XVII.—The Calciferous Glands of Earthworms.

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CONTENTS.

Introduction.

The calciferous glands of earthworms are well-known structures, which occur under a variety of forms, and have been the subject of a considerable amount of research. They are appendages of the œsophagus which occur in different segments in different genera and species; and the usual view of their morphological nature, put forward by Beddard (1) in 1895, and for long generally adopted, is that their epithelium is the œsophageal epithelium thrown into various degrees of folding. Beddard describes these different degrees in a number of different forms.

Since the appearance of Beddard's Monograph, the most noteworthy papers dealing with the morphology of the glands are those of Harrington (12) and Combault (6, 7, 8), to which may be added Ribaucourt (21); all these deal with the Lumbricidæ only. The last-mentioned author considers the glands in the course of a general study of the Lumbricidæ of Northern France; Harrington and Combault are both largely concerned with the physiology of the glands. But it is with the morphological views put forward by these latter authors that we have to do in the present communication.

Briefly, Harrington, to use his own words, holds the secretory epithelium to be a greatly hypertrophied vascular wall, representing both the intima and the endothelium; the glandular cells belong, in other words, to the vascular system. Combault says the same—the histology of the adult and of the embryo seems to show that the tissue of the glands is mesodermal and vascular in its origin; later, he modifies this so far as to say "it is very difficult to state precisely from which embryonic layer the organs are formed."

That the view of the mesodermal origin of the glandular epithelium has gained some adherents is shown by the following quotation from a recent elementary textbook: "These glands are not true glandular diverticula of the œsophagus, but are mesodermal in origin and are merely the walls of the blood-vessels." Since we believe this view to be entirely erroneous, and since one or other species of earthworm is a universally adopted subject of study in all elementary courses of zoology, it seems advisable to combat it, and to advocate a return to the, as we believe, correcter and simpler conception of the older authors.

We imagine that the mistakes of the writers we have mentioned arise in part from their having confined their studies to the Lumbricidæ, in which group the glands reach the highest degree of complexity. What we attempt in the present communication is therefore, firstly, to give an account of the simpler conditions met with in several forms which we have ourselves investigated, with a few notes on forms described by other authors. Secondly, to describe the glands, including their histological structure, in the common Indian genus *Eutyphœus*, in which they have not so far been the subject of investigation; the glands here are of a peculiar type, which is both interesting in itself, and capable of throwing light on the morphology of these organs in general. Thirdly, we deal with the Lumbricidæ; the condition in them is described at some length, because the earlier descriptions are short and, from a modern standpoint, inadequate; while the later, besides being, as we have already said, permeated by false morphological views, are, as regards their purely descriptive part, not at all easy to follow; a lucid account, giving even a moderate amount of detail, of the glands of the common Lumbricidæ does not exist. From these descriptions, and the considerations which attach to them, it will appear, we believe, that the glands are throughout the series what BEDDARD and the earlier authors always supposed them to be—foldings, which attain varying degrees of complexity, of the epithelial lining of the œsophagus.

The literature of the subject is very large, and may be divided under four heads:—

(1) Descriptions of the calciferous glands, from the morphological point of view, in a considerable number of worms.

(2) Descriptions of structures which may be homologous, or of a similar nature, though they differ considerably from the organs generally known as calciferous glands; such are the diverticula from the anterior part of the gut in the genus *Henlea* (Enchytræidæ), certain structures in *Buchholzia* (Enchytræidæ) and in *Limnodriloides winckelmanni* (Tubificidæ; MICHAELSEN, 18), the so-called Chylustaschen in certain genera of Ocnerodrilinæ, and the unpaired diverticula of *Eudriloides* and *Stuhlmannia* (Eudrilinæ).

(3) Descriptions of the form and situation, and sometimes of the disposition of the lamellæ, of the glands in various genera and species, in systematic papers; these occur in abundance, since the organs are of importance from a systematic standpoint, but they do not give any histological detail.

(4) Papers on the physiology of the glands.

Of these, the last three do not concern us, and even of the first group it is scarcely possible to give an adequate account here. All that will be attempted is to give a short *résumé* of the work of previous investigators on forms which are either those or allied to those which we have ourselves examined. This will be most suitably done in the body of the paper, as we take up the various types of structure.

Material and Methods.

We have investigated the following:—(1) *Pheretima hawayana* (Rosa), a widely distributed species of the Megascolecine branch of the Megascolecidæ; it is perhaps the commonest earthworm in Lahore, and the genus is the one which is studied as a type in the colleges of Northern India. (2) *Ocnerodrilus* (*Ocnerodrilus*) *occidentalis* Eisen, found sporadically in India; it belongs to the Ocnerodriline branch of the same family; it was not known to occur in the neighbourhood of Lahore till the course of the present inquiry, when some small worms, supposed to be immature *Helodrilus parvus*, were subjected to examination; these proved to be *O. occidentalis*. (3) *Octochætus barkudensis* Stephenson (Octochætinæ, a sub-family of the Megascolecidæ) has been described by one of us from the Chilka Lake, on the east coast of India. It is a small worm, and had to be investigated by means of sections; these, prepared for the purpose of the systematic description of the worm, have been used for the present paper. (4) *Eutyphœus waltoni* Michaelsen, also belonging to the Octochætinæ; it is common in the United Provinces, and the genus occurs here and there in the Punjab, but it is not known from near Lahore. We owe our specimens to the kindness of Professor Youngman, of the Department of Biology, Canning College, Lucknow. (5) Two species of *Helodrilus* which we have examined, *H.* (*Bimastus*) *parvus* (Eisen) and *H.* (*Allobophora*) *caliginosus* (Savigny), are common in Lahore. (6) *Lumbricus* sp., kindly sent us by Dr J. H. Ashworth, F.R.S., from Edinburgh; the worms were not fully mature, and the species was therefore not determinable.

Previous workers have recommended the avoidance of acid fixatives, as these destroy the calcareous concretions both before and after their discharge from the cells; the precaution as to acid fixatives has most force in work done with a physiological end in view, and it seems rather fanciful to say, as Combault does, that treatment with such an agent causes the epithelium of the glands to take on the appearance of a vascular endothelium. We have, however, used formalin mainly as a fixative for the worms that we have ourselves preserved; but in a few cases where we have used sublimate and acetic acid we cannot point to any marked differences in the gland-cells that could be put down to the difference of treatment. In none of the specimens examined, with the exception of the *Lumbricus*, were there any such accumulations of calcareous particles as to interfere with section-cutting; we have thus been spared a source of trouble which has been felt by some previous workers.

The *Ocnerodrilus* were fixed whole in Zenker's fluid. The *Octochætus*, which came from the collection of the Indian Museum, was not specially fixed for histological work, but we have no reason to complain of the results of fixation as shown in the actual sections; we have, however, been careful not to describe the histological appearances in greater detail than is warranted.

We have to thank Professor YOUNGMAN for the careful preparation and fixation of the specimens of *Eutyphœus*. Some worms that he sent us to Lahore alive were unfortunately dead or not in a suitable condition on their arrival, and he kindly then sent us a number of specimens opened under salt solution and fixed in formalin; others were fixed in sublimate-acetic; the alimentary canal had been freed of extraneous matter by feeding for twenty-four hours on damp blotting-paper, or by syringing out at the time of opening of the worm. Our thanks are also due to Dr ASHWORTH for a similar careful fixation of the specimens of *Lumbricus*.

The two staining methods that we have principally employed have been Delafield's hæmatoxylin followed by eosin as a counter-stain, and Dobell's modification of Heidenhain's iron-hæmatoxylin.

THE ALIMENTARY BLOOD SINUS.

A true conception of the morphology of the calciferous glands depends in the first place on an accurate apprehension of the relations of the vascular channels in the alimentary wall. The subject was exhaustively discussed, on the basis of the results obtained up to that date by the numerous investigators who had, specially or incidentally, worked at the problem, by LANG (14)—it occupies indeed a fundamental place in his *Trophocöltheorie*—and has since that time engaged the attention of a number of his school, as well as of VEJDOVSKY.

The vascular layer of the alimentary wall in the Annelida, which intervenes between the epithelium and the muscular coats, consists not of definite blood-vessels, but is of the nature of a sinus—rarely continuous all round the gut, mostly divided up into a number of anastomosing channels by adhesions between the epithelial layer on the one side and the muscular coat on the other; the usual condition is that of a copious network. According to LANG and his followers, this network has no proper walls; the blood bathes the epithelial cells on the one hand and the muscular fibres on the other. That flattened nuclei, of unknown origin, are to be seen in many cases on the walls of the sinus is undeniable; but they do not form an endothelial lining, and the peri-intestinal sinus, or network, remains essentially a space between the epithelium and the muscular layer.

This conclusion of LANG'S is supported by FREUDWEILER'S subsequent work in Enchytræids (10), by SCHILLER'S on *Arenicola* (24), and by STERLING'S on *Eisenia* and *Pheretima* (28). It is challenged by VEJDOVSKY (30, 31), who goes to the extreme of viewing the sinus as contained within the entoderm. "Choosing the Enchytræidæ as a starting-point, VEJDOVSKY shows that the peri-enteric sinus is crossed by thin protoplasmic strands passing between certain basal replacing cells of the intestinal epithelium, which bounds the sinus on its inner side, and a connective-tissue-like membrane which limits it externally; intimately associated with this membrane are a number of flattened, hemispherical, or sometimes stalked cells, which project into the sinus. External to the membrane are the muscular coats of the intestine and the chloragogen layer. The membrane (vasothel) is interpreted as having been separated from the intestinal epithelium; the cells in connection with the vasothel as having migrated outwards from the layer of replacing cells; and the strands which cross the cavity of the sinus as constituting evidence of the original unity of the outer with the inner wall of the sinus. The sinus is therefore contained within the entoderm." (The quotation is from a former paper by one of us, 26.)

Thus LANG and VEJDOVSKY (to quote again from the same paper) "agree that the origin of the vascular system is to be sought in the accumulation of fluid at the base of the layer of intestinal epithelium, but thereafter they part company. LANG holds that the original position of the fluid is between epithelium and surrounding muscular layer; VEJDOVSKY, that it is within the epithelial layer itself, since it is limited externally by the basement membrane of the epithelial cells and by certain, originally amœboid, replacing entodermal cells which associate themselves closely with the membrane." Whether or not, therefore, we consider the occasional nuclei on the outer side of the sinus as entodermal, and detached from the alimentary epithelium, there can be no doubt that the blood in the sinus directly bathes the base of the lining cell layer of the tube.

The investigations on the alimentary sinus in the Annelida have naturally been carried out mainly or altogether in reference to the intestinal region, and we do not know of any definite statement as to how far forwards the sinus extends with the relations that have been described. According to our preparations, that portion of the alimentary tube with which the calciferous glands are associated possesses in all cases a sinus with the relations described for the more posterior portion of the canal.

ON RODLET EPITHELIUM.

The cells of the calciferous glands and of the neighbouring part of the alimentary tube have often been described as ciliated, and in some cases they undoubtedly are so. In other cases, however, there occurs on their free surface a layer of rodlets, which has apparently hitherto escaped recognition, or has been mistaken for cilia. We place here, therefore, a short general account of rodlet epithelium.

The layer of rodlets (Stäbchen) is well known to occur not uncommonly on columnar epithelium, but its significance is apparently not very clear. SCHAFER (23) says: "Their free surface (the description is of columnar epithelium in general) is covered by a thick striated border, which may sometimes become detached in teased preparations." GURWITSCH (11): "A general occurrence in absorptive cells and excretory cells is the possession of a fringe of bristles,—*e.g.* in the epithelial cells of the gut which take up fat,—but not in secretory cells; it may be inferred that the object is to increase the surface, though this is not at present demonstrated." SCHNEIDER (25) in the section entitled "Nährzelle (Nutrocyte)," which he defines as epithelial cells, mostly pertaining to the enteroderm, always with extracytal differentiations (cilia, flagella, rodlets), seldom with intracytal (muscular fibrillæ), function nutritive: "The rodlets are short stiff structures, held together by a homogeneous substance, in which clear pore-like intervals are often seen"; in the figures they appear as fine lines between rectangular blocks of clear intervening substance; and it would seem that what we have called rodlets in the description of the epithelium of *Eutyphœus* corresponds rather to these blocks—at any rate we have been unable to see the fine bristles between these blocks of lightly-staining substance. He adds: "In many cases it seems as if the cementing mass between the rodlets were itself of importance for absorption."

HEIDENHAIN (13) states that the "brush-border" (Bürstensaum, also called the Stäbchenorgan) is present, as is well known, both in absorptive and secreting cells (thus differing from GURWITSCH); its typical representative being the intestinal epithelium of Vertebrates, the best investigated epithelium of this type; the border of the kidney cells has also been much discussed; numerous other objects possess the border, but have only occasionally been described and figured; it is found, for example, in the polynuclear cells of the decidua epithelium of the rabbit, and in the mantle epithelium of snails beneath the shell. The rodlets possess in general, like the cilia, basal corpuscles, by means of which they are implanted in the surface of the cell; they have been compared by FRENZEL to the basal non-mobile somewhat thicker portions of cilia (Fussstäbe)—which however do not occur in Vertebrates, and are especially seen in the intestinal tract of Worms and Molluscs; JOSEPH is said to have shown that in the intestine of the earthworm the epithelium is ciliated ventrally, while dorsally, on the typhlosole, it has the brush-border; in the transition zone the series of "Fussstäben" pass into the brush-border without break—and one may conclude therefore that in the ciliated part of the tract the immovable basal part of the cilia replaces functionally the rodlets, and has the same relation to absorption as these (what this is is not stated); HEIDENHAIN, however, does not admit a morphological homology. Between the Fussstäben there is sometimes a thin material, stainable and sometimes simulating a pore-cuticle; this may also be the case in the brush-order, in the intestine and kidney.

The figures of the rodlets in HEIDENHAIN show (1) a layer of very numerous lightly-staining threads, not all the same length, resembling cilia, with very marked basal corpuscles; or (2) apparently thicker rods, strictly parallel, and all the same size, with small intervals between them (the condition in *Eutyphœus*, as described below); or (3) relatively shorter rods, very close together. There is no figure like that in GURWITSCH—fine needle-like rods with a relatively large amount of cementing substance staining much more lightly in between them; but the figures of the basal portions or Fussstäben of cilia do show that condition—the spaces being filled up with an almost clear, slightly granular matter.

THE ŒSOPHAGUS IN THE GENUS PHERETIMA (Figs. 1, 2).

In the widely distributed *P. hawayana* the œsophagus is swollen segmentally in segments x–xiii, and constricted intersegmentally. The swellings are approximately globular; in horizontal longitudinal section the anterior may be seen to bulge slightly forwards, and the hindmost slightly backwards.

In these segments the epithelium (fig. 1) is thrown into prominent transverse folds, which may take up almost half the diameter of the tube, leaving only a narrow free channel in the middle; of these folds there may be about a dozen on each side in each segment. Neighbouring folds sometimes join and fuse at or near their free edges, at any rate on the dorsal and ventral regions of the œsophageal wall. Horizontal sections give evidence also of a ventral and of a less marked dorsal fold running longitudinally, the ventral being continuous from segment to segment; but these are not so conspicuous in transverse sections as might have been expected. Alternate transverse folds are sometimes regularly smaller; they might be called ridges, in distinction from the lamellæ, with which they alternate.

In these segments—especially well marked in xii and xiii—is to be seen a very striking system of transverse channels in the œsophageal wall; these vessels are about twelve per segment, are broad—equal in breadth, where they are best seen, to the interval between successive channels—and are not united by longitudinal connections. Above they join the supra-intestinal—a specialisation of the gut plexus (or sinus); below there is no median vessel, and the transverse channels are therefore continuous across the middle line.

The epithelium of this portion of the œsophagus (fig. 2) consists of cells which are shortly to markedly columnar, their average height being about 25 μ, and the extremes about 14 to 35 μ. The protoplasm has a fibrillar structure, the fibrillæ passing in a generally vertical direction (vertical to the surface of the cell); they frequently form a reticulum, especially near the surface, where they are more numerous than in the deeper parts of the cell. There are no rodlets or cilia; the surface of the cell consists of a deeper staining layer, homogeneous and compact, which receives and is continuous with the fibrillæ in the interior of the cell.

Cell partitions are apparently formed by vertical walls of the same nature as the intracellular fibrillæ; where the cells are cut tangentially to the surface of the layer the partitions are seen to constitute a honeycomb-like arrangement. These partitions are also continuous at the surface of the cells with the homogeneous surface layer. The rest of the cell is quite clear—as if it were merely empty spaces. The nucleus, often near the middle of the height of the cell, sometimes nearer the base, is round to roundly ovoid; the chromatin is in the form of scattered grains, with one large particle which is apparently constant.

In the middle of each lamella is an axis, also fibrillar in structure (fig. 2), and continuous with the fibrillæ of the cells and with the partitions between the cells. This axis is mostly, in our preparations, not divided by a blood film in its centre, owing to the fact that this portion of the alimentary canal does not retain its blood supply after fixation; in places, however, a satisfactory demonstration of the basal sinus between the epithelial and muscular coats of the œsophagus and of its extensions into the axis of the lamellæ is obtained. Flattened nuclei may be present in the axis. The circular and longitudinal muscular coats are both well marked.

Owing to the emptying of the blood spaces post-mortem in this portion of the tube our sections do not actually demonstrate the regular series of the transverse channels which are such a prominent feature of this portion of the œsophagus on opening the narcotised or just killed worm. There can be no doubt, however, that the channels are represented by the spaces at the base of the lamellæ, with which they correspond entirely in number and direction.

Other Simple Forms of Glands.

Of the same simple type, or only slightly more complicated, are the œsophageal swellings in a number of other Megascolecinæ. Thus Bourne (4) describes in *Megascolex cœruleus* a series of swellings of the œsophagus occupying segments x–xv; the inner wall is much plicated, raised into ridges and papillæ, and excessively vascular; smaller and larger concretions of calcium carbonate are usually to be found in this portion of the tube.

Miss Raff has studied the alimentary canal in a number of Australian worms (20); she distinguishes simple swellings, sacculated swellings, and diverticula; these portions of the œsophagus have a folded internal lining; the folds are very long and thin, and in the "calcareous glands" they have a very large blood supply. Thus in *Megascolex dorsalis* the swelling is of the simple type; in *Fletcherodrilus* the second stage occurs—there are lateral saccular swellings, but no duct separates them off from the central lumen. In *Cryptodrilus saccarius* (*Notoscolex saccarius*) there are five pairs of glands, separated off from the œsophagus by a distinct duct, each bean-shaped, with a large vessel running along its length on the dorsal side; microscopically, the very long folds of the lining stretch right across the lumen and are richly supplied with blood; the lining cells are ciliated, the cilia being visible with the low power.

A simple form of gland is described by Benham in *Plagiochæta punctata* (3). The folds of the œsophageal lining, present in segments x–xiii, become more marked in segment xiv, where they give rise to calcareous glands. Each gland is a large sac at the side of the alimentary tube, but extending ventrally and dorsally so as almost to surround the tube along with its fellow. The whole region is very vascular.

The Glands in the Genus Ocnerodrilus (Figs. 3, 4).

In the genus *Ocnerodrilus* there are present in segment ix, below and at the sides of the alimentary tube, a pair of ovoid sacs opening ventro-laterally into the œsophagus towards the hinder part of the segment, and lying with their blind ends directed forwards. These have been described by Beddard in *O. eiseni* (2), and by Eisen in *O. beddardi* (9). Beddard found the lumen of the sacs divided up by a network of anastomosing folds of epithelium, the subdivision being more complete towards the blind end of the gland. "The epithelium of the gland appears to be everywhere ciliated, and the alimentary tract from the orifice of the glands becomes ciliated. The structure of the glands is much like that of the calciferous glands of many earthworms, which are in some cases, at any rate, ciliated." BEDDARD here adds a note, "In *Acanthodrilus antarcticus* and in the young of *A. multiporus*. I do not know how far this ciliation is prevalent among earthworms."

EISEN is largely concerned with the vascular supply. The blood-vessel supplying the sac is single at its origin, where the sac originates from the œsophagus; it then breaks up into branches, which are grouped in bunches; the vessels unite again at the distal end of the sac, and in their course are parallel, and do not anastomose. The vessels cause the longitudinal ridges of the inner surface of the sac-wall, which are prominent, and sometimes so large as almost to divide the pouch into several parallel chambers; the inner lining of the pouch is ciliated.

MICHAELSEN, in the course of systematic studies (16, 17), has examined the glands of *O.* (*Ilyogenia*) *calwoodi* and *O.* (*I.*) *africanus*, which he prefers to call "chylesacs" (Chylustaschen). In the former species the broad lumen is partly narrowed by septa, and contains considerable calcareous masses; the blood-vessels of the sac unite at the free end to form a vessel which then runs freely. In the latter species the lumen is divided by a number of septa, longitudinal in direction, which spring from the wall and meet in the axis of the sac so as to give a wheel-like appearance to a transverse section; the number of radiating septa may be as many as seven; the external wall as well as the septa are rather thick, and are provided with a system of very narrow canals (Chylusgefässe).

BEDDARD gives no figure, and EISEN'S figure of a longitudinal section scarcely affords a good conception of the essential structure. We therefore give a reproduction of a transverse section through the sac of one side of *O.* (*Ocnerodrilus*) *occidentalis* (fig. 3), showing the ridges of the interior, and the relations of the blood sinus—an extension over the sac of the general gut sinus. The muscular layer over the sac is extremely thin, or in places absent; the sinus is then bounded on its outer side by the peritoneal coat, together with a distinct basement membrane.

We cannot discover cilia within the sacs; the cells may be covered by a fluffy secretion, beneath which the surface of the cells is as a rule, though not always, quite sharply defined; or the cells may show on their surface a fine thready raggedness; or the surface of the cells may be quite clear of any appendages or adventitious matter.

The neighbouring portion of the œsophagus shows an interesting condition of the epithelium (fig. 4). In segment ix, in the part adjacent to the opening of the sacs into the œsophageal lumen, and in segments x and xi, the epithelium bears a layer of rodlets, 7 μ in height, with the usual palisade-like arrangement, practically non-staining; the free border of the layer appears crenulated in the sections. The surface of the cells beneath the rodlets stains more deeply than the rest of the cell; in the deeper half of the epithelial layer is a series of oval vacuole-like spaces; the nuclei are round, at the middle of the height of the cells, just superficial to the layer of vacuoles. Cell outlines are not distinguishable; the protoplasm of the superficial half of the layer is close and granular, of the deeper half is rather clearer. Outside the epithelium is an almost continuous blood sinus; the muscular layer is very thin.

In three specimens of this species from the Ross Andamans, sectioned by one of us some time ago in the course of systematic work, the rodlets in segment x appear as if beginning to be transformed into cilia; they slope backwards, and have no longer the regular palisade arrangement. In xi they become typical cilia—thin wavy filaments, 20 μ or perhaps much more in length; they are especially marked at the place where the narrow œsophagus widens to form the intestine, at septum 11/12; here they form a tuft which projects backwards from the narrow neck into the following wider portion. Further back, in the intestine, the epithelium is covered by a thin cuticle-like layer, which, however, is not homogeneous, since it stains in its basal half, though the superficial part is colourless.

The Glands in the Genus Octochætus (Figs. 5, 6).

Beddard in his Monograph (1) gives a short description of the condition in the young *O. multiporus.* The gland is single, and projects forwards in the mid-dorsal line on the œsophagus; where it joins and opens into the œsophagus it begins to extend laterally as well, coming to cover the whole surface of the gut except in the mid-ventral line. The lining epithelium is arranged in numerous folds, some penetrating further towards the lumen than others. The gland epithelium is in general cubical, and therefore lower than the columnar epithelium of the œsophageal tube; but the free edges of the folds are thicker than the rest, since the cells are here more columnar; in the peripheral portions of the gland the cells are ciliated.

We have examined *O. barkudensis* (27) in transverse sections. Here the glands are paired, large, lobed and asymmetrical, occupying segments xv and xvi; but the openings of the two glands are at the same level. The glands are essentially diverticula of the œsophagus, containing a great number of thin lamellæ arising from the wall and projecting into the interior, ending in a free edge near where the lumen of the gland debouches by a narrow duct into the œsophagus (fig. 5).

In the peripheral parts of the glands there are numerous "bridges" between neighbouring lamellæ; and, though the specimen is not injected, and for the most part the enveloping sinus is not marked, some of the lamellæ are distended with blood—a sheet of blood between two layers of epithelium.

The cells of the epithelium of the lamellæ are for the most part much flattened, and the lamellæ extremely thin; in the periphery of the gland the cells are more cubical, transparent, sometimes filling up the peripheral end of the crypt between two adjacent lamellæ. In the crypts are small transparent crystalline-looking particles, probably calcium carbonate, which appear to have been formed within the cells of the peripheral portions of the lamellæ; these cells are often much vacuolated, and sometimes throughout a relatively large region entirely disintegrated. A certain number of the cells are ciliated, especially those towards or at the free edge of the lamellæ (fig. 6).

The duct by which the interior of the gland communicates with the œsophageal lumen is narrow and short, lined with low columnar epithelium which is heavily ciliated. Rodlets, but not distinct cilia, appear as a layer on the lining epithelium of the œsophageal lumen for a short distance on each side of the entry of the ducts.

The Glands in the Genus Eutyphœus (Figs. 7–10).

The Glands as seen in Dissection.

If a large species of *Eutyphœus*, such as *E. gigas*, be taken for dissection, it will be seen that the region of the alimentary canal corresponding to segment xii is slightly swollen, but not sharply delimited from the rest of the tube. On opening this portion by a median longitudinal incision a number of transverse lamellæ will come into view on each side (fig. 7) in such a way as to leave a median vertical channel in the middle; their dorsal edges are not attached to the inner face of the œsophagus, so that a T-shaped lumen is visible in a transverse section of the tube. The lamellæ of either side may be spoken of as constituting a gland; the pair of glands are thus contained within the gut—not appendages which project outwards from the gut.

The individual lamellæ cannot be freely separated from each other, since they are attached to and held together by a vertical wall along their inner borders; this wall partitions off the interlamellar clefts from the central lumen of the œsophagus, which thus forms a median corridor; the interlamellar clefts are, however, open above. In addition, a large blood-vessel may be seen running longitudinally along the upper edge of the vertical wall, or, in other words, along the upper and inner edge of the gland on each side.

Structure of the Glands as studied in Sections.

Sections taken in various directions confirm the above description of the glands as consisting of a large number of vertical transverse lamellæ on each side of a central lumen, a vertical longitudinal wall on each side separating off the lamellæ from the central lumen, and a system of included interlamellar spaces open above (*cf.* fig. 8). In addition, it is seen that a number of the lamellæ are incomplete, attached to the vertical partition and not reaching outwards as far as the lateral wall of the gut; or attached to the lateral wall and not reaching the vertical partition. Neighbouring lamellæ may sometimes be united by synapticula; or a lamella may split into two, the two reuniting at some distance and thus enclosing a long slit-like space. The lamellæ and vertical wall consist of a double layer of epithelium; the muscular coat of the œsophageal wall surrounds the whole, and sends no extensions into the lamellæ or vertical wall.

Vascular Supply of the Glands.

The large vessel in the dorsal edge of the vertical wall (fig. 10) has already been mentioned; it is continued back behind the level of the glands for some distance in the œsophageal wall before it disappears in the general gut sinus.

There is also a sinus in the vertical partition (not visible in fig. 10), which communicates on the one hand with the vessel just mentioned, and on the other is continuous with the sinuses in the lamellæ. These latter are potential or actual, according as the part of the gland is engorged or empty of blood (fig. 9); they separate the two layers of epithelium of which the lamellæ are composed. These lamellar sinuses become, at their peripheral margins, a series of circular sinuses in the œsophageal wall. Leading off from the front end of the glands is a vessel on each side which lies in the lateral wall of the œsophagus. The whole organ is thus permeated throughout with blood.

The Epithelium of the Glands.

(*a*) *On the Lamellæ.*—In the average condition the cells are approximately cubical, about 10 μ in height, and each projects as a low rounded, dome-shaped swelling into the interlamellar space. The nucleus is rather superficial, usually in the dome-shaped swelling; it is roundly ovoid, 5–6 μ in long diameter, with scattered granules of chromatin, and one larger darkly-staining particle.

The surface of the cell is often seen to be disintegrating, and then may best be described as shreddy; here and there long cilia-like threads are given off from the surface; the resemblance to cilia may be very close (some acid-fixed preparations). The epithelium appears for the most part as a single layer; but in places a number of superficial cells are seen, which appear to be disintegrating *in toto*—staining only very lightly, and being thrown off along with their nuclei. In addition, small solid crystal-like particles are being produced and thrown off in certain regions, or in certain preparations (fig. 9).

The epithelium of neighbouring lamellæ is continuous round both the external and internal ends of the interlamellar spaces.

In well-fixed preparations a basement membrane is often not to be made out; it is best seen in badly-fixed specimens (fixed without opening the worm) where acid fixatives have been used (Zenker's fluid). Here the glands are in places skeletonised; the epithelial cells have become detached, and the basement membrane is left to indicate the position of the lamellæ; the membrane may appear as a single or double layer in each lamella—potentially double, no doubt, throughout, and corresponding to the two layers of epithelium which compose the lamella.

Between the two layers of cells there are seen numerous nuclei, much flattened or of an elongated ovoid shape. A number of ovoid or rounded nuclei are also contained in the deeper portions of the epithelial cells themselves.

(*b*) *On the Vertical Partition.*—The vertical partition consists of a double cell layer enclosing a blood sinus (fig. 10); the cells on the lateral face of the partition are continuous with and similar to those of the lamellæ; those on the median face are of the nature of columnar œsophageal epithelium. The basement membrane of the layer on the median face is extremely stout—3 μ in thickness; it forms the median boundary of the partition sinus. The basement membrane of the outwardly facing layer of epithelium is much thinner, and is continuous with that of the lamellæ. The vessel (more correctly sinus) in the upper edge of the partition is covered by columnar cells similar to those on the median face of the partition.

No muscular layer intrudes between the epithelial layers of the vertical partition.

(*c*) *The Occurrence of Rodlets on the Œsophageal Epithelium.*—If a transverse section of any but the most anterior part of the glands be examined the columnar epithelium on the median face of the vertical wall will be seen to bear a layer of short rodlets, perpendicular to the surface of the cells; these are stiff and straight, staining only lightly, of appreciable thickness, and 7·5 μ in height; they are placed close together, and about six placed side by side in one plane take up a space of 10 μ (fig. 10). The remarkable thing in their appearance is that they form a regular palisade, are exactly parallel to each other, and of exactly the same height. The free edge of the cell below the rodlets stains deeply.

It has been said that the rodlets are not present on the vertical partition in the most anterior part of the gland region. They are present on the dorsal wall of the œsophagus, beginning rather behind the level at which they appear on the vertical partition; they disappear towards the dorso-lateral region of the gut wall.

In following a series of transverse sections from the anterior end of the glands backwards there will be seen, in the region in front of the rodlets, a thinner, more homogeneous layer on the columnar cells, in which distinct rodlets are not visible. This may, on the dorsal wall, simulate a cuticle, 2·5 μ thick; and it becomes transformed into the layer of rodlets as we pass backwards in the series. The same passage of a homogeneous cuticle-like layer into rodlets may be seen in the body of the glands, on the free edge of the vertical partition; on following the epithelial layer over this edge the rodlets of the inwardly-looking face of the partition change gradually into such a layer, rather more than 2 μ thick. (Compare also the replacement of the rodlets in *Helodrilus parvus* by a homogeneous cuticle-like layer behind the region of the glands, as described later.)

The rodlets are continued backwards for some segments behind the glands, as a layer 7 μ high on the œsophageal epithelium. The palisade arrangement may be less regular, but the structures are rod-like, not hair-like.

Rodlets are not seen on the cells of the lower portions of the lamellæ of the glands; but they are present on the upper halves, more or less, and on the free upper borders of the lamellæ; here they may have a remarkable resemblance to cilia, and are less regular and appear thinner than the typical rodlets. They are directed obliquely upwards, towards the free upper edge of the lamella, and being more or less separated from each other do not form a regular palisade (fig. 9). They seem to be intermediate between typical rodlets and typical cilia, and again have some resemblance to the ragged hair-like appendages of the cells lower down on the lamellæ.

General Remarks on the foregoing Genera.

So far there can be no doubt that the calciferous glands are to be considered as foldings of the œsophageal wall, and their epithelium as a continuation of the œsophageal epithelium. The condition described in *Eutyphœus* is the most complicated; the genus is to be derived from *Octochætus* (though not directly—the intermediate stages having been lost, or not yet discovered); and the calciferous glands of *Octochætus* have therefore been withdrawn, in *Eutyphœus*, within the œsophagus instead of projecting as considerable diverticula at the sides. Looked at from another point of view, the glands of *Eutyphœus* show us the extreme term attainable by a series of transverse lamellæ; their internal borders have fused together, so forming the vertical partition which separates off the interlamellar spaces from the general cavity of the œsophagus, and the communication of the interlamellar spaces with the œsophagus takes place only by means of their slit-like upper ends.

The Calciferous Glands in the Lumbricidæ (Figs. 11–13).

Historical.

It is in the Lumbricidæ that the glands have been most fully investigated by previous workers. Lankester was the first to examine them in any detail (15), though Morren had given a rough figure without any accurate description. Lankester calls them œsophageal glands, and places them in segments xii and xiii (corresponding to xi and xii in our present nomenclature). The first pair, in the first of the two segments, are round and full, very vascular, and firmly attached to the wall of the œsophagus, but do not appear to have any communication with the interior; their wall is thin, and they contain each a single hard crystalline mass, or numerous smaller bodies; the crystalline substance effervesces on the addition of acid. "I have frequently found the crystalline bodies passed into the œsophagus and lodged in the capacious crop." The second and third pairs of glands are both placed in the next segment, and are a little smaller than the first pair; their walls are much thicker, but no less vascular; they contain a milky secretion. In section, there are seen an inner epithelial coat, a vascular region, and an outer more delicate membrane forming the sheath of the organ, on which the externally visible vessels extend; these vessels are shown in the figure as running longitudinally, parallel and numerous on all three pairs of glands.

Claparède (5) identified three pairs of lateral pouches, the first two pairs in segment xi, the third in segment xii. He describes the glands as consisting of many gland follicles, the follicular cavities being the spaces between a number of lamellæ which are placed perpendicular to the axis of the œsophagus; each follicle occupies the interval between the epithelial layer and the muscular coat. The lamellæ consist of a double layer of cells, with vessels and connective tissue in their centre. These vessels are radially-directed branches of a series of longitudinal vessels in the thickness of the wall, and empty themselves peripherally into the vessels of the outer layer of the œsophagus. At first it was thought that the follicle could discharge the secretion into the œsophageal lumen by the separation of the epithelial cells of the œsophageal lining, but this appears not to be the case; "an geluugenen Durchschnitten finde ich einzelne Spalten des Epithels, welche die Mündungen der Follikel offenbar darstellen. Ob aber jeder Plattenfollikel eine einzige solche Mündung oder deren mehrere besitzt, ist nicht ausgemacht."

PERRIER (19) gives an abstract of CLAPARÈDE'S account, but in saying "ces feuillets sont placés entre la couche vasculaire et les couches musculeuses de la paroi œsophagienne," he gets further from the mark than his original.

BEDDARD, in his Monograph (1), does not give a separate description, but after giving a general account of the glands in their other and less complicated forms, adds that in *Lumbricus* only the most anterior gland on each side opens into the œsophagus, the hinder glands opening into each other and into the first pair.

The textbooks, even when treating *Lumbricus* in detail as a type for study, are scanty or sometimes misleading. VOGT and YUNG mention three pairs of thickenings, symmetrically situated in segments xi and xii—follicular glands intercalated between the vascular and muscular layers of the œsophageal wall, supplied with numerous blood-vessels. MARSHALL and HURST were apparently the first to give the situation of the glands correctly; the œsophageal pouches are a pair of short lateral diverticula of the œsophagus in segment x; the œsophageal glands are two pairs of lateral protuberances on the sides of the œsophagus in segments xi and xii; they are hollow, and their cavities, which are subdivided by a large number of horizontal lamellæ, contain a milky calcareous fluid; they are local thickenings of the glandular walls of the œsophagus, and their numerous cavities open into the œsophageal pouches. SEDGWICK mentions the name, but nothing more. PARKER and HASWELL present a paraphrase of MARSHALL and HURST, adding that the milky appearance of the fluid is due to its containing numerous particles of carbonate of lime. SHIPLEY and MACBRIDE are short, and not quite accurate; the œsophagus "has three pairs of lateral pouches developed on its walls. These pouches secrete calcareous particles, and hence are termed calciferous glands." We do not think that a student would arrive at an adequate conception of the glands from any of these descriptions.

We have previously given the outstanding points in the conceptions of the more recent writers, and shall criticise these more in detail after describing the glands themselves.

General Outline of the Structure of the Glands in Helodrilus.

In segment x the œsophagus suddenly widens to form a pair of pouches (œsophageal pouches); the tube also dilates, though less and less in successive segments, for a short distance behind this, and is constricted at the situation of the insertion of the septa into its walls.

The following measurements will give an indication of the outline of the tube in this region; they are taken from a young specimen of *H. caliginosus*:—

In segment ix, diameter of œsophagus ·22–·24 mm.

In segment x, transverse diameter of whole, including the pouches, ·61 mm. Vertical height of central part of œsophagus ·24 mm., of pouches ·37 mm.

At septum 10/11 the tube is ·35 mm. high, ·28 mm. broad.

In segment xi, ·37 mm. high, ·4 mm. broad.

In segment xii, ·37 mm. high, ·33 mm. broad.

At septum 12/13, ·37 mm. high, ·28 mm. broad.

In segment xiii, ·37 mm. high, ·35 mm. broad.

At septum 13/14, ·37 mm. high, ·28 mm. broad.

In segment xiv, ·35 mm. high, ·28 mm. broad.

A series of transverse sections shows that the pouches in segment x are lateral diverticula of the gut, with widely-open mouths, and longitudinally-ridged internal lining (fig. 11). On following the series of sections backwards the distal portions (the centrally directed ends) of the ridges are seen to fuse with those of their neighbours, and in this way, when the fusion of all is complete, a series of longitudinal tunnels is formed. These extend backwards through segments xi–xiv; the lumina of the tunnels are lined by an epithelium which is continuous at their anterior ends with that of the œsophageal pouches, and so with that of the œsophagus. As in *Eutyphœus*, the muscular coat is entirely outside the glands, which are differentiations of, and included entirely within, the epithelial layer.

The more detailed description will be most conveniently made by following out a series of sections through the successive segments; for this purpose we select a young specimen of *Helodrilus caliginosus* fixed in formalin. The slight differences observed in an adult of the same species, and in *H. parvus*, will be briefly described afterwards.

The Young Helodrilus caliginosus.

The Alimentary Canal in segment x.—In the region immediately in front of the calciferous glands the epithelium of the œsophagus is thrown into about a dozen longitudinal ridges; there is no layer of rodlets, and no cilia; the muscular coat is thin, 4·5 μ in thickness.

At the level of the anterior part of the œsophageal pouches the epithelium of the œsophagus proper (the dorsal and ventral walls) is columnar—the cells extremely elongated, with almost rod-like nuclei. The wall of the anterior part of the pouches is but little ridged, and the lumen of the pouch is a large open cavity; the epithelium of the proximal part of the pouch, near its opening into the œsophagus, consists of cells which are relatively broader than those of the neighbouring part of the œsophagus proper, with more oval nuclei; the height of the cells diminishes further towards the lateral wall of the pouch, where they are shortly columnar or even cubical, and the nuclei may be spherical; there are no rodlets or cilia. The free margin of the cells of the pouches is very definite, as if each cell were bounded at its surface by a membrane. The blood sinus lies outside the epithelial layer of the pouch, and the muscular coat is very thin, hardly definitely measurable.

In the posterior half of the pouch prominent ridges begin—better perhaps called lamellæ. Each lamella consists of a double layer of cells, approximately cubical in shape; the texture of the cells of the central portions of the lamellæ appears loose (in the particular specimens described; but not in the *H. parvus* of fig. 11), as if the cells were disintegrating, and the cells enclose empty spaces of ragged outline. The cells have no rodlets or cilia; nor have they at any place in the tunnels to be described.

Some of these lamellæ immediately unite at their free ends with their neighbours to form tunnels (fig. 11); these are at first irregular in form, but elongated in a direction radial to the centre of the pouch. In a short time the lamellæ have all fused at their margins, and the series of tunnels is complete. From the first appearance of prominent lamellæ to their complete fusion to form tunnels there is a distance represented by only ten sections (·08 mm.).

When the tunnels are well established, the central lumen of the pouch is much diminished. Each layer of a lamella has a basement membrane, and sometimes the blood sinus can be seen extending up between the two layers of a lamella from where it lies, contained externally by the muscular coat. Occasionally, flattened nuclei may be seen in the sinus in the lamella, lying on the basement membrane bounding the sinus on one or other side, or between the two cell layers of a lamella if the sinus does not exist or is only potential there. When first established there are about 14 tunnels on each side, 28 in all.

Each lamella is now the partition between neighbouring tunnels; it contains in its axis, potentially at any rate, an extension of the gut sinus, which lies primarily internal to the muscular layer of the alimentary tube; and by the fusion of the central ends of the lamellæ a layer of epithelium lining the lumen of the œsophagus has been established, which is no longer directly continuous with the epithelium of the lamellæ.

Meanwhile the tunnels have been encroaching on the dorsal and ventral portions of the œsophageal wall, more rapidly on the dorsal than on the ventral wall; or, in other words, what was called above the œsophagus proper—the portion of the alimentary tube between the lateral pouches—has almost disappeared. Where the œsophagus passes through septum 10/11 tunnels surround the whole except in the mid-ventral line; they are now restricted in height, their section being shortly oval.

The Alimentary Canal in segment xi.—In the next segment after the œsophageal pouches (fig. 12) the œsophageal epithelium has been reconstituted as a definite layer, independent of the tunnels which have been separated off below it. It shows only a slight degree of ridging, and consists of elongated cells, broader at their free surface; their narrower, deeper ends are consequently separated (fig. 13). These deeper ends become divided up, and form, or become part of, a spongy reticulum, with large free spaces, which intervenes between the regular œsophageal cell-layer and the tunnels below. On this œsophageal epithelium rodlets now make their appearance; these constitute a layer of equable thickness, staining only very slightly, and are similar to those described in *Eutyphœus*; they become more distinct in subsequent segments; they never show any transition to cilia, as far as we have observed. The cells have a more deeply staining free border beneath the rodlets; the nucleus appears homogeneous, and not very sharply distinct from the cell-body.

The tunnels have a beautifully regular arrangement (fig. 12), and are in general much elongated—four to five times as high as broad—but shorter in the mid-dorsal and mid-ventral lines, especially the latter. Occasionally small lamellæ arise within the tunnels, and these, on being followed back, are seen to unite with one of their neighbours, thus splitting into two a previously existing tunnel, and increasing the number of tunnels. In this way a considerable increase in the number is to be accounted for; when first established, in segment x, the number was seen to be about 28, while in front of septum 11/12 it has risen to between 60 and 70 (69 lamellæ, including one or two incomplete ones); this number is maintained approximately (64 lamellæ in segments xii and xiii) throughout the rest of the gland.

The cells of the tunnels are more or less cubical; the protoplasm is homogeneous, and stains more lightly than that of the cells lining the œsophageal lumen; the nuclei are ovoid; and there is a very evident basement membrane to the layer. The end of the tunnel, which is towards the œsophageal lumen—which may be called its roof—is sometimes closed by a flattish cell (fig. 13, *y*); but often the roof is indefinite, and the cavity of the tunnel appears to be in communication with the loose spongy space which intervenes between the layer of tunnels and the layer of œsophageal epithelial cells (as at *x*). This space is merely crossed by fine trabeculæ with occasional nuclei.

In each lamella is a blood sinus—an extension from the general gut sinus which lies within the muscular coat external to the tunnels; the lamellar sinuses, which may be potential only, are bounded by the basement membrane of the cell-layers, and are dilated at the central ends (towards the œsophageal lumen) (*int.*, fig. 13). The basement membrane is always complete round the inner ends of the sinuses, though the protoplasmic layer may be thin—merely an extension from the central ends of the cell-layers of the lamellæ, or even only a portion of the spongy reticulum beneath the epithelial layer of the œsophagus. These internal dilatations are oval in section; the junctions of the sinuses in the lamellæ with the outer, or general gut sinus, are triangular (*per. sin.*, fig. 13).

Nuclei are occasionally seen in the sinuses of the lamellæ—flattened against the basement membrane of the epithelial layers, and almost unaccompanied by protoplasm (*n.*, fig. 13); or, it may be, more ovoid in shape and accompanied by a certain amount of protoplasm. Much flattened nuclei may be seen, without any protoplasm, between the two layers of basement membrane in the axis of a lamella, where the sinus is only potential. Nuclei, flattened or rounded, and without or with accompanying protoplasm, are to be seen in numerous places on the wall of the general gut sinus between the layer of tunnels and the muscular coat of the œsophagus; but these are very far from forming a continuous investment.

The Posterior Portion of the Gland.—The tunnels become lower in the next segments (xii and xiii), and lower still in xiv; they disappear altogether in front of septum 14/15. In the hinder part of the gland the epithelial lining of the œsophagus becomes regularly ridged longitudinally once again.

The lumina of the tunnels are small, and their roofs (toward the œsophageal cavity) are more often definitely closed by the opposition of the cells constituting their sides. The nuclei between the two layers of a lamella are few.

There is no evident communication between the cavities of the tunnels and that of the œsophagus in the posterior part of the gland; we cannot definitely state that there is no possible passage from the one to the other, as a few sections are damaged. The point is again referred to further on.

The Adult Helodrilus caliginosus.

A series of transverse sections of a specimen fixed in sublimate and acetic acid, and stained in Delafield's hæmatoxylin and eosin, was compared with the above. The structure is identical with what has been described already, except in a few details.

The epithelium in the anterior half of the œsophageal pouches is more ridged than in the young example; and the cells here are more markedly columnar—more like those of the œsophagus proper, the nuclei being oval to rod-like. The nuclei of the cells, however, stain less deeply, and so are not so sharply differentiated from the cell-body, compared with those of the proper œsophagus.

The roofs of the tunnels are closed by a cell; or by extensions of the cells at the sides of the tunnels which fuse together over the roof; or by an indefinite fibrous or granular extension of the sponge-work of the deeper layers of the œsophageal lining; or, finally, the roof may not be completely closed, and the cavity of the tunnel may apparently communicate with the spaces of the loose sponge-work just mentioned.

The central ends of the sinuses in the lamellæ are dilated, as in the young example; but here the dilatation is triangular in shape, not oval; the base of the triangle, which is towards the œsophageal lumen, is broad, and the angles of neighbouring triangles may almost meet; so that, under the low power, the straight and almost continuous bases of the triangles simulate, all taken together, a continuous basement membrane of the œsophageal epithelium.

Towards the hinder end of the gland, where the œsophageal epithelium has again become regularly ridged, the loose reticulum beneath it disappears, so that the whole epithelial layer becomes denser in its texture; the intervals between the neighbouring angles of the triangular dilatations of successive sinuses are necks through which the epithelium of the œsophageal lumen is continuous with the epithelium of the tunnels. The whole extends to the hinder end of segment xiv.

There are no definite openings of the tunnels into the œsophageal lumen; there are, perhaps, very occasionally in segments xi and xii indications of the possibility of a communication; but these passages resemble, and may actually be, accidental breaks in the continuity of the œsophageal epithelium, and appear to us to be of no morphological importance whatever. They quite obviously do not occur in connection with all or the majority of the tunnels, and the tunnels are continued back beyond these breaks.

The number of lamellæ, at one place 62 or 63, become further back 68–72.

Helodrilus parvus.

The anterior part of the œsophageal pouches, in segment x, is almost smooth. Further back, the epithelium of the œsophageal lumen bears very marked rodlets, which come out with extreme distinctness in a chrome-hæmatoxylin stained preparation. These persist to the end of segment xiv; here the canal widens, and the layer of rodlets is replaced by a homogeneous, lightly staining, cuticle-like layer.

The texture of the deeper portion of the œsophageal epithelium is even looser than in the foregoing species; there are large clear spaces, unoccupied even by trabeculæ or strands.

In segment xi there are 27 tunnels, and 30–32 further back; in another specimen 38–44 were counted. The tunnels were not, in any of our specimens, much elongated in a direction radial to the axis of the œsophagus—they were never more than twice as long as broad. The nuclei of the cells of the lamellæ may often be on the free edge of the cell, even forming projections on the surface; a few nuclei are placed deeply in the cell. The roofs of the tunnels are often open, the cavity of the tunnel being thus in communication with the loose space beneath the epithelial lining of the œsophagus; or a wide opening at the top of a tunnel may be spanned by a delicate fluff with nuclei in it. The tunnels are very low in segment xiv, and disappear before the end of the segment; they die away by merging into the loose cells below the layer of œsophageal epithelium.

The inner ends of the sinuses in the lamellæ are always oval in section, not triangular as in the adult *H. caliginosus*, and are always sharply bounded by a basement membrane.

Towards the end of segment xiii there are appearances suggesting the opening of one or a few tunnels into the crypts between the folds of the œsophageal epithelium; but no actual opening could be demonstrated satisfactorily.

The Glands in the Genus Lumbricus.

It has happened that the structure of the glands was by no means so easy to make out in the specimens of *Lumbricus* at our disposal as in those of *Helodrilus caliginosus* and *H. parvus.* This is partly due to the damage caused by calcareous concretions in the case of *Lumbricus*; the glands seem to have been functioning actively, and the œsophageal pouches in particular were much torn in the sections of *Lumbricus* when they came to be examined. The swellings of the œsophagus were more marked in *Lumbricus*, and consequently overlapped from segment to segment, rendering the appearances at first sight rather confusing. The diagrammatic clearness with which the structures were displayed in the case of many or most of our specimens of *Helodrilus*, and the freedom from damage by calcareous particles, has rendered our description of them easy, and it is hoped satisfactory.

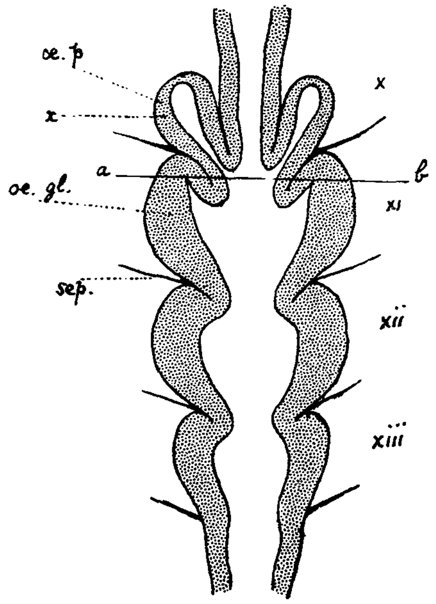
In *Lumbricus* the condition is essentially the same as in *Helodrilus.* In segment x are a pair of subspherical sacs, the œsophageal pouches; in xi are seen a pair of lateral swellings, with somewhat the appearance of stout sausages, applied by their inner curved surfaces to the sides of the alimentary tube; in xii are a similar pair of swellings, of equal size with those in xi; the section of the tube in xiii is somewhat dilated, and subspherical in form, the swelling being general; in xiv the œsophagus is narrower, but at the hinder end of the segment it may widen to form the beginning of the crop. The wall of the œsophagus is longitudinally striated by blood channels in segments xi–xiii.

Microscopically, the epithelial lining of the œsophagus is irregularly ridged and folded in segment ix, in front of the pouches; the ridges become regular and longitudinal in direction as the tube passes through septum 9/10. There is one considerable difference between the pouches of segment x in *Helodrilus* and *Lumbricus*;—the openings of the pouches into the œsophageal tube are at a much more posterior level in *Lumbricus*; instead of opening into the œsophagus by a wide mouth in segment x, the pouches communicate with the œsophageal lumen in the anterior part of segment xi (text-fig. 1), and hence throughout segment x they appear in sections on each side as separate sacs.

Longitudinal lamellæ are present within the pouches over their whole circumference; they are larger on the mesial wall of the pouch, where they extend into its interior so as to take up more than half the transverse diameter of the pouch. The union of the lamellæ to form tunnels takes place, however, only on the outer wall. When this happens, the lamellæ unite, each with its neighbours, at about half their height; and there thus extends for some distance a series of ridges, coexistent with and internal to the series of tunnels, the ridges representing the central halves of the lamellæ and the tunnels being situated between their peripheral portions.

The epithelium of the pouches resembles that of the œsophageal tube; on the surface of the cells in both situations is a fine, completely colourless and non-staining border.

Towards the hinder end of segment x the epithelium of the tunnels changes its character; it becomes cubical, and shows a number of hair-like tags, which soon appear as definite long cilia. In some places the surface of the epithelium is



Text-fig. 1.

merely shreddy. The tunnels begin to elongate; they may now be 18 in number in each pouch.

The anterior part of the dilatation in segment xi bulges forwards so as to overlap the hinder part of the sac in x, and therefore both are cut in a number of sections (text-fig. 1).

The lateral dilatations in segment xi show about 35 tunnels on each side, including those which are incompletely divided by lamellæ which, springing from the periphery, do not reach the œsophageal lining. The mid-ventral lining is free from tunnels. The tunnels are in general much elongated in a radial direction. The cells clothing the lamellæ are in these specimens entirely disintegrated, and have thrown off very numerous globular granules which stain deeply with hæmatoxylin. The fine structureless border of the œsophageal epithelium changes into an irregular layer of rodlets in the hinder part of segment xi.

In segment xii the whole circumference of the œsophagus becomes surrounded by tunnels, which are, however, lower in the dorsal and ventral regions than elsewhere; there are about 50 in the half circumference. The disintegration of the epithelium is, in one of the specimens here described, though not in another, much less than in the preceding segment; the epithelium is approximately cubical, and there are no cilia, and no granules are being discharged.

The tunnels continue through segment xiii, where they are lower. Their epithelium is low, and not disintegrating. The œsophageal epithelium is now longitudinally folded again in a regular manner. Rodlets are present as far as xiii, but are absent in xiv. The tunnels die away in xiv.

The vascular relations of the gland are similar to those in *Helodrilus.*

A notable feature was the occurrence of numerous groups of "chromophil cells," of the same kind as those of the pharyngeal glands, on the œsophagus throughout segments ix and x.

Criticisms of Previous Work.

The papers which will be referred to in what follows are those by Harrington (12), Ribaucourt (21), and Combault (6, 7, 8). The latter author has a number of other papers, which, however, are largely physiological, and in part concerned with the circulation through the glands; his paper of 1909 (8) is to some extent a summing up of his results, and repeats much of his earlier communications.

A word on the position of the glands to begin with: Ribaucourt nowhere mentions their situation; Combault invariably places them one segment behind their proper position—the first pair of swellings, the œsophageal pouches, in xi, whereas they are in x.

It has been shown above that the glands (*i.e.* the tunnels) and the œsophageal lining membrane together constitute the epithelial layer, and (except the blood, which bathes the bases of the cells) no other constituent of the wall is present from the lumen of the gut outwards as far as the so-called external sinus. Combault therefore mistakes the constitution of this part of the tube when he writes of the glands as "un véritable manchon œsophagien . . . creusé dans le tissu conjonctif qui sépare l'épithélium œsophagien de la couche musculaire," or of "une couche de tissu conjonctif fasciculé où sont logés les sinus internes" (*i.e.* the dilated inner ends of the sinuses in the lamellæ); in this tissue one is supposed frequently to meet with muscular fibres. On what we believe to be the true view of the morphology of the glands there is no place for either muscular or fibrous tissue in this situation.

Before mentioning Harrington's view of the origin of the glandular epithelium, it is necessary to allude to the process of secretion as described by him. The cells of the glandular layer are irregular, and give an irregular appearance to the layer. After an active wave of secretion the cell projections may almost entirely disappear, being levelled by disintegration to the general surface. The cells form a syncytium, being fused at their bases; in a secretory cycle the protoplasm at first increases, so that the cells project as club-like processes; lime granules appear in the interior, the cytoplasm degenerates and the granules are thrown out; the cytoplasm in the cell projections is nearly all used up, and if there has been over-secretion the cytoplasm disappears almost down to the blood sinus;—"in its lowest terms . . . the secreting layer is very thin, and may be reduced . . . to the thickness of an ordinary blood-vessel scarcely the width of the nuclei which are embedded in it" (the meaning is not very clear). The nuclei also collapse or become cast out into the gland cavity during active secretion, exhaustion of the nucleus running parallel to exhaustion of the cytoplasm; indeed nuclei may be scarcely visible through loss of staining power, and may be distinguishable only by the inconspicuous nuclear membrane.

Now comes the peculiarity of HARRINGTON'S position. The nuclei are replaced by others which migrate from the blood sinus into the glandular layer; nuclei are seen in every possible position between partial and complete embedding in the glandular syncytium; "repeated observations have demonstrated beyond a doubt that these wandering cells or migratory nuclei are constantly and normally making their entrance into the gland cells at certain periods of the gland's activity." These migratory nuclei are attended by a thin protoplasmic film; they may be of the most extraordinarily elongated forms; the cytoplasm which is brought in fuses with the general syncytium, and the nuclei then become the typical nuclei of the glandular layer. Thus what happens is that "wandering cells migrate into an enlarged blood-vessel wall and undergo degeneration, during which the accompanying cytoplasm expands and is finally transformed into lime crystals."

And again: "The cells, which here replace the waste caused by secretion, are derived from the walls of the blood-vascular system. The unusual relations between the glandular and circulatory systems can be interpreted only by regarding the one-layered secretory lamellæ bounding the blood spaces as greatly hypertrophied vascular walls representing both the intima and endothelium."

The follicles are therefore an enlarged blood-vessel wall. It is true that the germ-layer theory seems to stand in the way; but according to HARRINGTON'S observations, the earliest blood corpuscles in the embryo, as well as the follicles themselves, are derived from the mass of yolk cells surrounding the cavity of the gut, and hence corpuscles and follicle cells have the same ultimate origin.

Such is HARRINGTON'S conception of the glands. In criticism it must be remarked that unless "an enlarged blood-vessel wall" is used in a sense very different from the usual one, the expression is wrongly applied to the follicular epithelium. In cases where a vascular endothelium has been described, it is a layer of naked cells lying on a basement membrane, outside which again is the muscular (or muscular and connective) coat of the vessel; here the basement membrane would be the innermost layer, and the endothelium would be outside this. But that the follicular epithelium cannot be anything to which the term blood-vessel can properly be applied is evident from the fact that it is absolutely continuous with the epithelium of the œsophageal pouches, and so with the œsophageal epithelium itself. If it were necessary to go further, the constitution of the glands in other families would be sufficient as proof of the identity of the epithelium of the follicles and of the œsophageal lining.

We entirely disagree, therefore, with HARRINGTON when he says: "It must be repeated that the first pair of glands are entirely different morphologically from the two posterior pairs, and are the only portions of the glandular œsophagus which are true epithelial diverticula." The difference is one of detail only; the ridges of the œsophageal pouches are, in the anterior part of their extent at least, parallel to and independent of each other; further back they fuse at their free edges and so form a series of tunnels, the so-called follicles of the œsophageal glands of segments xi–xiv;—that is all.

The same idea runs through the work of COMBAULT: "L'histologie de l'adulte et de l'embryon me semble montrer que le tissu des glandes de Morren est d'origine mésodermique vasculaire." The difference between the glandular cells and a vascular endothelium is due "avant tout" to a difference of technique; if one fixes by acid reagents (Bouin's solution) the cells, where not destroyed, "presentent assez bien l'aspect de l'endothélium vasculaire avec lequel elles semblent se continuer"; and in *Phœnicodrilus taste*, as described by EISEN, we actually do find the glandular cells represented by "un endothélium aplati très mince rapellant bien l'endothélium vasculaire." There is nothing here that requires further comment however.

COMBAULT'S views appear to have undergone some change during the progress of his series of papers; thus in a later paper he says that "chaque feuillet est lui-même constitué de deux assises—l'endothélium vasculaire et l'épithélium branchial." He is speaking of the lamellæ of the gland, which he looks on as a respiratory organ, and here states that in addition to the respiratory (*i.e.* glandular) epithelium there is beneath it a vascular endothelium; the glandular epithelium is not therefore a vascular endothelium. This view is, however, no more admissible than the first; it predicates two cellular layers on each side of the blood film in the lamellæ, whereas, as we have seen, there is universally only a single layer bounding the gut sinus on its inner side—the layer of the alimentary epithelium. That there are nuclei on the basement membrane, bathed by the blood stream, is undeniable, but they do not form an endothelial layer, and are in no sense a vascular endothelium. COMBAULT also begins to have doubts as to the mesodermic origin of the glandular epithelium: "Il est d'ailleurs très difficile d'affirmer d'une façon précise de quel feuillet embryonnaire dérive l'organe de Morren." It is, however, his first view—that the glands are mesodermic—that has been laid hold of by the author of the elementary textbook quoted in the Introduction, and that, more than anything else, we wish to oppose.

One of COMBAULT'S statements deserves a word of notice; he says: "Déjà

Beddard, au cours d'une étude sur les Eudrilides, s'etait refusé d'admettre la nature épithéliale des glandes de Morren, et voulait y voir des 'glandes vasculaires sanguines.' . . ." This is misleading. BEDDARD (1) speaks of the glands of the Eudrilidæ as being homologous with the ordinary calciferous glands, and as consisting of a mass of cells in which is a small lumen communicating with the œsophagus; the mass of cells is probably peritoneal in origin, and has increased in amount *pari passu* with the reduction of the glandular secreting surface. These glands must "be referred to the same category as the calciferous glands of other Oligochæta"; though their structure "seems to be irreconcilable with any other theory than that the glands in question have some secreting function in relation to the blood or eliminate effete matters from the blood; we have in fact a gland originally performing a function connected with alimentation converted into a quite different physiological path, and one which must bear some relation to the vascular system." BEDDARD had no doubt whatever of the origin of Morren's glands (the calciferous glands of the Lumbricidæ) or of any other calciferous glands from the œsophageal epithelium; though with overgrowth of the peritoneal covering the glands of the Eudrilidæ have now, apparently, taken on a different function from the original one.

HARRINGTON'S statement that the disintegrated cells are replaced by nuclei with a thin protoplasmic film, which make their way into the epithelial layer from the blood sinus, is rejected by COMBAULT. The latter author never found, in "quelques milliers de préparations," appearances recalling those figured by HARRINGTON, though he did observe diapedesis, due to irritation resulting from a too acid diet. (HARRINGTON had fed some of his worms on acid starch, or had kept them in water acidulated with lemon juice.) The definiteness of HARRINGTON'S statements, the number of his figures, and the evident care with which they have been drawn, are such that we do not think we are entitled to reject his account of the replacement of the cells forthwith. Somewhat similar cases of wandering nuclei are not unknown. ROHDE (22) finds nuclei of neuroglial origin within the ganglion cells of a number of Invertebrates, and refers to their having been recognised also in Vertebrates (*Delphinus delphis*); many cases of the fusion of follicle cells with growing ova are known—though here it is whole cells rather than nuclei that enter and fuse; the entry of supernumerary spermatozoa with, in many cases, the persistence of the additional male pronuclei, and the exchange of nuclei in the conjugation of Infusoria, are interesting analogies. ROHDE concludes: "Wahrscheinlich kommen in Tierreich gleich selbständig sich bewegende und wirkende Kerne, wie es die von mir beschriebenen Kerne der grossen Neurogliasyncytien sind, viel häufiger vor, als allgemein angenommen wird. Bekannt ist, dass junge Leucocyten selbst bei starker Vergrösserung einen Protoplasmaleib nicht erkennen lassen." Though HARRINGTON speaks of a thin protoplasmic film in these wandering cells, he usually calls them migratory nuclei; in the figures they are designated as such, and the protoplasmic film is absent or at least extremely delicate.

The supposed Posterior Openings of the Glands.

According to HARRINGTON, some of the secreted calcareous particles pass backwards in the tunnels, and break through the œsophageal epithelium into the digestive tract in segment xiv; this second outlet for the escape of the secretion has, he adds, not attracted the notice of previous workers. If the œsophagus be carefully opened along the mid-dorsal line, the milky fluid containing the calcareous particles may be seen issuing into the digestive tract from pit-like indentations in the side walls of the œsophagus just in front of the crop. According to COMBAULT, the second pair of orifices, discovered by HARRINGTON, are invisible to the eye and to a lens: "nous ajoutons que nous n'avons pu la délimiter nettement que sur les coupes en serie; on ne peut la voir qu'au microscope à dissection, mais sur une simple vivisection on se rend très bien compte de son existence à l'œil nu et mieux à la loupe par la fine trainée de liquide troublé qui s'en échappe."

We have previously explained that we have never, in numerous series of sections, been able to satisfy ourselves that such openings definitely exist; ruptures, quite possibly artificial, may occur in the epithelial lining of the œsophagus, and in this way the tunnels may be in communication with the œsophageal lumen. For example, a crack in the lining epithelium of the œsophageal lumen, in fig. 13, would place one of the tunnels in communication with the lumen. Such ruptures may possibly occur at times when the tunnels are full of secretion during life, and would be not unlikely to occur when the œsophagus was opened and its interior displayed, owing to the transverse stretching to which the epithelium would be subjected. It is in this way that we think the appearances of the escape of milky fluid from the hinder end of the glands, as seen by both HARRINGTON and COMBAULT, are to be explained. In any case there is no question of the whole, or the majority, of the sixty or so tunnels being in communication with the œsophageal lumen at their hinder ends—but merely of an occasional one here and there which bursts, so to speak; and COMBAULT's description of the glands as "un organ unique, cavité periœsophagienne ouverte aux deux bouts" is altogether inadmissible.

An appearance which we met with only in *Lumbricus* in our own preparations, and which is described and explained by CLAPARÈDE and COMBAULT, is the presence of a double circle of tunnels in some sections, one within the other. This led RIBAUCOURT to the mistaken idea of a continuous internally-placed series of tunnels and, superposed on this, a separate series in each of the segments occupied by the glands. The condition may be illustrated by text-fig. 1; it is a simple consequence of the bulging of the glandular mass between the septa, and its restriction at the sites of the implantation of the septa; a section taken along the line *a b* will evidently cut a double or even treble series of tunnels, which will appear as concentric circles. This external lobulation of the glands is very variable, even in the same species, as COMBAULT remarks: and he is quite right in maintaining that there is one single organ extending from end to end. Differences in the degree of lobulation had previously been shown for a considerable number of species by Ribaucourt.

Combault's main thesis is that the glands are respiratory organs; and though the present communication does not deal with the physiology of the glands, a few remarks seem called for on this subject. A primary contention is that the earthworms are really aquatic; "les lombrics sont en fait des animaux aquatiques au même titre que tous les animaux qui respirent dans la vase"; "les 'vers de terre,' ne pouvant vivre que dans la terre humide, s'accommodent très bien du régime purement aquatique, et, périssant à la moindre sécheresse, doivent être considerés, au point de vue respiratoire, comme des animaux aquatiques." The epithelium of earthworms is compared with that of the frog as a respiratory organ, to the disadvantage of the former; "l'épiderme est recouvert (in the earthworm) d'une cuticule très épaisse . . . l'épaisseur de la cuticule vient encore s'opposer aux échanges gazeux." Or again, "il suffit d'ailleurs, à notre avis, d'étudier la structure des téguments d'un Lombric, pour être persuadé de l'impossibilité d'une respiration uniquement cutanée."

Respiration takes place, according to Combault, by the aspiration of water into the œsophagus: "Des mouvements musculaires continuels aspirent et chassent l'eau dans une chambre œsophagienne, située en avant de l'organe de Morren." The presence of the glandular tissue in the substance of the œsophageal wall causes a narrowing of the œsophageal lumen, so that the water is forced to traverse the gland (*i.e.* the tunnels of the gland): "Les organes autrefois décrits sous le nom de glandes digestives de Morren constituent en réalité une chambre branchiale peri-œsophagienne; il s'agit d'un veritable manchon œsophagien communiquant avec l'œsophage à ses deux extremités par deux paires d'orifices. Ce manchon creusé dans le tissu conjonctif qui sépare l'épithelium œsophagien de la couche musculaire produit un rétrécissement de l'œsophage qui force l'eau à les traverser."

The glands are therefore gills—internal branchiæ; and "leur aspect est tel qu'ayant montré ces coupes à des histologistes sans leur donner aucun renseignement sur la provenance, ils prononcèrent tous le nom de 'branchies.'" This comparison leads the author to certain revolutionary morphological ideas; the insertion of the septa into the glands represents a first hint of the branchial arches of Vertebrates: "L'insertion des dissepiments semble chez les types évolués pénétrer l'organ de Morren et les lamelles branchiales sont en quelque sorte soutenues par un arc de tissu conjonctif, véritable ébauche d'arc branchial." Or again: "Nous tenons dès maintenant à rapprocher l'organe respiratoire des Lombrics, des glandes en T des Scyllidiens, et surtout de la corbeille branchiale de l'Amphioxus . . . la corbeille branchiale de l'Amphioxus peut être rapprochée de l'organe branchiale de Morren: par sa forme, par sa situation, par sa fonction et enfin par son aspect histologique. Un coup d'œil jeté sur une coupe passant par la corbeille branchiale de l'Amphioxus évoque aussitot le souvenir des coupes passant par l'organe de Morren."

These latter expressions of the author's views scarcely require criticism. With regard to the former—earthworms as aquatic animals—while some certainly can and do live in water or mud, and others in damp earth, a number even among the Lumbricidæ can endure a considerable degree of dryness. According to Szüts (29), though *Allobophora* lives mostly in damp soil, it may be found under very various conditions; *Eiseniella* is found in damp or swampy meadows; *Eisenia rosea* may be found in luxuriant garden earth, and also in less nutritive loamy soil, or even between the stones of pavements in towns; *Lumbricus* and *Octolasium* can live on high mountains, and in stony, sandy, siliceous or loamy earth. The idea of a current of water passing through the glands (even were there a definite opening at the hinder end) may be dismissed as fanciful.

Summary and Conclusions.

(1) The calciferous glands of earthworms were rightly interpreted by the older authors as foldings of the œsophageal epithelium. The simplest condition is that where there occur slight segmental bulgings of the canal, within which are a number of transverse folds of the epithelium.

(2) In many forms the bulgings become diverticula, with wide or narrow mouth. The extreme form under this head may be seen in, for example, *Octochætus barkudensis*, where the glands are large lobed sacs, in the interior of which are numerous thin lamellæ extending nearly across the lumen; the sacs communicate with the œsophageal canal only by a narrow neck or "duct."

(3) The condition in *Eutyphœus* may be considered to have arisen from the fusion, along their edges, of a series of parallel epithelial lamellæ, transverse in direction, on each side of the œsophagus. The interlamellar spaces are here open above near the dorsal wall of the œsophagus, but are closed below by the ventral œsophageal wall. The glands here cause but little external swelling, being as it were withdrawn within the œsophageal wall. This is the end term of a type of evolution which starts with simple transverse lamellæ.

(4) The condition in the Lumbricidæ originated in a series of longitudinal lamellæ. The mode of evolution has been comparable to what has happened in *Eutyphœus*—the inner edges of the lamellæ have fused. In this way a series of longitudinal tunnels has been formed, in and part of the epithelial coat of the œsophagus, and entirely within the muscular coat. These tunnels open in front, where the longitudinal folds begin, into the œsophageal pouches in segment x; they become progressively smaller, and cease in xiv without posterior openings.

(5) The epithelium of the glands is in all cases continuous with that of the œsophagus, and comparative anatomy shows that the various forms of glands are essentially due to various forms and degrees of complexity of the epithelial folds. The glands are therefore not mesodermal in origin, and are not merely the walls of blood-vessels, as has recently been contended.

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EXPLANATION OF FIGURES.

a., axis of lamella; *b.m.*, basement membrane; *cil.*, cilia; *crys.*, crystals, probably of calcium carbonate, within the gland; *d.v.*, dorsal vessel; *epi. œs.*, epithelium of œsophagus; *h.*, heart; *int.*, dilated internal end of lamellar sinus; *l.*, lamellæ of gland; *lam. sin.*, lamellar sinus; *l.p.*, lamellæ of œsophageal pouch, here not united to form tunnels; *lum.*, central lumen of œsophagus; *m.*, muscular coat; *n.*, nucleus in lamellar sinus; *œs.*, œsophagus; *œs. p.*, œsophageal pouch; *part.*, vertical partition (in *Eutyphœus*); *perit.*, peritoneum; *per. sin.*, peripheral sinus; *r.*, rodlets; *ret.*, reticular tissue and loose spaces beneath œsophageal epithelium; *sem. ves.*, seminal vesicle; *sept.*, septum; *s.i.v.*, supraintestinal vessel; *t.*, tunnel; *v.*, vessel in dorsal edge of vertical partition; *vent. v.*, ventral vessel; *x*, incomplete roof of tunnel; *y*, flat cell roofing tunnel; *z*, dilated end of lamellar sinus closed in by basement membrane and a thin protoplasmic layer.

Fig. 1. *Pheretima hawayana*; horizontal longitudinal section through the œsophagus in segment xii. × 50.

Fig. 2. The same; cells of a fold of the œsophageal epithelium; formalin, Delafield's hæmatoxylin and eosin. × 570.

Fig. 3. *Ocnerodrilus occidentalis*; transverse section through a calciferous gland, in front of its junction with the œsophagus. × 160.

Fig. 4. The same; epithelium of œsophagus in segment x, behind the entry of the calciferous glands; rodlets well marked; Zenker, Delafield's hæmatoxylin and eosin. × 290. No muscular coat is visible.

Fig. 5. *Octochætus barkudensis*; transverse section of œsophagus with calciferous gland of one side; rodlets on œsophageal epithelium not visible at this magnification. × 130.

Fig. 6. The same; part of calciferous gland, outer wall with lamellæ arising from it. Fixative not known; Delafield's hæmatoxylin and eosin. × 300.

Fig. 7. *Eutyphœus gigas*; dissection of œsophagus in segment xii, which is opened to show the calciferous glands within.

Fig. 8. *Eutyphœus waltoni*; calciferous gland of one side in horizontal longitudinal section. × 40.

Fig. 9. The same; lamellæ of calciferous gland in vertical longitudinal section; formalin, Delafield's hæmatoxylin and eosin. × 145.

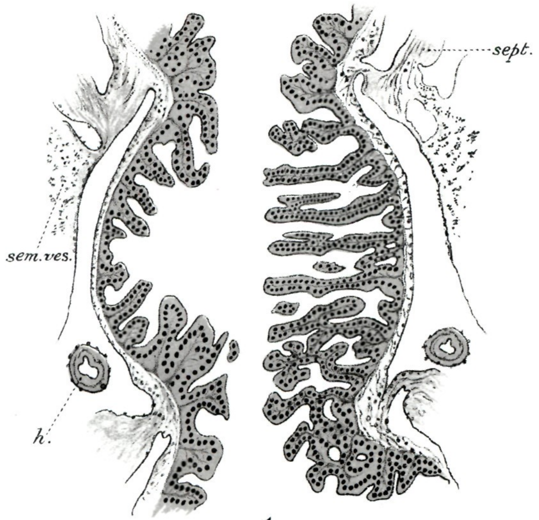
Fig. 10. The same; transverse section of part of calciferous gland, the vertical partition being cut transversely; one or two of the lamellæ are also cut, perhaps owing to the section being slightly oblique; formalin, Delafield and eosin. × 160.

Fig. 11. *Helodrilus parvus*; transverse section through alimentary tube in segment x of a young sexual specimen. The section is slightly oblique, and therefore shows a slightly different level on the two sides; on the right the section passes through the œsophageal pouch anterior to the appearance of prominent lamellæ; on the left lamellæ are present, which below are fusing together to form tunnels. Fixative not known; van Gieson's stain. × 180.

Fig. 12. *Helodrilus caliginosus*; transverse section through œsophagus of a young specimen in segment xi; tunnels established, rodlets as a fine border. Formalin, Delafield and eosin. × 125.

Fig. 13. The same; a portion of the œsophageal wall more highly magnified. Same preparation. × 550.

J. Stephenson and Baini Prashad: Calciferous Glands of Earthworms.



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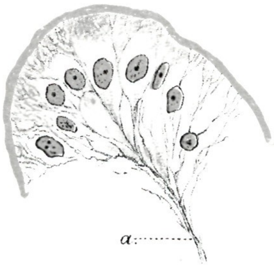

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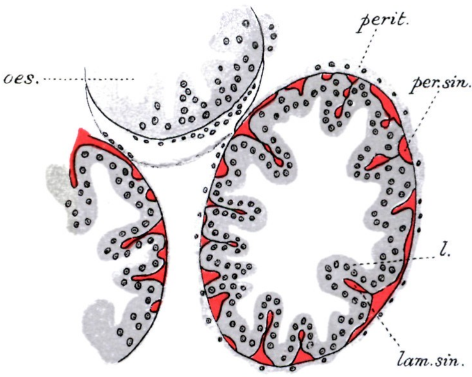

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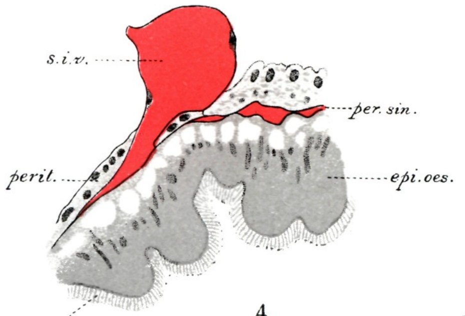

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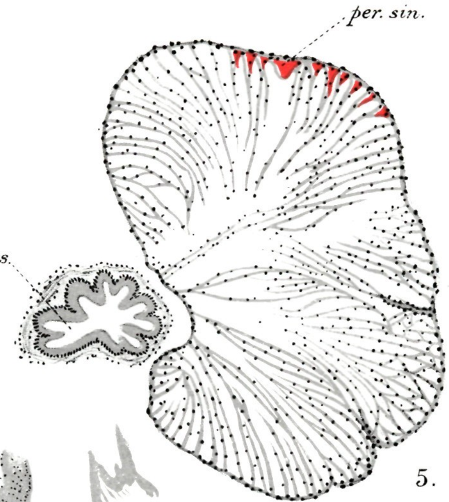

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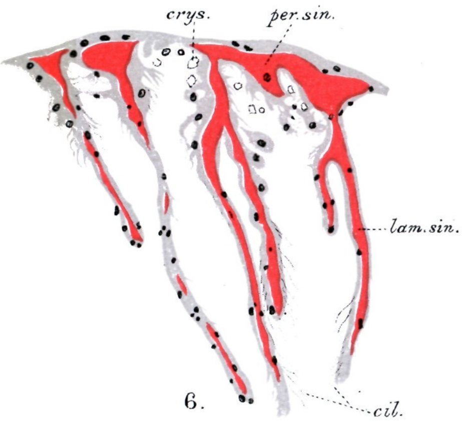

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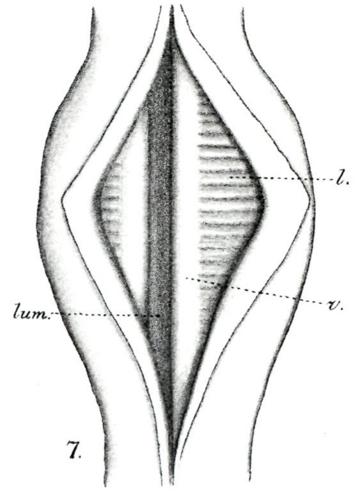

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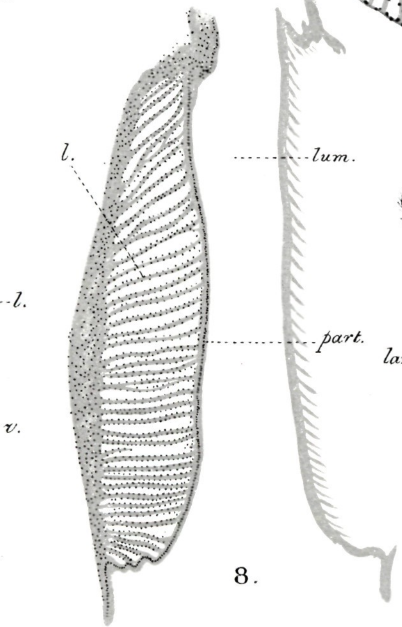

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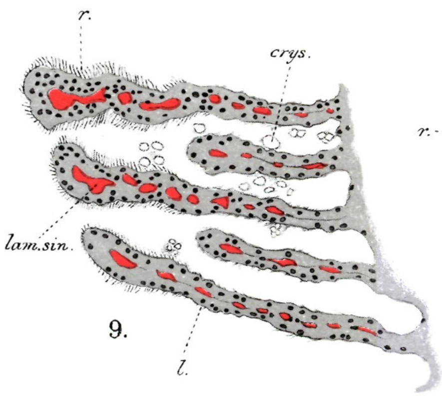

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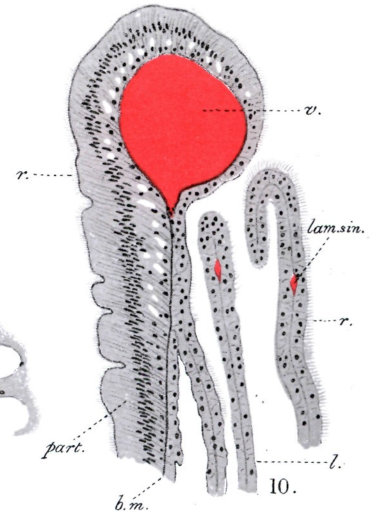

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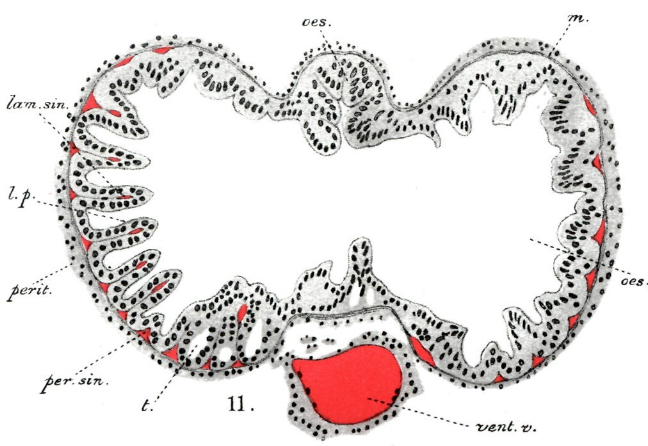

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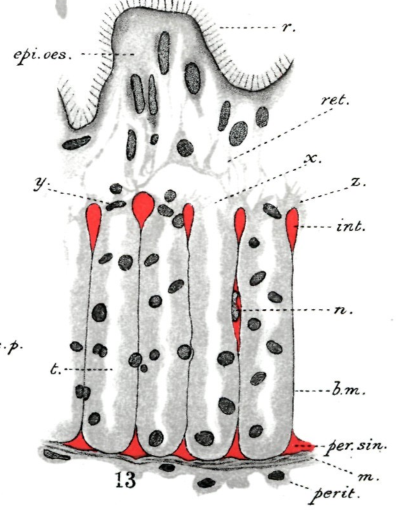
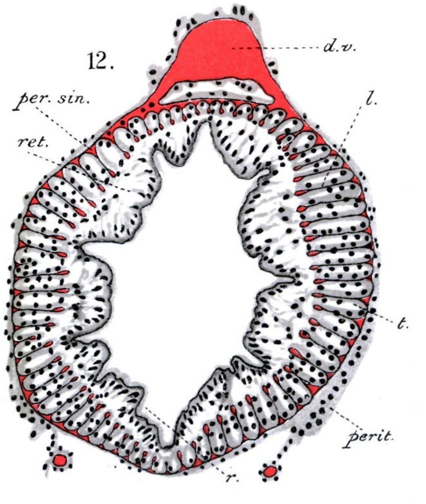


13



12.