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LXVIII.—*Critical Observations on Frenzel's Mesozoon Salinella: a Biological Sketch.* By Prof. STEFAN APÁTHY*.

In the 'Zoologischer Anzeiger' for 1891, no. 367, pp. 230 *et seq.*†, and in the 'Biologisches Centralblatt,' Bd. xi. pp. 577 *et seq.*‡, Frenzel described a new animal, on which he bestowed the name *Salinella* §. The creature is a tube provided with two apertures—mouth and anus—and its wall consists of a SINGLE LAYER OF CELLS. The cells on the ventral surface are similar to one another and finely ciliate; it is only around the mouth, which is not quite terminal in position, that certain of the cells are provided with stouter cilia. On the dorsal side the cells bear short setæ instead of cilia. The surface of all the cells which is turned towards the intestinal cavity is likewise finely ciliate. Food-particles are found in the intestine in a solid form. Frenzel is led to believe that intracellular digestion does not take place.

By the discovery of *Salinella* our store of facts received a very material addition, since the creature in question, as it appears to me, serves to a certain extent to fill the gap between *Volvox* and *Trichoplax*. For the comprehension of the most primary forms of multicellular life *Salinella* seems more important than the Orthonectids and Dicyemids, in which we find a genealogical stage, certainly a very ancient one, at the best merely restored by parasitism as a fully-developed animal.

A large number of questions of the highest biological importance can be connected with *Salinella*; but although in *Salinella* Frenzel furnishes an important contribution for our comparisons, he himself, in criticizing it and the problems connected with it, does not make sufficient use, for the purposes of comparison, of the store of facts already available. The result is that certain difficulties, which are indeed present,

* Translated from the 'Biologisches Centralblatt,' xii. Bd., no. 4 (Feb. 29, 1892), pp. 108–123.

† Ann. & Mag. Nat. Hist. ser. 6, no. 49, Jan. 1892, pp. 109–111, "A Multicellular Infusorian-like Animal."

‡ Ann. & Mag. Nat. Hist. *loc. cit.* pp. 79–84, "The Mesozoon *Salinella*."

§ Under the title "Untersuchungen über die mikroskopische Fauna Argentiniens," Frenzel publishes a detailed description, with figures, in the last part of the 'Archiv für Naturgeschichte' (53 Jahrg., i. Bd., 1 Heft, pp. 66–96, Taf. vii.). This was issued last December, but it did not come into my hands until later. In this paper Frenzel adds to his previous statements nothing that is essentially new; I therefore consider it unnecessary to discuss it further at present.

appear to him to be greater than, when considered from the comparative standpoint, they actually are.

In what follows I only hope to apply to an interesting concrete case nothing but what is well known and generally admitted, while venturing to add thereto certain reflections of my own.

"It is a well-known fact," says Frenzel in his second paper (*loc. cit.* p. 577*), "that between unicellular and multicellular animals there hitherto stretched a gulf which was wider than that between the vegetable and animal kingdoms; for indeed the two latter, in spite of the advances which we have made in knowledge, are even to-day hardly separable from one another." But the further our knowledge progresses the less will such a separation be possible, and the less moreover shall we consider it to be necessary: the animal and vegetable worlds have been developed in two different directions from a common basis, the non-nucleate Protoblasts. I totally disbelieve that it is permissible to institute such comparisons in the natural sciences. A gulf, if it is once present, can be neither smaller nor greater than any other.

Between animals and plants a gulf might well exist; but happily it does not. It is nevertheless only in relatively quite recent times that our store of facts has been so far enriched as to render it possible to bridge over the gulf, which, from the standpoint of earlier knowledge, was only too evident. It is possible that, among the forms at present existing, there is a gulf between Protozoa and Metazoa; it is possible, nay even very probable, that it does not really exist at all, and that our array of facts only needs to be further amplified in order to bridge it over. The transition also from the unicellular to the multicellular plants is to-day quite a gradual one: why should it be otherwise from the unicellular to the multicellular animals? Frenzel contributes a very considerable pillar to the bridge, and withal exerts himself, in developing his paper, to make the gulf appear deeper and broader than it is. Our science does not deserve such an extremely pessimistic conception of its present position; although in a general way I consider pessimism—but without relapsing into resignation and exclaiming "*Ignorabimus*"!—active pessimism, to be more fruitful than activity in an exaggeratedly optimistic direction. Frenzel, however, also overlooks stones which are already in existence for the building of the future bridge between Protozoa and Metazoa.

Frenzel moreover does the modern zoologist injustice when

* Ann. & Mag. Nat. Hist. *loc. cit.* p. 79.

he says (Biol. Centralbl. *loc. cit.* p. 577; Ann. & Mag. Nat. Hist. *loc. cit.* p. 80):—"In the systematic arrangement of the group (*i. e.* the Protozoa) we are even obliged, hard though it will be for every modern zoologist, to allow ourselves to be swayed by physiological considerations, since here the purely morphological and embryological foundations are insufficient." In cases in which "unfortunately far too little attention is paid" to a "by no means unimportant difference . . . perhaps in consequence of the fact that it arises in the first place from physiological conditions only," this does not occur because it would be hard for a modern zoologist to take physiological considerations into account, but because there are unfortunately still far too many zoologists who are one-sided in their views, *i. e.* not modern. It appears to me that precisely the perception that differences of a purely physiological nature exist between organisms, especially unicellular ones, which are not to be distinguished morphologically (*i. e.* anatomically and embryologically), is one of the most important acquisitions in biology; for it teaches us that the most essential differences—at least in my opinion—between organisms are independent of the degree of development which their organization has attained; and that protoplasm, or, better, Protoblasts—for independent protoplasm, without forming any kind of Protoblast or living being (*Lebewesen*), has no existence at all—is subject to material differences even in the non-organized condition.

Indeed, we must even arrive at the conclusion—in a manner which I will perhaps indicate more closely upon another occasion—that in the non-organized condition there already were AT LEAST as many original kinds of Protoblasts as there are to-day REALLY INDEPENDENT forms of living beings, or, we might say, QUALITIES OF LIFE; probably, however, there were many more. It may be that new qualities of life, in spite of the diversity of gradually developing forms of life, did not subsequently come into existence at all; for new and different FORMS OF LIFE may arise by gradual change of shape from apparently similar QUALITIES OF LIFE, the difference between which, though present from the beginning, does not become perceptible until a higher grade of development is reached. Yet it is probable that the qualities of life which were originally present cannot all have sustained the struggle for existence until now.

More or less visible gulfs between the various forms of life are and must be present, therefore, if we would in any way identify the idea of difference with that of a gulf. The apparent size of such a gulf may in the first instance depend

upon the paucity of our supply of facts; it is, however, on the other hand merely a matter of arbitrary valuation: essentially it makes no difference whether an abyss, which we cannot cross, is ten metres or a hundred metres wide. A difference is a difference, and can really be neither greater nor smaller than any other.

And wherefore must we exclude the Protozoa "from Hæckel's fundamental principle of biogenesis"? To what extent is our knowledge of the Protozoa to upset this principle? For if there really are living creatures which are to be EXCLUDED from the fundamental principle of biogenesis, the latter is entirely invalidated. But has it recently been proved that we are confronted with insuperable difficulties if we assume that, in the case of the Protozoa also, ontogeny recapitulates phylogeny? It is true that the number of distinguishable conditions of form through which the individual life of a unicellular animal passes is much smaller than that of the series of forms in its phylogeny must have been. Yet we see the same abbreviation—relatively still more—among the Metazoa also, and, just as in the Metazoa, the series of forms in the Protozoa often becomes somewhat more complete only in a cycle of several generations. In the same way larval adaptations and other cœnogenetic conditions of form must play a perhaps even greater part among the Protozoa than they do in the case of the Metazoa.

If phylogeny is really repeated in ontogeny it must be possible to rediscover in the individual development of a Protozoon THE INITIAL STAGE ALSO OF THE NON-NUCLEATE PROTOBLAST, THE STAGE OF THE MONERA. The same demand must, however, be presented to the Metazoa also; for in their case, too, phylogeny cannot have proceeded from the nucleate Protoblast, but rather from the non-nucleate primary stage of all living forms. But the ontogeny of every Metazoon has hitherto appeared to commence with the stage of the egg-cell (or the reproductive cell in general), therefore with the nucleate Protoblast. Yet I now find it possible, owing to the discovery of the general diffusion of centrosomes (attraction-spheres) and their, so to speak, leading rôle in cell-division, to trace back the ontogeny of the egg-cell also, and consequently that of all Protozoa, to the stage of the *Monera*. But the stage of the non-nucleate Protoblasts is at the present time always passed within the mother-cell, before delimitation of the daughter-cells occurs; for as soon as division has taken place in the centrosoma, the attracted area of which is equivalent to the unit of the Protoblast, therefore to its individuality, the parent individual has ceased to exist;

and the two daughter individuals are, although less separated than they subsequently become, already present before the nucleus has divided.

THE NUCLEUS OF THE PARENT INDIVIDUAL WHICH REMAINS UNDIVIDED BELONGS TO NEITHER OF THE DAUGHTER INDIVIDUALS; THE LATTER ARE THEREFORE IN THE STAGE OF THE NON-NUCLEATE PROTOBLAST. But since, for the FULL ACTIVITY of the Protoblast, the nucleus has become an organ of already indispensable importance, they must in the ontogeny receive a nucleus much earlier than may have been the case in the phylogeny. The appearance of important organs relatively earlier in ontogeny than in phylogeny is an occurrence which has indeed met with general acceptance since the writings of Fritz Müller. The unappropriated parent nucleus, which is left behind, is the more unable to lead an independent life, and relapses into its constructive parts: the daughter individuals hasten to divide among themselves this material, which is so important for the building-up of their further organization, and to construct from it a nucleus for themselves, after the pattern of that of the parent form. CONSEQUENTLY THE OBJECT ALSO OF THE MORE OR LESS COMPLICATED FORMS OF NUCLEAR DIVISION APPEARS TO BE NOTHING FURTHER THAN AN ONTOGENETIC ABBREVIATION OF THE PHYLOGENETIC PROCESS OF THE FORMATION OF THE NUCLEUS FROM THE MATERIAL SUBSTRATUM, TO WHICH THE HEREDITARY SPECIAL PROPERTIES ARE UNITED. THIS SUBSTRATUM, THOUGH NOT AS YET CONCENTRATED IN THE SHAPE OF THE NUCLEUS, AN ORGAN SUBSEQUENTLY SO IMPORTANT, CERTAINLY BELONGED ALSO TO THE NON-NUCLEATE STAGE IN THE PHYLOGENY*. Since, therefore, the nucleus, although as an organ more important than ever, has been to a certain extent dethroned, the Protoblast without a nucleus, no matter whether or not there still exist non-nucleate forms capable of independent life, may assume its rights once more.

The non-nucleate Protoblast, therefore, as the initial stage

* The further circumstance that daughter-cells which have been produced by simple fission do not (or less frequently) form other organs also (chromatophores, vacuoles in plants, cirelets of cilia, collars, &c. in Protozoa) quite afresh by themselves, but acquire them by division of the organs in question belonging to the parent-cell, must, I consider, likewise be regarded as an ontogenetic abbreviation of the original process of the origin of those organs. In cases, however, where the ontogeny of the cell reproduces its phylogeny more faithfully, *e. g.* in the development of unicellular and multicellular creatures from spores, the organs of the parent-cell, with a view to formation of spores, degenerate before division takes place, and the daughter-cells or their successors are obliged to reconstruct these organs, with the exception of the nucleus, afresh for themselves.

of development, can be rediscovered in ontogeny also, and indeed both among the Protozoa and the Metazoa as well. The ontogeny of a Metazoon individual does not commence with the stage of the fertilized or unfertilized egg-cell in process of division from which the Metazoon is built up; but the individual itself, which is represented by the mature egg-cell, has a past of its own which was possibly of great length, and which commenced with the non-nucleate stage within that germ-cell, from whose division into two it immediately proceeded as an unripe egg-cell.

I am unacquainted with any facts—it may be that my knowledge is insufficient for the purpose—which would render the theory of morphogeny inapplicable to the Protozoa, especially as, between the visible stages of the development of their organization, there may be others which are invisible. Development may even attain the highest stage of unicellular existence without evolving further organization; for it consists in a series of transformations of the PROPERTIES of the Protoblast, in imitation of the sequence of events in the phylogeny, wherein each arrangement of organs corresponding to the particular stage of development is only potentially combined with the succession of these transformations—that is, the latter includes only the capacity to produce such organization should circumstances require it.

In this manner it seems to me that the egg-cell ontogenetically arrives at the highest stage of unicellular existence which has been present in the phylogeny of that form of life; and all its daughter-cells and subsequent descendants, the constituents of the Metazoon body, have the capacity to reach the same stage, and must endeavour to reach it by the same way, starting from the stage of the non-nucleate Protoblast. The rapidity of the development varies according to the conditions under which the particular cell commences and continues to maintain its individual life. The greater portion of the cells of the Metazoon body, however, owing to the conditions which obtain at an earlier or later stage of the ontogeny of the latter, is compelled actually to develop the organization which belongs to this particular stage, although it may not be exhibited by other cells of the body. Those cells which, at whatever stage, really have to develop their organization, are hindered in their potential further development owing to immediate one-sided adaptation, are usually enfeebled in consequence of the performance of special functions, and never attain the highest stage of development, to which at their origin they were, so to speak, historically predestinated. It is only the reproductive cells, or, if two

kinds of them are present, only the egg-cells, which enjoy such favourable conditions as to virtually pass through in their own ontogeny the whole unicellular phylogeny of the species, and thereby to be able to transmit to their successors the complete character of that form of life.

Yet pretty frequently in the vegetable kingdom, but more rarely in that of the animals, cases also indisputably occur in which cells which had already adapted themselves to a special function, and which we should therefore be inclined to term working cells ("Arbeitszellen") in contrast to the reproductive cells, under certain circumstances rejuvenate themselves as it were, resume their virtual further development, and consequently, when they have arrived at the highest unicellular stage of their species, themselves become reproductive cells. But if, in consequence of excessive specialization or of the accumulation of aplasmatic cell-products, they have forfeited their capacity to virtually attain the highest unicellular stage, the daughter-cells which may be produced from them will also be unable to arrive at anything of the kind, and will never, even virtually, reach a higher stage of development than their parent-cell. For this reason the successors of already specialized tissue-cells can never do anything else than at the utmost develop, multiply, or regenerate the same tissue; and it is only in consequence of this that the working cells can never produce from themselves a new, independent, multicellular individual, similar to the mother.

Perhaps I am not mistaken if I consider that the theory of morphogeny appears to be inapplicable to the Protozoa only for the same reasons as those which are the cause of difficulties in the interpretation of the embryological stages among the Metazoa also—upon which, moreover, the differentiation of the body-cells likewise depends; and (briefly to repeat once more what has already been stated) these reasons themselves depend upon the fact that the different cells arrive at a different grade of virtual development, the highest possible stage of which is actually attained by the egg-cell alone: then, remaining stationary at an earlier or later stage, they display an organization which differs according to their conditions, at the same time adapting themselves in one direction and becoming far too much exhausted to be able to have a further future.

I will not, however, weigh every sentence of Frenzel's article so precisely, although indeed we only weigh that which appears to us to be worth weighing. Otherwise I might be charged with fault-finding. I hope nevertheless that Frenzel

is not one of those who are at once inclined to regard every reflection against their train of thought as "an attempt to pick holes" ("Anbohrungen").

In his article Frenzel lays most stress upon the supposed gulf between Protozoa and Metazoa, which is stated to be caused by the fact that the digestion of the Protozoon cell is intra-cellular, while among the Metazoa, on the contrary, where extra-cellular digestion prevails, the intra-cellular mode "is only met with in isolated and exceptional cases." In opposition to this I consider—and in so doing I am supported by the leading existing authorities—that the way in which the cell feeds in the Protozoa and Metazoa is least of all adapted to form a gulf between them. Quite on the contrary!

Among the Protozoa it may be a matter of momentary adaptation whether the digestion of one and the same animal is extra- or intra-cellular. And among the Metazoa intra-cellular digestion is not only not of isolated occurrence, but in the whole of the lower forms is, so to speak, predominant; in many, as *e. g.* in the Sponges, such a digestion is perhaps exclusively present. Moreover it is not "only the endoderm cells which can be concerned therein;" but also, and indeed chiefly, the amœboid cells of the mesenchyma, which, even in the highest Metazoa, as so-called phagocytes, continue to practise this faculty of theirs which they have retained from the Protozoon stage. Should we desire to construct a Metazoon out of Protozoa, we should not find, as Frenzel believes, any physiological difficulty at all in the mode of nutrition. Since the several individuals in the colony also would each digest for itself by the intra-cellular method, we could perfectly well get "beyond a simple Protozoon colony" and obtain a "typical Metazoon." If we take into consideration the more recent facts of comparative embryology and physiology among the lowest Metazoa, we arrive at the result that the several cell-individuals of the Metazoon, which continually relinquish more and more of their independence (in my opinion because the race of Protoblasts which is represented by them continually forfeits more and more of its vital energy), have on that account long retained the faculty of digesting their food for themselves. It is probable that this faculty was first lost in the ectoderm cells and then in those of the endoderm, while, on the contrary, the cells of the mesenchyma, even in the highest forms, are to-day still able to digest for themselves.

In opposition to Frenzel, we must entirely agree with Metschnikoff "that this mode of digestion represents one of the few properties of the Metazoon organism which have

been transmitted from the Protozoa, and consequently furnishes a CONNECTING LINK, however small it be, between the two groups"*. We should certainly be confronted with great difficulties, although not on the ground of nutrition, if we would construct Metazoa from Infusorian-like unicellular animals, such as the "larva" of *Salinella*. But we must not select precisely the most improbable possibility. The very earliest Metazoa are, as is generally agreed, to be derived from Flagellate-like creatures; and among the Flagellata it is really only a question of the stage of development whether the digestion of an animal is extra- or intra-cellular; the different conditions of form through which the cell passes in its life are also characterized by different modes of nutrition. In their different phases of life the Protozoa may resemble Amœbæ, Flagellata, or Ciliata, or may pass through all three conditions (Catallacta of Hæckel). The same is also true of a large number of cells in the body of the Metazoon. Should we actually wish to consider holophytic Flagellates as ancestral forms of the Metazoa, in which connexion a very pretty transition is realized by *Volvox*, it is easy to believe that, so soon as a communication between the central cavity and the exterior became established, or in some other way a gastral cavity arose, the cells gave up their holophytic mode of life, to pass for the first time to an extra-cellular method of digestion. We even find that real highly organized plants are also capable of digestion on occasions, and indeed of extra-cellular digestion, like the insectivorous plants. In criticizing the relationships of the Flagellates it is of no importance whatever whether a particular form possesses holophytic or saprophytic nutrition; not only among closely allied genera are some holophytic (e. g. *Chlamydomonas* and *Cryptomonas*) and the others (*Polytoma* and *Chilomonas*) saprophytic, but the mode of nutrition also changes within the genus (the various species of *Euglena*); nay, it is even possible for one and the same form in its predominant phase of life to pass from the holophytic to the saprophytic mode of existence by losing its chlorophyll (e. g. *Chlorogonium* and *Carteria*). The transition is, however, very easy between saprophytic forms, and therefore such as really do not digest, and those which are capable of digestion, and as a matter of fact the digestion is for the most part intra-cellular, in correspondence with the amœboid form which has been assumed (e. g. in septic Monads), though

* E. Metschnikoff, 'Untersuchungen über die intrazelluläre Verdauung bei wirbellosen Tieren,' Wien, 1883, p. 2.

occasionally also extra-cellular. For how could we designate otherwise than as extra-cellular digestion the capacity of certain Bacteria to dissolve by their secretions caoutchouc and other substances which are difficult to assail and to absorb them as nutriment?

That extra-cellular digestion is of such limited occurrence among the Protozoa, nay even that it can only take place under exceptional circumstances, is solely due to external conditions, which render extra-cellular digestion a physical impossibility for the majority of the Protozoa. Under the term digestion we understand only the process of the conversion of solid nutriment into a solution or into a fine emulsion. In this the chief part is played by the digestive secretions and ferments. In extra-cellular digestion the food is exposed to the influences of the cell-body externally to the latter; in intra-cellular digestion, however, this takes place within the body of the cell. Now how should a Protozoon, supposing it to be possible for the digestive juices to be produced at all without immediate stimulation of the protoplasm, secure their effect upon the food outside its body? The Protozoon must, in order to be able to digest, in order to render possible the operation of the digestive juices upon its food, incorporate its nutriment. But if this can also take place outside the cell, in consequence of the position of the cells in the colony, it will be possible to omit the incorporation of the food into the cells.

It is therefore in no way wonderful that the change in the mode of life of the former Protozoon, produced by living together with other cells in the consolidated, individualized, and differentiated colony, or in the Metazoon, should entail an alteration in its habits. In the first place it was of great advantage to be able to store up in an intestinal cavity much more nutriment than the several cells were in a position to secure all at once. An intra-cellular digestion was no longer unavoidable; but it gradually became for the majority of the cells of the body also impossible. THE VERY FACT OF THEIR REMAINING TOGETHER IN A COLONY, AND THEIR INCAPABILITY TO LIVE INDEPENDENTLY, ARE SIGNS OF THE INDIVIDUAL DEBILITATION OF THE SEVERAL PROTOBLASTS; in consequence of further exhaustion the majority of the cells, and gradually also the endoderm cells, forfeit the capacity for active, amoeboid changes of form; in compensation for the rest of the colony, however, the endoderm cells become specialized for the preparation of digestive juices and ferments, *i. e.* the consequence of their debilitation is the transformation of their protoplasm to digestive juices, and moreover without the application of a

direct stimulus to it. The great caducity of endoderm cells (and of gland-cells altogether) is a character of very general occurrence.

Were we able, says Frenzel, "still to regard the latter (*i. e.* the intestinal cells) at all events as Protozoon cells, this view would be absolutely inadmissible for the former, the cells of the mesoderm and ectoderm" I do not at all see why. The intestinal cells with intra-cellular digestion correspond to holophytic Protozoa; the rest of the cells of the body correspond partly to saprophytic Protozoa, because, thanks to the labours of other cells, they need only to feed, but not to digest their food; in part, however, the body-cells (especially those of the mesenchyma) are likewise holophytic Protozoa, and remain so even when the intestinal cells have long lost the faculty of intra-cellular digestion. In more primitive cases the intestinal cells themselves digest; they subsequently lose this faculty, and henceforth expend their energies in the production of digestive juices; the latter, however, are not sufficient for the digestion of the food-matter, and the wandering amœboid cells have to assist more or less with their power of intra-cellular digestion. The intestinal cells continue to be Protozoa, with which other body-cells, likewise corresponding to Protozoa, live together in a kind of symbiosis: their services to one another are reciprocal, so that their functions are consolidated into a physiological whole. Not only do the intestinal cells feed the rest, but a large portion of the latter also make provision for the intestinal cells: oxygen is in the widest sense food, just as much as albumen, fat, and carbohydrates.

I believe that I have sufficiently demonstrated in the foregoing that it is precisely the physiology of digestion which causes least difficulties in deriving the Metazoa from the Protozoa; but also the other "gulf" between Protozoa and Metazoa, which Frenzel likewise emphasizes, and which is occasioned by the multilaminar character of the Metazoa, appears to us less great when we take into consideration the following facts.

As a single-layered multicellular animal we are now also acquainted with *Salinella*, besides *Volvox*. The next stage, with the representatives of which we have closer acquaintance as adult animals, already consists—to leave *Trichoplax adharens* out of consideration—of three layers, since in them a mesoderm, or, better, mesenchyma, is already present between ectoderm and endoderm; for of animals which in the adult stage also would correspond to the typical Gastrula, and consist merely of ectoderm and endoderm, we have no knowledge.

The most cogent proof that the ancestral form of the Metazoa was the *Gastræa*—an animal with intestinal cavity and oral aperture, composed of ectoderm and endoderm, without mesoderm—is therefore wanting. WE REQUIRE THIS FORM, HOWEVER, AS A TRANSITIONAL STAGE, ONLY IF WE WOULD HAVE THE NEXT STEP IN THE SEQUENCE OF THE PHYLOGENETIC DEVELOPMENT, STARTING FROM THE BLASTULA-FORM (*BLASTÆA*), TO CONSIST IN AN INVAGINATION.

It is true that for a *Gastrula* to arise by invagination is MECHANICALLY the simplest mode of further development, and therefore it is that ontogeny, which always strives after abbreviation and simplification, so often adopts this method, especially among the higher types; therefore, on the other hand, it is also natural and easily explainable that the next stage in ontogeny after the *Blastula* is the *Gastrula* without mesoderm. But the question arises whether a similar formation of a *Gastrula* is also the PHYSIOLOGICALLY simplest possibility in the further development from the *Blastæa*. It does not appear to me that it is. The method of forming the endoderm which is physiologically the simplest, and therefore probably genealogically the oldest, is that which commences with immigration into the inner cavity of ectoderm cells, which have been forced out of connexion with the epithelium and have become amœboid, *i. e.* formation of the endoderm by apolar multilocular inward growth (Metschnikoff). The growth is apolar, because only by subsequent adaptation (accumulation of yolk) could the original polarity of the ovum be so far increased as already actually to effect a differentiation of the *Blastula*-cells, a greater difference between the hypoblast and epiblast. The cells which penetrated into the cavity of the *Blastula* afterwards gradually arranged themselves again in the manner of an epithelium to form the endoderm, after the communication of the *Blastula*-cavity with the exterior by means of the blastopore had furnished an incentive thereto. Perhaps an open *Blastæa* of this kind is even more archaic than the closed vesicle, and in that case the incentive alluded to would not have subsequently occurred, but would have been present from the beginning. I would remind the reader of the development of *Volvox*, where the young but already perfect colonies close their opening only after leaving the parent.

Now it cannot have happened either that all the immigrant cells were utilized for the formation of the endoderm, or that with the completion of the endoderm the immigration from the ectoderm at once came to an end; it is much more probable that the cells of the mesenchyma also should be

augmented in the same way from among the endoderm cells, which were by this time multiplying to excess. But then it is absolutely impossible to see why precisely such a form of animal should exist, as one in which only so many ectoderm cells become amoeboid as are necessary for the formation of the endoderm, in order not to leave any over in the shape of so-called mesoderm. The formation of the endoderm was indeed neither the object nor the cause, but merely the consequence of the immigration. As a matter of fact, such a bilaminar animal as represented by the *Gastræa* can neither have existed in phylogeny nor be in existence to-day.

That the *Gastrula* is nevertheless present in ontogeny is, as has already been mentioned, to be explained from the fact that the immediate incentive to the further development of the body from the *Blastula*, which in phylogeny was a more physiological process, dependent in a higher degree upon the individuality of the cells, has here, in ontogeny, become a more mechanical necessity. The phylogenetic method is longer, and therefore in ontogeny it is adopted merely in the case of very primitive forms (certain Porifera and Cnidaria), as opposed to which the more developed forms have gradually selected a shorter, because more mechanical, way to the same end.

Now the various colonies of Flagellata, and especially *Volvox*, present us with the highest stage of colony-formation among unicellular creatures, nay even with the most primitive multicellular animal, which already appears to possess an integral individuality. At the same or a somewhat higher stage, but developed from other unicellular ancestors, we also find *Salinella**, likewise an animal formed of an epithelial layer of cells, with an internal cavity. Now more and more cells—probably because they are weaker or stronger than their neighbours, and perhaps also because, owing to the axis of fission having been possibly somewhat oblique, they were situated more towards the interior—become continually forced from the epithelial position (if they are stronger than the rest they set themselves free), and passing into an amoeboid stage reach the inner cavity. It is possible that *Trichoplax adhaerens* corresponds to precisely this stage, in which, with the communication between the internal cavity and the exterior, the incentive to a secondary epithelial

* That cells are found upon the ventral surface which are somewhat differently constituted to those upon the dorsal side, is in this case (as also in that of *Trichoplax*) the immediate result of the creeping, and no longer floating, mode of life, and would in itself indicate no higher position than that of *Volvox*.

arrangement of the cells which have wandered into the original cavity is also wanting. But so soon as a communication was constituted between the cavity of the *Blastula* and the exterior by means of a mouth-opening, there was also provided the incentive for the immigrant cells to arrange themselves again like an epithelium, this time as an endoderm, and to pass from the *Gymnomyxa* form into a *Corticata* phase once more. Thus we already have the true Metazoon, a *Cœlenterate*, or one of the *Porifera* before us. In this series of stages we nowhere miss the *Gastræa*.

A greater difficulty than those advanced by Frenzel appears to me to consist in the fact that it is not easy to form an idea as to how the single individuality of the Metazoon has arisen from the separate individualities of the Protozoa, which at first composed a loose colony as ancestral form. This, however, is at once a question which directly touches upon the relationship between the soul of the Protozoa and that of the Metazoa, that is really the question of the soul in general!

Frenzel finally observes something also in the development of *Salinella* which is said to be difficult to harmonize with our previous knowledge. He speaks of a hypotrichous Infusorian-like unicellular animal, which he regards as the LARVAL STAGE of *Salinella*. "This nevertheless leaves a difficulty of considerable importance to be surmounted," he adds, "in that the transition from the single cell with intra-cellular digestion to the adult animal with extra-cellular digestion is enigmatical and completely unexplained." I would not consider this phenomenon to be so very enigmatical, even should the fact be established that the digestion of *Salinella* is really enzymatic, and not intra-cellular, like that of the majority of the lower Metazoa. This point, however, has already been sufficiently disposed of. Let us at once proceed to consider WHETHER A UNICELLULAR ANIMAL, WHATEVER ITS STRUCTURE, can be considered AS THE LARVA OF A MULTICELLULAR FORM.

That stage in the ontogeny of the multicellular animal which, while still unicellular, immediately precedes the multicellular condition, and is therefore the highest unicellular stage, we term, whether fertilized or unfertilized, the ripe EGG-CELL. In the case of *Salinella* we have before us—if I rightly comprehend the meaning of a phenomenon observed by Frenzel—the product of an act of copulation, we might say a zygospore; there can in this case be no question of an actual egg-cell, for there is no difference to be observed between the two copulating cells, and in fact in *Salinella* there are no special reproductive cells at all. All the cells in the body have the power of multiplying the species, and, singularly enough, the colony does not first relapse into its constituents

(like, *e. g.*, *Pandorina*), but TWO ENTIRE ANIMALS become fused together and form a common cyst. Unfortunately Frenzel was unable to trace the further phenomena within the cyst. It is, however, hardly possible to imagine anything else than the fusion of each pair of cells of different origin. If, as Frenzel writes, a continuation of cell-multiplication really takes place within the cyst, this in all probability happens before the copulation of the several cells. Unfortunately, too, Frenzel did not directly observe that the separate similar cells in the cyst pass into the unicellular Ciliate form which he has described.

Should that Infusorian really be a developmental stage of *Salinella*, it cannot nevertheless, as has already been stated, be termed a larva. The ova of many other animals also are capable of movements, particularly amœboid ones, and of feeding in the INTRACELLULAR fashion upon the neighbouring cells, such as is the case, among others, in *Tubularia* and *Hydra*; and not only can this be done by the unfertilized, immature, reproductive cell, but also, as is well known, by the fertilized one, as, for instance, in the case of certain Platyhelminthes, where, in addition to a larger number of yolk-cells, only a few fertilized egg-cells are found in the egg-capsule. The sole difference between *Salinella* and the other known cases of active egg-cells is that the latter have only to incorporate and digest the nutritive material which is already stored up for them; while on the other hand the fertilized ovum (or zygospore) of *Salinella* has itself to acquire its food by its own activity, in order to be able to proceed with the building-up of its body. Therefore it is that the faculty of reproducing the organization of the highest unicellular ancestral form in the highest unicellular stage of *Salinella* does not, as is the case in the majority of ova, remain virtual and latent. The necessity of accumulating the building-material for further development by its own activity only sets in in the case of *Salinella* earlier than in that of all other multicellular animals. In point of fact much more is demanded from an independent cell in *Salinella* than in higher animals, where the separate cells always retain less of the activity and independent energy of their unicellular ancestors. For the rest, however, the transition from the "cell with intra-cellular digestion to the adult animal with extra-cellular digestion" in the case of *Salinella* is by no means more enigmatical and unexplained than the fact that from egg-cells with amœboid digestion Metazoa develop whose body-cells—partly indeed themselves digest throughout life—for the greater part, however, are endowed with extra-cellular digestion or none at all.

The further ontogeny of *Salinella* also, subsequent to the already active unicellular stage, exhibits nothing extraordinary. Frenzel writes:—"For it is precisely the further development of this larva, incomplete though my study of it was, which proves that it does not develop into the perfect animal by means of ordinary division, much as a colony is formed from a single Choanoflagellate, but by a far more complicated process, which we may most fitly term endogenous cell-formation." We may, however, designate the segmentation of all Metazoa whatever, and even the formation of the daughter-colonies of the Volvocineæ, as endogenous cell-division ("cell-formation"). In very many cases the egg-cell has a distinct cell-membrane, and the processes of fission, in which segmentation consists, always proceed within this membrane; it often happens that it is only the already tolerably advanced larva or the almost perfect animal that leaves the cell-membrane of the parent-cell, the egg-cell. Even more distinct endogenous cell-division than in the case of the holoblastic ova is the segmentation in the meroblastic eggs, where, as for instance in the egg of the fly, the limits of the daughter-cells within the cell-membrane of the parent-cell are for a long time absolutely indistinguishable from one another.

It is indeed in the chief degree the circumstance that the daughter-cells remain in organic connexion with one another, and that they have no longer the strength to separate, which has replaced societies of cells by the higher category of colonies; and a still more intimate union of the cells, in connexion with their endogenous origin in the egg-cell and in consequence of their further individual debilitation, characterizes the Metazoa, and makes of them a single individual, an indivisible physiological whole.

That the daughter-cells and subsequent descendants of the Metazoon egg-cell have now no longer the power to separate from one another, and lead an independent cell-life like Protozoa or like the unicellular ancestors of the species, is a fact. It remains to be asked, what is the cause of this? It cannot be a change of habit owing to the living together for so long in the cell-colonies of the ancestors, for the latter is itself the first consequence of the cause for which we are seeking. I consider that the cause is to be found in a certain debilitation of the genus of Protoblasts with which we have to deal; and the latter is again nothing more than the consequence of that change in all protoplasms (vital qualities) which sets in as time goes on, even without special external influences, and which we are only able to detect through its combined effect

and its further consequences, and then term simply development. A continuous and inevitable change in the condition (mobile condition?) of matter in general is the common destiny of the universe, and is the equivalent of existence and the progress of the world. In speaking of phylogenetic development we refer this general change only to one special case, to that of living beings, where it proceeds at different rates according to the qualities of the Protoblasts, but everywhere essentially in the same direction and according to the same laws.

Certain cells in the Metazoon, owing to their peculiarly favourable conditions of life, attain to more of the original independent vital energy of the unicellular ancestors than do the rest: these cells are the reproductive ones. The egg-cell of *Salinella* proves the originality (low stage of development) of the species also through the very fact that, as a simple cell-individual, it possesses even more vital energy than does the egg-cell in all Metazoa. In a general way it is perhaps possible to advance the proposition, somewhat paradoxical though it appears, that THE HIGHER ORGANIZATION OF THE MULTICELLULAR INDIVIDUAL IS TO BE REGARDED AS THE CONSEQUENCE OF THE GRADUAL DEGENERATION OF THE SEPARATE CELL-INDIVIDUALS WHICH COMPOSE IT.

To briefly sum up what has been stated in the foregoing pages, I consider *Salinella* as a highly valuable and interesting discovery precisely because, in opposition to Frenzel's view, it at once fits in thoroughly well with our present biological theory as to the origin of the Metazoa, and, so to speak, fills a gap in the series of facts for our deductions. Frenzel is certainly quite right when he states in the concluding words of his article ('Biologisches Centralblatt'; Ann. & Mag. Nat. Hist. *loc. cit.*) that there are isolated links in Nature "for which we cannot find a place in our system, beautifully and ingeniously constructed though it is, and which tend to prove how little Nature is amenable to a dogmatic treatment on our part, a treatment which unfortunately appears to take the upper hand too much in the biological sciences, and which would gladly exclude everything which does not fit into its narrow frames." Happily, however, this great truth does not apply to *Salinella*! *.

Kolozsvár,
October, 1891.

* I have already given expression to views as to the simplest living beings, the impossibility of separating the ideas of life and individuality, and the import and causes of reproduction (fission) &c., which are in *Ann. & Mag. N. Hist.* Ser. 6. Vol. ix. 36