VII—On the Internal Anatomy of the Larva of the Rat-Flea, *Nosopsyllus fasciatus* (Bosc)

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Contents

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I—Introduction

Although a very extensive literature, covering a period of many years, exists on the anatomy of the flea larva, most of it deals only with the external anatomy. Previous studies on the internal anatomy are few and scarcely sufficiently detailed to throw any light on the affinities of the order Siphonaptera. It was therefore considered desirable that the whole question of the internal anatomy of the flea larva should be revised in the light of our existing knowledge of insect morphology. Consequently, a detailed study of the internal anatomy of the larva of *Nosopsyllus fasciatus* (Bosc) was undertaken to elucidate the various anomalies in the internal anatomy of the flea larva, and, if possible, to throw some light on the systematic position of the group. In order to complete the account of certain systems, a partial account of the prepupal stage has been included so as to facilitate the proper understanding of the pupa, an account of which is to follow.

The figures illustrating this paper are all camera-lucida drawings and have been finished by me in ink. In my description I have used the same terminology as is used by Snodgrass (1935) in his recent book. The specific names of fleas given in this account are corrected up to date by following the nomenclature adopted by Jordan (1933) and Wagner (1930).

My warmest thanks are due to Professor D. Keilin for the suggestion of the problem, for guidance, and for the friendly advice and criticism which he has from time to time given to me during the prosecution of the work. It is a pleasure indeed to record my gratitude to Dr. A. D. Imms, Dr. W. H. Thorpe, and Dr. V. B. Wigglesworth for timely help which they gave me unsparingly. I am grateful to Miss M. Rothschild for allowing me the use of her card catalogue of fleas. Dr. P. Tate has kindly read through and revised my manuscript and made several valuable suggestions, for which I am indebted to him. Finally I must not forget to acknowledge my indebtedness to Professor G. H. F. Nuttall, Mr. C. Warburton, Miss Mary Vincent, Dr. Ann Bishop, and Mr. A. W. R. Roberts for occasional help.

II—Material and Technique

An extremely flourishing culture of *N. fasciatus* was maintained in the laboratory by adopting methods described by Leeson (1932, p. 25). The original supply of this species was given to me by Professor P. A. Buxton of the London School of Hygiene and Tropical Medicine, to whom I acknowledge my indebtedness.

For the examination of the chitinous parts and the gross internal anatomy, the larvae were mounted in gum arabic (De Faure's fluid). Living material was examined in normal salt solution. For the study of the musculature, preparations mounted in Gilson's euparal proved very useful. Staining of chitinous parts with Ziehl's carbol-fuchsin gave very satisfactory results. Permanent preparations of

minute parts were made by following methods described by MINCHIN (1915, p. 444). These were stained either in Grenacher's borax-carmine or Mayer's haemalum. In making dissections of minute parts the preparations were lightly stained with Mayer's haemalum ; in this way the finer organs could be followed along their course, as some structures stain deeply while fat bodies do not stain.

The technique developed for sectioning was such as to give good histological detail. Considerable difficulty was experienced in the suitable fixing of the material. The earlier results were often far from satisfactory, in spite of great variation in fixing methods. Material intended for sectioning was fixed either in freshly prepared fixative of Duboscq-Brasil (alcoholic Bouin) or in freshly prepared Carnoy and Lebrun's fluid. The fixative penetrated with great difficulty into the objects. The entire larva was thrown into the fixative heated to 40° C., and, after a short time, it was cut into two pieces in the fixative. Then the object still in the fixative was transferred to a small tube which was placed in a bottle from which the air was exhausted by using the water vacuum pump for about two minutes. In the case of alcoholic Bouin, the tissue was left in it for about twenty-four hours at a temperature of 37° C. In this way fairly good results were obtained.

For staining I have used Mayer's haemalum, Delafield's haematoxylin, and Heidenhain's iron haematoxylin. These were counterstained mostly with eosin and in a few cases with orange G.

III—HISTORICAL

Amongst the earliest workers to whom we owe our knowledge of the external anatomy and habits of the flea larva, the names of LEEWENHOECK (1683), CESTONE (1699), VALLISNERI (1733), RÖSEL VON ROSENHOF (1749), DE GEER (1778), DEFRANCE (1824), WESTWOOD (1848), BONNET (1867), BLANCHARD (1868), and TASCHENBERG (1880) deserve to be mentioned. LABOULBÈNE (1872) gave a brief illustrated account of the external and internal anatomy of the larva of *Ctenocephalides felis* (Bouché) and described and figured its mouth parts and tracheal system. KÜNCKEL (1873) published a historical review of work done on the flea larva up to his time and described the larvae of *C. felis* and *N. fasciatus*. PACKARD (1894) described the structure of both newly hatched and fully grown larvae of *Ctenocephalides canis* (Curtis).

HEYMONS (1899, p. 231) gives a short account of the transformation of the mouth-parts of *Ceratophyllus gallinae* (Schrank), and his researches have greatly helped to elucidate the homologies of the mouth-parts of the adult flea. LASS (1905, p. 82) incidentally described the internal anatomy of the larva of *C. canis*, although he mainly devoted his attention to the anatomical and histological structure and the post-embryonic development of the female reproductive organs.

HARMS (1912) describes in detail the digestive system of the larva of *C. canis*. To OUDEMANS (1913) we owe an exhaustive account of the external anatomy of the larvae of *Hystrichopsylla talpae* (Curtis) and *Spalacopsylla bisbidentatus* (Kolenati). He

describes only nine pairs of spiracles, and it appears that he examined only the first- and second-stage larvae in which the second thoracic spiracles are closed. PATTON and CRAGG (1913, p. 459) give a short illustrated account of the internal anatomy of the larva of *C. felis*. BACOT and RIDEWOOD (1914) dealt with the external anatomy of the larvae of a number of species and were of the opinion that the structure of the mandible is of value in identifying different species and genera. MINCHIN (1915, p. 451) described the salivary glands of the larva of *N. fasciatus*. STRINDBERG (1917, p. 258) gives a brief account of the embryology of *Archaeopsylla erinacei* (Bouché) and is of the opinion that Siphonaptera, on the basis of his embryological studies, cannot be considered as having close relationship with Diptera.

For the most of what is known to us at present about the internal anatomy of flea larva, we are indebted to the work of PERFILJEW (1926). In his work he has acquainted us with the mouth parts, the digestive system, the salivary glands, the nervous system, and the reproductive organs of the larva of *Leptopsylla pectiniceps* (Wagner).*

HENDERSON (1928, p. 115) describes the external characters of the larva of *Xenopsylla cheopis* (Rothschild). WEBSTER (1929, p. 90) has found that the larvae of *X. cheopis*, *X. astia* (Rothschild), and *X. brasiliensis* (Baker) are indistinguishable on anatomical grounds. To SIKES (1930) we owe a correct and detailed account of the external anatomy of the larva of *Orchopeas wickhami* (Baker) and a short comparative account of the larvae of *N. fasciatus*, *X. cheopis*, and *X. astia*. HICKS (1930, p. 575) gives an account of the early stages of *Tunga penetrans* (Linnaeus).

WAGNER (1935) has recently described the changes in the mesenteron and the regeneration of the epithelium in *Pulex irritans* Linnaeus during the metamorphosis.

IV—THE HEAD

The head of the flea larva is of the prognathous type and is highly specialized. It is of yellowish-brown colour, and has a thicker chitinous covering than the rest of the body. It is elongate-oval in outline and its posterior margin is sharply truncated. The various sclerites of the cranium are completely fused together to form a compact head capsule, and there are no distinctly defined epicranial plates, frons, or clypeus. The labrum (figs. 10, 12, 58, *lr.*) is distinct and articulates with the cranium by a flexible membrane. The head capsule is strongly convex on the dorsal side and flattened on the ventral side. There are two rows of bristles on the head. The anterior row lies behind the level of the antennae and contains six bristles (two dorsal, two lateral, and two ventral in position, the last pair being the longest). The posterior row, which is close to the posterior margin, contains eight bristles (four dorsal, two lateral, and two ventral in position, the last two being the smallest). The

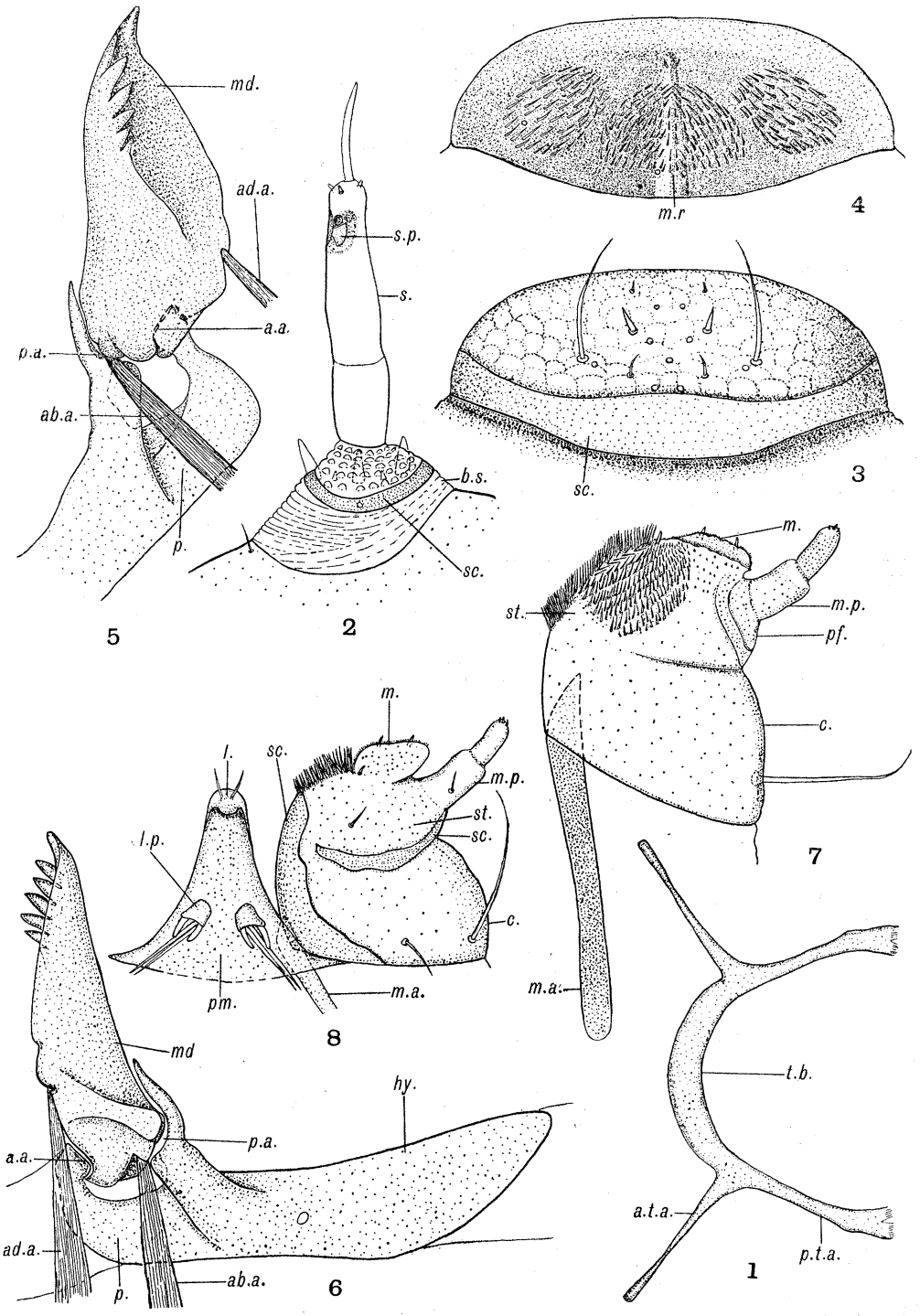
* I possess a reprint of PERFILJEW's paper in which the author himself has changed this specific name to *Leptopsylla pavlovskii* (Ioff) in his own handwriting; consequently it should be taken for granted that PERFILJEW described the larva of *Pectinoctenus pavlovskii* (Ioff), not that of *P. pectiniceps* (Wagner), but in my description I shall adhere to the printed name so as to avoid ambiguity.

head also bears three fine hairs around the base of each antenna (one posterior, one anterior, and one dorsal to the antenna). The " circular translucent areas " described by SIKES (1930, p. 247) are really *sensilla campaniformia* (fig. 14, *s.ca.*), which are sparsely scattered all over the head. On the ventral side there is a transverse area of weakened chitin behind the articulations of the maxillae and the prelabium with the cranium giving the appearance of a joint. There is also a narrow, longitudinal, ill-defined area of weakened chitin in the mid-ventral line from the base of the prelabium to the posterior margin of the head capsule.

The postoccipital ridge (fig. 11, *p.r.*) is well developed and it lies in the extreme posterior part of the cranium where it surrounds the occipital foramen dorsally and laterally. It gradually increases in size towards its lower ends where the posterior tentorial pits are situated. The extreme posterior position of the posterior tentorial pits, viz., near the margin of the occipital foramen, indicates that the longitudinal weakened area of the chitin in the mid-ventral line of the cranium referred to above is the postlabium and that the gula does not exist in the head capsule of the flea larva.

The subgenal area (fig. 6)—Immediately behind the points of articulation of the mandible and the maxilla of each side with the cranium there is a sclerite which I propose to call the subgenal area, though there is no subgenal suture defining it. This sclerite gradually becomes thinner on the dorsal side in front of the antenna of the side. Its thin dorsal extension in front of the antenna represents the epistomal ridge which (SNODGRASS, 1935, p. 111) defines the posterior limit of the clypeus. In the flea larva the latter is not well defined. The lower greater portion of the subgenal area, which runs behind the articulation of the maxilla with the cranium, is the hypostoma (*hy.*) and becomes thinner gradually along the antero-lateral side of the postlabium. Its upper portion—the pleurostoma (*p.*)—gives off two anteriorly directed processes enclosing a cup-shaped cavity. These two processes provide points of articulation for the mandible.

The tentorium (fig. 1) consists of the anterior and the posterior tentorial arms and a tentorial bridge (*t.b.*). Each anterior tentorial arm (*a.t.a.*) tapers gradually towards the anterior side into a thin cord of chitin and then again becomes thick and strongly sclerotized near the anterior tentorial pit. The latter is located midway between the anterior margin of the mound of the antenna and the point of articulation of the mandible of the side. The posterior tentorial arms (*p.t.a.*) are more strongly developed than the anterior ones. They take their origin from the posterior tentorial pits at the ventral ends of the postoccipital ridge. The tentorial bridge is a highly sclerotized transverse bar and lies in a notch in the antero-dorsal surface of the suboesophageal ganglion (figs. 9, 16, *t.b.*). No previous worker has described the presence of the real tentorium in the flea larva, and SIKES (1930, p. 249) has wrongly called the maxillary apodeme the tentorium.



FIGS. 1–8.—Fig. 1—The tentorium. × 436. Fig. 2—The right antenna. × 393. Fig. 3—The labrum, dorsal view. × 475. Fig. 4—The labrum, ventral view. × 475. Fig. 5—The left mandible articulating with the pleurostoma, dorsal view. × 652. Fig. 6—The left mandible with the subgenal area, ventral view. × 679. Fig. 7—The right maxilla, dorsal view. × 410. Fig. 8—The left maxilla and the prelabium, ventral view. × 450.

V—The Head Appendages

The antenna (fig. 2) consists of an elongated shaft (*s.*) placed on a dome-shaped membranous mound (*b.s.*). The upper side in the middle of the mound is strengthened by a semicircular sclerite (*sc.*), and on its lower side there are six chitinous sensory cones (*sensilla basiconica*) arranged in a semicircular row; three of them are large and alternate with the three smaller ones. The shaft is a long, narrow cylinder showing a pseudo-joint, which is absent in the antennae of the first- and second-stage larvae, and thus appears to be composed of two indistinctly separated segments. The distal half of the second false segment gradually narrows towards its free end, and the latter is surrounded by four small sensory cones with a seta projecting from its centre. There is an elongated pit on the posterior side of the distal segment of the shaft. It leads into a pear-shaped pit. There is another small pear-shaped pit close to it. These are the sensory pits or sensoria (*s.p.*). The proximal dome-shaped mound may be considered as the basal segment of the antenna, as the muscles of the antenna are not attached to the shaft, but to the base of the mound (fig. 58), which thus corresponds to the scape of other insects.

According to Laboulbène (1872, p. 268), Künckel (1873, p. 137), Packard (1894, p. 318), and Lass (1905, p. 83), the antenna is three-segmented, and they considered the terminal seta as the third segment comparable to the style of Diptera. Subsequent authors have always considered the antenna as single-segmented, ignoring, of course, the basal dome-shaped structure. In my opinion the antenna is distinctly two-segmented without taking into consideration the pseudo-joint of the shaft.

Morphologically the mouth-parts are of the biting and the grasping type, and they consist of a labrum, a pair of mandibles, a pair of maxillae, and a completely fused labium. A peculiar feature is a close association of the maxillae, the labium, and the hypopharynx to form an under-lip complex, in which the prementum and the hypopharynx are combined to form the salivarium.

The labrum (figs. 3, 4, 10, 12, 58, *lr.*) is sub-semicircular in outline and hangs transversely in front of the mouth and forms the anterior wall of the intergnathal preoral cavity. Its proximal margin is strengthened by a crescentic sclerite (fig. 3, *sc.*). On its upper surface it has a long hair and a short hair on each side of the median line shortly in front of the sclerite, a pair of spine-like hairs in front of them, and a pair of spinules near the free margin. There are also about four pairs of *sensilla campaniformia.* The lower surface has wrongly been designated the epipharynx (Sikes, 1930, p. 247). The true epipharynx of insects, as pointed out by Snodgrass (1935, p. 113), is a median lobe of the epipharyngeal wall of the labrum, which is absent in the flea larva. The proximal greater half of its epipharyngeal surface is provided with a median ridge (fig. 4, *m.r.*), which is continuous with that of the buccal cavity. The front end of this median ridge is provided with a pair of sensory spinules. The sensory hairs belonging to the central group are arranged on and around the median ridge. They are directed downwards and forwards. The sensory hairs belonging to the lateral groups are arranged on the

proximal sloping sides of the epipharyngeal surface. They are longer than those of the central group and are directed inwards and downwards.

The mandibles (figs. 5, 6, *md.*)—Each mandible is roughly triangular in shape with its apex, which is directed forwards, slightly bent inwards to form the terminal tooth. Its length varies from 0·075 to 0·086 mm. The outer margin is considerably thickened and the inner margin is extremely thin. The base of the triangle provides two points of articulation with the head capsule. The external side arches over the dorsal surface, so as to enclose a depression on the inner side. The anterior lessser half of this arched portion of the outer margin is provided with six teeth which gradually decrease in size from the anterior to the posterior end. The most common number of teeth of the mandible, according to my observation, is seven including the terminal one, although a very few specimens have only six teeth. BACOT and RIDEWOOD (1914, p. 166) give eight as the usual number for this species. The shape of the mandible depends upon the position in which it is examined. Fig. 5 represents the normal position of the mandible when at rest. The teeth are always directed mesially upwards. Usually one comes across a condition such as is shown in fig. 6 where the teeth appear to be attached to the external side of the mandible, which is brought about by the rotation of the mandible through an angle of 90°. BACOT and RIDEWOOD's drawings of the mandibles and those of PERFILJEW (1926, p. 104) and other previous workers are sketched in this abnormal position.

Each mandible, as in other pterygote insects, articulates with the pleurostomal margin of the cranium by well-developed anterior and posterior articulations. The anterior articulation (*a.a.*) is formed by a condyle on the upper process of the pleurostoma (*p.*) being received into a socket on the base of the mandible. The posterior articulation (*p.a.*) consists of a socket on the lower process of the pleurostoma receiving a condyle from the base of the mandible. The abductor apodeme (*ab.a.*) is inserted on the external basal angle of the mandible very close to the posterior articulation. The adductor apodeme (*ad.a.*) is inserted near the inner basal angle in a notch.

The maxillae (figs. 7, 8)—Each maxilla consists of three completely differentiated parts and a palp. The cardo (*c.*) is broadly articulated with the head capsule and bears two bristles on its lower surface. It is separated from the stipes (*st.*) by a groove on the external side which extends to its dorsal side. The posterior margin of the stipes is strengthened on the ventral side by a transverse sclerite (*sc.*), which runs anteriorly on the dorsal side to differentiate a small lobe-like structure, the palpifer (*pf.*), which is not clearly demarcated on the ventral side. The stipes has a single bristle on its ventral surface. Both the cardo and the stipes are strengthened by a thick sclerite (*sc.*) on their inner border, from which a lateral process runs along the ventral half of the posterior margin of the cardo. From SIKES's description and diagram (1930, p. 254) of the larva of this species, it appears that she has mistaken the cardo for the stipes and called the latter the palpifer. The proximal segment of the palp is broader than the distal one, and bears a single bristle. The distal segment is narrow and short, and has five short sensory pegs arranged in a circular

row near its apex. The mala (*m.*) is represented by an oval plate bearing two sensory pegs on the ventral surface near the posterior margin, and two on the dorsal surface near the anterior margin.

I cannot agree with SIKES (1930, p. 248) in regarding the oval plate as the galea, because there is no trace of lacinia and the part she called lacinia is the part of the stipes covered with hairs. There is no lobe on the inner and dorsal sides of the stipes as she considers. The hairy surface of the stipes extends almost to its base. It is difficult to imagine that the lacinia may extend right up to the base of the stipes and that the galea may be only confined to its anterior terminal end. I agree with OUDEMANS (1913, p. 246) and HEYMONS (1899, p. 231) in regarding this lobe-like structure as the mala, although, unfortunately, the complete absence of musculature of both the galea and lacinia makes it impossible to come to any definite conclusion. The stipes is covered on the upper and inner surfaces with fine hairs of different lengths which are arranged in longitudinal rows. These are directed forwards and inwards. These hairs were wrongly considered by KÜNCKEL (1873, p. 138) as " tranchant dentelé ".

In cross-section the maxilla (fig. 13, *mx.*) is roughly a four-sided structure. The outer side is convex, the ventral side is straight, and the inner side, which is also straight, is strengthened by a sclerite gradually increasing in breadth towards the posterior end. The dorsal side is concave with its concavity becoming deeper and broader from the anterior to the posterior end.

A strongly developed strand-like apodeme (figs. 7, 8, *m.a.*) is attached to the inner surface of the proximal portion of the cardo. Proximally it is hollow (fig. 14, *m.a.*), showing that it is formed by an invagination. It gives support to the main muscles of the maxilla. PERFILJEW's statement (1926, p. 106), " Die Chitinstränge nehmen am Lobus internus ihren Anfang ", is based on the wrong interpretation of facts. It appears that he thought the internal sclerite of the cardo and stipes and the maxillary apodeme one continuous structure. HICKS (1930, p. 582) has wrongly called the maxillary apodeme the stipes.

The labium (figs. 8, 9) lies between the maxillae. On account of the position of the single-segmented labial palps (*l.p.*) and the position of the labial suture, it appears that the portion called the labium by SIKES (1930, p. 249) and others is really the prelabium and that the postlabium, as mentioned before, has become completely fused with the ventral wall of the cranium. The cone-shaped portion in front of the labial palps is the true ligula (*l.*) and the portion behind them is the prementum (*pm.*). The single-segmented palp is nearly as broad as long and bears two blunt lobe-like sensory processes, which are lateral in position, and two long sensory bristles which are anterior and posterior in position. The ligula tapers gradually towards its anterior end and is provided with two sensory hairs near its distal end, which is bent downwards.

The sensory hairs of the ligula and the labial palps are supplied by bundles of sensory fibres coming from a group of sensory cells within the prementum. Thus the labial palps, which were considered by LABOULBÈNE (1872, pp. 268, 269),

BONNET (1867), and LASS (1905, p. 82) to be organs of locomotion, are purely sensory in function and have little to do with locomotion.

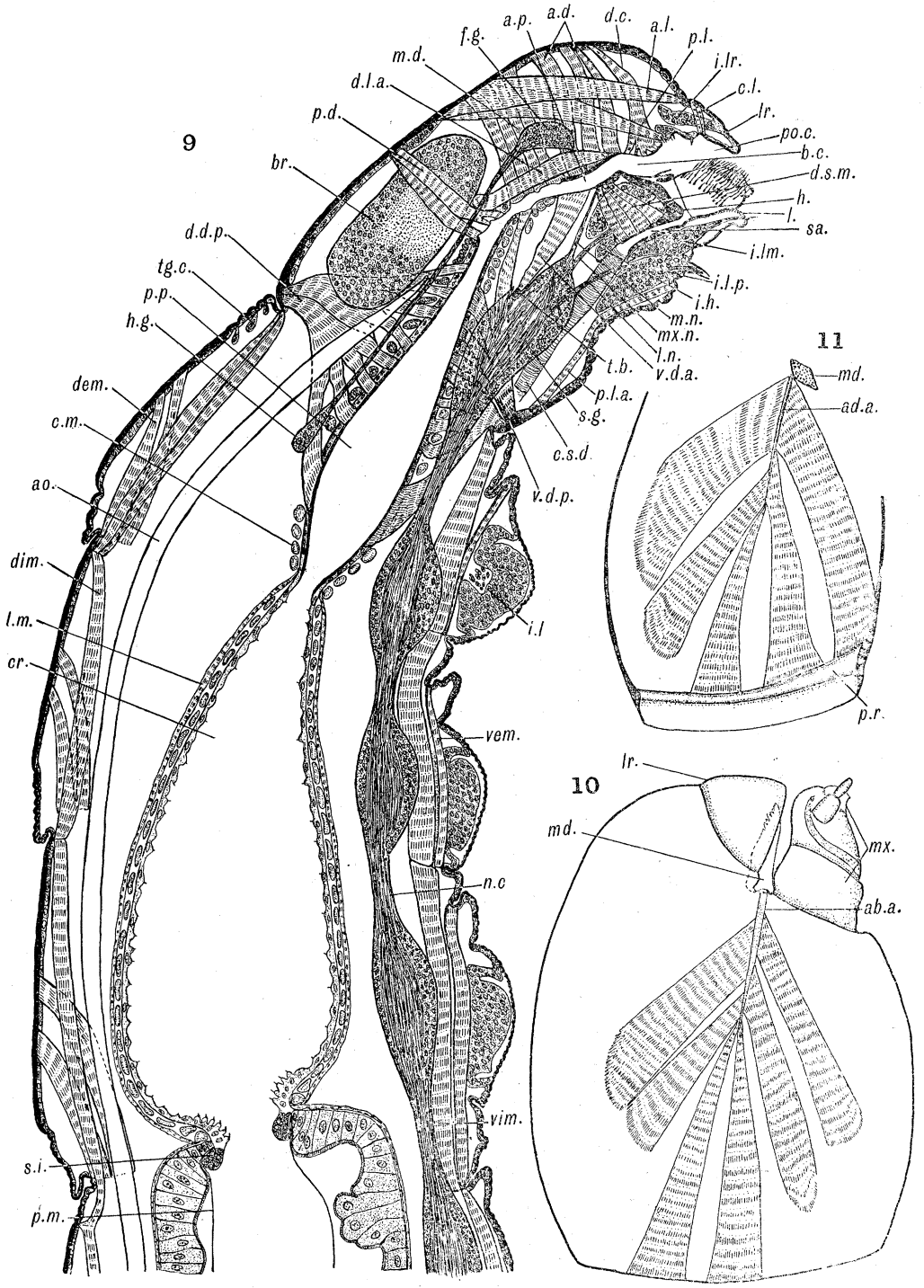
The hypopharynx (figs. 9, 18, *h.*) is a small cone-shaped structure which is located between the mouth and the prementum in the preoral cavity, and forms the dorsal wall of the salivarium (*sa.*). The external opening of the salivarium is strengthened on the ventral and lateral sides by a crescent-shaped chitinous thickening whose upper free ends are still more thickened to form lobe-like structures on either side of the hypopharynx (fig. 18, *h.*). These have been wrongly designated by SIKES (1930, p. 249) the superlinguae, which are absent in the flea larva. PERFILJEW (1926, pp. 105, 106) has wrongly described the ligula as the hypopharynx. HEYMONS (1899, p. 231) emphatically denies the presence of a hypopharynx in the larva of *C. gallinae.*

Function of the mouth parts—According to BACOT and RIDEWOOD (1914, p. 165), the mandibles are adapted for biting and nibbling. HEYMONS (1899, p. 231) considers the mouth parts to be of the chewing type but not of the biting type. As most of the teeth on the mandible are directed dorsal-wards and forwards, and cannot meet those on the opposite mandible, owing to the greater portion of the mandible lying between the teeth and its inner edge, it is difficult to imagine how they can crush the food. For this reason alone I cannot agree with SIKES (1930, p. 248) that the mandibles can break up the food into " small palatable particles ". I agree with PERFILJEW (1926, p. 105), who is of the opinion that they play the role of rasping and scrubbing the food, and then pushing it into the mouth. In these actions they are assisted by the hairs on the inner side of the maxillae and the labrum. I agree with SIKES in that the mandibles assist in locomotion by grasping with the terminal teeth the surface upon which the larva crawls.

VI—THE MUSCULATURE OF THE HEAD APPENDAGES

A peculiar feature of the head of the flea larva is that certain muscles of the cephalic appendages, which in most other insects usually take their origin on the tentorium, arise in the flea larva, owing to the poor development of the tentorium, either on the postoccipital ridge or on the lateral arms of the sclerite of the anterior pharynx.

The antennary muscles (figs. 14, 15, 58)—Each antenna is moved by three muscles. Two of them have their origins on the lateral arm of the sclerite of the anterior pharynx (*a.p.*). One of them is inserted in the middle of the lower margin of the basal segment and moves the antenna downwards. It is therefore called the depressor of the antenna (*d.a.*). The other is inserted in the middle of its anterior margin and moves the antenna forwards. This is named the flexor of the antenna (*f.a.*). The third muscle, which takes its origin from the anterior arm of the tentorium close to the tentorial bridge and has its insertion in the middle of its posterior margin, moves the antenna backwards and therefore it is called the levator of the antenna (*l.a.*).



FIGS. 9–11.—Fig. 9—Lateral sagittal section of the head and thorax of a third-stage larva. × 170. Fig. 10—Abductor muscles of the right mandible seen through the wall of the head capsule. × 234. Fig. 11—Inner view of the posterior portion of the left side of the head capsule showing adductor muscles of the left mandible. × 278.

The musculature of the labrum consists of muscles located within the labrum itself, and cranial muscles inserted on its base. The latter run between the dorsal dilators of the anterior pharynx.

The compressors of the labrum (fig. 9, *c.l.*) are two pairs of muscles running from either side of the median line immediately in front of the sclerite of the labrum, to be inserted on either side of the anterior end of the median ridge on the epipharyngeal wall.

The anterior labral muscles (figs. 9, 13, 14, 15, *a.l.*) are a pair of long muscles which arise from the middle of the roof of the cranium a little in front of the brain, in the region representing the frons, and are inserted close to each side of the middle of the posterior upper margin of the labrum. Their contraction raises the labrum as there is a thin articulating membrane separating the labrum from the cranium.

The posterior labral muscles (figs. 9, 13, 14, 15, *p.l.*) consist of a pair of muscles which take their origin from the roof of the cranium external to the origins of the anterior labral muscles and run downwards and forwards to the middle of the posterior margin of the epipharyngeal wall where it passes into the roof of the buccal cavity. Their contraction brings about the lowering of the labrum. The opposing action of these muscles to that of the anterior labral muscles is due to their more downward course and lack of any flexible articulating membrane behind the posterior margin of the epipharyngeal wall. It is probably these muscles which have wrongly been called the *musculus protractor cavitatis oris* by HARMS (1912, p. 184).

The musculature of the mandible has been wrongly described by SIKES (1930, p. 248), and it appears that she noticed only some of the fibres of the complex musculature of the mandible. Both the abductor and the adductor muscle fibres spread out posteriorly like a fan and are attached anteriorly to chitinous apodemes which are broad and dorso-ventrally compressed strands of the chitin.

The abductor muscles of the mandible (figs. 10, 14, 15, 16, *ab.*) form a group of six distinct fibres which are arranged in an upper, a posterior, and a lower set of fibres. The two fibres of the upper set take their origin from the dorso-lateral portion of the roof of the posterior part of the cranium. The posterior set has two fibres which are the longest, and which take their origin from the lateral portion of the post-occipital ridge. The remaining two fibres belonging to the lower set take their origin from the ventro-lateral portion of the cranium.

The adductor muscles of the mandible (figs. 11, 14, 15, 16, *ad.*), like the abductor muscles, are arranged into three sets, but of five distinct fibres; the lower set has only a single powerful fibre, representing two fused fibres, which takes its origin from the lateral and the hinder portions of the floor of the cranium near the posterior tentorial pit.

The musculature of the maxilla (figs. 12, 13, 14, 15, 16) is highly specialized, and it is difficult to compare it with that of any other insect and to interpret the arrangement in terms of the general scheme of musculature of a typical maxilla.

The abductor muscle of the maxilla (*ab.m.*) is an unpaired muscle which takes its origin from the lateral portion of the postoccipital ridge between the origins of the two posterior fibres of the abductor muscles of the mandible, and it runs downwards

and forwards to be inserted on the dorsal outer angle of the cardo. This muscle probably corresponds to the anterior dorsal muscle of the maxilla (SNODGRASS, 1935, p. 145).

The adductor muscles of the maxilla are three in number and are attached to a strongly developed maxillary apodeme (*m.a.*). A lower muscle (*l.ad.*) takes its origin in front of the origin of the posterior tentorial arm, and runs slightly upwards and forwards to be inserted close to the origin of the maxillary apodeme. The medial muscle (*m.ad.*) arises near the origin of the posterior tentorial arm and has its insertion on the free end of the maxillary apodeme. The upper muscle (*u.ad.*) starts from the lateral arm of the sclerite of the anterior pharynx, and meets the free end of the

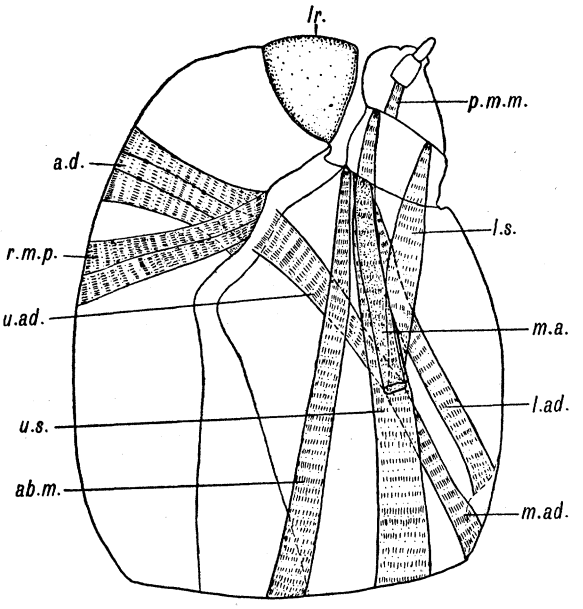


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FIG. 12—Side view of the head showing the maxillary muscles and some of the pharyngeal muscles. × 234.

maxillary apodeme. This last muscle from its position appears an exclusively ventral dilator of the anterior pharynx, but its connexion with the maxillary apodeme suggests that it plays some part in the movement of the maxilla as well. According to SNODGRASS (1935, p. 142), this muscle in other insects takes its origin on the tentorium.

The upper muscle of the stipes (*u.s.*) is a long muscle which starts from the post-occipital ridge at the level of the origin of the ventral fibre of the adductor muscles of the mandible, and runs forwards to be inserted on the posterior upper lateral angle of the stipes. This muscle probably corresponds to the cranial flexor of the lacinia. As the lacinia is not a distinct structure in flea larva this muscle, which according to SNODGRASS has a great morphological significance and is highly developed in other insects, has acquired connexion with the stipes.

The lower muscle of the stipes (*l.s.*) is a spindle-shaped muscle, which arises from the free end of the maxillary apodeme and runs outwards and forwards to be inserted on the lower posterior angle of the stipes. This muscle probably corresponds to the adductor of the stipes (SNODGRASS, 1932, p. 476).

The palpal muscle (*p.m.m.*) is a small muscle which starts from the middle of the posterior external margin of the stipes and is inserted at the base of the proximal segment of the palp.

The posterior labial adductors (figs. 9, 14, 15, 16, *p.l.a.*)—The labium possesses only a single pair of strongly developed muscles. They start from the ventral ends of the postoccipital ridge near the origins of the posterior tentorial arms, and are inserted on the ventral posterior margin of the prementum.

VII—THE CEPHALIC MUSCULATURE OF THE STOMODAEUM

PERFILJEW (1926) is the only author who has paid any serious attention to the extrinsic musculature of the stomodaeum of the flea larva, but his observations, as will be shown hereafter, are defective in certain respects.

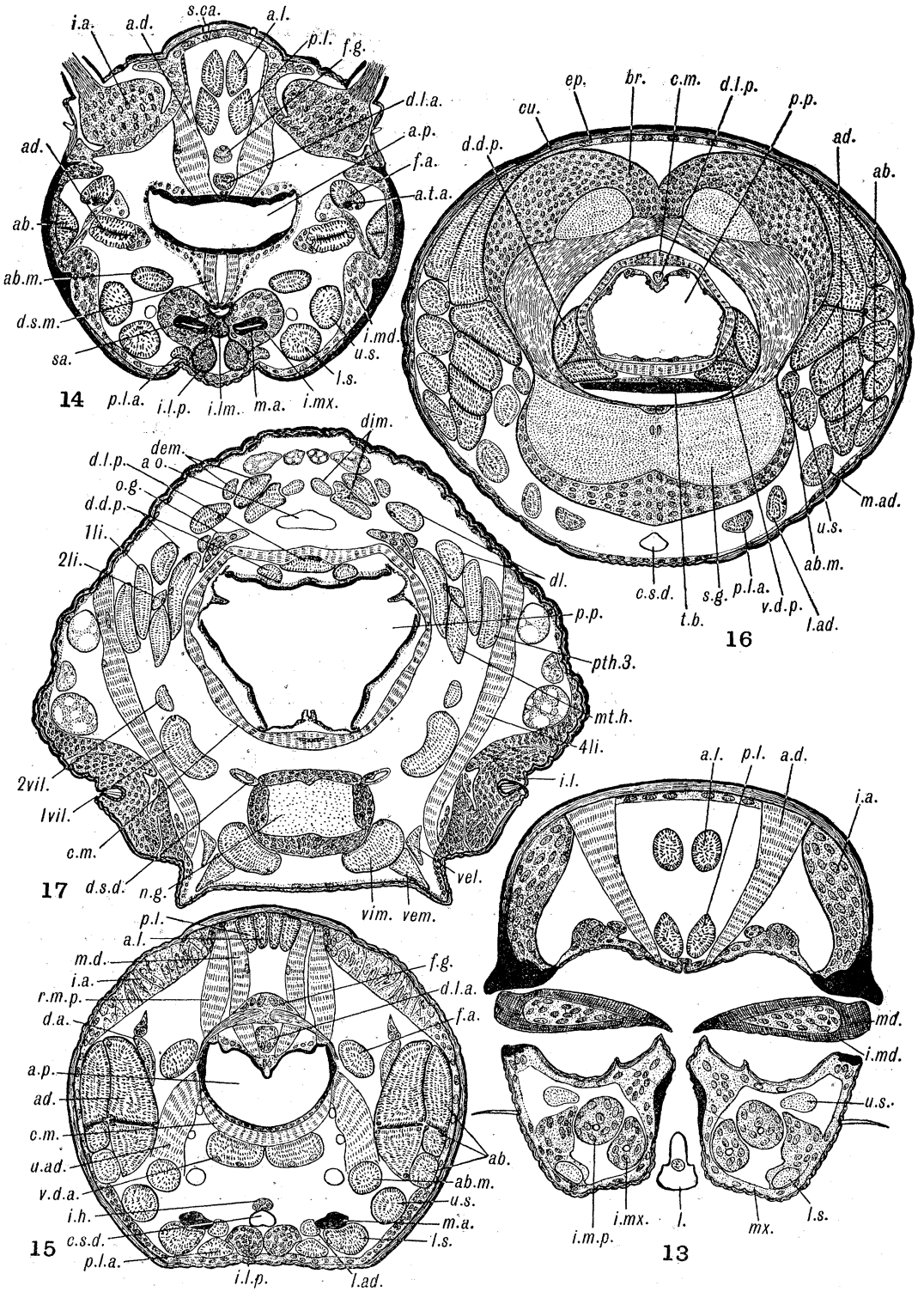
1—*Dilatores cibarii* (fig. 9, *d.c.*) are a pair of muscles each of which arises from the dorso-lateral region of the anterior part of the cranium corresponding to the clypeus and runs downwards and inwards to be inserted by three main roots near the middle of the roof of the buccal cavity (*b.c.*).

2—*The dorsal dilators of the anterior pharynx* are arranged in three paired sets and can conveniently be called the anterior, medial, and posterior dilators. The muscles of each side are inserted close to the median line of the dorsal wall of the anterior pharynx (figs. 14, 15, *a.p.*).

(*a*) *The anterior dorsal dilators of the anterior pharynx* (figs. 9, 12, 13, 14, *a.d.*) are three pairs of muscles which arise in a regular succession one behind the other from the cranium immediately behind the origins of the *dilatores cibarii*, and run similarly downwards and inwards to be inserted in the middle of the dorsal wall of the anterior portion of the anterior pharynx. The anteriormost pair of these is the *dilatores buccales* as it lies in front of the nerve connectives of the frontal ganglion (*f.g.*).

(*b*) *The medial dorsal dilators of the anterior pharynx* (figs. 9, 15, *m.d.*) are four pairs of muscles which arise from the dorso-lateral portions of the cranium immediately behind the anterior dorsal dilators. They run downwards and inwards to be inserted in the middle of the dorsal wall of the middle portion of the anterior pharynx.

(*c*) *The posterior dorsal dilators of the anterior pharynx* (fig. 9, *p.d.*) are two pairs of muscles which arise on either side of the middle line of the roof of the cranium immediately in front of the transverse commissures of the brain and thus lie in the notch formed by the two lobes of the brain. They run almost vertically downwards to be inserted on the dorsal wall of the junction of the anterior pharynx and the posterior pharynx. Each muscle of the anterior pair has two roots of insertions. PERFILJEW (1926, p. 109) calls these muscles the hinder oblique dilators (die hinteren schrägen Dilatatoren).



FIGS. 13–17.—Fig. 13—Transverse section through the head passing at the level of the cardo. × 416. Fig. 14—Transverse section through the head passing through the anterior region of the anterior pharynx. × 314. Fig. 15—Transverse section through the head passing through the middle region of the anterior pharynx. × 314. Fig. 16—Transverse section through the head passing through the middle of the brain. × 338. Fig. 17—Transverse section through the middle of the prothorax. × 333.

3—*The retractor muscles of the anterior pharynx* (figs. 12, 15, *r.m.p.*) are two pairs of muscles and the muscles of each side are placed closely to one another so as to form a sheet. The muscles of each side take their origin from the dorso-lateral wall of the cranium behind and external to the origins of the medial dorsal dilators of the anterior pharynx of that side. They run downwards and forwards to be inserted on the free end of the lateral crest of the anterior pharynx. These muscles have wrongly been considered as dilators of the anterior pharynx by PERFILJEW (1926, p. 109), and he calls them the anterior oblique dilators (die vorderen schrägen Dilatatoren). In my opinion, it is these muscles which correspond to the muscles named by SNODGRASS (1935, p. 285) the *retractores angulorum oris.*

4—*The ventral dilators of the anterior pharynx* (figs. 9, 15, *v.d.a.*) are two muscles which take their origin from the tentorial bridge (*t.b.*), and are inserted on the ventro-lateral walls of the anterior half of the anterior pharynx immediately behind its ventral transverse sclerite. It is probably these muscles which have wrongly been designated the *musculus retractor cavitatis oris* by HARMS (1912, p. 184). From PERFILJEW's diagram and description, it appears that he mistook these muscles for the direct continuation of the anterior fibres of the ventral dilators of the posterior pharynx, and he calls them the posterior ventral dilators (die hinteren ventralen Dilatatoren).

5—*The dorsal salivary muscles* (figs. 9, 14, *d.s.m.*) are two sheets of four closely placed fibres which arise from the ventral transverse sclerite of the anterior pharynx and run almost directly downwards to the middle of the dorsal wall of the salivarium (*sa.*). In other insects these muscles take their origin from the hypopharynx (SNODGRASS, 1935, p. 283). These muscles have wrongly been called, by PERFILJEW (1926, p. 109), the anterior ventral dilators of the pharynx (die vorderen ventralen Dilatatoren).

6—*The dilators of the posterior pharynx* (figs. 9, 16) are the most strongly developed muscles in the head capsule and are arranged in two sets, the dorsal and the ventral dilators of the posterior pharynx (*p.p.*). According to HARMS (1912, p. 187), the dorsal dilators are less strongly developed in the larva of *C. canis* than the ventral ones, which is not the case in the larva of *N. fasciatus.*

(*a*) *The ventral dilators of the posterior pharynx* (*v.d.p.*) are two powerful muscles each springing from the postocciput immediately behind the lower end of the post-occipital ridge of its side. They run inwards to be inserted on the ventro-lateral walls of the posterior pharynx. Each muscle consists of two large fans of fibres. The spreading fibres of the anterior fan run inwards and forwards and are inserted ventro-laterally on the anterior portion of the posterior pharynx, which lies in the head region. The spreading fibres of the posterior fan run inwards and backwards and are inserted ventro-laterally on the posterior portion of the posterior pharynx, most of which lies in the prothorax.

(*b*) *The dorsal dilators of the posterior pharynx* (*d.d.p.*) are muscles equally powerful as the ventral ones. They are two in number and each springs from the dorso-lateral

portion of the postocciput and runs inwards to be inserted on the dorso-lateral wall of the posterior pharynx. Each muscle consists of two large fans of fibres spreading on the dorso-lateral wall of the posterior pharynx in the same manner as in the ventral ones.

VIII—The Digestive System

The alimentary canal in the flea larva (fig. 35) is practically a straight tube with only two loops in the anterior intestine; as in other insects, it shows primary divisions into stomodaeum, mesenteron, and proctodaeum. The position and the shape of the various sections of the alimentary canal mentioned in the following account are as they are seen in a living larva in the normal extended condition. In a contracted larva they are liable to assume different positions in the body and in some regions different shapes. All the intrinsic muscles of the stomodaeum are striated as the extrinsic ones.

(A) The Stomodaeum

The stomodaeum (fig. 9) can roughly be divided into four regions : (*a*) the buccal cavity (*b.c.*), (*b*) the anterior pharynx (*a.p.*), (*c*) the posterior pharynx (*p.p.*), and (*d*) the crop (*cr.*), but in addition there is an intergnathal cavity which is called by Snodgrass (1935, p. 281) the preoral cavity (*po.c.*). It is bounded above by the ventrally concave epipharyngeal wall of the labrum (*lr.*), on the sides by the mandibles, and below by the labium and the maxillae. Harms (1912, p. 184) wrongly called this section the buccal cavity (die Mundhöhle). The hypopharynx (*h.*) lies within the preoral cavity and divides it into two regions. The region anterior to the hypopharynx is the cibarium and leads up into the mouth. The posterior narrow region, lying between the hypopharynx and the prementum, is called the salivarium (*sa.*) and into it opens the common salivary duct (*c.s.d.*).

(*a*) *The buccal cavity* (fig. 9, *b.c.*)—The mouth, which begins where the posterior margin of the epipharyngeal wall of the labrum terminates, opens into the buccal cavity which is a funnel-shaped structure. It is separated ventrally and laterally from the anterior pharynx by the latter's transverse sclerite and dorsally by the anterior insertion of the dorsal longitudinal muscle of the anterior pharynx (*d.l.a.*). Anteriorly the buccal cavity starts at the level of the anterior end of the hypopharynx and the posterior margin of the epipharyngeal wall of the labrum. Ventrally it is separated from the preoral cavity by a double wall ; the upper wall is the wall of the buccal cavity itself and the lower wall runs backwards to become fused with the inner proximal margins of the hypopharynx, prementum, and maxillae. Judging from its musculature and general appearance, it would seem that the greater part of this cavity belongs to the cibarium, and a considerable part of the true buccal cavity has been incorporated in the anterior pharynx.

The epithelial cells of the buccal cavity (fig. 19, *e.b.c.*) have distinct cell limits and the cells are longer than broad. Their inner surface is plain, whilst the outer surface is irregular on account of being swollen in places. The nuclei are more or

less oval with the chromatin condensed into big sparsely scattered granules of irregular size attached to the nuclear membrane. The cytoplasm is slightly basophil and has an alveolar appearance. The intima (*i.*) is extremely thin and smooth. The basement membrane and the intrinsic musculature are completely absent.

(*b*) *The anterior pharynx* (fig. 9, *a.p.*) extends from the buccal cavity to the anterior margins of the circumoesophageal connectives. At the beginning it is much compressed dorso-ventrally so that it is broader transversely than dorso-ventrally. It is crescentic in shape when seen in cross-sections (figs. 14, 15, *a.p.*) owing to the formation of the lateral crests. Further back this crescentic shape is intensified owing to the increase in its depth. The upper portions of the outer walls of these lateral crests are strengthened by longitudinal thickenings of the intima so as to form sclerotic plates. These two plates are connected together at the commencement of the anterior pharynx by a strong transverse thickening of the ventral intima of the anterior pharynx. This U-shaped sclerite (fig. 18, *sc.*) affords points of attachment for the pharyngeal muscles and certain other muscles of the head capsule. A similar sclerotic plate has been described by SNODGRASS (1935, p. 302) in the sucking pump of bees, and according to him its arms possibly " represent the oral arms of the hypopharyngeal suspensoria of more generalized insects ". In the roof of the anterior half of the anterior pharynx there is another sclerotic plate (figs. 9, 14, 15) formed by the thickening of the intima, which is fused with the lateral arms of the U-shaped sclerite. The lateral portions of the dorsal sclerite are slightly folded so as to form prominent ridges. These extend from the anterior to the posterior end. In the posterior half of the anterior pharynx there appears a dorsal median ridge which gradually increases in size from before backwards. The rest of the intima of the anterior pharynx is thin and smooth.

The epithelial cells of the anterior pharynx (fig. 20, *e.p.*) are more individualized than those of the buccal cavity. They are columnar in shape, viz., broader than long. The inner and outer surfaces are almost smooth. The nuclei are similar to those of the epithelial cells of the buccal cavity. The basement membrane is absent.

The intrinsic musculature is highly specialized. The longitudinal and circular muscles do not form complete layers but are represented by a few incomplete fibres. HARMS (1912, p. 185, pl. xiii, fig. 5) describes and figures in *C. canis* a transversely running muscle which according to him binds the upwardly bent sides of the anterior pharynx. This he considers to be the *musculus transversalis pharyngis* of other insects. I have failed to find a similar muscle in this larva. It appears to me that HARMS has mistaken the frontal ganglion connectives for a transverse muscle. The frontal ganglion connectives coming from the frontal ganglion look very much like a transverse muscle (*see* figs. 15, 18, *f.g.*).

The dorsal longitudinal muscle of the anterior pharynx (figs. 9, 14, 15, *d.l.a.*) is a powerful muscle connecting the anterior end of the anterior pharynx with the anterior end of the posterior pharynx. It lies in the dorsal trough of the anterior pharynx between the points of insertion of the dorsal dilators of both sides.

The circular muscles of the anterior pharynx (figs. 9, 15, *c.m.*) are four transversely running muscular arcs connecting the lower margins of the lateral arms of the U-shaped sclerite and thus surround this section ventrally behind the insertion of its ventral dilators (*v.d.a.*).

(*c*) *The posterior pharynx* (figs. 9, 18, *p.p.*) begins immediately behind the insertions of the posterior dorsal dilators of the anterior pharynx (*p.d.*). It differs from the anterior pharynx in having powerful complete circular muscles. It appears spindle-shaped when seen from the side and extends to the posterior end of the prothorax. It gradually enlarges for the first two-thirds of its length and then gradually decreases in diameter for the posterior third. In cross-section the lumen of its extreme anterior region is narrow and has the outline of a regular hexagon surrounded by complete circular muscles, but for its greater part the dorso-lateral and the ventral sides are shorter than the remaining three sides of the hexagon and they bend inwards so as to form internally directed longitudinal folds (*v.f.*, *l.f.*), thus making the lumen of the posterior pharynx sub-triradiate (fig. 17, *p.p.*). Thus the whole posterior pharynx is a spindle-shaped prism. The intima of the posterior pharynx is thicker than the general intima of the anterior pharynx. In the region where the three longitudinal folds are formed the intima is thick and smooth on the three large sides, but it is extremely thin and flexible on the short sides. This allows the dilation of the posterior pharynx at the time of feeding.

The epithelium (fig. 21, *e.l.*) is very much flattened and there are no cellular limits. Its internal and external surfaces are smooth and straight. The nuclei are larger than those of the epithelia of the preceding two sections. They are sparsely scattered and are flattened so that they appear elongate-oval in longitudinal sections. The basement membrane is absent. The intrinsic musculature consists of powerful circular muscles (fig. 18, *c.m.*). The fibres of these circular muscles give branches anteriorly and posteriorly in the middle of the dorsal side so as to constitute a dorsal longitudinal muscle (figs. 17, 18, *d.l.p.*). The absence of well-developed longitudinal musculature in both the sections of the pharynx is associated with the fact that the function of the longitudinal muscles is taken up by their dilators. HARMS (1912, p. 187) failed to find any longitudinal muscle in this section of the stomodaeum. The circular muscles at its junction with the crop are more closely placed and powerful.

Contrary to the usual practice of previous workers on the flea larva, I have designated this section of the stomodaeum the posterior pharynx, a name usually adopted for a similar section of the stomodaeum in Coleoptera and Orthoptera (SNODGRASS, 1935, p. 285). Owing to an abundant supply of the cranial dilators to this section of the stomodaeum, it is a mistake to call it the oesophagus, which name, as pointed out by SNODGRASS (1935, p. 352), is confined to " the narrow part of the stomodaeum following the pharynx that is not differentiated for purposes other than that of food conduction ". There is no section of the stomodaeum of the flea larva which could be called the oesophagus in this sense. On account of the presence of most highly developed musculature, both intrinsic and extrinsic, this section

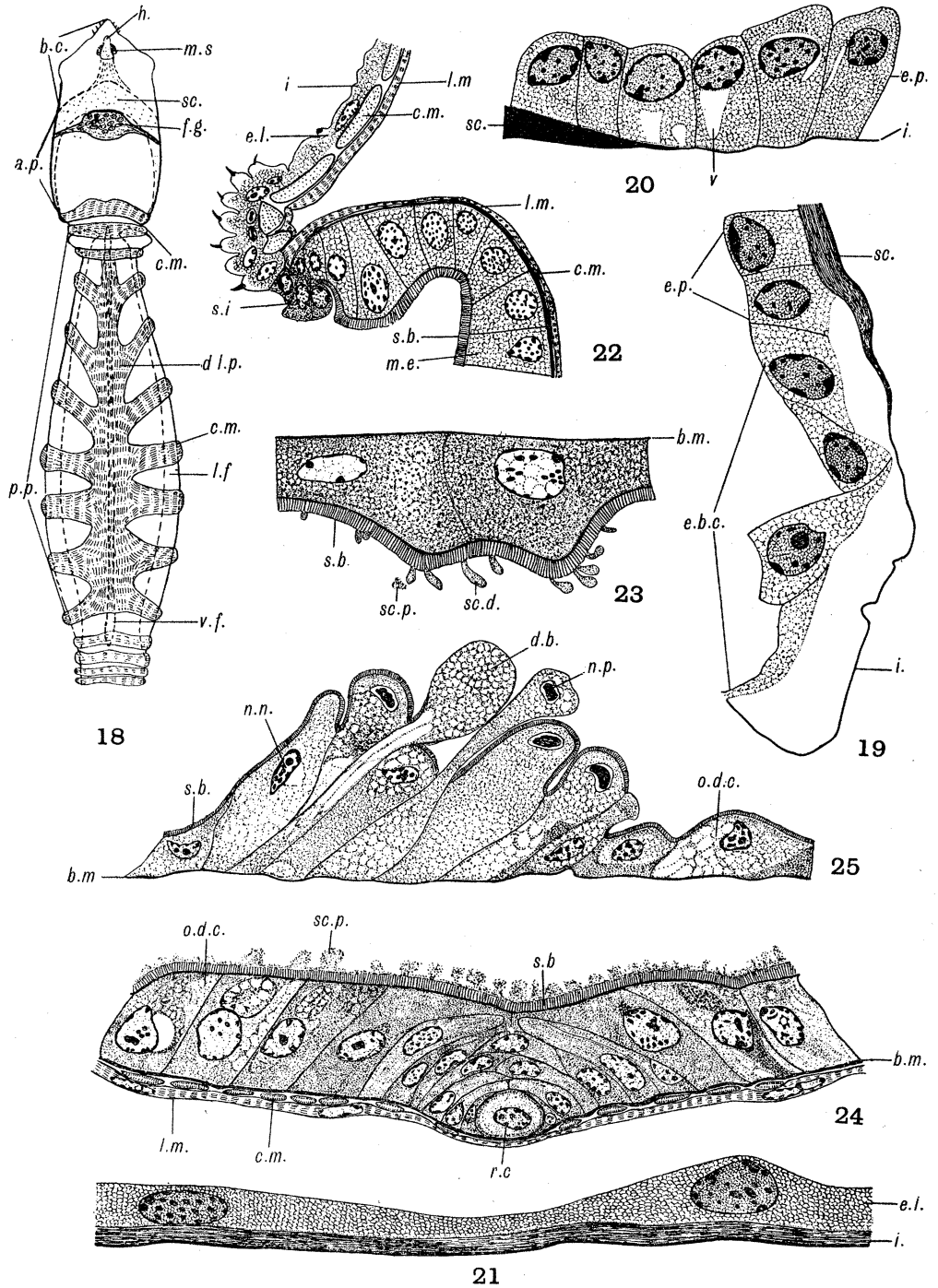
plays an important part in the ingestion of food through suction and is not a mere tube of passive food conduction.

From HARMS's description and figure (1912, p. 185, pl. xiii, fig. 6), it appears that the posterior pharynx of the larva of *C. canis* differs considerably from that of this species. To me it appears that these differences are more due to his erroneous interpretation of facts than to reality, as he based his account only on the examination of a few cross-sections of this organ.

(*d*) *The crop* (fig. 9, *cr.*)—The posterior pharynx passes near the hinder end of the prothorax into a cone-shaped sac, the crop. The shape of the crop varies according to the quantity of the food present in it. It extends up to the posterior end of the metathorax. When the crop is full the posterior end of the posterior pharynx appears to be invaginated into its anterior end like a stomodaeal valve. The epithelium (fig. 22, *e.l.*) is in the form of a syncytium with its outer surface plain and inner surface irregular and produced into lobes. The nuclei are sparsely scattered and are confined to the lobulated portions. They are round or oval and the chromatin is condensed into fewer and bigger granules than those of the nuclei of the posterior pharynx. The meshes of the cytoplasmic network are coarser than those of the posterior pharynx. The intima (*i.*) is extremely thin and plastic and forms, in certain places where the epithelium is swollen, dome-shaped protuberances each having a chitinous spinule at its apex. These dome-shaped protuberances are well separated ; they are scattered irregularly all over the crop and when seen in cross-sections give the false appearance of folds, and HARMS has mistakenly described them as longitudinal folds.

The musculature consists of inner circular muscles (*c.m.*) and outer longitudinal muscles (*l.m.*). The circular muscle fibres, though well developed and closely placed, are not so powerful as in the posterior pharynx. The longitudinal muscles are composed of six well-separated narrow fibres running from the anterior end to the posterior end of the crop. HARMS (1912, p. 189) failed to find longitudinal muscles of the crop in the larva of *C. canis*.

The stomodaeal valve (figs. 9, 22) is poorly developed and is represented by a circular constriction forming a circular fold internally at the junction of the crop and the mesenteron. It does not project into the mesenteron and acts merely as a sphincter. The stomodaeal wall and the wall of the mesenteron are well separated and the space between them is occupied by musculature of both the sections. At the junction of the stomodaeum and the mesenteron there is a complete stomodaeal imaginal ring (*s.i.*). The cells of the imaginal ring are well individualized and are much smaller than those of the mesenteron (*m.e.*) and are strongly basophil. Their cytoplasm is compact and homogeneous. In front of the imaginal ring there is an aggregation of the dome-shaped protuberances, which represents a poorly developed proventriculus and acts only as a valve and a poorly developed sifting organ. The epithelium of the proventriculus is a syncytium and has closely placed nuclei. According to HARMS (1912, p. 190, pl. xiii, figs. 7, 8), in *C. canis* this constriction is confined to the dorsal half, which opinion, I believe, is due to an error of observation and that the ring is really complete. Consequently his statement, " Infolge dieser eigen-



FIGS. 18–25.—Fig. 18—Dorsal view of the anterior portion of the stomodaeum. × 200. Fig. 19—Epithelium from the dorsal side of the buccal cavity of a third-stage larva with two epithelial cells of the anterior pharynx above, the intima of the buccal cavity is torn off from the epithelium, longitudinal section. × 2143. Fig. 20—Epithelium from the dorsal side of the posterior region of the anterior pharynx of a third-stage larva, longitudinal section. × 2291. Fig. 21—Epithelium of the posterior pharynx of a third-stage larva, longitudinal section. × 2000. Fig. 22—Longitudinal section through the stomodaeal valve of a third-stage larva. × 571. Fig. 23—Two digestive cells showing the phenomenon of secretion formation. × 1111. Fig. 24—Longitudinal section through the wall of mesenteron of a third-stage larva showing the transformation of regenerative cells into the digestive cells. × 1105. Fig. 25—Longitudinal section through the mesenteric epithelium showing the process of disintegration in the digestive cells. × 729.

tümlichen Verhältnisse ist bei unserer Larve ein vollständig geschlossener Imaginalring, wie er sich bei sehr vielen Insekten am Übergang des Vorderdarms in den Mitteldarm findet, nicht ausgebildet", is incorrect, as there is no known case in insects in which the imaginal ring is incomplete as he considers to be here the case. WAGNER (1935, pl. iii, figs. 1, 7) observed a complete imaginal ring in the larva of *P. irritans*.

(B) THE MESENTERON

The mesenteron (fig. 35, *me.*) is in the form of an elongated sac and stretches as a straight tube from the anterior end of the first abdominal segment to the posterior end of the sixth abdominal segment. It shows variation in its diameter at different places on different occasions and this is due to the presence of a variable quantity of food. Usually it becomes narrow towards the posterior end. It does not possess any caecal appendages or accessory structures of any sort.

The peritrophic membrane (fig. 9, *p.m.*)—The presence of the peritrophic membrane has been described for the first time in the order of Siphonaptera in the larva of *O. wickhami* by WIGGLESWORTH (1930, p. 607). It has also been reported in the larva of *P. irritans* by WAGNER (1935, p. 268). It is present in the form of an extremely delicate membrane in this larva. According to WIGGLESWORTH (1930, p. 596), in Diptera it is formed by a circular band of specialized cells confined to the anterior end of the mesenteron, and in the formation of this membrane a slight chitinous ring-like thickening on the opposite stomodaeal wall plays an important part and acts as an annular press. In the larva of *O. wickhami*, according to him, the annular press is formed by the thickened chitin of the margin of the stomodaeal invagination which is reflected over and is closely applied to the cells which secrete the peritrophic membrane. Such a chitinous annular press does not exist in the larva of *N. fasciatus*, but the stomodaeal imaginal cells (*s.i.*) form an annular thickening which presses against the mesenteric cells and thus may act as an annular press. As to the mode of formation of the peritrophic membrane, I cannot agree with WIGGLESWORTH that it is exclusively formed by the anterior mesenteric cells. It is extremely difficult, however, to come to any definite conclusion as to its mode of formation. I have often found it lying very close to the entire mesenteric epithelium, thus giving the appearance of having been formed from it.

The epithelium of the mesenteron (figs. 9, 22, *m.e.*) is much thicker than that of the stomodaeum and is made up of discrete cells with well-defined cell boundaries resting on a basement membrane. They are of two kinds, the large digestive cells and the small regenerative cells (fig. 24, *o.d.c.*, *r.c.*). The digestive cells form the functional epithelium of the mesenteron of the larva and possess a striated border on their inner surface.

According to HARMS (1912, pp. 191, 197), there are two histologically but scarcely morphologically differentiated parts in the mesenteron of the larvae of *C. canis* and *P. irritans*. The digestive cells of the anterior section are high with their irregular

inner surface forming villi, and he considers them to be exclusively secretory in function. Those of the posterior section, which are low and rectangular in shape and have a straight inner surface without forming villi, are, according to him, absorptive in function. WAGNER (1935, pp. 266–270), who examined the larva of *P. irritans*, has clearly shown that there exists no such differentiation into well-defined sections such as is mentioned by HARMS. I have not seen any such well-defined histological differentiation in the larva of *N. fasciatus* in any stage. The digestive cells (figs. 9, 22, 24, *o.d.c.*) are usually columnar in shape, but they vary a great deal in appearance according to the state of the digestive processes. In those parts (fig. 23) where the mesenteron is considerably widened they become flattened and sub-rectangular in shape. At certain times they (figs. 9, 25) project into the mesenteric lumen in the form of finger-like processes resembling villi, either individually or in groups, and thus give the mesenteron a shaggy appearance. These cells have a frothy appearance owing to the presence of large vacuoles and have been considered by HARMS as secretory cells and by WAGNER as cells in the secretory phase. There is no definite distribution of these cells, as was already pointed out by WAGNER (1935, p. 270), and they are scattered throughout the mesenteron but are more numerous in the anterior region than in the posterior region. They always alternate with either columnar or rectangular cells. My personal observations have led me to conclude that there is no differentiation of digestive cells in conformity with the dual function of secretion and absorption, and each cell is capable of performing both functions as is the case in most other insects. In this respect I am in complete accord with WAGNER's statement (1935, p. 270), "dasz der physiologische Charakter der Epithelialzellen des Mitteldarmes nur ein zeitweiliger ist, d.h. jede Zelle kann, unabhängig von ihrer Lage, potentiell entweder eine sekretorische oder eine resorbierende Funktion verrichten". The cytoplasm is granular and basophil in cells devoid of bigger vaculoes but in cells with larger vacuoles it is spongy and eosinophil. The nuclei show variation in form and size and they are spherical to ovoid in shape and occupy different positions in the cells. The chromatin is condensed in the form of sparsely scattered unequal granules, of which one is usually larger than the others. According to HARMS, some of the nuclei have the chromatin condensed into a ball in the centre and surrounded by a halo. These nuclei were apparently undergoing pycnotic degeneration, and such nuclei are found in cells undergoing disintegration in this larva as well.

The discharge of secretion products by vesicular extrusions in the form of big vacuoles following the destruction of the striated border has been described by HARMS (1912, p. 193) in the larvae of *C. canis* and *P. irritans*. He observed the absence of nuclei in some of these cells and some disintegrated cells in the mesenteric lumen, and consequently he believed in the possibility of the destruction of some of these cells during secretion formation. According to WAGNER (1935, p. 266), the secretion takes place in the form of big secretory spherical droplets (Sekretkugeln) of different sizes, most of which are homogeneous, but many of which are granular and vacuolated and have a frothy appearance and are formed from the frothy proto-

plasm (" schaumiges Protoplasma ") of the cells in the secretory phase. According to him, some cells are destroyed during the process of the energetic secretion.

The digestive cells, as pointed out before, at certain times have irregular forms and they project into the mesenteric lumen to such an extent that they block a considerable portion of it. In sections these processes are often cut in different positions and look like spheres of frothy protoplasm of different sizes, some nucleated, some enucleated. Most of these, in sections which I have examined, were surrounded by striated border and, when examined in adjacent sections, they show continuation with the digestive cells, and are thus parts of the digestive cells. In my opinion, it is possible that some of the secretory spheres and degenerate cells observed by WAGNER may be nothing else but frothy cells cut in different directions. WAGNER (1935, p. 267) has counted thirty-nine such degenerate cells in the anterior section of the mesenteron of a two days old first-stage larva, and it is hardly possible for the regenerative cells of a two days old larva to cope with such a great loss. According to my observations, this great protrusion of some of the digestive cells into the lumen is either due to one or both of the following two causes. Firstly, it is in abundance in certain regions of the mesenteron of third-stage larvae, which are either completely devoid of food or where there is very little food. Thus the protrusion of cells is possibly the result of either contraction of the circular muscles or of excessive absorption of the nutritive substances or may be due to both causes. In larvae in which the mesenteron is full of food, such protrusions of cells are absent. Secondly, the cells project enormously into the lumen at times when they undergo the process of disintegration (fig. 25, *d.b.*). In partially fed first-stage larvae less than twenty-four hours old, the protruded cells were absent. According to my observations, the presence of large vacuoles and the projection of cells have little connexion with the act of secretion, as secretory products (figs. 23, 24, *sc.p.*) are always much more abundant outside the low cells than outside the high cells. According to YUNG-TAI (1929, p. 53), " La présence des gouttelettes graisseuses d'une taille quelconque coincide le plus souvent avec certains aspects indiquant une dégénérescence des cellules qui les renferment ", and I am fully in accord with him. The first conclusion of mine finds support in the description and diagrams of WAGNER as the enlarged protruded cells said by him to be in the secretory phase are always in regions where the diameter of the mesenteron is much less than where the so-called absorbing cells are located. WAGNER (1935, p. 270) himself observed in a grown-up larva only a few weakly protruding cells at the anterior and the posterior end of the mesenteron, showing thereby that the protrusion of cells is a transitory phenomenon and has nothing to do with secretion formation.

I cannot agree with WAGNER's suggestion, " dasz bei Flohlarven die sich von den Krypten absondernden Zellen zunächst resorbierende Zellen sind und erst später beginnen Sekret auszuscheiden ; ist die Ausscheidung des Sekretes energisch— dann geht die Zelle bald zugrunde, ist der Prozess ruhiger, so lebt sie weiter, kann sich aber doch nicht mehr in eine resorbierende verwandeln ". According to my observations, the digestive cells recently transformed from the regenerating cells

are at first secretory (fig. 24, *o.d.c.*), later on absorptive, and then undergo disintegration.

It appears that both these foregoing authors have confused three distinct processes, viz., the absorption, secretion, and disintegration happening in the digestive cells. According to my observations, these three distinct processes occur on different occasions, but there is an overlapping of one over the other. During absorption the cells are highly vacuolated and the vacuoles are bigger in size and are formed as a result of absorbed substances being taken in the cell. The vacuoles in the cells in the absorptive phase are occupied by fat droplets in life, as is mentioned by YUNG-TAI (1929, pp. 51, 76). At certain times, due to the conditions mentioned above, the digestive cells protrude into finger-like processes projecting into the lumen. They show greater affinity for eosin. The striated border, except when the cells undergo disintegration, is always intact.

During the secretory phase, the cells are more basophil and the vacuoles are fine. In addition, in these cells there are strongly basophil inclusions which are considered by YUNG-TAI (1929, pp. 69, 76) to be secretory products. The secretion products are discharged in the form of extremely fine homogeneous vesicular droplets (*sc.d.*) which ooze out through the canals of the striated border, as is shown in fig. 23. There is no destruction of the striated border such as is mentioned by HARMS. Finally, these droplets burst and the secretion lies outside the striated border (figs. 23, 24, *sc.p.*) without injuring the latter. Thus the secretion formation is purely merocrine. These fine droplets have often been confused with big bud-like vesicular extrusions which are the result of cell disintegration, and it is thus that the controversy as to the method of secretion formation has arisen. The disintegration of cells (fig. 25, *d.b.*) takes place by the formation of highly vacuolated big spherical buds. The wall of these buds is always devoid of striated border. These buds increase in size enormously and become separated off from the main cells. Sometimes they contain a nucleus undergoing pycnotic degeneration (*n.p.*). This disintegration has been interpreted by WAGNER as a method for the energetic discharge of secretion products in the larva of *P. irritans*, and by some workers in other insects. This interpretation has been challenged by YUNG-TAI (1929, pp. 54, 76, 83) and by HENSON (1929, pp. 93, 101). According to both these authors, the secretions are always in the form of a diffusible liquid and the buds and globules given off from the digestive cells have all the characteristic appearances of cytoplasmic disintegration products. The disintegration, according to my observations, always takes place in the protruding cells but never in the low cells. From WAGNER's description it appears that the same occurs in *P. irritans*.

The regenerative cells (fig. 24, *r.c.*) are much smaller in size and have a dense chromatic texture. They are arranged in groups called nidi between the bases of the digestive cells against the basement membrane. They are concealed between the bases of large digestive cells and are not visible either from the internal or external aspect of the mesenteron, except a little before the defaecation period, when they project outwards into the body cavity as button-shaped swellings (fig. 73, *me.*).

According to HARMS (1912, p. 197), in the larvae of *C. canis* and *P. irritans*, and according to PERFILJEW (1926, p. 112), in the larva of *L. pectiniceps*, the regenerative nidi are more numerous in the anterior half than in the posterior half. They are equally abundant all over the mesenteron of the larva of *N. fasciatus*, but they protrude externally and increase in dimensions progressively from before backwards, and thus they appear at certain periods of the third-stage larva to be more prominent in the anterior half than in the posterior half. It is possible that both the foregoing authors examined the larvae at this stage and thus thought them to be more numerous in the anterior half than in the posterior half. The cytoplasm is homogeneous and strongly basophil. The nuclei are comparatively large as compared with the size of the cells and are provided with equal sized chromatin granules.

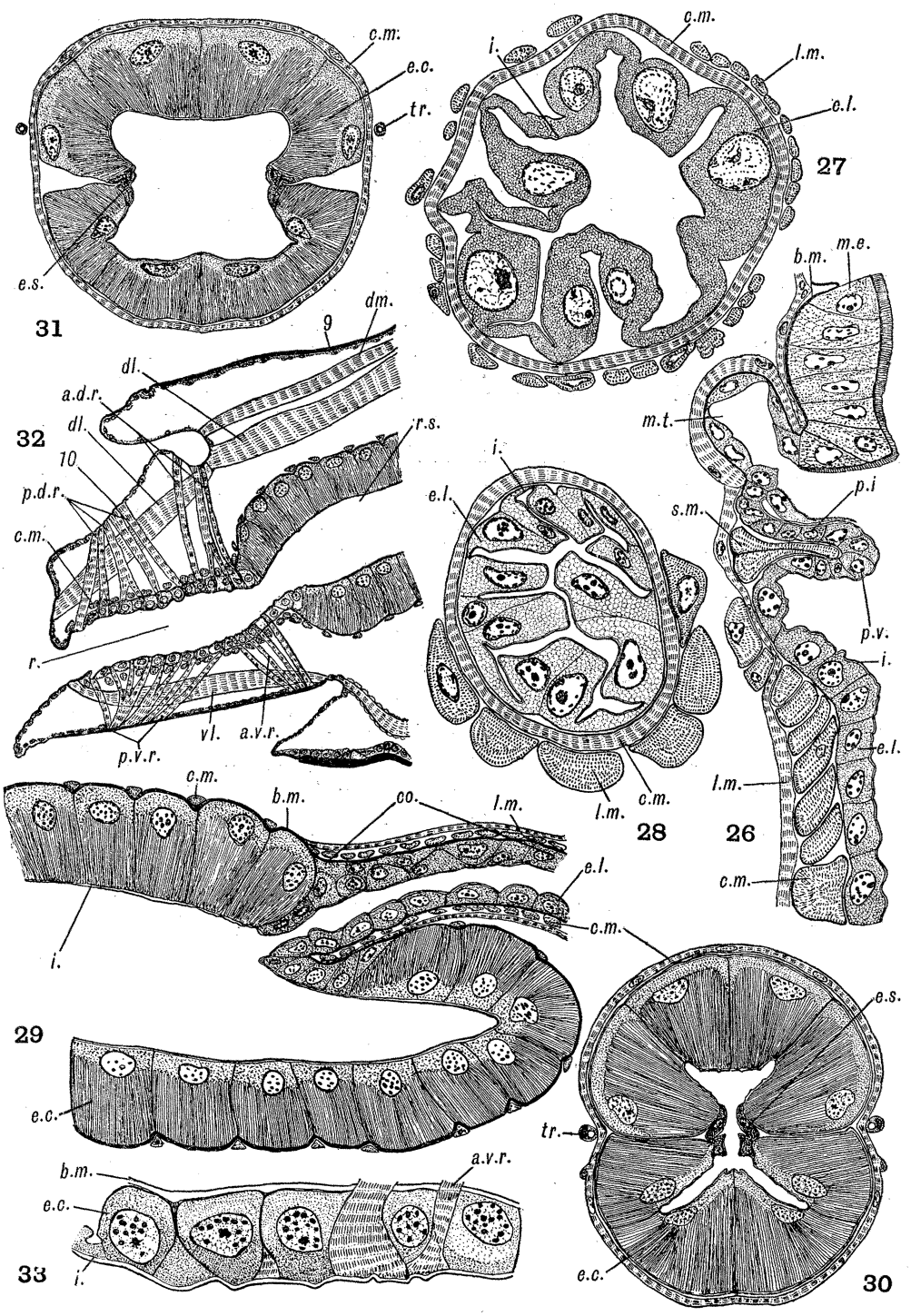
The replacement of digestive cells by proliferation of regenerative cells has been described by HARMS (1912, p. 195). According to WAGNER (1935, p. 271), there is a transformation of the regenerative cells into the usual digestive cells in the larvae of different stages. I have observed a similar transformation in an early third stage. Fig. 24 clearly shows that there is a complete gradation in size from the smallest regenerative cells to large columnar digestive cells. It may be presumed, therefore, that cell differentiation at the expense of regenerating cells (*r.c.*) takes place, thus suggesting their recent formation from regenerative cells. The next question is whether there is a complete or partial replacement of digestive cells accompanying each moult. The facts given by WAGNER are insufficient to lead to any definite conclusion as to complete replacement, and I have not followed the changes in all the three different larval stages, but that partial replacement accompanies each moult is certain.

The musculature of the mesenteron (fig. 22) is more weakly developed than in the stomodaeum and the proctodaeum. It consists of inner fine circular fibres (*c.m.*) and outer closely placed numerous longitudinal fibres (*l.m.*).

(C) THE PROCTODAEUM

The proctodaeum (fig. 35) commences in the beginning of the seventh abdominal segment and is differentiated into five regions : (*a*) the pylorus (*py.*), (*b*) the ileum (*il.*), (*c*) the colon (*co.*), (*d*) the rectal sac (*r.s.*), and (*e*) the rectum proper (*r.*).

(*a*) *The pylorus* (*py.*) is a well-defined sub-spherical chamber which lies immediately behind the mesenteron. There is a well-developed complete internal circular fold (fig. 26) in about its middle, which is composed exclusively of proctodaeal imaginal cells (*p.i.*) and which serves as a pyloric valve (*p.v.*). The latter structure is thus exclusively of proctodaeal origin and not of ventricular origin as mentioned by HARMS (1912, p. 198) in the larva of *C. canis*. The working of the pyloric valve is controlled by two powerful circular sphincter muscles (*s.m.*), which are enclosed within the external cavity of this fold. The smaller anterior section of the pylorus in front of the valve is extremely thin-walled as it is lined with proctodaeal imaginal



FIGS. 26–33—Fig. 26—Longitudinal section through the wall of the pylorus. × 868. Fig. 27—Transverse section through the ileum. × 894. Fig. 28—Transverse section through the colon near the bend where the longitudinal muscles are crowded on one side. × 1061. Fig. 29—Longitudinal section through the junction of the colon and the rectal sac, on the upper side it passes through a fold of the colon. × 439. Fig. 30—Transverse section through the rectal sac in the contracted condition. × 503. Fig. 31—Transverse section through the rectal sac in the dilated condition. × 281. Fig. 32—Median longitudinal section through the tenth abdominal segment showing the musculature of the rectum. × 218. Fig. 33—Epithelium of the ventral wall of the rectum close to the rectal sac. × 1364.

cells and is completely devoid of circular muscle fibres. It is bounded anteriorly by the high cells of the posterior end of the mesenteron forming a sort of fold. The greater posterior portion of the pylorus is thick-walled and is lined with ordinary larval epithelial cells, similar to those of the ileum, but not thrown into longitudinal folds. The two anterior circular muscles (*c.m.*) of the posterior pyloric section lie outside some of the longitudinal muscles (*l.m.*) of the pylorus. The cuticular intima (*i*) of the pylorus is thin and smooth.

(*b*) *The ileum* (*il.*)—The pylorus is followed by a U-shaped ileum. The anterior end of the lower limb, which is in direct continuation with the pylorus, is enlarged so as to form a funnel-like dilatation, which is wrongly considered to be the pylorus by HARMS (1912, p. 198) in the larva of *C. canis*. It runs backwards to the middle of the eighth abdominal segment and bends upwards. The upper limb runs parallel to the lower limb as far as its anterior end.

The epithelium (fig. 27, *e.l.*) is thrown into longitudinal folds which enclose external cavities. Their number varies from six to nine, but six of them are always bigger and more prominent than the others. These folds are more strongly developed in the anterior funnel-shaped portion than in the posterior portion. The epithelial cells are more or less rectangular in shape and well individualized. They become longer in the posterior region. They become swollen in the regions of folds and the nuclei are found in the swollen portions. HARMS (1912, p. 200) failed to recognize the cell boundaries in the larva of *C. canis*. He only based his conclusion on the examination of transverse sections, and I have also found that in the transverse sections the cell limits are not recognizable. But, on the other hand, the cell limits are easily recognizable in longitudinal sections and whole mounts. The cytoplasm is homogeneous and does not show any trace of striation as mentioned by HARMS. The nuclei are spherical to ovoid in form with coarse, sparsely scattered chromatin granules, of which one is usually larger than the others. The basement membrane is thin. The cuticular intima is thin and smooth but may take an irregular course on the folds.

The musculature consists of an internal layer of powerful circular fibres (*c.m.*) whose number corresponds exactly to the number of circular rows of the epithelial cells. The longitudinal muscles (*l.m.*) are arranged in widely spaced fibres. They are continuous anteriorly with the longitudinal muscles of the mesenteron. The musculature of the ileum and the colon is much more strongly developed than that of the mesenteron.

(*c*) *The colon* (*co.*) is narrower and shorter than the ileum. It runs at first forwards then backwards. The epithelial cells (fig. 28, *e.l.*) appear individualized even in the transverse sections. The folds, which are more prominent than those of the ileum and block the lumen, are formed, unlike those of the ileum, simply by the projection of cells and do not enclose any external cavities.

According to PATTON and CRAGG (1913, p. 460, pl. lvii, figs. 5, 7), the narrow part of the hind gut (colon) of the larva of *C. felis* " has on it near its termination a small

clump of round cells (fig. 8), of unknown function and origin, placed at one side ". But according to PERFILJEW (1926, p. 115) such a group of round cells does not exist in the larva of *L. pectiniceps*, although he found a group of cells at the junction of the colon and the rectal sac enclosed within a common covering. These cells, according to him, have comparatively bigger nuclei rich in chromatin, which are centrally situated. In the larva of *N. fasciatus* I did not find any trace of a clump of round cells as is described by PATTON and CRAGG, nor of a group of special cells such as is mentioned by PERFILJEW. I have often come across, both in transverse sections and whole mounts, the crowding of longitudinal muscles on the inner side of the bend. This makes the epithelial cells more conspicuous on the other side of the bend, and it is just possible that the clump of cells described by PATTON and CRAGG may be due to a similar cause.

(*d*) *The rectal sac* (fig. 29) is without a doubt the most outstanding structure in the whole alimentary canal. It is unusual both in gross and histological anatomy. The colon is not directly continued by the rectal sac, but it opens into the latter on its dorsal side some distance from its anterior end which terminates blindly so as to form a rectal caecum. The dorsal wall of the colon is continued directly with that of the rectal sac, but its ventral wall is invaginated into the latter so as to form a semicircular rectal valve on the ventral side. The rectal sac, which is an enormously thick-walled tube, runs straight backwards from the beginning of the seventh abdominal segment to the junction of the ninth and tenth abdominal segments. It is the broadest section of the proctodaeum and lies dorsally to the ileum. The rectal sac in cross-section (fig. 30) is 8-shaped and is formed of two enormously thick-walled longitudinally running gutter-shaped halves which are dorsal and ventral in position. The free margins of these gutters are connected on each side by an extremely thin longitudinal strip of the epithelium (*e.s.*). Its caudal end narrows abruptly as it joins the rectum proper without any indication of a valve.

The intima (*i.*) is smooth and is almost as thick as that of the rest of the proctodaeum. The epithelial cells are of two kinds. Each gutter is composed of enormously large cells (*e.c.*), and in cross-sections four to six cells can usually be distinguished, thus showing that each gutter is bounded by about four cells at one place. Each cell is columnar to cubical in form and is about 32 μ in width and about 25 μ in depth. The cytoplasm of the cells of the upper gutter is basophil and granular near the basement membrane, but the remainder part is strongly eosinophil and is radially striated. The nuclei of these cells are always near the basement membrane, but in the cells of the lower gutter the basophil portions and the nuclei are always near the intima. The nuclei are spherical to ellipsoidal in form and are about 11μ in diameter. Each nucleus is filled with closely placed, medium sized, subequal, chromatin granules.

The epithelium (*e.s.*) of the lateral portions is extremely thin and is about 5 μ in thickness, and the cell boundaries are not differentiated and thus form a syncytium. The nuclei are extremely small and are elongate-oval and flattened. The cytoplasm is homogeneous and basophil and is devoid of any kind of striation. The

basement membrane (fig. 29, *b.m.*) is well developed and often in sections one sees it separated from the epithelial cells and carrying with it the circular muscles.

The musculature consists of only circular muscles (*c.m.*) which are powerfully developed and in number correspond almost exactly to the number of circular rows of cells of both the gutters, and each muscle is lodged in a slight depression between the two adjacent circular rows of cells. There is no trace of longitudinal muscles in the larva of *N. fasciatus*, but HARMS (1912, p. 203) describes them as poorly developed in the larva of *C. canis*.

While examining different series of sections, I was struck by a fact which clearly shows that the radial striations in the bigger cells act as muscle fibres and control the dilatation of the lumen of the rectal sac. As shown in fig. 30, the lumen is reduced and is star-shaped and the lateral insinkings are very deep. In another specimen (fig. 31) I found the lumen in cross-section was wide and almost quadrangular. The lateral insinkings were shallow and the epithelial cells (*e.c.*) comparatively narrow.

This curious section of the proctodaeum has been called the rectum by HARMS (1912, p. 200) and LASS (1905, p. 84), and the colon (" Dickdarm ") by PERFILJEW (1926, p. 116). Both these names are inappropriate for this section. Taking into consideration its function and the presence of an anterior blind end, it is reasonable to call it a rectal sac.

(*d*) *The rectum proper* (fig. 32, *r.*) differs considerably from the rectal sac (*r.s.*) both morphologically and histologically. It occupies the whole of the tenth abdominal segment. Its diameter is much less than half of that of the preceding section and is broadest near its commencement, but gradually narrows towards the posterior end. It (fig. 34) is provided with six longitudinal folds projecting into the lumen. Three of these folds, the dorsal and the ventro-lateral ones, are much bigger than the other three which alternate with them and are thus dorso-lateral and ventral in position. The cavity thus appears star-shaped in cross-sections. This arrangement of folds, unlike that in the larva of *C. canis* (HARMS, 1912, p. 205), is preserved for the entire course of the rectum.

The intima (fig. 33, *i.*) is thin and smooth, but has a wavy appearance. The epithelial cells (*e.c.*) are columnar to cubical in shape and are well individualized. They are considerably smaller than in the preceding section, being about 10 μ in length. The nuclei are sub-spherical. The cytoplasm is homogeneous and is devoid of any striation. HARMS (1912, p. 205) has described the cells as having striations in the larva of *C. canis*, but I believe he was led into a mistake by considering the striations of the dilator muscles as belonging to these cells. The basement membrane is better developed than in the preceding section.

The intrinsic musculature (figs. 32, 34) consists only of circular muscles (*c.m.*) which are very closely placed. The number of circular muscles corresponds to the number of the circular rows of the cells as in the preceding section, and the muscles are equally powerful. The last muscle of this series acts as an anal sphincter. I have failed to find any trace of longitudinal muscles though HARMS (1912, p. 205)

described and figured longitudinal muscles in this section. To me it appears that he has mistaken the dilators of this section for longitudinal muscles, as some of the former do take a longitudinal course and in transverse sections they look like the cut ends of longitudinal muscles outside the circular muscles.

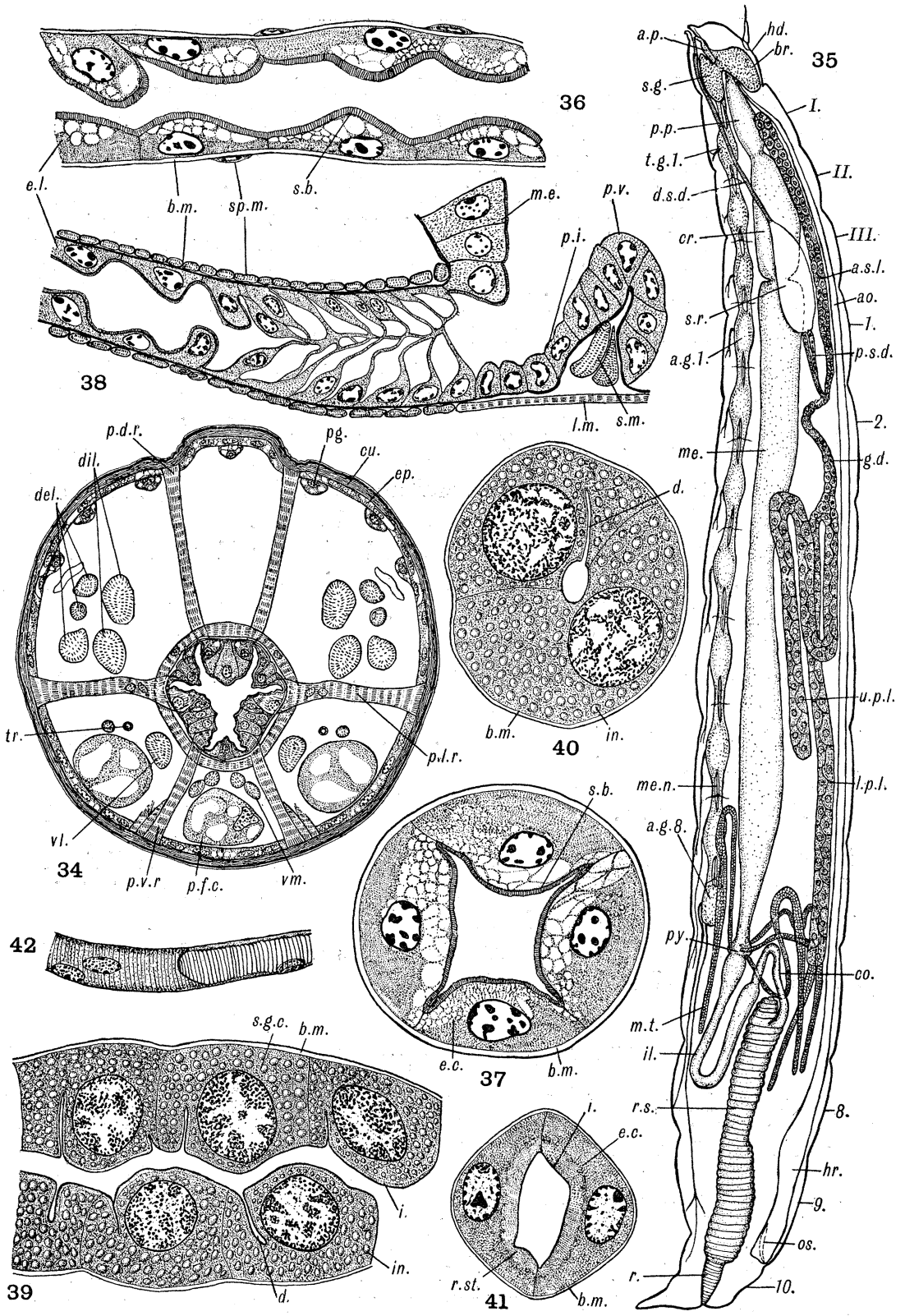
There is a well-developed extrinsic musculature (fig. 32) of this section which acts as its dilators. It consists of a large number of fibres, which are arranged into an anterior and a posterior group. The muscles of the anterior group (*a.d.r.*, *a.v.r.*) start from near the anterior margin of the tenth abdominal segment and are inserted on the proximal region of the rectum, while those of the posterior group (*p.d.r.*, *p.v.r.*) start from the middle of the segment and are inserted on the posterior greater part of the rectum. Muscles in each group are further arranged into three paired sets (fig. 34). The dorsal dilators (*p.d.r.*) are inserted on each side of the median dorsal line on the dorsal angle of the star-shaped cavity. The lateral dilators (*p.l.r.*) are inserted on the lateral sides, on the lateral angles of the lumen, and the ventral dilators (*p.v.r.*) on the ventral side, on the ventral angles.

This section has wrongly been called the anal sphincter (der Analsphinkter) by HARMS (1912, p. 203). The only reason he gives for this curious denomination is "die Ausbildung von starken Dilatatoren als Sphinkter charakterisiert wäre". These dilators of the proctodaeum occur in many insects, especially in the lepidopterous larvae. Their distribution is never confined to any definite section of the proctodaeum and as such their presence or absence does not justify the giving of a new name to a section of the proctodaeum. The rectum goes straight to the T-shaped anus as in *C. canis*.

According to PACKARD (1895, p. 316, fig. 1), the proctodaeum of a recently hatched first-stage larva of *C. canis* forms a straight tube without showing any morphological and histological differentiation into its various parts and is not even differentiated from the mesenteron. Such a condition does not exist in the larva of *N. fasciatus*. In a recently hatched first-stage larva of this species the proctodaeum shows the same differentiation and arrangement of its parts as are found in the third-stage larva, which are described above.

IX—THE MALPIGHIAN TUBULES

There are four long and slender Malpighian tubules (fig. 35, *m.t.*) lying free in the body cavity, as in the adult. They arise separately from the pyloric region (*py.*) in front of the proctodaeal imaginal ring, thereby showing that they open at the junction of the mesenteron and the proctodaeum. A longitudinal section (fig. 26, *m.t.*) at this level shows that the mesenteric epithelium (*m.e.*) is separated from the epithelium (*e.l.*) of the proctodaeum by a Malpighian tubule. Two of them open into the two lateral sides of the pyloric region and the other two open into its dorsal and ventral sides respectively. There are no ampulla-like dilatations at their junctions with the pyloric region. Morphologically three distinct regions can be distinguished in each Malpighian tubule. The proximal one-third portion is



FIGS. 34–42.—Fig. 34—Transverse section through the posterior half of the tenth abdominal segment. × 424. Fig. 35—Side view of a third-stage larva showing the natural position of the internal organs. × 34. Fig. 36—Longitudinal section through the distal portion of the proximal region of a Malpighian tubule. × 1211. Fig. 37—Transverse section through the proximal region of a Malpighian tubule. × 1171. Fig. 38—Longitudinal section through a Malpighian tubule near its origin. × 1222. Fig. 39—Longitudinal section through a portion of the salivary gland. × 645. Fig. 40—Transverse section through a lobe of the salivary gland. × 900. Fig. 41—Transverse section through the proximal salivary duct. × 1200. Fig. 42—A portion of the common salivary duct, posterior portion is cut to show the taenidia. × 778.

narrower than the middle third which is the broadest portion. The terminal third is slightly broader than the proximal portion.

Each Malpighian tubule is lined with large polyhedral cells (fig. 36, *e.l.*) with well-defined cell boundaries resting on a well-developed basement membrane (*b.m.*). The outer surface of the epithelium is smooth, but the inner surface is wavy owing to the swelling of each cell in its middle. As the swollen portions of cells of one side usually alternate with those of the other side, the lumen has a wavy appearance when seen from one side. Throughout its entire length, when seen in transverse sections (fig. 37), a Malpighian tubule is composed of a ring of four large cells (*e.c.*) and, consequently, the lumen usually appears star-shaped in transverse sections. The inner surface of the epithelial cells is provided with a distinct striated border (*s.b.*), as in other insects, and it is of the " honeycomb border " (" Wabensaum ") type in which rod-like elements are fused together. I cannot agree with HARMS's statement (1912, p. 208), " Gegen das Lumen werden die Zellen von einer zarten Chitinintima abgegrenzt ; ein Stäbchensaum, der bei den Malpighischen Gefässen mancher anderen Insekten beschrieben worden ist, ist bei unserer Larve nicht vorhanden ", as there is no known insect in which there is a cuticular lining to the Malpighian tubule such as he mentions, and a well-developed inner striated border is present in the larva examined by me. The basal striated zone of the cells of the Malpighian tubules, which has been observed in some insects, is entirely absent. The nuclei are oval with a few coarse chromatin granules in each. The cytoplasm is compact and homogeneous near the basement membrane and is strongly basophil ; but below the striated border it is eosinophil and highly vacuolated. The vacuoles are of irregular shapes.

This presence of vacuoles of different sizes below the striated border has been considered by some as fixation artefacts, by others as representing the normal vesicular secretory phenomena (WIGGLESWORTH, 1931, p. 440). It is this vacuolated region of the cells which contains excretory spherical globules of greenish-yellow colour in the living condition. These products are in greater abundance in the cells of the middle region than elsewhere and gradually decrease in quantity from the distal to the basal end of the proximal region. The epithelial cells lining the proximal portion are of two kinds. Near its junction with the pyloric region the cells (fig. 38) are devoid of striated border and produced into long processes which are fused with each other so as to form a loose network in the lumen. Such a structure has never been described in any other insect, and it is difficult to come to any definite conclusion as to its exact significance. The remaining part of the proximal region is lined with ordinary epithelium with striated border. The cells are much flattened, and the lumen is consequently comparatively larger in this region than in other parts. The epithelial cells in the middle region are the largest, and their inner margins project into the lumen to such an extent that they almost occlude the passage. In the distal region the epithelial cells are of medium size and the lumen is of comparatively smaller dimensions than that of the proximal region. According to HENSON (1932, p. 287), in *Hepialus* the part of the Malpighian

tubule lined with striated border is of endodermal origin and the proximal part devoid of striated border is of ectodermal origin. It is just possible that in the flea larva the part produced into processes may be of ectodermal origin and the rest may be of endodermal origin. In general appearance the proximal cells of Malpighian tubules resemble more the cells of the proctodaeal imaginal ring than any other cells in the pyloric region.

External to the basement membrane of the proximal one-third of each Malpighian tubule there is a muscular network. The network is formed by spirally running muscles (figs. 36, 38, *sp.m.*) which are continuous with the longitudinal muscles of the mesenteron. On account of their minute size it is difficult to determine the exact number of muscles involved in the formation of the network. These muscles form loose spirals except near the basal region where they lie very close to one another. The nuclei of these muscles are elongate-oval. According to HARMS (1912, p. 207), there is a peritoneal covering (" Peritonealhülle oder Serosa ") to the Malpighian tubule of the larva of *C. canis*. From his description it appears that he has mistaken these spirally running muscles for the peritoneal coat. The distal two-thirds of the Malpighian tubule is completely devoid of tissue outside the basement membrane. Peristaltic movements occur in living Malpighian tubules in the proximal region and bring about the transference of the excreted matter from the Malpighian tubules into the pyloric region. The blind end of each Malpighian tubule is provided with a strand of fine tissue devoid of nuclei.

The entire Malpighian tubule is either translucent and colourless or faintly greenish-yellow. There is no white and opaque part as in *Rhodnius prolixus* (WIGGLESWORTH, 1931, p. 429), as it contains only a clear fluid without any solid matter.

X—THE SALIVARY GLANDS

MINCHIN (1915, p. 451, pl. xxvii, fig. A) described the salivary glands of the larva of this species and noted the considerable difference both in size and in complication of parts from those of the adult. This complicated structure of the salivary glands of the larva is, I believe, associated with the production of silk at the time of the formation of the cocoon, as in lepidopterous and hymenopterous larvae.

The salivary gland (fig. 35) of each side consists of three elongated tubular lobes lying in the body cavity on the respective side of the alimentary canal. Of these three lobes one runs forwards and the other two backwards. MINCHIN was wrong in stating that two lobes run forwards. The anterior lobe (*a.s.l.*) runs forwards as far as the middle of the prothorax and narrows posteriorly to form a sort of glandular duct. The posterior two lobes correspond to the posterior single lobe of *C. canis* (*vide* PATTON and CRAGG, 1913, p. 460, pl. lvii, fig. 6). It appears that the posterior lobe in this species has become doubled, as there is a single glandular duct (*g.d.*) common to both of these lobes. One of these two lobes is shorter than the other. The lower lobe (*l.p.l.*), which has been called the posterior lobe by MINCHIN, extends as far as the anterior end of the seventh abdominal segment. The upper lobe (*u.p.l.*),

which departs from the lower lobe in the posterior end of the second abdominal segment, at first runs backwards to the middle of the fourth abdominal segment, then bends and runs forwards to the posterior end of the second abdominal segment. It again bends and runs backwards to the anterior end of the fifth abdominal segment. From the junction of the two posterior lobes a glandular duct (*g.d.*) runs forwards to meet the glandular duct of the anterior lobe in the anterior end of the second abdominal segment. Often the glandular lobes show variation as to their arrangement in the body cavity. The proximal salivary duct (*p.s.d.*), which is narrow proximally but is dilated where it passes into an elongate-oval thin-walled dilated reservoir (*s.r.*), arises from the junction of these glandular ducts, and runs forwards and downwards. From the other end of the reservoir the distal salivary duct (*d.s.d.*) runs forwards. The two distal salivary ducts from the two sides of the body unite into a common median salivary duct in the anterior region of the prothorax. The common salivary duct (fig. 9, *c.s.d.*) runs forwards and opens into the salivarium (fig. 9, *sa.*), which is a pocket of the ventral wall of the head between the base of the prementum and the base of the hypopharynx.

The salivarium or silk press (figs. 9, 14, *sa.*) is a long, narrow, cylindrical tube extending from the base of prementum to the base of ligula. It is lined with thicker intima than that of the common salivary duct and is devoid of the spiral taenidia of the latter. Its diameter is less than half the diameter of the common salivary duct. There is a median ridge running along its dorsal side. The dorsal salivary muscles (*d.s.m.*) are inserted on each side of this ridge. The labial salivary muscles are absent. The spinneret of the lepidopterous larvae is also absent. It functions very much as does the silk press of the lepidopterous larvae. It appears that the dorsal salivary muscles act as dilators of the press lumen and the elasticity of the infolded dorsal wall of the organ acts antagonistically.

Each glandular lobe, which has on an average a diameter of 71 μ, has an extremely narrow lumen, which, on account of the thickness of its wall, is not visible in the mounted preparations. The wall of each glandular lobe (figs. 39, 40) is composed of three layers. The basement membrane (*b.m.*) is a thin hyaline and structureless layer which is completely devoid of nuclei. The epithelium is constituted by a single layer of large-sized polyhedral cells (*s.g.c.*) with well-defined cell boundaries. Through its entire length, when seen in tranverse sections, each glandular lobe is composed of a ring of two cells. The cells have their inner border swollen in the middle, and as the enlarged portions of the cells of one side alternate with those of the other side the lumen has a wavy appearance. Each cell is about 47 μ long and about 43 μ in its broadest portion and possesses a minute cuticular ductule (*d.*) which extends from the lumen into its body. The cuticular intima (*i.*) lining these ductules is as thin as that which lines the inner surface of the cells, and possibly they serve to increase the secretory surface of the cells. The cytoplasm is strongly basophil and granular and has the appearance of a network. In the meshes are found different sized globules, of a homogeneous substance, which do not stain so strongly as the reticulum, but are eosinophil in mature larvae. These inclusions (*in.*) are

probably either connected with secretion or are some kind of stored products. These globules become broken into still smaller spherical globules and increase considerably in number before cocoon formation. The cytoplasm is always homogeneous and granular near the intima. Each cell contains a very large spherical nucleus, 27 μ in diameter, which is extremely rich in chromatin. The chromatin is found in the form of extremely fine granules which at places become crowded so as to form masses of different form and size. The intima is extremely thin and transparent. It is completely devoid of taenidia unlike that of lepidopterous larvae (*vide* BORDAS, 1909, p. 154).

Histologically the glandular ducts show the same arrangement as in the glandular lobes, except that the individual cells are comparatively smaller, being 34 μ long and 16 μ in the broadest portion, and so are the nuclei, being only about 16 μ in their largest diameter. They are devoid of globular inclusions in young larvae and the cytoplasm is homogeneous and granular. But in larvae a little before pupation there are a few inclusions like those of the glandular lobes. The glandular ducts should be considered as parts of the glandular lobes, but they are much narrower with an average diameter of 29 μ.

The histological structure of the proximal salivary duct is quite different from that of the glandular duct and the distal salivary duct. The epithelial cells lining it are thin as compared with those of the glandular ducts and they are flattened with their inner border projecting, being swollen in the middle. As the swollen parts of the cells of one side alternate with those of the other side the lumen has a wavy appearance. The intracellular ductules are absent. The lumen is surrounded by two cells at one place (fig. 41). Each cell is about 28 μ long and about 5 μ in its broadest portion. The cytoplasm is strongly basophil and homogeneous in the external greater part of the cell, whilst the internal lesser part, next to the intima (*i.*), is strongly eosinophil and shows radial striations (*r.st.*). The radial striations play a part in widening the lumen and thus act like muscle fibres. The nuclei are oval and not so rich in chromatin as those of the glandular cells. The chromatin is arranged into bigger, unequal, loosely arranged granules, of which one is always the largest. The intima (*i.*) is slightly thicker than that of the preceding two sections and without any taenidia. The proximal salivary duct has a diameter of 12·5 μ. In the lumen of this duct, well separated from its wall before the time of cocoon formation, is found the silk thread.

The reservoir is lined with thin smooth intima, outside of which there is an extremely thin layer of epithelium in which cells are not individualized. The very sparsely scattered nuclei are flattened and elongate-oval and have comparatively little chromatin in the form of a few big granules and very fine granules uniformly scattered throughout.

Histologically the distal salivary ducts and the common salivary duct (fig. 42) differ considerably from the proximal salivary duct. They are provided with taenidia in their thick intima. Externally to the intima there is a thin layer of flat epithelial cells which do not show distinct cell limits. The epithelium of these

regions is thicker than that of the reservoir and the nuclei resemble those of the epithelium of the reservoir except they are larger and are not so sparsely scattered.

The lobes of the salivary glands become dark brown when treated with Lugol's iodine solution, showing thereby that they are rich in glycogen. It is possible that the globular inclusions seen in sections of the lobes may be composed of glycogen.

XI—The Circulatory System

The dorsal blood vessel (figs. 35, 43) stretches from the posterior end of the ninth abdominal segment to the head, where it ends in the region of the brain. It is differentiated into an anterior narrow section, the aorta (*ao.*), and a posterior dilated section, the heart (*hr.*). The two sections pass into each other gradually and there is no well-marked line of demarcation between the two, except that the heart is much broader than the aorta. It (figs. 44, *hr.*, 45, *ao.*) is suspended from the dorsal body wall by fine radiating structureless strands attached to the epidermis.

The heart is confined to the posterior half of the eighth and whole of the ninth abdominal segment. It has two swellings and thus it is two-chambered. The terminal chamber ends abruptly. In the living condition I have observed pulsation only in the heart. There are only two pairs of ostia belonging to the two chambers of the heart. Those belonging to the posterior chamber (fig. 44, *os.*) are much bigger than those of the anterior chamber. They are confined to its posterior end and lie deep in ventro-lateral inflexions of the wall of the heart. These ostial pouches protrude within the lumen of the heart so as to form valve-like flaps having the true ostia at their free inner ends. The ostia belonging to the anterior chamber are extremely small as compared with those of the posterior chamber and they are lateral in position. I have only seen them in transverse sections. There are no internal valves separating the chambers of the heart, and the construction of ostial flaps is such that they cannot work as inter-ventricular valves. The wall of the heart is formed of striated muscle tissue. There is no connective tissue outside it.

The aorta—The heart is continued anteriorly by the slender aorta which runs forwards as a straight tube, without any swellings, immediately below the mid-dorsal portion of the body wall as far as the middle of the prothorax (fig. 9, *ao.*),

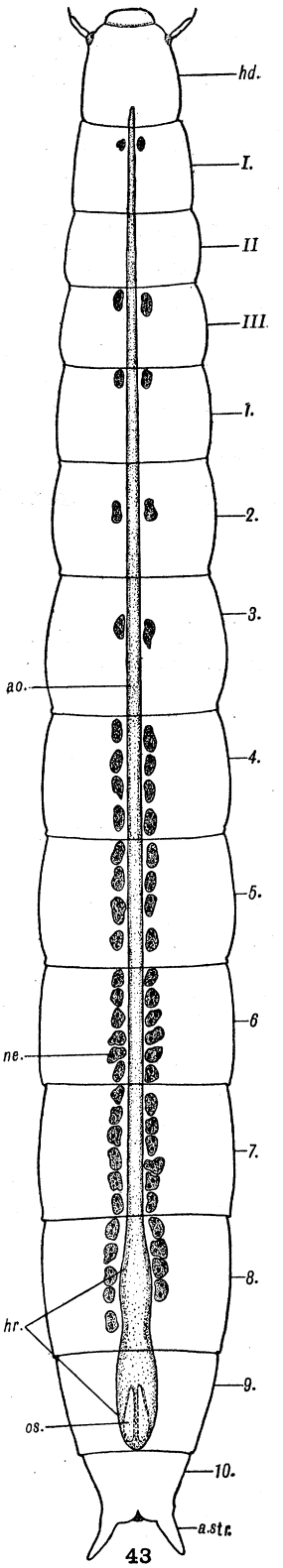


FIG. 43—Dorsal view of a third-stage larva showing the dorsal blood vessel and arrangement of naturally stained nephrocytes. × 45.

where it descends and comes to lie close to the dorsal wall of the posterior pharynx. It narrows towards the anterior end and has a narrow terminal opening below the posterior third of the brain. There are no ostia in its wall.

The dorsal diaphragm (fig. 45, *d.d.*) is poorly developed and is represented by web-like conjunctivo-muscular tissue full of large fenestrae. The muscular element is poorly developed and is confined to the external region where it is connected laterally with the tergum. These muscular elements on both sides of the diaphragm are the remnants of the dorsal transverse body muscles. The filaments of the network in the greater middle portion of the diaphragm are completely devoid of muscular elements and look like structureless, tendon-like, elastic fibrils which are mostly attached to the ventro-lateral walls of the dorsal blood vessel, and in a few cases they are continuous below the heart with the fibrils from the opposite side. The alary muscles are completely absent.

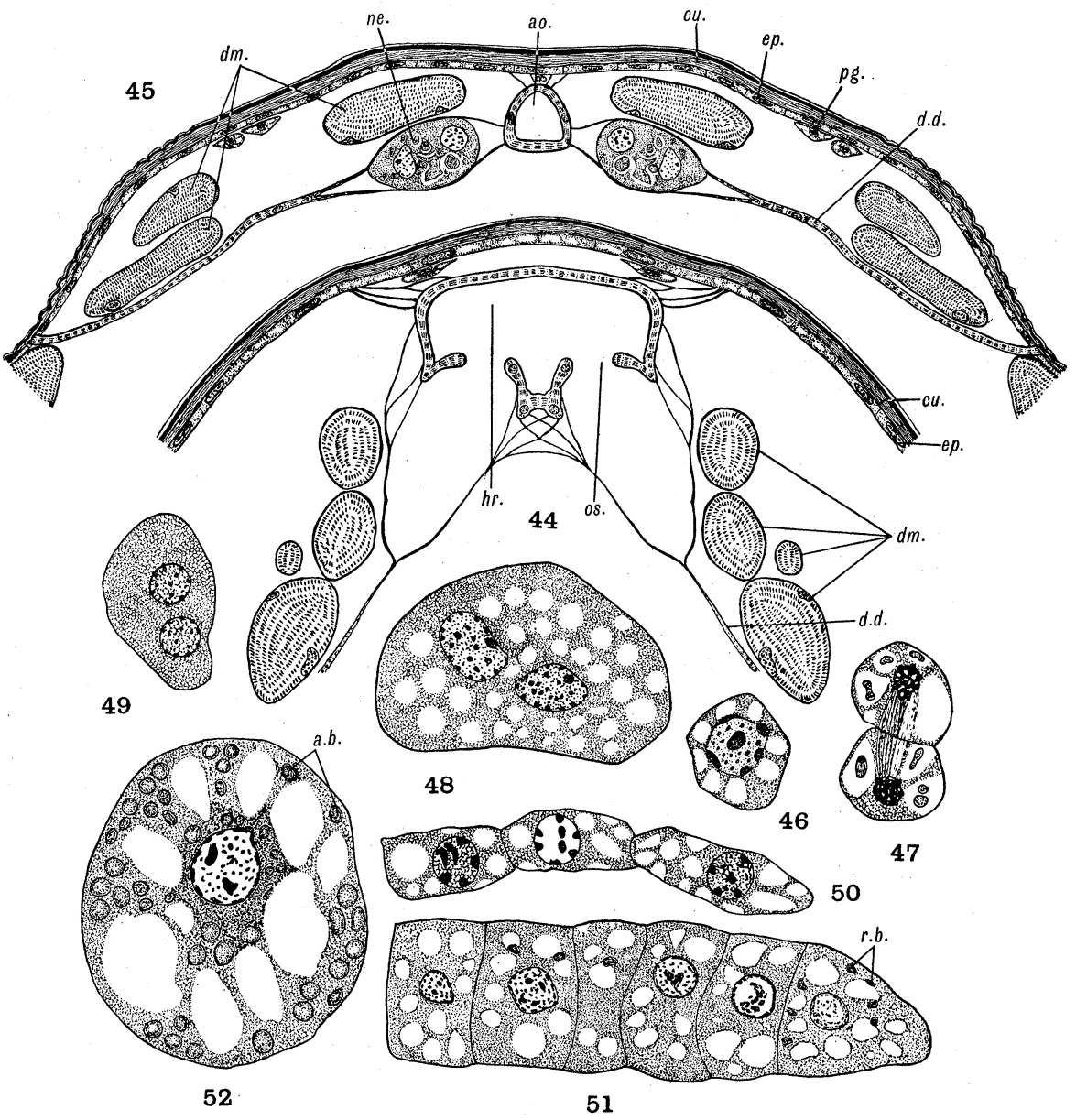
XII—The Phagocytes

In the flea larva the haemocytes are all of one kind and they also act as phagocytes. They are fairly numerous in recently hatched larvae. The phagocytes in the body cavity resemble the haemocytes present in the dorsal blood vessel, showing thereby that the phagocytes are purely blood cells. Normally the phagocytes are sub-spherical, but they assume different forms during their phagocytic activities. Their cytoplasm (fig. 46) is always highly vacuolated. The nucleus is spherical to ovoid with the chromatin condensed into a few big granules. They are about 8 μ in diameter and do not increase enormously in size, as is the case with *Calliphora erythrocephala* Mg. (Pérez, 1910, p. 14), when they have engulfed other tissues. They multiply by mitotic division even when they are full of inclusions (fig. 47). The function of the phagocytes is essentially that of engulfing and digesting the different larval elements which have undergone previous disintegration during the metamorphosis. I have never seen an instance in which the phagocytes have attacked and entered a normal healthy tissue. They only attack tissues in which signs of disintegration are apparent.

They are very abundant in all stages round the ventral nerve cord. Murray and Tiegs (1935, p. 443) believe them to originate in the pericardial tissue.

XIII—The Nephrocytes

In the flea larva only the pericardial or dorsal nephrocytes are present, there being no trace of the perioesophageal or ventral nephrocytes. The pericardial cells are arranged in two linear series of one cell thickness, one on each side of the dorsal blood vessel closely applied to its side in the pericardial sinus. The cells of each row are well separated from one another. They (fig. 45, *ne.*) are held in position close to the sides of the dorsal blood vessel by elastic fibrils extending from the dorsal diaphragm (*d.d.*) to the dorsal blood vessel. The nephrocytes (fig. 43,



FIGS. 44–52.—Fig. 44—Transverse section through the posterior chamber of the heart with its neighbouring parts of the dorsal sinus. × 687. Fig. 45—Transverse section through the dorsal sinus in the region of the seventh abdominal segment showing aorta and dorsal diaphragm. × 620. Fig. 46—A phagocyte of a defaecated larva. × 2012. Fig. 47—A phagocyte with inclusions undergoing mitotic division. × 1625. Fig. 48—A nephrocyte from the eighth abdominal segment. × 1750. Fig. 49—A prothoracic nephrocyte. × 1857. Fig. 50—Parietal fat cells of a recently hatched first-stage larva. × 1800. Fig. 51—Visceral fat cells of a third-stage larva. × 640. Fig. 52—A visceral fat cell with albuminoid bodies. × 1000.

ne.) are found almost in all segments from prothorax to the eighth abdominal segment and their total number is fairly constant, namely, from twenty-six to twenty-nine on each side of the dorsal blood vessel. They are usually arranged in segmental groups, especially in the anterior segments. The number of cells in each segmental group shows slight variation and the number of cells of the two sides of each segment may also vary. A pair of nephrocytes is present near the anterior margin of each of the prothoracic and metathoracic segments, but they are absent in the mesothorax. In the abdominal segments the following arrangement is found. The figures given first refer to the right side :—

I, 0–1, 0–1 ; II, 1, 1 ; III, 1, 1 ; IV, 3–5, 3–4 ; V, 4–5, 4–5 ; VI, 6, 6–7 ; VII, 4–6, 5–6 ; VIII, 5, 4–6.

The nephrocytes belonging to the first three abdominal segments are always near the anterior margin. Those of the prothorax are much smaller than the others, being only 14 μ in length, while the others are about 24 μ. The nephrocytes (fig. 48) are elongate-oval binucleate cells. The chromatin is reduced to a few sparsely scattered granules of which one is usually the largest. Vacuoles of different sizes are present in all except the prothoracic nephrocytes (fig. 49).

While examining a number of specimens which were starved for about a week to rid the alimentary canal of blood, I found two larvae which showed nephrocytes naturally stained a deep green to greenish-dark in colour. The coloration was due to the accumulation of a large number of small granules of some foreign material within the cytoplasm. The shape and form of the nephrocytes varied considerably, and this was due to their being packed with granules. Fig. 43 represents one of these larvae in the living condition, slightly compressed under a coverslip. A similar phenomenon was observed by KEILIN (1924, *a*, p. 222) in the larvae and pupae of *Lonchaea chorea* F., and he considers it " an interesting case demonstrating the natural function and distribution of these cells ".

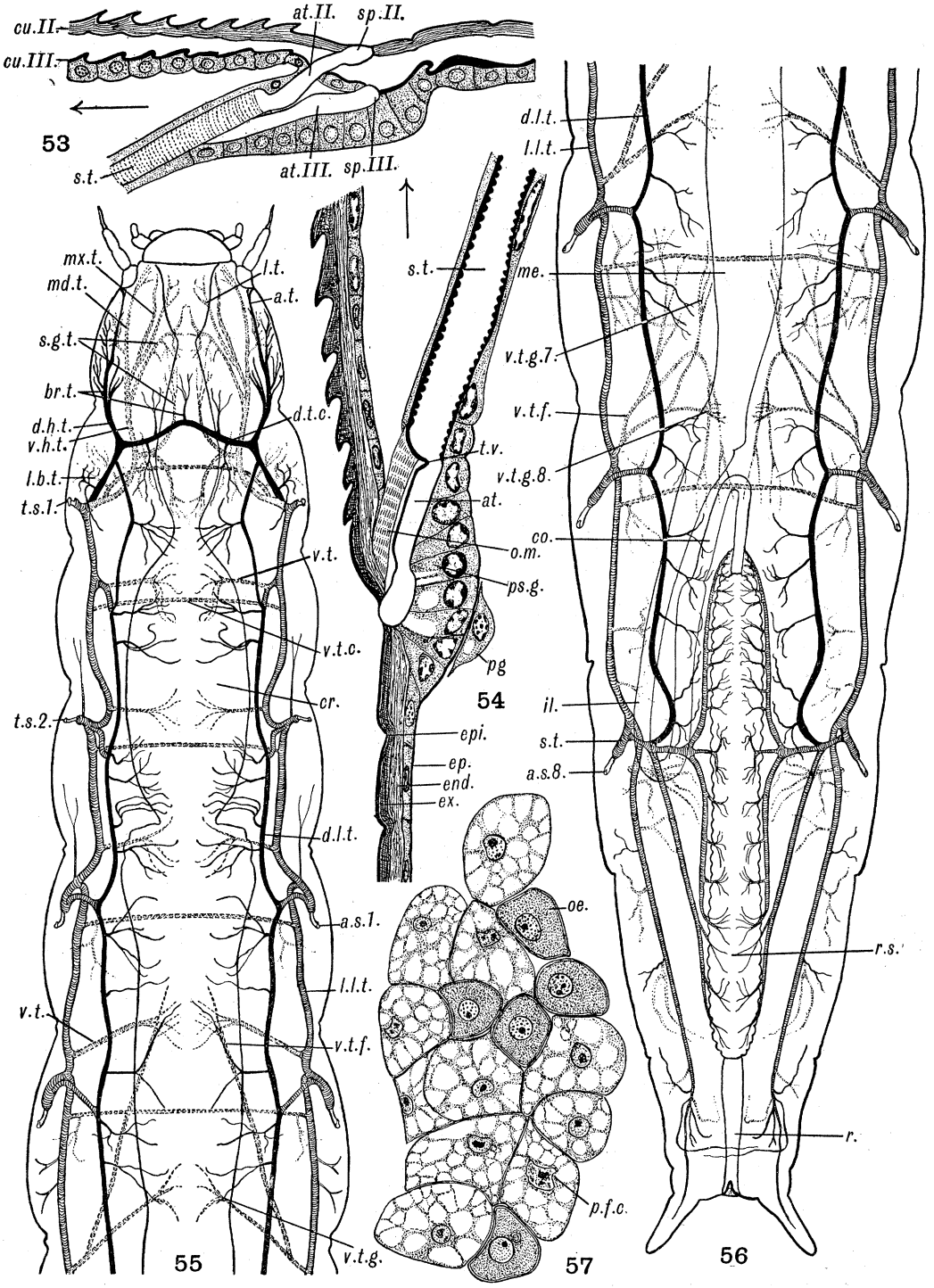
As to the nature of the foreign material which caused the coloration of the nephrocytes in the case of the flea larvae, the only suggestion that I can offer is that these larvae may have fed upon the larval faeces and thereby ingested the excretory product of the Malpighian tubules, which is of green colour. This green substance was then taken up by the mesenteric epithelial cells and passed on to the blood in the body cavity whence it has been taken up by the nephrocytes.

Regarding the function of nephrocytes, there is a great difference of opinion. These cells possess the property of absorbing ammonia carmine, when the latter is artificially introduced into the body either directly by injection or when administered with the food, and of retaining a precipitate of carmine in their cytoplasm. It is for this reason, and for their property to store up certain waste products either due to metabolic activities or taken within the body by chance, that these cells have been considered to be excretory in function. But according to HOLLANDE (1922) these cells play a part in breaking down complex colloids, which are transformed by ferments produced in the cells into crystalloids. These are then thrown into the blood and from which they are removed by the Malpighian tubules. This property

of absorbing carmine is predominantly due to their power of absorbing colloids. HOLLANDE (1916, pp. 67, 74) also considers that these cells absorb albuminoid substances from the blood into which they diffuse from the alimentary canal, and then transform them into assimilable substances. During the metamorphosis, according to HOLLANDE, the albuminoid substances in these cells are of different origin. I have never found albuminoid susbstances in the nephrocytes of the flea larva, although they are fairly abundant towards the approach of metamorphosis in the larval fat cells. On the other hand, the nephrocytes possess globular inclusions of different sizes towards the approach of metamorphosis (fig. 45, *ne.*) ; but these are formed as the result of disintegration of their cytoplasm and ultimately they are destroyed by globular formation during the metamorphosis.

XIV—THE FAT BODY

In the flea larva only the trophocytes are present and the urate cells are absent. Throughout the larval life the fat cells show well-defined differentiation into parietal and visceral fat cells. The parietal fat cells are present in all the body segments and show a somewhat segmental arrangement. They are arranged in a single thin layer situated between the integument and the body wall muscles. In a recently hatched first-stage larva (fig. 50) they are elongate-oval cells about 10–16 μ in length connected together at the ends. Throughout the third stage they occur as isolated cells, normally of oval form (fig. 57, *p.f.c.*), but they may assume different forms owing to mutual compression. Their largest diameter is about 46 μ. The visceral fat cells, on the other hand, form two elongate and compact, trilobed masses of more or less quadrangular cells (fig. 51) throughout the larval life. Each mass lies on one side of the alimentary canal and is in intimate association with the gonads, the salivary glands, and the Malpighian tubules of its side. In the living condition the fat cells are opaquely white. Fat globules of large size are present in the fat cells of the recently hatched first-stage larva. These globules increase in number and size during the growth of the larva. At about the time of defaecation the visceral fat cells (fig. 52) elaborate albuminoid bodies (*a.b.*) and these increase in number during the transitional period, while the parietal cells remain completely devoid of them until the late prepupa and thus form albuminoid bodies much later than the visceral fat cells. The visceral cells dissociate themselves from one another during the metamorphosis and form large spheres full of albuminoid bodies, which float freely in the body cavity. The albuminoid bodies are arranged in the cytoplasmic meshes surrounding the fat droplets and are highly eosinophil. With the increase of albuminoid bodies in the fat cells there is a corresponding decrease in the amount of fat. The nucleus is spherical to oval in form, rich in chromatin which is usually condensed into granules of unequal size. It undergoes slight distortion due to the pressure exerted by the fat globules during the metamorphosis. A few small, highly refractive bodies (fig. 51, *r.b.*) of irregular form are sometimes found in the visceral fat cells.



FIGS. 53–57.—Fig. 53—Side view of the seventh abdominal spiracle and atrium showing the formation of these structures of a third-stage larva behind those of a second-stage larva. × 1000. Fig. 54—Longitudinal section passing through the seventh abdominal spiracle of a third-stage larva. × 1111. (The head of arrow indicates in figs. 53 and 54 the anterior side.) Fig. 55—Tracheation of head, thorax, and first two abdominal segments of a third-stage larva, dorsal view. × 100. Fig. 56—Tracheation of the last five abdominal segments of a third-stage larva, dorsal view. × 100. (Darkly shaded ones are dorsal tracheae and the others are ventral tracheae in figs. 55 and 56.) Fig. 57—Oenocytes with the surrounding parietal fat cells of the second abdominal segment of a third-stage larva. × 372.

XV—The Respiratory System

The spiracles—There are ten pairs of functional spiracles in the third-stage flea larva and thus it is of the holopneustic type. Two pairs belong to the thorax and eight pairs to the first eight abdominal segments. The mesothoracic spiracles (fig. 55, *t.s.*1.) have shifted forwards so as to come to lie in the posterior portion of the prothoracic tergum, and they have wrongly been called by previous workers prothoracic spiracles, as it is a well-known fact that the prothoracic spiracles are completely absent in larval or adult insects. Their peculiar location, namely, in the posterior half of the prothorax, suggests that they have migrated forwards from the following segment, as all the remaining spiracles are found in the anterior half of the segment to which they belong.

According to Keilin (1924, *b*, p. 127), the primitive position of spiracles of an insect is the anterior intersegmental membrane of the segment to which they belong, as the ten pairs of spiracles of an insect can only possibly correspond to the ten intersegmental spaces of the eleven spiracle-bearing segments of the body. The shifting of the mesothoracic spiracles on to the prothorax and the backward migration of other spiracles have been clearly demonstrated by him in the larva of *Mycetophila cingulum*. Keilin's contribution as to the primitive position of spiracles in insects has not gained the importance it deserves. According to Lehmann (1926, p. 367), in the embryo of *Carausius morosus* Br. the spiracular rudiments are formed on the lateral sides of the anterior end of the segment. The different positions gained by spiracles are due to their migration and to the important fact that in adult insects there is a secondary segmentation (*vide* Snodgrass, 1927, p. 7), and not only the primitive anterior intersegmental membrane but also a posterior part of the preceding segment called the precosta has become fused with the anterior margin of the following segment. As a result of this, the spiracles have come to lie in the anterior region of the segment and have thus lost their primitive intersegmental position. The location of the spiracles on the anterior margin of the pleural region of their segment is a well-known fact (*vide* Weber, 1933, p. 429).

During moulting of the flea larva (fig. 53), I have observed that the atrial pits of the next stage (*at.III.*) are formed a little behind those of the preceding stage (*at.II.*) in all the spiracles except the first pair of spiracles. The proliferating cells of all the spiracles except the first pair are confined to the posterior sides of the atria while in the first pair of spiracles they are found all round the atria. The relative positions of the first pair of spiracles of the three stages of the flea larva clearly show a tendency towards their anterior migration, as in the first-stage larva they are very close to the posterior margin of the prothorax, while in the third-stage larva they are much in front of its posterior margin. These observations of mine on the anterior migration of the mesothoracic spiracles and the posterior migration of all the other spiracles lend support to Keilin's conclusions based on the study of larvae of the Mycetophilidae and Scatopsinae.

The spiracular aperture is keyhole-shaped, with its broader end facing anteriorly in the case of the first pair of spiracles and facing posteriorly in the case of others. Each spiracular aperture (fig. 54) leads into a tubular chamber, the atrium (*at.*). The atrium is less than half as broad as the spiracular trachea (*s.t.*). The atria of the thoracic spiracles are considerably shorter than those of the abdominal ones. The spiracular tracheae and atria of the thoracic spiracles run directly outwards to the surface, but those of the abdominal ones run backwards before they open by the spiracles. The spiracles are simple apertures devoid of any kind of external closing apparatus and thus they are permanently open. There is no trace of fringed processes forming a filter apparatus, such as is found in lepidopterous larvae. The peritreme is also absent. The wall of the atrium is smooth. A very simple kind of internal closing apparatus is present. It consists of a semicircular pouch-like inpushing of the anterior wall of the atrium, just before its junction with the spiracular trachea, which forms an internal fold that acts as a valve (*t.v.*). The occlusor muscle (*o.m.*) arises on the tergal wall immediately in front of the spiracle and is inserted on the proximal end of the spiracular trachea. By its contraction the fold increases in size and is pressed against the posterior wall of the atrium, and thus the entrance into the spiracular trachea is closed. The opening of the tracheal orifice is caused by the elasticity of its chitinous wall which regains its former position. The above described closing mechanism is present in all the abdominal spiracles. The closing apparatus of the first thoracic spiracle is of a different nature, but, owing to the difficulty of examining it in a suitable position, I could not determine its exact nature. The same difficulty was experienced in determining the nature of the closing apparatus of the metathoracic spiracle. The first pair of thoracic spiracles are the largest and the metathoracic ones are the smallest. The latter are closed and non-functional in the first- and second-stage larvae, which are thus of the peripneustic type.

On the posterior side of the atrium there is a group of broad eosinophil cells (fig. 54, *ps.g.*), some of which possess vacuoles. These cells appear to have a double function. They play a part in the formation of the new spiracles at the time of moulting and at the time of metamorphosis. The presence of vacuoles in some of them in the upper region indicates that they also form perispiracular glands such as are present in some Diptera (*vide* KEILIN, TATE, and VINCENT, 1935, p. 257). These cells in the living condition contain refractile globules of different sizes very similar to those observed by the aforesaid authors. These cells probably secrete some kind of oily or waxy substance which prevents the wetting of the spiracle and thus act as hydrofugal organs.

Tracheation of the head (fig. 55)—The tracheation issuing from the first pair of thoracic spiracles (*t.s.*1.) is considerably different from that of the other spiracles, as from these primarily mesothoracic spiracles proceeds the tracheal supply not only of the prothorax and of the mesothorax but also of the head. The spiracular trachea of the first thoracic spiracle gives off two main branches, one running backwards and the other forwards. The anterior branch divides near its origin into

the dorsal and ventral head trunks. The dorsal head trunk (*d.h.t.*) sends branches to the antenna (*a.t.*), the dorsal muscle fibres of the mandible, the brain (*br.t.*), and the dorso-lateral region of the head and the prothorax. The ventral head trunk (*v.h.t.*), near its proximal end in the prothoracic region, gives off a transversely running branch which ramifies on the posterior region of the suboesophageal ganglion, (*s.g.t.*) and on the prothoracic ganglion, and thus it is comparable with the visceral branches of the hinder region. The main branch of the ventral head truck runs forwards into the head and supplies the mandible (*md.t.*) and its lower muscle fibres, the maxilla (*mx.t.*), the labium (*l.t.*), and the anterior region of the suboesophageal ganglion (*s.g.t.*). The dorsal head trunks of the two sides are connected by a dorsal transverse commissure (*d.t.c.*) in the anterior region of the prothorax, which gives off branches to the dorsal musculature of the prothorax and the head and the posterior part of the brain (*br.t.*). The ventral head trunks are similarly connected by a narrow ventral transverse commissure which supplies tracheae to the ventral muscles and to the prothoracic leg buds (*l.b.t.*). Taking into consideration the ramification of the two head trunks, it appears that the dorsal head trunks correspond to the dorsal longitudinal trunks and ventral head trunks to the lateral longitudinal trunks of the body.

Tracheation of the thorax (fig. 55)—This resembles in its general plan that of the abdomen, but it departs from the general plan in the prothorax and the mesothorax. The spiracular tracheae of both pairs of thoracic spiracles are considerably shorter than those of the abdominal spiracles, especially those of the mesothoracic spiracles. The posterior main branch of the mesothoracic spiracle divides into two main trunks in the anterior half of the mesothorax. The inner and dorsal trunk becomes continuous with the dorsal longitudinal trunk (*d.l.t.*), and the outer and ventral trunk joins with the lateral longitudinal trunk (*l.l.t.*) of the posterior region. In the prothorax and in the anterior half of the mesothorax there is no continuation of the dorsal longitudinal trunk, and its place is taken by a narrow longitudinal trachea connecting the dorsal head trunk and the inner dorsal branch of the posterior main branch originating from the mesothoracic spiracle. It sends one branch to the dorsal body wall musculature and the dorsal parietal fat tissue, as is the case with the branches of the dorsal longitudinal trunk. The visceral branch belonging to the mesothorax (*v.t.*), which ramifies on the mesothoracic ganglion, does not arise from the lateral longitudinal trunk but from the inner dorsal branch before it becomes continuous with the dorsal longitudinal trunk.

Tracheation of the abdomen (figs. 55, 56)—The tracheation originating from the first seven pairs of spiracles is fairly uniform in its arrangement, but it has undergone a great complication in connexion with the eighth pair of spiracles. Each spiracular trachea gives off two main branches, one going upwards and inwards and the other downwards. The upper branch again divides into an anteriorly running and a posteriorly running branch, and these upper anterior and posterior branches from the spiracular tracheae of consecutive segments unite so as to form the dorsal longitudinal trunk (*d.l.t.*) of each side, which sends branches to the heart, the dorsal

portion of the parietal fat tissue, and the dorsal musculature of the body wall. The lower branch similarly gives off an anterior and a posterior branch which unite with those of neighbouring segments to form the lateral longitudinal trunk (*l.l.t.*). The lateral longitudinal trunks of the two sides are connected with each other by a ventral transverse commissure (*v.t.c.*) in the anterior half of each of the segments from the mesothorax to the seventh abdominal segment. The ventral commissures send a few branches to the ventral body wall musculature and the sternal portion of the parietal fat tissue. This ventral commissure, according to SNODGRASS (1935, p. 430), is formed by the anastomosis of the two ventral tracheae in each segment, and, according to this author and to LEHMANN (1926, p. 336), the ventral trachea supplies the ventral musculature and the ventral nerve cord. In the flea larva ventral transverse commissures do not supply the nerve cord. In each of the above-mentioned segments each lateral longitudinal trunk sends an internal branch which ramifies on the ganglion of its segment, the visceral fat tissue, and gonads in the segments in which they lie. These branches lie in front of the ventral commissure and they correspond to the visceral branches of the basic scheme of tracheation of LEHMANN. There is a very poor supply of tracheation to the stomodaeum, mesenteron, and the anterior section of the proctodaeum, and no special branch large enough to be seen in the mounted preparations could be traced to the above-mentioned regions of the alimentary canal. The visceral trachea (*v.t.*) of each of the segments, from the metathorax to the second abdominal segment, is composed of a single main branch ramifying mostly on the ganglion of its respective segment, but the visceral trachea of each from the third to the sixth abdominal segment divides near its origin into two branches, one going to its ganglion (fig. 55, *v.t.g.*) and the other to the visceral fat tissue (fig. 55, *v.t.f.*). In the seventh abdominal segment the visceral trachea is larger than all the preceding ones and gives off four branches, two (fig. 56, *v.t.f.*) of which ramify on the visceral fat tissue and the other two (fig. 56, *v.t.g.*7, *v.t.g.*8) on the seventh abdominal ganglion and the last terminal complex abdominal ganglion. Each of the lower branches of the spiracular tracheae of the metathoracic and the first abdominal spiracles gives off an anteriorly running small trachea ramifying on the lateral musculature of the body wall and the lateral portion of the parietal fat tissue.

Each eighth spiracular trachea (fig. 56, *s.t.*) gives off, as usual, a lower main branch and an upper main branch. The anterior branch of the lower main branch forms the terminal section of the lateral longitudinal trunk, and its posterior branch runs backwards and gradually narrows towards the tip of the anal strut and may be considered a direct continuation of the lateral longitudinal trunk. It supplies branches to the dorsal, lateral, and ventral muscles of the body wall and the parietal fat tissue of these regions. The upper branch from the spiracular trachea gives off three main branches. The anterior of these forms the terminal section of the dorsal longitudinal trunk. The middle one gives off three branches which ramify profusely on the lateral wall of the anterior three-quarters of the rectal sac (*r.s.*). The posterior one similarly ramifies on the terminal quarter of the rectal sac. These are

the visceral branches of the eighth spiracle, and their terminal parts are lodged in the lateral groove of the rectal sac (*see* fig. 30, *tr.*). There is no ventral transverse commissure in the eighth segment.

XVI—The Oenocytes

The oenocytes are found in all the three stages of the flea larva. They are colourless and are distributed as free cells among the cells of the parietal fat tissue. They (fig. 57, *oe.*) show variation in their form and size owing to their compression by the surrounding fat cells, but normally they are sub-spherical in form. They occur in the pleural regions of all the first nine abdominal segments. The presence of oenocytes in the ninth abdominal segment of the flea larva is a point of great interest. According to most investigators (Snodgrass, 1935, p. 411), the oenocytes originate in the embryo from the ectoderm at places just posterior to the spiracles in the first eight segments. Thus the association of the oenocytes with spiracles is purely incidental and has no morphological significance. As a matter of fact, the oenocytes are ectodermal in origin and their presence in the ninth abdominal segment in which the spiracles are absent clearly indicates that the formation of oenocytes is not confined to any particular part of the ectoderm, as is often considered to be the case. They are smaller than the surrounding fat cells, being only 21–29 μ in the larger diameter. Their number on each side of a segment varies from five to eight. Usually they are found away from the epidermis but sometimes, a little before second larval ecdysis, some of these oenocytes are embedded in the epidermis with one end, which is narrow, closely applied to the cuticle and the other broad end projecting into the body cavity, thus showing that new oenocytes are formed from the epidermis. They are often found arranged in groups of closely placed free cells and are not held together by fine branches of tracheae, as is the case with Lepidoptera and Trichoptera (*vide* Snodgrass, 1935, p. 411).

Each oenocyte has a well-developed external limiting membrane. The cytoplasm is strongly eosinophil and homogeneous. Each cell possesses one nucleus, which is large and spherical with the chromatin usually in the form of a big granule, the nucleolus, and numerous very fine granules. In one oenocyte in a third-stage larva there were two nuclei.

As to the function of oenocytes, there are different views. Some earlier workers (Pantel, 1898, and Berlese, 1899–1901) thought them to be excretory in function. According to Glaser (1912, p. 222), they secrete an enzyme which oxidizes reserve food material stored up as fat. Hollande (1914) considers them in a sense as complementary to fat cells in that they form, and keep in their cytoplasm, deposits of wax. Koller (1929, p. 288) suggests that they secrete a hormone which induces moulting. Wigglesworth (1933, p. 307), however, is of the opinion that they are concerned in the formation of the new cuticle by synthesizing the protein or the cuticulin elements of the cuticle.

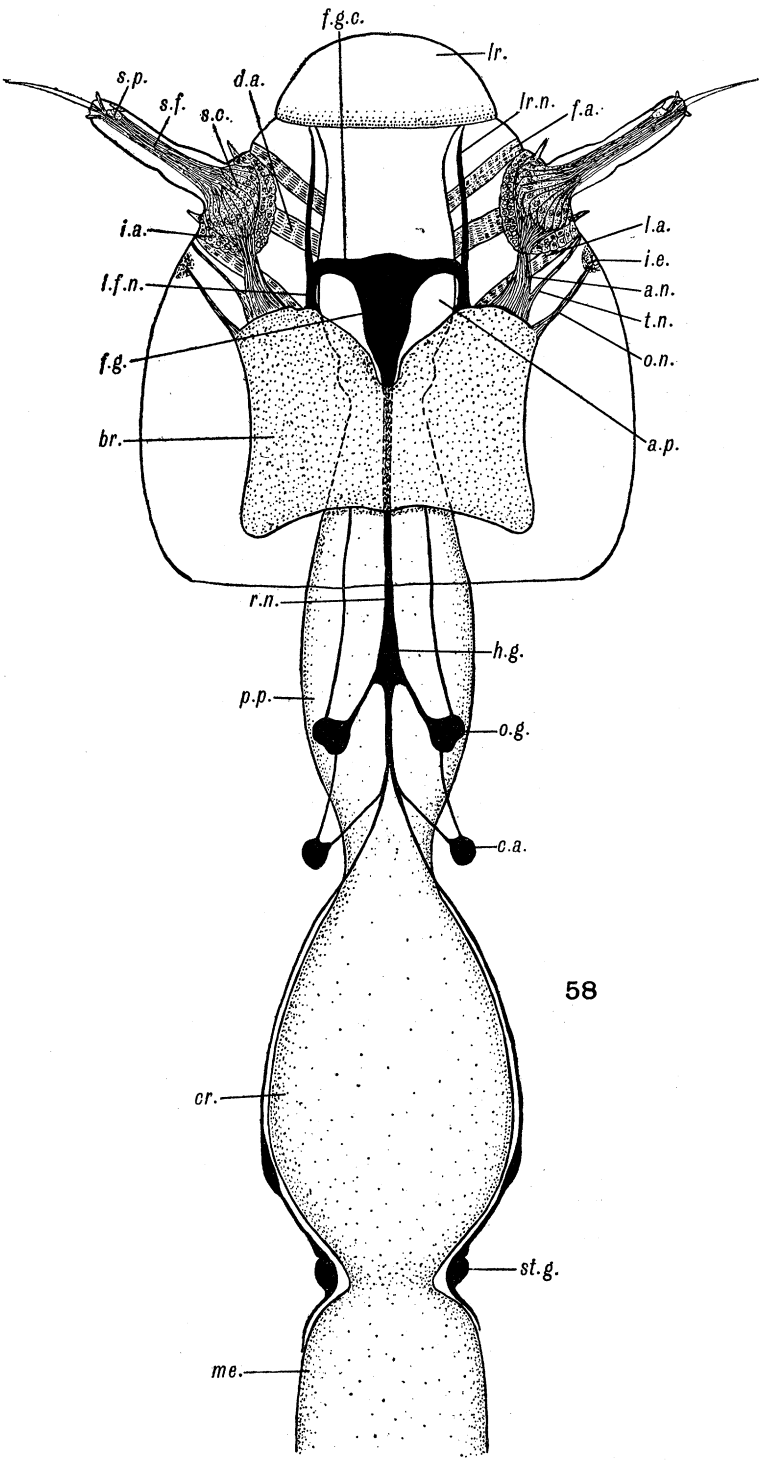


FIG. 58—Dorsal view of the head and the stomodaeum showing the stomodaeal nervous system and the antennal sense organs and musculature. (Diagrammatic.)

XVII—The Nervous System

The central nervous system (fig. 35) is composed of the brain (*br.*), the suboesophageal ganglion (*s.g.*) lying in the posterior half of the head capsule, and a ventral chain of eleven ganglia in the body.

The brain (fig. 58, *br.*) is bilobed in its anterior lesser part and forms a single compact mass in its posterior greater part. It gives off three nerves on each side from its antero-lateral margin. The labrofrontal nerve (*l.f.n.*) originates as a short, stout nerve from the lower part of the antero-lateral margin of the brain. It divides into an inner branch, the frontal ganglion connective (*f.g.c.*), and an outer branch, the labral nerve (*lr.n.*). The antennary nerve (*a.n.*) arises on the antero-lateral margin of the brain at a higher level than the labrofrontal nerve. Before entering into a group of sensory cells at the base of the antenna, it gives off a small branch, known as the tegumentary nerve (*t.n.*), to the head integument. A third rudimentary nerve arises from the anterior dorso-lateral corner of each lobe of the brain and goes to a group of cells which are different from the ordinary epidermal cells, representing imaginal cells of the adult eye. Taking into consideration its origin and its ultimate distribution, I consider it to be a rudimentary optic nerve (*o.n.*). Its poor development is associated with the absence of eyes in the flea larva. Posteriorly the brain gives off a pair of nerves which form the roots of the oesophageal ganglia (*o.g.*).

The suboesophageal ganglion is a dorso-ventrally compressed single mass, and its paired nature is only noticeable in sections (fig. 16, *s.g.*). It is slightly notched (fig. 9, *s.g.*) dorsally about the junction of the anterior third and the middle third, so as to enclose the bridge of the tentorium (*t.b.*). Anteriorly it sends off paired nerves to the mandibles (*m.n.*), the maxillae (*mx.n.*), and the labium (*l.n.*).

The ventral nerve cord (fig. 35) is provided with eleven ganglia, three thoracic (*t.g.*) and eight abdominal (*a.g.*), and extends to the posterior end of the sixth abdominal segment. The three thoracic ganglia are situated near the middle of their corresponding segments. The first five abdominal ganglia, on the other hand, lie close to the anterior intersegmental membranes of their respective segments. The sixth abdominal ganglion is located in the middle of the fifth abdominal segment, and the seventh and eighth ganglia lie in the sixth abdominal segment. Each ganglion is connected with its adjacent ganglion by a pair of well-separated connectives. Each of the first ten ganglia gives off a pair of principal nerves to its own segment, which bifurcate near their origins. The terminal ganglion (*a.g.*8.) sends off two pairs of long stout nerves. The proximal pair, which originate from the middle of the terminal ganglion, ramify in the eighth abdominal segment. The distal pair, which arise from the posterior end of the terminal ganglion, run backwards and supply the ninth and tenth abdominal segments. The terminal ganglion is therefore to be regarded as a compound ganglion formed by the fusion of the three primitively distinct ganglia of these three segments.

The stomodaeal or stomatogastric nervous system (fig. 58)—The frontal ganglion (*f.g.*), which lies above the anterior pharynx (*a.p.*) between the anterior and medial

dorsal dilators of the two sides (fig. 15, *f.g.*), is sub-triangular in shape, with its apex directed backwards. Its two anterior angles give off two nerves known as the frontal ganglion connectives (fig. 58, *f.g.c.*), which form a bridge over the front end of the anterior pharynx and then run backwards close to the lateral sides of the anterior pharynx to the brain (*br.*). Posteriorly it gives off a median recurrent nerve (*r.n.*), passing above the mid-dorsal line of both sections of the pharynx (*a.p.*, *p.p.*) and beneath the brain and the aorta. Behind the brain the recurrent nerve is swollen so as to form a medium-sized hypocerebral ganglion (*h.g.*). The hypocerebral ganglion gives off a pair of short nerves to the oesophageal ganglia (*o.g.*) which are situated near the hinder end of the posterior pharynx (*p.p.*) and lie dorso-laterally to it on each side. The oesophageal ganglia are connected directly with the posterior margin of the brain by a pair of nerves, the roots of the oesophageal ganglia. A short distance beyond the hypocerebral ganglion, the recurrent nerve divides into two lateral branches. Each lateral branch, near its origin, gives off a nerve to the corpus allatum (*c.a.*) of its side, which lies opposite to the junction of the posterior pharynx and the crop (*cr.*). Each corpus allatum is directly connected with the oesophageal ganglion of its side by a connective. The two lateral branches of the recurrent nerve then run laterally to the crop and each ends in a large ingluvial or stomachic ganglion (*st.g.*) situated close to the junction of the crop and the mesenteron (*me.*). Each lateral branch in addition possesses a slight ganglionic thickening in front of the stomachic ganglion. The latter sends off nerves which are distributed on the mesenteron.

The ventral sympathetic nervous system (fig. 35) consists of ten longitudinal median nerves (*me.n.*) each lying between a pair of interganglionic connectives. Every median nerve originates from the posterior part of the ganglion situated in front of it and gives off a pair of lateral branches which go to the respective spiracles. In the thorax each median nerve does not extend beyond its point of bifurcation into lateral branches, but in the abdomen it is continued by a thin filament going to the following ganglion. At the point where the lateral branches are given off each median nerve forms a small triangular swelling.

The sense organs—The eyes are totally absent and there is hardly any trace of the photo-receptive tissue, but, nevertheless, the flea larvae are negatively heliotropic to ordinary white light. This photo-negative property of the flea larva suggests the presence of the photo-receptive tissue. The optic nerve, as mentioned before, is poorly developed. It is only a little before metamorphosis that the above-mentioned (p. 513) imaginal cells of the adult eye appear. The response of the flea larva to ordinary white light may be purely due to reflex behaviour to light (Imms, 1931, p. 105).

Specialized sense organs are found at the bases of the antennae and of the maxillary and labial palps. Morphologically these three kinds of sense organs are very similar. Each consists of a chemo-receptive type of sensillum consisting (fig. 58) of a group of fusiform cells (*s.c.*) continuous at one end with the nerve fibres and drawn out at the other end into extremely long distal processes forming a compact fasciculus (*s.f.*)

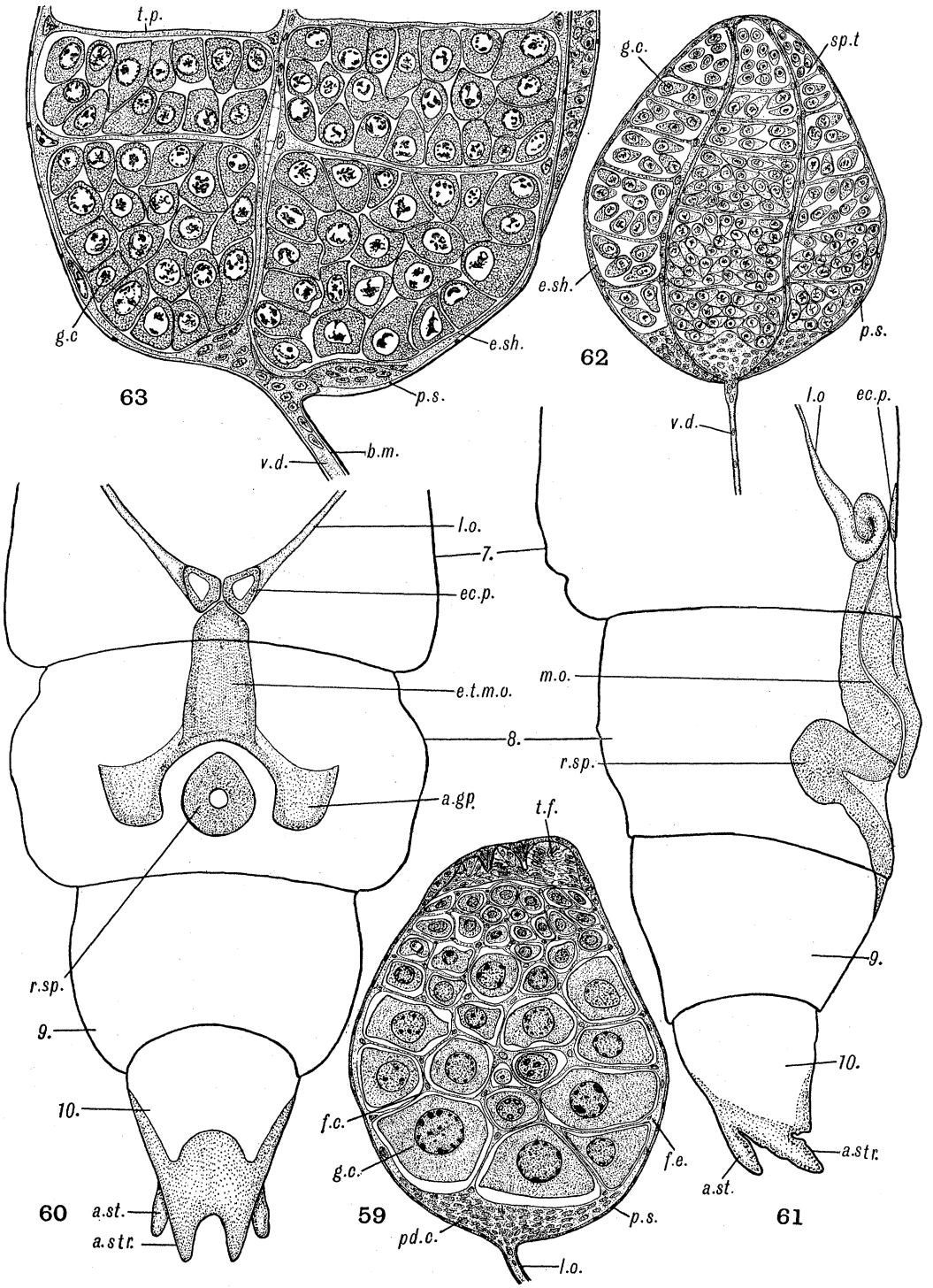
which goes to the cuticular processes. The antennae, in addition to the cuticular processes, possess pit-like sensoria (*s.p.*) having thin non-sclerotized wall. *Sensilla basiconica* are also found in connexion with the above-mentioned parts, and I have found only *sensilla campaniformia* on the head region.

XVIII—The Reproductive System

The rudiments of the gonads of the third-stage larva lie in dorso-lateral positions close to the mesenteron and occupy various positions between the fourth and sixth abdominal segments. They are surrounded on all sides except the distal end by the visceral fat tissue. The gonads of the two sides do not lie at the same level, the left one being anterior in position. They differ in form, size, and structure in the two sexes. The larger gonads, which are elongate-oval, are the male gonads and the smaller ones, which are pyriform in shape, are the female gonads. Perfiljew (1926, pp. 122, 123) has wrongly considered the four-chambered larger gonads as those of the female and the single-chambered smaller ones as those of the male. He was led into this mistake on account of the presence of four ovarioles in the ovary of *L. pectiniceps*, which he thought corresponded to the four lobes of the larger kind of gonads of the larva, although a careful study of Lass's description and diagrams (1905, p. 85, pl. v, figs. 2, 3, 4) would have prevented him from making this serious mistake. I have traced the post-embryonic development of the male gonads up to the adult stage, and the quadrifollicular condition is retained in the adult, although no worker has ever mentioned this fact before.

(A) The Female Reproductive System

The female gonads—The ovarial rudiments are a pair of pyriform bodies which are smaller than the testicular rudiments, being only 143 to 179 μ in the larger diameter. Each ovarial rudiment (fig. 59) is unichambered and is surrounded by a peritoneal sheath (*p.s.*) in which extremely small nuclei are discernible. The peritoneal sheath, at the time of division of the ovarial rudiment into ovarioles, becomes inflected between the lobes. Internally to the peritoneal sheath there is a thin layer of follicular epithelium (*f.e.*), which rests on the basement membrane forming the so-called tunica propria. The cavity of the gonad is occupied by loosely packed germ cells (*g.c.*) which gradually increase in size and show gradation of differentiation from the anterior to the posterior end. Each germ cell is surrounded by widely spaced small cells, the follicle cells (*f.c.*). Those belonging to the peripheral germ cells are in direct continuation with the follicular epithelium, showing thereby that the follicle cells are of the same origin as the latter. At the base of the ovarial rudiment there is a large group of small proliferating cells (*pd.c.*) which are continuous with the follicular epithelium and form a sort of plug. These give rise to the ovariole pedicels and the follicular egg tubes of the adult. At the distal end of the ovarial rudiment there is another group of small cells continuous with



FIGS. 59–63.—Fig. 59—Longitudinal section through the ovarial rudiment of a third-stage larva. × 397. Fig. 60—Ventral view of the terminal abdominal segments of an early female prepupa showing the ectodermal rudiments of the reproductive system. × 150. Fig. 61—Side view of the terminal abdominal segments of a late female prepupa showing the ectodermal rudiments of the reproductive system. × 150. (The darkly shaded portions in figs. 60, 61 represent the regions where the ectoderm has proliferated.) Fig. 62—The testicular rudiment of an early third-stage larva. × 307. Fig. 63—Longitudinal section through the basal portion of a testicular rudiment of a late third-stage larva. × 387.

the follicular epithelium, in which signs of division into short, thick, solid strands of cells corresponding to the number of the future ovarioles are present. These develop into the terminal filaments (*t.f.*) of the adult ovarioles. The terminal filaments of the ovarial rudiments are extremely narrow strands of structureless tissue. From the general arrangement and appearance it appears that the distal and proximal groups of small cells, the cells of the follicular epithelium, and the follicle cells are of the same origin. The female germ cells are comparatively fewer and larger than the male germ cells. Their nuclei are very large.

The lateral oviducts (fig. 60) of the third-stage larva are extremely fine straight cords (*l.o.*) which have small sparsely scattered nuclei and in which there is no visible sign of lumen. They are of mesodermal origin and extend to the posterior margin of the venter of the seventh abdominal segment. In the prepupa they are connected with two closely placed, though separate, pyriform ectodermal pouches (*ec.p.*) which open on the seventh abdominal venter. The presence of these pouches on the seventh abdominal segment, which are apparently formed as ectodermal invaginations, is a point of great morphological importance, as in primitive insects each lateral oviduct had its individual opening on the seventh abdominal segment, and this primitive condition is retained in the adult Ephemeroptera. Thus the primitive condition is repeated in the ontogeny of the flea.

The median oviduct is absent in the larval stage, but its formation starts at the close of the third larval stage. Immediately behind the ectodermal pouches of the lateral oviducts there is a median thickening, due to proliferation (fig. 60, *e.t.m.o.*) of the ectoderm on the venter of the eighth abdominal segment, which forms the median oviduct. The ectodermal pouches of the lateral oviducts are then closed and their ducts become continuous with each other and with the median oviduct. In this way the terminal female genital aperture is shifted towards the posterior half of the eighth abdominal venter. In the prepupa (fig. 61, *m.o.*) it is fully formed and is lined with cuticle which is continuous with that of the body wall. The anterior small section of the median oviduct is formed by fusion of the posterior parts of the ectodermal pouches of the lateral oviducts.

The rudiment of the spermatheca (figs. 60, 61, *r.sp.*) is formed as an invagination of the integument close to the posterior margin of the eighth abdominal venter. It is well developed even when the median oviduct is only represented by the ectodermal thickening. At an early stage it is represented by a mass of proliferating cells having a small cavity opening near the posterior margin of the eighth abdominal venter some distance behind the definitive terminal aperture of the median oviduct when it is formed. The terminal aperture of the median oviduct and the spermathecal aperture at first open separately on the body wall. Towards the end of the prepupal stage a ventral inflexion of the body wall between the eighth and ninth abdominal segments lead to the formation of the vagina of the adult, and in this way the aperture of the spermathecal rudiment and the aperture of the median oviduct become internal, the former lying on the dorsal side of the vagina, which is continuous anteriorly with the median oviduct. The above-mentioned arrangement is attained

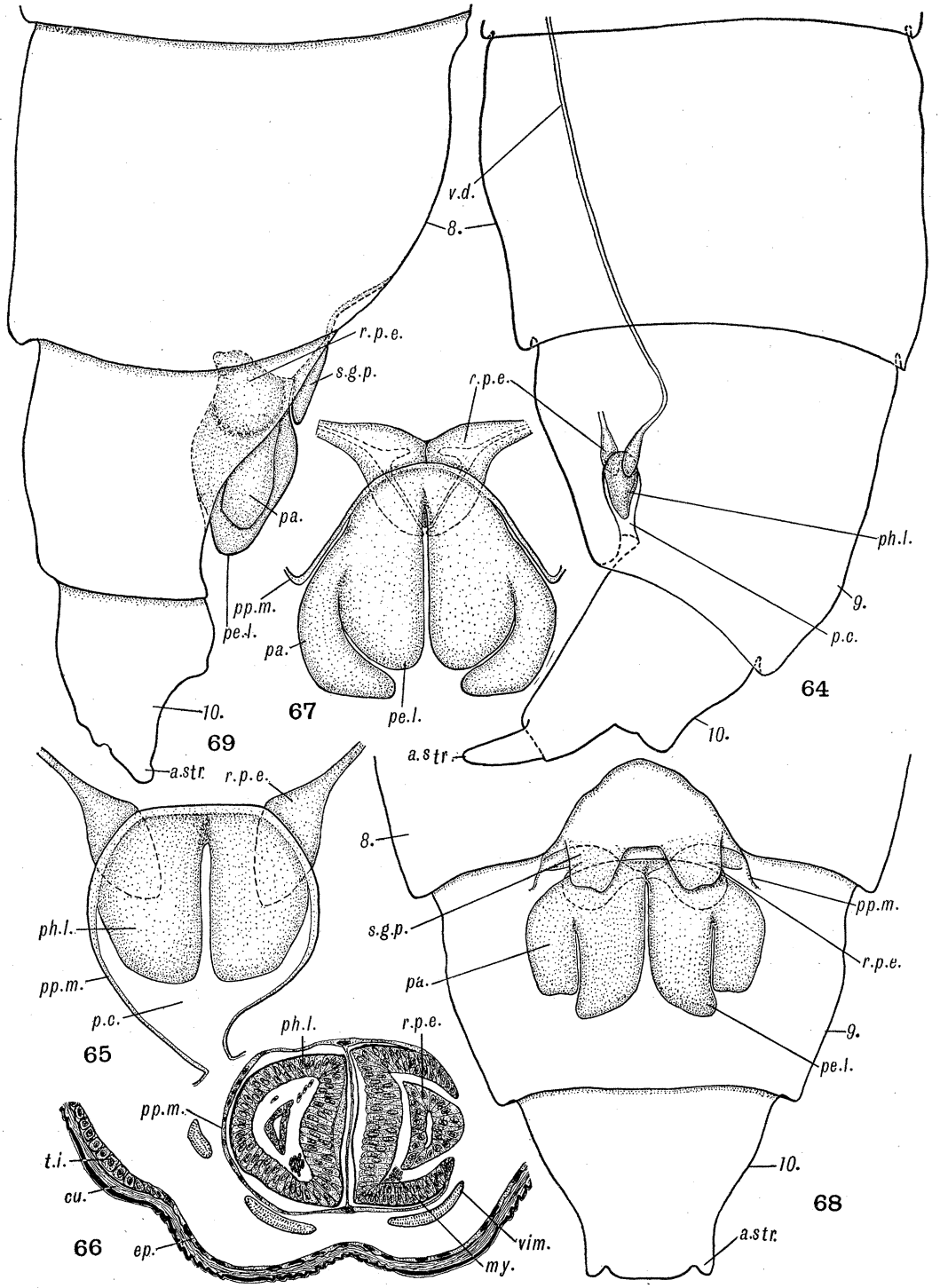
at the close of the prepupal stage and is retained, with considerable modification, in the adult.

The rudiments of the ovipositors (fig. 60) only appear in the prepupa in the form of ectodermal proliferating thickenings on the eighth abdominal segment. These are the anterior pair of gonopods (*a.gp.*). They are present in the pupa but disappear in the adult. The gonapophyses belonging to the ninth abdominal segment are not present at any stage of development of the flea.

(B) The Male Reproductive System

The male gonads—The rudiments of the testes (fig. 62) are comparatively much larger than the ovarian rudiments, being about 300 μ in the larger diameter. Each testicular rudiment is composed of four distinct sperm tubes (*sp.t.*), or testicular follicles, which are enclosed in a common peritoneal sheath (*p.s.*) in which extremely small, sparsely scattered, nuclei are present. While teasing a testicular rudiment, the peritoneal sheath sometimes breaks and the four lobes become free, showing thereby that it is formed of four separate tubes. Normally each testicular rudiment is a single compact structure on account of the close approximation of the internal walls of the sperm tubes within the peritoneal sheath. The wall of a sperm tube (fig. 63) consists of a thin layer of epithelium (*e.sh.*) in which cells are not individualized. The cavity of each sperm tube is divided into chambers by transverse partitions (*t.p.*), which are continuous with the epithelium forming the sperm tube wall and are structurally similar to it. The number of transverse partitions decreases with the age of the larva. In young third-stage larvae there are about eight partitions, but in defaecated larvae only four are present. These transverse partitions play the role of the sperm cysts of other insects. The germ cells (*g.c.*) are loosely packed in the chambers of each sperm tube and are comparatively much smaller than the female germ cells. They show great variation in form and each possesses a large nucleus. The germ cells in the terminal chamber of each sperm tube are comparatively smaller than those in the remaining chambers and are primary spermatogonia. The Versonian or apical cell is absent. In the prepupal stage the spermatids of the posterior chamber of each sperm tube show gradual transition into spermatozoa. At the base of each sperm tube there is a large group of small proliferating cells which are in direct continuation with the epithelium of the sperm tube wall. These give rise to the vasa efferentia of the sperm tubes. The anterior group of small cells, which in the ovarian rudiment give rise to terminal filaments of the adult ovarioles, is not present in the testicular rudiment. The terminal filaments which are found in the ovarian rudiments are also absent.

The vasa deferentia (figs. 62, 63, 64, *v.d.*) of a third-stage larva are a pair of long, translucent, thread-like structures of uniformly narrow diameter with sparsely scattered nuclei. No apparent sign of a lumen is visible and each vas deferens appears to be a solid cord of cells, which is so fine that it becomes slightly swollen where the nuclei are present. The cell boundaries are not defined. A well-



FIGS. 64–69.—Fig. 64—Lateral view of the terminal abdominal segments of a male third-stage larva showing the reproductive system. × 127. Fig. 65—Ventral view of the phallic lobes with the rudiments of the paired ejaculatory ducts of a third-stage larva. × 422. Fig. 66—Transverse section through the phallic lobes of an early third-stage larva. × 323. Fig. 67—Ventral view of the phallic lobes of a late third-stage larva showing their fission into parameres and penis lobes and the separate external openings of the paired ejaculatory ducts. × 222. Fig. 68—Ventral view of the terminal abdominal segments of an early male prepupa showing the three pairs of genital appendages. × 136. Fig. 69—Side view of the terminal abdominal segments of a late male prepupa showing the three pairs of genital appendages. × 169.

developed limiting basement membrane (fig. 63, *b.m.*), which is continuous anteriorly with the peritoneal sheath (*p.s.*) of the testicular rudiment, is present. The vasa deferentia are mesodermal in origin.

The ejaculatory duct—Each vas deferens (figs. 64, 65) is continued posteriorly by a large pyriform ampulla (*r.p.e.*) of small proliferating cells which are strongly basophil like the cells of the rudiments of the inner pair of genital appendages (*ph.l.*). Similar structures in other insects have been considered by some workers to be of ectodermal origin. In the flea they eventually give rise to the paired ejaculatory ducts and accessory glands of the adult, and hence they should be regarded as the rudiments of the paired ejaculatory ducts. In the early third-stage larva (fig. 66) each of these rudiments (*r.p.e.*) lies in the cavity of the rudiment of the inner genital appendage (*ph.l.*) of its side. I failed to find any trace of the external openings of these rudiments either in sections or in entire mounts of the early third-stage larva. They are either absent or too small to be detected. In the late third-stage larva and in the early prepupa (fig. 67, *r.p.e.*) each rudiment opens externally by a narrow duct lined with cuticle on the mesial side of the inner genital appendage of its side close to its origin. Thus in the ontogeny of the flea there are two well-separated male gonopores situated on the inner side of the inner pair of rudiments of the genital appendages, which is a primitive feature, and this primitive condition is permanently retained in the adult Ephemeroptera and some Dermaptera (*vide* SINGH-PRUTHI, 1924, *b*, pp. 78, 79; IMMS, 1931, p. 40, figs. 28C and D; and PALMÉN, 1884).

The presence of two male gonopores on the inner pair of genital appendages, which are considered appendages of the ninth segment, is a point of great morphological importance, and it militates against the idea advanced by SINGH-PRUTHI (1924, *b*, p. 67, and 1925, p. 763) that in insects the paired ejaculatory ducts have their external openings between the eighth and ninth abdominal segments. On the contrary, in the flea larva, the adult Ephemeroptera and some Dermaptera, they clearly open on the ninth segment. Thus the paired ejaculatory ducts cannot possibly correspond to the median oviduct (vagina or uterus) as SINGH-PRUTHI has suggested. The common ejaculatory duct is absent in the larva and it is formed only in the early prepupa by fusion of the penis lobes, and in its formation only the internal walls of the penis lobes (figs. 67, 68, 69, *pe.l.*) take part, while the outer walls surround it completely so as to form the wall of the phallus or aedeagus. The fusion of the penis lobes at first occurs only on the dorsal side, then later the ventral edges also fuse.

The male external genitalia—The rudiments of the external genitalia (figs. 64, 65) first appear in the early third-stage larva in the form of a pair of thick-walled ectodermal diverticula at the anterior end of an invagination of the ventral conjunctival membrane between the ninth and tenth abdominal segments. These are the rudiments of the inner pair of genital appendages which SINGH-PRUTHI (1924, *b*, p. 63) has called the paramere-lobes and SNODGRASS (1935, p. 587) the phallic lobes (*ph.l.*). The invagination of the body wall is flask-shaped (*p.c.*) and lies in the body cavity

above the sternum of the ninth abdominal segment, the neck of the flask opening behind the ninth abdominal segment. There is a thin, longitudinal, cellular partition in the cavity showing that the cavity is formed by the approximation of two separate invaginations. This double invaginated cavity is nothing else but the paired peripodial cavity of the paired phallic lobes and should not be considered to be the genital pocket or cavity, as has been done by some workers, *e.g.*, SINGH-PRUTHI (1924, *a*, p. 860) and MEHTA (1933, p. 43) in ontogenetic studies on the male genitalia of insects. The real genital cavity is formed only after all the other parts of the male genitalia are fully formed. Moreover, the phallic lobes which lie at first at the bottom of the peripodial cavity, are everted as the growth (fig. 67) proceeds during the late prepupal stage, and come to lie outside the body as hanging appendages of the sternum, as is the case with the leg buds, and the cavity is completely obliterated. The original double nature of this cavity also indicates that it is formed as the result of close approximation of the peripodial cavities of two appendages of the two sides and is not a single genital cavity.

Each phallic lobe (fig. 67) splits into two by the appearance of a horizontal longitudinal fissure which starts from its posterior end in the late third-stage larva. The outer elements are the rudiments of the parameres (*pa.*), while the inner elements are the penis lobes (*pe.l.*) which fuse in the prepupa to form the aedeagus. The aedeagus increases in size much more rapidly than the parameres and becomes curved upwards so as to look like the beak of a parrot.

In the prepupa (fig. 68) a second pair of rudiments appears in a shallow peripodial cavity independently and in front of the phallic lobes, as in Lepidoptera (MEHTA, 1933, p. 43), on the ninth abdominal venter. These are the rudiments of the true gonopods of the ninth abdominal segment which have been called by SINGH-PRUTHI (1924, p. 63) the subgenital plates (*s.g.p.*), and by SNODGRASS (1935, p. 592) the harpagones. This late and independent origin of the subgenital plates is a point of great morphological importance, as some workers consider that the phallic lobes and the subgenital plates are formed by the subdivision of an original pair of rudiments borne on the ninth abdominal segment (*vide* IMMS, 1931, p. 39). If these two pairs of appendages, which have been called phallic lobes and subgenital plates, are really true gonopods, or parts of them, their independent origin clearly indicates that they are two separate pairs of gonopods. As no segment in insects has more than one pair of appendages, this led KERSHAW and MUIR (1922, p. 210) to believe that the appendages of the eighth abdominal segment have shifted on to the ninth abdominal segment. This shifting of appendages from the eighth to the ninth abdominal segment they actually observed in the earlier stages of Homoptera. As nobody else has seen this migration of appendages, even in Homoptera (SINGH-PRUTHI, 1924, *b*, p. 73, and METCALFE, 1932, p. 471), it is now taken for granted that the subgenital plates are the true gonopods of the ninth abdominal segment in almost all insects in which they are present, and are not those of the eighth abdominal segment as KERSHAW and MUIR thought.

As to the homologies of the phallic lobes, there is no agreement. Some consider

them gonapophyses homologous to the endopodites of the crustacean limbs and in this way comparable with the posterior gonapophyses of female insects. SNODGRASS (1935, p. 590) doubts if the gonapophyses are retained by the pterygote insects. He discredits the association of gonapophyses with the formation of the aedeagus of insects for lack of positive ontogenetic evidence. According to him, the aedeagus is an independent median outgrowth of the body wall ; but the formation of the aedeagus by fusion of the penis lobes, as mentioned above in the flea, has been observed by various other workers, *e.g.*, DEWITZ (1875), ZANDER (1900, 1901, 1903), SINGH-PRUTHI (1924, *b*, 1925), and MEHTA (1933), in other insects. The idea that the subgenital plates are coxites and that the phallic lobes represent the endopodites of the gonopods of the ninth abdominal segment (SINGH-PRUTHI, 1924, *b*, p. 71) does not harmonize with facts observed during the post-embryonic development of some insects. If these two pairs of genital appendages represent the biramous condition of the Crustacean limbs, why should two parts of the same limb have independent origin one after the other ? The independent origin of the subgenital plates, as observed by me in the flea and by MEHTA in Lepidoptera, occurs also in Coleoptera, as is clear from SINGH-PRUTHI's description and drawings (1924, *a*, p. 861, text-figs. 1, 2). These two structures of different origin cannot possibly belong to the same appendage. The presence of separate peripodial cavities for the phallic lobes and their independent origin place them in the same category as the subgenital plates. In my opinion, the phallic lobes are either some special developments of doubtful homology found on the ninth abdominal segment, or they are gonopods of the tenth abdominal segment. The latter view finds support in that during the embryonic development of some orthopterous insects (WHEELER, 1893, pp. 117, 124, and HEYMONS, 1891, 1895, p. 85) the primary mesodermal vasa deferentia are either attached to the ectoderm of the tenth abdominal venter or in some cases they terminate in ampullae located within the rudiments of the appendages of this segment. In the adult Ephemeroptera the vasa deferentia open at the base of appendages of the tenth segment, and the subgenital plates, the appendages of the ninth segment, are also present. In insects the phallic lobes are always found in association with the male gonopore which in most insects is behind the ninth segment. In the flea larva the formation of the peripodial cavities of the phallic lobes at the junction of the ninth and tenth abdominal segments makes it impossible to decide whether these structures are in association with the ninth or the tenth abdominal segment. The possibility that these represent appendages of the tenth abdominal segment is not to be lost sight of until it is definitely disproved.

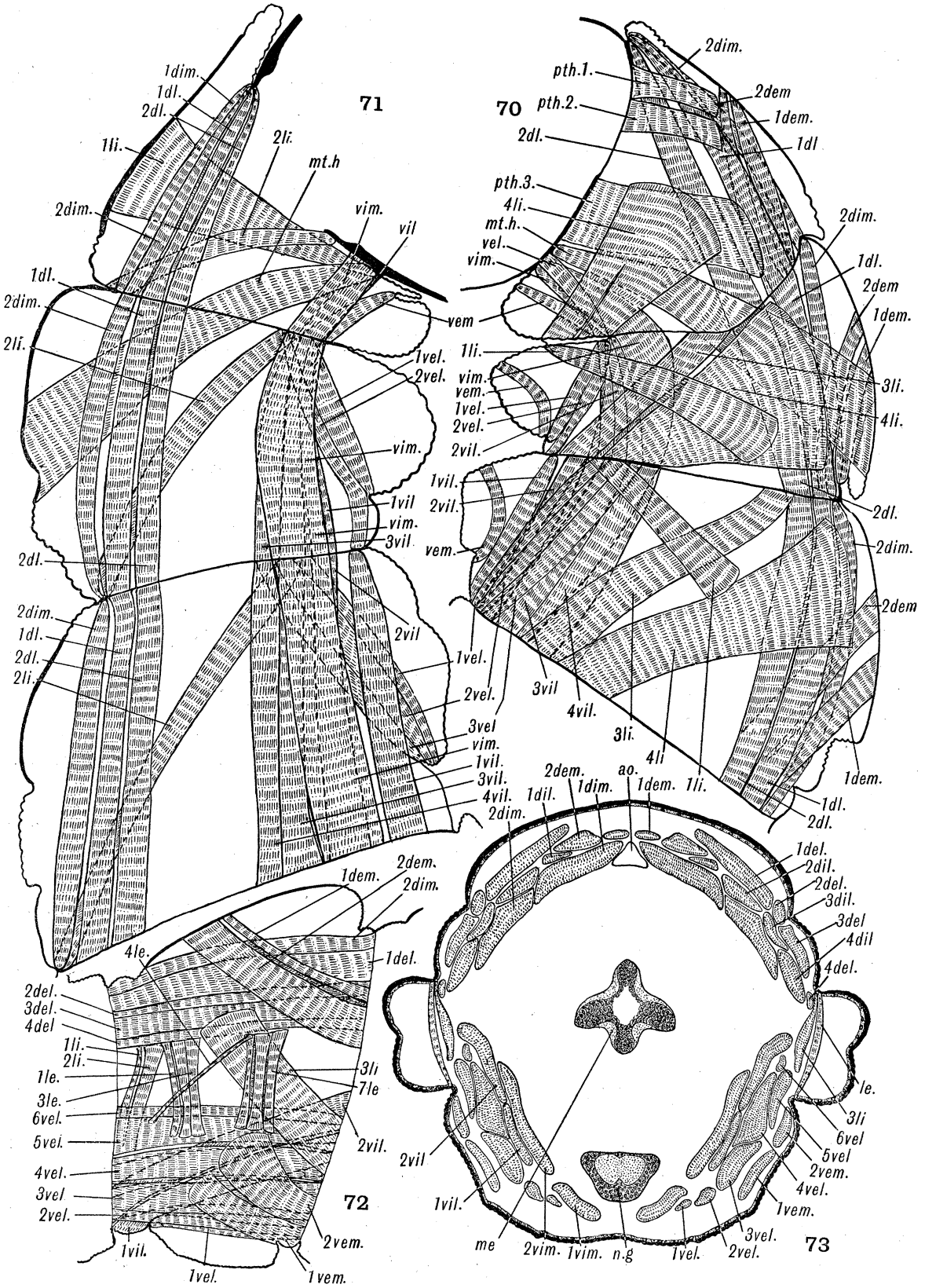
XIX—THE THORACIC MUSCULATURE

In the thorax (figs. 70, 71) there is a well-developed muscular system consisting of the dorsal longitudinal muscles, the ventral longitudinal muscles, and the dorso-ventral muscles, which, following SNODGRASS's scheme (1931, p. 32) for the abdominal

musculature, are designated here dorsal, ventral, and lateral muscles respectively. The dorsal muscles are arranged into three distinct sets, namely, the median internal dorsals (*dim.*), the median external dorsals (*dem.*), and the lateral dorsals (*dl.*). The last do not show any further division into external and internal muscles. In all the thoracic segments the dorsal muscles show uniformity of arrangement and each set on each side is composed of two distinct fibres. The median external dorsals (1, 2*dem.*) are short muscles confined only to the posterior part of their respective segments, while the others are of the full segmental length. The ventral muscles are arranged in four sets, namely, the median internal ventrals (*vim.*), the median external ventrals (*vem.*), the lateral internal ventrals (*vil.*), and the lateral external ventrals (*vel.*). The median internal ventrals are powerful muscles one on each side of the mid-ventral line of all the thoracic segments. The median external ventrals are not of segmental length and there is one on each side of all the thoracic segments. The lateral ventral muscles show variation in the three segments and will be described separately. All the lateral muscles of the thorax originate from the intersegmental folds, and hence they correspond to the internal lateral muscles of the abdomen. The external lateral muscles of the abdomen are not represented in the thorax. They are four in number in each of the last two thoracic segments and are tergo-sternal in arrangement. They are strongly oblique muscles arranged into two sets of two muscles. The muscles of one set (1*li.*, 2*li.*) run forwards and the muscles of the other set (3*li.*, 4*li.*) run backwards. One muscle (2*li.*, 3*li.*) of each set runs from the intersegmental fold of one side to the intersegmental fold of the other side of the segment and thus are of segmental length. The other two are connected only on one side with the intersegmental fold. The prothorax has only three lateral muscles (1*li.*, 2*li.*, 4*li.*) and the third internal lateral is absent.

The prothoracic musculature is considerably different from that of the other thoracic segments on account of the presence of a number of additional muscles which are concerned with the movements of the head. All the special muscles which control the movements of the head, with one exception, arise from the protergum and are called protergal muscles of the head. Two of these are inserted on each of the dorso-lateral sides of the posterior margin of the head capsule. These are dorso-lateral protergal muscles (*pth.*1, 2) and they originate from the anterior half of the protergum. On each side a powerful lateral protergal muscle (*pth.*3) springs from the posterior half of the protergum and is inserted on the lateral side of the posterior margin of the head capsule. The lateral internal ventrals are only two unequal sized muscles (fig. 17, 1*vil.*, 2*vil.*) on each side. The lateral external ventral (*vel.*) is only a single muscle on each side. The first internal lateral muscle (fig. 71, 1*li.*) is more deeply situated and is more powerful than those of the other two segments.

The mesothoracic musculature—There is only one mesotergal muscle of the head (fig. 71, *mt.h.*) on each side. It springs from the posterior half of the meso-tergum and is inserted on the ventro-lateral portion of the posterior margin of the head capsule. The lateral internal ventrals (1–3*vil.*) are three muscles on each side and the lateral external ventrals (1, 2*vel.*) are only two in number. Of the laterals



FIGS. 70–73.—Fig. 70—Side view of the thorax showing the superficial thoracic musculature (seen from outside). × 202. Fig. 71—Side view of the thorax showing the deeper thoracic musculature (seen from inside). × 228. Fig. 72—Side view of the first abdominal segment showing the musculature. × 154. Fig. 73—Transverse section through the middle of the first abdominal segment showing the arrangement of abdominal muscles. × 229.

all the four muscles are present and the fourth lateral internal (4*li.*) is a very powerful muscle.

The metathoracic musculature—Only the typical muscles of the thorax are present. The lateral internal ventrals (1, 2, 3, 4*vil.*) are four in number on each side and the lateral external ventrals (1, 2, 3*vel.*) are only three on each side.

XX—The Abdominal Musculature

The abdominal musculature consists of dorsal and ventral longitudinal muscles and lateral muscles. The transverse muscles are only represented by a few poorly developed incomplete dorsal fibres in the dorsal diaphragm (fig. 45, *d.d.*). These muscles are only present in the lateral portions of the dorsal diaphragm, and the muscles of one side are not connected with those of the other side to form a continuous septum. In describing the abdominal musculature, I have followed the system of classification and nomenclature adopted by Snodgrass (1931, pp. 32–42). The musculature of the first eight abdominal segments is fundamentally the same and is repeated with only minor variations in each of these segments. A detailed description of the musculature of the first abdominal segment (figs. 72, 73) only will be given. The musculature of the last two segments is characterized by the complete absence of the lateral muscles, and there is a gradual tendency towards the reduction in the number of the longitudinal muscles. In the terminal segment (fig. 34) there are only five dorsal muscles (*del.*, *dil.*) and four ventral muscles (*vl.*, *vm.*) on each side. Owing to the poor development of the transverse muscles, the division of the longitudinal muscles into median and lateral groups cannot be exact, but an attempt to divide them purely on the basis of topographical arrangement of muscles has been made.

The dorsal muscles (figs. 72, 73)—These are twelve muscles on each side, arranged into four groups. The median internal dorsals (1, 2*dim.*) are only two in number and are strongly developed. The median external dorsals (1, 2*dem.*) are two short, unequal and strongly oblique muscles, the posterior muscle (1*dem.*) being the weaker of the two. On account of their marked downward course they help the lateral muscles in compressing the segment. The lateral internal dorsals (1–4*dil.*) and lateral external dorsals (1–4*del.*) are each four in number. The paradorsal muscles are absent.

The ventral muscles (figs. 72, 73)—These, like the dorsal muscles, are also twelve in number on each side and are arranged into four sets. The division into different sets is more well marked in this case. The median external ventrals (1–2*vem.*) are two short, thick, oblique muscles which run upwards anteriorly and each spreads like a fan on the posterior half of the lateral portion of the sternum. The median internal ventrals (1, 2*vim.*) are two powerful muscles of segmental length. The lateral external ventrals (1–6*vel.*) are six in number. The third, fourth, and fifth lateral external ventrals (3, 4, 5*vel.*) are much stronger than the other three. The lateral internal ventrals (1, 2*vil.*) are two equally powerful muscles.

The lateral muscles are arranged into two sets, the external laterals (*le.*) and the internal laterals (*li.*). They compress the body dorso-ventrally. The external laterals (1–7*le.*) are seven in number on each side. Six of them, which are straight vertical muscles, are arranged in anterior and posterior sets each of three muscles. The seventh muscle (4*le.*) is a strongly oblique, thin, long, muscle which is confined to the anterior half of the segment lying outside the other external laterals. The internal laterals (1–3*li.*) are three in number on each side and lie externally to the lateral longitudinal tracheal trunk. The anterior two (1, 2*li.*) have their lower ends inserted in the anterior intersegmental fold of the segment and take a slightly oblique course upwards and then terminate close to the anterior margin of the tergum. The posterior internal lateral (3*li.*), which is the most powerful muscle of the lateral muscles, has its lower end inserted on the posterior intersegmental fold and runs obliquely upwards and forwards to the middle of the lateral side of the tergum.

XXI—The Integument

The cuticle (fig. 77) is differentiated into epicuticle (*epi.*), exocuticle (*ex.*), and endocuticle (*end.*). The outer surface of the cuticle, where it is sclerotized, is smooth, but in the unsclerotized parts it is produced into extremely minute backwardly directed denticle-like spines (figs. 74, 75, *d.s.*, 54) giving it a shagreened appearance. These spines are arranged in circular rows. The epicuticle forms a thin homogeneous layer of yellow colour. The exocuticle is well differentiated and thick in sclerotized regions, where it is of yellowish-red colour. In unsclerotized regions it is this portion only which forms the spines and it is not sharply differentiated from the endocuticle. The tips of spines are sclerotized. The endocuticle is horizontally lamellate and is strongly basophil.

The epidermis consists of six kinds of cells : (1) the so-called proper epidermal cells, (2) the tonofibril cells for the insertion of muscle fibres, (3) the cells of bristles or hairs termed trichogens, (4) the socket-forming cells known as tormogens, (5) the gland cells, and (6) the cells of the imaginal disks.

The epidermal cells of a recently hatched larva (fig. 75, *ep.*) and of a larva ready to moult (fig. 53) are usually cubical in outline with spherical to ovoid nuclei. The epidermis in these cases is always thicker than the cuticle. In old larvae the epidermis is of much less thickness than the cuticle (fig. 45, *ep.*, *cu.*). The cell limits are ill defined. The cells become considerably enlarged and flattened and have a polygonal outline in surface view. The nuclei are large, elongate-oval, and flattened with their long axes parallel to the general surface of the body. The chromatin is condensed in a few small, equal-sized granules.

The tonofibril cells (fig. 78) are characterized by the conversion of part of the cell into tonofibrillae (*tf.*). In most cases the plastic part of cells is absent. It appears that in these cases the whole cell is converted into tonofibrillae.

In the flea larva there are two kinds of setae. The larger kind is called a bristle and the smaller one is called a hair. Structurally both are similar and are uni-

cellular processes of the body wall. Both are lodged on sclerotized parts and never spring from the unsclerotized parts of the body. Each of them possesses all the usual elements of a seta. The trichogen (figs. 75, 76, *trg.*) is a huge pear-shaped cell protruding into the body cavity, with a large spherical nucleus having its chromatin condensed into big unequal-sized granules. The trichogens usually take an oblique course, and it is very seldom that one sees them connected with setae in sections. It is for this reason that HARMS (1912, p. 177, fig. 3) has sketched a bristle without a trichogen. Their presence can best be seen in whole mounts. Each tormogen (*tmg.*) is a sub-cylindrical cell larger than the ordinary epidermal cell but smaller than the trichogen. Its basal portion surrounds the basal neck-like portion of a trichogen.

The gland cells (fig. 77, *tg.c.*) are much larger in size than the ordinary epidermal cells and project into the body cavity like the trichogens. Each cell is pyriform, being connected with the cuticle by a narrow neck and possesses three (rarely two) nuclei rich in chromatin which is condensed into big unequal-sized granules. I did not see any intracellular outlet duct in the cytoplasm. The gland cells are only found in the dorsal region of the prothorax close to its articulation with the head. Their function may be that of moulting glands.

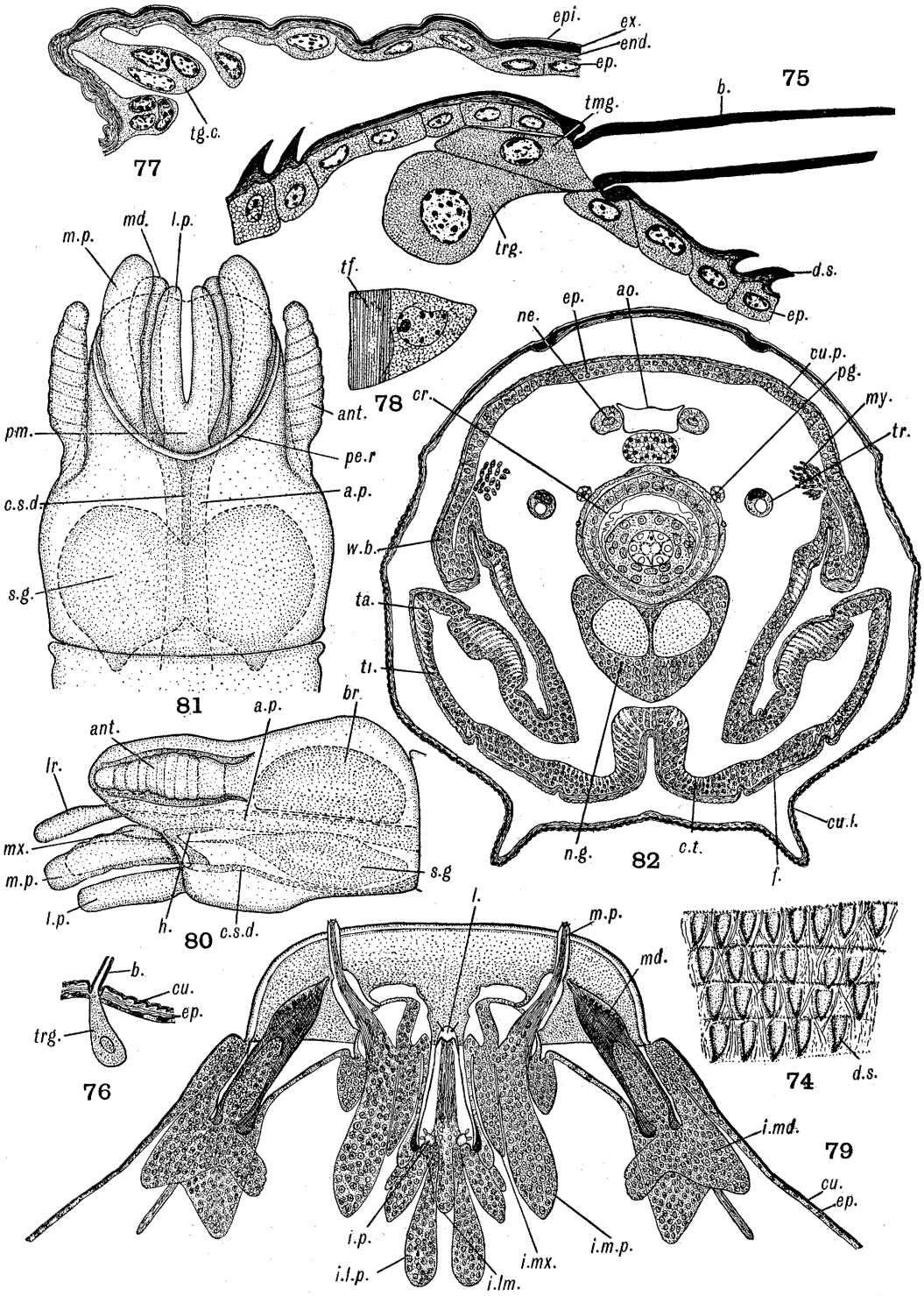
Owing to the pronounced flattening of the ordinary epidermal cells (*ep.*), the imaginal cells (fig. 66, *t.i.*) always look bigger than the former in sections, but in reality they are smaller.

XXII—THE IMAGINAL BUDS

The imaginal buds of the antennae, mouth parts and legs are present in the recently hatched first-stage larva and are easily distinguished from the surrounding tissues by their strong affinity for staining reagents. In all probability they arise in the embryo and undergo further development only in the late third-stage larva. The imaginal buds of the wings, genitalia, and other structures make their appearance either in the third-stage larva or in the prepupa. In the description of imaginal buds I have adopted the terminology used by TOWER (1903, p. 528) in connexion with the wing buds of Coleoptera, as the different types of buds described by him are also found in connexion with other parts of insects.

(A) THE CEPHALIC IMAGINAL BUDS

The head of the flea larva passes without any great modification into that of the adult, unlike that of the Muscidae. The imaginal buds of the mouth-parts (figs. 9, 79) in the third-stage larva are of the enclosed type. They are formed within the corresponding parts of the larva and are club-shaped, with their broader ends projecting into the head cavity. In addition to these buds, there are thickenings of actively proliferating ectodermal cells at places where the larval mouth-parts are connected with one another near their bases.



FIGS. 74–82.—Fig. 74—Surface view of the cuticle showing the arrangement of denticle-like spines. × 1000. Fig. 75—Longitudinal section through the integument of a recently hatched first-stage larva, passing through a bristle. × 2000. Fig. 76—A bristle with a trichogen of a third-stage larva. × 323. Fig. 77—Longitudinal section through the dorsal prothoracic integument near the junction of the head showing tegumentary glands. × 1200. Fig. 78—A tonofibril cell of a dorsal dilator of the posterior pharynx. × 2000. Fig. 79—Ventral view of the mouth parts of a third-stage larva showing their imaginal buds. × 366. Fig. 80—Lateral view of the head of a prepupa. × 139. Fig. 81—Ventral view of the head of a prepupa. × 141. Fig. 82—Transverse section through the mesothorax of a late prepupa at the level of wing buds. × 232.

The imaginal buds of the antennae—The largest and most prominent of the cephalic buds are those of the antennae (fig. 14, *i.a.*). They are placed at the bases of the larval antennae, and their cells are in intimate association with those of the antennary sensilla which they surround and form bulb-like swellings. They are of the recessed type and thus resemble the buds of the legs and not those of the head appendages. In the prepupa (figs. 80, 81, *ant.*) the antennae are directed forwards unlike those of the adult and the pupa. Each shows signs of division into the three primary segments of the adult antenna, the third segment or club being indistinctly nine-segmented. The antenna lies in a depression on the dorso-lateral region of the head of its side.

The imaginal buds of the eyes (fig. 58, *i.e.*) are represented by a pair of special thickenings of the proliferating ectodermal cells just behind the antennae in the late third-stage larva.

The imaginal bud of the labrum (fig. 9, *i.lr.*) is an unpaired long, club-shaped structure which in the prepupa (fig. 80, *lr.*) becomes everted, and its lower surface is continuous with the dorsal wall of the anterior pharynx and its upper one with that of the cephalic wall after forming a deep bend.

The imaginal buds of the mandibles—Each of these is sub-triangular in shape (figs. 13, 14, 79, *i.md.*) with the apex lying in the lumen of the larval mandible and the base projecting into the head cavity. In the prepupa (fig. 81, *md.*) it is represented by an unjointed club-shaped appendage of the head.

The imaginal buds of the maxillae (figs. 13, 14, 79)—Each maxillary rudiment is represented in the third-stage larva by two anteriorly connected club-shaped buds protruding into the head cavity. The inner, which is the smaller of the two, is the bud of the maxilla proper (*i.mx.*), and the outer one, which encloses the maxillary sensillum, is the bud of the maxillary palp (*i.m.p.*). In the prepupa (figs. 80, 81) each maxilla is a club-like structure showing faint indication of four segments. The basal segment has an indistinctly defined swelling (fig. 80, *mx.*) on its internal side which gives rise to the maxilla proper of the adult, and the four-segmented club-like structure (*m.p.*), which is highly developed and prominent, is the maxillary palp.

The imaginal bud of the labium (figs. 9, 14, 15, 79) consists of three anteriorly connected centres of proliferations. The two lateral ones (*i.l.p.*) are larger than the median one and are formed in connexion with the labial palps (*l.p.*). The median one (*i.lm.*) is found in connexion with the prelabium and lies above the lateral ones. In the prepupa (figs. 80, 81) the labium is a fork-like structure. The two arms represent labial palps (*l.p.*) and they do not show any sign of segmentation. The basal small unpaired portion is the prementum (*pm.*). The ligula, which is well developed in the larva, has completely disappeared. There is a gradual recession of the epithelial cells of the larval ligula into that of the bud of the prelabium.

The imaginal bud of the hypopharynx (figs. 9, 15, *i.h.*) is a club-shaped mass of proliferating cells with its broad end closely applied to the anterior end of the common

salivary duct (*c.s.d.*). In the prepupa (fig. 80, *h.*) it is extremely small and remains concealed between the bases of other mouth-parts. HEYMONS (1899, p. 235) failed to find its presence in *C. gallinae* and in consequence he emphatically denies its presence in all the stages of flea.

(B) THE THORACIC IMAGINAL BUDS

The imaginal buds of the legs—In the first-stage larva these are in the form of small ectodermal proliferation centres, and this condition is retained up to the third larval stage when they become pushed inwards. The peripodial cavity has a wide external opening and thus the leg bud is of the recessed type (figs. 9, 17, *i.l.*). HARMS (1912, p. 176) has wrongly described the peripodial cavity of the leg bud in the larva of *C. canis* as closed. From his description and drawing it appears that he only examined a longitudinal section passing through the leg bud near its base where the peripodial membrane passes into the leg evagination, and thus he failed to see the presence of the wide opening of the peripodial cavity which HEYMONS (1899, p. 232) rightly described in the larva of *C. gallinae*. The growth of leg buds is very much accelerated in the defaecated larva and the prepupa. In the former the leg buds begin to protrude from their respective peripodial cavities and in the early prepupa (fig. 82) differentiation into a basal segment representing the coxa and trochanter (*c.t.*), and into femur (*f.*), tibia (*ti.*), and tarsus (*ta.*) takes place by formation of faint constrictions. Owing to lack of space between the pupal and the larval skin, the leg buds at first move upwards and then turn forwards.

The imaginal buds of the wings—SHARIF (1935, p. 462) recorded for the first time the presence of wing buds in the pupae of three species belonging to two different families of the Siphonaptera. They are only found on the mesothorax, and no such structures are found on the metathorax. There is no perceptible trace of them in the larval stage. In the prepupa (fig. 82, *w.b.*), each wing bud makes its first appearance in the form of a thickening in the pleural region which develops into a conical evagination of the body wall enclosing an extension of the body cavity. The ectoderm of the evaginated portion is thicker than that of the neighbouring parts and the cells show signs of active proliferation. The wing buds at no stage are lodged in the peripodial cavities. Their late and superficial formation without any peripodial cavities should in no way discredit their being called wing buds, as in some Coleoptera (TOWER, 1903, p. 528 ; POWELL, 1904, 1905 ; and MURRAY and TIEGS, 1935, p. 413) the wing buds make their first appearance in the prepupa, have no peripodial cavities, and from the beginning lie outside the body. There is a considerable diversity in the time of first appearance of wing buds in different insects from a late embryonic period to the pupal stage. In the Lepidoptera the wing buds are found in the youngest larva and in all probability arise in the embryo. In some Nematocera, according to WEISMANN and others (*vide* TOWER, 1903, p. 526), the wing buds appear just before pupation, while in Brachycera they arise in the embryo. In the Coleoptera, according to TOWER, there is a great variation in the time of first appearance of

wing buds. In some they appear at the end of the larval life and in others they appear earlier and are even present throughout the larval life. In their development and general appearance the wing buds of the flea resemble the simple type of wing buds of TOWER (1903, p. 528), which, according to him, is the dominant type of wing development in Coleoptera. The imaginal bud which develops in the prepupal stage as a rule never sinks deeply beneath the ectoderm and consequently the peripodial membrane is reduced to a minimum, and there is no formation of the peripodial cavity. The wing buds of the flea prepupa are not specially supplied with tracheae as in other insects, but a few phagocytes and a large group of myoblasts (*my.*) are always found near their origins.

In the larval stages the cells of the wing rudiment do not differ in any way from those of the neighbouring ectoderm, but in the prepupal stage they proliferate and are smaller than those of the surrounding ectoderm and form a thick layer which appears to be composed of several layers of cells. This thickness and multi-layered condition is due to crowding of cells in the wing bud which is caused by rearrangement of the cell contents so that nuclei lie at different levels. Each cell reaches from the inner to the outer side of the wing bud, but the position of nuclei at different levels give it the multi-layered appearance, though in reality it is single layered.

In the prepupa the growth of wing buds is very rapid, so that in the late prepupa they are very conspicuous and hang downwards and backwards. They are thick and fleshy in general appearance. In cross-sections they look very much like the wing buds of Coleoptera (*vide* TOWER, 1903, pl. xvii, figs. 28–31; and MURRAY and TIEGS, 1935, p. 412, text-fig. 4).

POWELL (1905, p. 10) is of opinion that the simple type of wing development as is found in most Coleoptera lends support to the hypothesis that wings in insects have arisen as lateral outgrowths of the tergum or pleural regions of their respective segments. The recessed and enclosed types of wing development, in my opinion, are mere contrivances to accommodate these early formed structures within the body so that they may not unnecessarily encumber the larval life and are secondary features. The simple type of wing development resembles very much the wing development in the Heterometabola, and therefore it should be considered a primitive feature.

(C) THE ABDOMINAL IMAGINAL BUDS

In addition to the buds of the genitalia, of which an account has already been given in connexion with the reproductive system, there are imaginal buds which are formed in connexion with the seventh and tenth abdominal segments. These are imaginal buds of the antepygidial cones, anal struts, and anal stylets. These are of the simple type.

The imaginal buds of the antepygidial cones—In the prepupa there is a pair of finger-like evaginations of the thickened ectoderm at the posterior dorso-lateral margins of the seventh abdominal segment.

The imaginal buds of the anal struts (figs. 60, 61, 68, 69, *a.str.*) are formed as cone-

shaped thickenings of the ectoderm in connexion with similarly named structures of the larva on the tenth abdominal segment in both sexes. Their formation in the female is earlier than in the male. These structures are only retained up to the pupal stage and disappear in the adult.

Imaginal buds of the anal stylets (figs. 60, 61, *a.st.*) are formed as a pair of finger-like evaginations of the thickened ectoderm on the dorso-lateral sides of the tenth abdominal tergum of the female prepupa.

XXIII—Summary

The internal anatomy of the flea larva is revised in the light of our existing knowledge of insect morphology. A brief summary of previous work on the anatomy of the flea larva is given. The head and its musculature is described in detail. Owing to the poor development of the tentorium, some muscles of the head, which in most other insects usually originate on the tentorium, arise in the flea larva either on the postoccipital ridge or on the lateral arms of the sclerite of the anterior pharynx. The musculature of the maxilla is highly specialized.

There are two pharyngeal chambers. The posterior one with its powerful cranial dilators is an important organ of suction. The stomodaeal valve is poorly developed and is represented by a circular fold which does not project into the mesenteron. It is exclusively formed by the cells of the stomodaeal imaginal ring. The peritrophic membrane is not exclusively formed by the anterior mesenteric cells. There are no histologically differentiated parts in the mesenteron. The digestive cells do not show any differentiation in conformity with the dual function of secretion and absorption, and each cell is capable of performing both functions. The secretion formation is purely merocrine, and there is no disintegration of cells resulting in the energetic discharge of secretion products. The disintegration of cells by formation of bud-like vesicular extrusions is distinctly a different process and has nothing to do with secretion formation. Accompanying each moult, there is a partial replacement of the digestive cells at the expense of the regenerating cells. The pyloric valve is exclusively formed by the proctodaeal imaginal cells. The rectal sac is composed of two different kinds of cells. The bigger cells have radial striations which take part in controlling the dilation of its lumen.

A peculiar kind of network, formed by the processes of the cells of a Malpighian tubule near its opening into the pylorus, is present. There is only a striated zone on the inner surface of the epithelial cells of the Malpighian tubule. A detailed histological account of the salivary glands is given. The lobes of the salivary glands are rich in glycogen.

The heart is two-chambered and the dorsal diaphragm is poorly developed. The alary muscles are absent. The phagocytes are purely blood cells, and during metamorphosis they only attack larval tissues in which signs of disintegration are apparent. Only the pericardial nephrocytes are present, and they are arranged in two linear

series of one cell thickness, one on each side of the dorsal blood vessel. The larval fat cells show well-marked differentiation into parietal and visceral fat cells.

All the spiracles except the first thoracic pair shift during the course of post-embryonic changes towards the posterior ends of their respective segments. A very simple kind of internal closing apparatus is present in all the abdominal spiracles. There is an elaborate supply of tracheation to the rectal sac. The presence of oenocytes in the ninth abdominal segment shows that they have no special association with the spiracles, as is suggested by some authors.

A detailed account of the nervous system is given. The chemo-receptive type of sensilla are present at the bases of the antennae and of the maxillary and labial palps. As the eyes are absent, the response of the flea larva to ordinary white light may be due to reflex behaviour to light.

The larger four-chambered gonads are the male gonads, and the smaller single-chambered pyriform ones are the female gonads. The lateral oviducts of the prepupa are connected with a pair of pyriform ectodermal pouches which open on the seventh abdominal venter. Only the anterior pair of female gonopods are present. In the late male third-stage larva the paired ejaculatory ducts open by two male gonopores on the mesial sides of the inner pair of genital appendages. The subgenital plates arise independently and later than the phallic lobes. It is considered that they are homodynamous, and in view of this the phallic lobes may be considered appendages of the tenth abdominal segment.

A detailed account of the thoracic and the abdominal musculature is given. The movements of the head are controlled by four special pairs of muscles. Three pairs originate in the prothorax and the fourth pair in the mesothorax. The epidermis is composed of six kinds of cells. The tegumentary gland cells are found in the dorsal region of the prothorax close to its articulation with the head. The imaginal buds of different structures are described. The imaginal buds of the wings are first formed in the prepupa and are of the simple type, as is the case in most Coleoptera.

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XXV—KEY TO LETTERING OF TEXT-FIGURES

a.a., anterior articulation.
ab., abductor muscles of the mandible.
a.b., albuminoid bodies.
ab.a., abductor apodeme.
ab.m., abductor muscle of the maxilla.
ad., adductor muscles of the mandible.
a.d., anterior dorsal dilators of the anterior pharynx.
ad.a., adductor apodeme.
a.d.r., anterior dorsal dilators of the rectum.
*a.g.*1., *a.g.*8., first, eighth abdominal ganglion.
a.gp., anterior gonopod.
a.l., anterior labral muscle.
a.n., antennary nerve.
ant., antenna.
ao., aorta.
a.p., anterior pharynx.
*a.s.*1., *a.s.*8., first, eighth abdominal spiracle.
a.s.l., anterior salivary lobe.
a.st., anal stylet.
a.str., anal strut.
at., atrium.

at.II., *at.III.*, atrium of the second, third larval stage.
a.t., trachea to the antenna.
a.t.a., anterior tentorial arm.
a.v.r., anterior ventral dilators of the rectum.
b., bristle.
b.c., buccal cavity.
b.m., basement membrane.
br., brain.
br.t., tracheae to the brain.
b.s., dome-shaped basal segment.
c., cardo.
c.a., corpus allatum.
c.l., compressors of the labrum.
c.m., circular muscle.
co., colon.
cr., crop.
c.s.d., common salivary duct.
c.t., coxa and trochanter.
cu., cuticle.
cu.II., *cu.III.*, cuticle of the second, third larval stage.
cu.l., larval cuticle.
cu.p., pupal cuticle.
d., ductule.
d.a., depressor muscle of the antenna.
d.b., disintegration bud.
d.c., dilatores cibarii.
d.d., dorsal diaphragm.
d.d.p., dorsal dilators of the posterior pharynx.
del., lateral external dorsal muscles.
1*del.*, 2*del.*, 3*del.*, 4*del.*, first, second, third, fourth lateral external dorsal muscle.
dem., median external dorsal muscles.
1*dem.*, 2*dem.*, first, second median external dorsal muscle.
d.h.t., dorsal head trunk.
dil., lateral internal dorsal muscles.
1*dil.*, 2*dil.*, 3*dil.*, 4*dil.*, first, second, third, fourth lateral internal dorsal muscle.
dim., median internal dorsal muscles.
1*dim.*, 2*dim.*, first, second median internal dorsal muscle.
dl., lateral dorsal muscles.
1*dl.*, 2*dl.*, first, second lateral dorsal muscle.
d.l.a., dorsal longitudinal muscle of the anterior pharynx.
d.l.p., dorsal longitudinal muscle of the posterior pharynx.
d.l.t., dorsal longitudinal trunk.
dm., median dorsal muscles.
d.s., denticle-like spine.
d.s.d., distal salivary duct.
d.s.m., dorsal salivary muscles.
d.t.c., dorsal transverse commissure.
e.b.c., epithelium of the buccal cavity.
e.c., epithelial cell.
ec.p., ectodermal pouch.
e.l., epithelial layer.
end., endocuticle.
ep., epidermis.
e.p., epithelium of the anterior pharynx.
epi., epicuticle.
e.s., syncytial epithelium.
e.sh., epithelial sheath.
e.t.m.o., ectodermal thickening of the median oviduct.
ex., exocuticle.
f., femur.
f.a., flexor muscle of the antenna.
f.c., follicle cell.
f.e., follicular epithelium.
f.g., frontal ganglion.
f.g.c., frontal ganglion connective.
g.c., germ cell.
g.d., glandular duct.
h., hypopharynx.
hd., head.
h.g., hypocerebral ganglion.
hr., heart.
hy., hypostoma.
i., intima.
i.a., imaginal bud of the antenna.
i.e., imaginal bud of the eye.
i.h., imaginal bud of the hypopharynx.
il., ileum.
i.l., imaginal bud of the leg.
i.lm., imaginal bud of the labium.
i.l.p., imaginal bud of the labial palp.
i.lr., imaginal bud of the labrum.
i.md., imaginal bud of the mandible.
i.m.p., imaginal bud of the maxillary palp.
i.mx., imaginal bud of the maxilla.
in., inclusion.
l., ligula.
l.a., levator muscle of the antenna.
l.ad., lower adductor muscle of the maxilla.
l.b.t., trachea to the prothoracic leg bud.
le., external lateral muscle.

1le., *2le.*, *3le.*, *4le.*, *7le.*, first, second, third, fourth, seventh external lateral muscle.
l.f., lateral fold.
l.f.n., labrofrontal nerve.
li., internal lateral muscle.
1li., *2li.*, *3li.*, *4li.*, first, second, third, fourth internal lateral muscle.
l.l.t., lateral longitudinal trunk.
l.m., longitudinal muscle.
l.n., labial nerve.
l.o., lateral oviduct.
l.p., labial palp.
l.p.l., lower posterior lobe of the salivary gland.
lr., labrum.
lr.n., labral nerve.
l.s., lower muscle of the stipes.
l.t., trachea to the labium.
m., mala.
m.a., maxillary apodeme.
m.ad., medial adductor of the maxilla.
md., mandible.
m.d., medial dorsal dilators of the anterior pharynx.
md.t., trachea to the mandible.
me., mesenteron.
m.e., mesenteric epithelium.
me.n., median nerve.
m.n., mandibular nerve.
m.o., median oviduct.
m.p., maxillary palp.
m.r., median ridge.
m.s., mouth opening of the salivarium.
m.t., Malpighian tubule.
mt.h., mesotergal head muscle.
mx., maxilla.
mx.n., maxillary nerve.
mx.t., trachea to the maxilla.
my., myoblasts.
n.c., ventral nerve cord.
ne., nephrocyte.
n.g., nerve ganglion.
n.n., normal nucleus.
n.p., nucleus undergoing pycnotic degeneration.
o.d.c., ordinary digestive cell.
oe., oenocyte.
o.g., oesophageal ganglion.
o.m., occlusor muscle.
o.n., optic nerve.
os., ostia.
p., pleurostoma.
pa., paramere.
p.a., posterior articulation.
p.c., peripodial cavity.
p.d., posterior dorsal dilators of the anterior pharynx.
pd.c., pedicel forming cells.
p.d.r., posterior dorsal dilators of the rectum.
pe.l., penis lobe.
pe.r., peristomial ridge.
pf., palpifer.
p.f.c., parietal fat cell.
pg., phagocyte.
ph.l., phallic lobe.
p.i., proctodaeal imaginal cells.
p.l., posterior labral muscle.
p.l.a., posterior labial adductor.
p.l.r., posterior lateral dilator of the rectum.
pm., prementum.
p.m., peritrophic membrane.
p.m.m., palpal muscle of the maxilla.
po.c., preoral cavity.
p.p., posterior pharynx.
pp.m., peripodial membrane.
p.r., postoccipital ridge.
p.s., peritoneal sheath.
p.s.d., proximal salivary duct.
ps.g., perispiracular gland.
p.t.a., posterior tentorial arm.
*pth.*1., *pth.*2., *pth.*3., first, second, third protergal head muscle.
p.v., pyloric valve.
p.v.r., posterior ventral dilators of the rectum.
py., pylorus.
r., rectum.
r.b., refractive bodies.
r.c., regenerating cells.
r.m.p., retractor muscles of the anterior pharynx.
r.n., recurrent nerve.
r.p.e., rudiment of the paired ejaculatory duct.
r.s., rectal sac.
r.sp., rudiment of the spermatheca.
r.st., radial striation.
s., shaft.
sa., salivarium.
s.b., striated border.
sc., sclerite.
s.c., sensory cells.
s.ca., sensillum campaniformium.

sc.d., secretion droplet.
sc.p., secretion product.
s.f., sensory fibres.
s.g., suboesophageal ganglion.
s.g.c., salivary gland cell.
s.g.p., subgenital plate.
s.g.t., tracheae to the suboesophageal ganglion.
s.i., stomodaeal imaginal ring.
s.m., sphincter muscles.
s.p., sensory pit.
sp.II., *sp.III.*, spiracle of the second, third larval stage.
sp.m., spiral muscle.
sp.t., sperm tube.
s.r., salivary reservoir.
st., stipes.
s.t., spiracular trachea.
st.g., stomachic ganglion.
ta., tarsus.
t.b., tentorial bridge.
tf., tonofibrillae.
t.f., terminal filament of the adult ovariole.
*t.g.*1., first thoracic ganglion.
tg.c., tegumentary gland cell.
ti., tibia.
t.i., tegumentary imaginal cells.
tmg., tormogen.
t.n., tegumentary nerve.
t.p., transverse partition.
tr., trachea.
trg., trichogen.
*t.s.*1., *t.s.*2., first, second thoracic spiracle.
t.v., tracheal valve.
u.ad., upper adductor muscle of the maxilla.
u.p.l., upper lobe of the salivary gland.
u.s., upper muscle of the stipes.
v., vacuole.
v.d., vas deferens.
v.d.a., ventral dilator of the anterior pharynx.
v.d.p., ventral dilators of the posterior pharynx.
vel., lateral external ventral muscle.
1*vel.*, 2*vel.*, 3*vel.*, 4*vel.*, 5*vel.*, 6*vel.*, first, second, third, fourth, fifth, sixth lateral external ventral muscle.
vem., median external ventral muscle.
1*vem.*, 2*vem.*, first, second median external ventral muscle.
v.f., ventral fold.
v.h.t., ventral head trunk.
vil., lateral internal ventral muscle.
1*vil.*, 2*vil.*, 3*vil.*, 4*vil.*, first, second, third, fourth lateral internal ventral muscle.
vim., median internal ventral muscle.
1*vim.*, 2*vim.*, first, second median ventral muscle.
vl., lateral ventral muscle.
vm., median ventral muscle.
v.t., visceral trachea.
v.t.c., ventral transverse commissure.
v.t.f., visceral trachea to the visceral fat body.
v.t.g., visceral trachea to the ganglion.
*v.t.g.*7., *v.t.g.*8., visceral tracheae to the seventh, eighth abdominal ganglion.
w.b., wing bud.
I., *II.*, *III.*, first, second, third thoracic segment.
1.–10., first to tenth abdominal segment.