

# The Anatomy of the Female Genital Tract of the *Pupipara* as observed in *Melophagus ovinus*.

By

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With Plates II—III and 1 Figure in Text.

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## Introduction.

The female reproductive organs of the small group of dipterous insects known as the *Pupipara*, of which the common sheep-tick (*Melophagus ovinus*) is the most familiar representative, has long interested entomologists. The large size of these organs, their odd outward resemblance to the human female genital tract (Pl. II, Figs. 1 and 2), the very small number and peculiar arrangement of the ovariole tubules, the unique position of the receptaculum seminis, and other structural features have lead to the investigation or notice of them by RÉAUMUR (17), NITZSCH (14), CUVIER (3), LYONET (15), DUFOUR (4, 5, 6), BLANCHARD (1), v. SIEBOLD (19), and LEUCKART (10). But none of these authors, with the exception of the last named, has furnished a correct account of their structure. LEUCKART, however, who in accuracy of observation and in the interpretation of observed facts was well-nigh infallible, gives a full and in the main correct description of these organs. His investigation was, however, made 40 years ago, before modern methods of technique were in vogue, and the unusual interest attaching to the subject in the field of insect morphology has led me to make a fresh examination of these organs with a view to completing and extending his work.

The sheep-tick is an exceedingly common insect in America and Europe, the American tick being undoubtedly identical with the European species. The adult female insect (Pl. II, Fig. 1) is about 6 mm long. The head is small and triangular in shape and bears rudiments of antennae (*ant*) and eyes (*eye*), and a long proboscis

(*prob.*) The thorax is relatively small and is segmented, the meso- and metathorax each bearing a pair of large spiracles (*sp*). There are no wings or rudiments of any, but rudiments of halteres are present. The abdomen is a large, pear-shaped body-division, much flattened dorso-ventrally; it is unsegmented and is covered by a tough, leathery cuticula. It bears seven pairs of spiracles somewhat smaller than those on the thorax, two of which are near its anterior and two near its posterior end. The entire body is covered with long, bristly hairs.

The female genital tract occupies the position usual in insects, in the ventral, posterior portion of the abdomen (Pl. II, Fig. 1). It is made of the following parts: paired ovaries (Pl. II, Figs. 1, 2 *ov*); two short paired oviducts (*pa.ov*); a median unpaired oviduct formed by the fusion of the proximal ends of the paired oviducts and consisting of two portions, a narrower proximal portion (*med.ov*), and a widened distal portion, which has the function of a receptaculum seminis (*rec.sem*); the median efferent duct, which passes to the vulva and is usually called the vagina in insects, but which I shall in *Melophagus* divide into two portions, an extensive anterior portion, the uterus (*U*), and a shorter posterior portion, the vagina (*vag*); and, finally, the two pairs of milk-glands, which join the anterior end of the uterus (Pl. II, Figs. 2, 3 *m.gl*).

As to the position of these organs in the body, the vagina and the uterus lie near and in a plane parallel to the ventral abdominal wall. The median, unpaired portion of the oviducts, in the virginal female, lies in a plane perpendicular to that of the uterus (Pl. II, Fig. 3 *med.ov*), and in the old female in a plane at an acute angle to that of the uterus (Pl. II, Fig. 2). I wish to emphasize these facts as LEUCKART describes all the different parts of the genital tract as lying in very nearly the same plane (see his Figs. 1, 2, 3 and 4, Pl. I), and his figures have been copied into several text-books (see CLAUS' *Lehrbuch der Zoologie*, Fig. 495). It is only in sections, which, of course, LEUCKART could not have had at his disposal at the time when his paper was written, that the true position of these organs can be seen, and a dissection of them must inevitably disturb their relations with the surrounded viscera. The receptaculum seminis, constituting the distal end of the unpaired portion of the oviducts, is also in the median line, and from it the short paired portions of the oviducts proceed to the right and left to the two ovaries. The richly branching milk-glands are very extensive organs and wind

among the viscera throughout the abdomen. All of these organs will be described in detail further on.

The relative size of the genital tract is large, even in the virginal female, where its length is two-thirds that of the abdomen (Pl. II, Fig. 3), while in the old female its size depends entirely on the age of the growing larva, when one is present, in the uterus. The sheep-tick is, in common with the rest of the Pupipara, an ovoviviparous animal. The young animals are born one at a time and at intervals, in the Summer-time, of several weeks. The entire embryonic stage and the greater portion of the larval stage are passed in the mother's uterus, the young animal being born as an old larva. About twelve hours after the larva is born the puparium is completed and the »Tonnenpuppe« begins its metamorphosis<sup>1</sup>. The name »Pupipara« is thus a misnomer as BLANCHARD and LEUCKART have shown, as the sheep-tick is not a pupa-bearing insect, and rests on a misconception of LATREILLE, who named the group. In an insect, whose uterus is either empty or contains an egg or a very young larva, the genital tract is, as in the virginal animal, about two-thirds the length of the abdomen (Pl. II, Fig. 1), but the presence of an old larva in the uterus distends the reproductive tract in all directions, so that it may become quite as long as the abdomen and half as wide and half as thick (Pl. II, Fig. 4).

### The vulva.

The vulva is a half-moon-shaped slit, 0,40 mm long, transverse to the longitudinal axis of the body and situated at the posterior end of the body near the ventral surface (Pl. II, Fig. 1 *vul*). It is 0,27 mm antiad and ventrad of the anus (Pl. II, Fig. 1 and 3 *A*) from which it is separated by a thick chitinous plate (*ch.pl*) well studded with small chitinous bristles. Each lip of the vulva is bounded by a projecting chitinous ridge which, coming from above and below, almost close the opening. The anterior and most ventrally situated lip represents the concave side of the half-moon (Pl. II, Fig. 1). It is composed of a pair of chitinous plates, one to the right and the other to the left of the median line. These plates do not, however, meet in the median line except at their posterior, median margins where they are connected by a median, rectangular thickening (*spur*).

<sup>1</sup> A description of the larva of *Melophagus* will be found in »Beiträge zur Kenntnis der Pupiparen: die Larve von *Melophagus ovinus*« von H. S. PRATT, in Archiv für Naturgeschichte, 53. Jahrg., 1893.

This thickening projects into the vulva in the form of a spur and is seen especially well in a sagittal section (Pl. II, Fig. 3 *spur*). The anterior edges of these paired plates are much thickened and form distinct ridges. The posterior, convex lip of the vulva is a chitinous plate thickly beset with spines which, as above mentioned, extends back to the anus (Pl. II, Figs. 1 and 3 *ch.pl*). The margin of this plate which forms the lip is thickened to form a ridge which projects eave-like over the vulva from above (Pl. II, Fig. 3 *ch.pl*). The continuity of this ridge is broken in the median line by a median indentation (Pl. II, Fig. 1 *ch.pl*). The plate itself is bounded on both the right and left sides by a deep groove (Pl. II, Fig. 6 *gr*), which forms a ridge in the body-cavity, the significance of which for the attachment of muscles for the control of the vulva will be explained further on.

The vulva, it will be seen, is a valve-like slit which is capable of great distension. The larva, at the time of birth is a cylindrical object with a diameter of about 0,78 mm. The vulva, thus, through which it must pass, must stretch in all directions and more than double its capacity at the time of a birth. It is probable that both lips take part in this stretching but it also seems probable that the posterior (dorsal) lip has the principal share in it. The muscles which join the dorsal wall of the vagina and the posterior lip of the vulva with the ridge-like invagination of the body-wall (Pl. II, Fig. 3 *p.R*), which is situated just dorsad of the anus, undoubtedly have for their function the raising of them at the time of a birth and thus increasing the capacity of both vagina and vulva, as will be further explained in speaking of the vagina.

### The vagina.

The vulva opens into the vagina. This is a tube of the same width as the vulva which extends 0,33 mm forward to the posterior end of the uterus (Pl. II, Fig. 3 *vag*). The vagina is not a cylindrical tube but varies its shape between its anterior and posterior ends. At its posterior end it is a dorso-ventrally compressed tube with three shallow, longitudinal grooves in its dorsal wall, one in the median line and the other two at the extreme right and left sides. These three grooves increase rapidly in depth (height) anteriorly as far as the beginning of the uterus, where they abruptly terminate, so that near its anterior end a cross-section of the vagina presents the appearance represented by Pl. II, Fig. 5. The median groove



is a continuation of the median indentation of the posterior (dorsal) lip of the vulva mentioned above and a sagittal section of the vagina, which would pass through this groove its entire length, would represent the dorsal vaginal wall as becoming rapidly higher anteriorly as far as the beginning of the uterus (Pl. II, Fig. 3 *vag*). A comparison of this section, however, with the cross-section (Fig. 5) shows at once that the portions of the dorsal vaginal wall to the right and left of the median line do not thus increase in height. The two lateral grooves of the dorsal vaginal wall (Fig. 5) are continuations of the grooves mentioned above (Fig. 6 *gr*) which bound the plate (Fig. 1 *ch.pl*) forming the posterior lip of the vulva. The cuticula of the dorsal wall is hard and yellow like that of the outside of the body and is studded with small, chitinous bristles, deflected towards the vulva. The cuticula of the ventral wall is thicker than that of the dorsal wall but is not hard and yellow and contains no spines.

The vagina is very evidently an infolding of the outer body-wall. Its cuticula and hypodermis are identical with those of the body-wall and a direct continuation of them, and its muscles undoubtedly also belong to it. These muscles form several distinct groups of fibres and the function of all of them is to increase the capacity of the vagina during the growth of the larva and at the time of a birth. The most important of them is, perhaps, a paired group of fibres which connects the dorsal vaginal wall and the posterior (dorsal) lip of the vulva with a broad ingrowth of the body-wall situated directly dorsad of the anus (Pl. II, Fig. 3 *p.R*). These muscles appear fan-shaped in longitudinal section (Pl. II, Fig. 3 *d.vag.mus*); they surround the end-intestine, which runs through them and divides them into two equal divisions. Laterad of this group of fibres on each side are muscles-fibres which connect the lateral portions of the dorsal wall of the vagina with the dorsal body-wall (Pl. II, Fig. 5 and 6).

The significance of the folds of the dorsal vaginal wall will be clearly seen from their relation to these muscles. When the latter are contracted the folds are lifted and the capacity of the vagina thereby very largely increased. This takes place not only during birth but also during the growth of the young larva in the uterus. The spiracles of the larva, as is so common among Diptera, are on the hinder end of the body. They are thus directed towards the maternal vagina (Pl. II, Fig. 4 *lar.sp*), and the air necessary for the respiration of the larva must come through that organ. The figure

above referred to shows that the lumen of the vagina has been increased in size in response to this need of the larva.

Another important group of muscle-fibres is the thick bunch transverse to the longitudinal axis of the body which covers the dorsal surface of the ingrowth of the body-wall above mentioned (Pl. II, Fig. 3 and 6 *p.t.mus*). The ends of the fibres are attached to two ridges formed in the body-cavity by the two grooves (Fig. 6 *gr*) which form the lateral boundaries of the chitinous plate extending from the vulva to the anus and mentioned above. These muscles are, perhaps, the largest group of muscle-fibres in the animal's body. Their function is obvious: by their contraction they raise the plate forming the posterior lip of the vulva and thus very much increase the capacity of that slit-like opening during a birth. Reinforcing these muscles are also a number of fibres which pass from the above-mentioned ridges to the dorsal body-wall.

The ventral wall of the vagina is but poorly supplied with special muscles, there being here no extensive bands or groups of fibres but only a few scattered fibres which pass from it to the ventral body-wall (Pl. II, Fig. 3 *vag.mus*).

### The uterus.

The uterus is a broad, dorso-ventrally compressed tube stretching from the anterior end of the vagina forward to the median oviduct (Pl. II, Figs. 1, 2, 3, 4 *U*). Its actual shape and size are entirely dependant upon the age and the sexual condition of the animal. The virginal uterus represented in Fig. 3 has a length of about 1 mm, which is about half the length of the abdomen, and extends forward to within 0,8 mm of the forward end of the abdomen. The presence of an egg (Pl. II, Fig. 1) in the uterus changes its shape but slightly, but when the egg hatches and the young larva begins to grow, the uterus rapidly becomes stretched out of all semblance of its former shape. The presence of the full-grown larva in the uterus distends that organ forward until it reaches the anterior end of the abdomen (Pl. II, Fig. 4). The small intestine of the mother is crowded by this great growth of the larva into the anterior, dorsal portion of the abdominal cavity, and the voluminous rectum is pressed against the dorsal body-wall. The larva, which at this time occupies with the uterus half the space in the abdominal cavity, can easily be seen through the ventral abdominal wall. It appears as a glistening, white object occupying the entire median portion of the abdomen.

A young larva or an egg can also be detected, but less easily; it lies in the forward portion of the uterus and appears near the centre of the abdomen.

In its finer structure the uterus presents no new features, but some interesting modifications of the usual conditions. Its walls are a direct continuation of those of the vagina. The thickness of the cuticula at the posterior end of the uterus equals that of the cuticula of the vagina, but this thickness gradually diminishes toward the forward end and in its forward half the uterus is lined by such an extremely thin and delicate cuticula that it is often difficult to detect. The matrix of the cuticula is the usual single-layered epithelium. This is surrounded by a thickly woven layer of branched muscle-fibres forming a network about the entire uterus which branch without regularity and are of varying thickness (Pl. III, Fig. 7). The strands immediately next to the uterine wall appear to be smaller than those toward the outside. The function of this network is evident. It is primarily, by the contraction of its fibres, to bring about parturition at the proper moment, but it must also serve to strengthen and support the wall of the uterus while that organ is heavy with the growing larva. On the outer surface of the muscle-sheath run longitudinal bundles of unbranched muscle-fibres which connect the uterus with the ventral and anterior portions of the abdominal wall. Also a few fibres pass from the dorsal uterine wall around the rectum to the dorsal abdominal wall. The most important of these longitudinal groups of muscles are those which pass from the forward portions of the uterus to the anterior and ventral abdominal body-wall (Pl. II, Fig. 3 *l.mus*). These are attached to the dorsal, ventral, and lateral surfaces of the uterus and find their forward attachment principally on two ridges of the abdominal wall which project into the body-cavity. We see thus that the uterus is provided with an extremely strong musculature, composed of two distinct systems of fibres; the branched fibres forming the sheath immediately about it and the longitudinal fibres which connect it with the body-wall. The function of the latter is undoubtedly to hold the uterus in position. They are strong elastic bands which bind the uterus to the body-wall but whose length can change with the varying size of the uterus. But these muscle-fibres are not the only means of support with which the uterus is supplied. From the most anteriorly placed abdominal spiracles a pair of strong tracheal trunks pass to the uterus, just in

front of which they break into a number of branches which pass around it on all sides (Pl. II, Fig. 3 *tr.*).

The uterus is composed of two distinctly different divisions, the posterior half, the walls of which are in all respects like those of the vagina, and the anterior half, whose walls are of quite a different character in that they have the thin, delicate cuticula already mentioned, and are besides thrown into thick folds so that the lumen is very irregular in shape and in the empty uterus is often entirely closed. It is into this anterior portion of the uterus that the egg arrives when it has been extruded from the ovary and where it remains while the embryonic development proceeds. The young larva on hatching also occupies the same place but gradually grows towards the posterior end until it fills the entire uterus.

### The milk-glands.

At the anterior end of the uterus its dorsal surface is pierced by an opening through which the two pairs of milk-glands communicate with it (Pl. II, Fig. 3 and 4 *op.m.gl.*). LEUCKART (10) states wrongly that there are two openings, one for each pair of glands and one in front of the other, and that they are in the dorsal wall of the median oviduct. The forward pair is composed of two thick, short tubes averaging 0,5 mm each in length and 0,06 mm in diameter, whose proximal ends are fused to form a single tube (Pl. III, Fig. 8 *a.m.gl.*, Pl. II, Fig. 2 *a.m.gl.*). The hinder pair is composed of two large, extensively branched, tubular structures which also fuse at their extreme proximal ends to form a single vessel (*p.m.gl.*). The median, proximal ends of the two gland-pairs meet at the opening in the wall of the uterus and are there bound together by a sheath of muscle-fibres (Fig. 9). The function of these two pairs of glands is to furnish the milk-like fluid which serves as food for the growing larva. The forward, club-shaped pair has probably largely lost this function and become more or less rudimentary, and as is usually the case with rudimentary organs they show a considerable amount of individual variation. They are often so small as to be found with difficulty or may reach the considerable development represented in Fig. 8. They may even be found much larger than these and LEUCKART (10) has observed cases in which the distal ends of these glands branched dichotomically like the posterior pair. In Hippobosca, according to DUFOUR (4), the anterior glands are long branched structures.

The nutriment of the larva in Melophagus is undoubtedly furn-



ished principally by the posterior pair of glands. This nutriment consists of a fluid containing a mass of round or oval disc-shaped bodies which are presumably fat-bodies; they are fairly constant in size having an average diameter of 0,01 mm. The secretion of these glands is thus extremely similar to milk. It is poured through the opening already mentioned into the anterior end of the uterus where the larva sucks it into its mouth. During the entire uterine life of the larva its anterior end is constantly at the anterior end of the uterus, the increase in length which the larva undergoes resulting in its extension towards the posterior end of the uterus until that organ is completely filled. The mouth of the larva, however, does not change its position in the uterus, and would be thus constantly bathed in the milk-like secretion (Pl. II, Fig. 4 *lar.M*), which is sucked in by a complicated sucking apparatus I have already described in another place (PRATT, 16). For the sake of completeness, I will briefly describe this organ again. Directly back of the larva's mouth, in its pharyngeal cavity, is a muscular tongue-like organ (Pl. II, Fig. 4 *mus.ton*), ventrad of which the oesophagus passes to the sac-like stomach. Dorsad of the muscular tongue is a sac whose dorsal wall is connected by a median, longitudinal muscle with the dorsal body-wall. The muscular tongue contracts and dilates regularly like the beating of a heart, about forty times a minute: the dorsal longitudinal muscle must also contract, although I have never been able to observe it in the live animal. As a result of these movements the milk is drawn into the mouth of the larva and forced through the oesophagus into the stomach, which is at all times completely filled. The beating of the tongue probably goes on without interruption during the entire uterine life of the larva. As soon as it is born, however, and thus removed from its food supply, the beating ceases, and during the day or two which intervenes while the larva is preparing to enter upon the pupal stage and the first part of the metamorphosis, the young animal is nourished by the milk which was already in the stomach at the time of birth. The milk rapidly decreases in volume during this period and by the middle of the metamorphosis is entirely exhausted.

The finer structure of the milk-glands presents the following features. The extreme proximal, median ends of the two gland-pairs are bound together just before the opening into the uterus by a common muscle-sheath (Pl. III, Fig. 9), composed of irregularly arranged, striped fibres.

**The Anterior Pair of Glands.** The epithelium of which these glands are composed is made up of cells which have but little secretive function, those cells near the distal ends of the glands being somewhat higher than the others (Pl. III, Fig. 8 *a.m.gl.*). Surrounding the proximal, fused ends of the glands are muscle-fibres, irregularly arranged (Pl. III, Fig. 10 *a.m.gl.*). Distad of the point of bifurcation of the tubes, the inner most fibres no longer appear. The outer most fibres persist, however, and for a short distance form a common sheath around the ends of the diverging tubes and hold them together. They also surround each tube after they have ceased to form this common sheath for about a quarter of its length. The distal three-quarters of the glands have no muscles around them. The entire structure is bounded externally by a *membrana externa* (Pl. III, Fig. 8 *mem.ex*) and internally by a thick *membrana interna* (*mem.in*), both of which are structureless. In a longitudinal section of these glands their lumen appears bounded by serrated lines which fact is due to the projection of the inner ends of their epithelial cells into the lumen.

**The Posterior Pair of Glands.** The fused portion of these glands is very short, the two glands joining immediately before entering the uterus (Pl. III, Fig. 8). The free portion of each is composed of two distinct divisions, the branched, distal portion in which the secretive alone resides, and the unbranched, proximal portion which is but the outlet or duct of the other. The epithelium of this duct is composed of flat cells which project into its lumen; surrounding this are two layers of muscle-fibres. A thick *membrana interna* (Pl. III, Fig. 8 *mem.in*) lines the lumen and a *membrana externa* (*mem.ex*) surrounds the muscles on the outside of the ducts. The distal portion of the glands is by far the larger part of them. It branches very extensively, apparently usually dichotomically (Pl. II, Fig. 2 *p.m.gl.*), and fills up a greater part of the entire space in the abdomen which is not occupied by other organs. Its epithelium is composed of large cells, 0.04 mm high, four or five times as large as those of the epithelium of the duct. The nucleus is large and invariably contains one or two large nucleoli. The protoplasm of the cells appears coarsely granular in stained specimens and often contains large vacuoles. The *membranæ interna* and *externa* are present on every part of the glands, but no muscle fibres are on the distal, branched portion.

### The oviducts.

It has already been mentioned that the oviducts of the sheep-tick are very highly modified from the typical condition. Their proximal ends are fused and form a single, median vessel 0,33 mm long, which joins the uterus a trifle posteriorly to the latter's anterior end. In the virginal female this median oviduct lies in a plane perpendicular to that of the uterus (Pl. II, Fig. 3): thus it has a dorso-ventral position, whereas the uterus lies parallel to the ventral abdominal wall. As the female becomes older, however, and the uterus through frequent bearing becomes larger and longer, the proximal end of the median oviduct gets carried forward so that its original perpendicular position is lost and gives way to one in which the median oviduct meets the uterus at an acute angle (Pl. II, Fig. 2 *med.ovi*). And when the uterus is distended to its greatest extent by the presence in it of a large larva this angle becomes almost obliterated, and the median oviduct is brought to lie directly on the dorsal wall of the uterus. The short, paired, distal ends of the oviducts join the median, unpaired portion just described to the right and left respectively (Pl. II, Fig. 2 *pa.ovi*). These are very short and vary in length with the condition of the ovary as will be explained later, and each bears at its extremity the ovoid ovary.

The function and purpose of this peculiar fusing of the proximal ends of the oviducts, which, so far as I know, is not to be met with to the same extent outside the group of Pupipara, is to provide a reservoir for the sperm of the male animal in the female, in other words, to improvise a receptaculum seminis. The sheeptick has no receptaculum seminis of the form usual in insects. The extreme anterior end of the uterus, which appears as a small projection in front of the point of juncture of the median oviduct with it, may be a rudiment which is homologous to the receptaculum seminis of other insects, and has been so interpreted by LEUCKART (10). All of the other brachyceran dipters, so far as I know, are provided with a receptaculum seminis, and the ancestors of Melophagus and the other pupipars were undoubtedly no exception to the rule. But probably the enormous distention of the uterine wall, which has resulted from the retention of the growing larva in the uterus, has led to the extinction of the receptaculum seminis as a functional organ. Its place, then, is taken by the fused ends of the oviducts; this acts as a receptacle of semen and is constantly filled with it.

It was v. SIEBOLD who first demonstrated this fact (19). DUFOUR (4 and 5) called the anterior milk-glands the receptaculum seminis; LEUCKART corrected him.

But it is not the entire median oviduct which is thus filled with sperm and functions as a receptaculum seminis, but the dorsal or distal end of it (Pl. II, Fig. 2 *rec.sem*) which is considerably wider than the remainder of the median oviduct and forms a distinct compartment in it. LEUCKART calls this the Fundus. Its lumen has a width of 0,15 mm in the adult female against a width of 0,01 mm in the portion of the median oviduct immediately adjoining the uterus. It is slightly arched on its dorsal surface and the paired oviducts meet it to the right and left. These are very short and of unequal length. When in either ovary an egg is present which is fully matured or nearly so, as is the case with the left hand ovary in Fig. 11, the oviduct on that side is apparently almost obliterated through the crowding of the egg into it (Pl. III, Fig. 11): when, however, the largest egg is still small and immature as in the right hand ovary, the oviduct on that side may have a length of 0,23 mm. And between these extremes we find all intermediate stages.

The finer structure of the oviducts presents the following features. The structure of the proximal portion of the median oviduct is similar to that of the uterus. The epithelium of the fundus and of the paired oviducts is peculiar in being composed of very high, narrow cells giving the wall a much greater thickness than that of the remainder of the median oviduct. Surrounding the epithelium is a network of muscle-fibres similar to that of the uterus but somewhat thinner. Their arrangement is also somewhat more regular than that of the uterus, there being a more definite arrangement into circular and longitudinal muscles. The ental fibres are distinctly circular while the ectal ones are longitudinal although their arrangement is not regular but such that they form a more or less regular network about the circular fibres. Among the muscles are numerous connective-tissue fibres.

The membrana interna is very delicate in the median oviduct. In the paired portions, however, it is very thick and is thrown into long folds which are longer than the cells they abut and project into the lumen so as almost to fill it, leaving only a very narrow passage in the center of the vessels (Pl. III, Fig. 11 *pa.ov?*). These folds are all inclined toward the fundus and their function is obvious: they form a system of valves which prevent the flow of the sperma-



tozoa stored in the fundus towards the ovarial sacs. The passage of the egg, on the other hand, from the ovary into the fundus would not be hindered.

### The ovaries.

The ovaries of *Melophagus* have much about them which is peculiar and have in consequence attracted the attention of entomotomists ever since the time of RÉAUMUR. On account of the difficulties attending a successful dissection of them, however, it was LEUCKART who first correctly described them. All of the earlier investigators, often misled by a curious desire to homologise them with the human ovaries, to which they bear a certain superficial resemblance, described the ovary of *Melophagus* as containing but a single ovariole which contained but a single ovum. And this false notion still largely prevails and is propagated by certain illustrations which appear in some of the best text-books. Fig. 495 in CLAUS' »Lehrbuch der Zoologie« and Fig. 160 in GEGENBAUR'S »Comparative Anatomy« (English translation) are taken from LEUCKART'S Fig. 1 (l. c.) and incorrectly described, conveying the notion above mentioned.

The ovary of our insect appears as an ovoid body of variable size (Pl. II, Fig. 2 *ov*). In a superficial examination one sees none of the parts usually found in an insect's ovary; i. e., ovarioles, egg-follicles, etc. The whole organ seems rather to consist of but a single ovariole containing but a single follicle with its ovum and nutritive cells. As a matter of fact, the peritoneal covering which encloses the ovary is of extraordinary thickness, thicker, perhaps, than in any other insect and forms an elastic sac within which lie two ovarioles (Pl. III, Fig. 12). The walls of this sac are made up of muscle fibres and connective-tissue and are a direct continuation of the outer covering of the oviducts and the uterus (*peri.cov*). Each of the two ovarioles within the sac consists of two follicles and a germarium; no distinct terminal thread is present, although the terminal portions of the germarium may be considered as such a structure. The ovarioles are attached by means of their germaria to the inner, distal surface of the peritoneal sac and at no other place, hanging, thus, free within the sac (see woodcut No. 1, also Fig. 12). The ovariole is bounded on its outer surface by a structureless tunica propria (Fig. 12 *tun.prop*) and by an inner peritoneal covering composed exclusively of connective-tissue fibres which project from the inner surface of the distal end of the peritoneal sac (*in.peri.cov*).

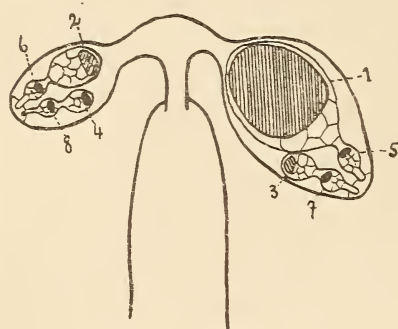
It will thus be seen that however different in shape from the typical insect ovary that of *Melophagus* shows no fundamental peculiarities. We find here the three structures one may expect to find in any insect ovary, to-wit; 1) the peritoneal covering; 2) the tunica propria; 3) the germinal epithelium. The first is peculiar only in being excessively developed, the latter two are not peculiar in any way.

*Melophagus* possesses almost the minimum number of ovarioles, *Campodia*, according to GRASSI (7), possessing but one. The following insects also possess but two, according to LUBBOCK (13, p. 343), *Lixus* and *Anthonomus* among the beetles, *Schizoneura corni*, an Hemipteron, *Chelonus*, a Hymenopteron, and according to LEUCKART (10), *Hippobosca* and *Braula*, also Pupipara. The greatest number of ovarioles is found in the termite in which the ovary, according to SHARP (18), is composed of 3000 ovarioles. Between these limits we find the greatest variation: according to LUBBOCK the honey-bee may have 170, Cicada 50, Elater and *Coccinella* 30, and Butterflies 4 to 12. There is, we see, the greatest variation in the number of ovarioles within the different orders of insets, nearly related insects often differing very greatly. There is, undoubtedly, in each case a single embryonic Anlage for all the ovarioles of each ovary, as has been shown, for example, among others by HEYMONS (8) for the cockroach, and by WEISMANN (20) for *Musca*, and by WHEELER (22) for *Xiphidium*, and by myself (16) for *Melophagus*, and this is true whether the ovary has a metameric origin as is the case in *Xiphidium* or appears before the metameres have become fully established. The number of ovarioles which actually becomes characteristic for any given species depends entirely on the life-conditions of that species and not on any hereditary conditions. If a large number of eggs must be produced in any given species a large number of ovarioles becomes the rule and vice versa. *Melophagus* produces probably not more than a dozen eggs a year. The ovarioles, it seems to me, cannot have metameric value except in some Thysanura as shown by GRASSI (7), their enormous variation between 1 and 3000, and their great variation often in near relatives, precluding this.

*Melophagus* possesses with a very few exceptions, the minimum number of follicles in each ovariole. A few of the Hemiptera (*Coccus*, according to LUBBOCK) have but a single follicle in each ovariole. These insects have, however, a large number of ovarioles and thus produce many more eggs than *Melophagus*. *Hippobosca* and *Braula* according to LEUCKART have three in each ovariole, *Musca*

has three or four, *Blatta* has ten, *Periplaneta*, according to WHEELER (21) has thirty and the *Lepidoptera*, according to LUBBOCK have from twelve to one hundred.

There are thus in the ovary of *Melophagus* but four developing ova at any one time, two in each ovariole, and in the two ovaries there are but eight ova. The two ovarioles within each ovary, and also the two ovaries themselves, are further peculiar in being very dissimilar in size. As the entire embryonic and a greater portion of the larval growth goes on within the uterus, this organ naturally retains each egg within it a long time, and receives the different eggs from the ovaries one at a time and at long intervals, probably of several weeks. The two ovaries alternate in furnishing the next egg, and within each ovary the two ovarioles alternate in performing



Textfig. I.

this duty. The accompanying diagram shows the order in which the eight ova in the four ovarioles leave the two ovaries, the numerals indicating the order of succession. The result of this arrangement is that there is always one ovum of the eight in the two ovaries much larger than the others, it being the one whose turn will next come to descend into the uterus, and the ovary

which contains it will be much larger than the other ovary. Likewise within the ovary the follicle which contains this ovum will be much larger than the other three follicles. These facts are very well shown in the plates. In Fig. 11, in the smaller ovary (the one to the right of the reader), the two ovarioles are as near the same size as any I have observed; the smaller ovariole (*ovar.2*) having a length of 0,17 mm, the larger one (*ovar.1*) having a length of 0,35 mm. The largest follicle in this ovary (*fol.2*) has a length of 0,26 mm, the next largest (*fol.4*) has a length of 0,15 mm. The two smallest follicles (*fol.6* and *fol.8*) do not differ much in length, they measuring 0,066 mm and 0,05 mm respectively. In the larger ovary (the one to the left of the reader) the ovariole containing the largest follicle (*ovar.1*) has a length of 0,87 mm, the smaller ovariole (*ovar.2*) has a length of 0,22 mm. The largest follicle (*fol.1*) in this ovary has a length of 0,77 mm, the next largest (*fol.3*) has a length of 0,16 mm; the two smallest follicles



(*fol.5* and *fol.7*) do not differ in size, their lengths being 0,08 mm and 0,06 mm respectively, which is very nearly the same as the lengths of the smallest follicles in the opposite ovary. The mature ovum measures 1,2 mm in length and 0,30 mm in width; it occupies almost the entire space within the peritoneal sac, and impresses its shape upon it, the follicles containing the other three ova being exceedingly small and being crowded into a narrow space at the distal end of the ovary. The lower or proximal end of the ripe ovum crowds the oviduct, partly obliterating it.

When, now, the ripe ovum is extruded, the ovary at once shrinks by the contraction of the muscles-fibres in the peritoneal sac to a very small size and the follicular epithelium, which had surrounded it, and the remains of its nutritive cells disintegrate. The ovary becomes about 0,64 mm long and 0,24 mm wide. Its shape also changes: when it contains the ripe ovum it has almost its exact shape and size, after the ovum is extruded it becomes an elongated structure, slightly larger toward the proximal end (Pl. II Fig. 2, *ov.* and Fig. 12). The walls of the peritoneal sac hang loose about the ovarioles (Fig. 12). The separate peritoneal coverings of the ovarioles also hang loose about them and project from their lower ends towards the oviducts and often contain scattered epithelial cells, the disintegrated remains of the last mature follicle (Pl. III, Fig. 12, *dis.fol.ce*).

The duty of furnishing the next ovum now shifts to the opposite ovary, which, of course, is now the larger of the two: it is a piriform structure and measures 0,9 mm by 0,5 mm. It is at this time that the two ovaries are the smallest in absolute size, and also that the youngest embryo is present in the uterus. As the growth of the embryo and the larva proceeds the two ovaries are constantly increasing in size, until finally when the larva has attained its maximum size and is ready to be born, the largest ovum in the largest ovary has again attained full size and is ready to be extruded. It is at this time that the two ovaries have attained their maximum size. The larva in the uterus is then born and that organ being emptied, soon afterward the ripe ovum passes in its turn from the ovary through the receptaculum seminis, where it is fertilized, into the uterus.

**Histology of the ovary.** Peritoneal covering. This is composed of two distinct tissues, a) a layer of striped, branched and anastomosing muscle-fibres among which are a small number of connective-tissue fibres, which form the outer portion of the peritoneal sac, and b) a layer of branched and anastomosing connective-tissue



fibres which form the inner portion of the peritoneal sac and also a coating about the ovarioles (Pl. III, Fig. 12 *peri.mus* and *peri.con*). Entering the peritoneal sac from the body-cavity are numerous small tracheae and nerves. The branched muscles are best studied in a small ovary. In large ovaries in which the principal ovum is well developed, the muscles are so much distended that it is often impossible to distinguish their striation, and they may appear more like an irregular mesh-work of anastomosing connective-tissue fibres. At the side of a small ovary the muscles appear as broad fibres with a round or elliptical cross-section (Fig. 12 *per.mus*) containing many nuclei; in a flat view they appear as broad, irregularly shaped muscle-cells, anastomosing freely, each cell containing a nucleus (Pl. III, Fig. 15). There are no straight, unbranched muscles-fibres connecting the ovary with other organs or with the body-wall as is the case with the vagina and the uterus, the nerves and tracheae entering the ovary being the only suspensory apparatus attached to it.

The connective-tissue fibres composing the inner layer of the peritoneal sac are always easily distinguished in sections from the muscle-fibres. They form a distinct layer beneath the muscles, the thickness of which is considerably less than that of the muscle-layer (Fig. 12). Where the peritoneal sac is stretched by the presence of a large ovum, the muscle fibres do not show their striations, as has already been mentioned, and the connective-tissues fibres of the inner layer and the muscle-fibres of the outer one have the same appearance, except that the former are smaller in cross-section and contain far fewer nuclei than the latter. The interspaces between the muscles contain numerous delicate strands of connective-tissue which pass among them from the inner layer. The outer surface of the peritoneal sac is covered by a *membrana externa*. According to LEUCKART's description the inner surface of the peritoneal sac is also lined with a structureless membrane which is a continuation of the intima of the oviducts. This membrane does not appear in my preparations.

But connective-tissue fibres not only form the inner surface of the peritoneal sac but they fill the distal end of the sac and form a coating around the ovarioles (Pl. III, Fig. 12). In a very small ovary containing very young ova, such as is figured in Figure 12, the peritoneal covering of the separate ovarioles may be studied very favorably. The distal end of the ovarian sac is seen to contain a mass of connective-tissue fibres in which are imbedded the distal ends of the ovarioles.

Figures 13 and 14 represent two cross-sections of the distal tip of the ovary, Fig. 13 being slightly proximad of Fig. 14. In both we see the outer muscular layer surrounding the connective-tissue within: Fig. 13 shows the distal termini of the ovarioles (*ovar*), Fig. 14, being just distad of these termini and not containing them. The peritoneal covering of the separate ovarioles is closely applied to those follicles which contain large ova (Pl. III, Fig. 11 *in.peri.cov*). This is not the case, however, at the narrow necks which connect the follicles, where it passes directly from one follicle to the other. In ovarioles containing very small ova their peritoneal coverings are but loosely applied to the entire structure (Pl. III, Figs 12 *in.peri.cov*). The peritoneal covering of the ovarioles often extends below the largest follicle toward the oviduct where they terminate abruptly and freely. The actual condition of this end of them differs very greatly in different cases. In the ovary represented in Fig. 12, the follicles being extremely small, the inner peritoneal membrane is seen extending far below each ovariole. It consists of a broad band of connective tissue which extends from the lower end of the ovarioles to the beginning of the oviduct and there ends abruptly; it contains a few scattered cells (*dis.fol.ce*) which represent the remains of a disintegrated follicle which has discharged its ovum.

In large ovaries the lower end of the peritoneal covering of the separate ovarioles is much less noticeable. Often, as in both ovaries represented in Fig. 11, it does not extend at all below the largest follicle in each ovary, but simply forms a covering around its lower end in all respects like that at its sides. When a ripe ovum is extruded the peritoneal membrane covering its follicle is ruptured.

It will be interesting now to compare the peritoneal covering of the ovary of *Melophagus* with that of other insects. In the majority of insects we find that it consists of a more or less closely woven membrane of fibrous connective-tissue which surrounds each ovariole: imbedded in it are often striated, branched muscle-fibres, nerves and tracheae. There are, however, the greatest differences in the actual extent of the peritoneal membrane in different insects. It may be entirely wanting, as, according to BRANDT (2, p. 3), it is in *Perla*, *Nemura*, *Baetis*, *Coccus* and the viviparous Aphids. In the cricket (*Gryllus*) it is present, but feebly developed, and consists of long, thin, net-like, anastomosing connective-tissue threads, which are spun around and among the numerous ovarioles. They do not form a membrane, however, about each separate ovariole, but at the outer

rim of the ovary they form a distinct membrane which surrounds that organ and binds the ovarioles into a compact mass. In *Tipula* similar conditions prevail, but in addition to the connective-tissue fibres, muscles-fibres are also present. In both cases the peritoneal membrane is continuous with the outer covering of the oviduct and also of the terminal thread. Very commonly, however, the peritoneal fibres, instead of merely being spun among the ovarioles or forming a membrane about all, are woven into a distinct membrane about each one, and in this case the membrane about the entire ovary is usually not present. Thus in *Rhizotrogus*, *Notonecta*, and *Carabus*, according to LEYDIG (11, p. 602), each ovariole is covered with a thick peritoneal covering, and the membranes of all the different ovarioles meet at the distal end of the terminal thread in a common membrane which connects with the outer covering of the heart. In *Musca*, a very near relative of *Melophagus* and the pupipars, the conditions are similar. The peritoneal membrane, according to LEYDIG (11, p. 574), covers each ovariole rather loosely. The different follicles of an ovariole are separated from each other by a very narrow neck, and here the peritoneal covering is not applied closely to the tunica propria, but passes directly from one follicle across to another. At the distal tips of the ovarioles their peritoneal membranes fuse and in this common membrane are branched muscle-fibres. There is no connection between the ovary and the outer covering of the heart.

BRANDT (l. c. p. 7) sums up his chapter on the peritoneal membrane in insects as follows. It is usually present, and consists of connective-tissue in which may be muscle-fibres; but it is an accessory and not a necessary part of the reproductive tract. Its function is to hold together the ovarioles. The muscle-fibres, when they are present, serve two purposes, they assist in binding together the ovarioles and also cause the peristaltic motion which has been observed in the ovaries of *Pulex*, *Pieris* and other insects.

Considering *Melophagus*, now, in the light of the foregoing, we see that its peritoneal membrane, the character and structure of which at first sight seem so aberrant, is really peculiar only in its great thickness and extent. The portion which forms the outer sac finds its counterpart in many groups of insects in the membrane which surrounds and holds together the ovarioles, but in no other insect, so far as I know, is it so thick and composed of two distinct layers, and nowhere do the muscles play so important a role. There are no muscle-fibres in the peritoneal covering of the ovarioles in *Melo-*



phagus, which is unusual where this covering is as thick as it is in this insect. It is not unusual for these coverings to fuse beyond the end of the terminal thread and form a common mass of connective-tissue at the distal end of the ovary. In *Musca*, this fused portion contains muscle-fibres, and it seems to me that the outer peritoneal sac in *Melophagus* with its thickly woven layer of muscles may be a further development of the muscle and connective-fibres which in *Musca* are present at the distal of the ovary. In no other insect, so far as I know, does the peritoneal covering of the ovarioles fail to be continuous with the outer covering of the oviduct, and that this is the case in *Melophagus* is probably due to the fact that the outer covering of the oviduct finds its continuation in the peritoneal sac.

The ovarioles. Each ovariole consists of a short, thick germarium or terminal chamber and one or two follicles, and is bounded on the outside by a delicate tunica propria. The germarium in a small ovary is about 0,05 mm long and 0,025 mm thick at its base, and is imbedded for about a third of its length in the fibrous mass at the distal end of the peritoneal sac (Pl. III, Fig. 12 *ger*, Fig. 13 *ger*). The germarium tapers towards its tip where it contains but one or two nuclei. It is surrounded by a tunica propria to its tip. The contents of the germarium are small, compact nuclei all of the same size and appearance imbedded in protoplasm, no cell-walls being demonstrable. The germarium is separated from the youngest follicle by a constriction. In a very small ovary the smaller of the two ovarioles does not contain the usual two follicles, but a single mass of germ-cells in which differentiation has but just begun (Pl. III, Fig. 12 *ovar.2*). The first signs of differentiation in the young follicle is a division of its cells into peripheral and central cells, the former being smaller than the later and arranged in a regular, peripheral layer. This layer is destined to become the follicular epithelium of the two follicles of the ovariole, the inner cells to become the nutritive and egg cells. Covering the common follicle is a tunica propria, which does not end at its lower end, but extends alongside the larger ovariole to near the lower end of the ovary and contains the disintegrated remains of the follicle which last discharged an ovum (Pl. III, Fig. 12 *dis.fol.ce*). Very soon the inner cells at the lower, posterior end of the common follicle begin to increase greatly in size; the extreme posterior one of these cells becomes distinctly different in appearance from its fellows and somewhat larger than them and acquires a nucleus which contains far fewer chromatine



granules than the nuclei of the other cells, and a nucleolus, and thus develops into the ovum of the future lower follicle of the ovariole (Pl. III, Fig. 12 *ovar.2*). Almost simultaneously with its appearance, but yet a little later, the nutritive cells of the same follicle differentiate (*n.ce*). They are a trifle smaller than the young ovum but have nuclei which contain numerous chromatine granules and can be easily distinguished from it. The ovum, nutritive cells, and follicular epithelium, which have thus become differentiated in the lower portion of the common follicle, are at first not separated by any constriction from the still undifferentiated cells which are destined to form the upper or younger follicle of the ovariole. They grow rapidly, however, and increase in size, and soon a constriction appears which separates them from the upper portion of the common follicle, and thus divides this structure into the two follicles, in the lower one of which the distinctive cellular elements have all differentiated, while in the upper one differentiation has so far lagged behind that the cells only show an indistinct separation into outer, follicular epithelium and central cells, as is shown in *ovar.1* Fig. 12 and also in both ovarioles in the right ovary and *ovar.2* of the left-hand ovary in Fig. 11.

*Ovar.2* in each of the ovaries of Fig. 11, being the smaller of the two in each, the development of its follicles is almost entirely checked after the condition above described has been attained, by the enormous growth of the lower follicle of the other and larger ovariole of the ovary. Thus we see, for example, that after the lower follicle of the smaller ovariole has reached the condition represented by *fol.4* in Fig. 11, it remains stationary during the increase in size of its large neighbor, *fol.2*, and until this follicle has become mature and has discharged its ovum. The same fate also follows *fol.3*, Fig. 11, which is no larger than *fol.4*, although it is older, and also the largest follicle in Fig. 12, which has just become the chief follicle in the ovary by reason of the recent extrusion of the ovum from this ovary, is no bigger than *fol.3* and *fol.4*, Fig. 11.

If we could follow, now, the growth of the larger ovariole (*ovar.1*) in the small ovary represented by Fig. 12, we should notice that now that its lower follicle has become the largest follicle in the ovary and is given a chance to grow (by the disappearance of the ripe ovum in the other ovariole), it increases in size very rapidly. Its smaller follicle, however, which up to this time has undergone no development except into outer, follicular, and inner cells, would

not for some time grow at all. The nutritive cells and ovum of the large follicle of the larger ovariole would all increase very rapidly in size. The ovum is always at the lower end of the follicle; its nucleus is large and centrally situated and contains a very few chromatine granules and a nucleolus. The nutritive cells for a long time increase in size about as fast as does the ovum and have very large nuclei richly charged with chromatine granules. The tunica propria covers the entire ovariole; it is stretched to disappearance about the larger follicle after this has become of large size, but always appears on the narrow neck connecting the two follicles in the form of a tube containing scattered cells. On the lower side of the large follicle (that looking towards the receptaculum seminis) the tunica propria usually passes smoothly around the follicle, as is shown in Fig. 11; in some cases, however, the ragged end of the tunica may be seen extending beyond the follicle towards the oviduct (Pl. III, Fig. 12 *tun.prop*). In no case does the tunica propria extend as far as the oviduct.

When finally a follicle becomes the largest one in the two ovaries and its ovum is the next one to pass into the uterus, its growth becomes very rapid. Its nutritive cells also increase greatly in size and soon attain their maximum volume. The ovum, which up to this time has grown in size at about the same rate as the nutritive cells, now rapidly outstrips them and is soon larger than all the nutritive cells together (Pl. III, Fig. 11 *fol.1*). The nutritive cells now begin to decrease in bulk, and at about the same time the follicular cells begin to make their appearance and form a membrane between them and the ovum, the follicular cells which bound the nutritive cells on the outside becoming stretched and irregular. The follicular cells which surround the ovum increase in number as it does in size so that they always form a regular, columnar epithelium about it. The nucleus of the ovum, which has remained near its centre now loses its nuclear wall, becomes amoeboid and migrates to its periphery where it decreases very much in size. The nutritive cells decrease rapidly now in volume and the ovum increases until it has assumed the shape characteristic of insect eggs and the nutritive cells being deprived of a greater part of their substance are reduced to a mere remnant. The delicate chorion forms. The nucleus of the ovum has by this time migrated back to the centre of the ovum and that body soon after bursts its tunica

propria and passes into the uterus. I did not observe the extrusion of the polar bodies.

It will be interesting, now, to compare the ovarioles and egg-follicles of *Melophagus* with those of other insects. As is well known KORSCHOLT (9) following LUBBOCK (13), LEYDIG (11), and others, has shown that the indifferent, germinal cells in the germarium differentiate in the youngest follicle into the follicular epithelial cells, the ovum, and the nutritive cells if these be present. My own observations on *Melophagus*, as will already have been noticed, clearly confirm this view. These investigations, purely anatomical in character, do not, however, stand in harmony with the results of the embryological investigations of HEYMONS (8) and WHEELER (22) on certain Orthoptera. These authors have found that the follicular epithelial cells and the ova in this group of insects, are separate and distinct from each other from the time of their inception in the mesodermic somites of the embryo, so that there can be no indifferent germ-cells in the germarium. In the Orthoptera, however, the germarium of the adult insect is exceedingly small: it may, in fact, be said hardly to exist at all in the same sense as in the higher insects. It certainly does not contain indifferent cells. Judging from the figures of KORSCHOLT (Figs. 1—7), the short germarium contains two kinds of cells throughout its entire extent, the large ova within and the smaller follicular cells on the periphery which are continuous with the follicular epithelium of the remainder of the ovariole. In the upper end of the germarium there is a small agglomeration of the smaller cells, and they alone are found in the terminal thread. In the higher insects, on the other hand, a voluminous germarium is usually present, and it contains apparently indifferent cells which develop into follicular, nutritive, and egg-cells. It is my opinion, however, that further investigation in the embryology of the holometabolic insects will show that in them also the germinal and follicular cells are separate and distinct from their inception and that in some forms the adults will be found to possess a germarium consisting of two kinds of cells instead of indifferent cells.

Insect ovaries are divided by KORSCHOLT (9) and most of the text-books into two classes, those in which nutritive cells are present and those in which there are none. The first class is found in the Orthoptera and other of the lower insects, the second is found in the higher insects and may be subdivided into three subgroups according to the position of the nutritive cells. The first subgroup



contains those ovaries in which the nutritive cells are in the germarium and this structure is unusually large; it is present in the Hemiptera and certain Coleoptera: the second subgroup contains those in which the nutritive cells are in separate apartments of the ovariole, each apartment being immediately above an egg-follicle; it is present in the Hymenoptera: and the third subgroup contains those in which the nutritive cells are included in each follicle with the ovum, being situated just above or distad of it; it is present in the Diptera. The ovary of *Melophagus* belongs to the last named class. The ovariole is, as has already been pointed out, almost exactly similar to that of *Musca*. As KORSCHULT shows, the tunica propria in *Musca* is also ruptured as it is in *Melophagus* when the ovum descends from the lowest follicle into the oviduct, so that the connection between the ovariole and the oviduct is maintained by the peritoneal membrane alone, but *Melophagus* differs from *Musca* in that it is the outer peritoneal sac (which does not exist in *Musca*) by which this is accomplished, the peritoneal covering of the ovariole rupturing with the tunica propria.

### Methods.

The greater portion of this investigation was carried on at Haverford College. The material was obtained chiefly from the neighborhood and from Cold Spring Harbor, L. J., although some ticks which had been obtained in Germany were also used. I could see no difference between the American and the German ticks. The animals were killed by decapitation and then fixed in a saturated corrosive-sublimate solution heated to 50° C. The abdomens were then in many cases stained in borax-carmin and sectioned in the three principal planes. These sections show the position of the genital tract with reference to the surrounding organs. The finer histological details of the ovaries could, however, be studied to advantage only on genital tracts which had been dissected from the animal and then sectioned, as then only could that organ be cut in definite planes. It was found that a much more successful dissection could be made after the abdomen had been thoroughly hardened than when it was fresh on account of the great delicacy of the organs. This dissected material was stained either in toto with borax-carmin or on the slide with EHRlich's haematoxylin.

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## Explanation of the Figures.

All of the figures except Fig. 2 were drawn with the aid of a camera lucida.

### Abbreviations:

<i>ant</i> , antenna;	<i>mus.ton</i> , muscular tongue;
<i>a.m.gl</i> , Anterior milk-glands;	<i>n.ce</i> , nutritive cells;
<i>a.R</i> , anterior ridge;	<i>op.m.gl</i> , opening of milk-glands;
<i>A</i> , anus;	<i>ov</i> , ovary;
<i>b.w</i> , body-wall;	<i>ovar</i> ; ovariole;
<i>b.w.mus</i> , body-wall muscles;	<i>ovi</i> , oviduct;
<i>ch.pl</i> , chitinous plate;	<i>o</i> , ovum;
<i>dis.fol.ce</i> , disintegrating follicular epithelium;	<i>pa.ovi</i> , paired oviduct;
<i>d.vag.mus</i> , dorsal vaginal muscles;	<i>peri.con</i> , peritoneal connective tissue fibres;
<i>eye</i> , eye;	<i>peri.cov</i> , peritoneal covering;
<i>fol</i> , follicle;	<i>peri.mus</i> , peritoneal muscle-fibres;
<i>ger</i> , germarium;	<i>p.m.gl</i> , posterior milk-glands;
<i>gr</i> , groove;	<i>p.R</i> , posterior ridge;
<i>head</i> , head;	<i>p.t.mus</i> , posterior transverse muscle-fibres;
<i>in.peri.cov</i> , inner peritoneal covering, that around the ovarioles;	<i>prob</i> , proboscis;
<i>I</i> , intestine;	<i>proth</i> , prothorax;
<i>lar</i> , larva;	<i>r</i> , rectum;
<i>lar.A</i> , larval anus;	<i>r.gl</i> , rectal gland;
<i>lar.M</i> , larval mouth;	<i>rec.sem</i> , receptaculum seminis;
<i>lar.P</i> , larval pharynx;	<i>sper</i> , spermatozoa;
<i>lar.S</i> , larval stomach;	<i>sp</i> , spiracles;
<i>lar.sp</i> , larval spiracles;	<i>spur</i> , spur;
<i>l.mus</i> , longitudinal muscles;	<i>tr</i> , trachea;
<i>med.ovi</i> , median oviduct;	<i>tun.prop</i> , tunica propria;
<i>mem.ex</i> , membrana externa;	<i>U</i> , uterus;
<i>mem.in</i> , membrana interna;	<i>v</i> , vacuole;
<i>mesoth</i> , mesothorax;	<i>vag</i> , vagina;
<i>metath</i> , metathorax;	<i>v.vag.mus</i> , ventral vaginal muscle-fibres;
<i>m.gl</i> , milk-gland;	<i>vul</i> , vulva.
<i>mus.sh</i> , muscle-sheath;	

### Plate II.

Fig. 1. Ventral aspect of an adult female sheep-tick showing an outline of the genital tract with an egg in the uterus.  $\times 9$ .

Fig. 2. The upper (dorsal) surface of the genital tract dissected from the animal's body.  $\times 33$ .

Fig. 3. Sagittal section of the abdomen of a young female sheep-tick showing the position of the genital tract. The position of the dorsal vaginal

muscles (*d.vag.mus*) is represented by dotted lines. They would not appear in the section as they are paired organs.  $\times 70$ .

Fig. 4. Sagittal section of the abdomen of an old female tick showing the uterus containing a full-grown larva.  $\times 39$ .

Fig. 5. Portion of a cross-section of the abdomen of the tick showing a cross-section of the vagina with the surrounding organs. The plane of the section is marked in Fig. 3 by dotted line \*.  $\times 59$ .

Fig. 6. Portion of a cross-section of the abdomen through the chitinous plate between the vulva and the anus. The plane of the section is marked in Fig. 3 by dotted line †.  $\times 59$ .

### Plate III.

Fig. 7. Branched muscle-fibres dissected from the wall of the uterus.  $\times 875$ .

Fig. 8. The anterior pair of milk-glands and the proximal portions of the posterior pair.  $\times 130$ .

Fig. 9. Cross-section of the extreme proximal ends of the two pairs of milk-glands showing them bound together by muscle-fibres. The plane of the section is marked in Fig. 8 by the dotted line \*.  $\times 340$ .

Fig. 10. Cross-section of the two pairs of milk-glands somewhat distad of the cross-section represented in Fig. 9 showing them no longer bound together by muscle-fibres. The plane of the section is represented in Fig. 8 by the dotted line †.  $\times 340$ .

Fig. 11. Longitudinal section of the two ovaries the paired oviducts and the receptaculum seminis. *ovar.1* and *ovar.2*, the two ovarioles of each ovary; *fol.1, 2, 3, 4, 5, 6, 7, 8*, the different follicles in the order in which they discharge their ova.  $\times 78$ .

Fig. 12. Longitudinal section of a small ovary. *ovar.1* and *ovar.2*, the two ovarioles.  $\times 200$ .

Fig. 13. Cross-section of the tip of an ovary showing the ends of the germaria by which the ovarioles are attached.  $\times 200$ .

Fig. 14. Cross-section of the tip of an ovary distad of the germaria.  $\times 200$ .

Fig. 15. View of the muscle-fibres of the ovary.  $\times 340$ .

Fig. 1.

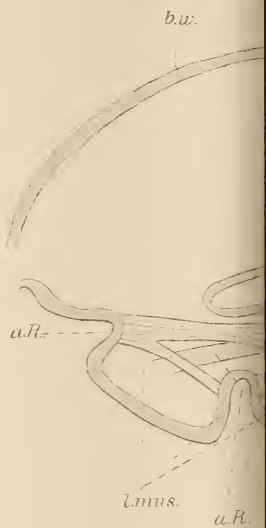
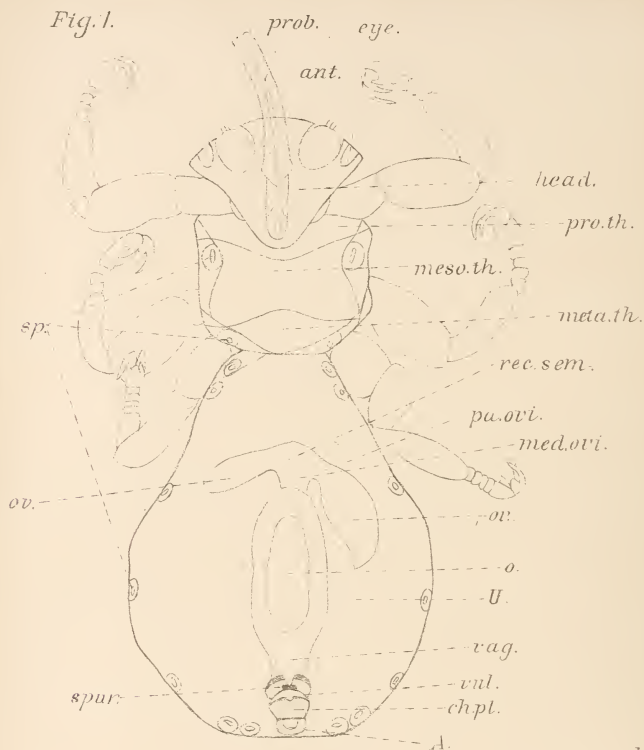


Fig. 2.

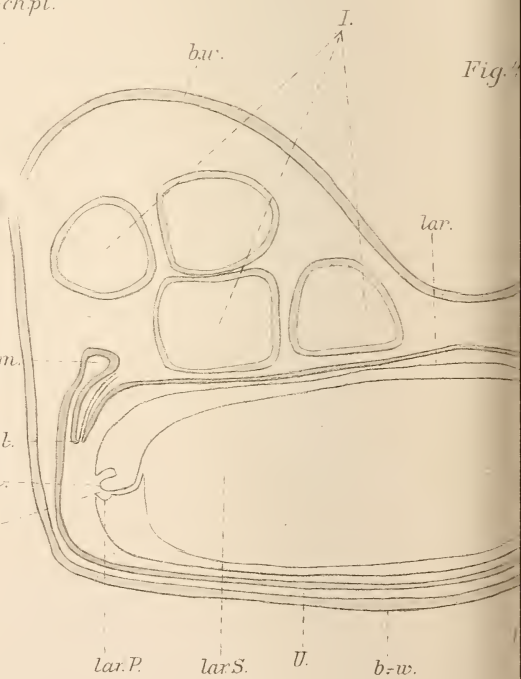
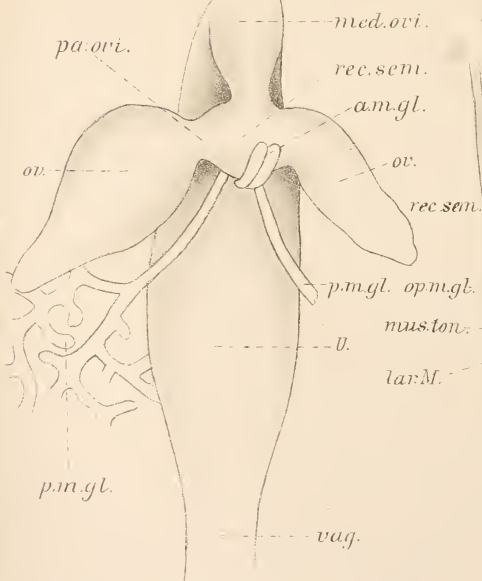




Fig. 3.

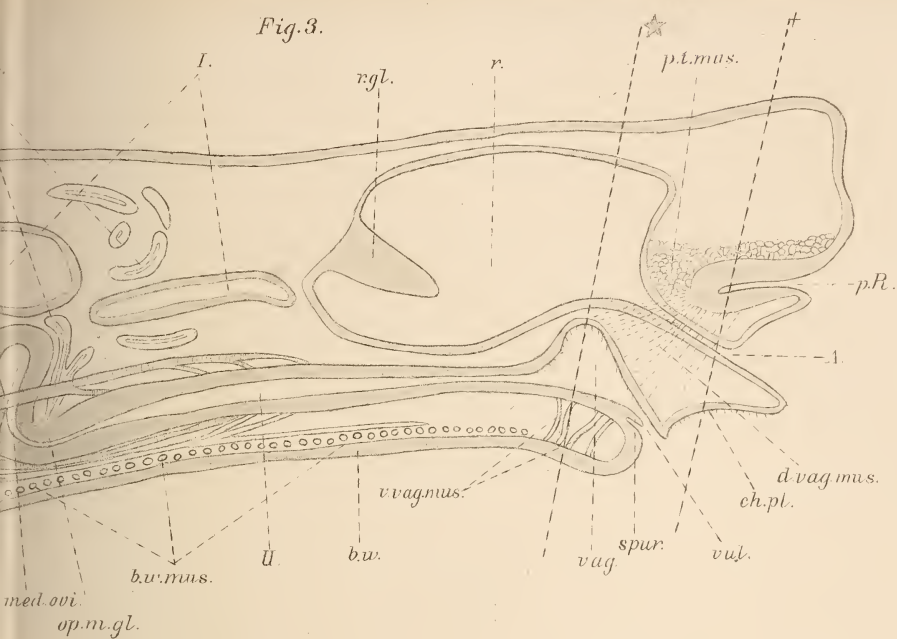


Fig. 5.

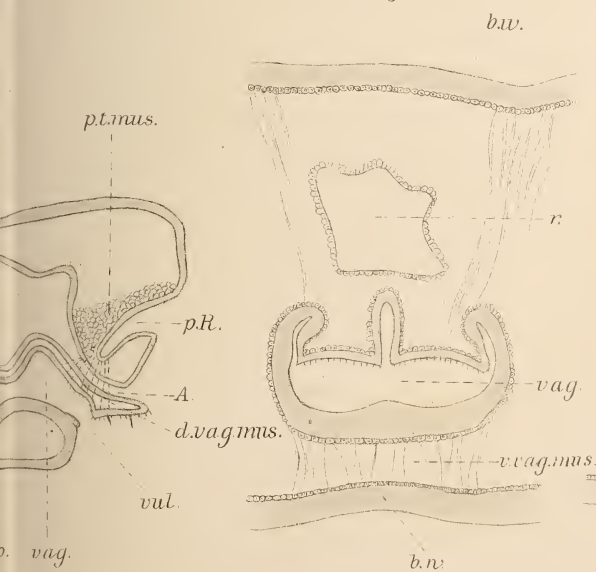


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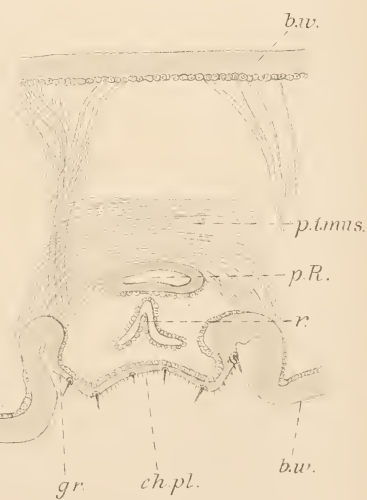


Fig. 1

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ant.



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Fig. 3.



Fig. 4

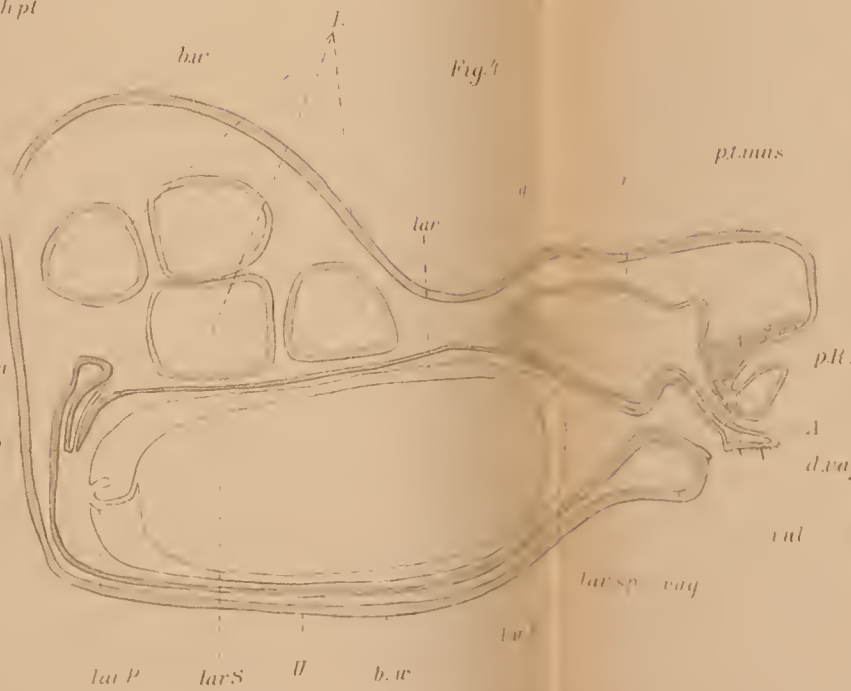


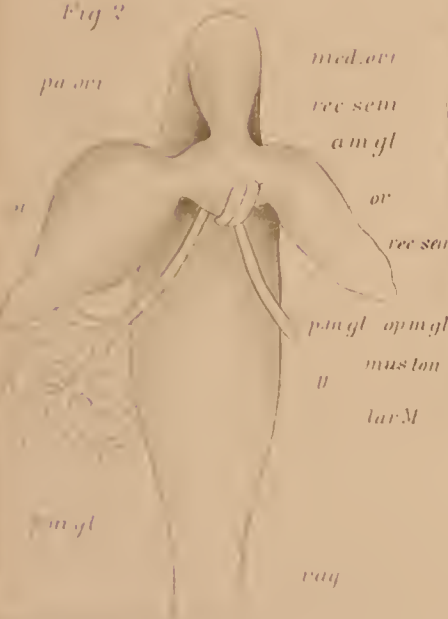
Fig. 5.



Fig. 6



Fig. 2



pa.ori.  
med.ori.  
rec sem  
a m gl  
or  
rec sem  
p. m gl  
op m gl  
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lar M  
m gl  
vag

Fig. 7.

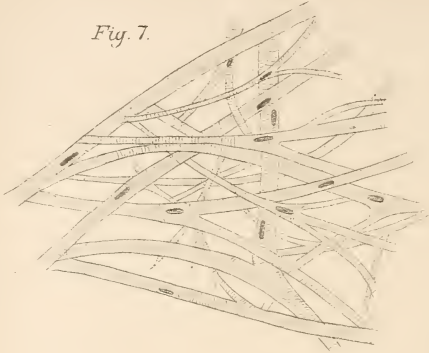


Fig. 9.

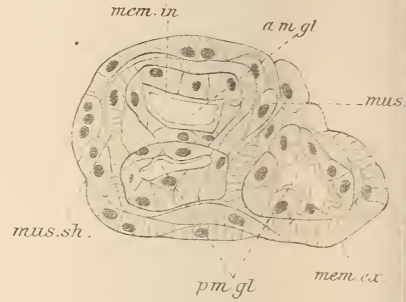


Fig. 8.

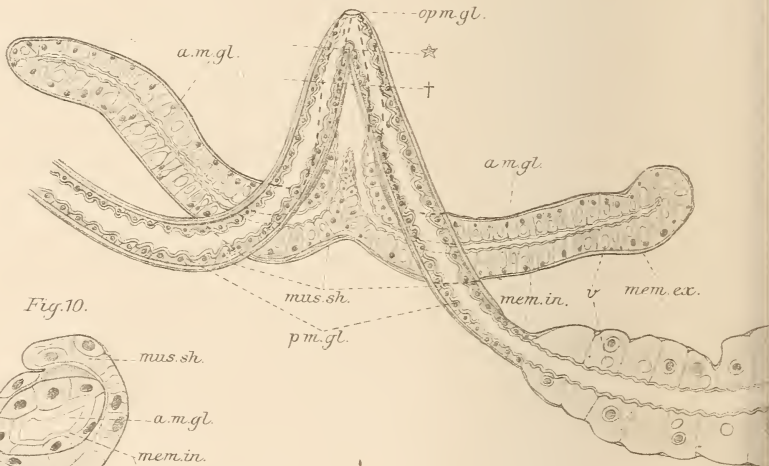


Fig. 10.

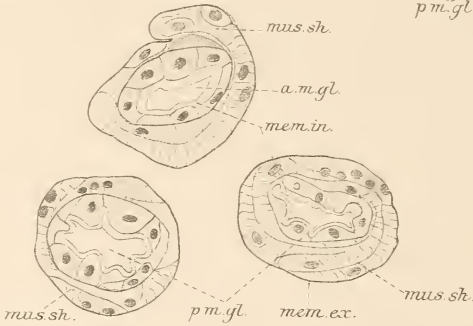


Fig. 11.

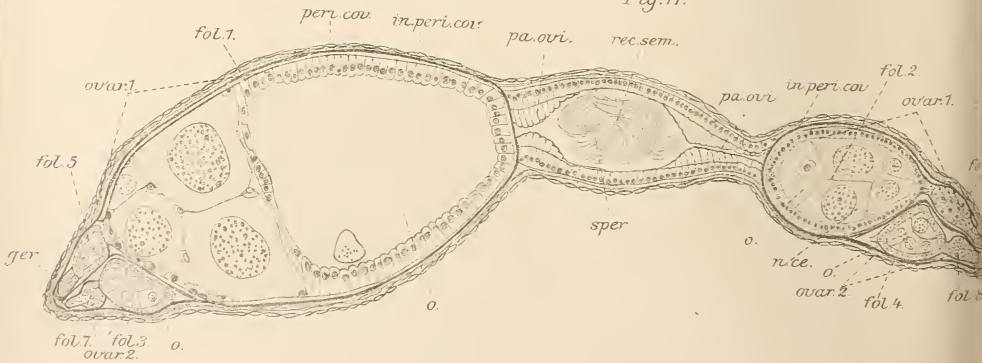


Fig.12.

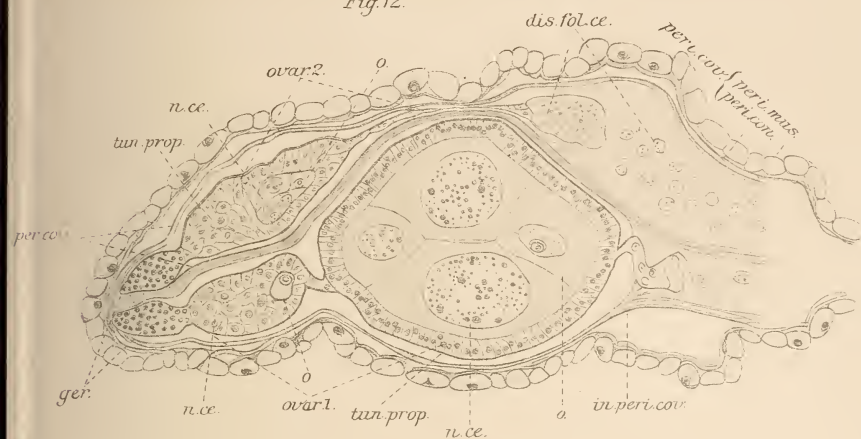


Fig.13.

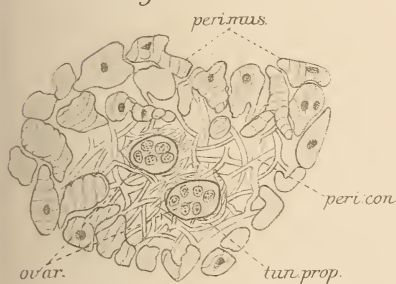


Fig.14.



Fig.15.

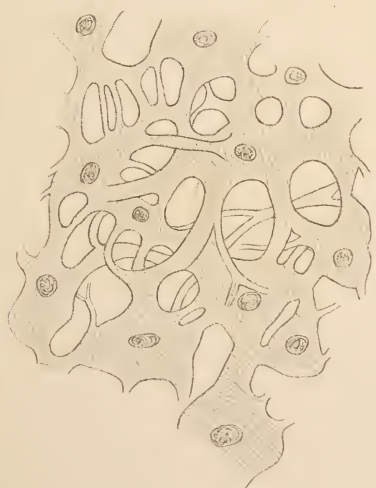




Fig. 7



Fig. 9



Fig. 12

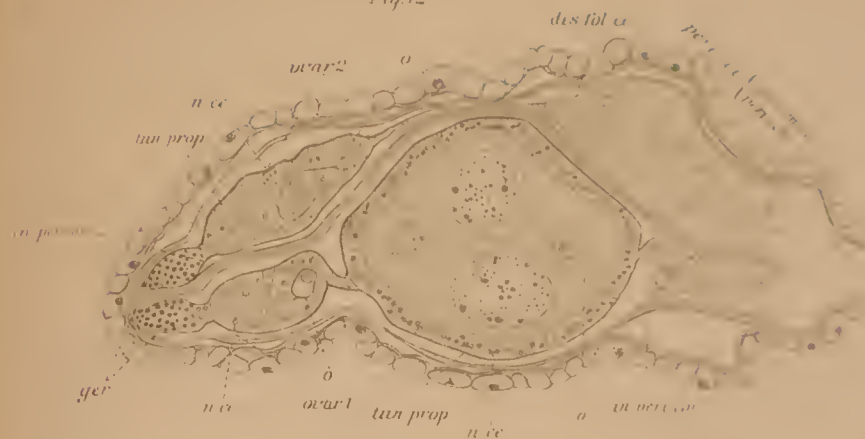


Fig. 8

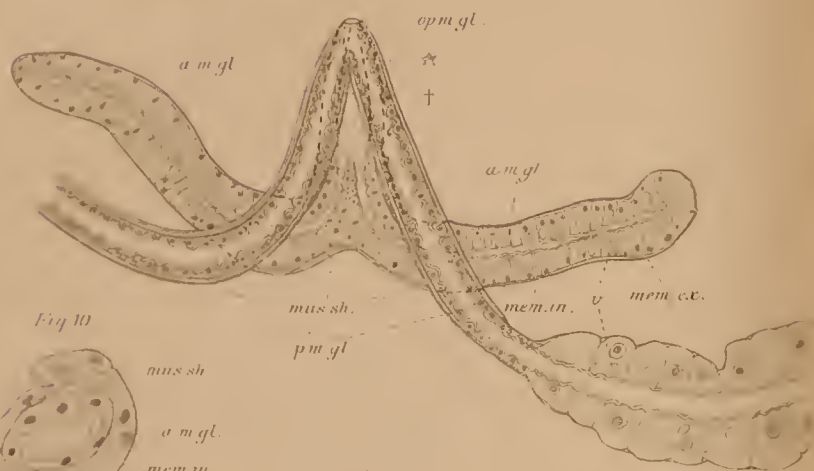


Fig. 10

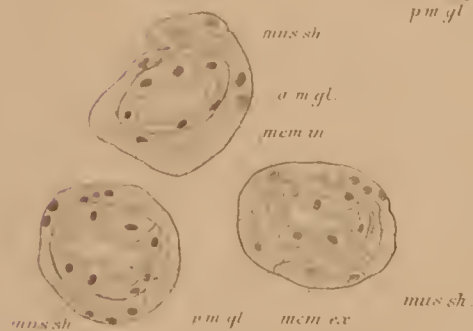


Fig. 11

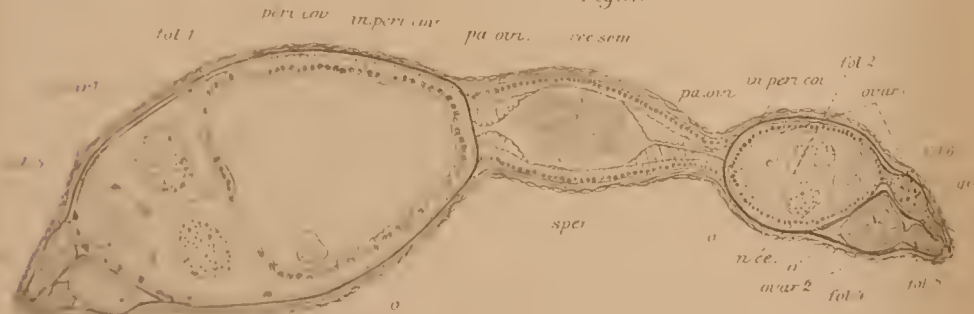


Fig. 13



Fig. 14

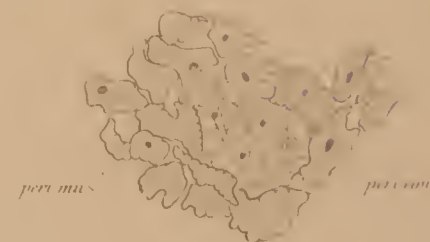
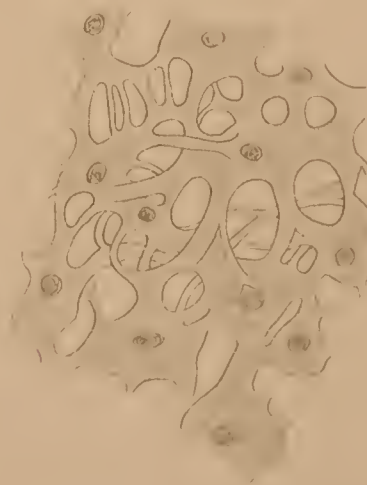


Fig. 15



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Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Zeitschrift für wissenschaftliche Zoologie](#)

Jahr/Year: 1899

Band/Volume: [66](#)

Autor(en)/Author(s): Pratt Henry Sherring

Artikel/Article: [The Anatomy of the Female Genital Tract of the Pupipara as observed in Melophagus ovinus. 16-42](#)