

Name der dem Ver- suche unter- worfenen Species.	Angewandtes thermisches Mittel.	Hervorgebrachte Veränderung in den Schnuppenfarben bezw. Farbenzeichnung durch das künstliche thermische Mittel.	Bezeichnung der entstandenen thermischen Aberration.
<i>Vanessa C-album.</i>	Kälte (Eiskeller)	{ Oberseite dunkler mit großen schwarzen Flecken. Unterseite stark verdunkelt. Zunahme von interferenzfarbigen weißen und grünen Schuppen. } Corrl.	unbenannte Kälteform.
	Wärme	{ Wesentlich lichtere Farben. Compens? }	
<i>Vanessa cardui.</i>	Kälte (Eiskeller)	{ Etwas düsterere Farben. Der weiße Fleck etwas größer. } Corrl.	Kälteform noch unbenannt. noch unbenannte Aberration.
	Wärme.	{ Lichtere Farben. Compens? }	
<i>Vanessa prorsa.</i>	Kälte (Eiskeller)	{ Übergangsfarben zur helleren Winterform ( <i>Vanessa levana</i> ). Auftritt blauer interferenzfarbiger Flecken. Verdunkelung der weißen Binde des Hinter- flügels. } Corrl.	Übergang zur Kälteform.
<i>Papilio machaon.</i>	Kälte (Eiskeller)	{ Verbreiterung der schwarzen Pigment- schuppen. Zunahme der interferenzfarbigen blauen Schuppen. Die gelbliche Grundfarbe zeigt einen Stich in's weißliche. } Corrl.	Winterform des <i>Pap. mach.</i>

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

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(Fortsetzung.)

It follows from this, that »mesenchyme«<sup>18</sup>, occurring 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

<sup>18</sup> 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.

phylogeny a complete invagination is effected, an accelerated imitation of the same occurring 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<sup>19</sup>. 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<sup>20</sup> and in the phenomena of phagocytosis<sup>21</sup>.

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<sup>22</sup>. 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.

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<sup>19</sup> For review of the work on monocytic and polycytic digestion in Coelenterata, see S. J. Hickson, *loc. cit.* p. 3.

<sup>20</sup> »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.

<sup>21</sup> M. A. Ruffer, *Q. J. M. S.* XXXII and E. Metschnikoff, *Zeitschr. f. wiss. Zool. et Biol. Cent.* etc.

<sup>22</sup> A. T. Masterman, *loc. cit.* p. 7.

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 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 ingestive 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 ingestive 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 ingestive 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.
Stomodaeum	Ingestion	Ectodermal
Enteron	Digestion	Endodermal
Proctodaeum	Egestion	Ectodermal

#### Ontogenetic Origin.

Epiblastic.

Hypoblastic.

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<sup>23</sup> and the emigrant cells should 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.

<sup>23</sup> 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) 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.

In the Echinoderma<sup>24</sup> 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<sup>25</sup> 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.
- 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<sup>26</sup> and it has also been shewn that ingestive cells from the typhlosole wander into the coelom and after conducting monocytic egestion, are carried thro the exterior together with the waste residua by the nephridia<sup>27</sup>. (Fig. 3.)

Again, in the Capitellidae<sup>28</sup> though the nephrotomes are present yet the nephridia in some cases terminate in the skin, and are not carried direct to the exterior.

<sup>24</sup> H. E. Durham, Trans. Royal Society. 1887.

<sup>25</sup> A. T. M. loc. cit.

<sup>26</sup> » 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.

<sup>27</sup> Kükenthal, Jena Zeits. XVIII, 1885.

<sup>28</sup> H. Eising, Fauna u. Flora G. v. Neapel XVI. 1887.

2) The origin of the sexual cells in Proterosporgia is from the transformed and immigrating flagellated cells at the exterior and these eventually leave the colony as sexual elements<sup>29</sup> so that in origin and fate they correspond with primitive ingestive cells, and again in sponges<sup>30</sup> 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.

(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 (nephrocinic) 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<sup>31</sup>, Gephyrea<sup>32</sup>, Polychaeta, etc. and the history of the nephridial funnels in the Vertebrata<sup>33</sup> points to a secondary separation of the two functions.

<sup>29</sup> W. S. Kent, loc. cit.

<sup>30</sup> »New individuals are produced from the union of ova and spermatozoa, which develop from wandering amoeboid cells in the mesoderm«. W. J. Sollas, Encycl. Brit. »Sponges« 1885.

<sup>31</sup> S. F. Harmer, Journ. Mar. Biol. Assoc. N. S. Vol. I. No. 2.

<sup>32</sup> See Text-books upon Sipunculus, Echiurus, Arenicola. etc. See also A. Hubrecht, Niederländische Arch. f. Zool. 1881 upon the Amphineura Compare also Sagitta.

<sup>33</sup> Rückert, »Entwicklung der Excretionsorgane«. Ergebnisse der Anat. und Entw. I. 1891.

Fig. 3.

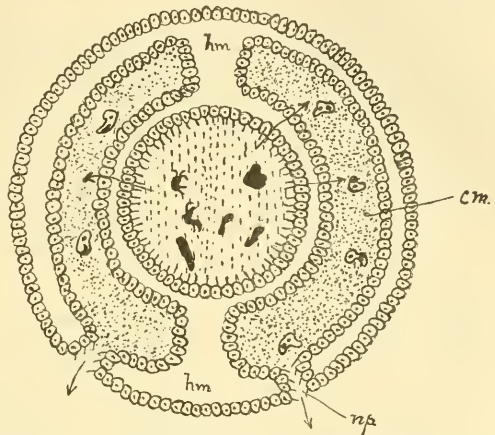


Fig. 3. Transverse section of triploblastic coelomate Metazoan with polycytic processes and monocytic ingestive into the coelomic digestive tract and egestive through the nephridial apertures. *cm* Coelom with nutritive fluid (dotted), *hm* haemocoel. *np* nephridial opening.

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<sup>34</sup>, 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<sup>35</sup>. Egestive processes do, however, no doubt exist. Thus if foreign bodies be introduced into the »body cavity« of insects<sup>36</sup>, 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<sup>37</sup>. (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

<sup>34</sup> I leave out of consideration the disputed homology of the dorsal organ.

<sup>35</sup> Kowalevsky, Biol. Centralblatt. Bd. IX.

<sup>36</sup> H. E. Durham, Q. J. M. S. XXXIII.

<sup>37</sup> R. Wiedersheim, loc. cit. und Über die mechan. Aufnahme der Nahrungsmittel in der Darmschleimhaut. Festschr. Vers. deutsch. Naturforsch. u. Ärzte Freiburg 1883. — A. E. Schäfer, loc. cit.

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 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

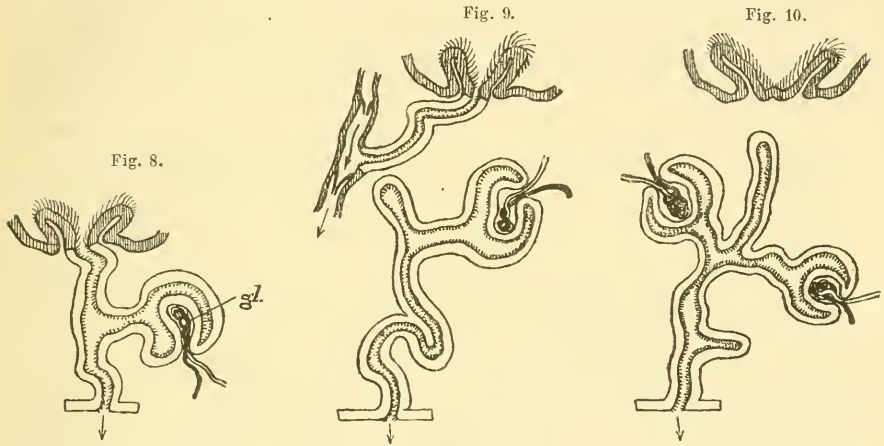


Fig. 8. Further complication of excretory elements, with formation of glomerulus (*gl*). Monocytic egestion. (Vertebrate kidney.)

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.)

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<sup>38</sup> (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.

<sup>38</sup> »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.



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<sup>39</sup> (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<sup>40</sup>.

The modifications of these funnels through the Cyclostoma, Amphibia, etc., bear out to some extent the history indicated by the Amphibian ontogeny<sup>41</sup>.

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 unrea-

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

<sup>40</sup> T. Boveri, Zool. Jahr. Abth. für Morph. V.

<sup>41</sup> It is obvious that the above derivation from coelomic pores metamericly 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 (monoeytic) is diffuse, hence are entirely excretory, are not segmented and drain the primary body-cavity. Compare: Gegenbaur, Comp. Anat. and R. S. Bergh, Kosmos. 1885.

sonable 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)<sup>42</sup>.

If we suppose the primitive Chordate hermaphrodite ancestor to have been protandrous<sup>43</sup> 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<sup>44</sup>. This is usually explained as an effect of the great reduction in size of the individuals, an hypothesis which one would hesitate to accept if any other were tenable. Upon the recognition 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

<sup>42</sup> F. M. Balfour, Journ. Anat. and Physiol. X. 1875.

<sup>43</sup> G. B. Howes, Linn. Soc. Journ. Vol. XXIII. p. 544. — A. T. Masterman, Scottish Fish. Board Rep. 1895.

<sup>44</sup> In *Toxosoma* 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 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.

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 to the colony of one of its individuals with the accompanying formation of a »brown body«. Harmer<sup>45</sup>, Ostroumoff<sup>46</sup> 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 zoecium, 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 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<sup>47</sup>, 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<sup>48</sup>.

<sup>45</sup> Quart. Journ. Mic. Journ. XXXIII.

<sup>46</sup> Arch. Slaves de Bish. t. II. 1886.

<sup>47</sup> 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.

<sup>48</sup> Flame-cell organs are, however, very common, confirming the purely excretory function of these structures.

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*)<sup>49</sup> 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<sup>50</sup>.

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<sup>51</sup>.

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<sup>52</sup>. 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

<sup>49</sup> »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*.

<sup>50</sup> »During its growth the spicule slowly passes from the interior to the exterior of the sponge, and is finally . . . . . cast out as an æffete product.« W. Sollas, *Encycl. Brit. Sponges* p. 47.

<sup>51</sup> In the *Ceratas* the skeleton is a polycytic secretion of spongin, which phylogenetically, has replaced the monocytic skeleton. A gradation of types shew this.

<sup>52</sup> 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.

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<sup>53</sup>.

### 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 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 coe-

<sup>53</sup> See Note I. above.

lom 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 haemocoel cavity<sup>54</sup> 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 haemocoel, 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 haemocoel cavity as here described, differentiates into the vascular system<sup>55</sup>, 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 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<sup>56</sup> 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<sup>57</sup>.

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 results of polycytic digestion diffuse through the endoderm, and simply re-inforce the nutritive fluid

<sup>54</sup> It will be noticed that in *Hydra*, the hydroids and the typical gastrula, the 'primary body-cavity' or 'haemocoel' 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*.

<sup>55</sup> 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.

<sup>56</sup> E. R. Lankester, Proc. Roy. Soc. Vol. XXI.

<sup>57</sup> C. A. McMunn, Q. J. M. S. XXV: with bibliography.

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<sup>58</sup>. 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<sup>59</sup>, 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 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,

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<sup>58</sup> »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.

<sup>59</sup> *Loc. cit.*

but the respiratory and excretory functions are predominant, and also that the coelom in these forms contains a nutritive fluid.

(Schluß folgt.)

### 3. On the secondary spiracles on the legs of Opilionidae.

By J. C. C. Loman, Amsterdam.

eingeg. 15. März 1896.

We are indebted to the skilful investigations of H. J. Hansen<sup>1</sup> for the discovery of spiracles on the legs of some *Opilionidae*. They were found only in the Family of *Phalangioidea* Thor., which is however widely spread, species being known to exist in nearly all parts of the world. In this family the tibia of each leg possesses two minute spiracles, one proximal, situated on the backside of its basis quite near the patella, the second, distal one, on the fore and upper part at a little distance from the metatarsus. The external opening of the spiracle leads into a kind of respiratory cave of the form of a lens, situated immediately beneath the skin, and the trachea opens itself through the interior wall of this cave. As for the variations of position and size in different genera I may refer to the description of Hansen. On the whole the differences are slight. After many measurements I found the average diameter of the proximal spiracle of *Phalangium opilio* L. to be 0,14 mm, that of the distal being always a little smaller, only 0,11 mm.

The tracheal system of Opilionids, as hitherto known, consists of two big tracheae originating from stigmata, situated in the groove between the fourth coxa and the abdomen. Each foot receives two smaller branches from the principal one, which are to be seen running down the femur and the patella. One of these a little larger than the other, communicates with the proximal spiracle of the tibia, whereas the second passes down the tibia and reaches the distal spiracle, its branches going as far as the tarsus.

Now the tracheae of Opilionids, as far as we know or may guess, are formed in early stages of development by invagination of the ectoderm, and therefore it seemed of interest to investigate whether these secondary spiracles had a similar origin as the main trunks.

So I searched after very young harvest-men during the spring of 1894 and 1895 and succeeded in collecting some dozens, most certainly belonging to different genera, probably *Phalangium opilio* L. and *Acantholophus spinosus* Bosc, but, as young Opilionids differ from the adult ones in nearly all systematical characters (external structure, colouring, etc.) it is impossible to determine the species, they belong to, with absolute certainty.

<sup>1</sup> Dr. H. J. Hansen, Entomologiske Meddelelser, 1893. p. 198.



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