Ueber doe Anwendung des Capillarelektrometers für das Studium der Muskulären Einzelschwankung / von Prof. Burdon Sanderson.

Contributors

Sanderson, Burdon.
Physiologische Gesellschaft zu Berlin.
University of Glasgow. Library

Publication/Creation

[Leipzig?] ; [Wien?] : Toeplitz & Deuticke?], [1898]

Persistent URL

https://wellcomecollection.org/works/vu7amw3q

Provider

University of Glasgow

-1900

Separatabdruck aus dem „Centralblatt für Physiologie" vom 11. Juni 1898, Heft 6.

Ueber die Anwendung des Capillarelektrometers für das Studium der muskulären Einzelschwankung.

Von **Prof. Burdon Sanderson**, Oxford.

Die Anwendung des Capillarelektrometers zur Untersuchung der elektrischen Erscheinungen, die bei der Muskelthätigkeit zu Tage treten, wurde von Prof. Hermann kritisch beurtheilt in einer wichtigen Schrift, die vor 2 Jahren in Pflüger's Archiv (LXIII) veröffentlicht wurde. In dem ersten Theile der Abhandlung wird theoretisch besprochen, inwiefern die Angaben des Instrumentes für das Studium von Actionsströmen zuverlässig sind; das Uebrige enthält eine anerkennende Besprechung der von mir im achtzehnten Bande des „Journal of Physiology" veröffentlichten physiologischen Beobachtungen. Diese Experimente bezogen sich auf den Gastrocnemius; ich habe meine Erwiderungen auf Hermann's Kritik hauptsächlich darum aufgeschoben, um Gelegenheit zu haben, bei der Wiederholung meiner Beobachtungen einen parallelfaserigen Muskel für den Gastrocnemius zu substituiren. In den vielen hunderten von Beobachtungen, die ich in den letzten 18 Monaten gemacht habe, benutzte ich ausschliesslich den Sartorius. Prof. Hermann meint, dass die durch meine Methode erzielten Resultate für kurzandauernde Veränderungen unzuverlässig seien (a. a. O., S. 448), und dass die Resultate mit den durch anerkannte Methoden erlangten nicht übereinstimmen. Er findet, dass die doppelsinnige Einzelschwankung des Muskels bis zur Unkenntlichkeit entstellt wird. Er gibt zu, dass die wahre Curve aus der photographischen construirt werden kann (S. 449), hält aber Burch's

8

Methode für mühsam und zweifelt daran, dass sie absolut zuverlässig sei; die Curve sei zu steil und dabei zu niedrig, um gemessen zu werden, und sei einer ganzen Reihe störender Umstände ausgesetzt.

Trotz dieser Anklage fahren wir fort, den Apparat zu benützen. Mein College Gotch ist augenblicklich mit einer mühevollen Untersuchung über die Reizschwankung des Nerven beschäftigt und auch ich setze meine Arbeit damit fort, in der Ueberzeugung, dass sie trotz ihrer von Hermann dargelegten „Tücken" (S. 456) zuverlässig ist.

Nach einer Theorie des Elektrometers, welche von Prof. Hermann im Jahre 1886 dargelegt wurde, ist die Geschwindigkeit der Bewegung des Quecksilbermeniscus jederzeit dem darauf wirkenden Strome proportional. Dieses Verhältnis wird ausgedrückt durch die Gleichung $\frac{dp}{dt} = hi$, worin h eine dem Instrumente eigene Constante bedeutet. Da nun, während ein Strom durch die Capillare fliesst, die einwirkende Potentialdifferenz durch die Polarisation p ausgeglichen wird, so kann man i durch $\frac{E-p}{w}$ darstellen. Wenn man voraussetzt, dass die Ablenkung der Polarisation proportional ist, so kann man schreiben: $\frac{dy}{dt} = h\frac{E-y}{w}$. In dieser Form ist die Gleichung aur die Erklärung der Elektrometercurven direct anwendbar und kann leicht in Burch's Darstellungsweise übertragen werden.

I. Herleitung der Curven der monophasischen, respective diphasischen Einzelschwankung nach der Hermannschen Theorie. Die Beziehung zwischen den beiden Vorgängen, respective der Bewegung der Säule y und der Aenderung der Stromstärke i, durch welche sie bedingt ist, kann graphisch dargestellt werden, indem wir E und y auf dieselbe Einheit beziehen, z. B. 1 Millimeter der Scala des Capillarelektrometers, auf der man y misst. In dem Elektrometer, das ich in meinen Experimenten benützte, entsprach 1 Millimeter ungefähr 1 Millivolt; d. h. also unter $^1/_{100}$ Volt Potentialdifferenz, wenn man es bis $E = y$ steigen liesse, würde es 1 Centimeter über dem Ausgangspunkte stehen bleiben. Die Abbildung (Fig. 1) ist nach diesen Angaben verfertigt worden. Nach der von Hermann gegebenen graphischen Darstellung der monophasischen Einzelschwankung (siehe Fig. 7, O a b, S. 452) dauert die Abnahme der Reizwelle dreimal so lang wie die Zunahme, es werden also die Veränderungen, welche respective an der proximalen und distalen Elektrode stattfinden, durch A B C und D E F dargestellt. Es wird ausserdem vorausgesetzt, dass die Ableitungspunkte um 8 Millimeter von einander entfernt sind und dass die Leitungsgeschwindigkeit 1200 Millimeter pro Secunde beträgt, und dass der Process für den Augenblick keinem störenden Einflusse ausgesetzt ist. Wenn wir aus irgend einem Punkte auf der Linie A B C eine Senkrechte auf D E F fällen, welche die Curve α durchschneidet, so ist die Differenz $kE-y$ der zwei Theile, (k wird eingeführt, um E auf dieselbe Einheit wie y zu beziehen) in welche die Senkrechte durch α zerschnitten ist, proportional der Tangente des Inclinationswinkels der Curve α an dem Durchschnittspunkte. Sie ist bei 0·005 Secunden am steilsten, wo die Tangente des Inclinationswinkels etwa = 1. Bei 0·009 Secunden erreicht die Curve ihren Höhepunkt (k E—y = 0). Nach 0·012 Secunden ist die absteigende Inclination (Tangente des Winkels) 0·5, nach 0·015 Secunden 0·25 u. s. w. Die Curve α stellt die theoretische diphasische Curve des Sartorius bei meinem Elektrometer unter den genannten Bedingungen dar. (Abstand der Elektroden 8 Millimeter, Leitungsgeschwindigkeit 1200 Millimeter).

Wenn die zweite Phase D E F unterdrückt wird, was der Fall ist, wenn die distale Ableitung am abgetödteten Ende des Sartorius stattfindet, so stellt β die Elektrometercurve der Einzelschwankung dar.*) In einer von irgend einem Punkte aus in A B C auf die Axe gefällten Senkrechten würde der Theil über β der Differenz k E—y entsprechen. In dem ersten Theile bis etwa 0·007 Secunden ist β mit α identisch. Bei 0·01 Secunden ist die noch aufsteigende, aber abnehmende Inclination = 0·5. Bei 0·014 Secunden erreicht die Curve ihren Höhepunkt und nimmt dann sehr langsam ab. Von dem Abschlusse der zweiten Phase aus wird sie keinem äusseren Einflusse unterworfen, sondern nimmt die Form einer Curve an, bei der gleich abständige Ordinaten proportional sind (logarithmische Curve).

Bei längerem Zeitintervall zwischen der ersten und zweiten Phase (Aufschiebung der zweiten Phase um 0·004 Secunden, siehe D E F) würde die Curve die Form γ besitzen. Sie erreicht bei 0·012 Secunden ihren Höhepunkt und bei 0·0156 Secunden ist ihre absteigende Inclination 0·85. Sie verfolgt die monophasische Curve β länger und weiter als α. Folglich ist ihre Amplitude grösser. Ihre Senkung ist steiler, so dass sie mehr symmetrisch erscheint.

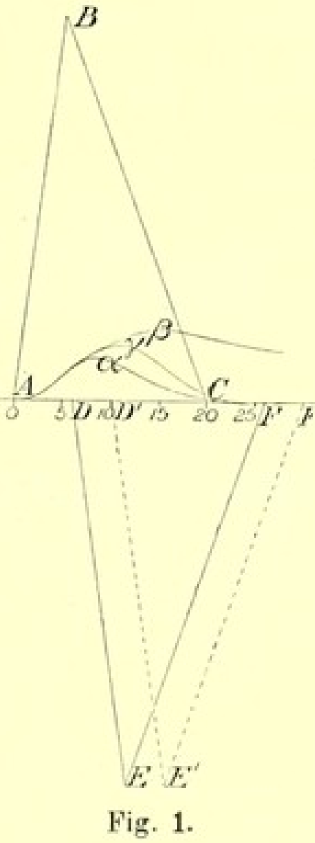

Fig. 1.

II. Vergleichung der photographischen Curven des Sartorius mit den theoretischen Curven. Wir müssen jetzt untersuchen, inwiefern die photographischen Curven eines curaresirten, mit ableitenden Elektroden versehenen Sartorius sich in Einklang befinden mit den oben beschriebenen theoretischen Curven. Dazu finde ich es am zweckmässigsten, einen wenigstens 12 Stunden in 0·6procentiger Kochsalzlösung conservirten Sartorius zu benutzen. Bei einem solchen Sartorius bekommt man, bei einer Temperatur (der Kammer) von 0·6° C., eine Leitungsgeschwindigkeit von 1000 bis 1500 Millimeter.

---

*) Der Endtheil der Curve β (Fig. 1) ist zu meinem Bedauern nicht ganz genau gezeichnet. Der Höhepunkt soll, der Beschreibung im Texte gemäss, im Durchschnittspunkte der Curve mit B C sein.

Fig 2, gibt genaue Abbildungen von drei photographischen Curven α, β γ, welche mit den gleichnamigen theoretischen Curven correspondiren. Der Abstand der ableitenden Elektroden war bei α und β 8 Millimeter, bei γ fast noch einmal so gross. Die distale Elektrode war am tibialen Ende des Sartorius, die Entfernung der Reizstelle von der proximal ableitenden Elektrode 12 Millimeter.

Die Curve der monophasischen Schwankung β culminirt erst 0·03 Secunden bis 0·04 Secunden nach dem Anfange der Bewegung der Säule. Bis zu diesem Punkte verfolgt sie den Lauf der theoretischen Curve genau; nachher sind sie verschieden. Die Muskelcurve verfolgt nie den Lauf der Depolarisationscurve des Elektrometers, wie sie es thun würde, wenn bei dem Ende der eigentlichen Schwankung die beiden Ableitungsstellen äquipotential würden. In ihrem Laufe macht sich einige Zeit nach der Reizung eine dauernde, aber nicht sehr grosse Abnahme der vorher existirenden Potentialdifferenz bemerkbar. Die Curve der diphasischen Schwankung ist während einer Periode, die von dem Zeitraume zwischen der ersten und zweiten Phase abhängt, mit der monophasischen identisch. Bei beständiger Fortpflanzungsgeschwindigkeit variirt diese Periode mit der Distanz zwischen den Elektroden. Wenn die Ableitungsstellen nahe zusammen stehen, hat sie die Form α; wenn der Abstand grösser ist, hat sie die Form β u. s. w. Die Uebereinstimmung dieser Curven mit den theoretischen von Fig. 1 ist bemerkenswerth.

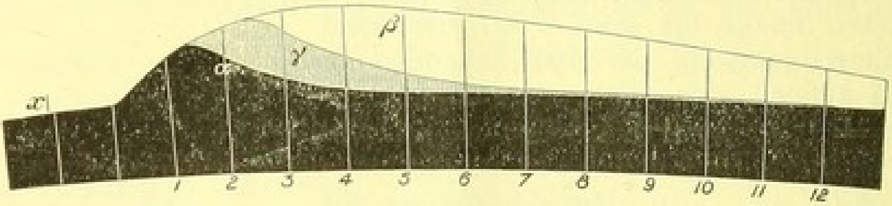

Fig. 2. Drei photographische Curven desselben Muskels (Sartorius). α und γ zwei Doppelschwankungen mit verschiedenem Abstande (bei α 8 Millimeter, bei γ 15 Millimeter) der ableitenden Elektroden. β Curve der einsinnigen Schwankung, x Reizmoment. Die polaren Ordinaten entsprechen Hundertel einer Secunde. Distale Elektrode am tibialen Ende des Sartorius. Entfernung der Reizelektroden von der proximalen ableitenden Elektrode 12 Millimeter. — Beim Gastrocnemius fand ich vor vielen Jahren, dass die photographische Curve der einsinnigen monophasischen Schwankung dieses Muskels eine Eigenschaft besitzt, welche so oft bemerkbar war, dass sie charakteristisch schien. Die Curve zeigte ein rasches Steigen, das von einer langsameren Bewegung („Hump") gefolgt wurde. Beim Sartorius ist diese Eigenschaft nicht bemerkbar.

Von den drei Curven hat die monophasische die beständigsten Eigenschaften. Ihre Form wird durch Aenderung der Entfernung zwischen den Ableitungsstellen nicht beeinflusst, vorausgesetzt, dass der Sitz der Reizung gleich weit entfernt ist von der proximalen Elektrode. Bei der oben beschriebenen Ableitungsweise ist sehr wenig Unterschied zu bemerken in der Wirkung eines directen und eines indirecten Reizes.

Trotz der Verminderung der Fortpflanzungsgeschwindigkeit bei erkälteten Muskeln kann man sie doch vortheilhaft zum Studium der Schwankung benutzen. Denn insofern die Dauer der Veränderung in jedem einzelnen Elemente auch durch Kälte verzögert wird, bleiben die Zeitverhältnisse normal. Bei einer späteren Gelegenheit werde ich zeigen, dass die Curven bei niederer Temperatur nicht nur längerdauernd, sondern auch grösser sind als bei der gewöhnlichen. Der Zweck dieser Mittheilung ist, zu zeigen, dass der Vergleich der theoretischen mit den photographischen Curven des Elektrometers einen guten Beweis liefert, dass letztere selbst bei kurz andauernden Veränderungen zuverlässig und brauchbar sind.

Ich kann meine Mittheilung nicht beendigen, ohne hinzuzufügen, wie sehr ich Herrn Hermann für seine deutliche Auseinandersetzung der Theorie verpflichtet bin. Die einzige Anklage, die ich gegen Hermann machen möchte, bezieht sich auf seine Benutzung der Ausdrücke: „Deformirung", „Verzögerung" u. s. w. Die Curve γ der Fig. 1 ist gewiss nicht „deformirt", obgleich sie mit A B C keine äusserliche Aehnlichkeit darbietet. Nicht weniger ist, nach meiner Meinung, die gleichnamige Curve γ der Fig. 2 eine treue Uebersetzung der Curve der Veränderung, durch welche sie producirt wurde. In Bezug auf den Satz von Hermann (S. 443): „Der Grad der Promptheit und Treue der Reaction hängt, wie sich leicht ergibt, ausschliesslich von dem Product rt etc.", möchte ich bemerken — Promptheit: Ja! Treue: Nein! Bei meiner Curve γ der Fig. 1 ist $r = {}^1/_{40}$. Wenn ich ihm den Werth ${}^1/_4$ gegeben hätte, würde sie weniger verzögert gewesen sein, aber hätte A B C nicht wahrer dargestellt. Ich gebe zu, dass dies nur eine Wortfrage ist, aber in der Wissenschaft haben auch Worte ihren Werth.

Ich hoffe, in kürzester Zeit im „Journal of Physiology" weitere wichtige Bemerkungen von Hermann zu besprechen.

Im Selbstverlage. — K. u. k. Hofbuchdruckerei Carl Fromme in Wien.

(Separat-Abdruck aus dem »Zoolog. Anzeiger« No. 501. 502. 503. 1896.)

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.

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 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-mouth[1], 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« areincluded 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 ingestion[2] 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 mbrella, the sub-umbrellar cavity thus formed being lined by a layer which both structually and ontogenetically belongs to the outer layer The umbrella serves the double function of locomotion and ingestion[3]. 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 appreciable[5] degree in ingestion.

Fig. 11.

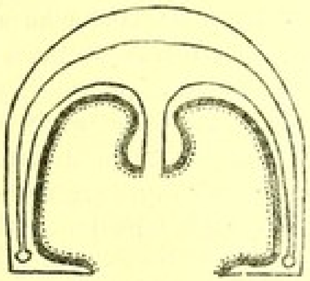

Fig. 12.

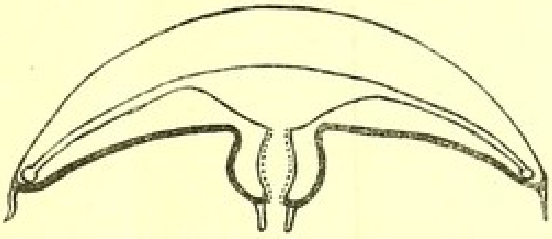

Fig. 11. Diagramm of Hydromedusa, showing locomotive-ingestive area (locomotory = black lined) (ingestive = dotted).

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

In a Ctenophore, such as *Cydippe*, (Fig. 13) the sub-umbrellar ity, as is proved by the transitional form *Ctenaria*[6] has been com- y invaginated to form what is usually known as the stomach, e 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 food-passage 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.

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.

Fig. 13.

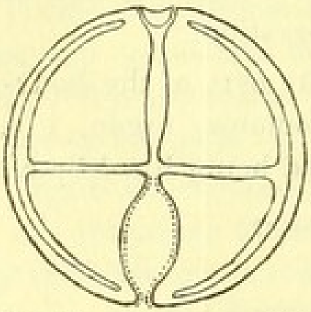

Fig. 13. Diagram of Ctenophora, showing ingestive (dotted) area, and fresh form of locomotion, not indicated.

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 stomodaeal ingestive area, so from the walls of the Vertebrate hypertrophied ingestive tract (primitive groove) the elongated dorsal nerve area (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 order [8]. 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 area[9]. 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 colony[12].

---

[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.

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 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

Fig. 1 u. 1a.

Fig. 2 u. 2a.

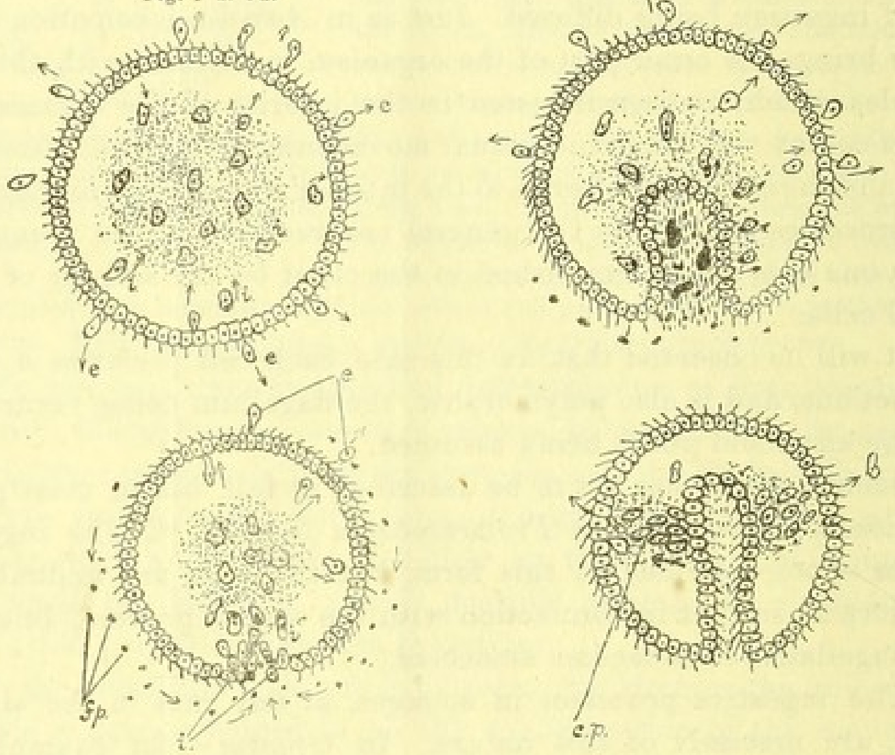

Fig. 1. Transverse section of monoblastic multilateral colony of cells with diffuse monocytic ingestion, digestion and egestion. The dotted area in this and the following figures (1a, 2, 2a, 3) represents the area of predominatingly nutritive fluids, whilst the white parts represent the area of predominatingly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

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 dissimilarty 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 Metschnikoff[15], 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 Echinoderma[17] to some extent, follows this plan. The larval stages of such a form as Amphicxus (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).

It follows from this, that »mesenchyme«[18], occuring in ontogeny of any organism must be regarded as the survival of or return to the first stage in evolution of the coelom, and that the direct formation of the mesoblastic pouch by invagination is an acquired process in which the tissue-cells have lost their individuality.

Summarising the above, we may state:

That in the scheme of Metazoan alimentary processes, from the actively ingestive area migrate inwards the single cells, which later perform the digestive function, and at any particular part of the ingestive area at which ingestion is most active there in the course of phylogeny a complete invagination is effected, an accelerated imitation of the same occuring in ontogeny: precisely the same migratory ingestive movement accounting for both the evolution of endoderm and of the mesoderm.

In polycytic ingestion, a further area of tissue cells becomes subservient to ingestion, and forms a special pseudo-endodermal area, known to morphologists as the stomodaeum.

The significance of the distinction between monocytic (intracellular) and polycytic (extracellular) digestion is well known, but the part which must be emphasised here is that in the evolution of the digestive processes of the Metazoa the unattained ideal is the perfection of the polycytic digestion to the entire exclusion of monocytic processes[19]. Although in the digestion of proteids and carbohydrates the polycytic method becomes predominant yet the monocytic ingestive and digestive processes survive in the highest types in connection with the absorption of fats[20] and in the phenomena of phagocytosis[21].

---

[18] From this point of view, the ontogenetic occurrence of »mesenchyme« represents the phylogenetic evolution of monocytic organs, by the indefinite delay of the alimentary mechanical movements, and this is succeeded by polycytic tissue invagination of »mesoblast«. The »mesenchyme« representing the lower type is naturally abbreviated out of occurrence in higher types. — Compare: O. and R. Hertwig, Die Coelomtheorie. 1881.

[19] For review of the work on monocytic and polycytic digestion in Coelenterata, see S. J. Hickson, loc. cit. p. 3.

[20] »Thus we arrive at the result that, in the lower Vertebrates, — and, with certain limitations, in the higher types also, — active or mechanical processes take place in digestion«. R. Wiedersheim, Comp. Anat. Vertebrates. — E. A. Schäfer, Internat. Journ. of Anat. and Hist. Vol. II. P. I. 1885.

[21] M. A. Ruffer, Q. J. M. S. XXXII and E. Metschnikoff, Zeitschr. f. wiss. Zool. et Biol. Cent. etc.

The perfection of the polycytic digestion is then the key-note of the principles upon which the metazoan digestive system is elaborated. On the other hand, at the base of the metazoan tree is the sponge group in which there is no polycytic digestion whatever[22]. The pores are polycytic digestive organs, and the canals represent a polycytic enteric cavity; to some extent the osculum may be regarded as a polycytic anus. All food particles, however, which are made use of by the sponge must be absorbed by each flagellated cell, separately, and thus monocytically. In fact the Porifera are to be regarded in this respect as colonies of Protozoa that the ingestive and digestive functions are carried on, monocytically, by the independent and individual energies and actions of single cells lining the inner cavities. Interdependence between the respective cells of the colony only commences when digestion has been effected and a distribution of the liquid products of digestion takes place. This distribution of assimilated material to all the colony allows of a certain amount of specialisation in certain cells to sexual, skeletal and protective functions, which feature brings the Porifera into line with the protozoa. These points may be summarised by a physiological classification of animal organisms:

1) Protozoa: Unicellular or multicellular with monocytic ingestion, digestion and egestion.

2) Porozoa (Porifera): Multicellular animals with polycytic ingestion and egestion and monocytic digestion.

(Many polycytic ingestive apertures.)

3) Metazoa: Multicellular animals with polycytic ingestion, digestion and egestion.

(One polycytic ingestive aperture.)

In the Porozoa and Metazoa all the monocytic processes also persist to a greater or less degree.

Just as polycytic ingestion is essentially connected with the stomodaeum, so polycytic ingestion is connected with the endodermal tissue, and in this tissue arise digestive glands.

The fact that an animal absorbs solid food necessitates the elimination of the indigestible residue from the organism. This process is known as Egestion.

Turning to the Protozoa we find that monocytic egestion is effected by simple contraction of the protoplasm resulting on the extrusion of the foreign body through a temporary or permanent anus.

In Amoeba, the waste residue may leave the body at any spot in

---

[22] A. T. Masterman, loc. cit. p. 7.

the cell-surface exactly as the ingestive function may also be active at any point. In fact there is diffuse monocytic egestion.

In the higher Protozoa, the egestive function becomes more confined to one particular point in the limiting surface and there the temporary or permanent anus is formed. The evolution of the monocytic egestive aperture in the Protozoa is parallel to that of the ingestive opening or cell-mouth.

In the Metazoa, the function of polycytic egestion is directly connected with that of polycytic ingestion. The residue from the polycytic digestion, or in the case of the sponges of the residue of food which has not been monocytically ingested, leaves the body through the polycytic egestive aperture or anus. This may be synonymous with the polycytic mouth in the lowest forms, but where they are separate, some part of the outer-layer is invaginated to form an organ of egestion, known in ontogeny as the proctodaeum, so that the Metazoan alimentary canal has three polycytic members corresponding to the three physiological functions of alimentation:

Organ.	Function.	Phylogenetic Origin.	Ontogenetic Origin.
Stomodaeum	Ingestion	Ectodermal	Epiblastic.
Enteron	Digestion	Endodermal	Hypoblastic.
Proctodaeum	Egestion	Ectodermal	Epiblastic.

The want of certainty with regard to the Phylogenetic origin of the polycytic anus obscures also the history of the proctodaeum.

It has been seen that in the Metazoa monocytic ingestion consists not only of an ingestion of food particles into the substance of the cell, as in the Protozoa, but also of the subsequent immigration of the cell to the interior of the organism: in the monoblastic form into the segmentation cavity and in the diploblastic organism, into the »mesogloea«. In a precisely parallel manner the monocytic egestion as occurring in the Metazoa consists not only of the ejection of the indigestible residue from the cell as in Protozoa, but of the expulsion of the whole cell with its contents from the organism. This process appears to be one of very general occurrence in the Metazoa and is an important factor in the determination of their morphology. It is quite distinct from the excretory processes[23] and the emigrant cells should

---

[23] It is however quite likely that in many cases the ek-phorocytes will give reactions indicating the presence of excretory liquids in them. It is possible that the organism may make use of these cells to carry away its excreta (cf. autumnal leaves)

be known either as egestive cells or ek-phorocytes and not as »nephrocytes«: many so-called excretory organs appear to belong truly to the monocytic egestive function.

In studying the monocytic egestion one need not necessarily follow out the whole metabolic circuit, for although normally ingestion takes place, in diplo- or triploblastic forms, at the endoderm layer, yet the ingestive cells are to be found in the interior (coelom) and if foreign particles be introduced, artificially, into the coelom, the seat of monocytic digestion, they are got rid of by the organism by the normal egestive methods.

These experiments have not been conducted for all the metazoan types of organism but sufficient data are to hand to show a parallel series to the ingestive processes.

In the Echinoderma[24] the ek-phorocytes appear to leave the organism by any part of the outer layer which is suitable, such as the branchiae. They leave the coelom and wander through its outer wall and the ectoderm to the exterior. Although Durham shewed only the egestion of foreign particles from the coelom, the whole circuit may be followed out by feeding Asterias with pigments, which are then ingested through the endoderm layer, appear in the coelom, enclosed in leucocytes and eventually are expelled through temporary pores in the branchiae.

In the sponges[25] metamorphosed choanocytes leaving the ingestive layer pass into the mesogloea and through the ectoderm to the exterior, carrying with them the egestive residua.

We thus see that although, in the Echinoderma, the coelom is definitely established yet the monocytic egestion is of the same diffused type as in the sponges. There are no definite egestive openings from the coelom to the exterior.

In the higher coelomata, the coelom opens, however, by definite apertures to the exterior, (coelomic pores, nephrostomes) and it is more than probable that these are definitely connected with the monocytic egestive function.

The evidence for this statement lies under several heads:

1) Direct evidence of egestive cells carried to exterior by nephridia.

2) Relationship of the sexual cells, or gonocytes.

---

just as later it makes use of the egestive current in Coelomata, but it must also be remembered that the ek-phorocytes themselves are masses of disintegrating protoplasm, and de facto abounding in liquid nitrogenous excreta.

[24] H. E. Durham, Trans. Royal Society. 1887.

[25] A. T. M. loc. cit.

3) The consideration of cases in which no ciliated internal apertures are present, either undeveloped or lost.

That solid particles are borne to the exterior through the nephridia of Lumbricus is a demonstrable fact[26] and it has also been shewn that ingestive cells from the typhlosole wander into the coelom and after conducting monocytic egestion, are carried tho the exterior together with the waste residua by the nephridia[27]. (Fig. 3.)

Again, in the Capitellidae[28] though the nephrotomes are present yet the nephridia in some cases terminate in the skin, and are not carried direct to the exterior.

2) The origin of the sexual cells in Proterospongia is from the transformed and immigrating flagellated cells at the exterior and these eventually leave the colony as sexual elements[29] so that in origin and fate they correspond with primitive ingestive cells, and again in sponges[30] the gonocytes are not recognisable from the ingestive amoebocytes and suffer the same emigrant fate.

From these and other examples we may conclude that:

(a) Gonocytes and ek-phorocytes belong primitively to the same layer (ingestive area), both phylogenetically and ontogenetically, the one charged with reserve material the other with digestive residua.

Fig. 3.

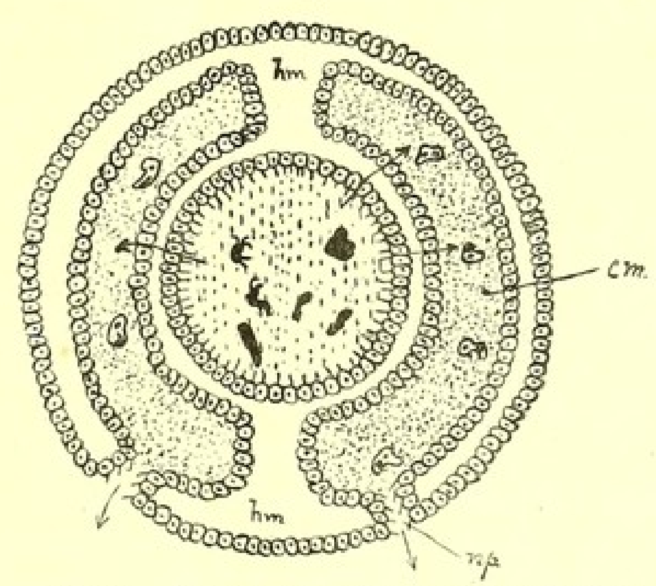

Fig. 3. Transverse section of triploblastic coelomate Metazoan with polycytic processes and monocytic ingestive into the coelomic digestive tract and egestive through the nephridial apertures. *cm* Coelom with nutritive fluid (dottet), *hm* haemocoele. *np* nephridial opening.

---

[26] »When a worm has been made to eat powdered carmine, the passage ...... from gut to yellow cells, from yellow cells to body-cavity, and thence out by the excretory tubes, has been traced«. J. A. Thomson, Outlines of Zoology.

[27] Kükenthal, Jena Zeits. XVIII, 1885.

[28] H. Eisig, Fauna u. Flora G. v. Neapel XVI. 1887.

[29] W. S. Kent, loc. cit.

[30] »New individuals are produced from the union of ova and spermatozoa, which develope from wandering amoeboid cells in the mesoderm«. W. J. Sollas, Encycl. Brit. »Sponges« 1885.

(b) Their subsequent course through the organism is similar.

Hence there is every probability in favour of supposing that the apertures which we know to serve for the discharge of the gonocytes will also be found to subserve the same function for the ek-phorocytes.

Most authorities agree that the mode of dehiscence of ova through the nephridia (nephrodinic) is a very primitive method and that the evolution of separate sexual ducts (idiodinic) is a secondary adaptation.

Thus the nephridia are known to function as gonaducts in many primitive Coelomata such as Archi-annelida[31], Gephyrea[32], Polychaeta, etc. and the history of the nephridial funnels in the Vertebrata[33] points to a secondary separation of the two functions.

The Gonocytes then, frequently, avail themselves of the nephrostomes and coelomic pores to dehisce to the exterior, so that there is ground for believing that the ek-phorocytes, of similar origin and fate, follow the same course and are discharged through the coelomic pores or nephrostomes.

3) In several of the most important animal types there is ground for believing that the nephridia have never existed and in some at least of these, e. g., Echinoderma, we have seen that it is easy to demonstrate that the egestive cells find their way to the exterior at other parts of the organism[34], but in others there is ontogenetic evidence that the nephridia, or at least the nephrostomes have atrophied.

Amongst these may be noted: 1) The Arthropoda; 2) The Vertebrata; 3) The Polyzoa.

1) The Arthropoda. If we assume the above hypothesis with regard to the function of the nephrostomes, we must also assume that in the case of atrophy of the nephrostomes, the egestive cells must either cease to leave the organism or must find an exit elsewhere. Yet another alternative there is, that the immigration of egestive cells is checked. As above alluded to, the elaboration of the polycytic digestive processes causes a correlative disappearance of the monocytic mechanical ingestion and hence also a disappearance of the monocytic egestion. The development of digestive glands, salivary, and hepatic, in the Arthropoda may thus be the indirect causes of the atrophy of the nephrostomes, so that excretion only is effected by the closed green glands, shell glands and malpighian tubules[35]. Ege-

---

[31] S. F. Harmer, Journ. Mar. Biol. Assoc. N. S. Vol. I. No. 2.

[32] See Text-books upon Sipunculus, Echiurus, Arenicola. etc. See also A. Hubrecht, Niederlandsche Arch. f. Zool. 1881 upon the Amphineura Compare also Sagitta.

[33] Rückert, »Entwicklung der Excretionsorgane«. Ergebnisse der Anat. und Entw. I. 1891.

[34] I leave out of consideration the disputed homology of the dorsal organ.

[35] Kowalevsky, Biol. Centralblatt. Bd. IX.

stive processes do, however, no doubt exist. Thus if foreign bodies be introduced into the »body cavity« of insects[36], they are taken up by wandering cells and are deposited in certain parts of the organism, more or less permanently.

The Arthropoda will be later referred to again.

2) **The Vertebrata.** In this group it has been shewn that there is a gradual differentiation of the glandular elements of the intestine and a corresponding reduction of the mechanical (monocytic) ingestive processes[37]. (**Schäfer**, **Wiedersheim**.)

In an exact correlation to this, the nephrostomial funnels become atrophied, so that in the Sauropsida and Mammalia the funnels do not appear appreciably to perform an active function in the whole life of the organism. In the larval Amphibian, on the other hand, the funnels (pronephric) are active and there is great probability for supposing that they form the normal points of exit for the egestive cells. Theoretically we would expect that, if the necessity for the exit of egestive cells from the organism be removed (by reduction of monocytic ingestion) then the loss of protoplasm to the organism involved

Fig. 8.

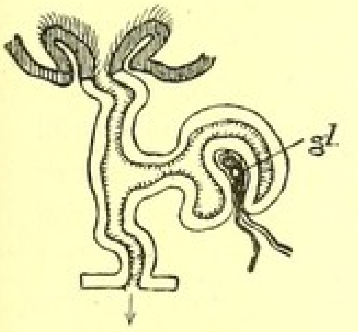

Fig. 9.

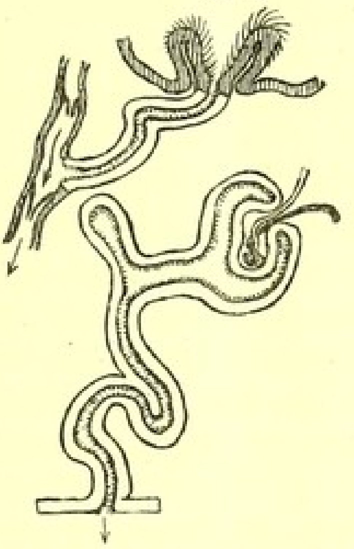

Fig. 10.

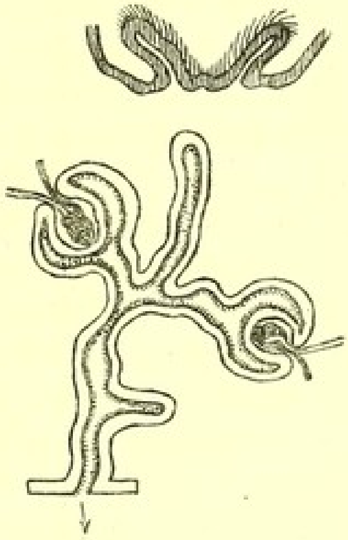

Fig. 8. Further complication of excretory elements, with formation of glomerulus (*gl*). Monocytic egestion. (Vertebrate kidney.)

Fig. 9. Secondary connexion of nephrostome with renal vein, monocytic ingestion vestigial, except in fat-absorption (?). Cells returned to vascular system. (Ontogeny of *Rana*.)

Fig. 10. Further complication of tubules of Vertebrate kidney, completely and solely excretory in function, and nephrostome closed. (Vertebrate kidney.)

---

[36] H. E. **Durham**, Q. J. M. S. XXXIII.

[37] R. **Wiedersheim**, loc. cit. und Über die mechan. Aufnahme der Nahrungsmittel in der Darmschleimhaut. Festschr. Vers. deutsch. Naturforsch. u. Arzte Freiburg 1883. — A. E. **Schäfer**, loc. cit.

by this exit would be avoided by some adaptation culminating in the complete atrophy of the funnels, and the retention of the ek-phorocytes in the system.

Searching for a repetition of phylogenetic history in the ontogeny of the frog, we find in this connection that first the funnels open freely (Fig. 8) into the body cavity (pronephric and mesonephric) and that later the mesonephric funnels obtain a secondary connection by opening into the venous system[38] (Fig. 9).

This extraordinary anatomical fact can be perfectly accounted for by the above hypothesis, i. e., that it is an adaption to save the loss to the organism of the egestive cells, which are thus returned to the vascular system.

If one holds that the ciliated funnels function for carrying excretory waste products to the exterior then the venous connection is utterly unexplainable.

Later than this, the nephrostomes in the Amniota atrophy altogether and the kidney becomes transformed into an excretory organ (Fig. 10).

In the lowest Chordata as the Hemichorda, there are simple pores or short ciliated tubes, leading from the coelom to the exterior[39] (proboscis pores, collar pores) an advance upon the diffuse and generalised ways of exit in the Echinoderma, though the ontogeny of the latter points to a definite series of pores in the bilateral ancestors of the group (Durham).

This is succeeded in the Cephalochorda by metameric nephrostomial funnels opening freely into the coelom and the branchial chamber throughout life[40].

The modifications of these funnels through the Cyclostoma, Amphibia, etc., bear out to some extent the history indicated by the Amphibian ontogeny[41].

---

[38] »In tadpoles of 18 to 20 mm length, the nephrostomial tubules break away completely from the Wolffian tubules, and acquire openings at their inner ends into the renal veins, on the ventral surface of the kidney«. A. M. Marshall, Vertebrate Embryology.

[39] W. Bateson, Q. J.M.S. Vol.XXIV—XXVI. — G. H. Fowler, Festschr. für Rud. Leuckart. 1892. — S. F. Harmer, »Challenger« Zoology XX. Appendix.

[40] T. Boveri, Zool. Jahr. Abth. für Morph. V.

[41] It is obvious that the above derivation from coelomic pores metamerically repeated precludes the likelihood of the nephridia being derived from branched flame-cell excretory organs. In this case the branching nephridia of *Capitellidae* (Eisig, loc. cit. p. 18), of *Pontobdella* (A. G. Bourne, Q. J. M. S. 1884), and of *Perichaeta* (F. E. Beddard, Q. J. M. S. XXVIII) must be assumed to be secondarily acquired, in a precisely similar manner to the reduplication of nephr. funnels in the Vertebrate phylum. Flame-cells and their tubes belong to the stage in phylogeny in which egestion (monocytic) is diffuse, hence are entirely excretory, are not

The morphology of the nephridial funnels is further complicated by the fact that from the condition where some of the nephrostomes function for discharge both of gonocytes and ek-phorocytes (a stage represented in ontogeny of Amphioxus by the period where the perigonadial coelom communicated freely with the pronephric funnel, and its mesonephric homologue in *Scyllium* [Boveri]) to that in which some funnels function solely for the exit of gonocytes whilst others having lost their egestive function atrophy, the tubules only remaining.

In the development of any pronephric (or for that matter mesonephric) tubule the funnel and tubule are first formed before the cells lining the walls take on an excretory function or become closely connected by glomeruli to the vascular system, so that it is not unreasonable to assume that the excretory function of the tubules has been secondarily acquired and that the pronephros therefore first functioned for the egestion of ek-phorocytes and gonocytes and that later the excretory function was added to it. (see below.)

Upon the evolution of the mesonephros followed by the metanephros each of these organs in turn was better adapted than its predecessor for excretory functions mainly from the fact that each was nearer the point of exit to the exterior than the one before it.

This factor, however, has no bearing upon the gonocytic and egestive function and hence the primitive pronephric funnel persists for the re-productive function (Mullerian funnel)[42].

If we suppose the primitive Chordate hermaphrodite ancestor to have been protandrous[43] then one would expect the male gonocytes, ripening first, to be discharged by the mesonephric funnels, which are nearer to the exterior and the female to retain their original pronephric connection.

The separation between the Wolffian and Mullerian ducts may then be an expression of the separation between the ducts of the two sexes in one individual rather than between the excretory and sexual functions.

3) The Polyzoa. The absence of any definite nephridia in the marine colonial Polyzoa is a well-known morphological fact[44]. This

---

segmented and drain the primary body-cavity. Compare: Gegenbaur, Comp. Anat. and R. S. Bergh, Kosmos. 1885.

[42] F. M. Balfour, Journ. Anat. and Physiol. X. 1875.

[43] G. B. Howes, Linn. Soc. Journ. Vol. XXIII. p. 544. — A. T. Masterman, Scottish Fish. Board Rep. 1895.

[44] In *Loxosoma* and *Pedicellina* have been described tubular excretory organs with blind flame-cell terminations. (Harmer, Joliet.) »It is probable that the flame cell termination, situated in the ‚primary' ‚body-cavity', is morphologically different

is usually explained as an effect of the great reduction in size of the individuals, an hypothesis wich one would hesitate to accept if any other were tenable. Upon the recogniton of the egestive function of the nephrostomes, we have, however, a reasonable explanation of either their atrophy or their not being evolved in the group in correlation to the evolution of a definite coelomic cavity.

We have seen that in a multicellular individual of the second order (Spencer) there is a sacrifice of a single cell (or individual of the first order) both for sexual (gonocytic) and egestive purposes (ekphorocytic), — in precisely the same manner in individuals of the third order colonial hydroids and polyzoa) there should by natural laws be a like sacrifice of a whole individual of the second order (polype or zooid) in the performance of the function of reproduction or egestion. This appears to be precisely what occurs in the hydroids and polyzoa. In the hydroids the egestive processes are not properly known, but the gonocytic function is conducted by the loss to the colony of one of its individuals (the medusa) which carries with it the gonocytes which in most cases wander into it, before departure, from various parts of the colonial individual.

The colonial Pedicellina apparently throws off intermittently polypoid cups, charged with detritus, and this has already been construed into an excretory process.

Again, in the Ectoprocta, there is a periodic loss the to colony of one of its individuals with the accompanying formation of a »brown body«. Harmer[45], Ostroumoff[46] and other observers agree in regarding this formation of a »brown body« as in part, at least, an excretory process. The latter definitely connects it with the absence of nephridia, and if the nephrostome has an egestive function there is every reason to suppose that the loss of the nephrostome would involve the formation of a mass of egestive detritus. There is no reason why an excretory function should not be united in the »brown body« with that of egestion. In the allied function of reproduction, in some forms (Flustra, etc.), the ova are found to occupy the whole zooecium, and presumably this involves the loss of an individual of the colony.

4) One interesting case may lastly, be cited, namely, that of the Hirudinea. In these animals the nephridial funnels although still present, do not open into a spacious coelom: the excretory part of the

---

from the ciliated funnel which opens into the ‚secondary body-cavity‘ in Chaetopoda, Mollusca, and Brachiopoda«. — S. F. Harmer, Q. J. M. S. Apr. 1885. — No egestive function is ascribed in this Essay to flame-cell excretory organs.

[45] Quart. Journ. Mic. Journ. XXXIII.

[46] Arch. Slaves de Bish. t. II. 1886.

nephridium being, however, well developed. In them also, we find that their very food and mode of life, as in truly parasitic animals, precludes all necessity for monocytic ingestion[47], and hence indirectly for monocytic egestion.

5) This case is closely allied to that of the endo-parasitic animals. In these, the food is in such a condition as to preclude the necessity for all ingestive processes, either monocytic or polycytic, and is ready for absorption into the tissues. Hence there is no necessity for either polycytic anus or for nephrostomes, and although, excretory organs are abundant, yet nephrostomes are invariably absent[48].

We have thus seen good reasons for holding that the nephrostome is egestive in function and not excretory, and upon this hypothesis can be explained the separate ontogeny of the nephrostome from the mesoblast, and its intimate connexion with the gonocytic function, whereas the excretory function (see below) essentially belongs to the ectoderm and there is no reason why it should be intimately connected with the sexual function. The close union of sexual and urinary functions is thus secondary.

Before leaving the monocytic alimentary processes we can note that it is from the immigrant ingestive cells that other monocytic organs are evolved.

The primary skeleton of Metazoa (this must be the only skeleton present in such forms as Halisarca)[49] consists solely of indigestible solid residua on their way to the exterior. In a slightly more differentiated state the sclerocytes secrete their own skeletal structures (spicules) but still continue their journey to the exterior. The spicules of sponges are said to arise in the »mesodermal sclerocytes« and to travel slowly toward the exterior[50].

If the travelling outwards be indefinitely delayed then a permanent endoskeleton may arise, or again, the deposit may form an exoskeleton in the outer tissues of the body[51].

---

[47] Compare also A. Sedgwick Q. J. M. S. XXVIII. »It is interesting to note the resemblance which would exist between the transverse section of Peripatus and the transverse section of a Leech, if the blood tracts of the former were more broken up and the nephridia of the latter did not open internally into the vascular system« and p. 20 preceding. See also A. E. Shipley, Stud. Morph. Lab. Camb. 1890.

[48] Flame-cell organs are, however, very common, confirming the purely excretory function of these structures.

[49] »Foreign bodies also contribute to the formation of the skeleton of some siliceous sponges, and occasionally form the entire skeleton, no other hard parts being present.« W. J. Sollas, Encyc. Brit. Sponges.

[50] »During its growth the spicule slowy passes from the interior to the exterior of the sponge, and is finally . . . . . . cast out as an ,effete product.« W. Sollas, Encycl. Brit. Sponges p. 47.

[51] In the Ceratosa the skeleton is a polycytic secretion of spongin, which phylogenetically, has replaced the monocytic skeleton. A gradation of types shew this.

A similar delay in the extension of the gonocytes may be carried on till late in life, and cause the phenomena of maturity, and again it may take on a cyclic activity giving rise to a rhythmic repetition at stated intervals, of the gonocytic discharge, just as a rhythmic discharge of the result of sclerocytic activity gives rise to »ecdyses«.

The connection of the monocytic egestive processes with pigmentary deposits has been pointed out by several observers[52]. In this case also one can conceive that the pigments first entered with the food, and were simple egestive residua, which travelled, like other monocytic faeces to the exterior, the influence of light upon the pigments, causing their direction to be towards the most intense illumination (Durham). As a matter of fact, the course of the egestive emigration has been worked out mainly by following up the fate of various pigments, after their introduction into the organism.

In the same way, as in the special alimentary processes, the monocytic skeletons, and other organs, may be replaced by polycytic, such as hairs, etc., which arise by the activity of several tissue cells, and their rudiments by polycytic invaginations[53].

Excretion.

In the consideration of true excretion of waste products of metabolism, it is obvious that the whole protoplasm of an organism must eliminate liquid waste products as an essential of its existence, but granted a ready interchange from cell to cell, then the cells in contact with the exterior will be those in which excretory organs make their appearance. The outer lining membrane or ectoderm has the advantage of position over the endoderm in quickly getting rid of the waste products so that in the latter will be developed only those excretions which can be utilised by the organism either directly or indirectly in the processes of digestion, and confined to the former (ectoderm) will be the function of getting rid of waste products which cannot be utilised in any way by the organism. Thus the lowest form of excretory organ will consist of the whole outside limiting ectoderm as in the case of sponges, the secretory activity of the ectoderm cells continually removing, from the body-fluid, the liquid waste products of the whole colony.

From what has already been said regarding the monocytic digestion in monoblastic forms, it is evident that in such form as in Fig. 1 digestion being effected by the cells which have migrated to the centre

---

[52] H. Eisig, loc. cit. p. 18. — H. Durham, loc. cit. p. 21. He gives a bibliography of works upon this subject. — S. Harmer, loc. cit. p. 26.

[53] See Note I. above.

the nutritive fluid set free by this process will diffuse from the centre outwards and as one reaches the outer layer the degradation products (or katabolic residua) will be predominant and will be removed by the secretory activity of the outer layer of cells or by simple diffusion through them to the exterior.

Somewhat the same distribution will occur in the higher diploblastic type (Fig. 2) the main difference being that here the beginning of polycytic digestion will set free digestive fluids in the enteric cavity which, diffusing through the endoderm, will supplement the digestive fluids arising from the monocytic digestion. (The nutritive fluid arising from the polycytic digestive activity is indicated Fig. 2 and Fig. 3.)

In the triploblastic type (Fig. 3), as already indicated, the monocytic ingestive cells migrate inwards from the endoderm into the coelom and these effect digestion, eventually leaving the coelom, with the egesta, through the nephridio-pores.

Thus the coelom is the seat of monocytic digestive activity and its fluid is a nutritive fluid containing all the nutritive products of monocytic digestion and hence also it is not surprising to find that from the walls of the coelom, in close contact with this fluid are evolved the muscles and sexual cells.

Outside the coelom is the space which represents the remains of the haemocoele cavity[54] but now no longer connected with nutrition as no monocytic digestion takes place in it; in fact, this cavity represents only the outer excretory zone of the haemocoele, as found in the diploblastic form.

Thus the body fluids in a typical coelomate form are divided in two areas, separated from each other by the walls of the coelom. The haemocoele cavity as here described, differentiates into the vascular system[55], which thus arises essentially as a system of vessels fulfilling the function of carrying the waste products of metabolism (excretory and respiratory) to the outer layer.

Thus in many of the lowest coelomata (such as the Polychaeta) in which a vascular system apart from the coelom, occurs, the function of the vascular fluid appears to be one of carrying waste products to

---

[54] It will be noticed that in Hydra, the hydroids and the typical gastrula, the 'primary body-cavity' or 'haemocoele' has atrophied in correlation to the atrophy of the physiological process of monocytic ingestive immigration. This is an additional reason for regarding these types as specialised from the primitive type as exemplified by Medusae with haemocoelic mesogloea, and Sponges.

[55] Although a disputed point, a balance of evidence appears in favour of the derivation of the vascular system from a specialised part of the segm.-cavity. See Hertwigs, O. and R. Embryology of Vertebrata.

the excretory organs (skin, nephridia, branchiae) and for that purpose the vascular system has branches from all the principal organs to the nephridia and skin and to the branchiae. The fluid itself also has a pigment diffused throughout it, either haemoglobin[56] or some allied compound. In *Glycera*, *Phoronis* and *Capitella*, the pigment is carried by cells, whilst in other Polychaeta, Hirudinea, and Turbellaria it is diffuse. Haemocyanin appears to serve the same function in Mollusca and Arthropoda[57].

The blood in these forms is no doubt also partly nutritive but probably so, only by virtue of absorbing the products of polycytic digestion.

In the diploblastic form, the nutritive resultsof polycytic digestion diffuse through the endoderm, and simply re-inforce the nutritive fluid derived from the monocytic digestive processes (Fig 2), but on inspection of Fig. 3 and a consideration of the relationship of the vascular system to the intestinal canal in such a form as Lumbricus will be absorbed, not into the coelom but into the vascular space. Hence, just in the proportion in which polycytic digestion predominates in comparison with monocytic digestion in an organism, so the vascular fluid will become more of a nutritive fluid and less of an excretory, and the coelom will proportionately lose its importance, and become reduced in size.

Thus, supposing the polycytic digestion to become predominant, and the food particles to be reduced to a soluble condition in the enteron and absorbed polycytically through the enteric wall into the vascular system, then the function of distribution of nutritive fluid will be relegated to the blood or vascular fluid, the coelom will no longer act in the distribution of nutritive products, and will become reduced in size, its cavity will remain only in connection with the sexual function, and the walls only in connection with sexual organs[58]. Such a case is never seen except in the extreme degeneration of parasites, because monocytic ingestion is never quite dispensed with, — in connection with the absorption of fat the monocytic ingestion appears to survive even in the highest Vertebrata[59], though in this case also a secondary adaptation (the thoracic duct) enables the monocytic ingestive cells charged with fat also to pass into the vascular system.

The addition of a nutritive function to the blood need not

---

[56] E. R. Lankester, Proc. Roy. Soc. Vol. XXI.

[57] C. A. McMunn, Q. J. M. S. XXV: with bibliography.

[58] »In the later Molluscs the walls of the vessels have swollen out in many regions and have obliterated the coelom. . . . . With regard to the Arthropoda, Prof. Lankester formulated the same view.« Nature, March 1888.

[59] Loc. cit.

necessarily mean a complete change of function, for the respiratory and excretory functions of blood still survive in the highest types, that is to say, the function of an intermediary between the tissues and the respiratory and excretory organs, but the respiratory pigment, no longer diffuse, is relegated to special carriers (red corpuscles) whilst the plasma becomes nutritive. A perfectly parallel case of transference of function is found in the allantois whose phylogenetic history indicates it to have acquired the function of nutrition, in addition to those of excretion and respiration.

One need not multiply facts in support of the above. The blood of all the higher animals is well-known to be nutritive in function, and to also subserve respiration and excretion, whilst authorities have already been quoted to shew that in the lower coelomata this is not so, but the respiratory and excretory functions are predominant, and also that the coelom in these forms contains a nutritive fluid.

We are now in a position to return to the Arthropoda, and other Coelomata, and to give a physiological interpretation to the peculiar history and fate of the coelom in these groups[60]. The root of the whole matter, as already said, is the elaboration of polycytic digestive processes, which again is due to the fact that the organism impresses into its services the products of the excretory activity of the endodermal cells. Thus the successive steps in the elaboration of polycytic digestion, and its results may be tabulated thus:

1) Utilisation of liquid excretory products of endoderm cells (Formation of secretory glands).

2) Absorption of the liquid nutritive fluid so obtained through the endoderm into blood system.

3) Rise of blood system, as predominantly nutritive in function. (Differentiation of whole blood system and of respiratory carriers, i. e. red corpuscles.)

4) Loss of nutritive function of coelomic fluid, consequent upon reduction of monocytic digestive processes. (Reduction in size and morphological importance of coelom, and of nephrostomes.)

5) Transference by secondary adaptation of the remnant of monocytic ingestive cells (fat absorbers) to the vascular system.

All these several processes depending upon general laws and upon fundamental properties and activities of protoplasm will proceed upon parallel lines in all the great branches of the Metazoa.

One need not recapitulate in detail the morphological facts of the origin and fate of the coelom shewn especially in the developement

---

[60] A. Sedgwick, loc. cit. — E. R. Lankester, loc. cit.

of Peripatus[61] and other forms and in the morphological comparison of the coelom[62] in different types which is well known to all zoologists.

So far as I am aware, no theory prior to this has been suggested to account for the facts from a physiological basis.

Returning for the moment to the consideration of excretion, reasons have been given for connecting excretion primitively with the general ectoderm, and the organs for excretion of salts and water appear to remain in this diffuse condition even in the highest Vertebrates[63], in the case of respiration the respiratory organ is formed in each group of organisms at whatever part of the animal is most suitable for interchange of the gases, so that the anatomical comparison of respiratory organs shows a very diverse and heterologous set of ectodermal and endodermal organs which, morphologically, have rarely any connection.

Fig. 4.

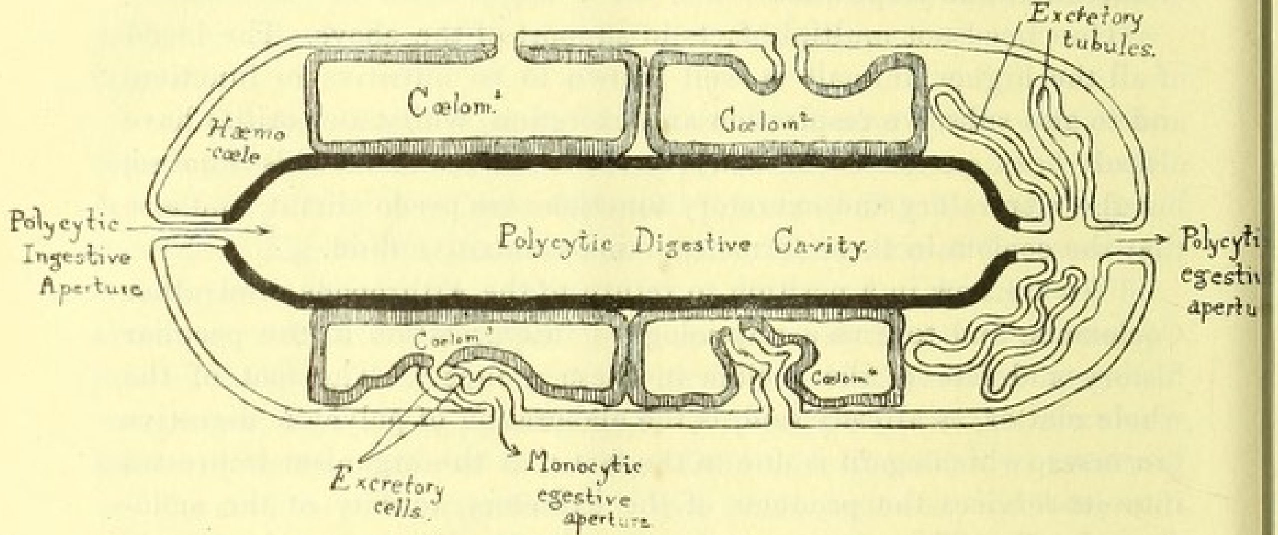

Fig. 4. Longitudinal section throug a triploplastic coelomate Metazoan with two pairs of mesoblastic pouches, showing the stages in evolution of excretory cells around the monocytic and polycytic egestive apertures. This form with a coelomic prostomial area probably represents the primitive ancestor of the Coelomata. Endoderm black, mesoderm shaded, ectoderm white.

In the case of »Nitrogenous« waste products a somewhat different state of affairs holds. These poisonous products must be got rid of as speedily as possible, so that excretory organs will tend to be developed

---

[61] In Peripatus »the functions of a perivisceral (or body) cavity are discharged by the vascular system, in which indeed the coelom is contained«. A. Sedgwick, Q. J. M. S. XXVIII. — A. Sedgwick, Developement of Peripatus. Q. J. M. S. XXV etc.

[62] E. R. Lankester, Q. J. M. S. XXXIV.

[63] In frog, waste respiratory pigment is got rid of through the skin (melanin). J. H. List, Biol. Centralbl. 1890 etc.

at any point of the ectoderm, at which a current leaves the organism. The chief points fulfilling this requirement are the monocytic egestive aperture (nephrostome) and the polycytic anus (Fig. 4) so that around each nephrostome and in the proctodaeal area nitrogenous excretory organs usually occur in the former case forming the main part of the nephridium, arising ontogenetically from the ectoderm, and consisting of active cells discharging their nitrogenous products into the nephrostomial duct, and in the latter case in the Malpighian tubules, arising ectodermally[64] and falling into the proctodaeum having precisely the same relationship to the polycytic anus as the nephridial cells to the nephrostomes (Figs. 5 to 10).

Fig. 5.

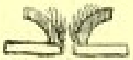

Fig. 6.

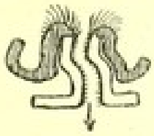

Fig. 7.

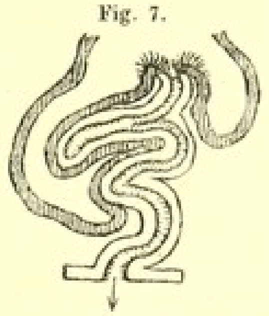

Fig. 5. This and the figures (8—10) represent the relationship of the organs of excretion and monocytic egestion, shown in phylogeny of nephridia. The complications in connexion with the sexual function have been ignored.

A coelomic pore for monocytic egestion (primary function). (Hemichorda and Cephalochorda.)

Fig. 6. Commencement of location of excretory cells on walls of ectodermal invagination.

Fig. 7. Increase of excretory surface by coiling as found in typical nephridium.

The same principles are involved in the excretory system of Amphioxus, where excretory cells[65] (ectodermal) are said to line the atrial cavity, where, of course, there is a current to the exterior not only from the nephrostomial openings, but from the branchial apertures.

From what has been said a »nephridium« must be regarded as a compound organ consisting of 1. An egestive aperture which is mesodermal in origin belonging to the coelom and egestive in function, the nephrostome, and 2. the true ectodermal excretory cells, lining a more or less complicated tube leading from the nephrostome to the exterior.

This is borne out by ontogeny[66] in so far as the nephridium

---

[64] »The Malpighian bodies arise as two pairs of outgrowths the epiblast of the proctodaeum.« F. M. Balfour, Comp. Emb. Vol. I. p. 414.

[65] P. Langerhans, Arch. für mikroskop. Anat. XII. 1876.

[66] E. B. Wilson, Journ. of Morphology. 1887. — Ed. Meyer, Mitth. Zool. Stat. Neapel. VII. 1887.

appears to arise normally, partly, the nephrostome, from the mesoblast, and partly, the tube, from the epiblast.

The history of the two series of organs can be traced from the diffuse egestion and diffuse ectodermal excretion of the sponges (and partly the Echinoderma) to the eventual extinction of the monocytic egestive organs and a perfection of the excretory organs till the Vertebrate kidney shews its nephrostomes only in ontogeny in the highest forms, whereas the excretory ducts and their connection with the vascular system are elaborated to a high degree of perfection (Figs. 5 to 10).

The Relationship to Ontogeny.

Note I. Reasons have been given for regarding the modifications of the alimentary processes to be the direct originators of other sets of organs, the instances of skeletal and pigmentary organs being taken as typical.

If in phylogeny the various organs arise from and are intimately connected with, the alimentary processes, then in ontogeny the same will result. The first signs of differentiation will appear in connection with the sustentative function, and mechanical ingestive processes will lead the way.

Thus ingestive cells wandering in from the monoblastic single layer will give rise to the inner layer, and the diploplastic form. From this inner layer again the ingestive cells give rise to the mesoblast or third layer, and again in the triploblastic type, — by further in-wandering from the mesoblast the skeletal, connective tissue, sexual and egestive organs arise. If all the organs of a type were monocytic throughout life, we might expect this form of development to prevail, but treading as it were upon the heels of the monocytic organs are the polycytic. Thus the polycytic digestive cavity is formed immediately and consequently upon the monocytic ingestion and again, upon this succeeds the polycytic ingestive area or stomodaeum. In a young form in which the monocytic ingestion and digestion can be dispensed with, the monocytic mechanical inwandering is hastened out of existence and a complete and direct formation of the polycytic organ (archenteric cavity) takes place.

Thus the complete invagination of a tissue of cells represents the formation of the higher type (polycytic) of organ.

It follows that the highest type of Metazoan ontogeny is represented by such a form as Amphioxus in which nearly the whole development proceeds upon the principle of tissue invagination, the lowest type being a form in which the organs are differentiated by successive migrating of single cells.

In the case of degeneration, if an organ degenerates, it will advert in mode of origin and in function to a simple type so that the polycytic digestive cavity atrophies in endoparasites; and, in the Tunicata can be selected instances shewing a gradation in the degeneration of the body-cavity, migratory cells replacing a solid proliferation of cells[67].

This theory at least offers an explanation of the mechanical ontogenetic processes, supposing them to be of a like nature as the mechanical processes involved in the successfully maintained mechanical processes of ingestion, digestion and egestion in the parent organism.

---

[67] A. Willey, Amphioxus and the ancestry of the Vertebrata.

Note II. Of other theories of the derivation of the diploblastic form, that of delamination[68] and also that of derivation from a syncytium[69] (granting the truth of the cell-theory) have a common drawback in that they assume that a division of cells follows, and is consequent upon, a physiological division of labour. There is no proof for this assumption, but, on the contrary, most known facts of karyokinesis and other phenomena of cell-division tend to shew that a normal cell divides into two like parts, and that after cell-division, a difference in form and function arises, due primarily to a difference in environment.

---

[68] E. R. Lankester, Q. J. M. S. XVII.
[69] A. Sedgwick, Q. J. M. S. XXV. etc.

Note II. Of other theories of the derivation of the diploblastic form, that of delamination 27) and also that of derivation from a syncytium 28) granting the truth of the cell-theory, have a common drawback in that they assume that a division of cells follows, and is consequent upon, a physiological division of labour. There is no proof for this assumption, but on the contrary, most known facts of embryogenesis and other phenomena of cell-division tend to show that a normal cell divided into two like parts and that after cell-division, a difference in form and function arises due primarily to a difference in environment.

---

27) E. R. Lankester, Q. J. M. S. XVII.

28) A. Sedgwick, Q. J. M. S. XXV. etc.

14.-1900

with comp.

A Meek

Abdruck aus:
Anatomischer Anzeiger.
Centralblatt für die gesamte wissenschaftliche Anatomie.
Amtliches Organ der Anatomischen Gesellschaft.
Herausgeg. von Prof. K. von Bardeleben in Jena. — Verlag von Gustav Fischer in Jena.
XIV. Band, Nr. 24, 1898.

Preliminary Note on the Post-Embryonal History of striped Muscle Fibre in Mammals.

By Alexander Meek, M. Sc., Durham College of Science,
Newcastle upon Tyne.

It is now some seven years since I began to interest myself in the changes taking place in muscle during growth. I was at that time giving lectures to farmers on the Natural History of the Farm Animals, and when lecturing on feeding my thoughts were directed to answering the question — how far is it possible for the farmer to form flesh in his stock? Are the fibres added to after birth or do they simply hypertrophy? It is only recently that I have had an opportunity of trying to give a solution by actual investigation, and as the results I have obtained so far bear one another out in an important point I think it well to present a preliminary communication on the subject.

The starting period of growth or post-embryonal existence is of course in Mammals a very unequal one, and a larger number of types must be examined before a general statement is possible. But in the Field Mouse (*Mus sylvaticus*), the Cat and the tame Rat, *hypertrophy of the fibres occurs accompanied by a reduction in their number* and I should think that this will be found to be true of all the Mammals, if not before, from a stage not long after birth.

It is convenient in speaking of growth changes to distinguish between proliferation of cellular elements and growth of these elements. And we cannot do better than borrow from Pathology the terms suggested by Virchow: *hyperplasia* for cell multiplication and *hypertrophy* for cell growth. For striped muscular tissue then we might say that during growth it undergoes hypertrophy accompanied by *aplasia*.

The muscles I have examined are 1) *the outer head of the triceps of the Field Mouse*, choosing for comparison a nestling and a pregnant adult. The middle third of the muscle was carefully cut out in each case, stained in borax carmine in bulk, differentiated in acid alcohol and cut into transverse sections. These were spread in succession on water on an albumenised slide. In this manner every fibre was rendered quite distinct. Many other stains were tried including several of the well-known double stains but for the purpose in view well-stained carmine sections left nothing to be desired.[1]

As fairly comparative a section as possible was chosen in each case and the fibres counted by means of an eye-piece micrometer ruled in squares. A paper similarly ruled in squares was filled in with the numbers as the fibres were counted.

Triceps of	No. of fibres	Average per square of 0.151 mm	Area of muscle section	Av. area of fibre
young Field Mouse from nest	10 070	114	1.95 mm	0.0002 mm
adult	4 613	17	4.96 mm	0.0013 mm

The above table requires little explanation: The area of the adult fibre in section is nearly seven times that of the young. It includes of course its share of the space in which it lies. The area of the muscle section was obtained by counting the number of squares of known area covered by the section. The area of the fibre was got by dividing the average number per square into the area of the square. These calculations, moreover, made with a different objective to that used for the enumeration will be found to be very confirmatory of the numbers in the first column.

A similar examination of 2) the biceps of the Cat at different ages was made with the following results:

Biceps of	No. of fibres	Average p. sq. of 0.0263	Area of muscle	Area of fibre
Cat 9 days old	83 514	7	8.4	0.0001
,, 20 ,, ,,	64 108	5.5	8.1	0.00013
,, 240 ,, ,,	37 830	1.15	22.8	0.0006

These cats all belonged to the same litter. The numbers of fibres were, however, not got by enumeration but by calculation. In the first two stages a portion was counted with a Leitz objective 7. Then by using different lower powers the number of squares covered in each case was noted. The number of squares with objective 7 contained in each of the other powers was determined by actual measurement with a micrometer slide; and thus the approximate number contained in the whole section was determined. Three such independent processes for stage 1 gave, for instance, 85 755, 83 585 and 81 200, the average being 83 514. When we consider the immense difference got in the different specimens, these numbers are quite near enough to show the general reduction which occurs.

3) The flexor profundus digitorum, with which is associated the flexor longus pollicis of the tame rat at 2 days old contained 3 020 and at 47 days old 2 275 fibres.

The results got in this preliminary investigation into the post-embryonal changes occurring in muscle fibre are weighty enough to justify immediate publication. I reserve for a future paper a more detailed examination of intermediate stages and an enquiry into how far the result may be modified by sex, variation, habit, feeding and breeding.

In my paper on post-embryonal development approached from a statistical Study of the Incisor Teeth of the Horse [1]), I showed that bone passed during life through processes of adjustment which could only be paralleled in pathological conditions. It was absorbed in response to pressure and deposited where pressure was removed. In muscle we have evidently similar processes going on. It is quite evident that the fibres which assert their position and those which are squeezed out of existence were not predestined to these fates by the evolution of determinants present in the ovum. The lucky fibres get into a better relationship with the nutritive supply through having a more telling position for taking part in the activity of the muscle. They increase and increase and their more unlucky neighbours have to give place to them. We have here indeed a survival of the fittest in a competition as keen as that say among the plants in a pasture or the branches of a tree.

8 July 1898.

---

[1]) The Veterinarian, 1897.

number contained in the whole section was determined. Three such independent processes for stage 1 gave, for instance, 62 760, 53 388 and 61 220, the average being 59 [illegible]. When we consider the immense differences got in the different specimens, these numbers are quite near enough to show the general reduction which occurs.

8) **The flexor profundus digitorum**, with which is associated the flexor longus pollicis of the same rat at 2 days old contained 4 020 and at 37 days old 2 275 fibres.

The results got in this preliminary investigation into the post-embryonal changes occurring in muscle fibre are weighty enough to justify immediate publication. I reserve for a future paper a more detailed examination of intermediate stages and an enquiry into how far the result may be modified by sex, variation, food, feeding and breeding.

In my paper on post-embryonal development appearances from a statistical Study of the Incisor Teeth of the Horse[1], I showed that bone passed during life through processes of adjustment which could only be paralleled in pathological conditions. It was absorbed in response to pressure and deposited where pressure was removed. In muscle we have evidently similar processes going on. It is quite evident that the fibres which are destroyed, the numerous fibres which are crowded out of existence were not predestined to these fates by the evolution of determinants present in the ovum. The lucky fibres get into a better relationship with the nutritive supply through having a more telling position for taking part in the activity of the muscle. They increase and increase and their more unlucky neighbours have to give place to them. We have here indeed a survival of the fittest in a competition as keen as that say among the plants in a pasture or the branches of a tree.

7th July 1905.

---

[1] See The Veterinarian, 1907.