ON DIGESTION IN HYDRA; WITH SOME OBSERVATIONS ON THE STRUCTURE OF THE ENDODERM. By M. GREENWOOD, *Girton College, Cambridge, Demonstrator of Physiology, Newnham College.* Plates VI. and VII.

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In the *Archiv für Mikros. Anat.* XXIX, Nussbaum published a paper on the "Divisibility of Living Substance." In this paper, after reviewing the specific characters of Hydra as described in the writings of earlier workers, he distinguished among such specimens as are destitute of chlorophyll, *Hydra fusca, Hydra grisea,* and the straw-coloured Hydra (*H. attenuata,* Roesel). Such characters as colour, the number of tentacles present, sharp or gradual passage of the Hydra's body into its narrower, paler foot formed the basis of classification.

When I began to make the observations which have led me to write this paper Nussbaum's account had not appeared, and I did not record the differences which existed before death in the specimens of Hydra which I examined. Since this is the case and since, further, I have been unable in later investigation to associate any certain variation in structure with variation in number of tentacles and in depth of tint, I apply the name *Hydra fusca* alike to forms which are bright brown or very dark brown, which have six, seven or eight tentacles and which taper gradually to their basal point of attachment—the sucker—or exhibit a cylindrical body and a well-marked narrower columnar foot. I do this with the greater confidence since Nussbaum[1] after describing the characters of the endoderm of *Hydra grisea* adds that in the case of *Hydra fusca* the structure is on the whole the same.

In the living membrane of the body cavity of any brown specimen of Hydra it is generally comparatively easy to distinguish two sorts of cells—the larger vacuolate endoderm cells with amoeboid ends and

[1] M. Nussbaum. *Archiv f. Mik. Anat.* XXIX. 1887.

retractile cilia, and, lying singly between groups of these, smaller cells destitute at all times of the vacuoles which form so conspicuous a feature of the endoderm generally, and (as far as I have seen) without amoeboid movement. Many descriptions of the larger vacuolate cells are given by various observers, since the time of Leydig (1854); it is only Nussbaum[1] and Jickeli[2] I believe who have described and figured cells of two kinds. To the smaller elements of the endoderm both observers give the name of *gland cells*; but while Nussbaum describes their appearance as varying in different specimens and therefore hints at the performance of correlated function, he brings forward no experimental evidence of their glandular nature, and such evidence is wanting in Jickeli's account. I may say at once that I shall have to record observations which seem to support the view that, during digestion especially, active secretory processes go on in these cells. And therefore, although these observations must be weighed against others not clearly in harmony with such an hypothesis, or not best explained by it, I keep the phrase used by Nussbaum and Jickeli and speak as they do, of *gland cells.*

Let me describe in some detail the points in minute structure which strike the observer of these two endodermal elements, and after such description deal with the manner in which they line the body cavity of Hydra and with local modifications found in the foot and round the lip.

Vacuolate endoderm cells. In the larger endoderm cells (Plate VI. *E* figs. 1, 2, 3, 4, 6) one may distinguish structural features which are relatively permanent, and others which slowly come and go. Thus cell substance, a nucleus with at least one well-marked nucleolus, and fluid forming a vacuole or vacuoles are discernible whatever the condition of the animal examined; they are not however always obvious, for changing circumstances bring one or another into relative prominence. Among the temporary constituents of the cell we may distinguish the brown or black pigment, and certain spherical deposits of proteid, probably of the nature of reserve material.

1. *The Cell substance* forms the external layer of the cell; it is somewhat massed towards the attached base, and more so at the free border which I will call the apex, here giving rise to a fairly conspicuous semilunar accumulation. (Fig. 1, Plate VI.) Bridles of cell

[1] M. Nussbaum. *Op. cit.*
[2] C. F. Jickeli. *Morpholog. Jahrbuch.* Bd. VIII. 1883.

substance, such as commonly pass from the perinuclear protoplasm of a vegetable cell to that layer of substance which lines the wall, are rare in the endoderm of Hydra, for the nucleus is excentric in position and projects inward from one lateral wall, but the apical mass of protoplasm in its inner part may be honeycombed by small vacuoles (fig. 1, *V*). It is in this apical mass that the slight power of amoeboid movement possessed by the cells becomes manifest, and in specimens examined in the fresh state it is exhibited by the formation of blunt hyaline projections which arise from the apex of each cell and are never probably more than one-fourth of the depth of the aggregation of substance from which they spring. Retractile cilia may also be given off from the endoderm into the body cavity, one or two taking origin in each cell. I do not believe that they co-exist with the blunt amoeboid protuberances, and I have not seen them in living, teased specimens: it may be then that the power of emitting a long cilium is lost with the integrity of the animal, the injury effected by rupture allowing only the formation of a lobate projection. (I ought to add that Nussbaum[1] describes the occurrence of ciliary action for some ten minutes after teasing a fresh Hydra, and says that later only blunt pseudopodia are formed.) That part of the protoplasm of the endoderm cell which is not immediately concerned in the putting out of a projection is, in the fresh state, very faintly granular, while the region which moves is hyaline; this differentiation is not however made permanent by hardening reagents, and I am unable to make any very definite statement of the nature of the structural details brought out by their action. The cell substance appears to me, after hardening in Flemming's fluid (and this is the reagent which gives the most satisfactory results), to show rather coarse and irregular granularity. While saying this I must add that no definite rounded granules occur; the appearance which greets one might indeed be ascribed to the presence of short fine fibres lying in many planes, or might even be taken as indicative of the existence of an inadequately defined, irregular network.

Two points in the disposition of the protoplasm of an endoderm cell remain, and demand notice. In the first place part of the substance of the lateral wall may bulge internally, forming spherical projections shaped after the fashion of those which hold the nucleus in place, and these at times enclose solid bodies,—the constituents of the cell to which

[1] M. Nussbaum. *Op. cit.*

I have already alluded as relatively temporary in their nature, and which I shall presently describe in detail. In the second place such spherical bulgings may exist and hold no solid matter but apparently a fluid; in this case they are apical rather than lateral in origin and project down into the main vacuole. (Fig. 2, *v*, Pl. VI.)

Thus we have in each endoderm cell an external sheath of substance with slight basal accumulation and more marked apical gathering bounding a central vacuole. Further, this substance displays great extensibility, and may gather fluid into itself to form scattered vacuoles, or may send out internally local extensions of itself which act as investments for solid particles of foreign matter.

2. *The Nucleus.* The nuclei of these endoderm cells are generally conspicuous, and hold at least one well-marked nucleolus. The nucleoli seem constantly dense and homogeneous in specimens hardened in Flemming's fluid or macerated in this fluid greatly diluted; the substance of the nuclei on the other hand shows, after the application of these reagents, irregular granularity, much like that displayed by the substance of the cell.

The nucleus is found most commonly in the lowest third of each cell bulging into the vacuole, and is bounded internally by a thin pellicle of protoplasm; occasionally however it may lie quite near the base, or again may be displaced apically. (Figs. 3, 6, nuc. Pl. VI.) The changes of position which come about in the nucleus and in any other solid bodies which may happen to be present in the endoderm appear comparable to the movements of chlorophyll corpuscles in the protoplasm of a plant cell under the stimulative action of considerable changes in illumination.

3. *The Vacuole.* In the foregoing statements, while I have wished to deal only with the cell substance and nuclei of the endoderm of Hydra, it has proved difficult to avoid reference to the fluid which constantly occupies the middle region of each large cell, and forms the third of those cell constituents which I regard as permanent. This fluid varies considerably in amount and not a little in disposition. Typically it exists as a large central vacuole unbroken by bridles of protoplasm, while the nucleus and any other differentiated solid matter which may be present project into it from the base, side or apex of the cell, and are held in place by an investing sheet of protoplasm. Sometimes (fig. 1, *V*, Pl. VI.) however fluid is gathered by the apical cell substance into tiny vacuoles in itself; this is a characteristic appearance during the early stages of digestive activity, and it is at a somewhat later time, that is to

say, after digestive activity has been marked that the total quantity of fluid present is the least. It is actually lessened because (I believe) it contributes to the secretion, which poured into the body cavity effects the solution of ingesta, and it is made especially inconspicuous at this juncture by the accumulation of the products of digestion. During hunger periods, on the other hand, fluid gradually gathers, and it is never so obvious as after long fasting. Thus the impression of marked vacuolation or the reverse which examination of an endoderm cell conveys is the effect of two co-operant factors,—accumulation or loss of centrally lying fluid, and presence or absence of the temporary constituents of the cell.

I pass now to the consideration of these temporary elements and, accepting for purposes of discussion the division I have above indicated, classify them as *nutritive spheres*, and grains or masses of *pigment.*

4. *Nutritive spheres.* These are figured at *n* in figs. 2, 3, 5, 6, 7, Pl. VI. and have been previously described, though with marked brevity, by all writers on the structure of Hydra. They are spoken of as "angular and rounded colourless bodies," as "colourless round or oval dense albuminous corpuscles," as "large pale globules occurring both in old and young animals but not in all specimens of any age;" and they are regarded by some writers as the colourless equivalents of the chloroplastids of *Hydra viridis.* Jeffrey Parker[1] may perhaps refer to them when he says that in a Hydra in full digestion the endoderm cells of the gastric region are "completely crammed with transparent spheroids."

These bodies vary in number and alter in appearance, in fact they pass through phases of deposition, of perfection, and of breaking down. I believe that only consecutive observation will adequately reveal the relation of these phases, while, at the same time, in ignorance of this relation the conception that can be formed of the sum of metabolic processes which make up the life of Hydra is but imperfect. I propose to describe the spheres as they appear and react when fully formed, and then to bring forward what evidence I have been able to gather of the nature of their building up and of the changes they undergo when being broken down.

a. Nature of the nutritive spheres. They occur typically at the sides and base of the vacuolate endoderm cells, and are solid and, in the fresh state, highly refractive and apparently homogeneous. When hardened they stain readily with borax carmine, picrocarmine and

[1] T. Jeffrey Parker. *Proc. Roy. Soc.* xxx. 1880.

haematoxylin, and their substance colours uniformly throughout; they do not reduce silver nitrate and are less stained by appropriately applied gold chloride than is the cell substance which surrounds them. Osmic acid brings about slight swelling and colours the spheres a pale yellow brown; they keep their homogeneous appearance however in this reagent, and it is only on one or two occasions that I have thought discriminative fractional solution might possibly show some complexities of structure. Thus 10 per cent. solution of sodium chloride breaks down the spheres, but does not dissolve all their substance, for a highly refractive myelin-like mass remains where a group of them existed before application of the reagent. On the other hand, in some strengths of some acids there is loss of homogeneity and indication of a sponge-like structure, normally supporting and made inconspicuous by the highly refractive element which the acid alters or dissolves. Apparently the spheres are proteid in nature; with iodine they colour less readily than does the cell substance in which they are embedded.

b. Origin of the spheres. We have to ask next, if not always present, under what conditions do they occur? They are very plentiful in well-nourished cells, or in cells that have reached the end of a period of digestive activity; they are on the other hand few in number, and indeed may be absent after long hunger. They form an index to the state of nutrition of the Hydra and seem to be present as a result of the ingestion and digestion of food. The exact manner in which they take origin from this becomes therefore a matter of interest, for it is conceivable that nutritive substance should be broken down in the body cavity into small spherical masses and that these should be subsequently ingested, or that there might be an initial absorption of substance in solution and succeeding precipitation or deposition in the form of solid spheres. That the endoderm does retain its power of ingesting solid substances, at any rate to a certain extent, is indicated by the presence of coloured fat drops in it during digestion when such particles happen to form a structural feature of the prey, and I certainly have seen in organisms undergoing digestion small masses of matter resembling the nutritive spheres, which were to be detected at the same time within the endoderm cells. There is however evidence, as I think weighty evidence, in favour of the view that the ingestive power possessed by the endoderm is usually potential rather than actively exerted,—that nutritive matter makes its entrance into the substance of the animal in a state of solution. This evidence is partly indirect and partly afforded by actual observation of the cells during the performance of a digestive act. Considering first the indirect evidence, we find that spheres are present in the tentacles and the foot of Hydra. Now the foot contains that extension of the body cavity into which an ingested animal never enters, and though it may be urged that formed masses of nutritive substance might be passed off from the main body of the prey, and ultimately by ciliary action or by a sort of peristaltic movement of the body walls come into the neighbourhood of the foot cells, I can only say that while a mass of faintly granular matter, staining but slightly, may during digestion fill the foot, I have not seen in such a mass actual dense spheres or even marked local accumulation of substance. In the same way the tentacles have nutritive spheres stored in their cells, and one can more easily conceive that they are supplied with fluid nourishment than that solid particles are driven into juxtaposition with them, and so held during enclosure. Indeed it seems likely to me that all cilia are retracted during a digestive act. Further, as the faintly staining granular matter to which I have alluded above, be it secretion or fluid nutriment about to be absorbed, is often present in digestion filling the foot of Hydra, so between the cells of the body and the prey (and this is commonly possessed of a well-marked cuticle) lies similar amorphous substance, presumably a precipitate thrown down by the hardening reagent from pre-existing fluid. Lastly, it seems probable (though I cannot yet give this statement great emphasis) that the nutritive spheres are formed whatever the sort of nourishment supplied, that is to say, they come alike from Crustacea, from spleen and from striated muscle fibre. Should this probability approach certainty in course of further investigation, it would be in harmony with the view that all food is taken up by the cell in solution and then deposited, rather than with that which supposes the nutritive spheres to be formed before their enclosure, from the changing prey.

But I have said above that a certain amount of direct evidence supports this view,—which I may perhaps call the view of intracellular deposition. It is of this nature; when discussing the characters of the fully formed nutritive spheres in an earlier part of this paper I pointed out that when perfect they lie along the sides and towards the base of the cell, projecting into the central vacuole. Sometimes, still fully formed, they are present in the free end separated from the body cavity only by the fairly constant apical accumulation of cell substance (figs. 3, 10, *n*, Pl. VI.). It is more usual however, when a cell actually engaged in digestion is examined, to find in this most internal region the sac-like infoldings of protoplasm which were described above, and were then distinguished from the projections which hold the fully formed spheres in place. These may have comparatively complex contents, holding for example a smaller dense sphere with fluid surroundings, or tiny, dense particles and spherules, or a loose, faintly granular basis, or even as many as two or three small spheres in fluid. In brief, these structures are distinguished from the perfect, typical spheres by lack of homogeneity in their substance and by apparent increase in fluidity; the increased amount of fluid forms a vacuole immediately within the supporting sheath of cell substance, or is mixed with the enclosed matter generally to give a mass of loose structure and small capacity for staining. Now I have said that these when present are typically apical in position, but that occasionally fully formed spheres have a like place in the cell. This occurs apparently in well-nourished cells at the end of a digestive period, so that it would seem that the turbid spheres are in process of deposition, those with homogeneous substance being perfect. I imagine that the deposition takes place in the apices of the cells (fig. 2, *v*, Pl. VI.), and the spheres as they are shaped come to occupy a more basal place; when digestion has ceased and the process of formation is no longer going on, then no turbid, unelaborated spheres are to be recognised but all are homogeneous (fig. 3).

Parallel instances of the deposit of proteid reserve material after absorption in a fluid form are not common among animals, but the process just described for Hydra at once recalls the formation of aleurone grains in the endosperm cells of plants. Here aggregations of proteid which may, according to Vines[1] be peptones, albuminates and globulins are thrown down as granules or spheres, and they have certainly as their more or less remote metabolic antecedent some soluble and diffusible nitrogenous body. And in glycogen, in the ethereal oil which occurs in sponges, in the "amyloid deposits" of Spongilla and the paramylum grains of some Infusoria we have examples of the temporary deposit of non-nitrogenous reserve material, while the coarse granules of vertebrate plasma cells and of certain white blood corpuscles have possibly nutritive value. In this last case it is of course probable that the granules are laid down by actual katabolism of the cell substance rather than that they have any direct connection with ingested proteid such as I would urge in the case of the nutritive spheres and proteid food of Hydra; and indeed since I found that for

[1] S. H. Vines. *Journ. of Physiol.* Vol. III. 1880—82, p. 113.

Amoeba only nitrogenous matter is readily efficient as food there is some ground for supposing that the nearly allied organisms cited can only deposit oil or starchy matter after profound change effected in proteid food or even in their substance. On the other hand Meissner[1] asserts that Infusoria have the power of digesting starch, so that carbohydrate food becomes at least a possible forerunner of any carbohydrate deposit these contain.

It has seemed to me worth while to instance these cases of storage in animal and vegetable cells when discussing the metabolism of Hydra, because they either show close similarity, or differ in detail rather than in type of action. And I wish to close the list by mentioning Allman's[2] description of the endoderm of Myriothela, the account which Ray Lankester[3] gives of some structural details of Limnocodium, and a statement made by Claus[4] in his memoir on *Charybdea marsupialis.* The endoderm cells of Myriothela are spoken of as containing numerous "refringent corpuscles" and a few brown granules. Specialised cells, to which I shall have to allude later, appear to hold most of the pigment which characterizes the animal, while in the tentacles a single layer of small cells surrounds the central cavity and is loaded with opaque spherules. Allman does not make any statement about the chemical reactions of these highly refractive bodies, but it seems to me probable when I recall the terms in which earlier writers have described the endoderm of Hydra, that the "opaque spherules" and "refringent corpuscles" of Myriothela correspond in structure and function to the nutritive spheres.

The statement made by Claus in his paper on *Charybdea marsupialis* is more definite. He is describing the histological variations exhibited by the endoderm in different regions and speaks of the cells of the sub-umbrellar gastric wall as high, and palisade-like. They have a shining well-marked protoplasmic border to their free edge and contain many highly refractive granules, colouring brown with osmic acid, and deep red with carmine. Claus adds, "It can hardly be doubted that we have to deal here with ingested albumen bodies, and that the deep cylindrical epithelium of the sub-umbrellar gastric surface acts in the absorption of albumen as does the intestinal epithelium of higher animals."

1 M. Meissner. *Zeit. f. Wissenschaft. Zool.* XLVI. 4. 1888.

2 Allman. *Philosoph. Transact.* Vol. CLXV. 1875, p. 551.

3 E. Ray Lankester. *Quart. Journ. Mic. Sci.* Vol. XXII. 1881, p. 119.

4 C. Claus. *Arb. aus. d. Zoolog. Ins. Wein,* 1878, S. 45.

In the endoderm of the gastric tube of Limnocodium Ray Lankester distinguishes three regions, *a*, the oral, *b*, the mid-gastric, *c*, the ingestive or proximal. The name given to the third region indicates its function; the cells of the mid-gastric region are inactive and the oral region is especially secretory. I hope to discuss later the probability that we have in certain elements of the endoderm of Hydra cells very much like the "secretion cells" of the oral region; it is the structure of the ingestive endoderm of Limnocodium however which is of immediate interest. Ray Lankester first gives diagrams drawn from the living animal and in the text describes the appearances seen; he then figures and gives an account of the tissue when hardened. The irregularly aggregated endoderm cells show in their substance, in the fresh state, "numerous dense-looking masses of an ill-defined shape which give to the cell substance a certain opacity." These lie near the nuclei. In the hardened cells may be seen "circular or oblong groups of oval bodies of a refringent substance which appear to correspond to the groups of large granules seen in the living specimens."

From this I gather that the bodies or granules are solid. But in further description of the endoderm it is stated that large vacuole-like spaces also occur, their substance being probably precipitated as a homogeneous or excessively finely granular solid by the action of the reagents; and again that the "substance filling the vacuoles is apparently identical with the substance filling the numerous oval spaces of the [refringent] bodies." This would lead one to suppose that fluid, at least at times, entered into their composition. Be this as it may they are evidently regarded by Ray Lankester as closely related to the absorption of nitrogeneous food, and if, as he suggests, they are concerned with the distribution of the "products of digestion and elaboration," their function does not differ very widely from that which I ascribe to the proteid spheres of Hydra.

Up to this time in speaking of these bodies I have dealt with their nature and the method in which they are formed; it remains to give some description of their disappearance.

c. Fate of the nutritive spheres. I believe that whereas hours suffice for deposition, however it may be effected, this disappearance is slow—a matter of many days, even of weeks. It is brought about by the agency of fluid, takes place at the apex of the cell, and may apparently be not merely a process of solution, but may imply the formation of distinguishable and stable bodies. For while apical infoldings of cell substance, such as I have described in detailing the process of absorption, may, when the Hydra is fasting, be seen to hold in fluid surroundings angular fragments of substance resembling the fully formed spheres in reactions (fig. 10, *d*, Pl. VI.) pigment and fat are also upon occasion present in the vacuolate endoderm cells (fig. 4, *p*).

The fat I have detected in a Hydra fed with prey in which none could be seen, and while it may lie freely it is at times apparently adherent to spheres; the pigment does not commonly occur in scattered grains but in particles bound together by a spherical basis. It is indeed a tempting hypothesis that both pigment and fat are formed by action on the stored-up proteid. The action is exerted by fluid,—the secretion of the endoderm cell, and is of such a nature that while the fat is the expression of the administration of very abundant nourishment, the pigment represents an excretory product, the useless element separated out by the cell's activity from the complex of valuable and unavailable matter which makes up the typical nutritive sphere. This is yet, I acknowledge, only an hypothesis; the pigment and the substance bearing it may have slight or even marked enclosing vacuole (fig. 4, *p*, fig. 11), but it is rare to find fat globules in fluid surroundings, and not always easy to establish connection between them and the proteid spheres on which they sometimes seem to lie. But the points on which I should like to lay emphasis are, the disappearance of formed proteid reserve material during long hunger; the apical localization of sheaths of cell substance holding fragments of proteid in fluid, the occurrence of fat in a nourished Hydra when it cannot be found in the prey, and the persistent connection of pigment grains with an amorphous basis. It may be that further work on the functional significance of the fat will decide whether it can be formed directly from dead proteid by the activity of the endoderm cell and its secretion, as it is known that a body connected with the fats is one result of pancreatic digestion in higher animals; I leave the point at present and pass to consideration of the pigment,—consideration which has been almost of necessity partially anticipated but which I am anxious to make somewhat more detailed.

5. *The brown pigment.* This acts alone as a colouring matter for *Hydra fusca,* and is present together with chlorophyll in the green Hydra. So constant are the references to it in all histological descriptions of these animals that it may be regarded as wrongly placed when included among the temporary constituents of the cell. I shall endeavour to show later however that there are some grounds for regarding it as excretory, and should such be its character the per-

manence is clearly only apparent, and due to succession of fresh formations which continually take the place of substance lost.

I propose, as in discussing the history of the nutritive spheres, to say here something about the chemical nature, the origin and the fate of this pigment; the first and last points have been unavoidably touched upon in describing the changes undergone by proteid matter in the economy of Hydra.

a. Nature of the pigment. It is generally spoken of as markedly resistent to chemical reagents, and the attempts I have made to dissolve it confirm the statement. All dilute reagents are without effect; after treatment with absolute alcohol it may still be detected in the cells, and in ether and chloroform there is no solution. Hydrochloric and acetic acids even when concentrated do not act as solvents, but by the action of strong nitric acid a change of tint is brought about; the little pigment masses become a dull greenish blue, sometimes even a bright blue and then grow colourless. They are in this state no longer distinguishable from the surrounding cell substance, all made turbid and irregularly shrunken by the action of so strong a reagent.

b. Origin of the pigment. It is almost invariably found with a basis of proteid substance which in the living cell is irregularly spherical or readily separates out in such a form on teasing. The colouring matter appears to be in two conditions; it impregnates the basis and, possibly because then diffused, is a brighter, lighter brown, and it occurs as small dark angular or crystalline fragments adherent to the substance which the lighter colouring matter stains throughout. Sometimes specimens of Hydra are found in which the diffuse pigment is conspicuous, while others are almost entirely tinted by well-defined lumps of pale or colourless substance bearing dark, angular, perhaps crystalline particles[1] (fig. 9, *a*, *b*, *c*, Pl. VI.). The former animals are bright brown when seen macroscopically; the latter a darker greener brown. The difference in colour brings to mind Nussbaum's distinction of *Hydra grisea* from *Hydra fusca* as partly depending on dissimilarity of tint; I must say however that the colour seems to me rather an individual than a specific character. It varies independently of variation in number of tentacles and in passage of the body into the foot, and the two conditions of the pigment may at any one moment co-exist in the same endoderm cell.

I could indeed imagine from appearances offered repeatedly by

[1] Cf. Howes. *Atlas of Biology*, Pl. XVII. figs. XV. XVI.

preparations that by some change in the colourless proteid basis a brown substance is chemically separated out, uniform in its diffusion at first, and later gathered into definite crystalline particles. And contrast of hardened with living specimens has made me think it possible that the brown pigment becomes less soluble as its separation is perfected, so that with change of form a chemical change goes hand in hand. I do not think that the chlorophyll of *Hydra viridis* is to be looked upon as a forerunner of the brown pigment. For in the actively metabolizing green cells of plants chlorophyll has not necessarily any such coloured decomposition product, although in dead and decaying organisms the green colour may change to brown. Further, I have not certainly seen transitional forms between chlorophyll corpuscles and pigment bodies, though Ray Lankester[1] suggests their occurrence. And finally the pigment is absolutely more abundant in *Hydra fusca* than in *Hydra viridis*, as well as relatively more obvious. It seems probable, as I shall have occasion to point out later, that nutritive spheres as well as chloroplastids exist in the green forms, and it is apparently rather in connection with them that here, as in *Hydra fusca*, the brown pigment takes origin.

c. Fate of the pigment. When a living Hydra is teased under the microscope, little masses of cohering pigment grains are sometimes seen to be turned out of the yet moving endoderm cells, much as carmine or starch is under certain circumstances passed from the substance of the Amoeba. This may of course be a phenomenon of lesion (for the injury inflicted by tearing must be severe), and may correspond to no normal discharge of pigment from the body; but certain statements of other investigators and of my own observations incline me to the view that the ejection represents, though perhaps in an abnormally explosive manner, a normal excretion of matter. On one occasion, when subjecting Hydra during some hours to intermittent stimuli from a weak interrupted current, I saw a mass of substance escape from the mouth of the animal. On examination this proved to be a collection of pigment bodies and some thread cells held loosely together by colourless gelatinous matter. Again, I have seen in the body cavity of one of the dark brown specimens above referred to a similar accumulation of pigment and nematocysts; here it would seem there had been discharge, without any immediate causal stimulation.

These records recall the statement made by Greef[2] that the

[1] E. Ray Lankester. *Quart. Journ. Mic. Sci.* Vol. XXII. 1882, p. 250.

[2] R. Greef. *Zeitsch. f. Wiss. Zool.* 20, 1870.

pigment grains in *Protohydra Leuckarti* have hyaline protoplasmic surroundings, and are in harmony with the account which Allman[1] gives of the brown pigment in Myriothela. In this animal he says the endoderm is many cells in depth, and the cells making up its most internal layer or layers (and therefore projecting into the body cavity) are loaded with dark brown granules. These are constantly thrown off, and their ejection from the mouth may be seen. Kleinenberg too in the case of Hydra implies a belief in varied loss or varied production of the pigment, for he says it changes in amount as the nutritional condition of the animal changes. This statement does not of course tell us whether increase or decrease of colouring matter goes hand in hand with hunger, but I have noticed that in the endoderm cells of a well-fed Hydra the pigment is generally difficult to distinguish, though sometimes it is to be found not now as normally at the apex of the cell, but moved down one side wall. In the endoderm of a fasting animal it is most conspicuous, partly because here the cells are comparatively empty and but few nutritive spheres strike the eye, but also I think because it is actually great in quantity (cf. figs. 3 and 4, Pl. VI.). I do not forget that Nussbaum[2] describes the tint of *Hydra fusca* as paling in long hunger, and that this at first sight appears contradictory of the statement just made. The contradiction is, I think, only apparent, for it must be remembered that long hunger means the disappearance of many opaque bodies,—the proteid spheres, and that possibly the highly vacuolate, partially empty cells are more transparent than are those loaded with reserve material. And the assertion that pigment is absolutely abundant in the fasting condition is not incompatible with the belief that at this time a slow discharge of it is going on, indeed the results of such discharge were, I imagine, seen in an experiment quoted above. Electrical stimulation or ingestion of fresh food stuff may be regarded as hastening the process, and their action recalls the fact that in the case of Amoeba[3] the enclosure of nutritive matter or the stimulus of contact with a pipette or microscope slide at times brings about the discharge of effete substance which the animal, left to itself, may carry about, enclosed, for many days.

If the account here given of the pigment of Hydra be true, if its fate be excretion, its origin proteid reserve material, it would yet seem unlikely that for each nutritive sphere laid down after the absorption

[1] Allman. *Op. cit.*
[2] M. Nussbaum. *Loc. cit.*
[3] *Journ. Physiol.* Vol. VIII. p. 278.

of digested food a group of pigment grains is eventually passed from the body. Rather, I imagine, bearing in mind the mobility of the protoplasm which makes up the endoderm cells, the readiness with which transportation of solids from one part of the cell to another is effected, and the irregularity of the coloured masses, that pigment grains which make up one group come from action on many spheres of proteid, and are finally aggregated before expulsion.

6. *Nematocysts.* The occurrence of thread cells in the endoderm of Hydra has been noticed by Huxley[1], by Parker[2], and by Jickeli[3]; Jickeli evidently regards them as developed there from special originating cells, while according to Hartog they are ingested. I may say, in confirmation of Jickeli, that they may often be seen with undischarged threads, and with the protoplasmic surroundings which characterize than in the ectoderm; at the same time I must add that emptied nematocysts do occur irregularly within or between the vacuolate endoderm cells, and may lie in vacuoles. Whenever prey is ingested many thread cells which have been discharged in its capture are introduced into the body cavity; thus the cells which I have described above as ejected with excreted pigment may have a double origin, coming from the place of their development,—the endoderm,—or passing out after accidental entrance with food.

7. *Temporary Vacuoles.* In an earlier part of this paper I placed "Fluid forming a vacuole or vacuoles" among the permanent constituents of the cell. It is however quite clear from what has been said lately that small temporary accumulations of fluid are of marked importance in the metabolic changes which the endoderm exhibits. I believe that just as the Amoeba's endosarc does not digest enclosures until a secreted vacuole lies round them, so here all solution of the nutritive spheres, all working, which has issue in the formation of pigment is effected proximately by fluid, ultimately by the protoplasm of the cell.

I have said that fragments of proteid reacting like the nutritive spheres may lie at the apex of an endoderm cell during hunger in marked fluid surroundings, and fig. 9, Pl. VI. represents an instance of the considerable vacuole in which pigmented proteid is at times found. Nussbaum[4] too describes balls, crystals and granules of a yellow or

[1] Huxley and Martin. *Elementary Biology.*
[2] T. J. Parker. *Quart. Journ. Mic. Sci.* xx.
[3] C. F. Jickeli. *Morphol. Jahrbuch.* Bd. VIII.
[4] M. Nussbaum. *Op. cit.*

brown colour as held in bladder-like formations in the apices of the endoderm cells, while Ray Lankester[1] in his account of the intracellular digestion of Limnocodium just alludes to "vacuole-like spaces or clearer portions of the cell substance containing very dark minute granules." It is of course only an assumption to regard any structures so briefly mentioned as corresponding in form or function with the pigment bodies of Hydra, but should investigation justify the assumption, we shall have in the vacuolar surroundings of these excretory substances another instance of the significance of vacuoles in certain metabolic processes. In the case of Hydra I cannot say to what extent this localized fluid is derived from the main vacuole, and its nature is as obscure as its origin. But that it is constantly present under appropriate conditions, and as judged by its effects has very distinct individuality, are conclusions almost necessarily drawn from any observation of the structure of the endoderm, conclusions which impose on one the obligation of mentioning the existence of the fluid even if cataloguing its constituents be out of the question. And with this brief account of it I bring to a close my description of the large vacuolate cells, and turn to consider the other elements of the endoderm, the "Drüsenzellen" of Nussbaum[2], and Jickeli[3].

The gland cells. These, according to Nussbaum, are ciliated. I have found that they generally appear with rounded apices (quite conceivably because in preparation their cilia have been retracted), and in living specimens do not readily show amoeboid movement; basally they taper to a long process, which passes to the supporting lamella, and gives them the pyriform shape noticed by Jickeli. Each cell has a nucleus not differing from those of the endoderm generally, and each has cell substance which forms here no sheath-like investment for a central collection of fluid, but is a solid mass in which certain temporary constituents of the cell at times lie embedded. These are solid spherical bodies, smaller than the typical nutritive spheres of the absorbing endoderm cells, but resembling them markedly under the action of staining reagents, or indeed of chemical reagents generally. Thus persistence under treatment with osmic acid, with assumption of a yellow brown colour, and loss of individuality in solutions of acids and alkalis characterize these spherules; they are swollen by dilute potash and in stronger solutions burst or become invisible; in 10 per cent.

[1] E. Ray Lankester. *Op. cit.*
[2] M. Nussbaum. *Op. cit.*
[3] C. F. Jickeli. *Op. cit.*

solutions of sodium chloride they dissolve. It is clear however that, if the name which I have adopted for the containing cells from the writings of earlier workers be truly indicative of their function there must be, underlying this apparent similarity, essential differences between the spherules and the proteid spheres which are formed when nourishment is abundant. And observation of the mode of origin and the fate of the smaller bodies makes it plain that such differences do exist. For it becomes clear not only that the spherules come and go, but that under suitable conditions specimens may be obtained which indicate the manner of their disappearance, and further that their occurrence is definitely related to the manifestation of digestive activity. I will first describe the varying appearance of the gland cells according as in any preparation they have or have not formed contents; and then, examining the conditions under which such variation occurs, I will endeavour to show that there are grounds for regarding the contained spherules as forerunners of some element of a digestive secretion, and as the complement of reserve material stored up by the vacuolate endoderm cells.

The gland cells are especially conspicuous when almost filled with homogeneous spherules; these, between the nucleus and the apex, are so abundant as to hide the protoplasm which holds them, and, since the nucleus lies rather near the base of the cell, it is but a small portion of cell substance that can be distinguished and observed. This is dense and stains deeply, and passes back apparently without marked histological change into the internal basal process. This process becomes so delicate that it is but rarely either in sections or teased preparations actually to be traced to the supporting lamella. (Fig. 5, *a* Pl. VI.) At other times the spherules are present, but are much reduced in size and often of angular shape, and each has fluid surroundings (Fig. 5, *b*); while after complete loss of formed contents two distinct appearances may be possibly presented by the cell. The first is that of a reticulum, the meshes of the network being large, while its separating bars are thin; here as before the protoplasm lying basally of the nucleus is unmodified. The last is no longer that of a honey-combed mass of substance; rather the gland cell is dense and irregularly furrowed and, ceteris paribus, smaller now than at any time. (Fig. 5, *d.*) Thus we have apparently a storage of matter in the form of spherules, and at times a loss of these spherules through the solvent action of fluid poured round them, probably by protoplasmic energy. After such loss the cell may look reticulate, apparently because regions, where was the solvent fluid, differ slightly from the protoplasm that has been acting as a supporting framework; eventually I think rearrangement of substance, loss of fluid or acquisition of fresh material, makes the cell pass into its last, furrowed condition and give but slight indications of structural differentiation.

We have next to deal with the functional significance of these histological changes. And in the first place I would state that the gland cells are most obvious in the endoderm of animals that have hungered for many days. Here the spherules are numerous and perfect, here too they gain additional prominence by the partial emptying of neighbouring cells,—by metabolic change in the nutritive spheres. In certain cases indeed while besides pigment masses, but little formed matter lies in the large vacuolate elements, the position of the gland cells is indicated by constant and striking clusters of spherules. When the endoderm is examined at the beginning of a digestive period the glands still show plainly (fig. 1, *g*, Pl. VI.), and after food has been within the Hydra for as long a time as two or three hours the spherules may be quite evident; the onset of absorption however, marked by initial vacuolar deposits and final separation of solid matter in the absorbing cells, appears to be bound up with solution of the spherules which we are thus impelled to call secretory. (Fig. 2.) At anyrate at the end of a digestive period the gland cells are so inconspicuous that I was at one time inclined to the view that they are lost bodily as secretion goes on; and though careful searching, revealing them, seems to negative such a suggestion, it shows them empty and shrunken, or at most holding fragmentary contents in fluid surroundings. (Figs. 3, 10.)

From these statements it would seem that there is good reason for dividing the endoderm of Hydra into secreting and absorbing elements, and that the use of the term *gland* finds justification in facts; I said however in an earlier part of this paper that some experimental results opposed such a theory, and it remains for me to bring forward this discordant evidence.

A Hydra that for two or three days has captured nothing may yet, if its food have previously been abundant, be described as well nourished. Examination reveals numerous fully formed nutritive spheres in its endoderm and very often fat is markedly present. Yet in such a specimen it may happen,—indeed this is commonly the case—that the gland cells are inconspicuous, or if detected are shrunken or contain only fragmentary spherules. Here is absence of secretory products with no immediately corresponding manifestation of digestive activity. Again, I have stated that well filled and conspicuous gland cells characterize the largely emptied endoderm of hunger, and have implied that this loaded condition must be regarded as a state of rest. I find sometimes however that in animals, which have fasted very long, there is partial solution of the secretory spherules, that is they lie, diminished, in little vacuoles. Here is change such as accompanies activity without any causal ingestive stimulus. One hypothesis appears to me to harmonize these statements. According to Langley[1] it is probable that in all vertebrates the granules of pepsin forming glands diminish in number when the animal remains without food longer than a certain time, so that the appearances of fasting cells may recall the condition of active secretion; if we suppose the cycle of development of secretory products to be very slow in Hydra it is conceivable that the solution without the stimulus of food corresponds to the vertebrate "fasting" state. Similarly the absence of spherules in well nourished cells may be due to the fact that their re-formation after secretion has not taken place. But should this hypothesis be regarded as offering a satisfactory explanation of the difficulties already mentioned, others, not easily obviated, appear. Thus I am unable to say how the spherules are deposited and whether the same appearances, that is fragments of substance in vacuolar cavities, indicate solution and deposition. Indeed the intracellular solution of solid spherules seems a clumsy way of developing a ferment from its antecedents. Yet while it is true that the formed contents of the gland cells tend to be gathered towards the free surface, I look upon it as a wholly improbable view that they are expelled bodily from the cells and then broken down or dissolved. Again, it seems hardly probable that an amount of fluid adequate for digestion should be derived from the solid gland cells, or even from the vacuoles in which their spherules are dissolved, and as I have said, the central vacuoles of the large endoderm cells do diminish during digestion. Since however there is *à priori* improbability in the view that the solids of a secretion should come from one cell while its neighbour supplies the water, and since normally a certain amount of fluid taken in by the mouth is present in the body cavity, it may be that the water necessary for digestion is thus obtained, the vacuoles of the endoderm cells being excretory rather than secretory in character.

These difficulties make one anxious not to omit the consideration of any other possible interpretation of the functional significance of the gland cells, and I therefore mention two suggestions which present themselves, but which have I think little support in facts. The first of

[1] J. N. Langley. *Journ. of Physiol.* Vol. III. 1880—1882, p. 275.

these is that we are dealing here with extra store-houses of reserve material, the substance stored resembling that which makes up the typical nutritive spheres. This suggestion has in its favour the close similarity which spheres and spherules exhibit; it is not inconsistent with the marked persistence of the spherules and their partial solution in long fasting, and similar partial solution which I once saw in a Hydra that, artificially bisected, grew presently into two perfect forms, might be explicable as response to an unusual demand on reserve material. But a generalization based on one experiment, especially an experiment in which an operation so severe as is bisection, is performed could not but be hasty, and as I have said the "solution" in long fasting is capable of explanation on the theory first stated. Further, spherules may be absent from a bud of Hydra which has not yet known scanty nourishment, and which does hold nutritive spheres within its vacuolate cells, and the persistent absence of pigment and fat in the "glands," and the constant lack of any central accumulation of fluid, seem to indicate that no function is performed by them so like that of the rest of the endoderm as would be the storage of nutritive matter. The second suggestion is that the small solid cells are young, and that vacuoles and pigment will be acquired later, their development making the cells like their neighbours in the endoderm. But they are not more markedly present in a bud than in mature forms, and should my interpretation of the functional meaning of each element in a vacuolate cell be the true one, it is clear that in development the separation out of fluid would precede the deposit of proteid reserve material. On the whole then I conclude that these views may be dismissed, the evidence in favour of the hypothesis that true gland cells are present being, if not overwhelming, too considerable to be disregarded. Nussbaum, though he gives good figures of the "glands" in their laden and reticulate conditions, does not, as I have said, discuss their function, but certain structures which exhibit many points of similarity with these cells of Hydra are described by Claus[1] in Charybdea, and by Ray Lankester[2] in Limnocodium, and there regarded as secretory in character.

In the oral endoderm of *Charybdea marsupialis*, according to Claus, three kinds of cells are to be found; flagellate cells, smaller than the rod cells occurring in other parts of the endoderm, goblet cells with mucous contents, and gland cells. These are cylindrical, with widened convex apices, and they hold numerous granules which colour deeply

[1] C. Claus. *Op. cit.*
[2] E. Ray Lankester. *Op. cit.*

with carmine and "represent a future secretion." Ray Lankester in his paper on the Intracellular Digestion of Limnocodium refers to this account, and regards the gland cells and goblet cells of Claus as young and older stages of the same structures. He compares them with certain cells found characteristically in the oral third of the gastric tube of Limnocodium; these are large, clear, nucleated bodies which, together with smaller young cells, are surrounded by some horny or gelatinous intercellular substance. A complete description of the young cells is not given, nor are there details of the stages through which one form grows into the other, but the appearance of Pl. IX. fig. 3, indicates that the young cells are denser and stain more deeply than do the adult "glands" into which they grow. I do not gather from Ray Lankester's account that special secretory granules are present during rest and are lost in each period of activity; rather he regards the cells as shed bodily when ripe, and presumably as broken down then into secretion. Thus ejected, they leave intercellullar spaces which the young cells fill by growth and development into the adult form. In taking the view that secretion is in Limnocodium derived from actual discharge of laden cells, Ray Lankester accepts an hypothesis which I found untenable in the case of Hydra; yet it seems to me that, granted this difference exists, there is room for interesting comparison of the two forms. I have shown above that the vacuolate absorptive cells of Hydra probably find a parallel in the cells which line the proximal third of the gastric tube of Limnocodium, and now we have to note in both animals the occurrence of specialised secretory cells. In Limnocodium indeed the separation of the two elements in space is more marked, but it must be remembered that only in the gastric cavity of Hydra is there general mixing of secretory and absorbing cells; the tentacles show no "glands," they are entirely absent from the extremity of the foot and in the upper part of that appendage are only rarely scattered. This statement of the localization of secretory cells in Hydra is a partial anticipation of the point I would next discuss,—the relation of the different endodermal elements to each other and to different regions of the body. I may perhaps include in the discussion a very brief notice of the histological variations which characterize certain of the endodermal lip cells, and which are discernible in the endoderm but especially in the ectoderm of the sucker.

Disposition of the endoderm cells. Those elements which are large and vacuolate greatly outnumber the smaller "glands." With slight modifications, to be described presently, they alone make up the lining of the hollow tentacles, and except for rare gland cells in its proximal portion they form a continuous boundary for the cavity of the foot. Round the gastric cavity proper both cells occur; the "glands," which are perhaps most striking in the upper third of the body, lying singly between groups of two, three, or six of the absorptive cells.

The mobility of the Hydra's body is very great, and the vacuolate elements of the endoderm are capable of considerable change of form and varying disposition of their substance. They lie side by side, cylindrical or cubical in shape when the whole animal is extended, or distended as it may be at times by food (fig. 1, Pl. VI.); they are comma shaped in general contraction of the body, bulging apically and becoming greatly attenuated at their attached bases. They are even sometimes thrown up into simulated villi (Pl. VI. fig. 10), after the fashion of the mucous membrane of the frog's intestine. But the gland cells, destitute of vacuole, can undergo less alteration of form and shrink and expand but little. Unless borne up on the side of a "villous" formation therefore by great attenuation of their basal processes, they lie far from the surface, when as in the contracted state of Hydra, the endoderm generally is deep; extension over prey on the other hand brings all the cells present to a level. (Cp. figs. 2 and 3 with fig. 1.)

I have said above that certain structural modifications other than those yet noticed remain, and demand brief consideration. The first of these is found in the *foot* and *tentacles*. In both regions the vacuoles of the large cells are very conspicuous (Fig. 6, Pl. VI.) and the cell substance is relatively scanty. Pigment groups and nutritive spheres occur, the pigment being indistinguishable in amount and disposition from that of the gastric tube, while the nutritive spheres are as a rule smaller than those found in the main part of the endoderm. In the *lip* certain cells constantly occur which I have represented diagrammatically in Fig. 7. Their substance is dense, and in the fresh state filled in its outer part with little shining granules which break down in acids and alkalis. Hardened, the cells stain readily and they appear punctate or granular according as the granules are preserved by the reagent used or are dissolved, making visible their supporting framework of substance. Nuclei are present but show no peculiarity, and the cells taper inwards to a process which is soon lost among the closely packed neighbouring pigmented cells. The endoderm of the *sucker* of Hydra has been described by Jickeli[1] as made up of a "second kind of gland cell." I have not been able to find any qualitative difference between these

[1] C. F. Jickeli. *Loc. cit.*

and the rest of the absorptive endoderm. There is, truly, marked diminution in size and the vacuoles are less conspicuous, still the cell substance is loose and not definitely structured, and pigment is commonly present. It is in the subjacent ectoderm figured at Plate VI. fig. 8, that obvious modification occurs, and here the structure recalls that found in the lip and already described. Only the shape of the cells is changed, for in the sucker they do not taper markedly but, very closely packed, run down to the supporting lamella as elongated cylinders. The peculiarities of form thus found at the oral and aboral extremities are probably to be associated with the performance of definite function, for while the sucker acts as an organ of attachment it is the lip which, when the Hydra is feeding, holds and advances over its food. For I must confirm the account of the act of feeding which Hartog[1] gives in his note "On the mode in which Hydra swallows its prey," and repeat that while the tentacles may arrest a moving animal and discharge their nematocysts into its body they are never used for tucking the prey into the interior of the Hydra, but remain extended and waving freely during its enclosure (cp. Pl. VII. figs. 1, 2). The lip, to use Hartog's expression, is drawn or pushed over food much as a glove may be advanced over the finger. But though I thus urge that these local modifications in structure are the expression of local differentiation of function, I can make no detailed statement of the exact nature of the connection. The granules which in appearance and reactions seem so like the secretory granules of many vertebrates may help to form some viscid secretion which acts as adhesive fluid. But speculation in the absence of experimental evidence seems idle; I pass then to consider another point which is of interest; the nature of the food of Hydra and the time and medium needful for solution.

Nature of the food of Hydra. I have never seen ingestion of inorganic or innutritious matter; this may be because the oral apparatus cannot readily deal with small particles, but since carmine in masses seems no more potent as a stimulus than when finely divided, I should imagine that here there was development of that initial discrimination in the choice of ingesta which I have before noticed as occurring in Actinosphaerium, and constituting one difference between this animal and Amoeba. Hydra is essentially carnivorous; Cypris, Cyclops, Tubifex, larvae of beetles and Trembly's "Millepieds" are all upon occasion readily eaten, and fragments of muscular fibre or of

[1] M. Hartog. *Quart. Journ. Mic. Sci.* Vol. xx. 1880.

spleen may be taken up greedily. Thus it comes to pass that the prey is sometimes larger and often longer than the animal which ingests; it is if necessary considerably doubled up inside the body cavity whose walls are put very much on the stretch, and in carrying through the act of enclosure the Hydra undergoes grotesque distortions of form. Death seems speedily to follow enclosure; at least movements of the prey cannot be detected for a time longer than five or seven minutes after the lips have closed over it. But I find it difficult to give details of the time occupied by the later stages of a digestive act. It seems possible that two or three hours may elapse without any uniform diminution of the spherules in the gland cells, and an equal length of time may still find the absorptive cells without nutritive spheres. In five or six hours solution has progressed considerably and absorption has begun, while it would seem that within twelve hours the débris of ingesta is rejected by the mouth. The act of ejection may be performed at an earlier time if the Hydra be brought roughly into contact with an instrument or fresh fluid. It seems possible to introduce with impunity very long periods of hunger between successive acts of feeding, (and this natural intermittence in ingestion would harmonize with my supposition that the secretory spherules once lost are but slowly reformed), but the animal is markedly capricious in its habit. Thus occasionally one wins response to the artificial administration of food to a well nourished Hydra, while at other times there is no ingestion even after a fast of many days.

The fluid medium in which solution of food goes on has apparently no acid reaction. For delicate litmus paper does not indicate the presence of an acid when the torn substance of a digesting Hydra is placed upon it, and an animal in like condition does not, when teased in it, redden a litmus solution obviously changed by hydrochloric acid less than ·2 per cent. Though it is probably of less value I may make the statement that animals, like the prey of Hydra, do not show the same changes when placed in acid as those exhibited by food teased from the body after ingestion or hurried to premature ejection. And when raw meat is taken in it undergoes a certain amount of digestion, as has been said, but it shows no separation into discs. In this connection I tried to test the effect of aqueous and acid extracts of Hydra on fibrin in various media; the experiment failed.

With this I bring to a close my account of the structure of the endoderm of *Hydra fusca*. In this account, since it is concerned only with the manifestation of digestive activity, I have omitted all description of possible nervous elements referred to by Nussbaum and Jickeli. And believing that hardly any histological character on which I have dwelt has been unnoticed by previous workers, I have been anxious during the course of the paper to institute comparisons on various points with statements which exist already. Such comparisons have made me think that hitherto lack of continuity in observation has led to the interpretation of what is really a phase of structure as a permanent histological condition.

I have simply to add a summary of the points of detail on which watching makes it seem well to lay most stress.

Summary.

1. The ingestion of solid matter is performed by slow advance over the prey of lip-like projections of the Hydra's substance (Pl. VII. fig. 1). During the action the tentacles for the most part remain extended, having previously been in contact with the prey and discharged their thread cells into it.

2. In any Hydra distinction can be drawn between body and foot. The foot ends in the sucker, is of narrower diameter than the body, and may join it sharply or pass gradually into it. Its endoderm cells are more markedly vacuolate than those of the body, and an ingested organism apparently never enters its cavity but remains in the body and often distends it greatly (Pl. VII. figs. 2, 3).

Entomostraca, Nais, beetle larvae or raw meat prove the most acceptable food, while innutritious matter and particles of very small size are not, it would seem, potent as stimuli to ingestion.

3. The digestion of enclosed food is effected entirely outside the endoderm cells which line the Hydra's body cavity, and among these cells two types may be distinguished.

a. Cells of pyriform shape destitute of large vacuoles; these hold many secretory spherules in hunger, and tend to be emptied during digestive activity.

b. Ciliated vacuolate cells which at times hold pigment. The water of the digestive secretion is probably, at any rate in part, to be associated with the vacuoles of these ciliated cells, for intracellular fluid is never so conspicuous as in the fasting state, nor so little marked as after abundant nourishment. In the body of the Hydra both types of

cells occur, the gland cells lying scattered between groups of the vacuolate structures; in the extremity of the foot and in the tentacles, gland cells are absent.

4. The pigment, which as brown or black grains attached to a proteid basis is often conspicuous in the endoderm, is resistent to most chemical reagents, but dissolves slowly in nitric acid. It is formed by the activity of the cells, and is probably at least as a rule, expelled into the body cavity during an act of digestion.

5. The formation of secretion by the endoderm, and the loss of pigment just described, are made inconspicuous during the later stages of a digestive act by the onset of absorption; this finds expression in the gathering of proteid matter within the vacuolate endoderm cells. This matter is deposited as a store of reserve substance in the basal part of the cells and eventually takes on the form of spheres; it is, I believe, absorbed as fluid, forms definite vacuoles bounded by the apical protoplasm of the cells, and is by the indirect action of the protoplasm converted into the insoluble form.

6. It would appear probable that the excretory pigment takes its rise in some residue of these proteid bodies, and possible that they may at times be the source of fat; at least well nourished specimens often show fat globules lying on or attached to the nutritive spheres of their endoderm cells. A large portion of the spheres however undergoes final solution, and, when dissolving, they probably constitute the "angular particles" of some authors.

7. When this solution is effected it takes place towards the apex of the enclosing cell; the little masses of proteid are moved upwards from their "resting" position, and by the then investing layer of protoplasm fluid is secreted round them.

8. At the lip of Hydra certain of the endoderm cells undergo marked modification, and structures resembling them take the place of the typical ectoderm formation at the sucker. These modified elements hold small granules in the fresh state, and when hardened appear granular or punctate, according as granules or spaces in which they have been are brought into prominence by the method of preparation. Vacuoles and pigment are absent.

9. The medium in which digestive activity goes on in Hydra is probably not acid.

Note. I have to subjoin a very brief account of the histological characters of the endoderm of *Hydra viridis*. In this animal the green bodies which Nussbaum regards as parasites, and which are as definitely looked on as chloroplastids by Ray Lankester, lie especially thickly towards the base of the vacuolate endoderm cell (fig. 10, Pl. VI.) and distally of them in well nourished specimens are the true nutritive spheres. These are never so conspicuous as in *Hydra fusca*, but in hardened preparations of the green form (where the chlorophyll has been dissolved out by spirit) they may be distinguished from the chloroplastids by their larger size, more irregular shape, more homogeneous appearance and often by position. The chloroplastids are round but frequently appear centrally punctate, or their substance may seem to be undergoing cleavage.

Gland cells do not form a conspicuous feature in the endoderm of *Hydra viridis*; they are present and hold no chlorophyll, and often seem to be destitute of spherules. It may be that the presence of chlorophyll has so changed the mode of nutrition of the green forms that digestive secretion is less active in them (and indeed I have never succeeded in feeding *Hydra viridis*); it may be on the other hand that "glands" are simply detected and examined with difficulty owing to the presence of numerous and conspicuous chloroplastids in the vacuolate endoderm cells.

EXPLANATION OF PLATES.

Plate VI.

Fig. 1. Vertical section through body-wall of digesting Hydra, early stage of digestion.

Fig. 2. Vertical section taken later in digestion, showing vacuolar deposit of nutriment in large endoderm cells and loss of the spherules of gland cells.

Fig. 3. Vertical section taken at the end of an act of digestion, showing emptied gland cells, and fully formed nutritive spheres.

Fig. 4. Group of cells teased from endoderm in hunger. To show connections of pigment in vacuolate endoderm cells, and persistence of secretory spherules. Oc. 3, Obj. F. Zeiss

Fig. 5. Cells isolated by teasing.
a. b. c. d. gland cells in different stages of activity
a. b. d. drawn with Oc. 3, Obj. D. Zeiss.
c. drawn with Oc. 3, Obj. F. Zeiss.
A. Absorptive endoderm cell from the animal in which *b.* was found. Oc. 3, Obj. D. Zeiss.

Fig. 6. Vertical section through foot cells of Hydra; digestive endoderm of same animal is drawn at Fig. 2.

Fig. 7. Vertical section through lip showing modified endoderm cells.

Fig. 8. Vertical section through modified ectoderm of sucker.

Fig. 9. Pigment of *Hydra fusca* as seen in specimens teased from diluted Flemming's fluid.

Fig. 10. Vertical section through body-wall of *Hydra viridis* to show simulated "villus," presence of gland cells, and coexistence of nutritive spheres and chloroplastids.

Except where otherwise specified the magnification throughout is that effected by combination of Oc. 3, Obj. D. Zeiss.

PLATE VII.

The figures in this plate have been drawn by Mr Wilson, of the Cambridge Scientific Instrument Company.

Fig. 1. *Hydra fusca*, enclosing a piece of striated muscle fibre (*m*). The lip is being gradually advanced over the food, the tentacles are extended.

Fig. 2. Ingestion is complete; the Hydra is distended by contained prey.

Fig. 3. Later stage of digestion; the distension is more localized in the hind part of the Hydra's body.

In all stages of digestion the distinction of "foot" and "body" is preserved.

Index of Symbols.

In all the figures.

Ec = ectoderm.
E = vacuolate endoderm cells.
g = gland cells.
nuc = nucleus.
p = pigment.
n = nutritive spheres.
V = temporary vacuole formed in the substance of the cell.
sp = secretory spherules of gland cells.
chl = chloroplastids of *Hydra viridis*.
m = modified cells of lip.
d = nutritive sphere undergoing solution.

Fig. 1

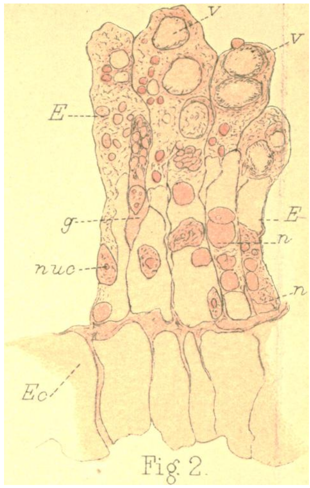

Fig. 2.

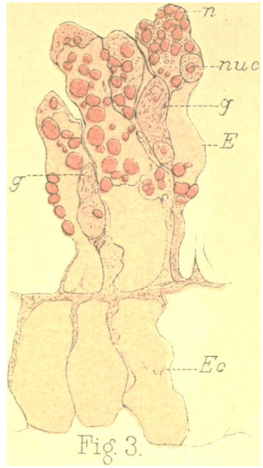

Fig. 3.

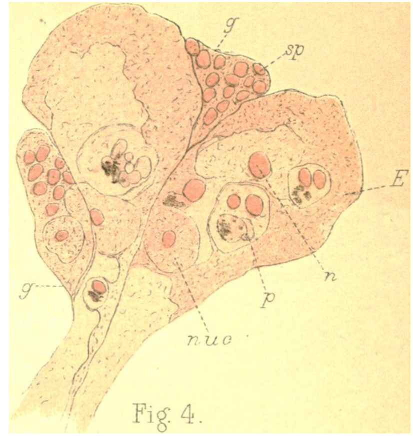

Fig. 4.

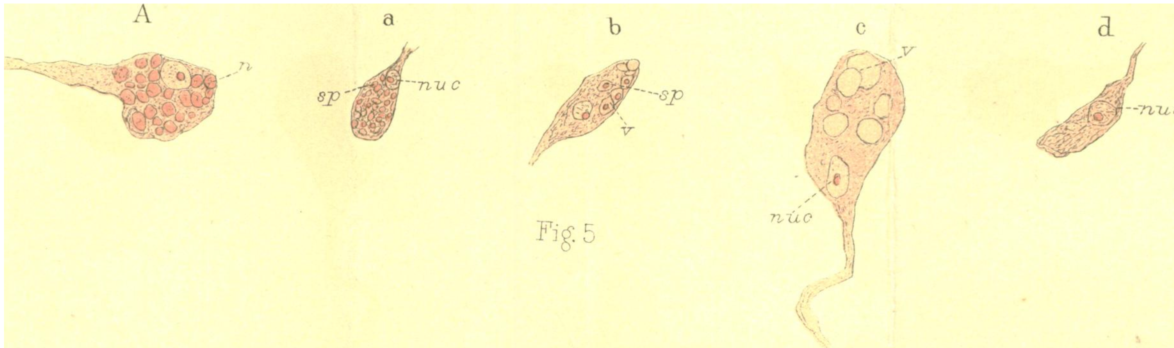

Fig. 5

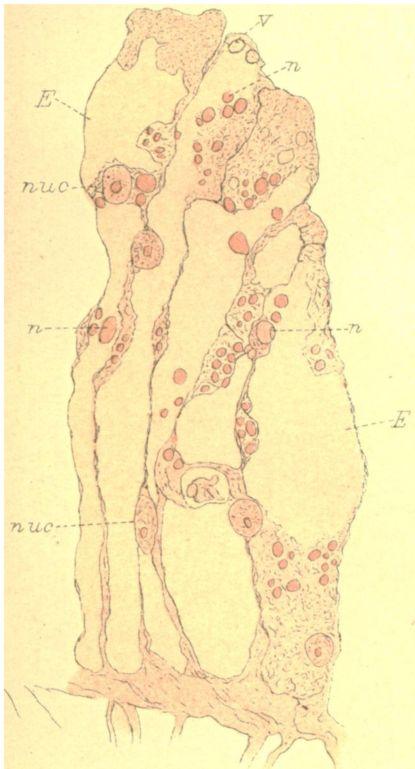

Fig. 6

Fig. 7.

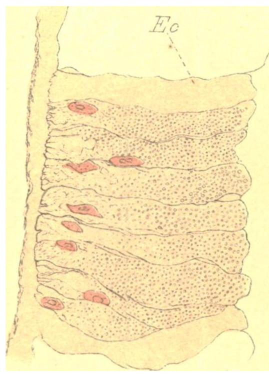

Fig. 8.

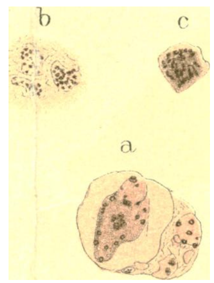

Fig. 9.

Fig. 10

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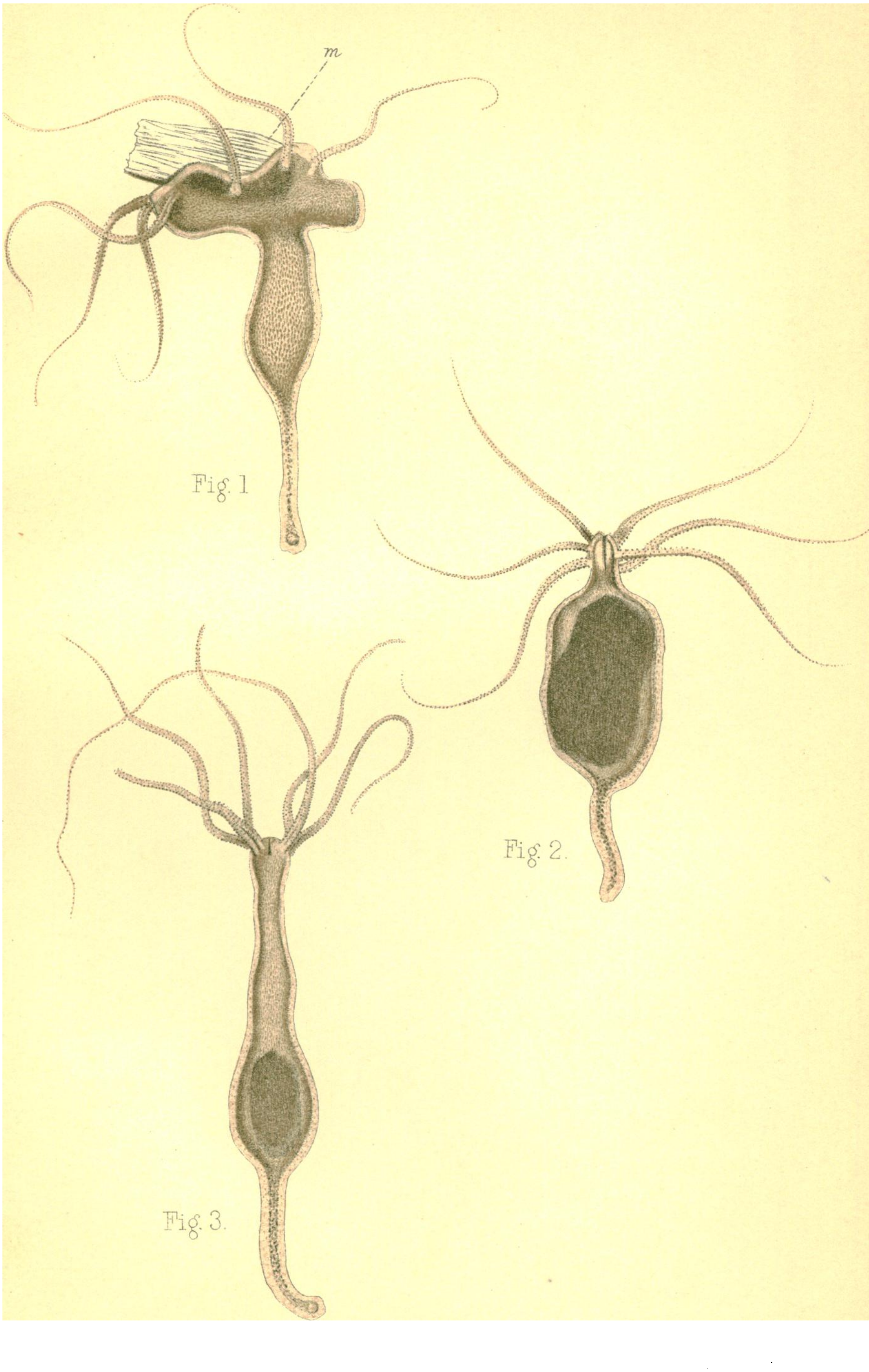

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