Gleichzeitig entsteht der Spieß aus dem achromatischen Theile des Kernes.

16) Die Spermatozoen haben auf gewissen Stadien bei allen Species einen typischen Schwanz mit Achsenfaden.

17) Der Achsenfaden bildet sich im Protoplasma der Spermatocyte (resp. Spermatide) zuerst als ein kurzes Stäbchen, welchem bisweilen einige Archoplasmakörnchen anliegen. Mit dem Kerne verbindet er sich erst nach dessen Umwandlung in die Chromatinplatte.

18) Da, wo sich Achsenfaden und Chromatinplatte verbinden, liegt am Rande der letzteren ein Zähnchen; das proximale Ende des Fadens paßt zwischen dieses Zähnchen und die Chromatinplatte selbst. Der Theil des Achsenfadens neben dem Zähnchen ist seinem Färbungsvermögen nach ein Homologon des Endknöpfchens anderer Arthropoden.

19) Die ganz reifen Spermatozoen, die sich vom Spindelreste befreit haben, sind beweglich (*Tarantula*).

20) Beim Übertritt in das Vas deferens wickelt sich der Spermatozoenschwanz auf und liegt dem Kerne an; der Kern selbst biegt sich so zusammen, daß sein vorderes Ende das hintere berührt, wobei er den eingerollten Schwanz völlig umfaßt. Wahrscheinlich verwandelt sich der Haupttheil des Achsenfadens in ein homogenes Kügelchen. So bilden im Vas deferens 'alle Spermatozoen stäbchenförmige oder längliche elliptische Körperchen, woran man weder Schwänze noch Spieße bemerken kann.

Neapel, 6. März 1896.

4. On some Points in the General Morphology of the Metazoa considered in connection with the physiological processes of Alimentation and Excretion.

By Arthur T. Masterman, B.A. Lecturer and Assistent Prof. of Natural History in the University of St. Andrews.

eingeg. 15. März 1896:

In the General Morphological comparison of Plants and Animals, the most important physiological factor which gives origin to the great differences in form between these two groups, will probably be acknowledged by all to be the fact that the protoplasm of the former is endowed with the power to subsist upon liquid aliment, whilst the great majority of the latter take into themselves solid food in one form or another.

The most obvious effect of this is that in the former a continuous

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protective envelope is possible, whilst in the latter a more or less permanent mouth and alimentary area are essential.

Taking, then, this necessity for solid nutrition in animals as the basis of their morphological differentiation, we can conveniently divide the processes by which an animal maintains its protoplasmic energy into three groups: namely.

1) Ingestive processes. 2) Digestive processes. 3) Egestive processes, and correlative to an elaboration of these we have the morphological differentiation of the three sets of organs: Ingestive, Digestive and Egestive organs.

Organs which occur as the result of the differentiation of a single cell, and functions conducted by cells either singly, or independently when the cells are in a mass, may be termed monocytic (in contradistinction to the form and function of tissues, which thus may be termed polycytic). The cell-mouth¹, cell-anus, and cell-digestive tract are thus monocytic mouth, etc., whereas the mouth of *Hydra* may be termed a polycytic ingestive aperture. Similarily, the digestion of food inside a cell, »intra-cellular« digestion, may be conveniently and comprehensively termed monocytic digestion, whereas »extracellular« digestion may also be known as polycytic digestion. Monocytic organs only are found in the Protozoa, whereas both occur in the Metazoa.

Under »Ingestion« are included all those organs which assist towards the ingestion of solid food. In the narrower sense this will mean apertures leading into the digestive area i. e. »mouths«, whatever their morphological value, but in the wider sense, it will comprise various organs developed in connection with the »mouth«, including such diverse structures as cilia, flagella, pseudopodia, tentacles, jaws, etc.

In a form like Amoeba, we find that it is quite impossible to distinguish between the functions of locomotion and ingestion, both are in the diffuse condition, and the ordinary contractile activity of the protoplasm serves for the ingestion of solid particles. In higher Protozoa illustrated by the Ciliata, there is a subservience of certain of the diffused locomotor organs to the special locomotor function of ingestion² in accordance with the location of the ingestive function to one particular organ the mouth. It follows from this, that the organ of ingestion being primitively a specialised part of the general locomotor system, must belong phylogenetically to the outer layer, the

¹ E. R. Lankester, Encyclop. Brit. »Protozoa«, 1885.

² A like development of ingestive organs from locomotor organs can be seen in the history of mouth-appendages in Arthropoda.

mouth or ingestive aperture marking the line of separation between the outer layer and the inner digestive tract.

In the Metazoa, we can perceive precisely the same evolution of ingestive organs from the locomotive organs. No known Metazoan is capable of enveloping its prey at any point of its surface, and then conducting digestion there, but the nearest approach to this condition is exemplified by the Coelenterata in many of which the half of the external surface forms an area of polycytic ingestion.

Thus, in a typical Hydromedusa, (Fig. 11) part of the body-wall is expanded outwards to form an efficient locomotory organ, i. e. the umbrella, the sub-umbrellar cavity thus formed being lined by a layer



Fig. 11. Diagramm of Hydromedusa, showing locomotive-ingestive area (loeomotory = black lined) (ingestive = dotted).

Fig. 12. Diagramm of Scyphomedusa, showing locomotory and ingestive areas indicated as in 11.

which both structually and ontogenetically belongs to the outer layer. The umbrella serves the double function of locomotion and ingestion³. Again, in a scyphomedusan such as *Aurelia*, (Fig. 12), there is an intermediate condition in which the functions of ingestion and locomotion are partially separated. Here a portion of the sub-umbrellar cavity is »tucked in «⁴ and does not assist to any appreciable⁵ degree in ingestion.

In a Ctenophore, such as *Cydippe*, (Fig. 13) the sub-umbrellar cavity, as is proved by the transitional form *Ctenaria*⁶ has been completely invaginated to form what is usually known as the stomach, the true mouth opening from this inwards. The locomotor function

³ In St. Andrews Museum are Medusae of some 4 inch. diametre, with no mouth or manubrium. The whole sub. umbr. cavity must here subserve digestion as well as ingestion.

⁴ Goette, Abhandlungen zur Entwicklung der Thiere, IV. 1886.

⁵ »It seems probable that the stomodaeum in all Anthozoa is simply a foodpassage and plays, at most, a very small part in the process of digestion.« S. J. Hickson. Science Progress. 1894.

⁶ E. Haeckel, Sitzgsber. Jenaische Gesellsch. 1878.

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of this part has been lost, and fresh locomotor organs are acquired, whilst the ingestive function of the stomach may be readily observed in the living Cydippe.

The ontogeny 7 of this form shews that the stomach repeats its ancestral history, and is invaginated from the epiblast. Above these

forms we nearly always find an area of the epiblast invaginated for the function of polycytic ingestion, well-known to Morphologists as the stomodaeum.

NB. Though quite a speculation - if we accept the homology of the Vertebrate blastopore (at any rate, in part) with the Invertebrate mouth, then the neural tube, in development and structure, answers to a hypertrophied stomodaeum or ingestive organ, a specialised part of the ectodermal locomotor system. As the Invertebrate oesophageal nerve ring takes origin in the phora, showing ingestive (dotted) stomodaeal ingestive area, so from the walls of area, and fresh form of locomotion, the Vertebrate hypertrophied ingestive tract (pri- not indicated. mitive groove) the elongated dorsal nerve area



Fig. 13. Diagram of Cteno-

(an elongated ring forming a cylinder) arises and persists after the ingestive function aborts. This function probably persists in the typical Chordate larva.

We can thus trace the gradual differentiation of both the monocytic and the polycytic ingestive organs, as exemplified by parallel series taken respectively from the Protozoa and the Metazoa, but these monocytic and polycytic elaborations of organs are quite independent of one another, and we have to follow up the function of monocytic ingestion in the Metazoa, and if possible attempt to elucidate the inception of polycytic ingestion therefrom.

In the transition from the Protozoa to the Metazoa the underlying principle is acknowledged to be the subordination of the monocytic individuality, and differentiation to that of the Polycytic, or in other words, the inception of the individuality of the unit of the higher order at the expense of that of the lower order⁸. Thus we shall expect to find in the ingestive process a cessation of further adaptations to favour monocytic ingestion in so far as it benefits the single cell, and the evolution of further processes by which the activity of the ingestive cell may benefit not only itself, but its surrounding cells.

Thus, if we take a spherical multicellular colony (Fig. 1) in which each cell has locomotor organs, either cilia or flagella. Supposing this colony to evolve upon the lines of monocytic differentiation, each

⁷ A. Agassiz, Embryo of the Ctenophorae. Mem. Amer. Acad. Arts and Sc. - F. M. Balfour, Comp. Embr. Vol. I.

⁸ H. Spencer, Principles of Biology.

cell must elaborate monocytic ingestive organs apart from locomotor organs, as in the solitary Protozoa; whereas if we assume that the monocytic differentiation ceases in favour of polycytic, then each cell will differentiate in time and not in space, will lose flagella when ingestion is effected and will, in accordance with the principles of polycytic differentiation migrate inwards from the locomotor area9. Thus each cell will perform in its turn the function of locomotion and ingestion and later, digestion. In fact, in this multicellular colony, there will be no division of labour between the cells, but each cell will play many parts. This stage may be compared to the stage of monocytic differentiation exemplified by Amoeba, the functions of locomotion and of ingestion being diffused. Just as in Amoeba, locomotion of the whole brings the outer part of the organism in contact with the food particles which are then ingested to the interior of the organism, so in this colony the whole individual moves into contact with food particles and these are transferred to the interior preparatory to digestion. The processes effected by the general contractility of the protoplasm in the one case are accomplished in the other by the activity of individual cells.

It will be observed that, in this case, each cell performs a series of functions, and is also polymorphic, the flagellum being contracted, and the amoeboid phase being assumed.

Such a colony has yet to be described in full, but in most points it is closely approached by *Proterospongia* (Savillia)¹⁰. The ingestive process is not described in this form, but the cells are undoubtedly polymorphic in that in connection with the sexual process, immigratory flagellated cells become amoeboid.

The ingestive processes in sponges, at any rate in the simpler forms, are precisely of this nature. In *Grantia*¹¹ for example the flagellated cells, upon being charged with food particles, withdraw their flagella, and becoming amoeboid, migrate into the so-called »mesoderm«. We thus find that *Proterospongia* illustrates such a low form of organism as we have mentioned, and in the sponges are to be found ingestive processes, dependent upon polymorphism of the cells, precisely similar to those suggested as primitive in the hypothetical multicellular colony¹².

⁹ This migration inwards is dependent upon the same laws as cause a food particle to migrate to the interior of Amoeba.

¹⁰ W. S. Kent, Month. Micro. Journ. Vol. VI. 1871.

¹¹ This migration has recently been stigmatised as »pathological«. The objection was to some extent forestalled in my paper. Annals of Mag. Nat. Hist. Vol. XIII.

¹² »It appears to me not impossible that the Coelenterata may have had an ancestor in which a digestive tract was physiologically replaced by a solid mass of amoeboid cells«. F. M. Balfour. Comp. Embr. Vol. I. p. 178.

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In the monocytic differentiation, the stage after diffuse ingestion appears to be the formation of a definite ingestive aperture with stomatic ingestion.

In the multilaterally symmetrical organism above described one must assume a pelagic habitat, with the environment equalised by a rotation about the centre. It is evident that the rotation about the centre of a sphere must be gradually replaced by rotation about an oral-aboral axis, and this must be caused by a differentiation of the locomotory cells, but the position of the rotatory axis is determined by



Fig. 1. Transverse section of monoblastic multilateral colony of cells with diffuse monocytic ingestion, digestion and egestion. The dotted area in this and the following figures (1a, 2, 2a, 3) represents the area of predominatingly nutritive fluids, whilst the white parts represent the area of predominatingly respiration and excretory fluids.

Fig. 1a. Transverse section of transitive form with located ingestive area.

Fig. 2. Longitudinal section of diploblastic radially symmetrical colony of cells, with monocytic ingestive, digestive and egestive, and also polycytic processes. (The shaded area represents that of the polycytic nutritive fluid.)

Fig. 2a. Longitudinal section of transitive form between 2 and 3, with two rudimentary coelomic pouches.

cp coelomic pouch at monocytic stage; e egestive cells; fp food particles; i ingestive cells.

the environment. In such a habit the only different factors in environment are differences in the surroundings of the upper and lower surface respectively, so that in further evolution involving also definite direction and combination of movement in the cells, a dorsiventrality will be induced with the formation of an ingestive aperture on the ventral surface. This is illustated by *Arcella* in monocytic differentiation and by Medusae in polycytic (Fig. 1a).

Hence in the transition between the two, the first stage from the diffuse condition will be a division of labour between the upper and lower cells, the ingestive cells forming the lower half and the locomotive cells the upper ¹³.

The cells will no longer be polymorphic, the division of labour in time being replaced by division in space and some cells will be ingestive troughout life, others locomotory throughout life.

If, as above stated, we assume the metazoan ancestor to be a pelagic organism, then it is evident that without assuming the survival of accidentally beneficial variations, a stimulus to heterogeneity, and to a condensation of the area of ingestion is found in the dissimilarity in environment between the upper and lower cells. This dissimilarity is most pronounced in the factor of light. It has been shewn ¹⁴ that the direct effect of increased light, within certain limits, upon monocytic organisms, is that of increased activity, so that the greater illumination of the upper surface cells would cause increased locomotory activity in those cells.

A different reactivity to light conditions might well explain the differentiation of upper and lower surfaces.

With the dawn of the polycytic individuality combined action between the locomotory cells is possible, and the result is combined action between the ingestive cells. Larger particles are brought round to the ingestive area, and these are enveloped, not by one cell but by the combined act of several cells, which also makes polycytic digestion possible. The final result of this line of evolution must inevitably be the formation of a polycytic ingestive aperture (mouth) and a polycytic digestive sac (Fig. 2). Monocytic ingestion will still take place, but the seat of actual immigration of the ingestive cells will be transferred to the hypoblast layer, whilst the archenteric cavity becomes the seat of polycytic digestion, and under the same evolutional laws a fresh area of polycytic ingestion, the stomadaeum, is formed. This theory of the evolution of the diploblastic from the monoblastic resembles in some particulars that suggested by Metschnikoff¹⁵, but the point to be especially emphasised here is that monocytic ingestion in the lowest Metazoa involves the mechanical movement of single cells to

¹³ See remarks by Balfour (Comp. Emb. Vol. I. p. 149.) on Amphiblastula larva.

¹⁴ Zopf, Encykl. der Naturwiss. Abth. I. Liefg. 1884.

¹⁵ E. Metschnikoff, Q. J. M. Sc. Jan. 1884 (Translation).

the interior, and that the hypoblastic invagination is the resultant expression of this activity.

Thus the ordinary movements of the cells in effecting throughout the life of an organism, the perpetual and necessary processes of ingestion may be made to account for the ultimate invagination of a hypoblastic tissue. The inwandering of single cells is replaced phylogenetically by the immigration of a whole tissue. All agree that the ontogenetic processes are, with few reservations, immensely hastened or accelerated epitomae of the phylogenetic processes. Thus, if the blastula be taken to represent the monoblastic larva, unless the ingestive functions are active, no inwandering of single cells will take place, but all are peripheral: A process of resultant immigration then takes place to form the gastrula. In this form again the ingestive activity is in abeyance, or there is no inwandering of single cells ¹⁶. If an accurate repetition of phylogeny were shewn in ontogeny we would expect single cells of the blastula to lead the way in migrating inwards, and later the whole area of ingestion. The gastrulation of the Echinoderma¹⁷ to some extent, follows this plan. The larval stages of such a form as Amphioxus (blastula and gastrula) are thus not identically similar to ancestral forms, but only to such forms with ingestive migratory cells in abeyance.

The theory here put forward regarding the origin of the diploblastic form from the monoblastic, and the relationship of hypoblastic invagination, has to recommend it several important points:

1) The actual mechanism of invagination is accounted for by an ingestive migratory force which occurs troughout life in lower forms.

2) The stages in invagination follow in the sequence of all evolution, from single-cell or monocytic immigration to polycytic or tissue-invagination.

The same arguments may be applied to the history of evolution of mesoblastic pouches from the hypoblast. After the establishment of the hypoblast this tissue becomes with regard to monocytic ingestion the outer limiting layer from wich the inwandering takes place. The invagination of hypoblastic tissue to form a mesoblastic pouch is thus the accelerated resultant of the inwandering activities of the single

¹⁶ It will be seen that, by this theory, the hydroids must be regarded as of a specialised type with reduced mesogloea in accordance an extinction of the process of immigration of ingestive cells. In the Medusae the immigration is present: "The mesogloea is occupied by in-wandering amoeboid cells derived from the endoderm The wandering endodermal cells are nutrient in function and represent so far isolated elements of the enteric canal system«. E. R. Lankester, Encyc. Brit. »Hydrozoa«.

¹⁷ E. Selenka, Zeitschr. f. wiss. Zool. Vol. XXVII, XXXIII, etc.

ingestive cells, and the cavity thus arising, i. e. the coelom, is the seat of the monocytic digestive processes.

Thus, just as in monoblastic forms, the single ingestive cells wandering inwards represent the first stage in the evolution of an internal enteric cavity, so in diploblastic forms such as Porifera the ingestive cells wandering into the mesogloea represent the first stage in the evolution of mesoblastic coelomic cavities (Fig. 2 a).

(Fortsetzung folgt.)

II. Mittheilungen aus Museen, Instituten etc. 1. The Term »Syzygy« in the Description of Crinoids.

Letter to the Editor.

eingeg. 28. März 1896.

With reference to the note on this subject that you kindly published for me in Zoologischen Anzeiger, 19. Bd. p. 57-61. Febr. 3, 1896, I have received many favourable expressions of opinion. It will advance the cause of reform if you will kindly permit me to quote two of the most influential.

Mr. P. de Loriol Le Fort, who has written more on both recent and fossil Crinoids than any author now living, says: »J'ai toujours compris comme vous le terme de Syzygie, c'est à dire en l'envisageant comme une mode d'union de deux articles, chacun des deux étant une unite. On ne peut pas dire d'une syzygie qu'elle est un mode d'articulation, une articulation indiquant toujours un mouvement possible«.

Mr. Frank Springer, who after the lamented death of Charles Wachsmuth, remains the leading authority on fossil Crinoids in America, writes: »I have read with much satisfaction your paper on , Syzygy ', and I endorse your proposed reform in every particular. I shall follow your plan in this respect in whatever I may do hereafter «.

It is not too much to hope that a general agreement may now be arrived at on this point. F. A. Bather.

British Museum (Nat. Hist.) 26 March, 1896.

2. New York Academy of Sciences, Biological Section.

March 9th, 1896. - Mr. F. B. Sumner read a paper on »The Descent Tree of the Variations of a Land Snail from the Philippines«, illustrated by a lantern slide. Mr. Sumner described the range in variation in size and markings in the shell, and arranged the varieties in the form of a tree of three branches diverging from the most generalized type. It was shown that these several varieties occupy the same geographical region and Mr. Sumner was of the opinion that their occurrence could not be explained by natural selection since if the colorations were supposed to be protective it would be impossible to explain the evolution of these three types. Prof. Osborn, in discussion, was inclined to take the same view. Dr. Dyar however, thought the explanation by natural selection not neccessarily excluded, since the variations seemed analogous to the dimorphism in Sphinx larvae, which has been shown by Poulton to be probably due to this factor. - The other paper was by Dr. Arnold Graf on »The Problem of the Transmission of Acquired Characters«. - Dr. Graf discussed the views of the modern schools of evolutionists and adopted the view that the trans-

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Autor(en)/Author(s): Masterman A. T.
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Artikel/Article: <u>4. On some Points in the General Morphology of the</u> Metazoa considered in connection with the physiological process of Alimentation and Excretion <u>190-198</u>