GLASGOW

Studies on the Anatomy
Of Tibicen Septendecim L.

Entomology
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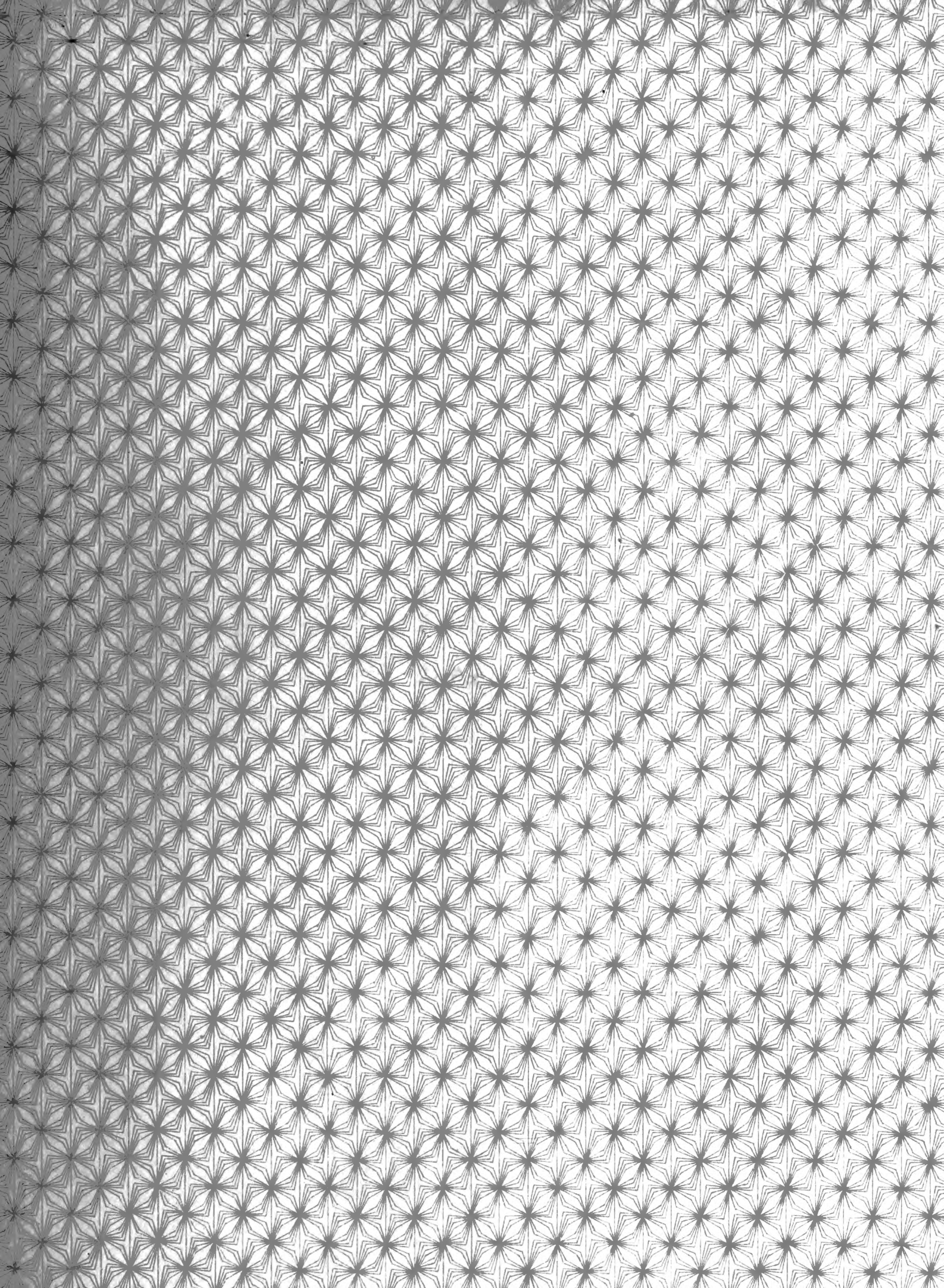

STUDIES ON THE ANATOMY OF TIBICEN SEPTENDECIM L.

BY

HUGH GLASGOW

THESIS

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THIS IS TO CERTIFY THAT THE THESIS PREPARED UNDER MY SUPERVISION BY

Hugh Glasgow

ENTITLED Studies on the Anatomy of Tibicen septendecim L.

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Instructor in Charge.

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6

CONTENTS

ANATOMICAL STUDIES ON TIBICEN SEPTENDECIM

INTRODUCTION

While the various external structures of the periodical cicada, including the mouth parts, musical apparatus and genital armature, have been studied and described more or less fully by a number of authors, the anatomy of the internal organs has remained practically untouched. The only recorded observations on the internal anatomy have been made on the digestive canal and these are quite superficial, being intended merely to determine whether or not the digestive system was really complete.

Until recently it was generally held among entomologists that the digestive system, in the male at least, was aborted, and that the male consequently took no food during the adult stage. Burnett~~e~~ appears to have been the first to advance this idea. In 1851 (Proc. Bost. Soc. Nat. Hist., vol. 4) appears the following note referring to an address by Dr. Burnett~~e~~. "He found that in the male in many instances there is scarcely a trace of a digestive canal or biliary apparatus, whereas in the female both are fully developed. This arrangement is adapted to the peculiar wants of each, the male living but a few days and the female much longer." Burnett~~e~~'s results seem to have

been accepted without question by entomologists for over fifty years, and Marlatt evidently had his work in mind when he stated in discussing the food habits of the cicada (Bull. 14, U. S. Bur. Ent., 1898, p. 72) "That the periodical cicada feeds at all has even been questioned, and it is quite possible that in some cases where it was supposed to have been feeding the action of the insect was misinterpreted. Such feeding is limited, at any rate, to the female, as in this sex only do we find a perfect digestive apparatus, that of the male being rudimentary." Five years later, Quaintance made the first really careful dissection of the digestive canal, in connection with his study on the food habits of the cicada. He says (Bull. 87, Md. Exp. Sta., p. 74) "Numerous dissections of both sexes under water show that the alimentary canal is not rudimentary, but is practically as well developed as in the female. The intestine in both sexes is small and threadlike, but continuous and sufficiently developed for insects subsisting on liquid food."

Of the superficial anatomy, the mouth parts especially have received careful study. In 1892, Smith described and figured the mouth parts of the cicada nymph. His work was supplemented by Marlatt in 1896, and by Meek in 1903. The oviposition is described and figured by Hyatt in 1896, and by Marlatt in 1898, while the mechanism of the external genitalia of the male was worked out by Apgar in 1887. The musical apparatus has been studied and described by Burnett in 1851, Love in 1895, and Marlatt in 1898.

MATERIAL AND METHODS

The material used in this study happened to consist entirely of the Cassini form, and was collected by Dr. J. W. Folsom in June, 1907 at Homer, Illinois. The specimens were killed in hot water and preserved in 95% alcohol after having had the abdomen opened to insure proper penetration. At the time the dissections were made, during the winter of 1907-08, the material was in very good condition for anatomical work.

Most of the following figures and descriptions are based upon gross dissections made under water, although serial sections were employed to some extent in working out the course of the Malpighian tubes.

DIGESTIVE SYSTEM

The Cicadidae in common with several other homopterous families present a characteristic peculiarity in the form of the digestive tube, namely, a recurrent portion of the mid or hind intestine that becomes closely united with the anterior part of the mid intestine or with the aesophagus. This unusual structure is known to occur in Coccidal and Psyllidae as well as in Cicadidae.

Mark found, in 1877, that in certain Coccidae the anterior end of the mid intestine forms a small spinal loop with the lower end of the oesophagus, and that the posterior end of this loop is firmly attached to the rectum. The remainder of the slender stomach then forms a large loop which fills a large part of the body cavity and just below its opening into the rectum forms a short caecum.

In 1885, Witlaczil worked out a similar structure in Psyllidae. He found that the intestine shortly beyond the point of insertion of the Malpighian tubes recurved, to wind several times about the anterior end of the mid intestine and then to proceed to the anus. He explains the origin of this peculiar structure as follows,- "Die erwahnte Darmverschlingung weist mehrere Windungen auf und ist von einer zelligen Haut umgeben. Sie erklärt sich so, dass eine nach hinten verlaufende Partie des Darmes mit einer zurücklaufenden verwachsen ist, worauf sich dieser ganze Theil nach einer Seite eingedreht hat. Man kann sich dies veranschaulichen, wenn man zwei Schnuren neben einander legt und sie mit dem

Finger inder Mitte eindrereht. Man findet dann in der Mitte der zusammengedrehten Stelle eine Umkehr der Drehungsrichtung, wie man sie auch bei den psylliden nachweisen kann."

The anatomy of the digestive system of the cicada has received considerable attention from foreign workers, especially among the French. Of these Dufour is easily first, and although his work is by no means perfect it is surprisingly accurate for the period in which it was done.

In 1833 he figured and described in detail the digestive apparatus of *Cicada orni*. This description was supplemented in 1839 by Doyere, who made certain corrections in Dufour's work, from dissections based upon *Cicada plebia*.

Since 1839, so far as I can learn, there is no record of further observations upon this subject except those mentioned in the introduction.

The digestive system of *T. septendecim* is in no way abnormal as compared with the descriptions for the two species studied by Dufour and Doyere. Its length, however, is considerably less than that given by Dufour for *Cicada orni*, but aside from this there is nothing in his description indicating a better development of any part of the digestive system of *C. orni* than that found in *T. septendecim*. Dufour gives the length of the digestive tube of *C. orni* as ten times that of the insect, while in *T. septendecim* I find, by actual measurement, that its total length, about 155 m.m., is not over six times the length of the body.

The following description of the digestive system is based upon dissections of the male. Numerous females were also dissected, in order to compare the relative development of the digestive tube in the two sexes. The stomach of the female is somewhat larger and heavier walled, as a rule, than that of the male, but aside from this there is no noticeable difference in the development of the alimentary canal in the two sexes.

The pharynx (Plate VI, ph.) situated in the median anterior angle of the head, consists of a ventral, chitinous, trough-like structure, terminating anteriorly in a narrow chitinous passage which empties into the epipharynx. This trough-like structure is closed dorsally by an elastic, transparent, semi-chitinous membrane, along the median dorsal side of which is a narrow chitinized ridge serving as a place of attachment for the eighteen to twenty paired muscles which operate the pharynx. When these muscles are relaxed,, as in preserved specimens, this membrane is strongly concave on its upper surface, fitting closely into the trough-like cavity of the ventral chitinous portion. By manipulating the muscles of the pharynx with finely pointed forceps its action can be readily observed. When the muscles are pulled, the dorsal membranous portion is drawn out, forming a more or less oval chamber with the ventral portion, nearly doubling the capacity of the latter. Immediately upon releasing the muscles the membrane springs sharply back into its normal concave position

by its own elasticity.

Posteriorly, the pharynx passes into the membranous oesophagus which, dilating just above the brain, forms a muscular enlargement (pp), the "pharyngeal pump," from the dorsal and lateral sides which originate a number of slender muscles, nine pairs in all. These muscles are attached at various points to the inner walls of the cranium or to the tentorium and are not wholly confined to the enlarged portion of the oesophagus, but two of the nine pairs are attached to its lower dorsal end just before it enlarges into the pharynx. Of the remaining seven pairs, four are comparatively short. These four short pairs are attached to the sides of the entargement (pp) and anchor it to the tentorium. The remaining three pairs are long and slender, originate on the dorsal side of the enlargement, and are attached at various points to the inner walls of the cranium.

From its dilated portion the oesophagus continues as a comparatively slender, muscular, thin walled tube which gradually increases in diameter as it approaches the stomach until at its lower end it forms an ill-defined crop which often equals or even exceeds the lateral area of the stomach (a) in diameter.

In the male the anterior end of the stomach commonly ends in the basal abdominal segment, but in the female it often projects up into the metathorax.

The stomach, the total length of which is about 90 mm., or three and one-half times the length of the body of the insect, consists of three principal regions, namely, a main, dilated portion (b), a lateral arm (a) and an intestine like tube (d). The dilated portion (b) varies somewhat in size and form, but averages about 7 m.m. in length. It is collapsed in preserved specimens and presents a wrinkled appearance, especially at its anterior end where the folds are quite pronounced. It is suspended from the oesophagus by a number of long, fibrous muscles (sm) which are attached to its anterior end. At its posterior end this dilated portion passes into the intestine like tube (d) which is about 80 m.m. long and of uniform diameter throughout. After a number of convolutions it returns to the anterior end of the abdomen and apparently empties into the stomach at (g). The third region of the stomach (a) is a lateral projection, from the right side of (b) near its anterior end, which extends laterally for a short distance and then bends suddenly forward, frequently projecting beyond the anterior end of (b). The lateral portions (a) is round and firm and appears quite heavy-walled, but in cross section (Plate V) its walls are seen to be moderately thin, the firm appearance being due to longitudinal folds in the walls which frequently fill the lumen completely. The whole is surrounded by a membrane which disguises the folds and gives the surface its characteristic, smooth appearance.

From the point where it seems to empty, the tube (d) passes up between longitudinal folds in the walls of (a), reaching to its extreme anterior end, and after making nearly a complete turn about it, emerges dorsally at (h). Almost immediately after emerging this tube passes into the intestine at (p). The point of union is characterized by a slight dilation and also by a marked difference in the color and texture of the two tubes. The intestine is quite thin-walled and fragile, usually collapsed in preserved specimens and of a glistening white color, while the tube of the stomach is thick-walled, firm, and rather gray in color.

From the pylorus (p) the intestine, which is about 50 m.m. long, passes down between the stomach and the dorsal wall of the abdominal cavity in three or four broad curves and just before reaching the rectum invariably forms a more or less spherical knot of convolutions, bound closely together by tracheal threads and connective tissue.

The rectum is a thin-walled muscular tube about 6 m.m. long, the anterior third of which is considerably dilated. This dilated portion narrows at its posterior end into a smaller tube of uniform diameter which terminates in the anus. The ileum opens at some distance down on the side of the dilated portion of the rectum so that the anterior end forms a broad muscular cul-de-sac.

I am unable to locate the pair of anal glands figured by Dufour in 1833. He has evidently mistaken the peculiar cluster of air vesicles which are located one on each side of the ab-

dominal cavity, in segments seven and eight, for anal glands. Each of these clusters is composed of eight or ten pear-shaped vesicles, all joined to a common center by short tracheae, and the whole connecting with the main tracheal system.

The apparently abnormal structure of the stomach was first described in 1825 by Dufour, but it was not until 1839 that Doyère worked out the true relation of the recurring portion. Plate III is a copy from the figure given in his "Note sur le tube digestif des Cigales," and I shall have occasion to refer to it in the following discussion as well as in connection with the Malpighian tubes as there are certain errors in his description which I wish to correct. In the above note he says: "E (Plate III) est le pylore. L'intestin EF après de nombreuses circonvolutions qu'il m'a été impossible de suivre et que l'on voit d'ailleurs figurés d'une maniere complete dans la figure I, empruntée à M. Léon Dufour (FC, fig. 2). Mais au lieu de se dégorger dans cette cavité, il ne fait que s' introduire dans les parois pour ramper, en serpant, entre les tuniques dont elle se composent, et ressortir en K, à pen de distance de l'orifice cardiaque B, sans aucune solution de continuité. C'est à partin de ce point seulement que M. Dufour lui donne le nom d'intestin."

"Ainsi, c'est le canal intestinal qui se replie vers la moitié de sa longueur, pour venir se suspendre à l'estomac."

The pylorus is not located at E, and EF is consequently not the intestine but merely a tubular prolongation of the

stomach. The intestine originates at a point slightly below K, this being the true position of the pylorus.

THE SALIVARY GLANDS

The salivary glands, which are figured in Plate I as they appear before dissection, and in Plate VI dissected out to show the relation of the different parts, are seen to be quite complex in structure. The more prominent glands (a.s.) and (d.s.) consist of two pairs of large, nearly equal clusters of blind tubes. In the anterior pair (b.s.) each cluster is composed of from twelve to fourteen stout tubes, pure white in color, very irregular in form and often branched. The greater part of this anterior pair is within the cranial cavity, completely filling the space above and in front of the brain. The posterior pair (a.s.), situated wholly in the prothoracic cavity are not simple glands, but are composed of at least three distinct sets of utriculi (i.s., m.s. and n.s.). The posterior set (n.s.) is composed of from ten to twelve comparatively straight, yellowish tubes which taper off abruptly at their anterior ends into slender ducts, uniting to form a very short common duct which passes through the center of the middle set of utriculi. This middle set (m.s.), disc-like in form, is composed of from fourteen to eighteen very short tubes, many of which are almost spherical. This middle set fits closely over the anterior end of n.s. The tubes composing these two sets are quite distinct, in color as well as in size and form. In the posterior set the tubes are yellowish and quite opaque, while in the middle they are much darker

but translucent and finely dotted with darker points. The anterior set (l.s.) is not so characteristic in form as the other two, being composed of from ten to twelve very delicate pure white vesicles of variable size, fitting closely to anterior side of (m.s.).

Situated just within the posterior angles of the head, back of the eyes is a pair of very small, spherical glands (d.s.), each composed of eight to ten pure white vesicles. Emptying through (d.s.) is a large tubular gland (e.s.). This tubular gland is dilated at its base where it often equals (d.s.) in diameter. From this point it passes into the anterior part of the cranial cavity, then turns back and passes through (b.s.) where it frequently becomes interlaced with the tubes of this gland. From here it continues, gradually becoming more slender, and ends blindly in the mesothoracic cavity.

The gland (d.s.) empties through the long slender duct (g.s.). The walls of this duct are lobulate, white and quite delicate, the glistening contents of the lumen being plainly visible through them.

The gland (d.s.) empties through the short, slender duct (h.s.) the walls of which are uniform and opaque. The ducts (g.s.) and (h.s.) as well as the gland (a.s.) empty into the common duct (i.s.) which is quite similar to g.s. in general appearance, but is considerably larger.

This duct (i.s.) unites with the corresponding duct of the opposite side to form a very short common duct just before emptying ventrally, at the base of the chitinous "injector" (k.m.), the structure of which was worked out by Meek in 1903. The "injector" consists of a short, cylindrical, thin-walled, chitinous chamber, the posterior end of which is depressed, forming an invagination which can be clearly seen through the thin walls of the chamber. The invagination, which serves as a plunger for the "injector," is operated by a pair of large, flattened muscles (l.m.). Anteriorly the "injector" empties into the hypopharynx.

THE MALPIGHIAN TUBES

The Malpighian tubes (m.) consist of two pairs of long, slender, white tubes, quite lobulate and delicate, which upon hasty examination appear to empty into the stomach separately, at a point somewhat below (g.). They were described by Dufour in 1833, (Recherches sur les Hémiptères, page 90), as follows: "Les vaisseaux hépatiques sont au nombre de quatre, très entortillés, variqueux, diaphanes et fragiles; flottans par un bout, ils s'insèrent isolément par l'autre entre le cul-de-sac de l'estomac et l'embouchure de la portion intestiniform du ventricule chylifiqu~~r~~e."

In his "Note sur le tube digestif des Cigales," page 84, Doyère makes the following addition to Dufour's description: "Le double rôle que jouait le ventricule chylifique et l'anse duodénale dans le transport des alimens, tel qu'il ressortait des faits announcés par M. Léon Dufour, expliquait jusqu'à un certain point cette autre singularitié que là précisement venaient s'inserer les vaisseaux hépatiques. Il n'en est plus de même si les faits sont tel que je crois les avoir vus; mais cette insertion, en effet, ne m'a pas semblé plus exister pour les vaisseaux hépatiques que pour l' intestin lui-même, et ils m'ont paru suivre dans la paroi estomacale un route tout-à-fait analogue à celle que suit l'intestin. Ils y entrent, se recourbent, reviennent sur eux-même, et ressortent. Il s'ensuivrait de là quelques conséquences assez dignes d' attention, et qui contredisent complètement l'opinion actuelle de savans sur ce point."

"1°.- Les vaisseaux hépatiques sont au nombre de deux seulement P.S. et Q.R. (Plate III).

"2°.- Leurs extrémités ne sont très probablement point flottantes.

"3°.- Leur point d'insertion nous est encore tout-a-fait inconnu."

From the point where they seem to enter the stomach the Malpighian tubes pass back between the stomach and the dorsal wall of the abdomen following the convolutions of the intestine more or less closely, and instead of floating free in the body cavity as described by Dufour, they follow the intestine into the compact knot of convolutions (i.e.), forming a confused mass, the parts of which are closely bound together, making their complete dissection quite difficult. Shortly after entering this knot the Malpighian tubes decrease somewhat in size, but instead of forming four blind tubes as Dufour figures them, they are actually continuous, forming two loops, the lower ends of which interlace with the convolutions of the intestine in (i.e.).

From the point where they appear to enter the stomach the Malpighian tubes pass up between separate longitudinal folds in the walls of (a.) at varying depths, frequently reaching nearly to the center, but commonly remaining nearer the surface. They do not extend so far anteriorly as does the tube (d.) and emerge with it at (h.), from which point they follow it to the pylorus (p.), where they empty into the intestine. Just before emerging at (h.) two of the four tubes unite to

form a common duct so that there are only three ducts which empty at (p.). From (h.) to (p.) the Malpighian tubes are tightly pressed against the walls of (d.) giving its lumen a characteristic three-lobed appearance. This complex tube is surrounded by a membrane which completely disguises its true structure.

The approximate course of the Malpighian tubes and of the tubular part of the stomach along (a.) is shown diagramatically in Plate IV. The tubes do not really follow a perfectly straight course, but adapt themselves to irregularities in the wall of the stomach.

In Plate V are shown cross sections of (a.) taken at three different places (6, 7 and 8). The section six is taken just below the point (h.) and shows the three ducts of the Malpighian tubes just after they emerge from (a.). Section seven includes the pylorus and eight was taken across the intestine at a point somewhat below the pylorus.

MALE REPRODUCTIVE SYSTEM

Plate VII

The internal reproductive organs of the male consist primarily of a pair of testes with their vasa deferentia, two pairs of accessory glands and an ejaculatory duct. These organs are interlaced and closely packed in the posterior end of the abdominal cavity, completely filling segments six, seven and eight.

The testes, about 3 m.m. in diameter, consist of somewhat flattened clusters of 150-200 more or less pear-shaped follicles, each of which communicates with the vas deferens by a short duct. The vasa deferentia are long, slender tubes dilating just before their union with the accessory glands (a.c.), into prominent seminal vesicles which often equal the accessory glands in diameter. In discussing the relative lengths of the vasa deferentia in different insects, Henneguy states in his text-book("Les Insectes," page 174) that "Dans la Cigale ils sont dis a quatorze fois la longueur du corps." This statement is rather surprising as in T. septendecim they are from 35-40 m.m. in length, which makes them rather less than one and one half times the length of the body of the insect. The accessory glands (a.c.) are blind tubes of much greater diameter than the vasa deferentia and considerably longer, being about 65 m.m. in length and increasing very gradually in diameter as they approach their junction with the

vasa deferentia. Immediately before this point they are strongly constricted and empty through very short, slender ducts. These glands are of a glistening white color, comparatively heavy-walled and firm near their blind ends, but becoming more delicate and thin-walled as they increase in diameter, until at their point of greatest dilation they become quite delicate. From their union with the accessory glands the vasa deferentia proceed as short slender ducts which empty independently of each other into the anterior end of the large muscular reservoir at the anterior end of the ejaculatory duct. This reservoir is an oval, heavy-walled, muscular organ, about 25 m.m. long by 1 m.m. in diameter, the structure of which is shown in cross section (Plate VII, fig. 11). Its wall is composed of three principal coats. The outer coat consists of a heavy layer of longitudinal muscles, and the middle of a somewhat thinner layer of circular muscles, while the inner coat is made up of large cells, doubtless glandular in function, which form regular projections into the lumen of the reservoir. The ejaculatory duct is a slender tube about 3 m.m. long, emptying at the base of the sheath enclosing the penis proper. This sheath is a thin-walled, chitinous cylinder about 3 m.m. long, recurving at its anterior end where it bears a second pair of small, round, somewhat flattened accessory glands (n.), between which the posterior end of the ejaculatory duct disappears. These glands are supported by a chitinous plate to which is attached the powerful muscles operating the penis.

The shield is held in place by the two heavy, chitinous genital hooks (h.), attached to the posterior dorsal edge of the ultimate segment of the abdomen. Attached to the free end of the chitinous sheath is a pair of curved, serrate, chitinous plates which also function as copulatory hooks.

The penis proper is a highly elastic, membranous tube, the mechanism of which has been described by Apgar, 1887.

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EXPLANATION OF PLATES

Plate I.

Fig. 1. Ventral aspect of the digestive tube and its appendages before dissection.

Plate II.

Fig. 2. Abdominal region of digestive tube dissected out.

Plate III.

Fig. 3. Stomach of Cicada plebia, taken from Doyère's "Note sur le tube digestif des Cigales."

Plate IV.

Fig. 4. Diagrammatic representation of the stomach showing the disposition of the Malpighian tubes, and of the recurrent tubular portion of the stomach, in the lateral arm a.

Plate V.

Fig. 5.- Stomach, showing places at which cross-sections in figures 6, 7 and 8 were taken.

Fig. 6. Section of a taken above the pylorus, showing the three ducts of the Malpighian tubes.

Fig. 7. Section across the pylorus, showing place of discharge of the Malpighian tubes.

Fig. 8. Section across the intestine somewhat below the pylorus.

Plate VI.

Fig. 9. Ventral aspect of salivary glands, dissected out to show the relations of the different parts.

Plate VII.

Fig. 10. Ventral aspect of the male reproductive system.

a---- lateral arm of the stomach.

AB--- jabot.

ac--- first pair of accessory glands.

al--- outer coat of longitudinal muscles of er.

an---anus.

as---posterior complex group of salivary tubules.

b---- dilated portion of the stomach.

B----orifice cardiaque.

BC---anse duodenale.

bs--- anterior group of salivary tubules.

c---- cardiac end of the stomach.

ce--- crop.

cl--- clypeus.

cm---muscles attached to the dorsal side of the pharyngeal pump.

cs----chitinous sheath enclosing the penis.

d---- recurrent intestine-like portion of the stomach.

DE--- estomac.

ds--- small, secondary salivary gland situated in the cranial cavity behind the eye.

e---- oesophagus.

E---- pylore.

EF---intestin.

em--- membrane surrounding the tube d from p to h.

ep--- epipharynx.

er--- muscular bulb at upper end of ejaculatory duct.

ej--- ejaculatory duct.

es--- accessory salivary glands.

gh--- genital hooks.

gs--- duct connecting the secondary salivary gland ds with as.

h---- place where the tube d emerges from a with the Malpighian tubes.

hd--- head.

hs--- duct connecting the gland bs with as.

hy--- hypopharynx.

i----ileum.

ie---knot of convolutions formed by the ileum just before it empties into the rectum.

il---inner coat of er.

is---main salivary ducts.

km---"salivary injector."

ll---middle wall of er, composed of circular muscles.

lm---muscles of the "injector."

ls---anterior division of the complex gland as.

m----Malpighian tubes.

mc---chitinous plate serving as the place of attachment for the muscles of the penis.

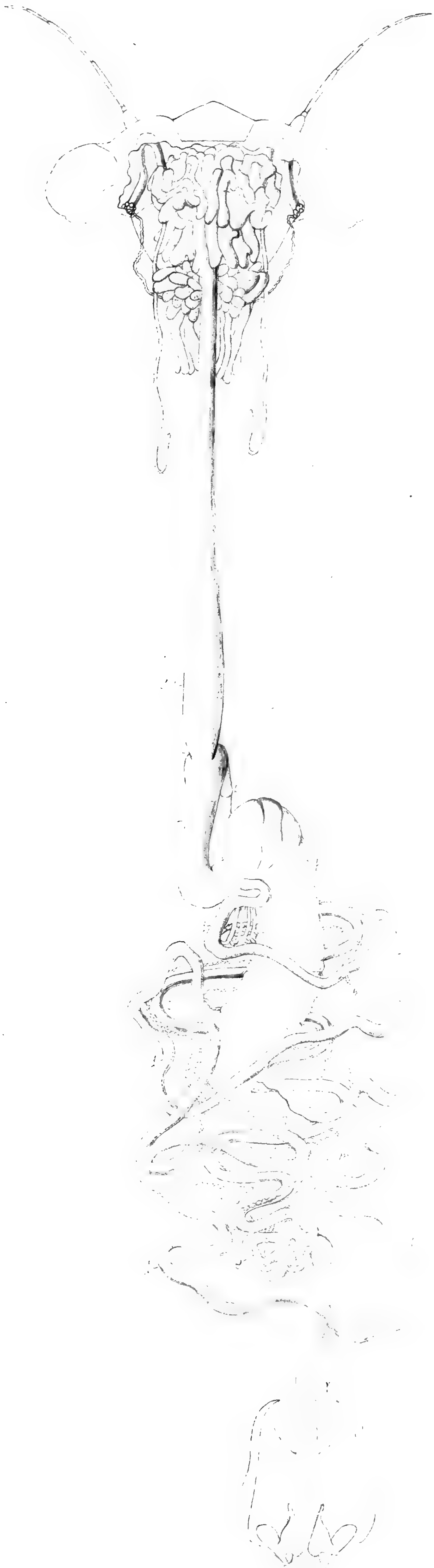
md---ducts of the Malpighian tubes.

ms---middle set of tubules in the complex gland as.

n----second pair of accessory glands.

ns---posterior set of tubules in as.

om---orifice of the Malpighian tubes.
p-----pylurus.
ph---pharynx.
pp---pharyngeal pump.
PS, PR---vaisseaux hepatiques.
r-----rectum.
sm---muscles by which the stomach is suspended from oesophagus.
sv---seminal vesicle.
t-----testes.
tm---muscles anchoring the pharyngeal pump to the tentorium.
um and un---the Malpighian tubes which unite to form the common duct vm.
us---ultimate abdominal segment.
v-----vas deferens.
vm---common duct formed by the union of the Malpighian tubes um and un.

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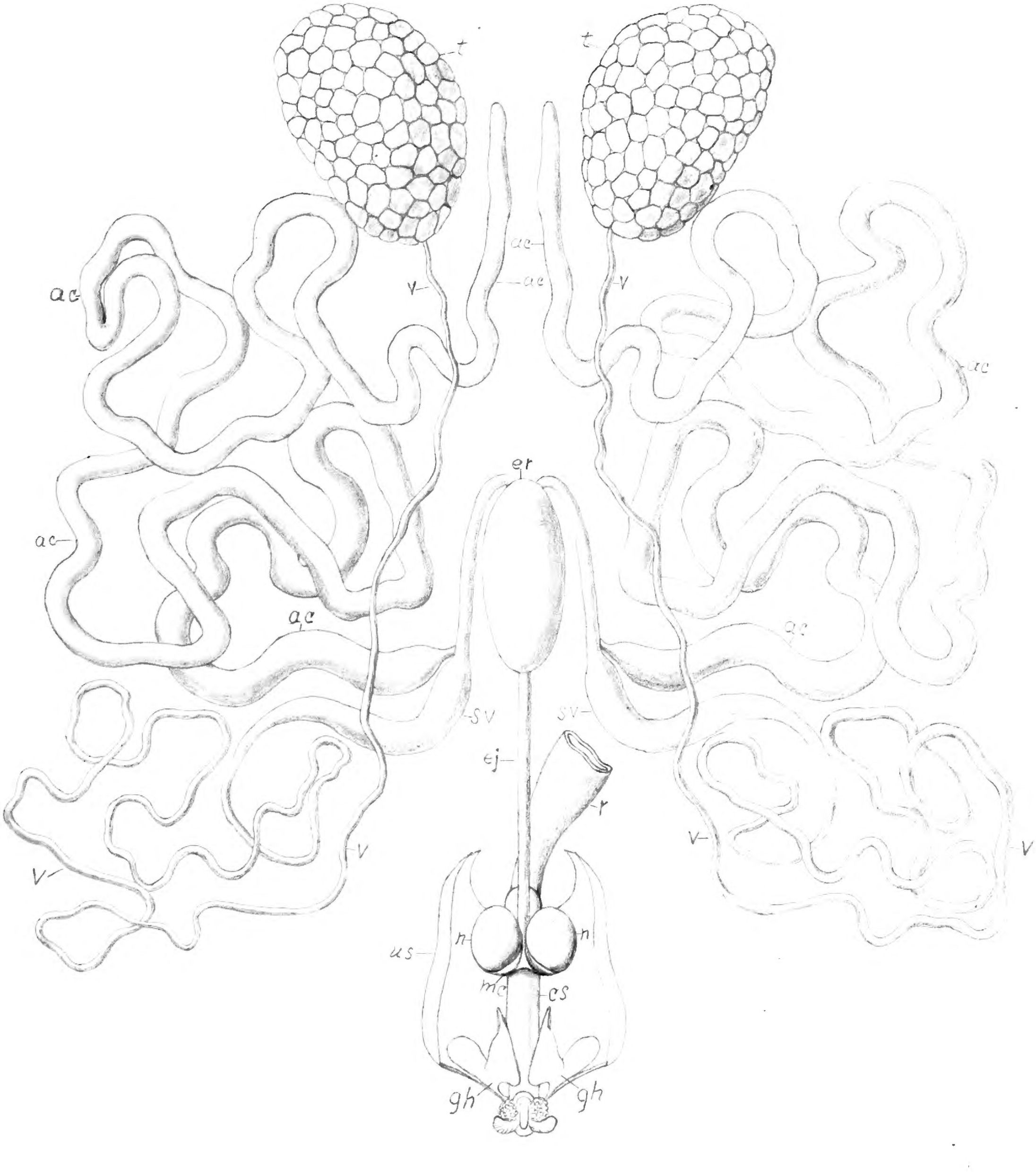
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