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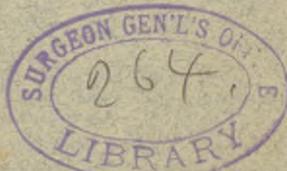
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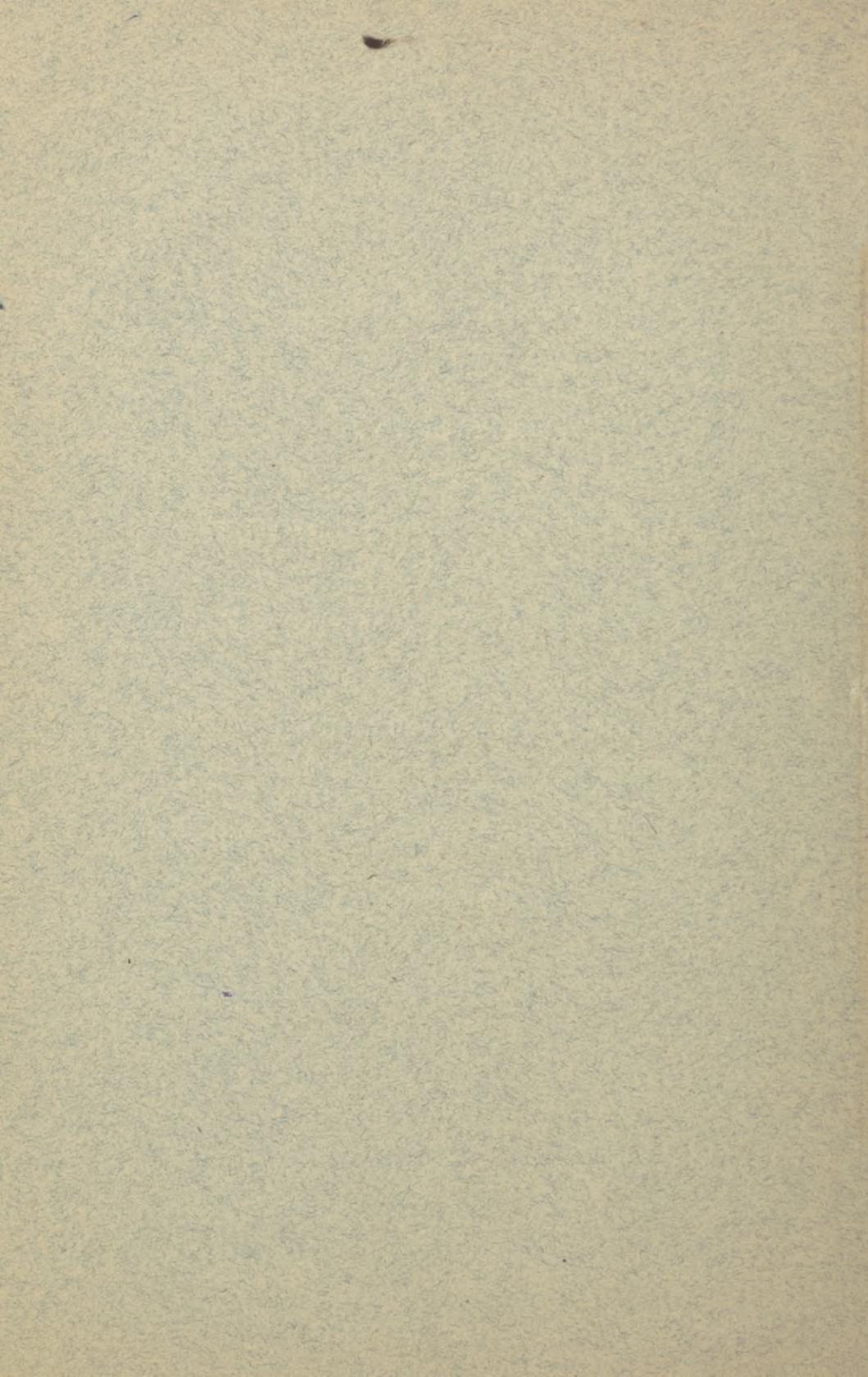
HISTOLOGY
OF THE
LOCUST (*Caloptenus*)
AND OF THE
CRICKET (*Anabrus*).

BY
CHARLES SEDGEWICK MINOT.

[Extracted from the Second Report of the United States Entomological Commission.]

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CHAPTER X.

HISTOLOGY OF THE LOCUST (*CALOPTENUS*) AND THE CRICKET (*ANABRUS*). (Plates II-VIII.)

By Dr. CHARLES SEDGWICK MINOT.

Insects have hitherto been but little studied by histologists. The science of general anatomy or histology, which was first established by Bichât in France, acquired a fresh importance and new meaning through the investigations of German naturalists, and above all through the great discovery of Schwann that all animals are composed, like plants, of certain minute elements or units, which are now familiar to all natu-

ralists under the name of cells. Cells are found only in living bodies; and it is very probable, though by no means certain, that no life exists outside of cells, or in any other bodies. For this reason, to determine the essential powers and peculiarities of cells, and to discover the modifications they undergo, is the fundamental problem of zoology and botany at present. Indeed, biology might almost be defined as the *science of cells*.

Since, however, microscopic anatomy, which is that branch of science which deals especially with the forms and appearance of cells, has been more actively prosecuted by medical men than by zoologists, our knowledge of the tissues of the higher vertebrates is much more complete than of the lower animals. Of the histological structure of insects singularly little is known, although they are particularly favorable objects for microscopic investigation. The most extensive series of observations are those of Leydig, which are summarized in part in his invaluable *Lehrbuch der Histologie*, published in 1858, and in part in shorter special papers scattered through various scientific journals of the last twenty years. Max Schultze has made several important contributions, and there are besides a few excellent single papers, by various authors, notably Dr. Von Basch, Landois, Claparède, Graber, O. Schmidt, &c. Several of Professor Rudolph Leuckart's pupils have made very valuable additions to our knowledge of insect histology. The writings of earlier naturalists contain many observations of importance, but the ground covered by them must now be gone over again and viewed from the stand-point of modern anatomy.

When I began the work the results of which are here described in detail,²²³ I found that very few histological observations had been made on the grasshoppers, or, indeed, on other insects. I feel that this is very unfortunate, because it prevents my judging of the accuracy of my own observations by comparing them with the results obtained by others. I must therefore anticipate that some at least of my conclusions will hereafter require modification.

I regret very much the incompleteness of this report, occasioned in large part by my inability to devote myself longer than a little over five months to the work. My results are derived chiefly from the study of the locust,²²⁴ to which I have added a limited number of observations on *Anabrus purpurascens*. I have endeavored to increase the value of the article by incorporating a considerable number of bibliographical references. I hope that with these additions this report will assist other American students in becoming acquainted with the present state of our knowledge of the histology of insects without having to search far and wide for the authorities. In brief, I attempt to give a bibliographical index to the general outline of the subject, and to describe in detail such

²²³ A preliminary report has been published in the First Annual Report of the Commission, pp. 273-277.

²²⁴ The observations are mostly made of the *Caloptenus femur-rubrum*, the common red-legged locust, and on *Edipoda sordida*.

of my own observations as I believe to be new. I shall give a more complete account of the digestive canal than of any other system. The figures on Plates II-VIII are numbered consecutively from 1 to 66.

In order to make the relation of the various organs to one another more evident, and at the same time to explain the classification of the tissues, which has been generally adopted upon embryological grounds, I figure and describe two sections through the abdomen of the grasshopper, Plate II, Figs. 1 and 2. They are both semi-diagrammatic, being intended to represent rather the general arrangement of the parts than their exact disposition in a particular section. To insure accuracy, however, the outlines of both the drawings were made with the camera lucida from actual sections, and these outlines were then changed only so much as was necessary to remove very slight irregularities.

Fig. 1 is a transverse section through the abdomen of a female at the level of the posterior part of the stomach. The outer wall *D, art., V*, is shaded and represented of nearly uniform thickness, which is not quite exact. Outermost is the cuticula, next the epidermis, or cellular matrix, and innermost the muscles—the three parts that make up the outer wall of the body. The same is true of the section through the male, Fig. 2. This section, however, is taken further back in the abdomen, being through the colon; compare Fig. 45 *col.* The walls of the abdomen are divided into a large dorsal arch, *D*, and a smaller ventral arch, *V*, the two being united on either side by an articulating membrane, *art.*, which will be described in speaking of the cuticula further on. The dorsal arch is really composed of the tergite and the pleurites fused together into one piece.²²⁵ Within the body walls, which form, so to speak, a continuous tube, there runs from mouth to anus a second tube of smaller diameter, the digestive canal, the general course of which is shown very clearly in a longitudinal section through a whole grasshopper, see Fig. 45. In a transverse section the digestive tract also appears (Fig. 1, *St.*, stomach, Fig. 2, *col.*, colon), separated by a considerable space from the body walls. In this intervening space there lie various other organs, notably those of reproduction. In the female, Fig. 1, it so happens that at the level of the stomach the sexual organs lie *above* the intestinal canal, while in the male, at the point represented in Fig. 2, the sexual organs lie partly above, partly below, the colon. In the female we notice first the round tubes of the ovary, *Ov*; second, the ovarian ducts, *ord.*, and, third, on each side the large uterus, *Ut.*, or upper end of the oviduct, into which the ovarian ducts open directly. In the male, on the other hand, we see the testes, *Te.*, lying above the intestine, the single tubes round in section, being embedded in or surrounded by connective tissue (*Leydig's zellig-blasiges Gewebe*), and below the colon, *col.*, lie the spermi-ducts or *vasa deferentia*, (*v. def.*) Finally, between the inner and outer tubes lie various muscles, the Malpighian vessels, and the numerous branches of the tracheæ. These are all left out in the drawing except a

²²⁵ Gruber Die Tympanalen Sinnesapparate der Orthopteren. *Denkschr. Wien. Akad.*, Bd. 36 (1876), p. 75.

few of the tracheæ, *Tr.*, and in Fig. 2 the muscle *r. m.*, to which I shall refer later.

In brief, the grasshopper is built up, 1, of the outer body wall; 2, of the inner tube, digestive canal; and, 3, of the organs which intervene between the two first. Accordingly, I shall describe, 1st, the outer body wall; 2d, the intervening tissue (mesoderm); 3d, the digestive canal and its appendages.²²⁶

Before entering into the special subjects, I would remark that the Orthoptera, and indeed all insects, are, it seems to me, remarkably favorable objects for histological investigations. As regards *Caloptenus* and *Ædipoda*, it may be mentioned in general that the cellular elements of their bodies are particularly large, and the nuclei of the cells distinguished by being, for the most part, strikingly granulated and seldom exhibiting distinct nucleoli.

ECTODERM.

Cuticula.—It is well known that insects have an external crust or shell, the cuticula, which is supposed to always consist mainly of a peculiar substance, chitine, often mingled with earthy salts, such as carbonate of lime and magnesia.

In both locusts and crickets the abdominal segments present differences in the characteristics of the cuticula of different regions. There are at least three distinct modifications—first, upon the dorsal arch; second, on the spiracular or articular fold, which intervenes between the two main arches; and, third, the main portion of the ventral arch—but in the locusts the dorsal and ventral portions are very similar. The dorsal arch, as seen in transverse sections (Fig. 3 *d*), is much the larger, covering the back and sides of the body, and the articular membrane, *art.*, is a comparatively narrow band. Upon the living locust, or one recently killed, it is easy to observe that the dorsal and ventral arches are movable upon one another in consequence of the extreme elasticity and flexibility of the articular membrane (Fig. 6, *art.*). Both the dorsal and ventral portions of the cuticula are rigid, and, in the locusts at least, present a faint striation parallel to the circumference of the section. This striation may indicate a fibrillar structure. The inner surface of the cuticula presents certain peculiarities in the distribution of a reddish-brown pigment, probably part of the matrix, but otherwise this surface appears quite smooth, while the external surface is somewhat roughened, and is beautifully sculptured in *Anabrus*, as I will shortly describe. The thickness of the cuticula is about the same in both arches; it has a yellowish tinge, shading off into brown at the posterior edges of the abdominal segments. The rigid portions of the cuticula are further characterized by the pores (*Poren-canülchen*) and hairs. The pores are quite large in diameter (see Fig. 4 *p*), and are widened at each end;

²²⁶ For the relation of these parts the reader may also consult chapter IX of the First Annual Report of the Commission, pp. 257-272.

they always run nearly perpendicular to the surface to the cuticula. Directly over each pore there sits a stiff chitinous tapering hair (Fig. 4 *h* and *h'*), which is generally slightly curved. This relation of the hairs and pores has also been described by Leydig,²²⁷ and is well known to naturalists. The hairs are all small, though very unequal in size, the difference in the extremes being much greater than between *h* and *h'* in Fig. 4. The hairs do not stand upright, but are so inclined as to point towards the posterior end of the body.

Each hair is constricted around its base (Fig. 63 *h*), forming a narrow neck, below which it expands again, spreading out to make the circular covering membrane of the hair pore. This membrane is very thin, but has a thickened rim. In consequence of this constriction these hairs are commonly said to be articulated. They are not homogeneous, but have a distinct medulla (Fig. 63 *h*), which is probably a prolongation of the cell which forms the hair. These cells have been described by Graber.²²⁸ They were formerly called "*Hautdrüsen*" by Leydig and others. They are, as it were, suspended from the inner side of the large pores as the hairs are from the outer. They are somewhat pear-shaped, and four or five times the diameter of the ordinary epidermal cells, and have correspondingly large *round* nuclei; their contents are very granular. There are usually two or three, rarely but one nucleus in each hair-cell. Graber suggests the name of *trichogens* for these cells. They are probably strictly homogeneous with the scale-cells of the Lepidoptera; the cells differ in the two orders of insects in that they bear a round hair in one case, a flattened hair in the other. The plausibility of this suggestion must, I think, strike every one who is acquainted with the account of the structure and development of the scales in butterflies given by Semper.²²⁹ If the homology is correct, these hair or scale cells must be regarded as specially characteristic of insects, or, possibly, of arthropods generally.

The articular membrane, though a part of the cuticula, has either no, or at most very few, hairs. In the locusts the cuticula at the joint is much thicker and paler in color than elsewhere (Fig. 5, *art.*), being not only thrown up into folds, but also covered with numerous minute pyramidal spines. In the locust the first abdominal segment lacks an independent articular membrane, its own entering into the formation of the sternocoxal membrane, or articular capsule of the third or metathoracic limb. On the sides of the segment a kidney-shaped piece of the cuticula undergoes peculiar modifications to enter into the formation of the tympanal apparatus.

In *Anabrus* the cuticula presents the following characteristics, besides those which have been mentioned as found in both it and the locusts:

First, there are projecting conical nodules scattered irregularly over it, as can be seen in a surface view. (Fig. 59, *b b.*) These cones are less

²²⁷ Leydig: Lehrbuch der Histologie, 1857, p. 111, Fig. 56.

²²⁸ Graber: Denks. Wien. Akad., xxxvi, p. 35 (1876).

²²⁹ Semper: Zeit. für wiss. Zool. Bd. viii, p. 328.

numerous, much thicker, and shorter than the cuticular hairs. They have rounded apices, and are inclined backward. They do not seem to correspond in any way to the hairs, for they do not rest over pores, nor have I seen any specially modified cells underlying them. As far as I have observed, they are mere local irregularities, each nodule being apparently supported by some four or six unmodified epidermal cells.²³⁰ The cones in those specimens I have examined are entirely wanting in the ventral arch, in the upper portion of the dorsal arch, but on the sides of the dorsal arches they are of considerably greater dimensions than upon the spiracular membrane, and finally they are larger and more numerous on the anterior than on the posterior abdominal segments. I have not, however, attempted to follow out the distribution of these structures in greater detail.

Second, the whole of the cuticula except the cones just described and the hairs, is divided into numerous minute fields (Figs. 63 and 65), each of which corresponds to a single cell of the underlying epidermis. Each field is bounded by a distinct polygonal outline, and its surface is either covered by a large number of extremely minute projecting points (Fig. 65), as on the dorsal arch, or is smooth as upon the articular membrane and ventral arch. Upon the sides of the dorsal arch and upon the spiracular membrane each field has a projecting spine or sometimes two or even three. Fig. 65 represents a surface view of part of the side of one of the dorsal arches. Upon the articular cuticula each spine springs from a short basal collar. Fig. 63 represents a surface view of the upper and anterior part of the dorsal arch. The fine sculpture is drawn only on a few of the fields, none of which have spines. The figure is intended to show that from the smooth circular area around the base of the hairs, *h*, the fine points of the sculpturing appear to radiate, while elsewhere they are only irregularly distributed. I have been unable to determine how this radiating appearance is caused.

The ventral arch has a quite smooth surface and but few hairs. The articular membrane has few hairs, a number of broad cones, and sculptured fields, bearing spines, which have a thick collar around their bases. The dorsal arch resembles this membrane generally, but differs from it by the simpler character of its spines, by their absence from its upper portions, and by its brownish tinge. The cuticula between the segments resembles the spiracular membrane.

The cuticula forms also the stigmata or openings of the tracheal system. Immediately around each opening the cuticula is perfectly smooth, while to form the stigmata it undergoes various modifications, which I have not studied. The cuticula of the thorax, head, and limbs I have not examined.

Epidermis.—The cuticula is secreted by an underlying layer of cells, the epidermis proper, often called the matrix or hypodermis, but inas-

²³⁰ I think it possible that the examination of sections, which the imperfect preservation of the parts prevented my making, will show that the cones are after all really produced by specialized cells. The surface views I have obtained are none of them thoroughly satisfactory in this respect.

much as this layer is homologous with the epidermis of other animals, it seems desirable to secure uniformity of nomenclature by adopting this name for the subcuticular layer of cells. I have not devoted much attention to this tissue. Its relations and proportionate size in locusts to the cuticula, *Cu.*, can be seen at *Ep.*, in Fig. 7. The cells composing it are cylindrical and form but a single layer, interspersed through which are numerous hair cells, as above described.

In *Anabrus*, the epidermis is composed of high cylinder-cells, which contain a great deal of granular pigment, often sufficient to completely hide the nucleus. Seen from the surface these cells present polygonal outlines (Fig. 56). When in such a view the nucleus is visible, the character of the cuticular matrix is at once evident, and it becomes certain that Leydig was entirely wrong in his assertion that the "hypodermis" of insects is formed by connective tissue and not by an epithelium. This mistake has already been carefully and accurately pointed out by Graber.²³¹

The coloration of *Anabrus* depends principally upon the pigment of the epidermis shining through the cuticula. Most of the cells contain dull reddish-brown granules, but scattered in among them are patches of cells bright green in color. I have observed no cells intermediate in color; on the contrary the passage is abrupt, a brown or red cell lying next a green one. Indeed I have never seen any microscopic object more bizarre than a piece of the epidermis of *Anabrus* spread out and viewed from the surface. My thought upon first seeing such a preparation was that my reagents must have played me some trick, but preparations made from alcoholic specimens, and examined in alcohol, without having been exposed, to my knowledge, to any other reagent, exhibited the same peculiarities.

The student will find observations on the coloration of the epidermis and cuticula of insects in an article by Dr. Hagen,²³² and a memoir by Leydig.²³³

Sense organs.—This would be the proper place to describe the sense organs, the eyes, and auditory apparatus, &c., but the extreme difficulty of preparing these organs satisfactorily induced me to neglect them entirely, in order to devote my whole time to the investigation of other points, concerning which results were more readily attainable. For the convenience of those who may wish to know the present state of our knowledge concerning these obscure structures, I quote below the titles of some of the more important recent papers,²³⁴ especially those which give references to the earlier publications.

²³¹ Graber: Denkschr. Wien. Akad. wiss. Bd. xxxvi. (1876), p. 33.

²³² Hagen: American Naturalist, vol. vi, p. 388.

²³³ Leydig: Bemerkungen über die Farben der Hautdecke, etc., bei Insekten. A. f. n. A., Bd. xiii, s. 536 (1876).

²³⁴ Leydig: Geruchs- und Gehörorgan der Krebse und Insekten. Müller's Archiv, 1860, p. 292.

Wolf: Das Riechorgan der Biene. Nova. Acta, xxxviii., No. 1.

Grobben: Ueber Bläschenförmige Sinnesorgane der Larve von *Ptychoptera contaminata*. Sitzber. Wien. Akad., Bd. lxxii. (1876).

(List continued on next page.)

Nervous system.—This requires special methods and unusual pains in determining its histological character. I was the less unwilling to let this omission remain, because the nervous system of insects has been the subject of elaborate histological investigations on the part of Professor Leydig,²³⁵ of Bonn, to whose work I may refer those who are desirous of further information on this subject.

A recent article, by Hans Schultze, in vol. xvi, page 57, of the *Archiv für mikroskopische Anatomie*, is valuable. There is also an extensive memoir by K. R. Krieger,²³⁶ on the nervous system of the crayfish, and another by Bellonci²³⁷ on that of *Squilla*.

In order, however, to illustrate the general structure of the nervous ganglia, I have given, in Fig. 11, a drawing of a section through the last abdominal ganglion of *Caloptenus*. The figure is somewhat diagrammatic. A ganglion consists of two parts, the central fibrous portion, from which the nerves arise, and the peripheral layer of ganglion cells, GZ. On each side of these are two nerve roots, one the dorsal, DR, the other the ventral, VR. These Professor Semper,²³⁸ in his article on strobilation and segmentation, homologizes with the roots of the spinal nerves in vertebrates, but I do not know how far his conclusions on this point have been accepted by zoologists. It will be noticed that the four nerve roots in Fig. 11 pass out from the central fibrous mass, through the cellular layer, which latter is thus divided into four fields.

The structure of the supràesophageal ganglion, the so-called brain, is very much more complicated in insects than was formerly supposed. It differs very essentially from any of the abdominal ganglia. The brain of insects has been recently investigated by Dietl,²³⁹ Flögel,²⁴⁰ and Newton.²⁴¹

Graber: Ueber die tympanalen Sinnesorgane der Orthopteren. Denkschr. Wien. Akad., Bd. xxxvi, (1876), 2 abth., p. 1.

—: Ueber neue Otcystenartige Sinnesorgane der Insekten. Arch. für mikros. Anat., Bd. xvi, p. 36 (1878).

Mayer: Sopra certi organi di senso nelle antenne dei Ditteri. Mem. Reale Accad. dei Lincei, Roma, 4 Maggio, 1879. (A criticism of Graber's paper on Otcysts.)

Grenacher: Untersuchungen über das Arthropodenauge. Klinische Monatsblätter für Augenheilkunde, Jahrg. 15, Beilageheft zum Maiheft, 1877.

Newton: Eye of Homarus. Quart. Journal Micros. Sci., 1875.

Lowme: On the modification of the simple and compound eyes of Insects. Phil. Trans. R. Soc., London, vol. 169, p. 577.

Bullar: On the Development of the parasitic Isopoda. Phil. Trans. Roy. Soc., London, vol. 169, p. 513, 514 (structure of eye).

Graber: Ueber das unicomale Tracheaten, und speciell des Arachnoideen- und Myriapodenauge. Arch. f. micros. Anat., xvii, p. 58 (1880).

²³⁵Vom Bau des Thierischen Körpers, Tübingen, 1864. Histologie des Nervensysteme der Arthropoden, pp. 214-226; bei Orthopteren, p. 262.

²³⁶Krieger: Ueber das Centralnervensystem des Flusskrebse. Zeitsch. f. wiss. Zool., xxxiii (1880), p. 527. Taf. xxxi-xxxiii.

²³⁷Bellonci, G.: Morfologia della sistema nervosa della *Squilla mantis*. Annali Museo civico stor. Nat. di Genova, vol. xii (1878), pp. 518-545.

²³⁸Semper: Arbeiten des Zool. zoot. Inst., Würzburg, Bd. iii.

²³⁹Dietl: Die Organisation des Arthropodengehirns. Zeit. f. wiss. Zoologie, xxvii, p. 488.

²⁴⁰Flögel: Ueber den einheitlichen Bau des Gehirns in den verschiedenen Insectenordnungen. Zeitsch. f. wiss. Zool., Bd. xxx, Suppl. (1877), p. 536.

²⁴¹E. T. Newton: On the brain of the cockroach, *Blatta orientalis*. Quatr. Jour. Micros. Sci., vol. xix (1879), p. 340.

Tracheæ.—The tracheæ of insects have long attracted the attention of comparative anatomists, and the curious spiral thread which lies within their interior has been frequently mentioned both by the older as well as the more recent writers. Those who wish to become acquainted with the opinions of the authors of the beginning of this century, will find a capital summary in Shuckard's *Burmeister*, p. 170. It may, also, be well to state that the tracheæ do not consist of an "external serous and internal mucous membrane," as quoted by Dr. Packard on pp. 40-41 of his invaluable "Guide to the Study of Insects," that idea of their structure being now known to be incorrect. The true structure of these interesting air tubes was not known until 1875, when Dr. Chun, one of Leuckart's pupils, published an article²⁴² on the "*Rectaldrüsen der Insecten*," in which he incidentally describes with approximate exactitude

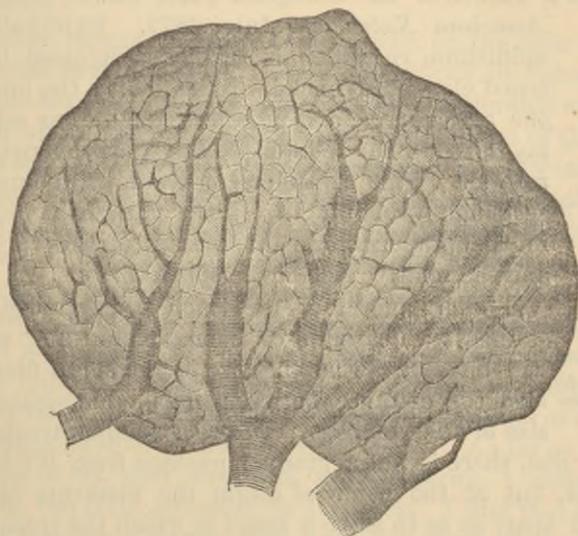


Fig. 6.—Testis of *Anabrus*, showing the ramifications of the tracheæ.

the structure of the tracheæ. Leydig²⁴³ had previously found that the inner membrane consists of two layers, and that the spiral filaments are not distinct and separate, but, on the contrary, intimately connected with the inner membrane. Leydig also found the tracheæ to have an outer layer, which contained nuclei, and which he wrongly supposed to be connective tissue, even venturing to say that no one could think of regarding it as an epithelium. Chun, in his paper above cited, was the first to show that Leydig was in error in making this statement, and that, in a variety of insects, the cellular matrix, which secretes the inner membrane and the spiral thread, is really an epithelium. At the same time I made similar observations on various insects, particularly on the large water

²⁴² Chun: Ueber den Bau, die Entwicklung und physiologische Bedeutung der Rectaldrüsen bei den Insekten. *Abh. Senkberg. Natforsch. Ges. Frankfurt*, 1876, Bd. x, p. 27. *Structur der Tracheen*, p. 39.

²⁴³ Leydig: *Arch. f. Anat. u. Physiol.*, 1855, p. 458. *Lehrbuch der Histologie*, p. 386. *Vom Bau des Thierischen Körpers*, p. 41.

beetle, *Hydrophilus piceus*. The results of my investigations were afterwards published in Paris.²⁴⁴ A few months later Graber also described the structure of the tracheæ, pointing out Leydig's error. Graber's observations are published incidentally in his article on the tympanal organs of the Orthoptera.²⁴⁵

I have found that the account I then published of the minute anatomy of the air tubes in *Hydrophilus* is applicable, almost without change, to the grasshoppers, and I have, moreover, been able to convince myself that the epithelium is not columnar, but a true pavement epithelium (*Pflasterepithel*) as I had previously found it to be in *Hydrophilus* and other insects. My own observations certainly imply that Dr. Chun is in error as to the nature of this layer in those species that he examined.

In order to avoid repetition I reproduce here a figure (7) of a longitudinal section of a trachea of the European water beetle, taken from the *American Naturalist*, July, 1877. Externally lies the epithelium *ep*, which is readily recognized by the flattened elongated nuclei. Next follows the inner layer of the cuticula, *cu*, and interiorly the darker colored inner layer, in which are imbedded the dark colored spiral filaments *f*. This arrangement recurs in a number of insects and probably in all, the variations being merely in the proportionate thicknesses of the various parts, and the relative size of the spiral threads.



Fig. 7.—Longitudinal section of large tracheæ of *Hydrophilus piceus*.

If short pieces of the tracheæ be pulled out, then stained with carmine or hæmatoxiline and mounted, it will be noticed that the size of the spiral filaments, and also the distance between them, diminishes with the size of the tracheæ. Where a smaller trachea springs from a larger one, there is not a gradual passage from the large to the small threads, but at the point of origin the filaments of the large tracheæ bend apart so as to leave a space in which the tracheal branch takes rise, beginning at once with small spiral threads.

The preparations we are now considering further show that there is not a single spiral thread, but several, which run parallel to one another, as I have shown before²⁴⁶, and end after making a few turns around the trachea. The single threads terminate not abruptly but by tapering down to a point and so disappearing.

The nuclei (Figs. 8 and 61) of the tracheal epithelium are elliptical in outline, much flattened, though considerably thicker than the body of the cells. Their long axis is more or less nearly parallel with that of the trachea, and they all have a very distinct and highly refringent nucleolus; sometimes two. The nucleoli are, I believe, always eccentrically

²⁴⁴ Archives de Physiologie Normale et Pathologique, 1876, p. 1, and in Ranvier's Travaux du Laboratoire, etc., 1876, p. 1.

²⁴⁵ Graber: Denk. Wien. Akad., xxxvi, p. 35.

²⁴⁶ Minot: Recherches histologiques sur les Trachées de l'*Hydrophilus piceus*. Arch. de Physiol. expt. 1876, p. 1.

placed. The nuclei can be seen in *Anabrus* in tracheæ that have been mounted in balsam, without being stained, for the flat cells are surcharged with unusually large, highly refringent, reddish-brown pigment granules of nearly uniform size (Fig. 61), hence the nuclei appear as clear ovals in the midst of the dark bodies of the cells.

The spiral threads are unusually delicate in *Anabrus* (Fig. 57), and lie quite close together.

In the finer branches of the tracheal system the structure is slightly modified (Fig. 8). In the first place, the nuclei are farther apart, showing that the cells are much larger than in the main tubes, and the nuclei appear much elongated, though their volume does not seem much, if at all, changed. The fine branches divide mainly by forking. In the crotch of the fork there often sits a triangular nucleus of entirely different shape from those on the other parts of the respiratory apparatus (Fig 7 n').

The peculiar elongated shape of the nuclei on the finer tracheæ renders it possible to follow the course of the delicate air tubes (in stained preparations) through the other tissues with considerable ease. Nevertheless it is advantageous in studying the distribution of the tracheæ in the various organs to examine them immediately after the insect is killed, because they are then injected with air, so that under the microscope the large tubes appear silvery and the fine branchlets as dark lines in the fresh tissue. It will then be found that their distribution is almost as characteristic of the single organs as is the course of the blood-vessels in vertebrates. Williams²⁴⁷ has reported some observations on this subject, but his statements are generally received with some questioning.

Sir John Lubbock²⁴⁸ has published a valuable and extensive memoir on the distribution of the tracheæ, containing the results of observations on a very large number of insects of all orders. As far as I have been able to express my own results in general terms, I believe they are confirmed by the facts recorded by Lubbock. I find that the distribution of the tracheæ depends, *first*, upon the shape of the organs, and, *secondly*, upon the size of those whose size is variable; whereby it must be remembered that *the tracheæ, as far as at present known, are exclusively confined to the connective tissue, including, of course, the fat body.* No epithelium is ever penetrated by the air tubes in any instances known to me, through either my own observations or the writings of others. I give descriptions of the distribution of the tracheæ in certain organs of *Caloptenus* and *Ædipoda*. Around the large organs (intestine, sexual organs), with interior cavities, the tracheæ ramify in all directions, as on the ovary, for instance, Fig. 13, forking so that the branches diverge at a wide angle. In the organs which have muscular walls, like the oviduct (Fig. 14), for example, the tracheæ run straight when the walls are distended, but have a sinuous course, as in the figure (14), when

²⁴⁷ Williams: Ann. Mag. Nat. Hist. (1854), vol. xiii, p. 194.

²⁴⁸ Lubbock: Distribution of the tracheæ of insects. Phil. Trans. 1860, vol. xxiii, p. 194.

the walls are contracted. This shows, as I also know from direct observation, that the tracheæ, though capable of great elongation, are more easily bent than compressed, so as to diminish their length. Around the organs of more elongated form the branches of the tracheæ run more longitudinally, as is shown by the air tubes of the muscles, which also present some peculiarities worthy of especial notice. A short thick trunk (see Fig. 12) arrives at the muscular bundle, and, dividing very rapidly, breaks up into a large number of delicate tubes, which penetrate between the muscular fibers, there terminating in tubes of exceeding fineness, which, at first sight, seem to form a network that might well be called a *rete mirabile*. A closer examination, however, reveals that it is not a real network, but rather an interlacing, confusing to the eye. The longitudinal direction of the tracheæ of the muscles presents a striking contrast to the system of divarication, represented in Figs. 13 and 14. The course of the tracheæ of the Malpighian tubes is also very curious. It is represented in Fig. 10. There is one large trachea which winds around the tube in a long spiral, giving off numerous small branches, which run to the surface of the tube, upon which they form delicate ramifications. Each tube has but a single main trachea, and I think the trachea continues the whole length of the tube, but of this last point I am not quite sure.

Many organs, as for instance the testis of *Anabrus* (Fig. 6 in the text), are supplied by a few large tracheal trunks, which give off many small branches, the ramifications of which penetrate the organ in question.

The fine terminations of the tracheæ have been investigated, as far as I am aware, only by Max Schultze,²⁴⁹ Weismann,²⁵⁰ and H. Meyer.²⁵¹

They all agree in stating that they end blindly in stellate and branching cells. Max Schultze discovered that these terminal cells are dyed black by per-osmic acid, so that they are then very sharply marked off from all the surrounding tissues. The tracheæ extend into the interior of these terminal cells. Graber²⁵² gives a singular account of the termination of the tracheæ in *Phthirus inguinalis*. I cannot but think that his description is based upon a false interpretation of his observations.

The development of the tracheæ has been studied by Weismann and Meyer in the papers just cited, and also by Semper,²⁵³ in an admirable paper on the development of the wings in Lepidoptera.

Dr. Williams, in his article published in the Annals and Magazine of Natural History for 1854, vol. xiii, maintained that the finer branches anastomosed, resembling in that respect the capillaries of vertebrates. Lubbock has already pointed out that the tracheal anastomoses are con-

²⁴⁹ Max Schultze: Zur Kenntniss der Leuchtorgane von *Lampyrus splendidula*. Arch. f. mikros. Anat. 1, p. 124; Tracheen, p. 130, ff.; figs. 4, 5, 8, and 9.

²⁵⁰ Weismann: Die Entwicklung der Dipteren im Ei. Zeitschrift für Wiss. Zool. Bd. XIII (1863), p. 193.

²⁵¹ H. Meyer: Ueber die Entwicklung des Fettkörpers, der Tracheen und der keimbereitenden Geschlechts-theile bei den Lepidopteren. Zeitsch. f. wiss. Zool. Bd. I, p. 174.

²⁵² Graber: Zeit. f. Wiss. Zool. XXII, 147 (1872).

²⁵³ Zeit. Wiss. Zool. VIII, p. 328.

fined to the larger branches. My observations on the grasshoppers entirely confirm Lubbock's opinion, and probably his conclusion may be safely made general for all insects.

Air-sacks and spiracles.—Concerning the latter I have made no observations, considering that an account of their structure belongs rather to the anatomist. Of the air-sacks I have only to say that in them the spiral filament is wanting, their inner walls being thrown up into quite high and somewhat irregular folds, but concerning the histological elements of the sacks I can add nothing to what is already known. The absence of the spiral thread had already been noticed by the older authors.²⁵⁴ The true air-sacks must be distinguished from simple tracheal dilatations.

MUSCLES.

By far the majority of the muscular fibres in *Caloptenus* and *Ædipoda* are transversely striated. Examined with a high power they are found to resemble closely the fibres of the common water-beetle, which has been so often figured and studied.²⁵⁵ First there is a broad dark band, then a broad light band, which is, however, divided in two by a narrow dark line, just as in the fibres of *Hydrophilus*, figured in the accompanying wood-cut.



FIG. 8.—Muscular fibre of *Hydrophilus picus*.—After Minot.

The way in which the muscular fibres are grouped together varies very much in different parts of the body. For instance, in some of the muscles of the head the fibres are not collected in bundles, but are more or less isolated, as appears with the utmost distinctness in a transverse section like Fig. 5, while the muscles of the thorax form bundles of more or less cylindrical form, as appears in Figs. 9 and 6 r. m. The single fibres are not round, as might be thought upon looking at one spread out longitudinally, but polygonal in section, as is seen in Fig. 5, the corners being rounded off. They are commonly four-sided, but sometimes three or five-sided. In every muscular bundle there are to be seen oval nuclei, whose long axes lie more or less nearly parallel with the direction of the muscular fibres. The nuclei are small and flattened, slightly granular, and many of them (Fig. 9) contain a small eccentric nucleolus. They are situated on the surface of the fibres, to which I think they belong, though they are perhaps the nuclei of the sarcolemma.

Besides the striated muscles there are also smooth fibres to be found around the intestine, as will be more particularly described hereafter.

²⁵⁴ *Burmeister*: Manual of Entomology, translated by Shuckard, p. 178.

²⁵⁵ *Ranvier*: *Traité Technique d'Histologie*, p. 477 ff.

Dr. T. Dwight: Structure and action of striated muscular fibre; in the Proc. Boston S. N. H. (1873-'74), vol. xvi, p. 119.

Engelmann: *Plüger's Archiv. für Physiologie*, Bd. vii, pp. 33 and 155, and Bd. xviii, p. 1, and many others.

This is not the place to describe the single muscles of the body, but there is one which I will mention, because its disposition can hardly be seen as clearly in any other way but in a section through the abdomen. The muscle in question is shown in Fig. 6 *r. m.*, and may be called the *M. respiratorius*, for it serves to approximate the upper and lower cuticular arches (Fig. 2 *D* and *V*) and so to diminish the capacity of the abdomen, hence it is to be concluded that it subserves the act of expiration. It has a broad attachment to the lower part of the side of the dorsal arch (cf. Fig. 2 *r. m.*) and a narrow insertion into the upper edge or rim of the ventral arch. It is surrounded by a network of fibrous connective tissue. Graber²⁵⁶ calls this muscle the "dorso-ventral." In the living grasshopper the respiratory movements of the two arches are readily seen.

ORGANS OF CIRCULATION.

These organs I have not examined with sufficient attention to justify the publication of my fragmentary observations. The two most recent articles on the heart are by Graber²⁵⁷ and Dogiel,²⁵⁸ both of whom refer to the older literature. I wish also to use this occasion to refer to the investigations of Graber²⁵⁹ on the pulsating ventral sinus of insects, and the discovery of ganglion cells in the heart of crustacea by Dogiel²⁶⁰ and Berger.²⁶¹ The student should also compare Burger's paper²⁶² on the so-called ventral vessel, which he shows to be really a cord of connective tissue surrounding the ventral ganglionic cord.

CONNECTIVE TISSUE.

In insects all the internal organs of the body are, so to speak, spun around by a web of fibrous and fatty tissue, which extends in the space between the outer body wall and the digestive tract, so as to surround all the intermediate parts. This is the connective tissue, which also acts as carrier or staging of the trachea. The arrangement of this network is such that the spaces left between the beams or threads of it form a system of lacunar spaces, which serve as channels for the circulation by being directly connected with the arteries on the one hand and the veins on the other. Indeed it is not improbable that the distinctive blood-vessels are nothing more than specialized lacunæ of the connective tissue, so that it would be eminently proper to consider the vas-

²⁵⁶ Graber: Denkschr. Wien. Akad., Bd. 36, p. 75.

²⁵⁷ Graber: Ueber den propulsatorischen Apparat der Insecten. Arch., f. mikros. Anat., ix (1873), p. 129.

²⁵⁸ Dogiel: Anatomie und Physiologie des Herzens der Larve von *Corethra plumicornis*. Mem. Acad. St. Petersb., xxiv, No. x (1877).

²⁵⁹ Graber: Ueber den pulsirenden Bauchsinus der Insecten. Arch. f. mikros. Anat., xii (1876), p. 575.

²⁶⁰ Dogiel: De la Structure et des Fonctions du Cœur des Crustacés. Arch. Phys., 1877, p. 401.

²⁶¹ Berger: Ueber das Vorkommen von Ganglienzellen im Herzen des Flusskrebse, Vienna, 1877, published by Gerolds Sohn.

²⁶² Burger, Dionys: Über das sogenannte Bauchgefäß der Lepidopteren, nebst, etc. Nederl. Arch. f. Zool., iii (1876), p. 97.

cular system under this head had the time at my disposal permitted my investigating it.

In the connective tissue we find, first, long fibres upon which sit small compressed and elongated nuclei (Fig. 6 *con.*), and which form a loose network; second, the pale round cells, with a nucleus at the periphery (Leydig's *zellig blasiges Gewebe*²⁶³): third, the fat-cells²⁶⁴ (Fig. 15); and, fourth, the connective tissue with stout trabeculæ and small meshes around the ovary (Fig. 17). I shall here speak only of the third and fourth kinds of tissue. The "*Fettkörper*" of the Germans, or the fat-body, is generally, and I think correctly, supposed to be merely a modification of the connective tissue. Fig. 15 is from a section cut from the object after it had been imbedded in paraffine, so that the action of turpentine on the cells, while the object was being prepared for imbedding, probably altered their appearance from what is natural by dissolving a portion of the fat they originally contained. In a preparation of this kind, which has been colored by hæmatoxiline, the outlines and nuclei of the cells appear very distinctly. The cells are nearly of uniform size, and so crowded together (Fig. 15) that their walls are flattened by mutual pressure. The nucleus is placed in the center of the cell and is nearly or quite spherical, and especially characterized by containing some fifteen to twenty or more large granules of nearly uniform size and darkly colored by the logwood, while the intervening spaces are quite pale and clear. The nature of the body of the cell is obscured by numerous indistinct lines and dots, the real nature of which I have been unable to make out.

Graber has described some interesting peculiarities in the fatbody of insects, especially in *Pthirus*.²⁶⁵ He found the cells in this insect to be elongated, charged with greenish pigment, with spherical nuclei. One end of the cells is pointed and free, the other is united with a cord of connective tissue, the ultimate course of which he could not follow. Graber suggests that these cords contain tracheæ running to terminate in the fat-cells themselves. Besides these Graber saw other fat-cells in which he discerned no nucleus. The presence of pigment in the fat-cells is very common. The pigment is usually green or yellow, but sometimes of other colors.

As regards the connective meshes with stout trabeculæ around the follicles of the ovary, I believe that Fig. 17 illustrates its appearance in the locusts better than any description I could give. I will, therefore, only call attention to the rounded form of the openings and their unequal size, and I have often seen them much larger than any in Fig. 17. Of this same ovarian tissue I have obtained very beautiful preparations from *Anabrus* (Fig. 62), showing both its fibrous character and the shape and form of its nuclei. The fibres are exceedingly fine, and show a tend-

²⁶³ Leydig Vom Bau des Thierischen Körper's. Tübingen, 1864, p. 29.

²⁶⁴ See particularly Leydig Ueber den Fettkörper der Arthropoden, Müller's Arch., 1863, p. 192.

²⁶⁵ Graber Z. Z., xxii, p. 152-157. Taf. xi, fig. 7 b.

ency to gather themselves into bundles, which, though they run in various directions, have a common trend parallel to the ovarian tubes. The interspaces of the network are, for the most part, of an elongated, rounded form, their long axes being parallel with the general trend of the fibres. The majority of the nuclei are irregularly oval in shape, and contain numerous granules, which are darkly stained by hæmatoxiline. Whether these nuclei belong to the fibrous tissue itself or to an endothelium covering it, I cannot say. The latter view seems to me more probable.

A very singular modification of this tissue may be found in the *tunica propria* of the Malpighian vessels of *Anabrus*. Spiral bands wind round the tubes. These bands are composed of a network of fine fibres, with small meshes and occasional granular oval nuclei, each of which is surrounded by a little *court* ("hof") of protoplasm. At first sight these bands might be taken for a nervous plexus, but closer examination reveals their true character. In the locusts, as will be described shortly, there is a trachea which winds round each Malpighian tube in a spiral. It is possible that a similar disposition exists in *Anabrus*, though I have not observed it. In that case the spiral bands of connective tissue in the latter insect may be the means of fastening the trachea to the walls of the Malpighian tube.

The trabecular or retiform modification of the connective tissue is probably very generally, if not always, to be found in all invertebrates above the *Cœlenterata*. It does not seem to me necessary to give extended references. I will, however, mention Grobben's figure.²⁶⁶

The nervous chain of Lepidoptera is covered in the abdomen, but not in the thorax, by a cord of connective tissue, originally described by Treviranus as a ventral vessel, "Bauchgefäss." Its true nature was first recognized by Leydig in 1862, and more recently it has been the object of a special study by Dionys Burger,²⁶⁷ who proposes for it the name of *chorda supraspinalis*. It is to be hoped that subsequent investigators will search for this organ in the Orthoptera and other insects in which we may reasonably expect to find it.

SEXUAL ORGANS.

I.—FEMALE ORGANS.

Ovary.—The ovary is composed of a number of separate tubes, each of which is more or less independent. They all have essentially the same structure histologically, the differences I have observed relating merely to the proportions of the parts to one another. Every ovarian tube begins in the thorax with a small cord (Fig. 64 *ch.*) of connective tissue, which is said to be attached to the heart.²⁶⁸ Graber states that in

²⁶⁶ Grobben: Die Geschlechtorgane von *Squilla mantis*. Sitzber. Wien Akad., Bd. lxxiv 1. Abth., p. 389. (Fig. 8 of plate.)

²⁶⁷ Burger, Dionys: Über das sogenannte Bauchgefäss, etc. Niederl. Archiv. für Zool., iii (1876), p. 97.

²⁶⁸ Leydig, Burmeister, Waldeyer, Lubbock, and others.

Phthirus, three cords spring from each ovarian tube, instead of one as in most insects. Leydig²⁶⁹ considers this cord to be hollow, while most other authors describe it as solid in the insects they have examined. Neither in the locust or the cricket have I seen any trace of an interior cavity. The cord is covered by an external membrane, very thin, and apparently homogeneous, except for the nuclei, which enter into its composition, and appear in stained preparations as dark bodies projecting above the general level of the membrane, which, in short, very closely resembles the *tunica propria* of the Malpighian tubes. In the interior of the cord are numerous granular oval nuclei (Fig. 64 *ch.*), their long axes being nearly parallel with that of the cords. If a cord be teased out with needles, each nucleus is found to lie in the middle of a spindle-shaped body, from either end of which a thread-like process runs out lengthwise of the cord. In what manner these threads terminate I do not know. This cord runs to the rounded tip of the ovarian tube, which begins quite abruptly, quickly attaining twice the diameter of the cord in *Anabrus* (Fig. 64), or three or four times in the locusts. From the tip downwards the tube is divided into compartments, each of which contains a single egg. The lower we go, the wider the tube and the more advanced in development the egg. Between every two fully-developed compartments the tube is somewhat constricted. In *Anabrus*, a long narrow piece sometimes intervenes between two adjacent compartments. In locusts, at least, the tubes are narrowed by a marked constriction just before they open into the oviduct. In *Anabrus* (Fig. 64 *a*), the commencement of the upper end of the ovarian tube proper is marked by the transverse direction of a few oval nuclei. Immediately below these are found rounded nuclei, and among them lie a few cells which have already assumed the distinctive characters of eggs; these latter cells are larger the lower their position. In this part of the tube (Fig. 64 *a b*) there is no distinct division into compartments. The corresponding region in locusts differs in that at the upper end or very tip I could distinguish only one kind of cells, which had clear nuclei and distinct nucleoli. Lower down some of the cells become larger than their fellows, and partly surrounded by them; still lower the large cells appear isolated, larger, and completely inclosed by a layer of cells that form a perfect epithelial follicular wall.

The remaining lower and largest part of the ovarian tubes is divided into distinct compartments or follicles. As we proceed downward in our examination of the tube we see that the egg-cells, which were at first spherical, become elongated in the direction of the axis of the tube, while at the same time the nucleus becomes indistinct, and the protoplasm of the original cell charged with yolk granules, the deutoplasm of Édouard van Beneden.²⁷⁰

It will thus be seen that the development of the eggs in *Caloptenus*

²⁶⁹ Leydig: Zum feineren Bau der Arthropoden. Müller's Archiv., 1855, p. 472-3.

²⁷⁰ Composition et Signification de l'œuf. Mém. cour. Académie Royale Belg., T. xxxiv, p. 1 (1870.)

and *Anabrus* is identical with that observed in other insects,²⁷¹ for which I refer the reader to Waldeyer,²⁷² Leydig,²⁷³ and particularly to the elaborate and accurate memoir of Dr. Ludwig.²⁷⁴

I wish to describe somewhat carefully the relation of the egg to the cells of the follicular wall in the locust. If a bit of the wall of one of the largest follicles be spread out on a slide and colored with carmine it will be seen that it is composed of very large and beautiful cells, Fig. 20. The cells are for the most part pentagonal in outline, a few being hexagonal. The nuclei are very large, taking up a great part of the cells, in the center of which they lie. They are slightly oval, though departing but little from a circular outline. They are darkly colored by carmine, and are filled with innumerable small granules, which prevented my ascertaining whether there is any nucleolus, though in many cases there seemed to be one of considerable size. A transverse section through the whole follicle, such as is reproduced in Fig. 19, shows that the cells form a single continuous layer, *Ep*, around the egg, *Eg*. Examined with a higher power, Fig. 16, such a section reveals the form of the cells. The free or outer surface of the epithelium, *Ep*, is nearly flat, while the side towards the egg, *Eg*, is dome-shaped. Between the epithelium and the egg there is a layer, *Sh*, of finely-granulated and very pale substance that is not colored by carmine or hæmatoxiline. This layer has its outer surface hollowed out into little cups, each of which is intended to receive the dome-shaped end of one of the epithelial cells, as is shown very plainly in Figs. 16 and 19, which represent sections in which the epithelium is artificially raised from the granular layer. In the normal condition the cells rest directly on the layer, and there is no clear space, as indicated in Fig. 16. It is to be added that the layer in question consists of three strata: 1, a very delicate external membrane, which rests against the epithelium; 2, the middle granular portion; and 3, a fibrous stratum, which assumes a roseate hue after staining with carmine, and which lies next the egg. The layer is formed in the follicles, and is probably secreted by the follicular epithelium. It is not to be found in the upper part of the ovarian tube. If I am not mistaken, it passes over with the egg into the oviduct, being destined to form part of the shell. I cannot help suspecting that it is this structure which has given rise to the opinion that, at least in some insects, the wall of the egg follicle passes off with the egg to form part of the shell.

In the egg proper of locusts, Figs. 16 and 19, *Eg*, the enormous masses of nutritive yolk deserve special mention, though I have been unable to determine their relation to the protoplasm of the egg.

The ovarian tubes have further an external tunic, which I have studied

²⁷¹ Excellent diagrams of the development of eggs in insects are given in Gegenbaur's *Grundzüge der Vergleichenden Anatomie*. 2 Aufl., p. 463, fig. 121, and an even better figure of *Vanessa urticae* is given by Waldeyer in Stricker's *Handbuch der Lehre von den Geweben*, p. 563, fig. 195.

²⁷² Waldeyer: *Eierstock und Ei*, Leipzig (1870), p. 86, and especially p. 90.

²⁷³ Leydig: *Eierstock und Samentasche der Insecten*. *Nov. Act. Caes. Leop.*, xxxiii (1867).

²⁷⁴ H. Ludwig: *Semper's Arbeiten*. Bd. I.

in *Anabrus* only, Fig. 64, *Tu*, continuous with the *tunica externa* of the cord *ch*. The appearance of the tunic is represented at *Tu*, the rest of Fig. 64 being drawn with the objective focused lower. The membrane is thin, delicate, and entirely distinct from the follicular epithelium, which has shrunk away from it, as seen in the figure. The external tunic is very transparent, and contains more or less nearly oval, flattened nuclei, with no distinct outline or apparent nucleolus, and containing a single layer of fine granules, all of which are darkly stained by hæmatoxiline. Apparently every granule lies by itself, and is separated from its fellows by a clear space, only very slightly tinged by the logwood. Toward the upper end of the tube the nuclei are smaller and lie closer together. They lend a peculiar character to the tunic, and remind one of the similar nuclei in the *tunica externa* of the spermatie tubes of locusts.

The peculiar net-work of connective tissue which surrounds the ovary, and which is represented in Figs. 17 and 62, has already been described.

Anterior cæcum of the oviduct.—By this name I designate the narrow convoluted anterior prolongation of the oviduct in locusts, which Dufour²⁷⁵ calls the “boyau borgne et flexueux, qui termine l’ovaire en avant,” and which is represented on his Plate II, Fig. 18 *c*. In a transverse section through the middle of the abdomen, the two cæca are cut across several times, *ovd*, in Fig. 1. It is then seen that they are tubes with thick walls and a cavity of moderate size. The main thickness of the wall is made up by the epithelium, the real character of which is obscure in my preparations, there being a great many oval nuclei scattered through it at all levels, while the limits of the single cells do not appear. Outside the epithelium is a distinct but thin layer formed by the connective tissue, tracheæ, and muscular fibres, which, as far as I can make out, seem to run circularly. It is very possible that in better preparations longitudinal fibres will be likewise found.

Uterus of locusts.—I employ this name to designate the enlarged upper end of the oviduct, or that division which Dufour in his classical memoir calls the “calice.”²⁷⁶ Of this organ I have obtained some very beautiful preparations from *Ædipoda sordida*. If the whole uterus just before the eggs descend into it be hardened in alcohol and then examined, it will be found to be compressed laterally. With a very sharp razor it may then be cut in halves, so as to obtain two flat pieces; some granular matter and coagulated secretions will be found adherent to the inner surface, which may be removed under alcohol by the careful use of a camel’s hair brush. The piece may then be colored with hæmatoxiline, and mounted, with the inner surface upwards, in Canada balsam. Part of such a preparation is represented in Fig. 21. The inner surface is seen to be lined by a beautiful epithelium, which is thrown up into broad transverse folds, with intervening depressions of about

²⁷⁵ Recherches Anatomiques et physiologiques sur les Orthoptères Mémoires à l’Acad. R. des Sci. Inst. France, 1834, p. 324.

²⁷⁶ Dufour: l. c. Planche II., fig. 18.

the same width; the folds are not quite regular, but sinuous in outline, though, roughly speaking, they are all parallel to one another. Under a higher power, the epithelium is seen to be composed of cells, which, viewed from above, present a polygonal outline, varying with each cell, as is seen in Fig. 23; the nuclei appear nearly in the center of the cells; they are oval, and coarsely granular, the granules being darkly colored by hæmatoxiline and all of nearly uniform size; I failed to detect any nucleolus. The relations of the epithelium to the remaining layers of the uterine walls appear best in longitudinal sections, because in them the folds are cut across. Fig. 22 is taken from a section of a uterus *distended* with eggs, and therefore with the folds very much drawn out. The cells of the epithelium, Fig. 22 *ep.*, are "*cylinder cells*," with the large nuclei lying somewhat towards their free or *inner* ends. Their appearance is better shown in the enlarged drawing, Fig. 18; they are sharply separated from one another; their protoplasm is finely granular, the granules being unequally distributed so that some parts of the cells appear clearer than others. The free surface of the cells is nearly if not quite flat, while their outer ends or those which rest upon the connective tissue (*conn.*) are often rounded; finally, the cells are not all of the same height. Outside the epithelium follows a layer of fibrous tissue, in which the tracheæ ramify, Fig. 22, and which contains numerous small, oval nuclei belonging to the cells of the tissue and elongated nuclei of the fine tracheal branches, as represented in Fig. 7. Outside the connective tissue lie the muscular layers, Fig. 22 *muc.*, the fibres of which are all smooth and not striated. They are arranged so as to form an internal circular, and a much more powerful external longitudinal coat, that is very distinctly shown in Fig. 22. Within, the epithelium is covered by a layer of fibrous matter, *Gr.*, that fills up the whole space between the uterine walls and the eggs. In many sections there are nuclei contained in this mass, closely similar to those in the underlying epithelium. As to the nature of this layer and the source of the nuclei I cannot venture an opinion.

The remaining portions of the efferent ducts of the female apparatus I have not investigated. I particularly regret my inability to give some account of the receptaculum seminis. The reader will find some unsatisfactory, because very brief, notices of the female appendices in Leydig's Textbook,²⁷⁷ and a more elaborate monograph²⁷⁸ by the same author giving a general account of the structure of the *receptaculum* in insects, but containing no new observations on the Orthoptera, though in a previous article²⁷⁹ Leydig has described the "*Samentasche*" in this order as being lined by an epithelium, which rests on a *tunica propria* and bears a chitinous cuticula, and outside of which is a thin layer of striated muscle. The part that Dufour²⁸⁰ calls the "*glande sébifique*" is really the

²⁷⁷ Leydig: Lehrbuch der Histologie, p. 544.

²⁷⁸ ——— Nova Acta, xxxiii (1867).

²⁷⁹ Müller's Arch., 1859, p. 86.

²⁸⁰ Dufour: Recherches sur les Orthoptères, l. c. 325, Pl. II, fig. 17 c.

receptaculum seminis. A description of the receptaculum and its ducts in *Phthirus* is given by Graber.²⁸¹

2.—MALE ORGANS.

The close analogy between the male and female genital systems in insects is shown by the correspondence of their divisions, and has been repeatedly pointed out. The analogy in the way in which the sexual products are developed, though attention has been called to it, has not been so often emphasized. The testes are elongated sacks or tubes whose upper ends terminate blindly and whose lower ends open into the efferent ducts. The spermatozoa begin their development in the cæcal end, in which, accordingly, we find the earliest stages always represented, while the more advanced zoosperms all lie further down in the sack, just as we find the youngest stages of the eggs in the upper, the oldest in the lower part of the ovarian tubules. The simplicity and distinctness of the parts and straightness of the seminiferous tubes in the grasshoppers renders the testes of these insects the very best object to demonstrate the development of the spermatozoa, with which I am acquainted, as in a single preparation all the principal stages are often distinctly shown.

Testis.²⁸²—The male glands are composed of tubes which, instead of ascending from below *forwards* as do the ovarian tubes, incline from below *backwards*. The whole set of tubes is inclosed in a common sack-like envelope (Fig. 6, p. 191, testis of *Anabrus*), and from this the tubes must be isolated. I have found the most convenient way of doing this to carefully harden a whole male insect in alcohol, and then to cut the whole abdomen in two along the median line, after which if a little pains is taken the single seminiferous tubes, which will be easily recognized lying over the stomach, can be isolated under alcohol with needles. The following account refers to locusts only. The general shape of one of the tubes is shown in Fig. 25. The upper end is rounded off, and from the tip downwards it widens very rapidly, the tube soon attaining its maximum diameter, which it then maintains through the rest of its upper half; the lower half gradually tapers down to a comparatively small tube. The whole, when isolated in the manner described, is more or less surrounded by connective tissue, as shown in the drawing, *conn*. The tube may be roughly divided into four segments as indicated by the numbered brackets of Fig. 25. The upper segment [I] is filled with aggregations of cells in various stages of transformation into spermatozoa, but still distinctively cellular in their appearance. In the second segment [II] the cells are gathered into distinct bundles, each bundle being as shown in the figure in a different stage of development, those lowest down being most advanced; in Fig. 25 each one of the dark masses represents one of the bundles, each of which is composed of a

²⁸¹ Graber: *Z. Z.*, xxii (1872), pp. 161-162.

²⁸² This account of the testis is taken mainly from *Caloptenus spretus*.

great many cells or spermatozoa, the dark portions indicating, however, only the heads of the zoosperms, the tails being many times longer, but very pale; it will be noticed that the shape of the bundles changes from above downwards, being broad with rounded ends in the upper part, and becoming narrower and sharply pointed lower down. In the third segment [III] the interior of the tube is entirely filled up with the long tails of the spermatozoa, the tails belonging to each set of heads being themselves gathered into a sinuous bundle, which are perhaps fifteen or twenty times as long as the bundles of the heads. Finally, the fourth segment is filled with globules of various sizes, highly colored by the hæmatoxiline, very slightly refringent, and closely crowded together, leaving room only for small interspaces and a few bundles of spermatozoa tails which extend down among them.

Before entering into the description of various details, which can be studied on the isolated tube, I will describe a transverse section through the upper part of the first segment, such a section as is represented in Fig. 24. The whole tube is formed by an external membrane, *Tu.*, and its interior is divided up by septae, *cys.*, into several distinct cavities, the *spermatocysts*, each of which contains a number of cellular elements, the *spermatoblasts*, all in about the same stage of development. In the walls of the spermatocysts there are a number of peculiar nuclei, so flattened that in a transverse section they appear as hardly more than a narrow dark line, as is indicated in the figure. The cells of the spermatoblasts are large and distinct, and are destined to be transformed each one into one or more spermatozoa. Near the top of the tube the spermatoblasts are round cells, the protoplasm of which is highly tinged with hæmatoxiline, and which are provided with a bulky central nucleus each, as is shown in Fig. 26. The nuclei are approximately spherical and very coarsely granular, the granulations being dyed almost black by hæmatoxiline. Judging from the analogy with other animals, the parts just described must be interpreted as follows: The whole of each *spermatocyst* arises from a single cell, in which the original single nucleus gives rise by division to the secondary nuclei, each of which becomes a *spermatoblast*, the original cell enlarging until it becomes a cyst; the mother nucleus also divides into nuclei like itself, which become transformed into the peculiar nuclei before mentioned, in the wall of the cyst. This is of course all hypothetical, not based upon direct observation, for in all the seminiferous tubes I have had an opportunity of examining the cysts and spermatoblasts were all fully formed. The most complete and satisfactory account which I am acquainted with of the development of the spermatozoon is that given of the frog by La Vallette.²⁸³ I would also refer those who wish to understand the great theoretical importance of these facts to the brief summary of the observations previously made, which I have published elsewhere.²⁸⁴

²⁸³ *La Vallette*: Archiv für Mikros. Anat., Bd. xii, s. 797, Taf. xxiv, xxxv (1876).

²⁸⁴ *Minot*: Theory of Impregnation. Proc. Boston S. N. H., 1877, vol. xix, p. 165.

Let us now return to the examination of an isolated tube. In it also we can recognize the single cysts, and we perceive at once that each cyst pursues its independent development, and gradually changes into one of the bundles that appear so very plainly in the second segment, Fig. 25 II. It will next be noticed that the further we descend the more numerous and the smaller the spermatoblasts in each cyst, the nucleus diminishing in size with especial rapidity. The nature of these changes appears in Figs. 26, 28, 29. Fig. 26 represents a few spermatoblasts from the upper portion of segment I; their characters have been already described. Fig. 28 is taken from lower down. Fig. 29 is taken from a transverse section of one of the upper bundles of the second segment. The cells have begun to lengthen, but the nuclei have not changed much. To this fact I shall recur directly.

Segments I and II, Fig. 25, correspond to two natural stages in the development of the spermatozoa; first, the multiplication of the spermatoblasts; second, the metamorphosis of the spermatoblasts into the spermatic threads (*Samenfäden*). It is therefore only in the first segment that we find the signs of division, which have been frequently noticed in the development of the male products in various animals (I may mention the Batrachians in particular²⁶⁵), but have, I believe, hitherto puzzled all naturalists, without exception. These signs of division are the cells, such as are shown in Fig. 27, which, instead of the ordinary nuclei, contain a number of very dark and very large granules, often somewhat irregularly distributed. I have been so fortunate as to obtain some of these cells isolated, and saw at once that they were in process of division, and upon closer examination, with a very high power (Tolle's immersion $\frac{1}{2}$ th), I was able to see that many of them were in the condition indicated by Fig. 27 A, elongated, constricted in the middle, the granules accumulated at the two opposite poles, and running between the two accumulations a faint striation. There can be no doubt that this represents the last stage of the division of the nuclei, by the formation of a *Kernspindel*, that remarkable phenomenon which has been so actively studied in Germany and Switzerland during the last two years by so many distinguished observers.²⁶⁶ This discovery naturally leads to a variety of theoretical considerations, which cannot be appropriately introduced here. I will add that I have observed several other stages in the formation of the *Kernspindel*, but as my investigations on this point are still incomplete, I will reserve further details for another occasion.

²⁶⁵ *Spengel*: Urogenital System der Amphibien. Semper's Arbeiten, iii, p. 1, plate ii, figs. 27-34, Spermatozoa of *Epicurium glutinosum*.

²⁶⁶ *Bütschli*: Studien über die ersten Entwicklungsvorgänge der Eizelle, etc. Senkberg. Natf. Ges., Frankfurt, Bd. x, p. 1.

— Zur Kenntniss der Theilungsprocess der Knorpelzellen. Zeitsch. Wiss. Zool., xxix, p. 206.

— Entwicklungsgeschichtliche Beiträge. Zur Kenntniss der Furchungsprocess bei *Nephelis*. Z. Z. xxix, p. 230.

O. Hertwig: Befruchtung, etc. Morph. Jahrb. i, p. 347; iii, p. 1 and p. 271.

H. Fol: Sur le Developpement des Ptéropodes. Arch. Zool. Expt. Gén. (1875), Tome iii, p. 104; also, same journal, T. V, Fasc. ii.

Compare also the writings of Auerbach, Strassburger, Balfour, et al.

Since the peculiar cells of Fig. 27 are signs of division they are not always present, but in some tubes they are absent altogether. The multiplication of the spermatoblasts by self-division is interesting because it shows that all the male elements do not arise directly from the mother nucleus, a fact of most profound theoretical meaning.

We must now pass to the consideration of the alterations of form which the spermatoblasts undergo after their multiplication ceases. As before stated, these changes occur altogether in the second segment of the tube. The body of the spermatoblasts begins to change before the nucleus, as is frequently the case with other animals,²⁸⁷ and is perhaps even the general rule. In the grasshopper the cells begin to elongate, the nucleus remaining in the upper part. There remains a small head of protoplasm around the nucleus, while the rest of the protoplasm lengthens out to form a long tail, so that when the spermatozoon is about half-developed it consists of a head with a small, spherical, granulated nucleus surrounded by a little protoplasm, which is prolonged into a thread-like tail. The further metamorphosis consists mainly in the elongation of the nucleus, it first becoming pointed at both ends and bulging in the middle, then growing more and more rod-like until it is quite filamentous and about six times its original length; meanwhile the protoplasm around the nucleus gradually disappears, forming probably the little thread that extends beyond the nucleus, and also contributing to the growth of the tail. The nucleus, while lengthening out, does not remain perfectly straight, but at a certain period of its formation is curved somewhat in the form of an S. The nuclei afterwards straighten out again forming the heads of the spermatozoa and they then lay themselves parallel to one another, and as they become more perfectly packed together they form the sharp-pointed bundles, which are so characteristic of the lower part of the second segment of the seminiferous tubes, Fig. 25, II. In a transverse section through the head of a bundle of spermatozoa, the heads appear as minute dots closely crowded together, while in a section of a younger bundle, Fig. 30, they lie at some distance apart.²⁸⁸

There now remain to be mentioned the very singular nuclei which appear in the walls of the seminiferous tubes in the lower three-quarters of their length. They are irregularly distributed, oval, very much flattened, quite large, and contain a few large granules, which alone are stained by hæmatoxiline, the intervening space remaining perfectly clear.

²⁸⁷ *La Vallette St. George*: Der Hoden in Stricker's Handbuch i, p. 522, especially figs. 183, 188, 189.

— Ueber die Genese der Samenkörper. 4. Mittheilung. Arch. Mikros. Anat., Bd. xii, p. 797.

Spengel: l. c.

Braun: Das Urogenital System der einheimischen Reptilien. Semper's Arbeiten, iv, p. 113. Hoden, p. 158 ff.

Kölliker: Handbuch der Gewebelehre, 5 Aufl., 1867, pp. 526-528.

Sertoli: Sulla Struthora delli Canalicoli seminiferi, etc. Archivio delle Scienze Mediche, vol. ii, p. 107 (1877).

²⁸⁸ For other accounts of the development of spermatozoa in insects the reader is referred to H. Moyer, Zeit. Wiss. Zool., Bd. i, p. 187.

I think these nuclei are probably the degenerating remains of the nuclei in the walls of the spermatocysts, and which I regard as the mother nuclei of the spermatoblasts.

Vasa deferentia of locusts.—These are long, nearly cylindrical tubes, the walls of which are composed of an interior lining epithelium and an external layer hardly one-fourth as thick as the epithelium, and composed of connective tissue and tracheae, and, as far as I have been able to observe, entirely without muscular fibres. The epithelium is formed of cylindrical cells, with large and distinct nuclei in the basal third of each cell. It is interesting to compare these ducts with the corresponding canals of crustacea, the histology of which has been recently studied by Grobben²⁸⁹ and by August Gruber.²⁹⁰ It now seems probable that further observations will soon render it possible to give a description of the minute structure of the male ducts which shall correctly record the typical form among arthropods.

Ductus ejaculatorius of locusts.—If we make a transverse section through the abdomen of a male *C. femur-rubrum* at the level where the ejaculatory duct runs straight along underneath the dorsum a section of the duct will be obtained of the appearance indicated in the unfinished drawing Fig. 33. The canal of the duct, *Ej. D.* is oval. Below, on either side, is the section of a large trachea, *Tr.* and *Tr¹.* The duct itself is lined by an epithelium, *Ep.*, the height of which is very great at the sides of, but inconsiderable above and below the duct, so that while the cavity appears oval in section the external outline of the epithelium is more nearly circular. Above and below, where the epithelium is narrow, there is but a single row of nuclei, but in the broad lateral portions the nuclei are at very various levels, though never outside a certain central zone of the cells, so that just below the inner, and likewise the outer, surface of the epithelium there is a clear space in which there lie no nuclei. The epithelium is surrounded by a muscular coat, *Muc.* of circular fibres, which form a layer of considerable thickness. This coat, as will be seen from the figure, is not really separated by the neighboring connective tissue. In fact, the external limits of the wall of the duct are not defined.

Vesiculae seminales of locusts.—These are blind cylindrical tubes of larger diameter than the *vasa deferentia*. They consist of an upper, wider, non-muscular, and a narrower lower division that has a muscular coat. The passage from the upper to the lower portion is gradual, not sudden.

A section through the upper part, Fig. 31, shows that its walls are formed mainly by a cylindrical epithelium, with slightly oval nuclei, nearly in the center of each cell. I think, but am not sure, that the nuclei are nucleolated. There is a delicate interior cuticula. I thought

²⁸⁹ Grobben: Beiträge zur Kenntniss der männl. Geschlechtsorg. der Decapoden, etc. Arb. Zool. Inst. Wien. (1878).

²⁹⁰ A. Gruber: Über zwei Süßwasser Calaniden, Leipzig, 1878. Beiträge zur Kenntniss der Generationsorgane der freilebenden Copepoden. Z. Z., xxxii (1879), p. 407.

in some sections that I could see cilia, but this point I could not settle to my satisfaction. There is a thin, but distinct, layer of connective tissue around the epithelium. The character of the epithelium is not the same throughout this upper division. In the lower part, when seen from the inner surface, the epithelium presents the appearance represented in Fig. 32, the nuclei being oval, of nearly uniform size, and quite closely crowded together. Higher up the nuclei are further apart and vary considerably in their dimensions; the outlines of the cells also appear more clearly as pentagonal. Near the rounded tip the distance apart of the nuclei is still greater, and they are more irregular in size. In some of the specimens I have examined the whole upper division of the tube was crowded with bundles of spermatozoa. In one tube I counted over 200 bundles.

The lower end of the upper division tapers off, the nuclei becoming smaller and even more crowded than in Fig. 32. The muscular coat appears thin at first, but, increasing, soon acquires its full thickness, the caliber of the tube diminishing at the same time. A transverse section of this lower part of the vesicula (Fig. 34) shows that the epithelial cells are very much smaller than in the upper portion (compare Fig. 34 with Fig. 31, both being equally magnified $\frac{17}{4}$); the walls, however, rendered very much thicker by the enormous muscular coat, Fig. 34 *Muc*, the fibres of which appear to be exclusively circular.

I have also made a complete series of sections through the posterior end of the abdomen of the male, some of which display very beautifully the relations of the parts, but these structures are so complicated that an elaborate investigation is necessary to secure a satisfactory interpretation of the sections. Therefore I must reserve the subject for another occasion.

DIGESTIVE CANAL.

Of the digestive canal I shall give a more complete histological description than I have of the other systems. Of the cavity of the mouth and of the œsophagus I shall say but little. The salivary glands I have not studied at all, for want of proper material. Those in the cockroach have been described by von Basch,²⁹¹ and also in the more recent superb monograph of Kupffer.²⁹² Leydig²⁹³ has made some valuable observations. The glands have likewise been studied in other insects by various authors, to whom I need not refer here.

In order to render my description easier to follow, I will preface my account by a brief review of the divisions of the digestive canal in locusts; my own investigations having shown that the divisions adopted by the older authors,⁴ and since generally introduced in all text-books,

²⁹¹ *S. Basch*: Untersuchungen ueber das Chylopoetische und Uropoetische System der Blatta orientalis. Sitzber. Wien. Akad., xxxiii (1858), pp. 234. Speicheldrüsen, p. 235, Taf. v, Fig. 11.

²⁹² *Kupffer*: Die Speicheldrüsen von Periplaneta orientalis und ihr Nervenapparat. Beiträge Anat. Phys., C. Ludwig gewidmet, p. 64, Taf. ix.

²⁹³ Müller's Arch., 1850, pp. 59-70.

are not quite sufficient. The descriptions, both general and histological, refer to the locusts unless expressly stated to refer to the cricket.

The best method with which I am acquainted for readily obtaining a general view of the course and divisions of the digestive tract is the following: Place a female (a male will do, but is not quite so good) in alcohol of about 50 to 60 per cent. for from 12 to 24 hours; then put it in strong alcohol (96 per cent.) for a day or longer; then, with a sharp razor, cut it carefully into halves along the median line, so as to have the right and left sides separately. Lay the pieces under alcohol, and carefully remove the contents of the digestive canal, which will then appear very plainly, its course being as represented in Fig. 45. The cavity of the mouth, *M*, ascends obliquely forward, and is generally found filled with a black mass, the coagulated "molasses" which grasshoppers pour out when caught or irritated. The cesophagus, *oe.*, is narrower, of uniform diameter, it curves upwards and backwards, terminating very nearly in the center of the head, where it opens into the very large crop, *Cr*. The crop extends through the posterior half of the head and the whole of the thorax; it attains its greatest diameter in the prothorax, behind which it descends, tapering off slightly, and ending in the proventriculus, *P*. The crop itself is divisible into two distinct portions: 1, the anterior (*Cr.*¹) lies in the head and prothorax, and is characterized by the somewhat irregular transverse ridges on its inner surface; in *Caloptenus spretus*, the Rocky Mountain locust, these ridges are somewhat less numerous and powerful than in *C. femurrubrum*; 2, the posterior (*Cr.*²), in which the ridges are longitudinal and much smaller and closer together than in the front segment; the shape of the posterior division is that of a truncated cone. The proventriculus (*Kaumagen*) *P*, is so much reduced in the grasshopper that it appears as hardly more than the terminal portion of the crop, instead of being a large and distinct segment of the digestive canal as in other Orthoptera. The *Kaumagen* opens into the large "chylific stomach" or ventricle, *ven.*, which extends along the ventral surface about half the length of the abdomen. At its anterior end it gives off the six blind pouches, so long known and so frequently described; in a longitudinal section only one of these can be seen (*Div.*) extending forwards underneath the crop. The first part of the intestine I propose to call the *Ileum*, *Il*. It appears at first sight as the direct continuation, or rather as the posterior division, of the stomach, from which, however, it is in reality perfectly distinct, both by its structure and by its separation through a peculiar valve, which I shall describe later. The Malpighian vessels open just underneath and in front of this valve. The second division of the intestine I call the colon, *col.*, a name sometimes applied by older authors to the rectum. The colon is smaller in diameter than any other part of the digestive tube; it ascends and opens into the rectum, *R*. The rectum extends horizontally directly underneath the dorsum; its diameter is about two-thirds that of the stomach; its inner

surface is thrown up into six longitudinal folds, the rectal glands, three of which are found in each half-section. The rectum opens into the short anal tube, *An.*, which opens externally on the back just in front of the upper clasper.

Crop.—Both divisions have their walls composed of the same layers: 1, an internal chitinous cuticula, which forms the hard covering of the ridges; 2, the underlying epithelium, the matrix of the cuticula, which seems to be pigmented, but unfortunately is not very distinct in my preparations; 3, an inner layer of longitudinal muscles; and 4, an external layer of circular muscular fibres. The muscular fibres of the crop are all striated. There is a layer of connective tissue between the muscles and the epithelium (Wilde), making five layers in all. As it is not distinct in my preparations I do not enumerate it with those I have myself made out. In the front division the ridges are transverse, somewhat irregular, but each one continuous and not formed of single teeth; they are much more numerous and closely crowded in *femur-rubrum* than in *spretus*. The inner covering of the ridges is the thick cuticula. Upon the posterior edge of each ridge there is a row of sharp chitinous spines which point inwards and backwards. The ridges are not all parallel, as is shown in Fig. 45. Those next the oesophagus are broader than the rest and are armed with several rows of spines. The posterior ridges become first slightly irregular, then zigzag, and so gradually change their direction until they become longitudinal and very regularly parallel. The area where the ridges are zigzag marks the limit between the two divisions of the crop. The two muscular layers are well developed in the front division, the longitudinal, which are of course transverse to the ridges, being particularly powerful.

The posterior segment of the crop, Fig. 45, *Cr.*², has longitudinal ridges. In a transverse section, Fig. 35, it is seen that the ridges are small, *rid.*, rounded on top, with small projecting cuticular spines of yellowish color, *s. s.* In each ridge the pigmented epithelium appears as a dark layer underneath the cuticula. The inner muscular coat, *L.*, of longitudinal fibres is but little developed in comparison with the enormous coat of circular fibers, *muc. C.* Thus we see that, in both parts of the crop, that muscular coat obtains predominance whose fibres run transversely to the direction of the ridges. An examination of the inner surface of the hind part of the crop reveals the fact that the ridges are not continuous, but composed of rows of imperfectly individualized oblong teeth, each of which is armed with a few small spines.

It will be seen that the general character of the crop is the same as in the cockroach, according to the descriptions of Basch,²⁹⁴ who adds that the epithelium corresponds to Ramdohr's "*flockige-Lage*," and is the same as the *membrana propria* of Straus-Durekheim and Burmeister. Finally, I must call particular attention to the recent capital memoir²⁹⁵ of

²⁹⁴ S. Basch. *Sitzber. Wien. Akad.* (1858), xxxiii, p. 242.

²⁹⁵ K. F. Wilde. *Untersuchungen über den Kaumagen der Orthopteren.* Arch. f. Naturgesch. Jahrg. xlv, 1. Bd., p. 135 (1877).

Dr. Wilde, of Leipzig, in which, p. 139, he gives the most accurate account of the crop and proventriculus of the Acridians and other Orthoptera which has yet been published.

The crop of *Anabrus* is not divided into two parts, and its cuticula forms no ridges, but is divided up into distinct fields (Fig. 60), each of which corresponds to a single epithelial cell, for in preparations colored with logwood, and examined from the surface, a sharply defined, round nucleus appears in the middle of each field. Each field has a spine, which rises from its posterior part and points backward. These spines are more developed than their fellows on the cuticula of the epidermis. The close resemblance of the two cuticulæ serves to corroborate the view that the crop of insects arises in the embryo, as a secondary invagination of the ectoderm.

Proventriculus.—Dr. Wilde, in the article just mentioned, speaks of the "*Kawmagen*" as the terminal portion of the crop, but I see no objection to considering it entirely distinct and fully equivalent to the proventriculus of other insects with which it is homologous, as Wilde has already pointed out. Wilde appears to have overlooked the fact that it is sharply limited both in front and behind, and in his figure (l. c., Plate IX, Fig. 2) the front limit is not marked.

An examination of the proventriculus opened, and spread out so as to expose the inner surface, shows that there are six large teeth, which present a triangular outline, the base facing frontwards, the apex pointing backwards. The ridges of the crop become zigzag just in front of the bases of these teeth close to which they terminate. Between the single teeth of the proventriculus there are a few parallel ridges, which are not continuous with those of the crop, and which terminate abruptly with rounded ends, at the level of the apices of the large teeth, that is to say at the entrance to the stomach. In the apical portions of the large teeth there is more or less pigment, while in the basal portions there is almost none. The base of the large teeth is notched; the apex rounded off; and their surface covered with a multitude of minute conical spines, which project up from the cuticula.

In *Anabrus* the proventriculus is fully developed, and resembles that of other crickets.²⁹¹ It consists, as in *Gryllus domesticus*, of two parts: one, anterior, serves as the communication between the crop and the proventriculus proper. This anterior part has no definite limit either in front or behind. Both parts are traversed by six rows of teeth, but, though the rows are continuous, the form of the teeth differs in the two parts. If a single row be examined it will be seen that the change from one form of tooth to the other is gradual, not abrupt. A transverse section through the posterior part of the proventriculus shows the disposition of the parts to be as drawn in Fig. 58. Externally is the muscular coat, consisting mainly of circular fibres, intermingled with tracheæ. I have not succeeded in detecting any longitudinal fibres in transverse

²⁹¹Wilde, l. c. Arch. f. Naturgesch., 1877, 1. Bd., pp. 159-165.

sections, though in surface views they appear very plainly; inside the coat of circular muscles all the fibres are transversely striated. The teeth form six distinct arches, and are united with the muscular coat only at their sides. The attachments of the adjacent teeth to the *muscularis* are separated by a longitudinal ridge, *a*, which runs unbroken through the length of the crop, separating the neighboring rows of teeth (compare a surface view Fig. 54 *a*). Each tooth is tripartite, having a central pointed division, *d'*, and two lateral protuberances, *d''*, which Wilde terms "molar" (*mahlzahnartig*). The shape of these is best explained by the figure. The whole proventriculus is lined by a continuous resistant cuticula, which rests upon a cylinder-epithelium, that varies greatly in height in different regions of the teeth, as is plainly shown in Fig. 53, *ep*. The epithelium rests on a layer of connective tissue *conn.*, beneath which is the space left by the dental arch; this space, *C*, corresponds to a large canal which runs under each row of teeth. Examined from the surface, Fig. 54, the same disposition of the parts can be seen, though less plainly. The central process of each tooth is pointed and inclined backwards, so as to slightly overlap the next following tooth. Certain of the anterior "molar" protuberances are distinguished from the posterior, by having three dark colored projections of their cuticula. The cuticula is armed with spines upon the central dental division, and with numerous bristles upon the "molar" protuberances and interdental ridge. A side view, Fig. 55, is also given in order to make the relation of the teeth to one another as plain as possible.

In the anterior part of the proventriculus the teeth are simpler in form, and the longitudinal ridge and "molar" protuberances are wanting. The cuticula gives off a dense coat of long hairs. The edge of each tooth is deeply serrated on both sides of its point, instead of being merely somewhat roughened as in the posterior part. Finally these anterior teeth are convex on their front, concave on their hinder sides. They become smaller as we go forward, the rows spreading apart as they widen out to form the crop.

Posteriorly the rows of teeth stop quite suddenly. The interdental ridge runs somewhat further on, and is rounded off at its termination. On the last five or six teeth the middle process gradually loses its prominence, and on the last two the "molar" processes are also very much reduced.

The total number of teeth in each row is twenty three or four, of which eight or nine belong to the anterior and fifteen to the posterior division. In *Gryllus campestris* and *domesticus* the crop, likewise, forms two divisions, in the posterior of which there are fifteen teeth in each row. It is to the posterior division alone that Wilde (l. c.) restricts the name proventriculus, but I cannot see what grounds he has for so doing, for the two parts have essentially the same characteristics.

Stomach.—This name I apply to the ventriculus of authors, the *Ochylusmagen* of the Germans, Fig. 45, *ven*. Of no part of the digestive

canal is our present knowledge so unsatisfactory as of this. The few observations that have been made are eminently incomplete. It is known that there is no thick cuticula; that the muscular layers are less powerful than in other parts, and certain other details, which a brief examination suffices to clear up. Frey and Leuckart²⁹⁷ pointed out that the walls of the stomach were not folded, but that the secretory surface was increased in some cases (in many Coleoptera, for instance) by the epithelium and connective tissue forming villi, a fact already noticed by H. Meckel.²⁹⁸ Sirodot²⁹⁹ subsequently showed that there are also gastric glands in many insects, and describes particularly (l. c., pl. 13, Fig. 3) how in the field cricket the gastric follicles occupy the interspaces of a network formed by the sinuous fibers of the connective tissue, "*tunica propria*" auct. I have found essentially the same structure to exist in grasshoppers (*Caloptenus* and *Oedipoda*). The description of the minute anatomy of the ventriculus which Leydig gives³⁰⁰ is very meager and insufficient, while that given of the epithelium and glands in the stomach of the cockroach by von Basch³⁰¹ will probably require some modification.

The walls of the stomach are composed of an internal epithelium, a layer of connective tissue, an inner layer of unstriated circular muscular fibres, and an external layer of longitudinal fibres of striated muscle. In studying these layers I have found it best to begin by viewing them from the inner surface. If the walls of the stomach be spread out and stained and then mounted in glycerine or Canada balsam, it will be seen that the nuclei of the epithelium are not uniformly distributed, but there are little clusters, each of which corresponds to a small gland or follicle; it can be further seen that each gland has a cavity or duct; each follicle lies in a cup of connective tissue, which separates it from its neighbors. If a piece of the wall spread out on a glass slide in a drop or two of water, is gently brushed with a fine camel's hair pencil, the epithelium can be removed, and if the specimen be then stained and mounted the structure of the remaining layers will be displayed as shown in Fig. 39. The connective tissue, *tunica propria*, forms a somewhat irregular network,³⁰² the meshes of which vary in size only between certain limits. In the figure the network is drawn somewhat darker than it appears in reality, in order to make it stand out more plainly. The spaces of the network are the cups before mentioned in which the gastric follicles lie. The tissue has a fibrous character and also forms the bottoms of the cups, as is shown by sections. Underneath the connective tissue follows the internal muscular coat, *In. m.*, composed of a great number

²⁹⁷ Frey und Leuckart: Anat. Physiol. Uebersicht. Thierreichs, 1855, p. 114.

²⁹⁸ Meckel. Mikrographie einiger Drüsenapparate niederer Seethiere. Müller's Arch., 1846. Die Eintheilung des Darmcanals bei den Insekten. Par. 4, p. 23.

²⁹⁹ Sirodot Recherches sur les secretions chez les Insectes. Ann. Sci. Nat. Zool. Sér. 4. Tome X, p. 183 (1858).

³⁰⁰ Leydig. Lehrbuch der Histologie, 1858, p. 337.

³⁰¹ Basch, l. c., Wien. Akad. Sitzber., xxxiii, 248, ff

³⁰² Compare Sirodot, l. c., Pl. 13, Fig. 3.

of pale fibres, running singly, and parallel to one another around the stomach. Between this layer and the *tunica propria* there are some indistinct *longitudinal* fibres that may be muscular; these fibres also appear in transverse sections. If my supposition as to their nature is correct, then there are two layers of unstriated muscles, the longitudinal layer being innermost, just as we found with the striated muscles of the œsophagus. Most externally are the longitudinal striped muscles, which are distributed in single bundles (*L*, *L*,) and do not form a continuous layer. Each bundle is composed of a number of fibres and pursues its own course; the bundles are not parallel, as will be evident upon glancing at the Fig. 39; sometimes two bundles unite, or one bundle connects two others; in spite of these irregularities, however, the trend of the muscles is lengthwise of the stomach. Finally, it must be mentioned that numerous tracheal branches penetrate the muscular layers and ramify both through them and also through the connective tissue.

A transverse section (Fig. 36) through the walls of the stomach exhibits further structural features. The epithelium is composed of cylindrical cells, with large, finely granular nuclei, in some of which a nucleolus can be distinguished; the limits of the single cells are not well defined. The follicles are formed by simple involutions of the epithelium, there being no apparent change in the general character of the cells except in their shape, which is not plain enough in sections for me to describe it with real accuracy. They are, however, certainly not spherical, as affirmed by Sirodot. The epithelium is covered by a cuticula, *cu.*, which also descends into the follicles, and is traversed by numerous pore-canals. I cannot make out any basement membrane, but apparently the epithelium rests immediately upon the connective tissue, *conn.* The manner in which this layer extends up between the follicles is seen very plainly in transverse section; it is comparatively thin, as is also the circular coat, *muc.*, of unstriated muscles. In the part figured it so happens that there are no longitudinal bundles of striated muscle, but the tracheæ, *Tr.*, appear very distinctly.

The ventricle of *Anabrus* differs from that of the locusts, as far as I have observed, only in unimportant details. The diameter of the glands is somewhat greater, as shown by the size of the "cups" of connective tissue (Cf. Figs. 66 and 39) in which they rest. The longitudinal muscles form more regular bundles than in the locusts, and fibres cross less frequently from one bundle to another.

Diverticula.—I employ this name for the six cæcal pouches, frequently called the *appendices ventriculares*. It has been commonly stated that these cæca do not differ in structure from the stomach, a statement which, though quite incorrect, is repeated even by so exact an author as Milne-Edwards, in his magnificent compilation of Anatomy and Physiology.³⁰³ Yet, that there is a great difference, had been noted in 1846 by H. Meckel,³⁰⁴

³⁰³ Milne-Edwards: Leçons sur la Physiologie. Tome v., p. 608-609.

³⁰⁴ Meckel: Müller's Arch., 1846, p. 38 ff.

whose observations are also cited by Leydig on p. 337 of his "*Handbuch*." Sirodot³⁰⁵ repeats the old and incorrect statement, while Gräber³⁰⁶ expressly states that their structure is not the same as that of the stomach, and that they are not "einfache Aussackungen des Chylusmagens." More recently M. F. Plateau³⁰⁷ has again called attention to the incorrectness of the old view.

In fact, a single transverse section of one of the diverticula (Fig. 37) demonstrates at once that its structure is entirely different from that of the stomach. Its inner surface is thrown up into longitudinal folds, generally twelve in number. These folds shine through the outer walls, and are, accordingly, indicated in the drawings of Dufour, Gräber, and others. The whole diverticulum has an external muscular envelope, outside of which are a few isolated longitudinal muscular bands. The folds within are formed mainly by the high cylindrical epithelium, which lines the whole interior of the cavity. The shape of the folds will be more comprehensible from the Fig. 37 than from any description I can give. They are not all of the same height, but they form two opposite groups, the folds in the center of each group being the highest. On either side and between the two groups there are smaller folds. Whatever the height of the folds, however, they all have the same general histological character, which is indicated by Fig. 38. The cells are large and cylindrical, slightly granular, those near the top of each fold being slightly pigmented with brownish matter that obscures their definition. The nuclei are large, oval, coarsely granular, and lie in the middle or lower parts of the cells. The cells are protected by a delicate but very distinct cuticula, in which I can detect no pore-canals, though it otherwise resembles the cuticula in the ventriculus. In the center of each fold there runs up a thin partition of fibrous tissue (Fig. 38, *conn*), which separates the epithelium of the two sides, and is itself an offshoot of the connective tissue, *tunica propria*, that intervenes between the muscles, *muc.*, and the epithelial layer. The tracheæ ramify throughout all the layers outside the epithelium; one of the main trunks running to the wall is shown at *Tr.* (Fig. 37). It sometimes looked as if there were glandular follicles in the bottom of the spaces between the folds, but of this I could not make sure.

Towards the tips of the diverticula the folds decrease in height as the diameter of sacks diminishes, until finally they disappear almost completely.

Gastro-ileal folds.—I have now to speak of some very curious and striking formations which seem to have escaped notice until now, for I find no description of them in any of the works on insect anatomy which

³⁰⁵ L. s., p. 157.

³⁰⁶ V. Gräber: Zur näheren Kenntniss des Proventriculus und der Appendices ventriculares bei den Grillen und Laubheuschrecken. Sitzber. Wien. Akad. (1869), lix, p. 33.

³⁰⁷ F. Plateau: Recherches sur les Phénomènes de la Digestion chez les Insectes. Mémoires Acad. Roy. Belg. (1875), tome xli, p. 75.

I have been able to consult. It is impossible to follow Dufour's account³⁰⁸ of the termination of the stomach and the origin of the intestine, for it seems to me not only incomplete but also inaccurate.

I have already referred to these folds, p 209, as the valve which marks the termination of the stomach. They are indicated in Fig. 45 as six dark spots, round in front, and lying at the anterior end of the ileum, *Il.*, so as to form a ring around the interior of the intestine. If this part of the digestive tract be opened, spread out, colored, and mounted, it will appear as represented in Fig. 46. In front lies the stomach, *ven.*, from which the epithelial lining has been removed, and which can therefore be readily recognized by the network of connective tissue before described and the isolated, longitudinal, muscular bundles. Behind the protuberances comes the ileum, *Il.*, which is traversed by six broad and low longitudinal folds, three of which appear in the figure. On the line between the ileum and the ventricle lie the strongly pigmented gastro-ileal folds. They are twelve in number, and all alike. Their shape is best indicated by the figure. They are rounded off in front, where they are broadest and stand up highest; they narrow down backwards; the pigment disappears, and they gradually fade out into the ileal folds; directly underneath them, and just at the posterior termination of the ventricle, there is a strong band of circular striated muscular fibers 0.14^{mm} wide.

These folds are found in *C. femur-rubrum*, *C. spretus*, and *Ædipoda sordida*, and probably in all grasshoppers. I have made sections of them from *Ædipoda*, Figs. 49, 43, and 44. Fig. 49 shows the general arrangement of the folds; there are twelve of them, all pedunculated with broad tops and thick stems. They are covered with an epithelium, the cells of which are smaller and for the most part not pigmented *between* the folds, and larger with a great deal of pigment *on* the folds, as also appears in Fig. 45. The muscular coat, *muc.*, is very powerful, and of even thickness throughout. Between it and the epithelium there is a well-developed tunic of connective tissue. Examined with a higher power it is seen, Fig. 44, that the epithelial cells are large, with an oval nucleus in the lower half of each cell. The cells in the valleys are not so high as on the folds, though the nuclei are not any smaller. The epithelium is covered by a thin cuticula, which is armed on the surface of the folds with minute conical spines, Fig. 44, *cu.*, which are generally, but not always, wanting between the folds; the spines are sharp-pointed and inclined backwards. The connective tissue is fibrous, and contains a good many small, granular, oval nuclei. The layer of circular muscles is composed of three or four parallel layers of bundles. I think there are some few longitudinal fibres between the muscular coat and connective tunic.

Returning now to the epithelium, we find cells in all stages of pigmentation. The pigment is in fine granules of various sizes; they first

³⁰⁸Dufour, Sur les Orthoptères, l. c., p. 314.

collect around the nucleus, Fig. 43, and as they accumulate they extend through all the rest of the cell, except the upper part underneath the cuticula, which portion always remains clear, as is seen in Fig. 44. Viewed from above the epithelial cells appear as polygonal pigmented fields, each separated from its neighbors by a clear line. Posteriorly the cells become less and less pigmented, and pass by gradual changes into the epithelium of the ileum.

Ileum.—The ileum is traversed by six longitudinal folds, with intervening furrows. Outside each furrow is a longitudinal muscular band. Viewed from the inner surface, the epithelium is seen to have an unusual character. The cells in the middle of each of the flat folds are quite large (Fig. 50 A), polygonal in outline, with large, round, granular nuclei, which stain very darkly with hæmatoxiline. Toward the furrows the cells become very much smaller, those at the edge of the furrow being not more than one-sixth the size of those in the middle (Fig. 50 B). Underneath the furrow, the longitudinal muscles (Fig. 50 L) are seen shining through.

A transverse section (Fig. 51) shows that the walls are double; the inner leaf is composed of epithelium, *Ep.*, and connective tissue, the outer leaf, of the circular muscles, *muc. C.* The furrows are indicated by the six bands of longitudinal muscles, *L L.* It is only opposite these bands that the two leaves are united, as is shown more plainly in Fig. 52. The epithelium, *Ep.*, rests directly upon and is intimately united with the connective tissue, so forming a single leaf, which then bends down, making a furrow, *F*, opposite the longitudinal muscle, *L L*, where it is united with the circular muscular layer, *muc C.* The consequence of this arrangement is that underneath each fold there is a very large longitudinal cavity between the *propria* and the *muscularis*.

The cuticula (Fig. 52), *cu.*, is thin, but probably chitinous; it resembles that on the gastro-ileal folds, except that there are no spines, but it is not in the least like the ventricular cuticula. It extends equally over the folds and the furrows.

The epithelium has round nuclei; the size both of the cells and of the nuclei diminishes rapidly towards the bottom of the furrows (Fig. 52), *F*. The bases of the cells are somewhat dome-shaped. The nuclei are surcharged with granules, and have a less distinct outline than the nuclei from other parts of the body.

The circular muscles are moderately developed. Each longitudinal muscular band consists of 10 to 15 single bundles. The fibres are striped.

Colon.—In the colon the six longitudinal folds of the ileum are continued, but their surface, instead of being smooth as in the ileum, is thrown up in numerous irregular curved and zigzag secondary folds, as is imperfectly indicated in Fig. 2, *col.* The cells of the epithelium are of uniform size, and contain, especially at the summits of the secondary folds, pigment granules like those in the cells of the gastro-ileal valve. The epithelium is covered by a highly refringent cuticula without spines,

and, like that on the ileum, it rests upon a layer of connective tissue, beyond which follows (1) an internal coat of longitudinal, and (2) an external coat of circular muscular fibres, which are striated.

Rectum.—The rectum of insects is remarkable for containing certain curious structures now generally known as rectal glands. They are incidentally mentioned by older authors, but Frey and Leuckart³⁰⁹ were, as far as I am aware, the first to recognize their general distribution and importance. Leydig³¹⁰ was the first to give an accurate account of their histological structure. Since then they have received but little attention until 1876, when Dr. Chun published his investigations,³¹¹ which were made under the guidance of Professor Leuckart. Chun extended his researches over a variety of insects, but gives no account of the glands as found in the grasshoppers, though he studied the closely allied Katydid (*Locusta viridissima*, l. c., p. 32). He describes the glands as six flat folds, formed by a high epithelium and well-defined cuticula; the connective tissue (*tunica propria*) is largely predominant; there is a coat of circular muscular fibers, and six external longitudinal muscular bands, corresponding to the furrows between the glands. This description is applicable also to the grasshoppers I have investigated, the only differences being in the structural details of the single layers.

Seen from the inner surface the epithelium presents a most curious and puzzling aspect, Fig. 53, because there are two kinds of nuclei at different levels; small, spherical nuclei nearest the surface, and larger nuclei of oval form deeper down. The small nuclei are less numerous than the large; in the portion represented in Fig. 48 there are 21 small and 49 large nuclei, or, in other words, less than half as many of the superficial as of the deep nuclei. As the two sets are at different levels they cannot both be in focus at once, hence in drawing Fig. 53 with the camera-lucida, the large nuclei were first focused and drawn, and then the smaller nuclei were drawn in the same way over the first. When we focus upon the large nuclei, the polygonal outlines of the cells can be seen in successful preparations as represented in the figure; as there are no spaces between the cells with the large nuclei, the cells belonging to the small nuclei do not extend so far down, though the cells of the large nuclei do reach up among the small nuclei, as can be seen in sections. The outlines of the cells to which the small nuclei belong, I have not been able to distinguish.

The small nuclei are spherical, very refringent, and have a sharp outline. The large nuclei are oval, their long axes lying generally lengthwise rather than transversely on the folds of the rectum. An epithelium presenting a somewhat analogous peculiarity has been described from the epididymis of mammals by Klein.³¹² He figures small darkly stained

³⁰⁹ Frey and Leuckart: Uebersicht des Thierreichs, 1855, p. 116.

³¹⁰ Leydig: Lehrbuch der Histologie, p. 337.

³¹¹ C. Chun: Ueber den Bau, die Entwicklung und physiologische Bedeutung der Rectaldrüsen bei den Insecten. *Abh.: Senckb. Natforsch. Ges. (Frankfort)* Bd. x, p. 27, mit drei Tafeln.

³¹² Klein: Observations on the structure of cells and nuclei. *Quart. Journ. Micros. Sci.*, XIX, (1879), p. 138, pl. VII, fig. 9.

cells lying at the *bases* of the high columnar ciliated epithelium. It is, however, uncertain whether these small cells lie between the others, or form a sub epithelial endothelium, similar to that described by Debove.³¹³

Underneath the epithelium appear the round nuclei of the tunica propria, and the very much elongated nuclei of the tracheal ramifications.

In a transverse section, Fig. 42, it is seen that each gland is a low flat fold of the epithelium; each fold is separated from its neighbor on either side by a deep but narrow furrow, *F, F'*, and is covered internally by a cuticula, which is quite resistant, highly refringent, and very slightly tinged with yellow. The epithelium, Fig. 41, is, as was to be expected from the presence of the two sets of nuclei, composed of two kinds of cells; 1st, cylindrical cells corresponding to the oval nuclei; in sections these nuclei appear round and are seen to lie in the basal portion of the cells; 2d, cells corresponding to the superficial nuclei; each of these nuclei is surrounded by a clear space, as indicated in Fig. 41, but this space has not a sharp outline as there represented; the shape of these cells I have been unable to determine.

The epithelium rests upon a layer of connective tissue, in which there are round granular nuclei, as before stated. Outside of the connective tissue there is a thin layer of circular muscular fibres, Fig. 42, *muc.* The tracheæ, with their distinctive nuclei, ramify throughout all parts of these two layers. Opposite each furrow there is a longitudinal muscular band, Fig. 42, *L II*, composed of some twenty or more striated bundles. Attached to the outer walls are found large tracheal trunks, *Tr.*, and Malpighian vessels, *M. v.*

At the points where the epithelium of the folds descends to form the intervening furrows, there is a little accumulation of pigment granules.

From the above description it will be seen that the rectal folds do not offer the least appearance of glandular structure; neither is any evidence deducible from their microscopic anatomy to indicate that their function is that of absorption. Neither does it appear to me that Chun, in his memoir, has elucidated their function in other insects, and the opinions he expresses with apparent confidence I cannot regard as anything more than speculative.

SUMMARY OF OBSERVATIONS ON THE DIGESTIVE CANAL.

If we now glance back at the descriptions above given of the histological peculiarities of the various divisions of the digestive canal, there are certain general features which deserve especial attention. In the first place it will be recognized that the digestive tract is composed of three main divisions: 1, the œsophagus, crop, and proventriculus; 2, the ventricle and diverticula; 3, the ileum, colon, and rectum.

In the first division there are two coats of muscles, an internal longi-

³¹³ Debove: Mémoire sur la couche endothéliale sous-épithéliale des membranes muqueuses. Arch. de Physiol., 1874, p. 19.

tudinal and external circular coat; the fibres are all striped. The lining epithelium is not much developed, but forms a thick, hard, and very refringent cuticula that is thrown up into ridges, that may be armed with spines. The chitinous lining, or the cuticula, is undoubtedly always secreted by an epithelium,³¹⁴ and does not belong in the series of connective tissues, as Leydig has maintained.³¹⁵ It will be seen that these features are common to all the subdivisions of the anterior segment of the digestive canal, the principal variations being in the form and development of the ridges, and the muscular layers, as I have already described in detail. The thick cuticula of the "*Vorderdarm*" has been observed in many insects,³¹⁶ and of all orders.

The second division of the alimentary canal is distinguished from the first by the epithelium being composed of very high cylindrical cells, which make up the greater part of the thickness of the walls; by the presence of a very delicate, and but slightly refringent, cuticula, and the absence of ridges; by the unstriated muscular coats, and, finally, by the development of glandular follicles and folds. The ventricle and diverticula have all these peculiarities in common, while no other part of the digestive canal resembles them in the least. Essentially the same peculiarities distinguish the "*Mitteldarm*" of *Phthirus inguinalis*, Leach³¹⁷, except that there are no glandular follicles. Landois³¹⁸ has wrongly homologized this part with the crop of the Orthoptera.

The third division (intestine and rectum) has an epithelium, the cells of which are intermediate in size between those of the first and second division. The cells are often pigmented; they are covered by a cuticula much firmer than that of the ventricle, but not so thick and hard as that of the first division. The very refringent cuticula is not transformed into ridges, though in some parts it is covered with delicate conical spines, which are very short. The epithelium and underlying connective tissue (*tunica propria*) are thrown up into six folds, which run longitudinally, being regular in the ileum and rectum (as the rectal glands), but very irregular in the colon. Outside the depression between each two neighboring folds there is a longitudinal muscular band, thus making six bands. This peculiar disposition of the longitudinal muscles does not occur in any other part of the canal; it is therefore especially characteristic of the third division. From this statement of the characteristics of the three divisions, it is evident that the gastroileal valves belong to the third.

The curious repetition of the number six may be pointed out here. I cannot but think it will be ultimately found to have some hitherto unsuspected meaning. There are six rows of teeth in the proventriculus,

³¹⁴ *Semper*: Ueber die Entstehung der Schuppen bei den Lepidopteren. *Zeit. Wiss. Zool.*, VIII. Cf. also, *Gegenbaur, Chun, Braun, et al.*

³¹⁵ *Leydig*: Vom Bau des Thierschen Körpers, p. 38, ff.

³¹⁶ For example: *Phthirus inguinalis* Leach. *Graber.* Z. Z. XXII, 141.

³¹⁷ *Graber*: *Zeit. Wiss., Zool.* XXII, 142-144.

³¹⁸ *Landois*: *Zeit. Wiss. Zool.*, XIV, p. 1, and XV, 502.

six diverticula arising from the stomach, and twelve longitudinal folds in each diverticulum. There are twelve (twice six) gastroileal folds, arranged in twos, each pair appearing as the double anterior termination of one of the six ileal folds, which, changing their character, extend backwards through the colon; finally, in the rectum there are six rectal glands.

The three divisions of the digestive canal are perfectly natural; their existence of itself suggests that they represent the three segments which are usually distinguished upon embryological grounds, namely, the *foregut*, *midgut*, *hindgut* (*Vorderdarm*, *Mitteldarm*, and *Hinterdarm*). This supposition is strengthened by Bobretzky's³¹⁹ observation that in decapods the embryological *foregut* forms the œsophagus and *Kaumagen*, while the midgut forms the follicular stomach and diverticula (liver). This is a strong confirmation of the conclusion that I have been induced to consider probable upon purely anatomical grounds. It seems to me, moreover, that Hatschek's³²⁰ observations also point to the same conclusion, viz, that the ventriculus (*Chylusmagen*), together with its appendages, represents the midgut, all in front being foregut, and all posterior to it arising from the hindgut.

The principal respects in which the middle division differs from the other two is by, 1, its glandular character; 2, the presence of a delicate cuticula, probably not chitinous; and, 3, of unstriated muscles. It seems to me now a legitimate problem in insect anatomy to determine whether these characteristics are applicable to the midgut of all insects.

In all parts of the digestive tract the succession of the layers is the same: 1st, a cuticula; 2d, an epithelium; 3d, connective tissue; 4th, muscles. Besides which there is stated to be a pavement epithelium (*serosa*) outside the muscles in some insects. This I have not observed in the grasshoppers, though it may be present.

Of the physiological functions of the single parts of the digestive canal little is really known, though some observations have been published by Sirodot and Plateaux.

I should like to interpolate here a comparison, which is curious and odd rather than of scientific value. After Malpighi had shown that the grasshopper had several stomachs, some of the older authors, according to *Colin*, considered these insects to be ruminants, comparing the various parts of their digestive canal with the divisions of the stomach in the true ruminants. Of course this idea is now entirely rejected, but it is nevertheless curious to notice that with our present knowledge we can trace an analogy between the crop and the rumen, the ventricle of the grasshopper and the sheep, while the diverticula with their leaf-like folds singularly imitate the structure of the psalter. Those who are not familiar with the anatomy of ruminants, will find a clear and excellent account in Huxley's *Anatomy of Vertebrated Animals*.

³¹⁹ Bobretzky: Zur Embryologie der Arthropoden (in Russian) as abstracted by Hoyer in Hoffmann und Schwalbe. Jahresbericht der Physiol. u. Anat. für 1873, p. 314.

³²⁰ B. Hatschek: Beiträge zur Entom. Lepidopteren. *Jena Zeitschr.* Bd. XI. (1877), (p. 17 des Separatabdruckes.)

MALPIGHIAN VESSELS.

The *vasa varicosa* of Malpighi have long attracted the attention and excited the interest of naturalists. The earliest histological description of them, however, with which I am acquainted, is comparatively recent—I refer to the article of H. Meckel.³²¹ Since then three general accounts of their structure have been published, one very full by Sirodot,³²² and another by Leydig,³²³ and the third and most important by Schindler,³²⁴ and they have been investigated by numerous other anatomists in a great many insects.

Their structure is very much the same in the grasshopper as in the cockroach.³²⁵ They are covered by a delicate external envelope (*tunica propria*), Figs. 40, 41, 47, 48, in which there occasionally appear small nuclei. They are lined by flattened epithelial cells with granular contents and large oval nuclei, which leave a round central cavity, Fig. 40. The canal, as observed in optical section, Fig. 47, is not straight, but somewhat sinuous in its course. Seen in transverse section, the outlines of the cells, Fig. 40, resemble those of truncated cones. There are generally four rows of cells around the inner canal, as indicated in Fig. 40. Some parts of the vessels are surcharged with reddish-brown pigment granules. The tubes are, as is well known, not of the same diameter throughout their length, but consist of a narrower and a wider portion. The Figs. 40, 42, 47, 48 all represent the narrower part. In the segment with the greater diameter the thickness of the walls remain about the same, so that the "*lumen*" of the vessel is increased. The nuclei are larger and more nearly round instead of oval.

³²¹ Meckel, l. c., Müller's Archiv. 1846, p. 41 ff.

³²² S. Sirodot: Recherches sur les Sécrétions chez les Insectes. Ann. Sci. Nat. Zool. Sér. IV. Tome x (1858), p. 251. Histologie, p. 268.

³²³ Leydig: Lehrbuch der Histologie, p. 464, § 426.

³²⁴ E. Schindler: Beiträge zur Kenntniss der malpighischen Gefässe der Insecten. Zeit. f. wiss. Zool., Bd. xxx. (1878), p. 587.

³²⁵ Basch. l. c. Sitzber. Wien Akad. xxxiii. (1858), p. 254.

EXPLANATION OF PLATES II-VIII.

All the figures on Plates II-VII, except those specially otherwise designated, are taken from preparations made from *Caloptenus femur-rubrum*. The figures on Plate VIII, are all from *Anabrus purpurascens*. All but three or four of the figures were drawn in outline with the *camera lucida*, and the details added afterward with free hand. The drawings, with the partial exception of Fig. 58, are nowise diagrammatic, but fall short in clearness of the actual preparations.

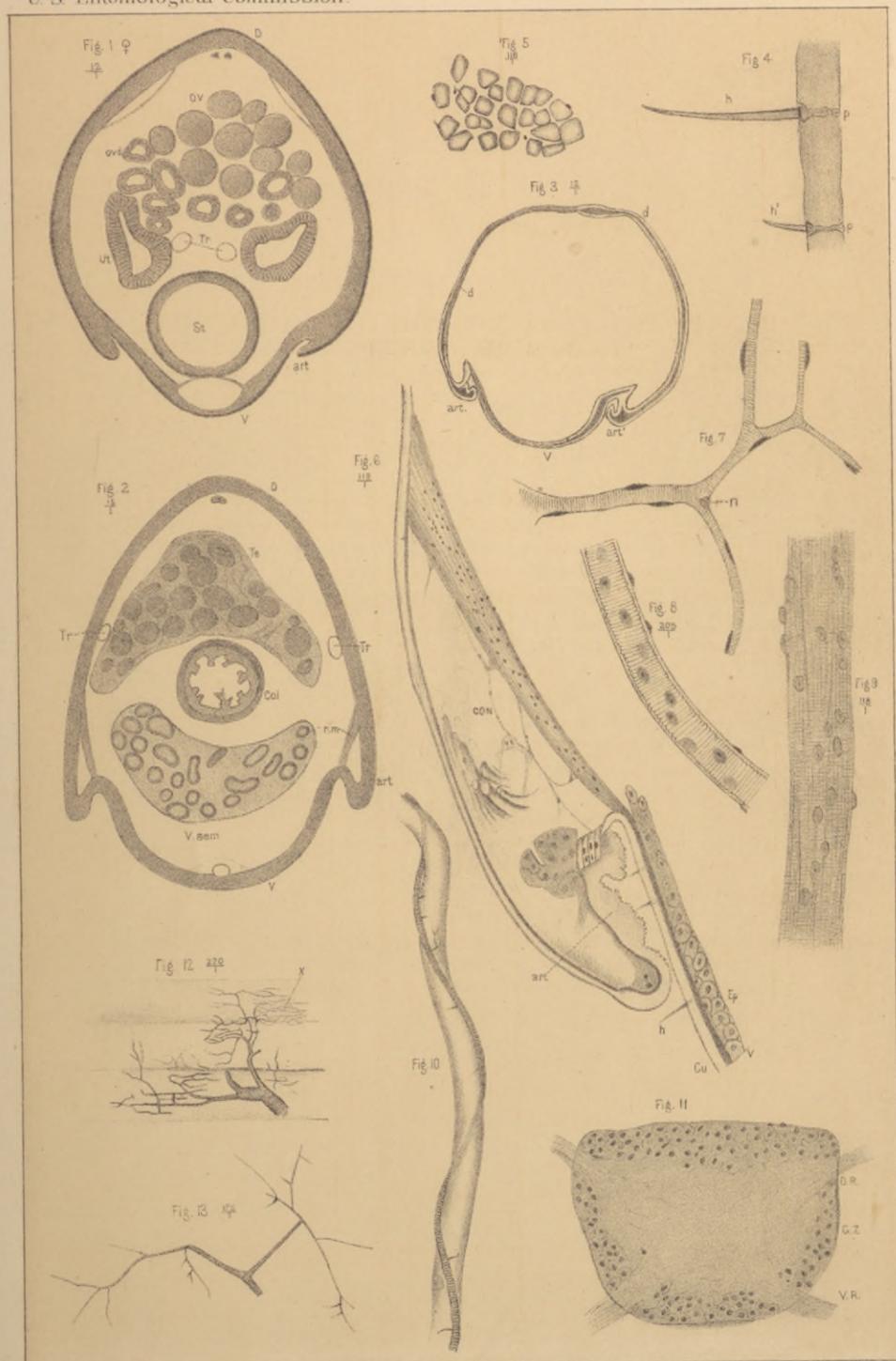
EXPLANATION OF THE LETTERING.

<i>An.</i> , anus.	<i>In. m.</i> , internal muscular coat.
<i>art.</i> , articulating membran	<i>L.</i> , longitudinal muscles.
<i>Bd.</i> , muscular band.	<i>M.</i> , mouth.
<i>ch.</i> , cord of ovarian tube.	<i>muc.</i> , muscle.
<i>col.</i> , colon.	<i>muc. C.</i> , circular muscles.
<i>conn.</i> , connective tissue.	<i>M. v.</i> , malpighian vessels.
<i>Cr.</i> , ¹ <i>Cr.</i> , ² crop, 1st, 2d segment.	<i>Oe.</i> œsophagus.
<i>cu.</i> , cuticula.	<i>Or.</i> , ovary.
<i>cys.</i> , wall of spermatocyst.	<i>Ord.</i> , anterior cœcum of oviduct.
<i>D.</i> , dorsal arch of body wall.	<i>P.</i> , proventriculus.
<i>d.</i> , ¹ <i>d.</i> , ² dental processes.	<i>p.</i> , pore canals.
<i>Div.</i> , diverticulum of stomach.	<i>r. m.</i> , musculus respiratorius.
<i>D. R.</i> , dorsal nerve roots.	<i>rid.</i> , cuticular ridges.
<i>Eg.</i> , egg.	<i>Te.</i> , testes.
<i>Ej. D.</i> , ductus ejaculatorius.	<i>Tr.</i> , tracheæ.
<i>Ep.</i> , epithelium.	<i>Tu.</i> , external tunic.
<i>F.</i> , furrow between intestinal folds.	<i>Ut.</i> , uteris.
<i>Gr.</i> , granular layer, inside epithelium.	<i>V.</i> , ventral arch of body wall.
<i>G. Z.</i> , ganglion-cells.	<i>Ven.</i> , ventriculus.
<i>h. h.</i> , ¹ cuticular hairs.	<i>V. R.</i> , ventral nerve roots.
<i>Il.</i> , ileum.	<i>V. sem.</i> , vesiculæ seminales.

PLATES II-VI, CALOPTENUS AND OEDIPODA;
PLATE VIII, ANABRUS.

PLATE II.

- FIG. 1.—Section through the abdomen of a female at the level of the posterior part of ventricle. *D.*, Dorsal arch; *V.*, ventral arch; *Ov.*, ovary; *Ovd.*, blind end of oviduct; *Ut.*, uterus; *Tr.*, trachea; *art.*, articulation between dorsal and ventral arches; *St.*, stomach.
- FIG. 2.—Section through the abdomen of a male at the level of the colon. *D.*, dorsal arch; *V.*, ventral arch; *art.*, articulation between the two arches; *Tr.*, tracheæ; *Te.*, testes; *col.*, colon; *r. m.*, respiratory muscle; *V. sem.*, vesiculæ seminales.
- FIG. 3.—Section of cuticula of abdomen. Letters as before.
- FIG. 4.—Section of cuticula, *p. p.*, pore canals; *h. h.*, cuticular hairs.
- FIG. 5.—Transverse section of wing muscles.
- FIG. 6.—Part of transverse section of abdomen to show the respiratory muscle *r. m.*; *D.*, dorsal arch; *V.*, ventral arch; *art.*, articular membrane; *Ep.*, epidermis; *cu.*, cuticula; *h.*, hairs; *conn.*, connective tissue.
- FIG. 7.—Fine tracheæ of rectum; *n.*, triangular nucleus in fork.
- FIG. 8.—Tracheal branchlet.
- FIG. 9.—Bundle of striated muscle from the head.
- FIG. 10.—Spiral trachea of malpighian vessel.
- FIG. 11.—Diagrammatic section of last ventral ganglion; *D. R.*, dorsal roots; *V. R.*, ventral roots; *G. Z.*, ganglion cells.
- FIG. 12.—Ramification of tracheæ in muscles; \times , fine terminations.
- FIG. 13.—Ramification of tracheæ on the ovary.



C. S. Minot, del.

HISTOLOGY OF THE LOCUST.

Text: Sinclair & See, Lith. Wash.

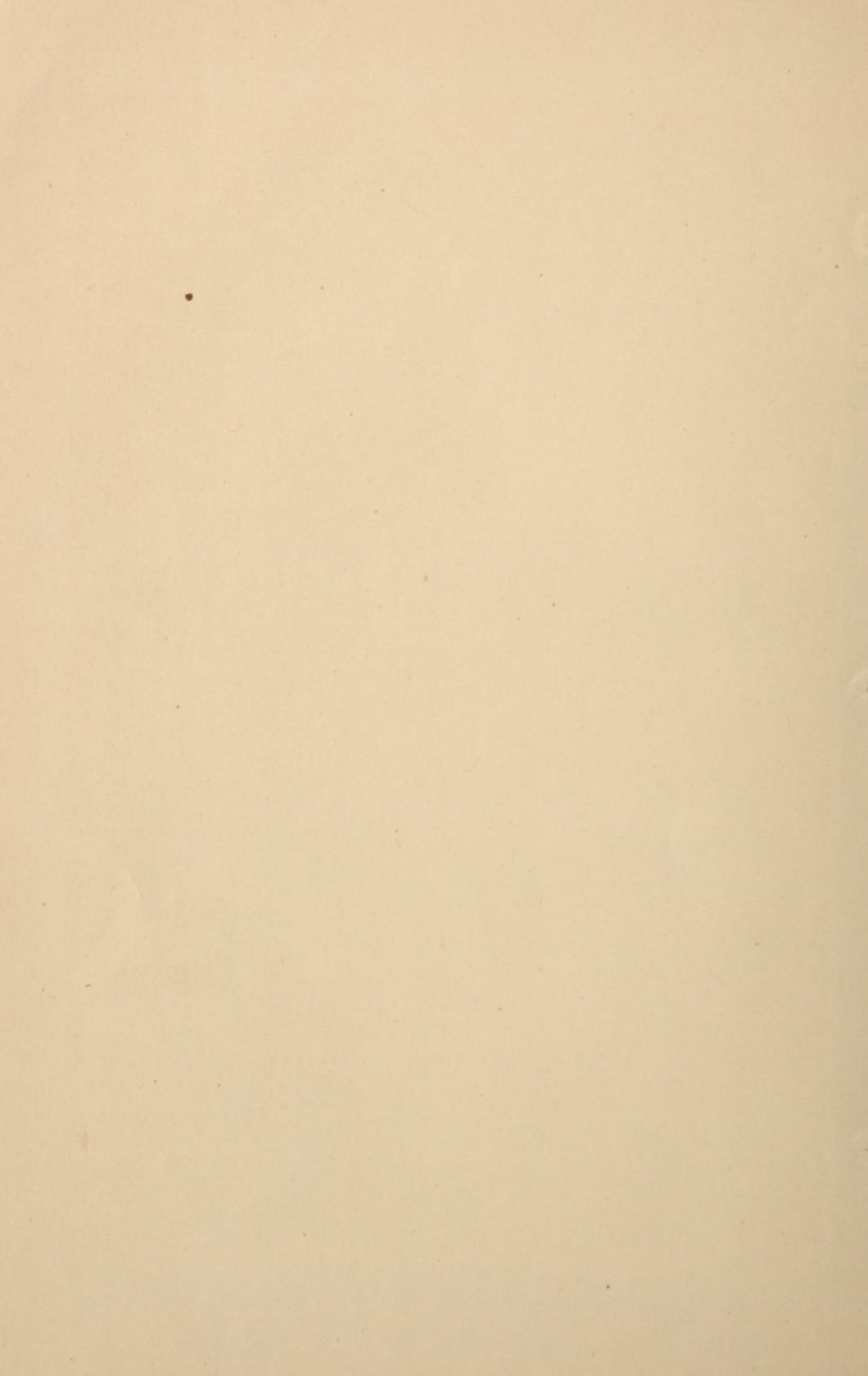


PLATE III

The illustration of a section of the fossiliferous
strata of the Devonian period is shown in the
figure. The section is a typical example of the
type of strata which is characteristic of the
Devonian period. The section is composed of
sandstone, shale, and limestone. The fossils
found in the section are typical of the
Devonian period. The fossils are
represented in the figure by the letters
A, B, C, D, E, F, G, H, I, J, K, L, M, N, O, P, Q, R, S, T, U, V, W, X, Y, Z.

PLATE III.

- FIG. 14.—Ramification of tracheæ on the oviduct (uterus.)
- FIG. 15.—Connective tissue cells (fat body?) from between the seminiferous tubes.
- FIG. 16.—Section of a ripe ovarian follicle; *Eg.*, egg; *Sh.*, shell (?) secreted by the epithelium, *Ep.*
- FIG. 17.—*Cedipoda sordida*. Connective tissue around the ovary.
- FIG. 18.—*Cedipoda sordida*. Epithelium of uterus seen in section.
- FIG. 19.—Transverse section of a whole, ripe ovarian follicle; *Eg.*, egg; *Ep.*, epithelium.
- FIG. 20.—Surface view of the follicular epithelium of the ovary.
- FIG. 21.—*Cedipoda sordida*. Inner surface of uterus.

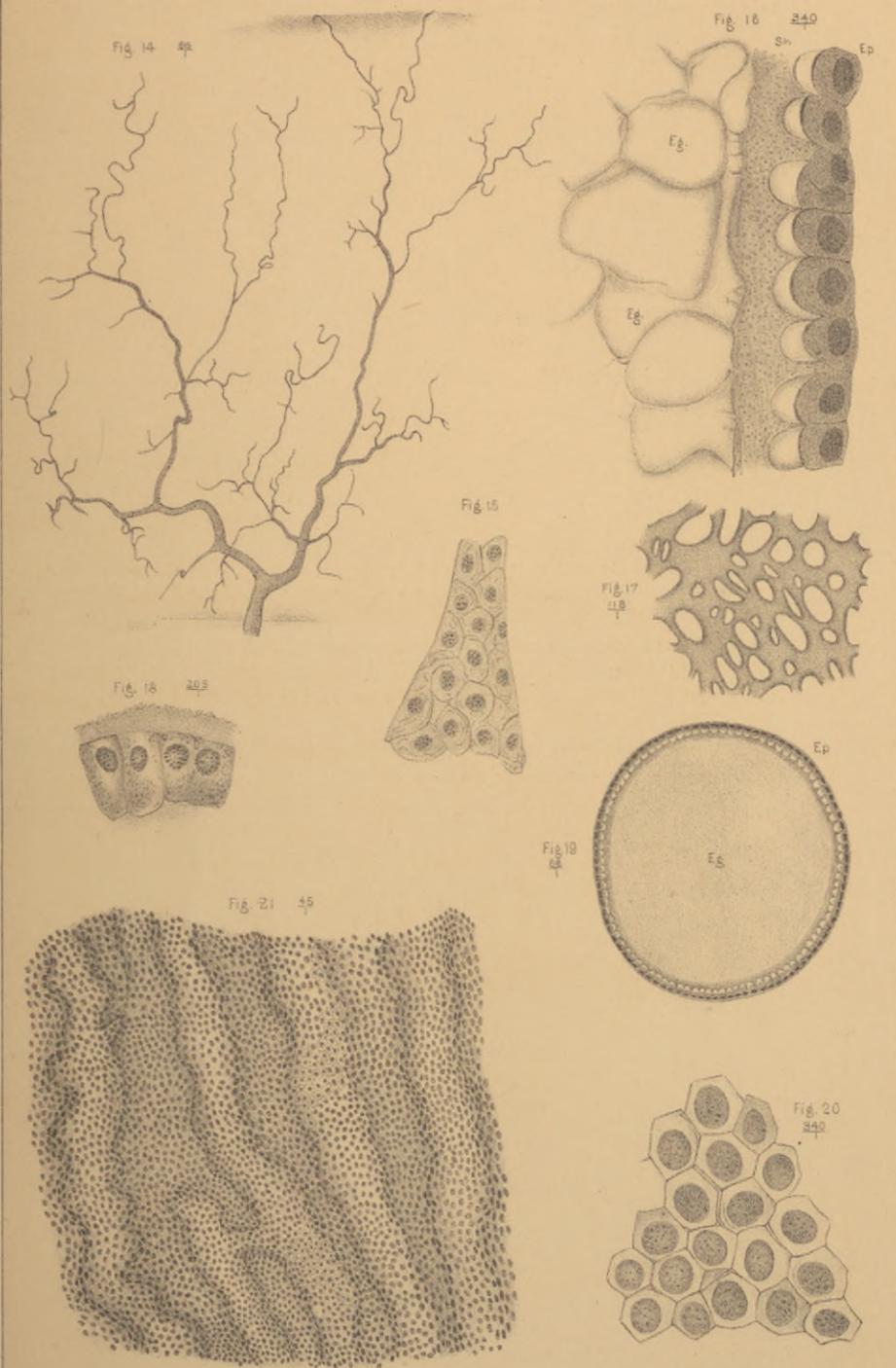


PLATE IV

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PLATE IV.

- FIG. 22.—*Edipoda sordida*. Longitudinal section of the uterus; *Gr.*, granular layer; *Ep.*, epithelium; *conn.*, tunica propria; *muc.*, longitudinal muscular coat.
- FIG. 23. *Edipoda sordida*. Surface view of uterine epithelium.
- FIG. 24. Section through the upper part (first segment) of seminiferous tube; *Cys.*, walls of the spermatocysts; *Tu.*, external tunic.
- FIG. 25.—*Caloptenus spretus*. Seminiferous tube, isolated; *conn.*, connective tissue; I, II, III, and IV, the four segments of the tubes.
- FIG. 26.—Young spermatoblast.
- FIG. 27.—Spermatoblasts just divided.
— — A, Spermatoblast in process of dividing.
- FIG. 28.—Older spermatoblasts.
- FIG. 29.—Transverse section of bundle of young spermatozoa.
- FIG. 30.—Transverse section of older bundle.
- FIG. 31.—Section of the upper part of a vesicula seminalis.
- FIG. 32.—Epithelium of the upper part of a vesicula seminalis.
- FIG. 33.—Transverse section of the ejaculatory duct, *Ej.*, D; *Ep.*, epithelium; *muc.*, circular muscle; *Tr. Tr.*', tracheæ.
- FIG. 34.—Transverse section of the muscular portion of a vesicula seminalis.

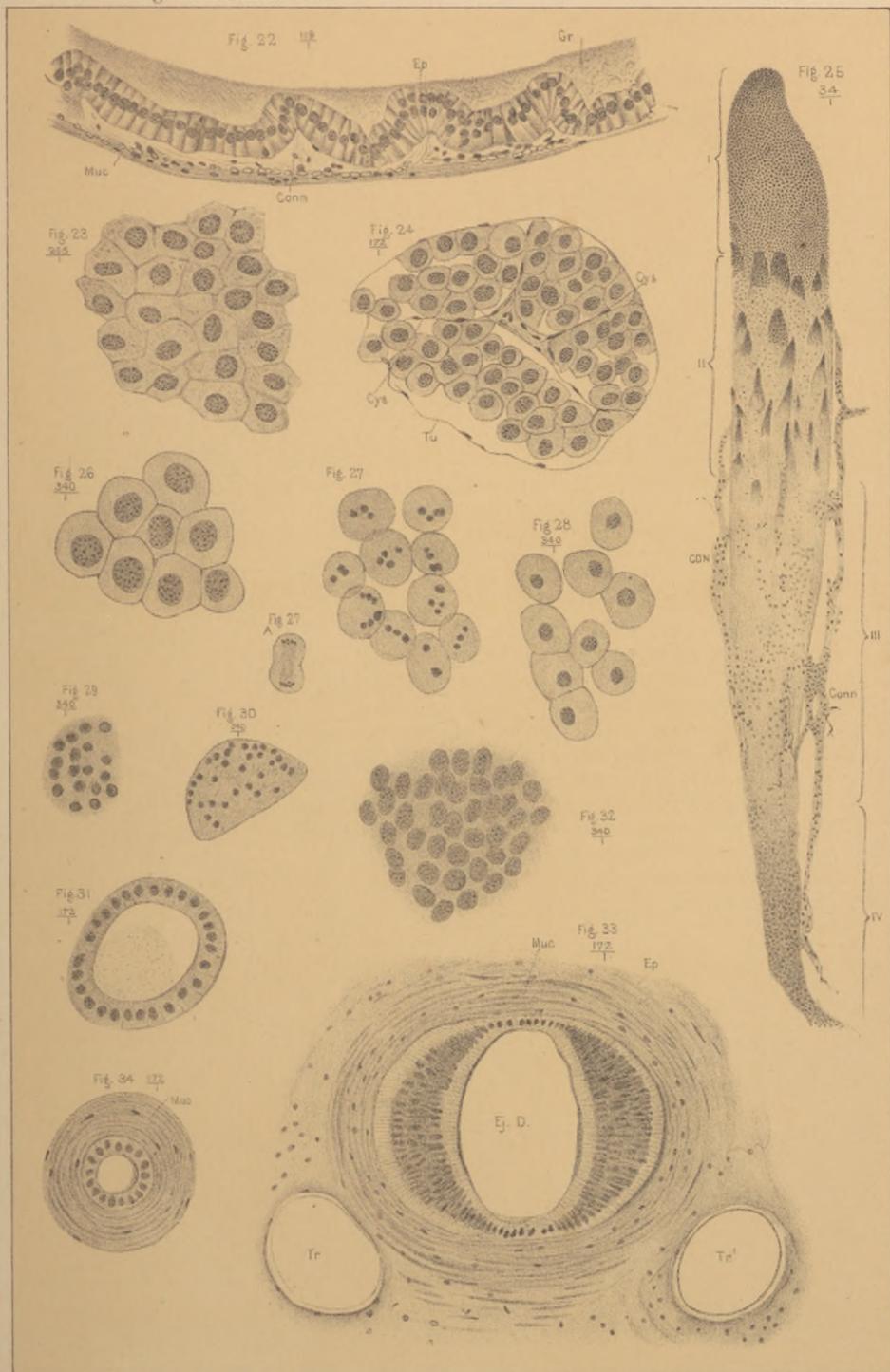


PLATE V.

- FIG. 35.—Transverse section of the hind part of the crop. *Ss.*, spines; *rid.*, ridges; *L.*, longitudinal; *muc. C.*, circular muscles.
- FIG. 36.—Section of the ventricular wall; *d.*, duct of follicle; *cu.*, cuticula; *Ep.*, epithelium; *conn.*, connective tissue; *muc.*, muscles; *Tr.*, tracheæ.
- FIG. 37.—Transverse section of a diverticulum. *Tr.*, trachea; *muc.*, circular muscular coat.
- FIG. 38.—Section of a single fold of a diverticulum; *conn.*, connective tissue or *tunica propria*.
- FIG. 39.—Inner surface of ventricle, with the epithelium removed. *In. m.*, circular; *L.*, longitudinal muscles.
- FIG. 40.—Transverse sections of three Malpighian vessels lying against the muscular walls of the rectum, *rect*.
- FIG. 41.—*Caloptenus spretus*. Section of the epithelium of the rectum.
- FIG. 42.—Transverse section of rectal folds. *F. F.*¹, furrows between the folds; *L. L.*, longitudinal muscle; *M. v.*, Malpighian vessels.

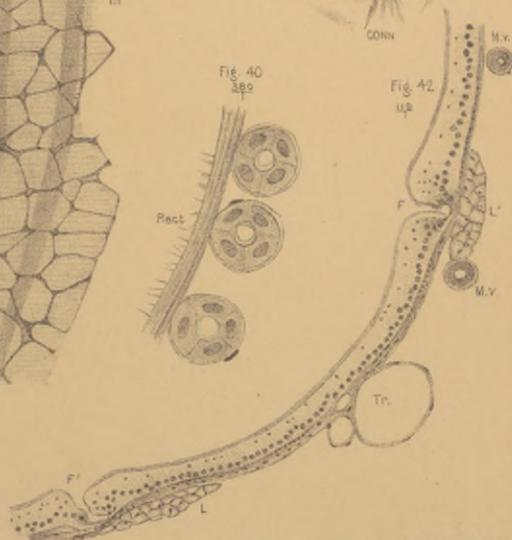
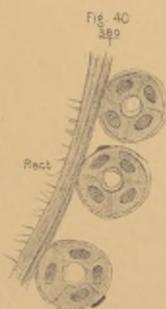
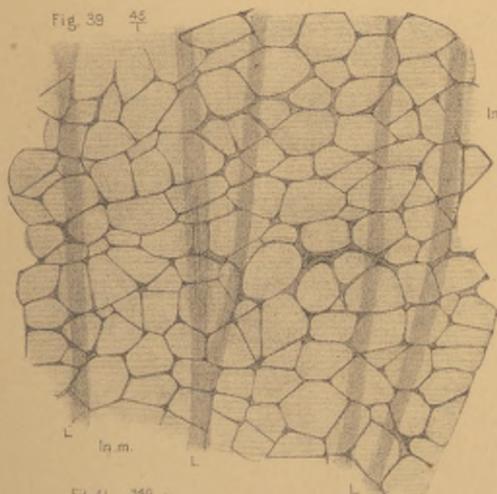
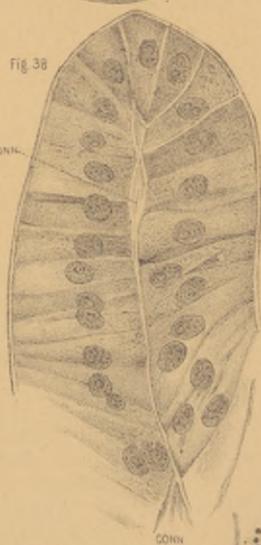
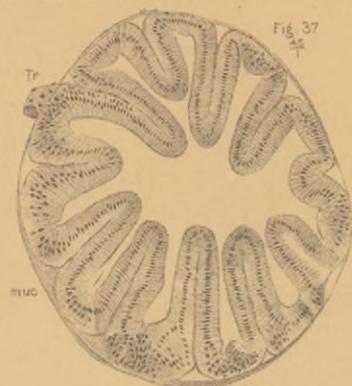
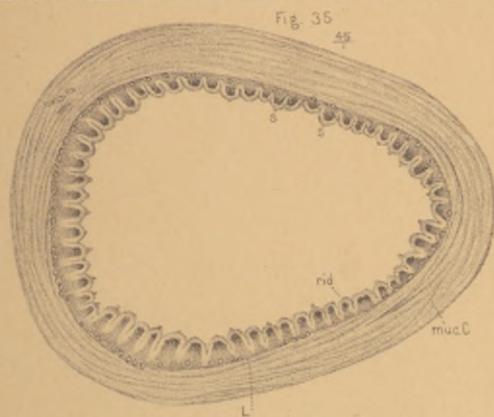


PLATE VI.

- FIG. 43.—*Oedipoda sordida*. Epithelial cells of gastro-ileal folds.
- FIG. 44.—*Oedipoda sordida*. Part of transverse section of gastroileal folds; *cu.*, cuticula; *muc.*, muscle.
- FIG. 45.—Longitudinal median section of *Caloptenus femur-rubrum*, female, to show the digestive canal. *M.*, mouth; *Oe.*, oesophagus; *Cr.*¹, anterior; *Cr.*², posterior division of crop; *p.*, proventriculus; *Div.*, diverticulum; *Ven.*, ventricle; *Il.*, ileum; *col.*, colon; *R.*, rectum; *An.*, anus.
- FIG. 46.—Surface view of the gastro-ileal folds. *Ven.*, ventricle; *Bd.*, circular muscular band under the folds; *Il.*, ileum.
- FIG. 47.—Optical section of Malpighian tube.
- FIG. 48.—Malpighian vessel.
- FIG. 49.—*Oedipoda sordida*; transverse section of gastro-ileal folds; *muc.*, muscular band; *Bd.*, of Fig. 45.
- FIG. 50.—Epithelium of ileal folds. *A.*, middle of folds; *B.*, furrow between folds; *L.*, longitudinal muscular bands.

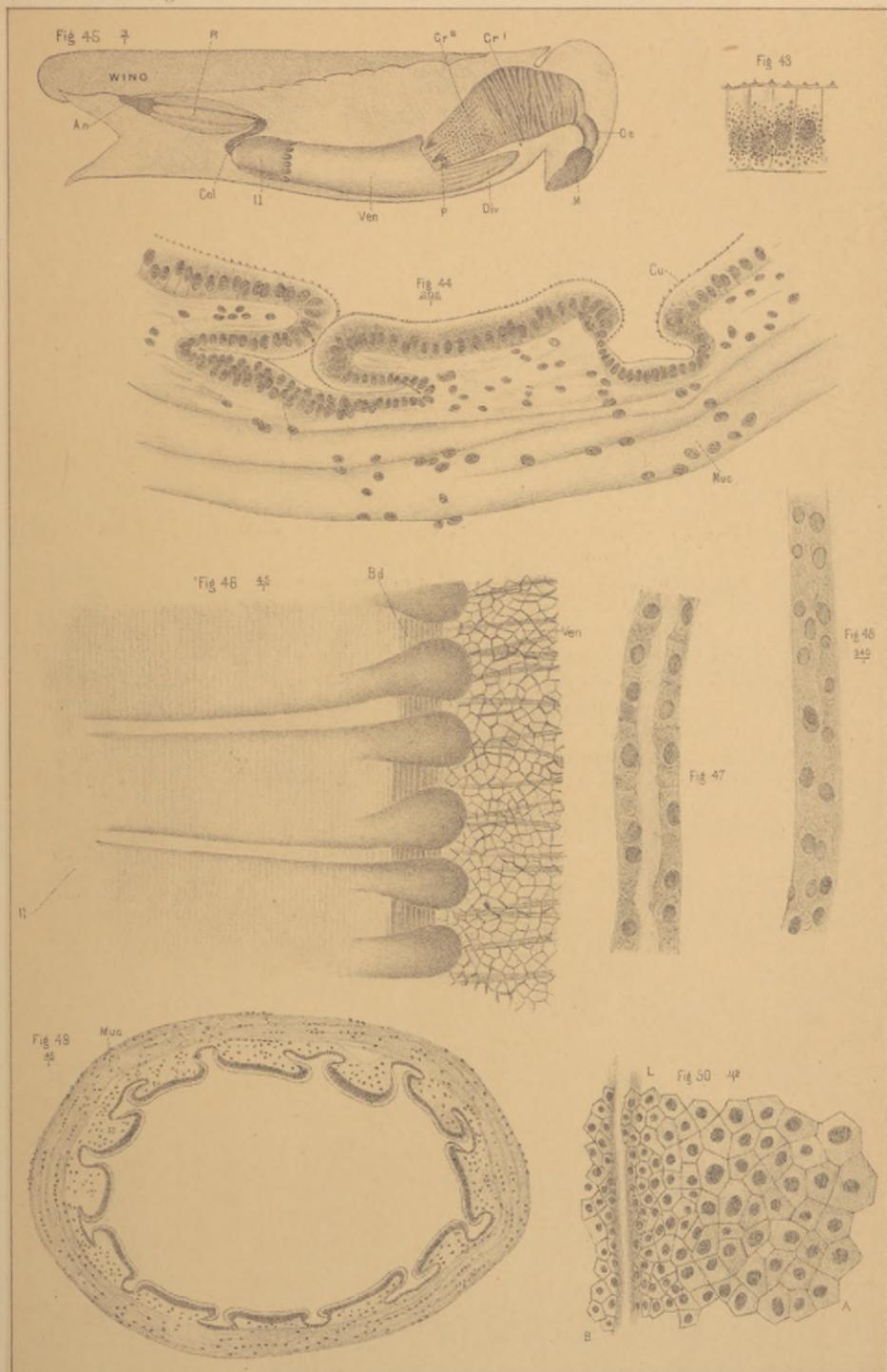


PLATE VII.

FIG. 51.—Transverse section of ileum. *L.*, longitudinal muscular bands; *muc. C.*, circular muscular coat; *Ep.*, epithelium.

FIG. 52.—Transverse section through the furrow between two ileal folds. *F.*, furrow; *cu.*, cuticula; *Ep.*, epithelium; *conn.*, connective tissue; *muc. C.*, circular muscles. *L.*, longitudinal muscular band.

FIG. 53.—*Caloptenus spretus*. Epithelium of rectal glands.

FIG. 54.—Surface view of the interior of the proventriculus; *d'*, central; *d''*, molar processes of the teeth; *a.*, longitudinal, interdental ridge.

FIG. 55.—Longitudinal section of the wall of the proventriculus.

FIG. 56.—Epidermal cells, seen from their outer surface.

FIG. 57.—Spiral threads of the same trachea.

FIG. 58.—Transverse section of the proventriculus; *d'*, central; *d''*, molar process of the teeth; *ep.*, epithelium; *conn.*, connective tissue; *a.*, longitudinal ridge; *C.*, subdental canal; *muc.*, muscularis.

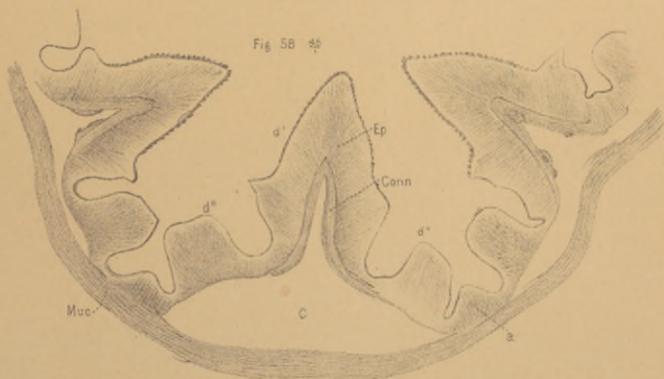
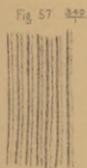
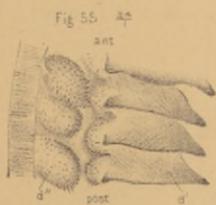
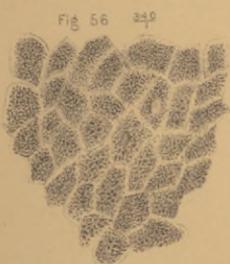
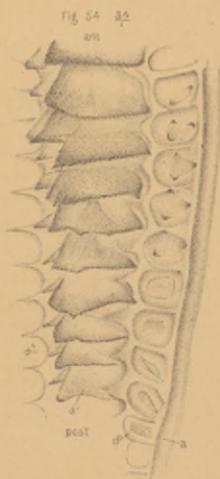
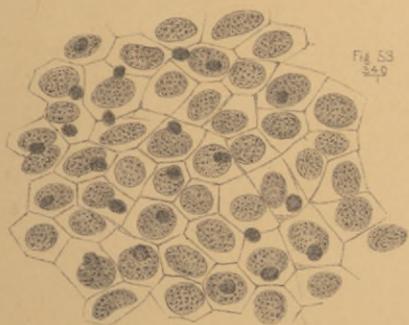
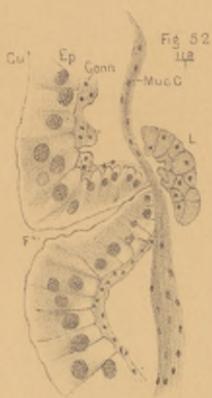
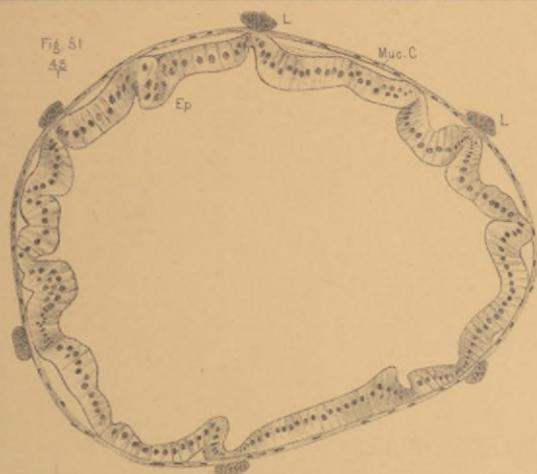


PLATE VIII.

- FIG. 59.—Cuticula from the lateral portion of one of the middle abdominal segments, to show the nodules *b b* and hairs.
- FIG. 60.—Cuticula of the crop.
- FIG. 61.—Tracheal epithelium, from a large trunk.
- FIG. 62.—Connective tissue from the ovary.
- FIG. 63.—Cuticula from the upper and anterior portions of the dorsal arch of one of the middle abdominal segments. *h.*, cuticular hair.
- FIG. 64.—Ovarian tube. *Ch.*, cord; *a-b*, region in which the eggs are first formed. *Tu.*, part of the external tunic. In order to draw this part the focus had to be changed.
- FIG. 65.—Cuticula from the side of the dorsal arch of one of the middle abdominal segments.
- FIG. 66.—Wall of the ventricle after removal of the epithelial and glandular cells.

