford's monograph of Psyllidae in 1914, and Awati's paper on P. mali are the chief ones, though I believe there are other European papers inaccessible to me. Of those mentioned the first and last are the only ones to discuss internal anatomy at all, and Awati only touches lightly on the tracheal and reproductive systems. The others take up the external anatomy in some detail but with several doubtful interpretations.

There has been a large amount of work done upon the structure and homologies of the Homopteran mouth, though the family Psyllidae has never been included specifically in these studies. Muir and Kershaw were prominent in this work, and others such as Meek and Marlatt, to whose papers I have not had access. These studies have culminated in the production of a recent paper by Snodgrass in the Proceedings of the Entomological Society of Washington upon the mouth parts of the cicada, in which he carries the analogy between the Homopteran and Orthopteran mouth parts as far as possible, and describes the anatomy in great detail. He reviews all the published theories on the homology of the setae and other parts, and demonstrates the weak points in each; he fails to give any alternative interpretation himself, saying that embryological work alone will ever solve the mystery.

In addition to these works many special papers on thoracic and abdominal sclerites, genitalia, and internal organs have been found useful. Only those papers to which I had access have been included in the bibliography, though there are certain other references which I should very much like to see as I believe they would have some bearing on my subject.

### TECHNIQUE.

Specimens for dissection were killed and fixed in hot water and preserved in 5% chloral hydrate. This method was found to give far the best results, and specimens so fixed could be washed, dehydrated in alcohol, and imbedded for sectioning, giving sections quite as normal as those fixed with a regular fixing fluid. For the most part, however, Gilson's fluid was used to fix specimens intended for sectioning. Dissection was carried out under the binocular, often using the highest power available. To determine the limitations of the sclerites of the exoskeleton, specimens were treated with strong caustic potash until nothing remained but the chitin, then an aqueous solution of methylene blue was used. This was necessary because the chitin contained no pigment; after staining the sclerites stood out clearly and the intersegmental membranes remained colorless. The same stain was used on the internal organs with excellent results.

Serial sections of the insect were cut in all three planes, five to ten microns thick. It was found necessary to section the head and pro- and mesothorax together and the abdomen separately, leaving out the metathorax as the hard endoskeleton of that region always broke and tore the softer tissues of the other parts. Individual organs, such as testes, ovaries, and glands, were imbedded and oriented under the binocular, and sectioned in the usual manner. Sections were



stained chiefly with acid haematin and eosin, but picrocarmine was useful in some cases and Giemsa's blood stain gave excellent results on tissues. The oil immersion lens was frequently employed to determine details in sections.

ACKNOWLEDGMENTS.

I wish to express to Mr. E.M. Du Porte, of Macdonald College, my hearty appreciation of his valuable assistance, advice, and encouragement throughout the course of this work. I would also thank Mr. Arthur Gibson, Dominion Entomologist, for the loan of a volume from the library of the Entomological Branch.

EXTERNAL ANATOMY.

HEAD.

(Figs. 1, 4, 9, 10).

The head is short and broad in dorsal aspect, triangular from the front, with the apex of the triangle deeply notched. (Fig. 1).

The Vertex is a large dorsal sclerite composing almost the entire front and top of the head; it is roughly triangular in shape with its apex at the frons, and is divided by a distinct median suture into two halves, each of which is depressed slightly near the centre. The two lateral ocelli occur at the extreme posterior lateral angles of the vertex, on top of the head when held in normal position. (Fig. 10).

The Frons is a minute triangular sclerite, scarcely larger than the median ocellus which it bears, situated between the bases of the genal cones at the end of the median suture of the vertex. A small, triangular, poorly chitinated sclerite, also part of the frons, extends back behind the genal cones with its apex at the median ocellus and its base attached to the clypeus (Fig. 21).

The Genae are two large ventral sclerites of the head greatly evaginated to form tapering cones which project downward (Fig. 1). In length they are equal to the vertex, and their surface is clothed with fine short hairs.



The Occiput is so greatly reduced that the only distinguishable part of the sclerite is a thickened ring around the foramen of the head, on the posterior margin of the vertex and genae.

Mouth Capsule (Figs. 21, 22):

In Psyllidae a very definite mouth capsule is attached to the lower posterior part of the head, and, while composed of sclerites belonging to the head capsule as well as modified trophi, the whole structure will be described under this heading. Owing to the greatly reflexed position of the mouth parts some confusion naturally arises in designating the position of certain sclerites, those which form the front in a normal insect being in a ventral position in Psyllidae, but in this work the condition will be described as it actually occurs.

The Clypeus is a triangular, slightly concave sclerite attached to the head at its broad end by means of the triangular frontal sclerite previously described. Distally a slight constriction in the ventral surface near the tip may indicate the position of the suture between clypeus and labrum; Davidson ('14) describing the mouth capsule of Eriosoma (Aphididae) calls the whole sclerite the clypeo-labrum. Crawford ('14) calls the distal portion the labrum, and the small tongue-like organ at the tip below the exit of the styli, the epipharynx. Davidson designates this organ the labrum, and reserves the term "epipharynx" for a thickening

of the floor of the pharynx. Owing to the lateral fusion of the dorsal and ventral elements of the mouth capsule in this region it was impossible to tell whether such a condition exists in P. mali.

The Tentorium takes a prominent part in the formation of the mouth capsule. The anterior arms arise from the clypeus on the outer margins near the widest or proximal end, and arch upwards and backwards to be joined at their greatest height by a cross bar, the modified central plate of the tentorium. The origin of the posterior arms is obscured by the general fusion of sclerites in the distal region of the capsule; they pass upwards and forwards to join the anterior arms at the central bar.

Lying beneath the posterior arms near their point of origin, and partly fused with them, two wider plate-like sclerites occur, generally conceded by workers on the hemipterous mouth to represent the maxillary sclerites. These, or the posterior tentorial arms, or both together, are fused laterally with the clypeo-labrum beneath, leaving a central opening for the passage of the styli. The two plates do not quite meet medially, but are joined by a short bridge.

Upon more minute and careful dissection I find a complex of exceedingly small sclerites forming the distal tube through which the styli pass, but I have been unable to work <sup>them</sup> out with sufficient accuracy to give a description.

The Styli, both maxillary and mandibular pairs, arise within the mouth capsule. Their proximal extremity is in the form of a long hollow cone which furnishes a secure attachment for the protractor and retractor muscles. All four of these cones will be found inside the mouth capsule, the maxillary pair being well up under the roof, attached to the under surface of the maxillary sclerites by a short chitinous apodeme which appears to act as a hinge upon which the stylus may swing forward and backward. The mandibular setae are united by a tongue-and-groove joint, while the maxillary setae lie along the sides, completing the minute channel through which the plant juices are sucked. Shortly after leaving the mouth capsule the styli bend directly upwards and back again forming a loop which passes between the connectives joining the suboesophageal and thoracic ganglia and even extends a short distance above them (Fig. 22). This is the normal position when at rest, but when the styli are protruded during feeding the loop would partially or entirely disappear. The distal part of the setae run down in a groove on the anterior surface of the labium.

The Labium consists of three segments: the first is attached by its narrow, attenuated, proximal extremity to the bridge which connects the maxillary sclerites, enlarging distally with a slight downward bend to its broad articulation with the second segment. The second segment is long and broad, the lateral margins rolling in to form a groove for the styli; it proceeds in a ventral direction, and bears at



its distal extremity the short, heavily chitinated third segment. These two segments together form the beak which projects from the ventral surface of the prothorax between the fore-coxae.

Other Appendages of the Head:

The Compound eyes are prominent hemispherical bodies situated on the sides of the head. In proportion to the size of the eye the individual ommatidia are large. The internal structure of the eye will be discussed under the nervous system.

The Antennae (Fig. 1) are borne in large antennal sockets upon the upper lateral angles of the genae, just mediad and below the compound eyes. Each consists of two short, stout, basal segments and eight elongated, cylindrical, distal segments, all strongly imbricated. The last two together are about equal in length to one of the other segments, and appear superficially to be one segment. Circular sensoria occur on the upper surface at the tip of segments IV, VI, VIII and IX, and very few minute hairs, probably sensory, may be found scattered along the entire length of the antennae. At the distal extremity of the terminal segment two long, stout setae are borne, equal in length to the segment on which they occur.

## THORAX.

(Figs. 3, 4, 5, 6, 9, 10).

### Prothorax:

The prothorax is very short in comparison to the size of the thorax as a whole.

The Pronotum is a single broad, short sclerite behind the head, extending less than half way down the pleura.

The Pleurites are readily visible as two narrow sclerites of almost equal size, the episternum and epimeron, divided by a distinct pleural suture. They extend from the margin of the pronotum to the fore-coxae, and bear attached to their lower margin a very small triangular sclerite, the trochantin, lying along the upper margin of the coxa. The pleural suture is oblique as in all members of the genus Psyllia, and meets the pronotum at its posterior lateral extremity.

The Prosternum is completely atrophied externally, but a deep slit-like invagination occurs between the coxae extending even between the connectives of the nervous system, to accommodate the labium and setae in their upward bend. The walls of this invagination are very thin and membranous, and are probably formed by the unchitinised prosternum, strengthened posteriorly by the modified profurcae.

In the pleural membrane between the pro- and mesothorax three small sclerites occur. One of these, the lowest, bears a spiracle and is, therefore, a peritreme, while immediately above it, separated only by a very narrow space, is another

larger and longer sclerite which in some members of the family is joined to the first. This, then, is also part of the peritreme which for some reason has become separated. The third sclerite, the uppermost of the three, is rather more circular, and it is generally conceded to be an accessory or intersegmental sclerite.

#### Mesothorax:

The mesothorax forms the largest part of the thorax, the sclerites being large and well developed.

Four notal sclerites may readily be distinguished in the mesonotum:

The Praescutum is broad at its posterior margin, rounded anteriorly with the front margin flexed upward to catch under the hind margin of the pronotum. Laterally a bridge-like sclerite joins the praescutum to the upper margin of the episternum. Crawford ('14) considers these to be processes from the praescutum, but Crampton ('09) interprets them as definite sclerites and calls them the praesegmental sclerites (Fig. 9).

The Scutum is a large and very broad sclerite composing a large part of the dorsum of the thorax. It is separated from the praescutum and scutellum by deep sutures and internal ridges. At its lateral angles it bears part of the articular wing processes, and articulates strongly with the dorsal margin of the episternum and epimeron. Upon each lateral anterior margin of the scutum, behind the praesegmental



sclerite, two very small knob-like sclerites occur, a larger anterior and a smaller posterior one, the paraptera. A third still smaller one occurs behind the wing base.

The Scutellum is a small, raised, central sclerite sending slender lateral axillary cords obliquely forward to the hind margin of the wing bases.

The Postscutellum is not evident externally, but has grown inwards to produce the post phragma (Fig. 3) in the form of a thin, bilobed, chitinous plate extending almost half way to the sternum, reinforced with chitinous rod-like thickenings to serve as a muscle attachment.

The Mesopleurites form a large plate strongly articulated to the sternum below and the scutum above, imperfectly divided by the pleural suture into episternum and epimeron, subequal in size. The wing base is a forked process borne on the dorsal margin of the pleurites. Internally, the pleural apodemes may be seen, formed by invaginations of the pleural suture near its base.

The Mesosternum is a large, undifferentiated ventral sclerite. At its posterior margin, between the mid-coxae, the mesofurcae (Fig. 3) arise within the body, somewhat larger than the profurcae and different in form being of the typical Y shape.

#### Metathorax:

The metathorax is greatly modified, the endoskeleton being most remarkably developed into a strong frame work of rods to serve as attachments for the very large muscles used in leaping and flying.

Exoskeleton:

Either the Praescutum and Scutum are fused together, or the former is suppressed leaving the scutum alone to form the anterior portion of the metanotum, a sclerite which extends down laterally to the hind wing process. On either side of the dorsal median line is a depression or pit, at the bottom of which are punctures in the cuticle which I believe to be the external openings of the thoracic scent glands (Fig. 10).

The Scutellum is very similar to the same sclerite of the mesothorax, sending down lateral axillary cords to the wing base.

The Postscutellum of the metathorax, or pseudonotum, is greatly enlarged and membranous, extending backward over the internal furcae, and merging into the intersegmental membrane of the abdomen.

The Metapleurites are greatly changed and forced out of position by the general modification of the metathorax. The episternum is a long sclerite extending obliquely from the front of the hind coxa up to the hind wing base, bearing the greater part of the wing articulation at its dorsal margin. In more primitive forms the spiracle is borne upon the episternum, Crawford ('14), but in Psyllia the peritreme is separated, and the intersegmental area between the mesothorax and the metathorax appears to be filled with two large accessory sclerites. My interpretation of this area does not satisfy me, and a thorough examination of related species is necessary to justify a specific statement.

The Epimeron is a triangular sclerite situated dorso-caudally to the episternum, having apparently been forced upward by the great development of the coxa. A deep oblique suture and internal ridge separates the episternum and epimeron from the trochantin, a narrow sclerite running along the upper edge of the coxa for the greater part of its length.

The Coxa is extraordinarily developed into a large heavily chitinated structure extending upwards and backwards beyond the middle of the pleuron. The articulation of the hind leg is at the anterior lower extremity, and is so constructed that the leg may move forward and backward through an angle of almost 180 degrees. The ventral margin of the coxa is slightly curved, and the posterior angles each bear a short chitinous tapering projection usually known as the meracanthus. Extending from the epimeron a narrow sclerite, the postcoxale, passes over the upper posterior portion of the coxa and extends half way down the posterior margin.

The ventral surface of the metathorax is entirely occupied by the coxae; the metasternum is not evident externally in P. mali.

Endoskeleton (Figs. 5, 6):

The internal structures of the metathorax are composed of the coxae, the sternum, and the highly developed furcae, with additional connecting rods of doubtful origin.

The Coxae have already been described in their external appearance, and we find that internally the posterior margin is very heavily chitinated, while the inner and upper portion is

composed of two thin oblique plates. The upper margin is marked externally by the very deep oblique suture at the lower margin of the episternum.

The Sternum is a complicated system of rods arising between the bases of the coxae and spreading apart, downward, and then upward to form an outer ring-like framework for the anterior portion of the metathorax. A median process also projects backward and articulates with the postcoxae behind the coxae.

The Metafurcae arise from a common point on the sternum near the origin of the median posterior process and project backward and upward, diverging to their termination as two decurved, inverted spoon-like processes in the extreme posterior dorsal region of the thorax, extending a short distance into the abdomen. Rods from the postcoxae and the coxae connect with the upper portion of the metafurcae, rendering the whole structure very rigid.

#### Wings: (Fig. 10)

The Fore Wing is almost rhomboidal in form. The venation is quite simple; only one principal basal vein occurs, a fusion of the radius, media, and cubitus. The media and cubitus branch from this a short distance from the base, the radius continuing in the same direction, joining the costa and subcosta at about one-third the length of the wing. Instead of fusing directly with the costal vein the radius runs along almost parallel to it, finally joining near

the tip of the wing; the enclosed thickened portion is the long pterostigma. The radial sector branches from the radius midway between the first fork and the costal vein, and runs through to the outer margin of the wing. The media branches off from the cubital petiole and forks once near its extremity. The cubitus forks typically. One weak anal vein occurs in the anal angle of the wing.

The Hind Wing is very thin and delicate, and faintly veined. The radial sector remains of the radius, the media is but a single vein, the cubitus is normal, and one weak anal vein occurs.

Legs: (Fig.2)

The condition of the legs is quite normal. The coxae are short, rounded bodies except those of the metathorax, which have already been described. The trochanter is short and cylindrical; the femur is elongated and slightly swollen in the hind leg to accommodate muscles used in leaping; the tibia is somewhat longer than the femur, slender and cylindrical, with a small spur at the base in the hind leg, and two simple spines and one double or even triple one, black and shining, at the distal extremity. The tarsus is two-jointed; two spines similar to those on the tip of the tibia occur on the first segment, and a pair of black curved claws is located at the extremity of the second segment.

ABDOMEN.

(Figs. 7, 8, 9).

The number of abdominal segments is greatly reduced in Psyllidae, and no satisfactory interpretation of the existing sclerites has ever been given. Thus, since any attempt to homologise the sclerites without very extensive phylogenetic and embryological studies would be pure speculation, the existing condition will be described, and if any theories are advanced they are to be considered as tentative and speculative only.

Five large, distinct tergites are visible, and a very short anterior tergite, the pleural extremities of which appear separated by a narrow space. Upon this separated triangular portion a rounded elevation occurs, studded with very minute stout spines. Beneath the cuticle a number of large, quadrangular, glandular cells are arranged in the form of a hemisphere, as nearly as I can ascertain. No pore could be seen in the cuticle or in the spines for the excretion of fluids, and the true function of this organ remains a mystery. No mention is made in any psyllid literature to which I have access of any such abdominal organ.

The number of distinct sternites in the male is six and in the female five. In addition to these several minute sclerites and peritremes may be found in the intersegmental membrane at the base of the abdomen, representing one or more suppressed segments.



Seven abdominal spiracles occur in P. mali, each situated in a distinct peritreme, located in the pleural membrane the last peritreme in the male has become fused with the sternite to which it belongs, but the dividing suture is still apparent.

### Genitalia.

The entire genital segment will be described under this heading for convenience, though in the strict sense of the term some of the sclerites should not be included.

#### Female: (Figs. 9, 11, 12)

In the female the genital segment consists of a dorsal and a ventral plate forming an enveloping sheath for the ovipositor within. The dorsal plate has been termed the "supra-anal" plate by Stough ('10), but the term is hardly correct since the sclerite bears the anus upon its dorsal surface. Crawford's name, the "dorsal valve", is confusing, as this term is usually reserved for a part of the ovipositor.

The Dorsal Plate is broad at its attachment to the abdomen and arches over the entire dorsum, extending down laterally almost to the middle line of the pleura. The lateral margins continue parallel to the dorsal surface, when viewed laterally, for a third of the length of the plate, then curve upward to meet each other at an acute point, thus giving a tapering form to the plate as seen from above. The

max  
wing to  
11 12.

surface is clothed with short hair-like setae, rather more thickly toward the extremity than at the base. On the dorsum in the median line near the base is found an elliptical area very lightly chitinised, in the centre of which the anus opens as a longitudinal slit. A heavily chitinised ring surrounds this area, in which a double row of openings for the wax glands occur; a portion of this ring is shown in fig. 25.

The Ventral Plate ("subgenital plate" of Stough; "ventral valve" of Crawford) is somewhat shorter than the dorsal plate, and rather concave, the lateral margins extending up the sides to articulate by a thin membrane with the basal third of the dorsal plate. From the point of separation of the two plates the lateral margins of the ventral plate converge abruptly to meet in a point rather less acute than that of the dorsal plate.

The Ovipositor (Figs. 11, 12) is so far modified from the primitive condition in female insects as to present a very difficult problem in homology. There are apparently four elements concerned in the formation of the organ: a ventral and a dorsal pair of valves, a median unpaired process, and a pair of inner valves.

The Ventral Valves are long blade-like processes curving upwards distally and terminating in a fine point which curves back again to the direction of the main portion; they are strengthened with a thicker chitinous band running along just within the dorsal margin. At their base these

valves have a small rod-like inferior apodeme projecting directly cephalad, and a strong heavily chitinated superior apodeme at right angles to the valve, curving forward slightly in the upper half. These two valves are normally in close apposition, and in their proximal half are united by a membrane. Fig. 12 shows these valves slightly drawn down from their normal position. Fig. 11 shows them from the dorsum, separated ventrally and spread apart.

The structures I have called the "dorsal valves" are broad plates strengthened dorsally and ventrally with rod-like thickenings, the ventral rod being prolonged forward to form the inferior apodeme. At the position where one might expect to find a superior apodeme a short projection articulates with the superior apodeme of the ventral valve nearly half way up its length. Running caudad the ventral and dorsal rods, at first wide apart, converge and unite, and at the tip the left and right valves join to form a single upper valve for the egg-duct. This median distal portion curves slightly downward at the tip, accommodating the tips of the ventral valves when in normal position.

The median, dorsal, rod-like process is seemingly "cartilaginous" in nature. It is attached to the other structures of the ovipositor just in front of the fusion of the two dorsal valves, and runs forward and upward, widening slightly toward its anterior extremity which is notched in the middle. At its attachment two narrow processes extend caudo-laterally,

on each side, which soon fuse and widen to form thick fleshy tongue-like plates on each side of the ovipositor tip. These tongues join the dorsal valves anteriorly. (Stough ('10) homologises them with the sting-palpi of stinging hymenoptera.

Mr. F.M. Du Porte, of Macdonald College, has been good enough to examine specimens of the ovipositor, and has given me the following speculative theory of the homology of the parts. The median dorsal process represents the ninth sternite, and the two fleshy tongues are the true outer or dorsal valves; the two rod-like thickenings extending forward are merely processes from these outer valves. A small triangular sclerite at the end of the median dorsal process connects it with the distal, partially divided dorsal point of the ovipositor, which sclerites represent the inner valves. The ventral valves are easily homologised with those structures in generalised insects.

In cleared and mounted preparations it appears as though the lower of the two rod-like thickenings of the lateral plates is concerned with the distal tip, or "inner valves", and the upper only connects with the fleshy tongues, or "outer valves".

It should be stated that the only connection between the ovipositor and the other abdominal sclerites is by a stout articulation at the base of the median dorsal process with the under surface of the dorsal plate of the genital segment; also by a thin membrane from the ventral plate which joins the ovipositor in the same region all around the lateral and ventral surfaces.

Male: (Figs. 7, 8, 13)

The male genitalia are much simpler than the female, but the fusion and reduction of parts makes it just as difficult to homologise them with the typical structures of male insects. The genital segment is composed of the following parts:- subgenital plate ("ventral genital valve" of Crawford); proctiger ("anal valve" of Crawford, "supra-anal plate" of Stough); copulatory organ, penis, or aedeagus; and forceps.

The Subgenital Plate is a deep concave sclerite forming three sides and the bottom of the genital segment; it is attached to the last normal abdominal sternite. Crampton ('20 a) interprets this as the fused basal segment of the gonapods, and the forceps as the distal segments, but the discovery of an internal sclerite, as described under the heading "proctiger", tends to disprove this theory.

The Proctiger is a short tubular organ bearing the anus at its tip. It is attached beneath the last normal abdominal tergite, and is directed slightly backward, then upward, then backward again at the tip. Its caudal surface bears a wide and long depression or hollow, formed apparently by an invagination of the wall. The whole surface, except the posterior groove, is clothed with short hairs.

At the caudal side of the base of the proctiger is attached the two-jointed penis, the basal joint of which curves down and then upward and backward. The greater part

of this joint is broad and slightly flattened dorso-ventrally, but near its extremity it assumes a rod-like form, enlarging at its distal extremity to form an articulation with the second joint. This second segment is shorter than the first, straight, slender and cylindrical except for the swollen tip and enlarged basal articulation. A very fine lumen runs through the two joints, opening beneath the tip, to give passage to the seminal fluid. Normally the second joint folds forward on to the first, and the two together are lodged in the posterior hollow of the proctiger.

On either side of the base of the penis the proctiger is prolonged in the form of flat ribbon-like bands of chitin which meet below and form a loop. From the posterior margin of the middle of this loop a poorly chitinated sclerite extends backwards, widening slightly and terminating in two points, one attached to each of the forceps. This sclerite lies within the walls of the subgenital plate forming in part the floor of the cavity thus created; from its position, and from the fact that the forceps adhere more readily to it than to the subgenital plate upon dissection, it might be inferred that it represents the remnant of the ninth sternite. Such an interpretation would of necessity be purely speculative, and would depend absolutely upon a correct interpretation of the other abdominal sclerites.

The Forceps are a pair of strong chitinous appendages situated apparently upon the posterior dorsal margin of the subgenital plate, but in reality I believe them to be borne



upon the internal ninth sternite, in which case they would represent the gonapods of primitive insects. They are roughly cylindrical bodies, swollen in the middle, curving outward basally and then upward, terminating in a sharp inward directed hook or claw.

INTERNAL ANATOMY.

DIGESTIVE SYSTEM

(Figs. 14-18).

In the family Psyllidae, and in the closely related families of the Coccidae and Aleyrodidae, the alimentary canal has become strangely modified to form a complete ring, the first and last parts of the mesenteron uniting for a greater or shorter distance. The gradual evolution of this type of digestive tract forms an interesting study in comparative morphology.

The Pharynx (Fig. 21) is a short tube within the mouth capsule more or less surrounded by the heads of the styli. It is fairly large at its base, where it surrounds the opening of the passage between the styli, and tapers anteriorly to merge into the oesophagus. That the chitinous intima is present to a marked degree is evidenced by the fact that the pharynx may be clearly seen after caustic potash treatment.

The Oesophagus (Figs. 21, 22) is a narrow tubular continuation of the pharynx passing from beneath up in front and back over the top of the central tentorial bar of the mouth capsule. Thence it passes directly through the central cavity of the thorax above the nervous ganglia to the abdomen. Its walls consist of an epithelial layer composed of granular protoplasm in which numerous small elongated nuclei are scattered, without distinct cell walls.

Mesenteron: The oesophagus passes into an enlarged, thick-walled chamber which Witlaczil calls the stomach (Figs. 14, 17 ant. chamber of mes.). Its cellular structure differs from that of the remainder of the alimentary canal owing to its apparently secretory function. The epithelial cells are very small and columnar, their free ends presenting a ragged irregular appearance as though the cells varied in their degree of secretory activity. The cell walls are not always distinct in the basal part, but the nuclei are clear and distinct; no intima nor striated margin is apparent.

From the posterior end of this chamber the mesenteron is in the form of a narrow tube, coiled, not spirally, but in a succession of U loops. The rectal extremity of the mid-gut is fused with this anterior part, and follows its convolutions as a very small tube adhering to the wall (Fig. 17), the contents, however, passing in the opposite direction. After leaving the coiled part the mid-gut expands and describes two complete circular coils, a larger and a smaller, which, however, are forced into various positions by the pressure of other internal organs. The part of the tube composing the small circle is reduced somewhat in diameter and bears four slender urinary or Malpighian tubules terminating in delicate suspensory ligaments. Two larger ones project forward, and two smaller ones project backward; their arrangement on the mesenteron will be best understood by referring to fig. 14. The walls of the mesenteron are composed of a single layer of large epithelial cells leaving

a small irregular, stellate lumen; the basement membrane is distinct, the protoplasm is coarsely granular, the nuclei are large and distinct, and there is a definite striated margin to the cell (Fig. 18). The structure of the Malpighian tubules is somewhat different; the cells are fewer, and are spaced alternately, so that the lumen is wavy in its long axis, (Fig. 14), oval in cross section. The protoplasm of the cells is more homogeneous than that of the mesenteron cells, rather more dense around the lumen, but no striated margin is present (Fig. 15). At the completion of the second coil the mesenteron becomes very small, and fuses with the wall of the anterior portion as described above. This fusion is so complete that it is impossible to separate the two tubes when dissecting, and the true condition can only be seen in section or in a stained and mounted preparation. After following up the series of U coils the rectal extremity of the mid-gut continues up the side of the anterior chamber in a larger, more expanded form (Fig. 16) until at the entrance of the oesophagus the rectum is given off.

The Rectum is a long slender tube similar in structure to the oesophagus, bending sharply caudad from the termination of the mesenteron and passing between the internal organs to the anus. In the female a slight swelling in the tube occurs just below the cuticle, compressed laterally, forming a small chamber behind the opening of the anus (Fig. 26). In the male the rectal tube passes straight through the proctiger to the anus without any enlargement.

The Salivary Glands are large, roughly cubical, white bodies lying in the thorax just above the posterior extremity of the mouth capsule, on either side of the suboesophageal ganglion. From the lower surface of these primary glands a secondary process, cylindrical and tapering to a slender rod of tissue, runs forward a short distance (Fig. 22). The salivary ducts leave the glands at a point on the basal portion of the secondary process, and, passing round on either side of the suboesophageal ganglion, unite at a median point beneath and enter the mouth capsule just in front of the connecting bridge of the maxillary sclerites. The salivary gland is composed of large glandular epithelial cells (Fig. 23) with well defined nuclei. The protoplasm is always found in several different conditions in the same gland; in some cells it is granular, in others reticular, and in a few very dense as though filled with a dark-staining secretion.

#### NERVOUS SYSTEM.

(Figs. 19, 22).

##### Central Nervous System:

This, in Psyllidae, as in all Homoptera, is greatly cephalised, and consists of three main parts: the supraoesophageal ganglion, or brain, the suboesophageal ganglion, and the thoracic ganglion, the last representing a fusion of all the thoracic and abdominal ganglia.

The Brain is a large triangular mass of nervous tissue in the head. The fundamental divisions, proto-, deuto-, and tritocerebrum are not distinct externally and special ~~intra~~ <sup>vitem</sup> staining would be necessary to demonstrate them in sections. They may, however, be located roughly by the position of the optic ganglia, the antennal nerves and the connectives respectively.

The Optic Ganglia are situated on either side of the anterior portion of the brain, being swollen into a lobe or bulb just behind the constriction at the base of the eye. On the anterior dorsal margin the lateral ocelli are seen, appearing externally as papillae that lie immediately behind the lens in the cuticle of the head. In section the three ganglia of each optic lobe are fairly distinct. The periopticon is a narrow mass of fibres and medullary substance interspersed with pigment cells, just beneath the basilar membrane. This connects by the external chiasma of long nerve fibres with the epiopticon, a larger, subspherical mass of punkt substance. This again transfers the stimulus by the internal chiasma to the opticon, the largest of the three ganglia. Thence the optic nerve passes into the brain. The central masses of punkt substance and conducting fibres are surrounded by large-nucleated ganglionic cells.

The Compound Eye, while not belonging properly to the nervous system, is best discussed here. Its small size makes it difficult to distinguish all the recognised component parts, but the condition appears to be as follows:- (Fig. 19)



The cuticle is modified to form the cornea, a series of hexagonal lenses separated by thickened chitinous divisions. Beneath the cornea the modified hypodermal cells are visible as deeply staining plates, two beneath each lens. Under this again the cone cells form a distinct layer, followed by the long, straight retinulae which gradually converge until they reach the basilar membrane. A great quantity of pigment is deposited in and around the retinulae so that no differentiation into rhabdomes and rhabdomeres could be demonstrated.

The Ocelli consist of an outer convex lens formed from the cuticle, and a group of retinal cells beneath, connecting with a nerve that passes to the brain. No cone cells exist, and only a small amount of pigment is present.

The structure of the brain is simple compared with that of most insects. No mushroom bodies exist, but a distinct central body is present. I have not been able to demonstrate the nerve paths with the ordinary technique of staining.

The Antennal Nerves are given off from the sides of the brain on the anterior ventral surface, just below the bases of the optic ganglia.

The Connectives which pass beneath the central tentorial bar in the mouth capsule to the suboesophageal ganglion are completely fused except for a very small median opening which permits the passage of the oesophagus.

The Suboesophageal Ganglion is almost as wide as the brain, but quite short. The connectives that leave it are

so large and swollen that it appears rather as though the ganglion itself were bifurcated to give passage to the loop of the styli. The anterior portion of this ganglion lies within the dorsal part of the mouth capsule, as seen in fig. 22.

The Thoracic Ganglion is a large quadrate mass of nervous tissue lying in the mesothorax. It is slightly flattened dorso-ventrally, and the lateral margins are convex. Two large nerves are given off from the posterior dorsal angles, and two similar ones from the ventral posterior angles, the latter close together. These are the main trunks which pass backward through thorax and abdomen innervating the various organs and tissues of the body. Numerous other nerves enter the thoracic ganglion, as may be seen by referring to fig. 19.

#### Sympathetic System:

I have not attempted to trace the course of the sympathetic system in this insect on account of the extremely delicate work that would be entailed. Portions of very fine nerves and small ganglia belonging to this system have sometimes been found during dissection in the region of the mouth capsule, but their actual position, origin, and course could not be traced.

#### REPRODUCTIVE SYSTEM.

(Pl. IV.)

#### Female:

The female genital organs consist of a pair of ovaries with oviducts leading to the vagina into which two lateral

accessory glands pour their contents. There is a single large sac-like seminal receptacle leading into the extremity of the vagina by a slender duct, and a single median accessory gland just cephalad of this. In addition, there is a fourth gland, small and spherical, with a very long slender duct opening in the roof of the egg-duct between the plates of the ovipositor near the tip.

The Ovaries (Figs. 28, 32, and Pl. V) in very early stages of development may be likened to a pair of minute spherical bunches of grapes, each "grape" being a follicle opening by a short slender tube into the end of the oviduct. This form is retained while the ovaries increase in size until late in August, when the follicles begin to separate out on more slender stalks, and evidences of two eggs in process of development within each follicle appear. After egg-laying commences in September the follicles are quite obviously double, and a mature egg can usually be found in the oviduct. In section (Figs. 32, 34) it is difficult to make out the structure on account of the avidity with which these organs absorb stain. If specially treated to overcome this difficulty we find that the walls are very thick in early stages, being composed of tall columnar epithelial cells with long narrow nuclei. The central portion, representing the developing egg, is separated from the follicular wall by a fine membrane. As the egg grows the wall of the follicle, which functions as a "nurse cell", gradually reduces, the cells drawing back until

only a strand of protoplasm connects each cell to the egg (Fig. 34) and finally the connection is severed completely. Meanwhile the egg, at first finely granular, develops a great number of fat globules and granules in the protoplasm, besides the pronucleus.

The Oviducts (Figs. 27, 28) are thick-walled tubes capable of great distension. They are of medium length, more or less doubled and creased, and unite to form a common duct just before their entrance to the vagina. The walls appear to be a syncyium, i.e. many nuclei in the protoplasm of the wall, but no cell walls visible. The lumen of the ducts in late summer is always found filled with a thick yellowish secretion.

The Vagina (Figs. 27, 28) is very complicated in structure, and I have not succeeded in working out all the details to my satisfaction. The anterior portion, directly after the entrance of the oviduct, is studded exteriorly with circular rows of minute papillae, of which each one appears to be an individual cell with its nucleus in the tip. In section they may be seen standing on the basement membrane, the epithelium of the vaginal wall being on the inside. Possibly my interpretation of the condition is not quite correct, and certainly further work is necessary to understand the nature and function of these papillae. One would naturally expect to find muscles in this region, but these structures cannot be interpreted as such. They extend down to the front margin of the attachment of the lateral accessory glands, which are

in the form of broad lobes flattened dorso-ventrally, with a broad attachment to the vagina and a long cylindrical process at the opposite side. Only one wall is glandular in function (Fig. 31) consisting of columnar epithelium with an irregular inner margin, while the other wall is composed of small cubical cells. From their position, and their condition of active secretion in late summer it would seem likely that these glands secrete the large amount of fluid found in the oviducts. Witlaczil calls these "cement glands", but without positive evidence to the contrary it would seem logical to consider another gland to be described below as the cement gland.

The internal structure of the vagina at the insertion of the lateral accessory glands is intricate; I have not yet succeeded in demonstrating the true egg passage. Two small rounded elevations below the accessory glands on the dorsal surface of the vagina always contain a dark-staining homogeneous substance; I have been unable to discover spermatozoa in them, and am unable to explain them at all.

The oviduct opens into the egg-duct of the ovipositor ventrad of this, while dorsad a curious structure occurs which receives the ducts from the median accessory gland and the seminal receptacle (Figs. 27, 28). A chitinous plate with thickened rod-like lateral margins projects backwards a short distance and then curves upward and forward, forming a cup-like receptacle the sides of which are formed by muscle fibres.

Within this receptacle is a bean-shaped body of cartilaginous substance into which the ducts above-mentioned pass. I am not clear as to the internal structure of this body, for there seem to be several cavities and passages in it; neither have I been able to establish the opening from the egg-duct or vagina. It seems evident that this structure is concerned with the copulatory activity of the insect or the fertilising of the eggs, or both. If the lateral muscle fibres contract pressure will be exerted upon the bean-shaped body, and thus in some way not yet understood it may act as a pump to force the seminal fluid up the narrow duct of the seminal receptacle.

The Seminal Receptacle is a distensible sac of enormous size in comparison to the other organs of the reproductive system. It is in the form of a short cylinder with rounded ends, and its walls are membranous with isolated circular epithelial cells imbedded at regular intervals in the membrane. The duct is long and slender, widening a little to join the base of the receptacle.

The Median Accessory Gland or Parovarium is a club-shaped, thin-walled gland which enters the bean-shaped body in front of the seminal duct. Its similarity to the parovaria of diptera (Nonidez '20) has prompted me to give it that name, but whether its function is to secrete an activating agent for the spermatozoa I am entirely unable to state. It is a delicate gland that is only seen in dissections when great care is taken, and I have never found it in sections.



The Cement Gland is a single, small, spherical gland leading by a very long, slender duct into the roof of the egg-duct between the plates of the ovipositor. It is difficult to make out the cellular structure of the walls of this gland as there are always larger or smaller vacuoles in the protoplasm filled with secretion (Fig. 33); scattered nuclei may be found around the peripheræ, but there are no definite cell walls. This gland is small and undeveloped in early summer, and is not found actively secreting until oviposition commences, which fact, coupled with the location of the opening of the duct where it may deposit its secretion upon the egg in passing, presents strong evidence in favor of the theory that this is a cement gland.

Male: (Figs. 29, 30, 35)

The male reproductive organs consist of a pair of bilobed testes connected with the central seminal vesicle by the vasa deferentia. The seminal vesicle opens to the penis by the long ejaculatory duct at the beginning of which is a structure probably functioning as an ejaculatory pump. A large sac-like accessory gland is situated on either side of the seminal vesicle and ejaculatory duct, opening into the former just above the pump.

The Testes are roughly cylindrical bodies tapering to a point at their distal extremity, from which a slender suspensory ligament arises. At their bases the two testes of each side

are united to empty into the vas deferens, a narrow tube which passes to the seminal vesicle. Structurally the testes are composed of a series of ring-like sections, enclosed by a follicular membrane, which become smaller and smaller toward the tip. These are partially visible externally and quite distinct in longitudinal section (Fig. 30). The two ultimate compartments contain undifferentiated germ cells; in the third the cells are much larger and hexagonal in shape, while in the fourth a group of small cells in the centre is surrounded by fully formed spermatozoa. In the fifth the central cells may plainly be seen elongated, and some in the act apparently of splitting longitudinally into spermatozoa. The remaining compartments contain masses of spermatozoa coiled around in a circle, with a few irregular groups in the centre. No definite grouping of the sperms occurs in this insect. A number of small, isolated, spherical cells may be found in the base of the testis, the nature and function of which I am unable to determine. Possibly with a more complete series of sections of testes prepared at different periods of maturation the complete process of spermatogenesis might be followed.

The Seminal Vesicle is a heart-shaped organ with the pointed end continued caudad to empty into the ejaculatory duct. It is in reality a double organ, being divided medially by a thin membrane, but the whole is invested with a thin membrane of connective tissue. The separate ducts from each half are distinguishable in cross section down to the ejaculatory pump. The vasa deferentia enter on each side of

the seminal vesicle in an upward direction, as seen in fig. 29. In structure the vesicle consists of a very thin wall with the interior crammed with deep-staining spermatozoa.

The Ejaculatory Pump (Figs. 29, 35) is a curious chitinous structure situated at the base of the seminal vesicle. It consists of two circular flanges a short distance apart, connected by a cylindrical tube; the anterior end is open to receive the ducts from the seminal vesicle, while the posterior end is funnel-shaped, tapering to form the stiff chitinous lining of the ejaculatory duct. Between the two flanges, arranged longitudinally around the central tube, a number of strands of muscle fibres are stretched. The contraction of these muscles must in some way put the contents under pressure and force the seminal fluid down the ejaculatory duct.

The Accessory Glands (Fig. 29) are somewhat similar to the paragonia of some diptera (Nonidez '20) in their location and nature. They are large membranous sacs on either side of the basal part of the seminal vesicle and ejaculatory duct opening into the ducts just above the ejaculatory pump. The anterior portion is always large and distended, while posteriorly they narrow down somewhat and cross each other behind the ejaculatory duct. This posterior lobe is the only part in which any cellular structure can be seen, the cells appearing as small circular areas in the membrane. The glands are always filled with a clear, homogeneous, slightly viscid liquid.

## CIRCULATORY SYSTEM.

I have been unable to determine anything with regard to the dorsal vessel beyond finding it in cross sections of the abdomen close to the wall of the dorsum. It appears as an irregular lumen with thin membranous walls swollen here and there at the nuclei. Witlaczil ('85) says that the dorsal vessel or heart extends from the seventh abdominal segment forward to the second, and the aorta continues into the thorax. He found five pairs of ostia in the heart.

## TRACHEAL SYSTEM.

(Fig. 20).

Owing to the delicate condition of the tracheae it was found impossible to work out the tracheal system in the adult. Witlaczil records the same difficulty. In the nymph the tracheae appear to be stronger, and when filled with air the main trunks may readily be seen through the body wall. I thought at first that each spiracle opened into a separate system with no connecting trunks, but these were later discovered in the abdomen, though not in the thorax. In fig. 20 a fifth stage nymph has been outlined, and all the tracheal system that could be traced has been inserted. Witlaczil figures and describes a much more complete system, so doubtless more can be demonstrated with fresh material properly treated.

## MUSCULATURE.

It has not been possible in the time at my disposal to undertake a detailed study of the musculature, which, in this insect, is very complicated, as the structure particularly of the metathorax would indicate. There appear to be a number of very large, cylindrical, horizontal, and vertical muscles in the mesothorax, but those of the metathorax are chiefly of a different type, being fan-shaped and composed of a great many deeply striated bundles which separate readily in dissection. These are probably muscles of the hind legs, capable of very sudden contraction to cause leaping. In the abdomen the muscles of the body wall are segmental and quite simple in arrangement, but those operating the genitalia are complex.

## GLANDS.

Wax Glands occur in the nymphs, and in the adult female, in both cases in a ring around the anus. The apertures in the chitinous cuticle (Fig. 25) have already been described under external anatomy. The glands are found in lobular masses directly beneath the cuticle (Fig. 26); they consist of tall columnar epithelial cells with a well defined nucleus at the base, and frequently a space filled with secretion between the cells.

Scent Gland: I have found glands in various degrees of entirety in the metathorax of late summer forms; I could not

find them in early forms but they must be present. I have never been able to isolate one completely and establish its external opening, but I believe them to open on the dorsum of the meta scutum. The complexity of the hard chitinous endoskeleton makes it practically impossible to dissect out such a delicate organ satisfactorily; sectioning of this region is quite impracticable because the chitin breaks and tears the soft tissues. The organ, as far as I can determine, is tubular in the male, but seems somewhat more complex and branched in the female. I have no evidence that these are scent glands, except that glands located in the thorax usually perform that function.

#### PSEUDOVITELLUS.

(Figs. 20, 24).

There is in the abdomen of nymph and adult an irregular yellow mass of cells, usually in close proximity to the digestive tract. In section they are medium sized cells with well defined nuclei and very coarsely granular protoplasm which usually appears to be grouped in areas around the nucleus (Fig. 24). The function of these cells, which are also found in Aphididae and Coccidae, has never been established. Davidson ('13) considers them nutritive for the developing embryos in aphids, hence the name "pseudovitellus" or false yolk; Witlaczil ('85) thinks they may be excretory in function.

#### ADIPOSE TISSUE.

The entire body cavity not occupied by the vital organs is filled with a white granular-appearing mass of fat cells in nymphs and young adults. In late summer, when the ovaries of the female are functioning and the males are near the end of life, the fat body seems to be absorbed to a large extent, but there is always a certain amount adhering to ovaries, testes and alimentary canal, held there by branching tracheae. In structure the cells are vacuolated and form a reticular network of protoplasmic strands enclosing fat globules of all sizes.

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EXPLANATION OF PLATES.

PLATE I.

- Fig. 1 Head, front view, with one complete antenna.  
2 Hing leg, lateral view.  
3 Mesothorax, caudal view, showing internal structures.  
4 Head and thorax, ventral view.  
5 Endoskeleton of metathorax, caudal view.  
6 Endoskeleton of metathorax, lateral view.  
7 Abdomen of male, lateral view.  
8 Genital segment of male, caudal view.  
9 Entire body of female, lateral view.

PLATE II.

- 10 Head, thorax, and wings, dorsal view.  
11 Ovipositor of female, separated and spread apart  
ventrally; dorsal view.  
12 Ovipositor of female, normal; lateral view.  
13 Male genitalia; caudal view, slightly from left side.

PLATE III.

- 14 Alimentary canal, dorsal view.  
15 Malpighian tubule, cross section.  
16 Anterior chamber of mesenteron, cross section,  
showing rectal extremity of mesenteron attached to  
wall.

- 17 Longitudinal section through anterior chamber of mesenteron showing rectal extremity and rectal tube. Also a section through the base of a U loop of the mesenteron with the rectal extremity fused with the wall on either side.
- 18 Mesenteron, cross section.
- 19 Nervous system, with the structure of one compound eye and optic ganglia; ventral view.
- 20 Outline of a fifth instar nymph, with as much of the tracheal system as could be determined.
- 21 Mouth capsule, heads of styli omitted; dorsal view slightly from left.
- 22 Mouth capsule with beak, nervous system, and one salivary gland in situ; lateral view.
- 23 Salivary gland, cross section.
- 24 A few cells of the pseudovitellus in section.
- 25 Portion of the circum-anal ring of chitin of the female bearing apertures for wax glands.
- 26 Wax glands and rectum of female, longitudinal section.

PLATE IV.

- 27 Vagina of female, showing structure of the bean-shaped body and its receptacle, lateral view.
- 28 Entire reproductive system of female, ovaries partially mature.

- 29 Entire reproductive system of male, dorsal view.
- 30 Testis of male, longitudinal section.
- 31 Lateral accessory gland of female vagina, cross section.
- 32 Follicle of ovary in early stage of maturation,  
longitudinal section.
- 33 Cement gland, longitudinal section.
- 34 Follicle of ovary in later stage of maturation,  
cross section.
- 35 Structure of the ejaculatory pump of male.

PLATE V.

Development of a single ovary throughout the  
season.



PLATE I.

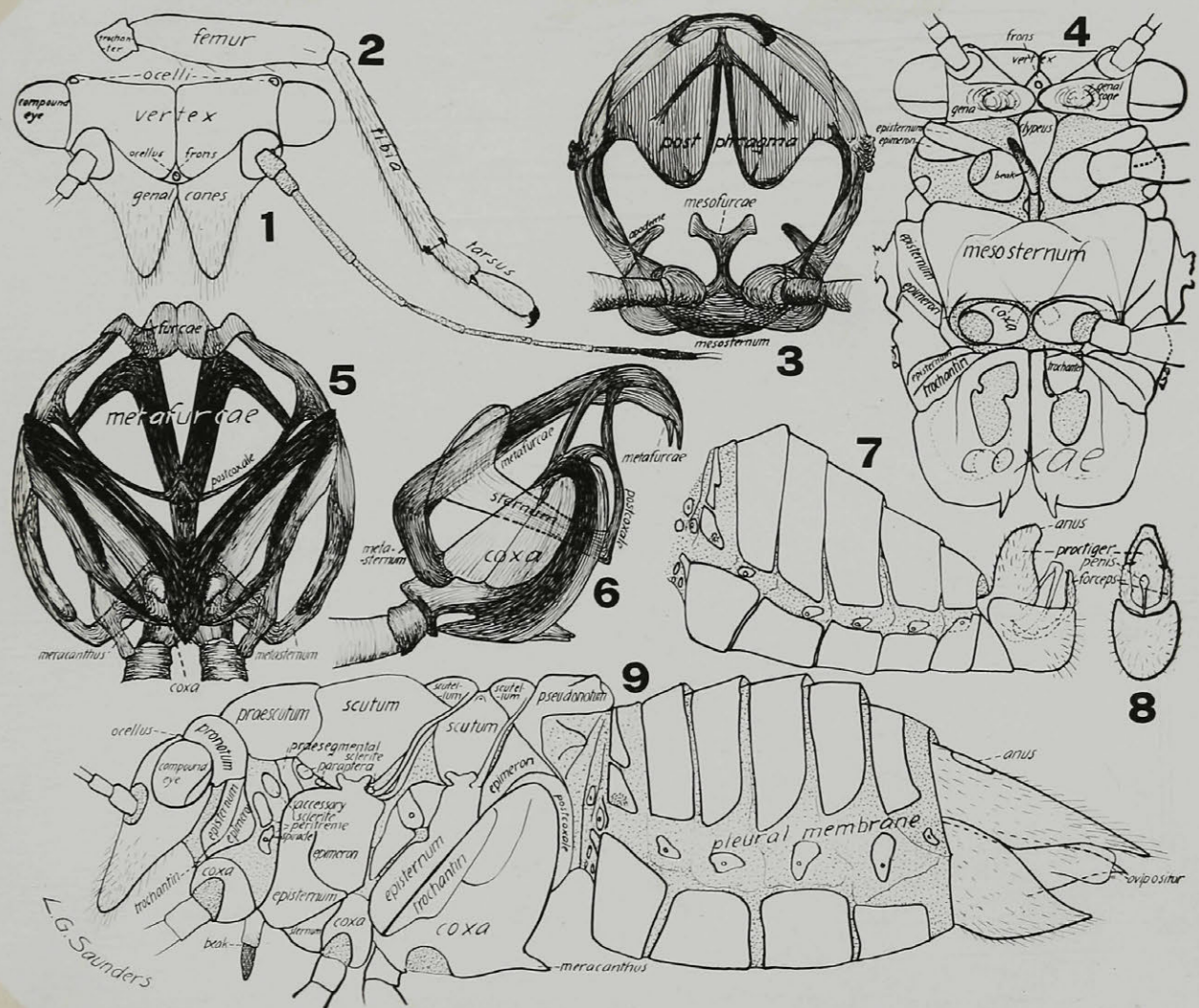




PLATE II.

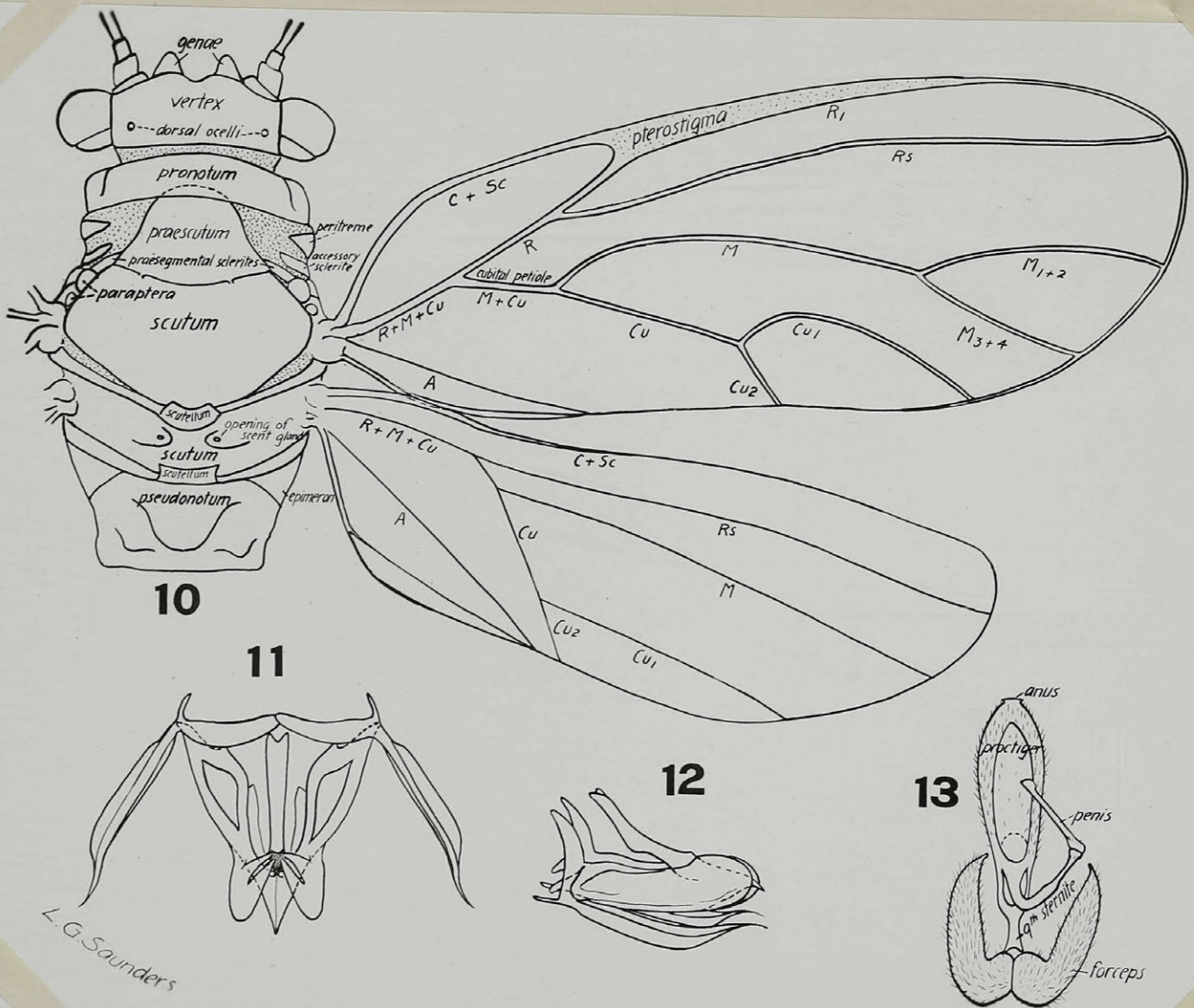




PLATE III.

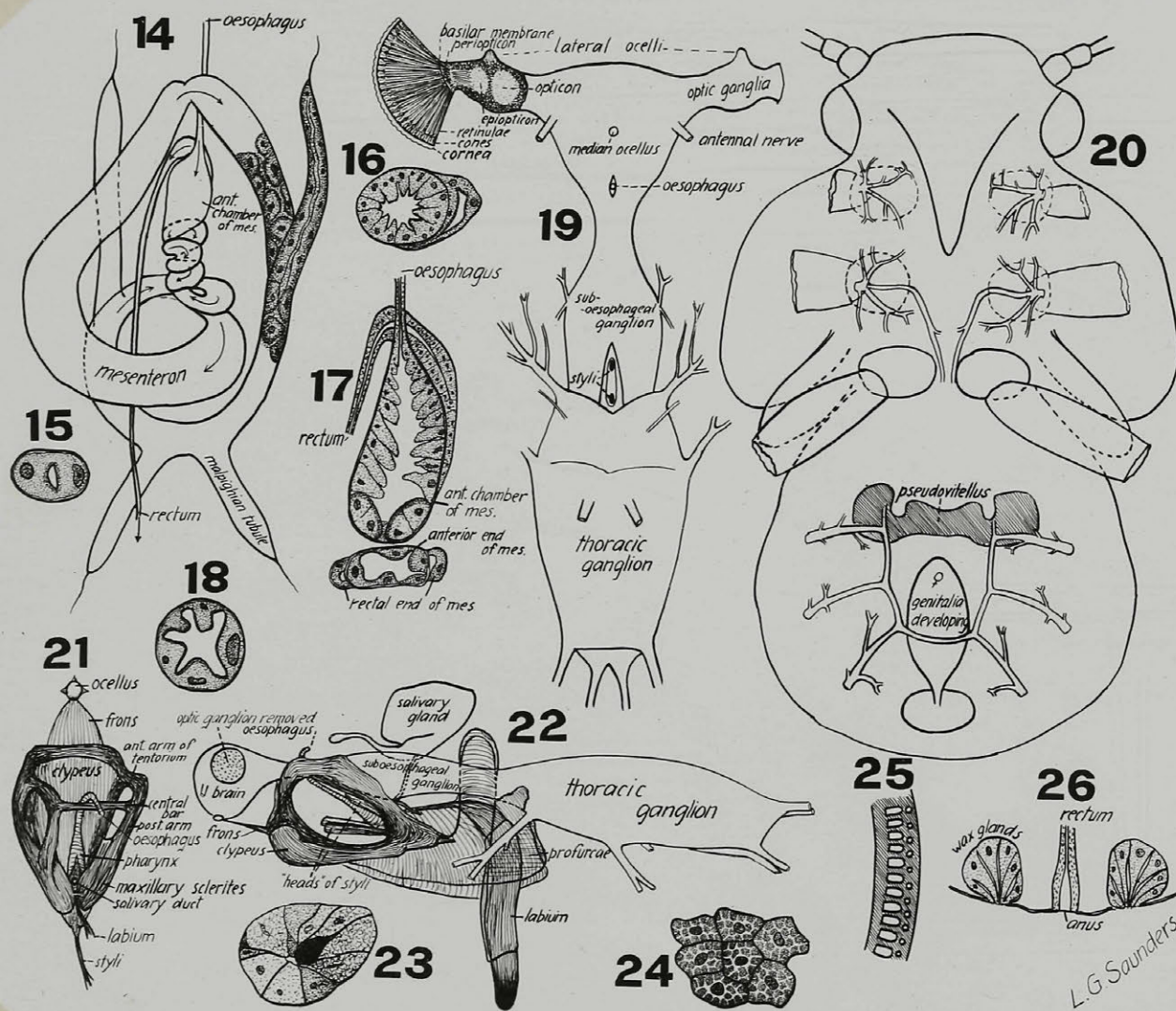




PLATE IV.

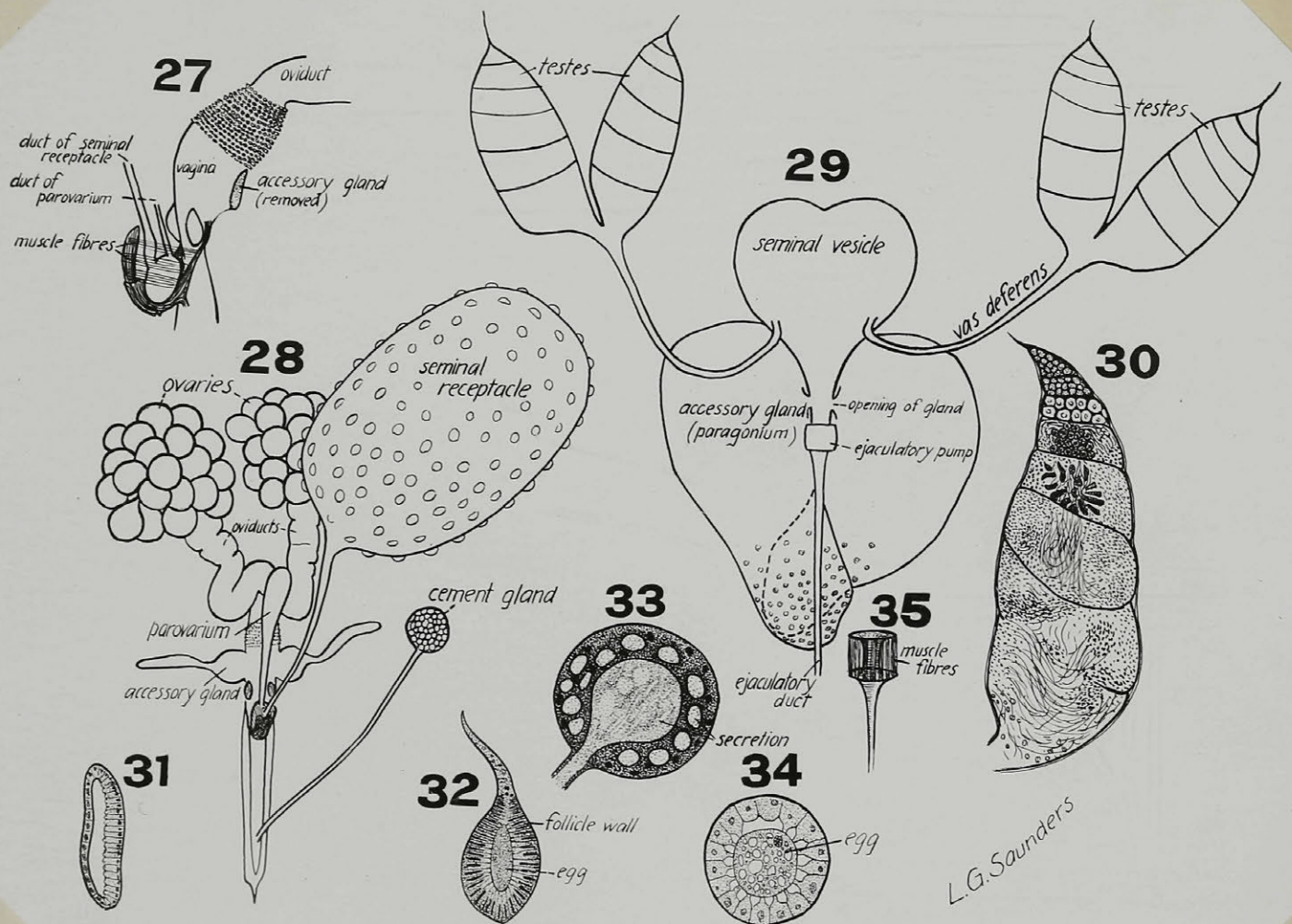
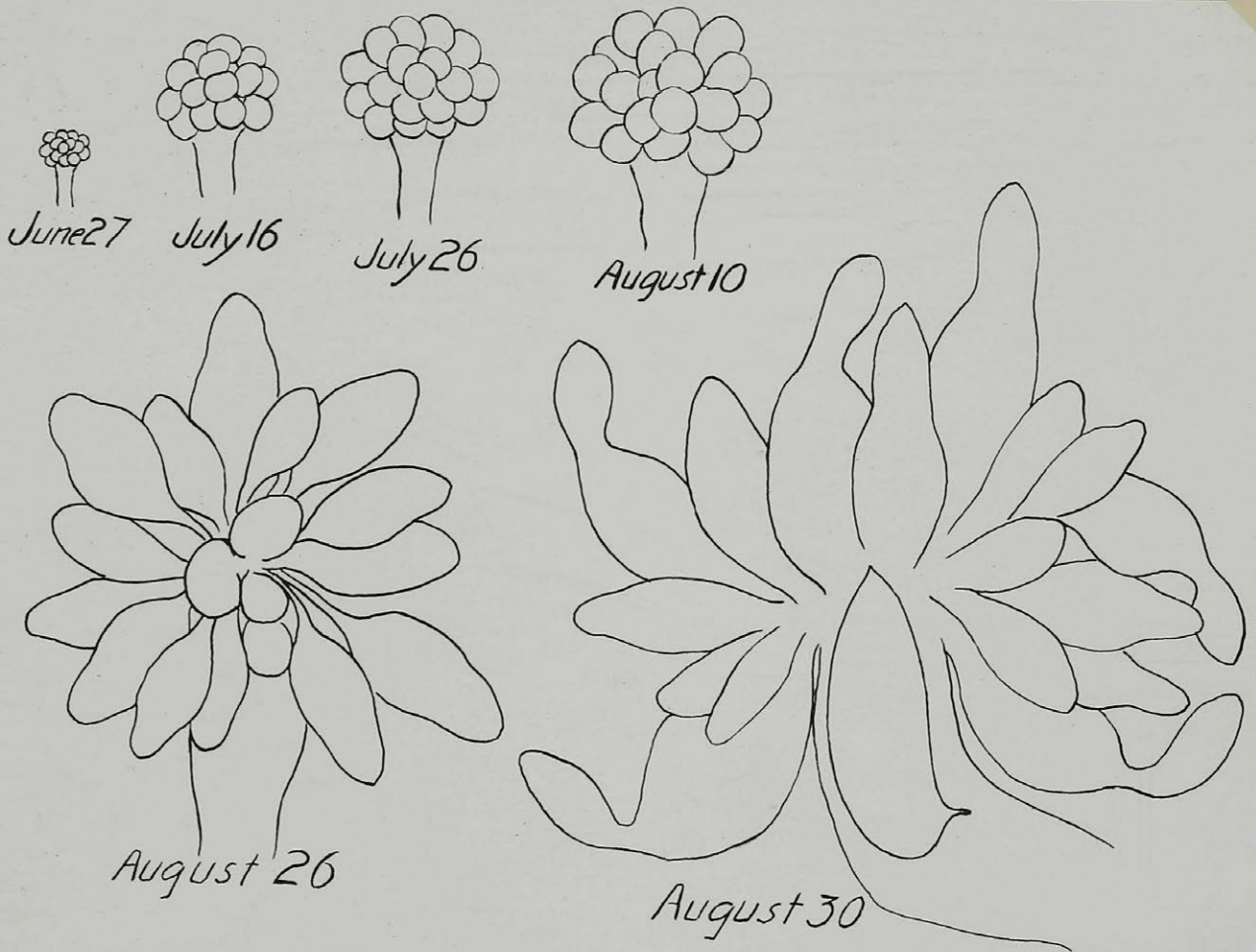


PLATE V.



Development of an Ovary of *P. mali* female throughout season







