

daß ich bereits so frei war, den Irrthum bezüglich der vermeintlichen Umwandlung von *Hydra grisea* in *viridis* selbst zu corrigiren.

Übrigens kann ich den Zweifel auch jetzt noch nicht unterdrücken, ob Herr Dr. Otto Hamann und ich wirklich dasselbe Object beobachtet haben. Schon in seinen früheren Arbeiten spricht Herr Dr. Otto Hamann von »jodhaltigen gelben Zellen«: ich habe meinerseits »jodhaltige« Zellen niemals beobachten können, außer wenn ich selbst Jod unter das Deckglas fließen ließ, um die gelben Zellen auf Stärke-Reaction zu prüfen.

2. Contributions to the Cell-Theory.

By Patrick Geddes.

I. A Theory of the Life-History of the Cell.

Our current conceptions of the groups of the Protozoa are apt to be based upon their most prominent and permanent characters only. One thinks of an Infusorian as a ciliated or flagellated organism of permanent form, of a Radiolarian as a highly differentiated Rhizopod, with two layers of protoplasm, a gelatinous envelope, and a siliceous skeleton, while in description of a Heliozoon special attention is paid to the radiating pseudopodia with their axial filaments. In lower forms, however, more attention is paid to the whole life-cycle. In the Amoeba the encysted state is almost as familiar as the active, in the Gregarine sometimes more so, while in such a remarkable Moneron as the *Protomyxa* of Hæckel it is hard to say whether the encysted, the amoeboid, the flagellate or the plasmodial is the most prominent stage. For here is no single permanent highly differentiated form, but an eventful life-history in which one protean mass of protoplasm passes through a cycle of at least four distinct phases.

Such discoveries as those of the life-history of Monads, of the ciliate embryo of *Acinetææ*, of the multiplication of Radiolarians by Zoospores or of the union of several *Actinosphaeria* or Gregarines into a plasmodium point in the same direction, — in fact the whole progress of recent research has largely lain in revealing the existence in even the most highly differentiated forms, of a life cycle almost as complete as that of *Protomyxa*.

In other words if we make a diagram of *Protomyxa*, exhibiting the encysted, the ciliated, the amoeboid and the plasmodial stages, an essentially similar life history may be sketched out for all the higher groups of Protozoa, with blanks it is true, but blanks which the progress of discovery is constantly diminishing and seems likely indeed

wholly to fill. In short a Heliozoon differs from *Protomyxa* (over and above its possession of a nucleus) merely in the excessively high differentiation and relative permanence of the amoeboid stage of its life cycle: the Monad or the Infusor has similarly developed its ciliated stage, the Myxomycete its plasmodial. In the *Protophyta* the resting or encysted stage certainly predominates, but they too show phases of the same life cycle, as the naked motile zoospores of so many Fungi and Algae (which as »a transition from plant to animal life« so perplexed the elder Botanists) and, the amoeboid stage into which these so often collapse, bear witness.

This view at once demonstrates the thorough unity and naturalness of the Protista, and affords a basis for their classification into series corresponding to the stages of the life-cycle. In the Palmellaceae or Schizomycetes the resting and motile stages are almost equally prominent, while in the Desmids and Diatoms and the Saccharomycetes the encysted stage predominates. The Protoplasta, the Foraminifera, the Heliozoa and the Radiolaria are of course referable to the preponderatingly amoeboid type, while the Infusoria represent the ciliated. The Myxomycetes far from having any relations to the Fungi stand on the whole nearest to the Moneron or Protomyxoid type, despite the excessive differentiation of their plasmodial stage.

Huxley has called attention to the importance of the alternation between the amoeboid and ciliated stages which he terms Myxopod and Mastigopod (Anat. Invert.) and Lankester has divided the Protozoa into Gymnomyxa and Corticata (Quart. Journal Microsc. Sc. XVIII); the present proposal includes both points of view.

Leaving the details of this classification to the completed paper let us consider the physiological aspects of this cycle. A mass of protoplasm is under constantly varying conditions, at one time receiving abundant energy — heat and food — from the environment, at another little or none, and thus a rhythm of more and less vital activity ensues. The amoeboid state, as every observer knows, varies extremely with food and temperature: Haeckel and others have shown that the ciliated stage is merely an exaltation of the amoeboid, and the cilium but a rhythmically contractile pseudopodium, while on the other hand the ciliated cell may collapse into an amoeba and the active Amoeba sink gradually into a quiescent spheroidal mass.

Vast importance has been attached to the cellulose wall as an assumed characteristic of plants, yet the coat of an Amoeba or of a Myxomycete is known to be composed of cellulose. Contracting muscle evolves much carbonic acid and water, with evolution of heat. Contractility implies waste; if contractility ceases these waste products will

not be formed and heat will not be evolved. The cell-wall which appears on the assumption of the quiescent state is therefore the equivalent of the carbonic acid and water, which were before being excreted — an incompletely oxidised waste product, which by reason of its insolubility and coherence acquires at once its permanent morphological importance and its protective use. The plasmodial stage which terminates the cycle seems an almost mechanical union of exhausted cells, and such cases as those of the union of *Actinosphaeria* and *Gregarines* formerly alluded to, furnish grounds for regarding the process of conjugation as specialised from that of plasmodial union. Division may take place at any stage, most frequently, however, after cell-union.

That this cell-cycle is not beyond the reach of experimental physiology, and that such a form as the amoeboid does really underlie that of apparently far more highly differentiated organisms are evidently shown by a very simple experiment. When a living *Actinosphaerium* is treated with dilute solution of ammonium carbonate, its pseudopodia are retracted or disappear, its stroma vanishes, and it sinks into a simple granular amoeboid mass with blunt pseudopodia and finally bursts and dies.

If division takes place continuously in the encysted stage the resultant multicellular aggregate is a vegetable, if in the amoeboid or the ciliated a more or less distinctly animal organism arises. In plants the cell cycle is represented almost solely by the resting-stage, though the ciliated phase lingers on here and there in the antherozoid, and the amoeboid in the oospore. In an undifferentiated aggregate like *Magosphaera* the cell-cycle is evident, in a *Sponge-Gastrula* equally so. The development of the tissues of all the higher animals from similar embryonic amoeboid cells ought to be interpreted in the same way. Some become quiescent and these develop an intercellular substance truly analogous to cellulose, but probably differing only in the non-economisation of nitrogenous matter, others are differentiated into muscular tissue or remain merely amoeboid, others become ciliated. And thus a classification of the normal tissues from the same point of view as that adopted for the *Protista* becomes possible. We recognise the utility and physiological import of the present hypothesis when we consider the cell theory in its functional as well as in its structural aspect. Since the activities of the body are the aggregate activities of its component cells, such phenomena as the variations of muscular and nervous tonus, of ciliary activity, and even those of rest and sleep, become intelligible as phases of the same rhythm of increasing and decreasing cellular activity.

Variation and disease are much akin, for pathological changes

are essentially those variations which happen not to be conducive to success in the struggle for existence, and all variations normal and pathological alike are ultimately cellular. The structural and functional aspects of the theory are here again available, the former yields us a means of classifying the normal and pathological variations of structure alike, the functional aspect of interpreting them, both of course in terms of »the cell cycle«. Pathologists are reducing tumours to a common type essentially that of cell multiplication in the resting stage, the formation of pus and perhaps disorders of the ciliary epithelia are degenerations to the amoeboid stage, while inflammatory changes may be interpreted as a temporary and excessive intensification of cell activity.

II. An Hypothesis of Cell-Structure and Contractility.

The amount of attention which has recently been paid to the internal structure of the cell has not as yet resulted in the establishment of any sufficiently comprehensive generalisation, and an hypothesis which attempts at once to unify the numerous hitherto uncoordinated observations as well as to throw light upon that theory of the cell cycle of which an outline has above been propounded, may be at least suggestive if not completely exhaustive. Let us survey a few of the main differences in protoplasmic structure which any such hypothesis must aim at unifying.

While the lowest amoeboid forms are simply granular, others are distinctly differentiated into clear ectoplasm and granular endoplasm. The immense variability of the size, form and general appearance among the Rhizopods has not been sufficiently allowed for, so that there is every reason for doubting, whether the vast majority of described species have any real distinctness. The elongated and reticulated, granular and circulating pseudopodia of the Foraminifera, or the radiating, clear, and scarcely contractile pseudopodia of a Heliozoon are however sufficiently characteristic and must be reckoned as fairly distinct differentiations of protoplasm. The remarkable changes visible in ova before and during fertilisation, the stroma of cells and the phenomena exhibited during cell-division require to be accounted for. Such an hypothesis too should aim at throwing light on the mystery of muscular structure and should deal even with such apparently peculiar phenomena as that aggregation of protoplasm described by Darwin as occurring in the cells of insectivorous plants, which when in active nutrition or when subjected to chemical, electrical and mechanical stimuli, exhibit the protoplasm aggregated into two portions — the outer more or less hyaline but containing irregular and constantly changing

streaks and granules of a more highly refracting and more fluid substance in which the colouring matter when present become accumulated¹. Darwin extended these observations to the protoplasm of root-cells and indicated its wide prevalence throughout the vegetable kingdom, and the object of the present paper is to extend and apply these observations still further.

On this view the granules of an Amoeba or Torula are (disregarding of course sap-vacuoles and fat globules) aggregation products, the clear ectoplasm when present being merely a portion of the homogeneous protoplasm in which aggregation is not occurring. The more or less granular character of the Amoeba would thus depend on the state of nutrition and the quality and quantity of external stimuli, and would naturally be least evident in the resting state. In the granular pseudopodia of a Foraminifer aggregation is in progress, in those of the Heliozoon not so. The granules of cells in higher animals may be similarly explained, while the opinion of Klein and other histologists, that the granules are the optical expressions of the intersections of a stroma or network of more highly refracting filaments traversing the protoplasm, may be correlated with this view when we remember that Darwin's aggregation masses are as frequently linear as spherical and that they may run in any direction.

The radiate arrangement of granules visible during the maturation and impregnation of so many ova I regard as again dependent upon aggregation, while even the striae in the division of the nuclear spindle seem to be of essentially similar nature.

In the insectivorous plant too it is clear that this process of aggregation is closely associated with contractility, but no movement can of course ensue; in the Amoeba however where no cell-wall impedes motion the irregular aggregation is accompanied by irregular contractility and this necessarily by changes of external form. The very mechanics of such movement becomes intelligible, for the surface tensions of an elongated aggregation-mass tend to draw it into spherical form even against resistance. It is inevitable to apply such an hypothesis to the specialised contractile tissue. In many Invertebrates one observer has described the muscles as striated, the next as homogeneous, and even respecting such permanently striated muscle as that of the Vertebrates the wildest discrepancies exist.

Rutherford² in what seems to be the most important paper in

¹ These observations were corroborated by Francis Darwin (Quarterly Journal Microscop. Science XVI), who showed that the granules did not consist of sap as some had supposed but were essentially protoplasmic in nature.

² On the Structure of Arthropod Muscle. Proc. Roy. Soc. Edinburgh 1883.

the literature of the muscle controversy explains these discrepancies by showing that each observer has figured his specimens in different states of extension. With slight contraction Flögel's granules disappear, then Dobie's globules; finally in completed contraction the two heads of adjacent sarcous elements come together and the fibril is momentarily homogeneous, the former complexity reappearing on extension. Such phenomena can readily be explained, if we regard the doubly refracting portions as aggregation granules whose union and separation is rendered linear by the bounding surface of the fibril, rendered symmetrical by the fixed points of Krause's membrane, and rhythmic by regularly applied nervous stimulus, the attractions and surface tensions of these globules and elongated masses thus effecting a contraction of the muscle, the elasticity and capillarity of the fibrillar sheath acting for its extension. The sum of the tendencies of the innumerable elongated aggregation masses of a muscular fibre towards the spherical form at once accounts for the shortening and broadening of the muscle and the overcoming of resistance. This view agrees too with what recent researches have revealed as to the development of muscular substance and with Strasburger's observations on the striated border of some active Amœbae. Such a hypothesis has innumerable corollaries, but it is sufficient for the present to point out its increased applicability to the cell cycle, since the increase and decrease of cellular activity upon which that depends should be largely associated with corresponding variation in aggregation.

Zoological Laboratory, School of medicine, Edinburgh, 6. June 1883.

III. Mittheilungen aus Museen, Instituten etc.

1. Zoological Society of London.

19th June, 1883. — The Secretary read a report on the addition, that had been made to the Society's Menagerie during the month of Mays and called special attention to a fine example of the Surucucu or Bush-maste, Snake of South America (*Lachesis mutus*), presented by H. Y. Barkley, Esq. of Pernambuco, on the 22nd of May. — The Secretary read an extract from a letter received from Mr. Albert A. C. Le Souëf, containing observations on the coloration of the plumage of the Satin Bower-bird (*Ptilonorhynchus holosericeus*). — Prof. E. Ray Lankester, F.R.S., read a memoir on the muscular and endoskeletal systems of *Limulus* and *Scorpio*, drawn up by himself with the assistance of his two pupils, Mr. W. J. Barham and Miss E. M. Beck. These investigations seemed to confirm Prof. Lankester's previously expressed views as to the near affinity of these two forms, hitherto usually referred to different classes of the Animal Kingdom,

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