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With the author's compliments

THE
VITALITY AND ORGANIZATION

OF

PROTOPLASM

BY

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Dr. EDMUND MONTGOMERY



AUSTIN, TEXAS:
GAMMEL-STATESMAN PUBLISHING COMPANY
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VITALITY

INTRODUCTION.

The problem to be here considered is that of vitality. The things we perceive consist of what is physically and chemically designated as "matter." This irrespective of whatever theory may be formed regarding the real consistency of what is thus designated.

In plants and animals this material substance is found to be alive. It manifests the peculiar phenomena that are called vital, and which essentially distinguish living beings from lifeless things. It is, therefore, above all, incumbent upon biology, as the science of life, to seek to ascertain the special conditions which give rise to the vital properties of the substance composing plants and animals.

The explanation of vitality to be here advanced has been arrived at as the result of many years of observation devoted to the vital phenomena of primitive forms of life, such as the Protozoa.

No general definition of life, such as philosophizing biologists have abundantly advanced, can here at all avail. Our insight into the processes which are operative in the manifestation of vital phenomena, has nowise been furthered by any of these conceptual abstractions.

But neither, it must be confessed, has biology, despite its minute investigations and diligent endeavors, as yet succeeded in disclosing the true nature of vitality. Guided by the cell-theory and purely mechanical principles, it has vainly searched for it in the minute structure, the intimate movements, and the chemical constitution of the single cells composing multicellular organisms; and quite especially in the striking occurrences accompanying their mitotic self-division. For, according to the cell-theory, complex organisms are made up of numberless autonomous vital units or elementary organisms, which multiply by means of self-division. Such complex or multicellular beings have then to be regarded, not as being themselves unitary individuals; but, on the contrary, as being in reality aggregates of elementary units.

In accordance with the cell-theory, each separate cell, as an autonomous vital unit, must be the bearer of all that essentially constitutes vitality. Hence the minute investigation of every phase of its vital manifestations, of every visible trace of the changes it undergoes.

But, however instructive in other respects, it can not be said that the result of all these patient and accurate observations, carried on by a host of competent investigators, has conduced to throw any decisive light on the real nature of vitality. It has failed to show how the substance which composes the cells comes to be actually alive; how it is empowered to maintain its vitality and identity under constant change;

how it is able to transform lifeless nutritive material into living substance; also by what means the cell gets to grow on its course towards self-division; and by what agencies such self-division is really effected. In fact, the intimate mode of operation of no fundamental vital process has yet been scientifically explained in current biology.

The difficulty of recognizing the real processes that give rise to vital activity and its visible manifestations was, moreover, perplexingly increased by the discovery of the mitotic self-division of the egg-cell. Here was seen what in keeping with the cell-theory, assisted by visible appearances, had to be considered a simple cell or elementary organism, containing, nevertheless, potentially all evolutionary or developmental dispositions, which under successive cell-divisions lead to the reproduction of a definite, intricately differentiated organism. Under this cell-theoretical aspect, that which constitutes the vitality of the germ cell, inclusive of its determinate vital potentialities, had to be considered either scientifically inscrutable, or it required for its plausible explanation—as amply exemplified in current theories—a set of far-fetched hypothetical assumptions, which have no slightest support in real occurrences, or indeed in any known modes of activity.

To clear the way for a correct insight into vital processes, it is important first to expose the insufficiency of the principal theories advanced in explanation of the vital manifestations displayed by the germ-cell or the germ-plasm during ontogenetic evolution. For in the plasm of the germ-cell and its ontogenetic evolution all vital potencies are concentrated. And attempts at their interpretation occupy themselves mostly with ontogenetic problems. The exposure of the radical insufficiency of current theories being accomplished, it would leave the way open to show more effectively by what natural means protoplasm, of which the germ-cell and all living beings essentially consist, really comes to be alive, to be in verity what it is rightly called: the living substance.

ONTOGENETIC PERPLEXITIES.

In the problem of the reproduction of definitely organized beings from morphologically all but undifferentiated germ-cells or germ-plasm, is to be found the most pregnant and significant task imposed upon biological research. In order to account for the ways and means by which this wonderful formative process is effected, sundry hypothetical conjectures have been offered by leading investigators. These have been generally conceived in analogy to prevailing physical theories. Ultimate elementary units are here also assumed as composing the substance of the germ-plasm, and are hypothetically furnished with whatever endowments are required for the attainment of the given end in view.

The explanatory difficulties which are encountered by supposing the germ-plasm to be composed of a cluster of elementary units are, however, so perplexing, that strangely extravagant conceptions have to be resorted to, in order to render the interpretation at all plausible. Yet the need of such exceptional hypothetical assumptions arises almost inevitably

from what is actually witnessed as taking place in ontogenetic evolution. For it is seen to start from a single cellular being, the germ-cell, which divides into two "daughter-cells;" these again divide, and so on and on, until by means of such successive self-divisions the vast cell-aggregate is formed, which constitutes the complex multicellular organism. Microscopically the complex adult organism appears to be thus composed of a countless number of elementary units, all the lineal offspring of the one parental germ-cell.

It is upon these plainly visible facts that the cell-theory is principally grounded. And its tenets seem not only ontogenetically evident, but appear to be, moreover, confirmed by the existence of colonial forms, constituted by a number of more or less closely united unicellular beings, such as enter, for instance, in the formation of *Volvox* and *Magisphocra*. Some of these colonies bear a striking resemblance to the blastula stage of *Metozoa*, and strongly suggest the formation of these by union of similar unicellular beings. On the strength of such manifest evidence the complex organism of plants and animals was declared to be, not really the unitary being seen as such by unaided vision; but to be, on the contrary, a populous commonwealth composed of a multitude of autonomous elementary individuals, busily dividing among themselves the divers ontogenetic and physiological labors, which result in the complex structure, and the harmonized vital functions of the vast cell-aggregate they constitute. This sociological interpretation of the constitution of the complex organism was elaborated by Virchow, Haeckel and others, and was generally accepted as a fundamental tenet of biology.

Though, even with the assistance of sociological analogies, it is rationally inconceivable how the unconscious co-operation of numberless elementary beings can result in the ontogenetic reproduction of the strictly predetermined, diversely constituted structures of an organic being, itself infinitely more complex and potent than any of the constituent cells; though, as conceived by the cell-theory, evolution of the adult organism through self-division of an elementary germ-cell, and its cellular progeny, is utterly incomprehensible, the cell-theory—seemingly enforced by visible demonstration—became notwithstanding a generally accepted doctrine, guiding biological research.

It follows from its acceptance, that all vital efficiencies reside exclusively in the sundry discrete cellular beings, as autonomous units. And as ontogenetic evolution starts from one single such fertilized or unfertilized autonomous being, the task thus given was to discover what endowments of the reproductive cell and its progeny lead to the diversified development ultimately represented by the manifoldly constituted tissues of the adult organism. How, then, does an epithelial cell, a muscle cell, a nerve cell, and all other varieties of cells; how do they come to be potentially represented in the germ-cell? And how does this minute, morphologically all but undifferentiated cellular being manage to evolve the huge structurally differentiated form of the adult organism?



To answer these questions, even when the phyletic factors necessarily involved are left out of consideration, taxes the ingenuity of biologists to the utmost. Conceived as being itself an elementary organism, the germ-cell, like other elementary organisms, can consistently be expected to reproduce by self-division its own likeness only; and not, as is actually the case, a morphologically most diversified and functionally utterly dissimilar progeny. Biologists, who regard the germ-cell as a genuine self-dividing elementary organism, have sought to attribute the successive differentiations and developments of its progeny to external causes and conditions, to which in the course of ontogenetic evolution the sundry cell-generations are diversely exposed. But, it must be asked, what imaginable external influences could possibly transform during ontogenetic evolution real elementary organisms, such as the germ-cell and its progeny are supposed to be, into muscular fibres, neurons, or merely into liver or lymphatic cells; these forming, moreover, one and all, integral constituents of a complex organism, whose form and structure are rigorously predetermined?

To render so inconceivable a process to some extent plausible, the germ-cell is sometimes, despite its alleged elementary nature, hypothetically endowed with all manner of latent potentialities, which are believed to be respectively awakened to activity by specifically corresponding external incitements. These are then held to give rise, each in its special way, to the development of the sundry definite kinds of cellular beings. And as dormant potentialities of the living substance which constitutes cellular beings are known in some instances to be forced by external influences into undergoing definite normal or abnormal modes of development, this hypothesis does not *prima facie* seem altogether fanciful. But in normal ontogenetic evolution no such specifically and adequately diversifying external causes can be detected. The reproduction of adult organisms of all kinds runs its course in essentially the same physical medium, and its specific distinctions, and therewith its structural differentiations, are evidently determined by inherent endowments of each special germ; are in fact, strictly predetermined.

The contents of the germ-cell, though not differentiated during ontogenetic evolution by external influences, must, however, in some manner possess within itself diversified potentialities, which in a suitable medium become then essentially self-evolving. In order to account for such manifoldly evolving endowments, the germ-cell is usually conceived as made up of a sufficient assortment of hypothetical vital units, such as gemmules, plastidules, pangenes, micelli, plasomes, biophores, etc., etc. And to the differentiated and differentiating endowments of these hypothetical vital units are then attributed the diversely evolving characteristics of the cellular progeny.

But here, under this supposition, another formidable difficulty arises to impede the progress of interpretation. For how does it come to pass that the original contents of the germ-cell, as an elementary organism, which as such would in all its progeny reproduce only its own likeness;

how does it happen that its sundry constituent elements have come to be so diversely endowed as to be now fit respectively and conjointly to evolve into the disparate tissues of the adult organism?

In explanation of this strange evolution of heterogeneous and progressively higher offspring from an originally elementary organism, phyletic influences are necessarily invoked. And their differentiating and developing effect on the ultimate vital units is then variously conceived by biologists; either as liability to assume specific modes of equilibration, or as phases of unconscious memory, or again as sundry tropic sensibilities, or as other still more occult ontogenetic efficiencies. These divers ontogenetic potencies are generally believed to be wrought upon elementary units during phyletic elaboration by diversifying nutritive influences, which are supposed to bring about a progressive development of their molecular constitution, and therewith development of their respective potential endowments. Each elementary unit is then imagined to become thus separately transformed into a specific germ of a specific tissue; and being so highly developed as now to be endowed with ontogenetic efficiencies enabling it conjointly with others to reconstitute the specific form and structures of the adult organism. It is clear, however, that under this mode of interpretation the visible germ-cell can no longer be regarded as being itself an elementary autonomous organism, as it was at first supposed to be; but has to be regarded as being, on the contrary, at most, an ordered aggregate of diversely and highly endowed constituent elements. And this being the case, self-division of the germ-cell into genuine daughter-cells has therewith become impossible. For a composite of disparate or definitely ordered units, whether nuclear, somatic, or of any other kind, can not be conceived as producing by mere division qualitatively equal parts, or genuine lineal offspring. Consequently, under the supposition that the germ-cell was originally, or has become phyletically, composed of diversified or definitely ordered units, the cell-theory, the acknowledged basis of ontogenetic interpretation, is thereby virtually abolished. For it is of the essence of the cell-theory that by means of self-division equal "daughter-cells" are being produced. Here, on the contrary, the division of the differentiated aggregate can result only in the case of disparate assortment of units, in the production of two heterogeneous parts so far as their composition is concerned. And in the case of a specifically ordered aggregate of equal units, division can produce only complementary halves or fragments of the ordered whole; but nowise genuine autonomous offspring.

In fact, under the assumption of ultimate vital units, the cells of complex organisms can be merely differently constituted clusters of such multiplied vital units, without individuality of their own, and therefore without being themselves autonomous elementary organisms. The cell-theory, by assuming that its cells are clusters of vital units, effects thereby its own dissolution.

Furthermore, on close inspection it becomes evident that, by assuming

the germ-cell to be composed of self-multiplying elementary units, the real problem of ontogenetic evolution has been simply shifted wholly unsolved from the visible germ-cell, as a whole, unto merely imagined constituents of the same. For it is now the vital units that reproductively evolve, not the germ-cell itself. And these hypothetical, ultimate units have not merely to reproduce themselves, but have, moreover, conjointly to reproduce the predetermined adult organism; all this declared to be happening without the least insight into how it is really accomplished.

And so we find ourselves again confronted by the double-sided riddle: How a group of specific reproductive elements, representing potentially the divers adult tissues, manage to originate and to become collected in the germ-cell? And how these autonomous units are then empowered conjointly to evolve the adult organism?

MOLECULAR THEORIES EXAMINED.

*Polarigenesis—Herbert Spencer.**

It is highly instructive and helpful to the view which will be here advocated, to examine some principal attempts at elucidation of the paramount vital and yet profoundly obscure problem of ontogenetic evolution; obscure under the hypothetical assumption that the adult organism consists really of a vast aggregate of autonomous elements.

In recent times the first serious, though purely speculative, effort of the kind, was published in 1866 by Herbert Spencer in his "Principles of Biology," as part of his comprehensive scheme of cosmic evolution. In this his ingenious hypothesis, besides trying to account for given biological phenomena, he aims also to show that organic forms are special products or outcomes of the general redistribution of matter and motion, which atomic mechanics declares to be underlying the formation of all visible things.

To render this mechanical mode of organic construction plausible, Spencer assumes the existence of highly complex organic molecules, which, in order to distinguish them from the molecules of lifeless organic substances, such as albumin, fibrine, protein, etc., he calls "physiological units." These physiological units serve him not only as building material, but they are also conceived as being the bearers of all vital and organic efficiencies. Each species of organism is held to be composed of a special kind of such units. And with the construction of the specific organic form in view, each kind of physiological units is endowed with appropriate "polarities."

"Polarity" consists with Spencer in the tendency of each physiological unit to aggregate with other such units into the form of the organism it helps to compose. Just as the atoms of a salt have the intrinsic aptitude to crystallize in a specific form. This interpretation of organic

*1880, "Mind," No. XIX. Herbert Spencer's, Darwin's and Haeckel's theories were criticized from essentially the same standpoint.

construction may seem to be plausible. But when we desire to learn something more definite regarding this all-efficient intrinsic endowment of each physiological unit, predetermining it to aggregate into the specific form of the adult organism it goes to compose, we are told that "it is a power of whose nature we know nothing;" "a name for something of which we are ignorant;" "a name for a hypothetical property, which as such needs as much explanation as that which it is used to explain."

Surely, this candid declaration amounts to a full confession that a wholly occult power, incapable of explaining anything, has been here arbitrarily invented, and made to account for all morphological and physiological phenomena of life. In mitigation of this sweeping confession of utter ignorance concerning the all-efficient power assumed to be inherent in physiological units, and in order to correlate it with atomic mechanics, Spencer states that polarity "is regarded as a resultant of forces and motions like those of sensible masses." If so, transmitted motion by impact can be the only influence that a physiological unit would be capable of exercising upon others. And this could result only, either in a rearrangement or vibration of their component elements, or in their bodily displacement, or in both these mechanical effects.

How physiological units can acquire under such mechanical actuation their all-efficient specific polarities, and how the minutely organized form and structures of a complex adult being can be evolved by their being mechanically shaken about, remains not only utterly enigmatical, but must be considered an egregiously inefficient hypothetical conception. Better to have adhered to the original confession of complete ignorance concerning the power that really actuates ontogenetic evolution.

But, furthermore, how does Spencer, who may rightly be regarded as the first and foremost promulgator of universal evolution in the modern scientific sense; how does he make the prodigious supply of physiological units arise, needed to compose the comparatively huge bulk of adult organisms? Incredible as it sounds, in utmost contradiction to his fundamental evolutionary principle, which asserts that "construed in terms of evolution, every kind of being is conceived as a product of modifications wrought by insensible gradations upon a pre-existing kind of being;" in outright contradiction to this irrefragable law of evolution, he lets the physiological units in countless multitudes come into being by sudden spontaneous generation. Considering that with Spencer the physiological unit is a product of endless phyletic evolution, in fact the highest product of evolution on our globe, its spontaneous generation in vast shoals out of mere nutritive material is in the highest degree startling. He tries to mask this assumed spontaneous generation by attributing to existing physiological units "the power of moulding fit material into other units of the same order." But it would be a truly miraculous power possessed by physiological units, if they were really capable by mere contact with lifeless nutritive material to transmute the same into eminently specific and complex beings of the same species

as themselves. Such sudden production of these his highest single beings on earth would afford a striking confirmation of the "special creation hypothesis," to whose refutation Spencer has bent all his energies.

But let a sufficient supply of physiological units be somehow furnished. From what source would they then derive their implied vitality? A physiological unit is, after all, conceived as a mere self-rounded chemical compound, though of a far more complex composition than other organic substances. At what stage of its phyletic elaboration could anything of a vital character have originated within it? Being, in fact, only a vastly complex chemical molecule, it could, if it really existed, be no more alive than any other chemical molecule. No manner of impressibility, due to its complex nature, could possibly invest it with any property that might rightly be called vital. And no ever so vast aggregate of them, however grouped, could display the least trace of vital activity.

The fundamental assumptions of Spencer's hypothesis of Polarigenesis having proved utterly inadequate, the hypothesis itself has to be pronounced an out and out failure.

The belief in the universal sway of atomic mechanics is accountable for this, and for similar theories of organic evolution. Starting with material atoms as building material, and taking their spatial arrangement into definite forms to be simply the effect of mechanical modes of motion, theorists are readily led to ascribe definite shapes, and with definite directions of tension to their hypothetical units, believed to compose definitely shaped bodies. The specific structure and form of the latter, whether of organic or inorganic consistency, are then conceived as resulting from the equilibration of the shapes and tensions of the component units. But in such atomo-mechanical structures, if by mosaic-like arrangement of such material units the highly differentiated frame of complex organisms could really be constructed, there would be found in it no possible nook or crevice for vital activities to enter, and become functionally operative. The juxtaposition of myriads of non-living elements, however grouped, can never result in the production of a living being.

*Pangensis—Darwin.**

Darwin formulated his "provisional hypothesis of Pangensis" under the conviction that like can produce only like; and under the further conviction that complex organisms are really aggregates of diversely constituted autonomous cellular beings. Accepting these prevailing biological doctrines, he found himself logically constrained to conceive the germ cell, not as a genuine elementary organism, but as an assemblage of reproductive "gemmules" derived from each different kind of adult cells. For the adult cells, as autonomous beings, have necessarily

* See also "Pangensis," p. 701; *Jenaische Zeitschrift für Naturwissenschaft*, vol. XVIII, 1882.

each in its kind to be represented in the germ cell. These germinal gemmules Darwin believed to be thrown off by the adult cells at random into the circulation; whereupon an appropriate collection of each kind finds eventually its way into every germ cell; wherefrom is then evolved in due order the respective kinds of cells by means of multiplication through self division of the corresponding gemmules.

In support of this hypothesis of reproduction, the consistent logical outcome of the conceptions involved in the cell theory, a number of highly fanciful adjunct hypotheses have to be invented. For no known agency can be imagined competent to collect into germ cells from out the widely scattered chaos of coursing gemmules of all sorts; to collect therefrom an exact assortment representing each separate kind of adult cells. And no known agency can furthermore be imagined competent to marshal such a reproductive aggregate of gemmules in due order of ontogenetic evolution, so as to make them construct the specifically organized structure of the adult being. Pangenesis, though a legitimate outcome of the cell theory, being thus forced to have recourse to various extravagant adjunct hypotheses, which transcend all legitimate inference, is a theory which has in consequence to be declared untenable.

With modifications Pangenesis has since served, nevertheless, as a necessary basis, upon which cell theorists have to build in order to account for the phenomena of reproduction. But in their very inception, pangenic theories carry with them their self destruction. For the specific cells from which the hypothetical gemmules are derived have evidently to be first in existence before they can throw off reproductive gemmules, and their existence and production can therefore nowise be accounted for by the self-multiplication of gemmules to whose existence and production they themselves give rise. Moreover, it is the ontogenetic reproduction of the divers adult cells which is to be explained, and, surely, it is not the least explained by assuming unexplained the reproduction of their hypothetical germs, to whose multifold reproduction they owe their existence. Real visible reproduction is here merely hypothetically delegated to the invisible reproduction of hypothetical units, without the least attempt to show in what reproduction itself really consists.

Pangenesis is obviously laboring under insuperable difficulties by building upon the cell theory as a given basis, and it ends by destroying this very basis, from which it confidently starts. For cells, according to the cell theory, accepted by Pangenesis, are declared to be autonomous beings. In fact Pangenesis rests on this supposition. But how can the cells be autonomous beings when Pangenesis itself is forced to dissolve them into clusters of self multiplying gemmules? In keeping with the hypothesis, cells can indeed consist of nothing but aggregates of self-multiplied gemmules, and are therefore not autonomous beings.

According to Darwin's hypothesis the expected ontogenetic result would, however, be attained only if the substance of the cells, which are supposed to throw off reproductive gemmules would be homogeneous

throughout. But cells prove to be, on the contrary, minutely differentiated and organized beings. This, at any rate, is the generally accepted view. Pangenesis would then require, as Darwin himself asserts, special gemmules representing each differentiation of the cellular structure, and this would so complicate the already untenable hypothesis as to amount, here also, to its complete overthrow.

Pangenesis has been shown to be not only self-destructive, but destructive also of the cell-theory, which it accepted as the foundation upon which to erect its fanciful superstructure.

Perigenesis—Haeckel.

Haeckel found himself unable to adopt Darwin's hypothesis of Pangenesis and offered in its stead, under the name of the "Perigenesis of the Plastidule," a different interpretation of heredity and ontogenetic evolution. Haeckel believes material atoms to possess certain psychical properties underlying their attractions and repulsions, and he assumes the plastidules or ultimate vital units of which he holds organisms to be composed, to be moreover endowed with memory, similar to that which Ewald Hering had ascribed to organic matter. To this psychical endowment of the plastidules he attributes the power of reproducing definite modes of motion caught up and impressed upon them during their phyletic interaction with external influences. Hereditary traits are thus held to be conveyed from generation to generation by means of these specifically memorized plastidule-motions, which in the form of complexly cumulating waves are transmitted from the reproductive germ-plastidules to such as are thereby newly produced in the course of ontogenetic evolution. With Haeckel, ontogenetic evolution consists, therefore, in a deployment and proliferating transmission of phyletically acquired wave motions emanating from the plastidules of the germ-cell. These transform by force of their specific wave-motion at all stages of the evolutionary progress nutritive material into equivalent plastidules, by whose co-operation the adult organism is eventually built up.

To this rather strange hylozoic hypothesis it may first be objected, that from a scientific, and also from a philosophical standpoint it has been found inconceivable how a psychical property, such as memory, whether conscious or unconscious, can possibly set going any kind of motion. The postulation of a psychical moving agent undermines the very groundwork of physical science. Allow any sort of psychical influence to move matter, and there can be no further dependence on a physically ordered cosmos. But scrutinizing Haeckel's conception somewhat closer than he has himself been led to do, it will be found that it amounts, after all, only to a statement of a chemical fact in terms of hypothetical motion. For in his own words: "Conditions of nutrition change the chemical constitution, and therewith the molecular motion of the plastidule." And so it turns out, that it is the chemical constitution of the plastidule which is underlying its so-called memory, as well as its hypo-

thetical wave-motion. It must, consequently, be at bottom the chemical constitution of the plastidule which undergoes developmental changes. And who will venture to assert that such evolving chemical changes are caused by the plastidule remembering, and therewith re-producing the series of wave-motions phyletically impressed upon it?

The ontogenetic problem consists essentially in accounting for the gradual chemical and structural evolution of the germ-cell into the disparate tissues of the adult organism, and, surely, a hypothesis attributing ontogenetic evolution to the reproduction of cumulating wave-motions originated by memory is on the face of it an inept fiction.

Moreover, it is wholly incomprehensible how a progressive wave-motion can at all be transmitted in all its phyletic complexity to random nutritive material, so as to coerce it into chemical compounds of the same elaborated constitution as that possessed by the original wave-emitting plastidules. A profuse multiplication of plastidules is required to build up the bulk of the adult organism. Can it possibly be furnished by mere contact of phyletically elaborated plastidules with nutritive material? No chemical compound whatever, much less one so highly wrought as a plastidule is held to be, can proliferate by transforming adjacent matter of a different kind into its own likeness. If this mode of proliferation really occurred, it would amount, in the case of a plastidule, to the spontaneous generation of the most highly evolved autonomous being in existence; for such the theory asserts it to be. The plastidules, as ultimate bearers of all vital efficiencies, are therewith conceived to be the real organisms, of which the adult being is then a mere ordered aggregate.

The ontogenetic problem seeks to find out by what means any kind of organism becomes reproduced, be it elementary or complex, be it a mere plastidule or the highest organism, and it is clear that Haeckel's hypothesis nowise contributes towards its solution. Nor does it contribute to the solution of the vexed problem of the formation of the germ-cell itself, as bearer of all ontogenetic potentialities. It leaves in the dark where its constituent plastidules originate, and how an appropriate assortment of the same comes to be collected in the sundry germ-cells. Nor, again, is it in the least clear how it happens that the plastidules are what may be really called alive. To hypothetically endow their component atoms and themselves with psychical faculties renders nowise their own vitality and that of the adult organism scientifically intelligible. Strangest of all, that Haeckel should call this psychically actuated vital theory "mechanical."

Furthermore, and finally, Haeckel, a cell-theorist par excellence, dis-integrates in this his molecular theory of reproduction the absolutistic "Zellenstaat," of which, according to his view, we ourselves, and other complex organisms are a mere collective appearance. For, assuming the cells to be mere clusters of individualized plastidules, their own autonomous individuality is completely lost by thus delegating all vital properties and activities to the plastidules composing them. Here also



this hypothesis of ontogenetic evolution, starting from the cell-theory, ends by refuting it.

Mechanico-physiological Theory—Naegeli.

In 1884 Naegeli published his elaborate "Mechanico-physiological Theory of Evolution." In this important work he also adopts the cell-theory, of which he was one of the principal originators. It underlies his explanation of phylogenetic and ontogenetic phenomena. Taking thus the multicellular organism to be an aggregate of unicellular organisms, the lineal offspring of an initial parent-cell, the question here again arises: First, as to the means by which the successive generations of daughter-cells constituting the multicellular organism have become differentiated in its divers, highly developed tissues? and second, how these widely differentiated cellular beings come to be as such potentially represented in the reproductive germ-cell of higher organism?

To answer these fundamental biological questions, Naegeli assumes the existence of a gradually developed germinal substance, which he calls "idioplasm." This reproductive substance he endows with an intrinsic tendency to undergo phyletic development, and also with the capability of being to some extent structurally and functionally influenced by external conditions; and he believes that it is the intrinsically originated and directed process of development which leads to phyletic evolution, whilst the external influences bring about adaptation to the environment.

The idioplasm or germinal substance is conceived by Naegeli as being segregated from plasm composed of micellæ, which elementary bodies he holds to be invisibly small organic crystals surrounded by a watery film. Primordially, micellæ are said to arise spontaneously in albuminous solutions. Whereupon by force of their molecular activities they arrange themselves into groups, which grow by intussusception of newly formed micellæ, and then, as such, multiply by self-division. Through summation of the molecular forces of groups, whose micellæ are similarly oriented, molar forces come into play, that initiate new chemical processes, by which specific plastic tissue-products are phyletically formed. And these being influenced in their formation, not only intrinsically, but also by external stimuli, are found to be adapted to their medium.

It is in this way that in the-course of phyletic evolution groups of idioplasmic micellæ become more and more differentiated, so as to constitute respectively the "Anlage" or germ of the variform cell-structures composing the complex organism. The idioplasm of the germ-cell of a multicellular organism consists, therefore, of as many divers idioplasmic germs, or differentiated groups of micellæ, as there are differentiated cells in the adult organism to be reproduced therefrom, and these are reproduced in the order in which the phyletic development of the specific groups of micellæ has taken place.

The germinal potency of the idioplasm is, by means of growth and

self-division, transmitted in its developed and developing condition to every cell, and is therefore continuous in phylogenetic as well as ontogenetic evolution. In lower plants every cell has complete reproductive power. In higher plants and in higher animals this power of reproducing the entire adult organism is, however, delegated to special germ-cells.

According to Naegeli's views, the idioplastic substance consists at every stage of phyletic development of single filaments of equal and equally oriented micellar groups. These filaments are believed to grow lengthwise by self-division of their micellar groups. In the course of further phyletic evolution, filaments whose micellar groups have become differentiated are developed alongside the primitive filaments, so as to form fasciculæ of diversely constituted micellar groups. In complex organism correspondingly complex strands of such filaments ramify in form of a network throughout the entire organism. These complex strands grow, as such, lengthwise through self-division of the micellar groups of which they consist. Each cross-section of idioplasm comes thus to contain a full assortment of micellar groups, and constitutes thus the "Anlage" or collective germ of the differentiated cells and tissues, to whose formation they give rise in the course of ontogenetic evolution.

With Naegeli propagation, the supreme vital phenomenon, is—as with Haeckel—merely mechanical division of overgrown groups of elementary units formed by the intussusception of more and more numerous like elements. To account for self-division of the germ-cell into an increasingly differentiated progeny, Naegeli does not, like Haeckel, endow his elementary units with a reproductive memory, acquired through unlike ontogenetic exposure to differentiating external conditions. He attributes organic evolution, with its increasing complexity of micellar structure and differentiation of vital functions, to an intrinsic tendency of the combining molecular forces of the idioplastic micellar groups to give rise to the formation of higher organic beings; and he maintains that evolution once started in a given direction tends to continue in the same.

Naegeli's answer, then, to the first question, which arises when organic reproduction is contemplated from the standpoint of the cell-theory; the question, namely, how a self-dividing elementary organism, such as the germ-cell is conceived to be, comes eventually to propagate the differentiated progeny which constitutes the variform tissues of higher organisms;—his answer to this vexed question consists in an elaborate, but vain, attempt to apply mechanical conceptions to the vital phenomena here involved. Naegeli's vital units, the micellæ, of which the entire organism is said to be composed, are mere crystals of organic matter possessing no trace of what really constitutes vitality. Intussusception of new micellæ into groups already formed, causing mere increase of their bulk, which he misnames "growth;" such mere aggregation of organic crystals can not rightly be considered a vital phe-

nomenon. Yet with Naegeli this mere aggregational increase of bulk is the fundamental and essential characteristic of life.

As to the alleged causes operative in organic evolution, it is scientifically inconceivable how the molecular forces of separate micellæ can affect the constitution of adjacent micellæ divided by a watery film, so as naturally to differentiate and to develop their respective chemical composition. The separate micellæ neither chemically combine, nor can they cause among one another any kind of nutritive elaboration. How, then, under such conditions, by mere multiplication of micellæ, and self-division of overgrown groups of the same, can these micellar groups come to be so diversely constituted as to form the respective germs of the differentiated tissues of higher organisms? And, above all, how come groups of crystalline micellæ to be at all alive, to be real bearers of vital properties? Cells can be here only mere clusters of micellæ themselves lifeless, and by no sort of grouping and combination of molecular forces across their watery film, can they be made to perform the vital functions of higher organisms; to perform, indeed, the vital functions of the most elementary organism?

And, surely, it is no less intelligible how idioplasm, which is held to consist of definite groups of divers organic crystals, can come mechanically, by combination of their molecular forces, to be intrinsically endowed with a tendency to phyletically evolve. It is obvious, therefore, that instead of a mechanical interpretation, an occult vitalistic principle is here introduced as the real cause of phyletic evolution, or as Naegeli calls it, "Autonome Vervollkommnung."

But conceding to Naegeli all he claims for his phyletically evolved idioplasm; conceding that the idioplasm of the germ-cell of multicellular organisms consists really of differentiated groups of micellæ, each representing the specific germ of a specific tissue of the adult organism; conceding all this Naegeli fails to show how the differentiated cells of the adult organism are actually reproduced by the idioplasm. For, first of all, it is scientifically unintelligible how micellæ, as vital and organizing units, can spontaneously form or crystallize out of albuminous solutions, or can be made to form in such solutions by the mere presence of already existing micellæ: and then it is visually and mechanically unrepresentable how a specifically arranged group of micellæ, and furthermore an entire cross-section of a complex strand of such groups, can divide and be thereby bisected into two equal parts, so that each part will contain an equal number of diverse micellæ, grouped in the same specific manner as in the parent groups. No such mechanical division of complexly variform groups is conceivable. An infusorium, as a unicellular being, would consist, according to Naegeli, of a specifically ordered and oriented group of micellæ. Try to divide it mechanically lengthwise, or in any other way, and nowise could two equal halves, equal as regards the specific grouping of their micellæ, be ever brought about. The division of an infusorium into two structurally equal beings is a specifically vital process transcending any mechanical mode of

division, and the same holds good for cross-sections of strands of idioplasm, which consist of manifold and divers groups or micellæ.

The cell-theory, Naegeli's original conception, is moreover virtually abolished by his conceiving the idioplasm as constituting a network of fasciculæ, ramifying as a continuous substance throughout the entire organism, and giving origin to the differentiated cells of the ontogenetically developing organism. This can only take place, as he himself asserts, by the specific micellar groups, which form the "Anlage" or germs, giving rise to "the production of soma-plasm." We have here no longer an elementary parent-cell, which proliferates by means of successive self-divisions; all daughter-cells remaining autonomous units in the aggregate, which is held to constitute the multicellular organism. It is here, on the contrary, a continuous substance, consisting of complex strands of divers micellar groups, whose every cross-section contains a full assortment of all micellar groups required to reproduce the different structures of the complex organism; it is a definite strand of such purely germinal substance, which from beginning to end directs and operates in every respect the entire ontogenetic reproduction.

The germ-cell, from which ontogenetic evolution takes its start, is then no longer an elementary, self-dividing organism, but contains instead idioplasm consisting of a full assortment of micellar groups, which have as such to produce the diverse cellular structures of which they are the "Anlage" or germ. This conception of an idioplastic germinal substance has been adopted by succeeding ontogenetic theories, which likewise falsely believe themselves to be grounded in the cell-theory.

Furthermore, by what imaginable means can in the course of ontogenetic evolution definite sets of specific micellar groups, composing a self-rounded cross-section of ontogenetically inactive idioplasm happen to become separately active within the complex strand of which they form a part, exactly in time and at the very place where required during ontogenetic evolution? And how can a specific micellar group of idioplasm as "Anlage," or germ, evolve by self-division or otherwise the specifically differentiated tissues, of which they are held to be the germs? How can they, for instance, not being themselves of muscular or neural consistency, produce muscular or neural tissue? It is clear that the entire problem of ontogenetic evolution is here also transferred wholly unsolved to hypothetical germs, consisting here of mysteriously originated, developed and arranged groups of organic crystals, themselves lifeless and ontogenetically inefficient.

It follows from the few objections brought forward, to which many more might be added, that Naegeli's mechanico-physiological interpretation of "Autonome Vervollkommnung," or phyletic evolution by means of intrinsic forces, and that of "Anlage," or ontogenetic reproduction by means of specific groups of micellæ, constituting the germs of specifically differentiated tissues; that these essential tenets of his theory are untenable. And as some of the principal assumptions of the

theory are adopted by other current views of ontogenetic evolution, the exposure of their fallacy can not be deemed superfluous.

The Continuity of Germplasm—Weismann.

It is evident that in sexual reproduction the spermatozoon conveys somehow more or less completely the traits of the male parent. And as its head is found to consist almost entirely of nuclear substance, and to originate from nuclear plasm; as, moreover, this nuclear head is seen to unite during fertilization with the nucleus of the ovum under specifically figured karyokinetic deployment; it lay near to look upon the nucleus as being the exclusive bearer of the germinal or reproductive substance. And, forming part of the nuclear material, the chromatic substance, by dint of its peculiarly regulated mode of fission and division, quite especially offered itself in the shape of so-called chromosomes as the veritable idioplasms, and was so designated by O. Hertwig and Strasburger.

On this carefully observed and established foundation Weismann reared his ingeniously elaborated and widely celebrated theory of the "continuity of the germ-plasm." The chromatic plasm is actually observed to be continuously and directly transmitted during mitotic division from one germ-cell to another. This direct observation of the continuity of what is taken to be germ-plasm seemed thus effectively to circumvent the insurmountable difficulties in the way of conceiving how a definite assortment of gemmules representing the different kinds of adult cells, and detached from the same, come to be collected in germ-cells. This "wonderful" germinal representation of all kinds of phyletically evolved cells, as autonomous beings, in one and the same germinal receptacle, constituted for Darwin the principal phylogenetic and ontogenetic riddle. He asks: "How can the use or disuse of a particular limb, or of the brain, affect a small aggregate of reproductive cells, seated in a distant part of the body, in such a manner that the being developed from these cells inherits the characters of either one or both parents?"

Weismann answers, that no kind of functional use or disuse ever affects the content of reproductive cells; that they exclusively reproduce their own phyletically inherited potencies, regardless of what modifications of structure or function may have been acquired by the organism during its individual life. Under this essentially different view the task of accounting for the acquirement and reproduction by the germ-plasm of the peculiarities of the structures of complex adult organisms was, however, only apparently facilitated. For granting that phyletic evolution has been impressed on the continuous germ-plasm, the question how this germ-plasm has come to be phyletically differentiated and developed, so as potentially to represent, and ontogenetically to reproduce, the multifold structural and functional characteristics of the adult organism, this fundamental question proves here to be not a whit less perplexing than the Lamarekian problem just quoted from Darwin.

Although it is a fact that the germ-plasm evolves all the diverse tissues of the adult organism, it remains yet to be discovered how it has acquired its differentiated efficiencies, and how it manages actually to realize the same during ontogenetic evolution. It was principally to answer these questions that Weismann formulated his theory. Taking the chromosomes of the nuclear plasm to be exclusively germ-plasm, he necessarily conceived their structure to be of a highly complex nature. For how otherwise could they evolve the diverse structures of the adult organism with all their specifically differentiated characteristics. The chromosomes must then contain special germinal representations for all the different specializations found in adult organism, and these representatives must occupy definite positions, and must be definitely grouped, in order systematically and in due sequence to evolve the differentiated structures. Each independently varying and inheritable trait of adult organisms, "even a mole on the skin, or a colored spot on the wing of a butterfly," Weismann believes to be representatively performed in the germ-plasm by specialized component units of the same. These specialized formative units he calls "determinants," because they are held respectively to determine the variform characteristics of the evolving structures of the adult organism.

In the chromosomes the determinants are conceived to be specifically grouped so as to form complete assortments, representing every kind of structural differentiation destined to appear in the adult organism. Such complete assortments of determinants, definitely arranged within the chromosomes, Weismann names an "id." And to explain certain biological phenomena he believes the chromosomes to be composed of a number of such ids, constituting what he names an "idant." The determinants themselves are held to be composed of a definite group of ultimate vital units, which Weismann calls "biophores." These biophores or lifebearers are, like the gemmules of Darwin and the pangenes of De Vries assumed to multiply by means of self-division. And Weismann not only allows his biophores or ultimate vital units, to multiply by self-division, but makes his determinants, in which the biophores are specifically grouped, likewise multiply by self-division as a whole. And in the same manner his ids, in which determinants in full assortment are specifically grouped. And finally also his idants, in which a number of ids are held to be contained. Thus all different members of his hierarchy of differently grouped biophores are assumed to be endowed with the same vital property as the biophores themselves. They propagate their kind, and must possess, consequently, all vital efficiencies involved in reproduction.

It is obvious that under this theory the phylogenetic problem has to consist in showing how the biophores as original life-bearers come to be specifically differentiated, and specifically grouped, so as to form the vast supply of divers determinants required; and how these determinants themselves come to be specifically grouped so as to form ids, and the ids again grouped so as to form idants. Now the question is, have we any

knowledge of agencies in nature that are competent to accomplish these tasks demanded by the theory? All phyletic evolution has here to be immediately and exclusively wrought upon the biophores composing the germ-plasm; for they are held to be the veritable life-bearers, and the idioplasm they compose to be the only phyletically evolved and evolving substance.

It is therefore relevant and essential to inquire by what known, or by what scientifically imaginable process the primordially equal biophores of the original germ-plasm can have been so profoundly affected that one set will now give rise to a liver-cell, while another set will determine the formation of a nerve-cell; while, in fact, divers sets or groups of biophores, all directly differentiated within the narrow confines of the chromosomes, will by self-division so propagate and so evolve as eventually to constitute the multifoldly differentiated structures and execute the harmonized and unified functions of the adult organism?

The biophores of the germ-plasm can be affected only by direct nutritive conditions. For, under Weismann's consistent theory, external stimuli, acting as evolutionally modifying agents, are strictly excluded. How, then can the sundry adjacent biophores composing the chromosomes be imagined to have been so differently exposed to nutritive conditions, as eventually to vary so widely, and to develop so prodigiously in their respective chemical constitution and formative potencies, as is here necessarily required? No nutritive process, no germinal selection, aided by ever so favored and prolonged natural selection can possibly have brought about this state of things, upon which Weismann's theory is grounded.

Weismann masks this cardinal difficulty of his theory by assuming that through mixture of male and female germ-plasm numberless varieties arise, which, by means of selection of those best suited for the struggle of life, the progressive development of organic beings is brought about. It is, however, evident that in order that progressive varieties can come at all into existence the biophores of the germ-plasm must have themselves first varied in the direction of useful organic progress. In fact, the very differentiation of male and female germ-plasm, with all their distinguishing peculiarities, can be due here only to differentiation of their respective biophores, of which the plasms are held to be entirely composed. All differentiation, and therewith all variation, and all progressive development, can originate only in the constitution of the biophores as ultimate vital units.

This being so, no differentiation into male and female germ-plasm could have occurred had their biophores not themselves undergone such differentiation. Let the respective biophores of male and female germ-plasm remain at their earliest stage of differentiation unchanged from generation to generation, and no new varieties could have arisen from their mixture. Without varieties of biophores there can result no varieties of organisms by mixing them. And if the biophores believed to compose the germ-plasm had failed to become themselves progressively

differentiated and developed, no progressive varieties of organic beings could have ever come into existence. No manner of mere grouping of biophores at a definite stage of their own development could give rise to tissues or organisms of a higher order than they themselves germinally represent. And with Weismann it is accordingly the specifically developed biophores of the determinants, and not the determinants themselves as specific groups, that are said to transform indifferent soma-plasm into specific tissues. Only after the biophores have singly dispersed, dissolving their grouped connection, do they come to exercise their marvelous structure-determining influence. In every instance variation, development and formative potency have in this theory to be attributed exclusively to the biophores of the germ-plasm.

Consequently, all phyletic and all ontogenetic efficiencies being incorporated in the germ-plasm biophores, natural selection, as such, can nowise bring about any kind of organic change or development. It can consistently with the theory only select varieties whose progressive potentialities have been predetermined in the biophores of the germ-plasm. Natural selection is therefore no formative factor in organic development, as often surreptitiously assumed. And so the task remains, untouched by Weismann's theory; the task to ascertain what conditions have really brought about the progressive phyletic development potentially incorporated in the germ-plasm of higher organisms. Naegeli endowed his idioplasm with an intrinsic propensity phyletically to develop, leaving thus progressive evolution a scientifically unexplained mystery. To believe, however, in accordance with the theory here examined, that mere nutritive accidental variations of the densely clustered biophores composing the vitally sequestered chromosomes of nuclear plasm, have been competent so wondrously to differentiate and to develop these hypothetical beings, that they have become thereby fit to produce by self-multiplication the divers organic tissues; and conjointly to form, moreover, the eminently purposeful somatic configuration of the unitary adult organism, an organism functionally adapted out and out, and through and through, to a definite environment, upon whose constant, manifold interactions its very being and life are dependent, and with which the germ-plasm biophores are said to stand in no remotest vital relation;—to believe and postulate so groundlessly incoherent a state of things, in order to explain the most interdependently coherent and aimfully elaborated product of nature; this hypothetical effort affords, surely, one of the most glaring examples of elucidating *obscurum per obscurius*.

But concede that the germ-plasm is really composed of biophores, and that these become in some way specifically differentiated and developed, as required by the theory; let these biophores multiply by self-division and form specific determinants; let, furthermore, definite assortments of such determinants group themselves into ids, in which all distinctive traits of the adult organism are representatively performed; and let, finally, a sufficient number of such ids be grouped so

as to constitute idants;—how, then, it must be asked, can these specifically arranged groups of divers biophores themselves multiply by self-division? How can the two resulting halves contain an equal assortment of all necessary determinants, without which no continuity of germ-plasm can exist, and without which the entire theory is vitiated in its most essential assumption? It is true that the chromosomes themselves, conceived as idants, are actually seen longitudinally to divide. But no appearance points to their really consisting of so complex an aggregational structure as is here hypothetically assumed. Division of determinants, ids and idants into two equal halves, under the supposition that they are composed of a diversity of self-dividing biophores, is simply inconceivable, as has been already stated in reference to any kind of specifically arranged group of diversified units. But Weismann's theory rests essentially on such equal division of specifically arranged groups of diversified units. For only division into equal halves can furnish successive generations with complete assortments of determinants: can, in fact, secure the continuity of the germ-plasm. Equal division of Weismann's germ-plasm being inconceivable, his theory is left without a sound foundation.

It would be therefore superfluous to expose the fallacies involved in additional assumptions that have to be made in order first to constitute the manifold different groups of biophores: and then to marshal them in their way to achieve the stupendous task of constructing the adult organism with all its peculiarities of structure and function.*

As regards the alleged unequal division of germ-plasm during ontogenetic evolution, which forms an essential tenet of Weismann's theory, it is effectively refuted by the demonstration of the formative totipotency of fragments of egg-plasm. This important discovery upsets, indeed, all his ingenious groupings of biophores, together with their surmised ontogenetic potencies.

It may here again be pointed out with advantage, that vital units, such as biophores are supposed to be, conceived as bearers of all essential vital properties, are thereby constituted also bearers of the real process and entire secret of ontogenetic evolution. For their own propagation by means of self-division consists in the complete ontogenetic reproduction of new beings. They must therefore contain within themselves all potencies that come into play during ontogenetic evolution and that underly the hereditary transmission of parental traits. And as the entire ontogenetic evolution of the complex adult organism is here wholly effected by the grouped progeny of proliferating biophores, the problem of ontogenetic evolution would, under this view, have to be solved, if it can be solved at all, not by making imaginary vital units hypothetically multiply and automatically group themselves into the organized form of the adult organism; but by showing how the phyletic

*This the present writer has to some extent attempted in a paper on "Molecular theories of organic reproduction," read before the Texas Academy of Science, December, 1895.

and ontogenetic evolution of a vital being, such as the assumed vital units are held to be, is really brought about. And this means here, that the entire problem under consideration has been relegated wholly unsolved to fanciful realms peopled by imaginary beings.

Nor, it must be confessed, is it in the least intelligible how biophores, however specifically developed, and emitted from determinants at the right time and in the right place, start suddenly into activity, transforming thereby indifferent soma-plasm or morpho-plasm into specifically constituted and specifically functioning tissues. As they do not themselves consist of, for instance, muscle or nerve substance, how can they by their mere presence and self-multiplication determine the formation of muscles or nerves, or of any other kind of tissue? Organic tissues can in this theory consist only of aggregations of self-multiplied biophores, which are able to determine or reproduce nothing but their own likeness.

It is obvious, that in this theory also, as in all other aggregational theories, the cell-theory by which it is guided in its exposition, becomes in the course of its application disintegrated. The cell, as a self-dividing autonomous being, has dissolved into a multiplicity of other autonomous self-dividing beings, and is no more itself.

Finally, it has become extremely doubtful, if not wholly disproved, that it is really a nuclear plasm, which may rightly be called germ-plasm, the plasm that actually undergoes ontogenetic evolution, reproducing thereby the adult organism?

It will be admitted that the fundamental assumptions of a theory, to be really serviceable, must be self-consistent, and must not logically lead to impossible interpretations of actual phenomena.

SUMMARY.

It has been shown, that, under the supposition that the germ-plasm destined to reproduce a complex organism is composed of elementary units; that under this aggregational view the leading theories of heredity and reproduction are untenable. Yet, assuming, as they mostly do, that higher organisms are really multicellular beings, composed of generations of autonomous cells, which are the lineal offspring of a mother-cell, itself an autonomous elementary organism; taking, in fact, the cell-theory as a safe foundation upon which to rear a theory of heredity and reproduction, they can hardly arrive at different conclusions. It seems, indeed, the only way to account for an elementary self-dividing being having come in the course of phyletic evolution to contain potentially the germinal differentiations, which under successive divisions give rise to so divers a progeny as constitute the sundry tissues of higher organisms.

A cell, being by definition an elementary organism, can legitimately reproduce by means of self-division only its own likeness. But here it is found to reproduce successively differentiated generations of offspring mostly more highly developed than it is itself supposed to be.

Somehow, then, the widely differing cells of multicellular organisms, when conceived in accordance with the cell-theory as autonomous beings, have to be all germinally represented in the reproductive cell. Hence Spencer's multifoldly polarized physiological units, Darwin's specifically differentiated gemmules, Haeckel's memory-endowed plastidules, Naegeli's intrinsically developing micellar groups, De Vrie's intracellurally competing pangenes, Weismann's nutritively differentiated and diversely grouped biophores, etc.

But by supposing the germ-cell, and still more by supposing the nuclear germ-plasm to be composed of differentiated elementary units, through whose multiplication and grouping the adult organism is constructed, you not only completely destroy the autonomous and elementary nature of the germ-cell itself, as defined by the cell-theory: but you dissipate during ontogenetic evolution the entire cell-theory, from which the evolutionary start was so confidently made. For each kind of cell that composes the adult organism can then be nothing but a cluster of the multiplied particular units, by which it was representatively preformed in the germinal substance.

Furthermore, the difficulty in the way of explaining by what means the vital units, supposed to compose the germ-plasm, have become so widely differentiated and diversely developed as now to be able to reproduce entirely different and more highly endowed cell-generations; this difficulty proves to be insuperable. For it is scientifically inconceivable how the originally equal units held to have composed the primordial mother-cell, all exposed to the same nutritive conditions, can have by any known, or legitimately inferred means come to be so widely differentiated and so highly evolved, as the theory demands. And if the varied external influences or stimuli, to which successive cell-generations have been exposed, are here invoked to account for their differentiations, then Darwin's untenable hypothesis of pangenesis is logically necessitated; each externally differentiated cell has therewith to emit germinal representatives, definite assortments of which have by some wholly unaccountable means to be collected within the reproductive cells. And this, surely, is a scientifically inadmissible assumption.

As to Haeckel's substituted hypothesis of perigenesis, by which he seeks to explain the progressive differentiations of ontogenetic evolution, it was found to be really based, not—as he contends—on the drastically unscientific hylozoic assumption of memorized wave-motions of the plastidules, but on their supposed differentiation of chemical constitution. At any rate, no less than in Darwin's pangenesis have distinct representatives of the diversely constituted cells of the adult organism to find their way into the germ-cell, which would necessitate supernatural intervention; for never could they, unaided by some *Deus ex machina*, reach their appointed destination.

Moreover, the differentiated and highly evolved ultramicroscopical units here hypothetically assumed have to multiply in prodigious numbers in order to build up the comparatively enormous bulk of the adult

organism. And this can take place only: either by spontaneous generation, as taught by Spencer, Haeckel and Naegeli, or by self-division, as assumed by Darwin, De Vries and Weismann. Under the first supposition, that of spontaneous generation, the essential tenet of the general theory of evolution is being egregiously contradicted. For this leading theory emphatically maintains that only by most gradual phyletic elaboration can such highly developed vital units have been produced. And here, in direct opposition of this irrefragible rule of evolution, countless numbers of just as highly constituted units are declared to be spontaneously and suddenly formed out of mere nutritive material. To such straits are foremost advocates of organic evolution pushed by the logic of their erroneous premises! Their highly complex organic units are conceived as specific chemical molecules. And no chemical molecule, even of the most elementary composition, can by its mere presence transmute different chemical molecules into its own likeness. Much less can the chemical units here assumed, which according to the theory are the most highly developed single beings in existence, have power to transmute by their mere presence or otherwise random nutritive material into their own consummately elaborated constitution. Nor can it be scientifically conceived when and where vital properties can possibly effect their entrance, or come into existence, among the groups of chemical units held to compose the tissues of adult organisms.

And here it is important to remark that we are indirectly touching upon the pre-eminently vital problem of assimilation, and therewith of genuine organic growth, which is something entirely different from mere increase of bulk through accumulation of separate units. It is safe to say that this essential vital activity, which underlies growth and reproduction, can nowise be scientifically interpreted by aggregational theories. A vital unit has no power to produce other vital units out of nutritive material, and cause thereby genuine organic growth, leading ultimately to the development of adult organisms, as maintained by Spencer, Haeckel, Naegeli and others.

The other alternative, adopted by Darwin, De Vries, Weismann, and their followers; the alternative, namely, of proliferation and increase of bulk by means of self-division on the part of the assumed vital units; this supposition leaves likewise the entire problem of assimilation unsolved. For it is clear, that in this case the ultimate vital units have first of all themselves to grow by assimilation of nutritive material before they can divide. And this is exactly the vital process that has to be explained. We desire to know how an organism grows from a germinal beginning to maturity under assimilation of nutritive material. And we learn nothing by being told that an organism grows to maturity because it is composed of constituent elements or units that grow to maturity and then divide. The process of growing to maturity by means of assimilation of nutritive material remains here entirely occult, and this obfuscation involves all ontogenetic evolution.



Likewise, wholly obscured, remains the process of proliferation by means of self-division. For how does a complex vital unit divide into two equal halves? To do so mechanically, as is usually believed, it would have to be a mere cluster of still more elementary equal units, while if it is conceived as an organic whole, whose component elements are diversely constituted and specifically arranged, it renders mechanical division into two equal parts impossible. We have here, then, in these assumed ultimate self-dividing units, to face, wholly intact, the entire ontogenetic problem, for whose explanation they are expressly invented.

Organisms of highly complex structure actually and visibly divide into two equal halves. How is this eminently vital feat accomplished? No valid explanation has yet been offered for it by current biology.

Without assimilation of nutritive material no genuine growth, and without growth no reproduction. For reproduction is essentially evolutionary growth of a germ to adult stature, by means of progressive assimilation.

Obviously, then, before the fundamental and essential vital processes of assimilation, growth and reproduction are themselves scientifically explained, no valid theory of ontogenetic evolution can possibly be formulated. In the current ontogenetic theories, instead of explaining assimilation, growth, and reproduction, these fundamental vital processes have been simply taken for granted, and ontogenetic explanation has merely consisted in a more or less ingenious grouping of assimilating, growing and reproducing hypothetical units.

The aggregational theory, the theory that the complex organism is formed of clusters of autonomous units, is found to break down at every stage, and under every mode of hypothetical assumption. It meets its most grievous break-down, however, when the unitary organism and the unitary functions, of highly constituted living individuals are made to be constructed and actuated by a multitude of autonomous elementary units. Nothing short of a constant miracle could under these conditions bring into existence and maintain the intricately organized constitution of higher forms of life, and superintend, moreover, the blending of their separate and different elementary functions, so as to assure their harmonious co-operation; could, in fact, constitute the higher organism a functionally and morphologically indiscernible whole.

The myriads of vital units, in order conjointly and aimfully to construct the minutely and exquisitely organized frame of higher organisms, and harmoniously to actuate its diverse and yet interdependent functions; in order to accomplish this prodigious task, these innumerable elementary beings would have to be endowed with psychical powers and co-operative skill infinitely surpassing anything we are conversant with even in the highest living beings.

These plain objections to aggregational theories, repeatedly urged by the present writer in English and German periodicals during the last twenty-five years have hitherto remained unheeded. They are, however, beginning to be corroborated by investigators occupied with experi-

mental ontogeny and experimental regeneration. The striking phenomena of regeneration, and the discovery of the formative totipotency of single blastomeres, and even of small fragments of egg-plasm, are forcing upon biologists the conception, that the complex organism has to be looked upon as essentially a unitary whole, and not as a mere aggregate of a multitude of inferior beings.

To apprehend at a glance why aggregational theories have necessarily failed to explain ontogenetic evolution one need only recognize that by assuming a specific germinal unit, of whatever sort, to be capable of reproducing a definite kind of cell as autonomous being, be it a liver cell, a nerve cell or any other cell; that by adopting this aggregational hypothesis the entire process of ontogenetic evolution is therewith already presupposed and left wholly unexplained. For the multicellular organism is being here regarded as a mere aggregate of diverse autonomous cells, and its collective germ-cells as mere clusters of germinal units, each of which possesses the powers to reproduce the kind of cell of which it is the special germ. And it is just as difficult to account for the evolution of a germinal unit into, for instance, a nerve cell, as it is to account for ontogenetic evolution in general. Ontogenetic evolution of the multicellular adult organism can consist here only in the separate ontogenetic evolution of the germs of each kind of its component cells. The ontogenetic process running thus its full course unexplained in each germinal unit, it is in relation of the multicellular organism likewise taken for granted in all its evolutionary stages, from its germinal beginning to its completed evolution ending in the adult organism.

It is, therefore, obvious that, despite most ingenious and diligent endeavors on the part of a great number of competent investigators, the sway of preconceived doctrines has prevented them from gaining insight into the real process of ontogenetic evolution. They have merely given minute attention to its morphological appearances and results, without the remotest understanding of their mode of production. This can not be attained before the conditions which give rise to the vitality of the living substance are first understood. For ontogenetic evolution is only a special outcome of that which constitutes the vitality of the living substance.

THE LIVING SUBSTANCE AND ITS VITAL PROPERTIES

INTRODUCTION.

Principally since Max Schultze's investigations Protoplasm has come to be generally recognized as the veritable living substance out of which organic beings are formed, as the specific chemical substance, which is the bearer of the vital properties, and which observably displays the same.

Realizing that, without a scientific insight into the process or processes that constitute the life or vitality of protoplasm, biology lacks a solid foundation, the present writer has devoted a number of years exclusively to the study of the vital properties of the living substance composing elementary forms of life. For we have here protoplasmic beings, morphologically all but homogeneous, which, nevertheless, move, react on stimulation, assimilate, grow and multiply. And these activities constitute admittedly the fundamental vital properties of all living beings, which are likewise essentially of protoplasmic consistency. By what means, then, is the living substance empowered to perform these sundry activities which constitute its vitality? Obviously, this is the question of questions underlying the science of life.

It has been shown that, without an explanation of assimilation and growth, ontogenetic theories lack a sound foundation, and must consequently miscarry. They necessarily fail to give a valid scientific interpretation of the ontogenetic phenomena which lead to the reproduction of the adult organism. For they use, unexplained, for basis of their interpretation that which is to be explained; namely, the vital process of ontogenetic evolution, only relegated here to the hypothetical vital units, which ~~the~~ ^{are} the assumed life-bearers. And this they do, either by making these units spontaneously arise in some mysterious manner, or by making them multiply by self-division. And all this clearly involves the entire mystery of reproduction, for the explanation of which these units were expressly invented.

The problem of ontogeny has, therefore, to be attacked from a different standpoint. The original vital properties that underly ontogenetic evolution have first to be scientifically explained.

In the realm of Protozoa, looked upon as unicellular beings, we have at our disposal for research a vast array of diversified, and yet most simple forms of life. As these diverse protoplasmic individuals all display the fundamental vital activities, by means of which they prove to be alive, it is evident that if that which constitutes life in general

can ever be explained, here we have offered to us the most promising field for investigation. In suitable specimens all vital phenomena are openly displayed in visible transparency. And it can not be denied, that the adequate scientific explanation of the vital phenomena of such protoplasmic beings, carries with it the explanation of the essential vital phenomena of all protoplasmic beings. The particular mysteriousness attaching to life as a natural phenomenon would then be effectively dispelled, so far as scientific interpretation is concerned.

But it is well to remind ourselves at this juncture, that the living substance with all its properties is revealed to us in the medium of our visual precepts. What we actually perceive are obviously visual phenomena arising within our own being. And, as such, they can be only symbolical, though definite, representations of the foreign existent whose activities are stimulating our sense of vision in specific ways. It is solely upon the evidence of these visual signs, consisting of definite spatial forms and movements, that we realize the presence and the activities of the foreign existent, and draw therefrom our conclusions concerning them.

This vicarious nature of our knowledge of the phenomena of life, accruing to us symbolically, chiefly in the medium of our sense of vision, accounts sufficiently for the back-ground of mystery legitimately attaching to vital manifestations. This epistemological fact has to be clearly borne in mind, in order rightly to correlate living being with the rest of sense-revealed nature. For the life of organic beings, though a far more complex phenomenon than other natural occurrences, is really no more nor less mysterious in its constitution and its activities, than are the constitution and the activities of unorganized and non-living substances. Perceptible nature in all its modes of appearance belongs to one and the same order of nature. No essential disparity in this respect obtains between bodies that display vital phenomena in out and out dependence on a non-vital environment, and such as display only what are called physical or lifeless phenomena.

The study of protoplasmic beings yields an interpretation of vital phenomena at least as scientifically complete, though not as accurately measurable as is afforded by the study of purely physical phenomena. These are likewise chiefly revealed and scientifically expressed in visual terms of expansion and motion, and, therefore, no less vicariously and symbolically, than is the case with vital phenomena.

VITAL MOTILITY.

To our sight the most salient evidence of being alive is the self-movement of organic individuals. An animal that no longer moves is held to be dead, or at least, to have its life suspended for the time being. And as regards protoplasm, the veritable living substance in plants and in animals, its vital motility is quite conspicuously the visible phenomenon, by which its being alive chiefly evinces itself. In case we succeed in disclosing the ways and means through which the motility of proto-

plasm is rendered possible, we shall have gained a scientific insight into that which principally constitutes it a living substance.

Selecting suitable protoplasmic individuals as objects of investigation, the sundry processes operative in the self-movement of their substance are readily detected. And here protozoa, belonging to the Sarcodina, afford the easiest and clearest view of the intimate workings that underly vital motility. By carefully watching the emission and retraction of their so-called pseudopodia; or rather by watching the outflow, stagnation, remelting and shrinking of the substance of their pseudopodia, the desired information can with certainty be gathered.

In order to arrive quite unmistakably at the correct interpretation of what are the actuating causes when protoplasmic pseudopodia are seen forcibly to flow out into space, eventually to come to a standstill, and finally to shrink, collapse and be reincorporated into the body of the protoplasmic individual; in order to gain an understanding of these fundamental vital occurrences it is best to select such amoeba, or such rhizopods as emit slowly long and broad pseudopodia, whose flow of granules and distinction of granular and hyaline substance clearly indicate what is really taking place. The most favorable specimens for the purpose I have met with were gigantic amoeba, whose long, blunt finger-shaped pseudopodia measured 0.2 mm. in diameter. And almost as favorable were gigantic difflua pyriformis, whose pseudopodia were often equally as broad, and at times about three times as long as the shell, though in this latter case they were much more slender in proportion to their length.

First, then, what causes the stagnation, shrinking and collapse, or the so-called contraction of the living substance composing the pseudopodia? Definite, unmistakable signs prove it to be due to chemical disintegration. The stagnation of the outflowing pseudopodia is seen to begin at the surface of contact with the medium, extending more and more deeply towards the axis of the protoplasmic cone or cylinder. This occurrence is clearly evidenced, first, by the slackening flow of the granules embedded in the substance near the surface, and, then, by that portion of the hyaline substance brought into contact with the medium becoming itself flocculent and eventually granular. Complete proof that the change here observed is, in fact, the work of chemical disintegration, is visibly given in vesicles, or so-called vacuoles, forming within the disintegrating substance, in which are gathered the effete fluid products of disintegration, presently seen to be eliminated.

Now, as to the influences that are causing this chemical disintegration, they are readily detected. Any sort of contact or external stimulation tends to decompose more or less profoundly the highly complex and explosive constitution of the protoplasm. In this "sensitiveness" to stimulation consists its so-called "irritability," formerly considered the very essence of vitality, or, at least, its most characteristic manifestation. On artificial stimulation an expanded pseudopodium, or an entire expanded amoeba will instantly shrink or contract. And if the

irritation be sufficiently intense the entire substance of the amoeba will contract into a globule. During the formation of a pseudopodium an expanding surface is offered to the stimulating influences of the medium, and the ensuing disintegration, accompanied by contraction, is very obviously an effect of these stimulating influences. The proximate cause of contraction is thus observably chemical disintegration induced by external stimulation. Normal stimulation functionally disintegrates the expanding living substance, and, in consequence of it, it contracts.

But something additional occurs during the contraction of protoplasm; something most essential to what constitutes its vitality, and which imparts to vital motility one of its most characteristic features. Each functionally disintegrated portion or particle of protoplasm serves as restitutive material to other disintegrated portions or particles. A chemically equilibrating vital commotion is thereby set going, which spreads more or less vividly throughout the entire protoplasmic individual. It is this process of reintegration by means of complementary chemical blending of adjacent portions of protoplasm that causes the remelting of the stagnated protoplasm of pseudopodia. And spreading from part to adjoining part it gradually involves the entire substance of the functionally disintegrated pseudopodium, whereby it acquires the tendency to contract into globular form. Shrinking thus within itself, it ends by being reincorporated into the substance of the protoplasmic body, with which it chemically blends.

This essential vital process of complemental restitution, by means of the chemical blending of portions of functionally disintegrated protoplasm, can most conspicuously be observed when two or more stagnated pseudopodia meet, and thereupon visibly coalesce, contracting into globular form. But in each separate pseudopodium stagnation on exposure to external stimulation is followed by a lively play of complementary restitution, by means of the chemical blending of adjacent portions of protoplasm to more and more complete reintegration, involving the entire substance of the pseudopodium as a formative whole, and causing the molecular commotion and the mass-movement in which the contractile phase of vital motility consists.

But something still more profoundly vital is implicated in that which causes a pseudopodium to be reincorporated into the body of the protoplasmic individual. Fragments of protoplasmic individuals have, as is well known, the tendency to reintegrate or regenerate the whole organism from which they are derived. A disintegrated pseudopodium is really a fragment of the protoplasmic individual from which it has issued, and its reincorporation is partly due to its own tendency, as well as to that of the rest of the protoplasmic being, to become fully reintegrated, and to form thus a unitary whole. We shall find in the course of our interpretation of vital phenomena that reintegration of the individual, as a whole, from fragments of the same, is playing the most essential part in ontogenetic evolution.

The living substance has generally been looked upon as pre-eminently

a contractil substance. But the reverse is really the case. The living substance is pre-eminently an expansil substance. Its contraction forms essentially part of the negative phase of vital motility, due to functional disintegration. Expansion, on the contrary, forms part of its positive phase, due to functional reintegration. You irritate or stimulate an amoeba sufficiently, and it contracts into a globule. You leave it then to its own resources, and it re-expands, pushing forth one or more pseudopodia. The intrinsic tendency of protoplasm is forcibly to expand or spread out during functional restitution. The formative expansion of a protoplasmic pseudopodium is the visible manifestation of the cumulative reintegration of the functionally deteriorated substance of the body from which it issues.

Pseudopodia during their outflow assume a more or less elongated shape, because on contact with the medium the substance of the surface solidifies and forms an envelope confining the flow of the expanding substance, which is seen to continue within the envelope or tube. This more or less rigid envelope is occasionally ruptured by an all too forcible inroad of new expanding substance, whereupon an additional pseudopodium issues from the ruptured spot, forming a side branch, and giving rise to complex phenomena of vital motility.

The real consistency of flowing protoplasm has been a great puzzle to investigators. It could not be considered a real fluid, nor a real viscid, nor a real celloid. For the manifold phenomena of its vital motility refused to be explained by any property, possessed by these different states of material consistency. The progressive reintegration of the substance which forms the pseudopodia is evidently that which gives rise to its apparent outflow. This apparent outflow is produced, not by anything resembling the flow of a genuine fluid, but by the progressive expansion of protoplasm during its cumulative reintegration. What takes place here is an eminently active and vital formative process, and no mere passive outspreading of any fluid or viscid substance. Nor is it caused by any mode of inhibition. I know well the astonishing formation of beautiful, flexible, winding, tube-like shapes, which shoot out of amorphous myeline when water is added to it.* But the formation of pseudopodia is entirely due to a process of cumulative chemical reintegration on the part of the living substance.

That the apparent outflow of pseudopodia consists really in a cumulative chemical elaboration of protoplasm can on close examination be clearly detected in suitable specimens. At first only densely and coarsely granulated substance issues from the protoplasmic individual. During its apparent flow the substance is seen to become progressively finer granulated, and finally a completely hyaline substance, the so-called extoplasm, issues as cumulating result of the chemical reintegration. In

*I have much experimented with the wonderful formative capacity of myeline, and have succeeded in imitating with it almost all forms of natural and morbid cells. The results were communicated in a paper read before the Royal Society of London, December 20, 1866.

contact with the medium the hyaline substance becomes functionally disintegrated, and therewith transformed again into granular substance.

Active expansion by force of chemical reintegration constitutes, then, the positive, progressive phase of vital motility, while contraction on external stimulation constitutes its negative, retrograde phase. Chemical reintegration winds up the spring of action relaxed by chemical disintegration. The force or energy expended during disintegration is thus restored during reintegration. This two-fold process underlies most fundamentally and essentially all vital activity.

The struggle and interaction between disintegration on external stimulation, and reintegration by force of intrinsic chemical affinities, taking place amid greater or smaller supplies of expanding substance, give rise in certain cases, and very conspicuously, for instance, in hairs of certain plants, and in rhezopods such as *Gromia oviformis*; this antagonistic and yet compensative process gives rise here to a most varied and complex display of partly progressive and partly retrogressive motions undergone by different portions of the protoplasm at one and the same time. And these manifestations of vital motility are further complicated by partial stagnations and partial remeltings of the same. All these blending and diverging phases of vital motility produce in such cases a most perplexing confusion of appearances, which, however, can all be disentangled and explained by using the light here thrown upon the actuating agencies of protoplasmic motility.

Various kinds of amoeba are met with, in which the antagonistic forces of disintegration and reintegration are completely harmonized or balanced; in which the retrogressive and the progressive phase of motility co-operate to form a continuously reconstructed and self-rounded protoplasmic individual. Nothing can be more instructive than to watch, and to gain an insight into what takes place in such morphologically unorganized, and yet organically and functionally unitary protoplasmic beings. An individual ovoid being is seen to flow evenly across the field of the microscope. From the interior of its body, toward the basal or aboral pole, where nutritive corpuscles are gathered, there issues what is seen as a continuous flow of granular material, expanding and getting finer and finer granulated, until quite in front there emerges a perfectly hyaline substance, forming what may be called the oral, most expanded pole of the ovoid being. This foremost product of cumulative reintegration presents thus its fully expanded surface to the medium. Suffering thereby functional disintegration through contact with the same, the disintegrated portion is thrust aside by the pushing forth of new expanding material, and is left sliding down along the sides, helping there to form the gradually contracting envelope, getting more and more granular, and closing in at the rear collapsed, and ready to reenter by means of complementary restitution the ascending current.

It is by means of this cycle of definitely interdependent activities that the form of the organism is maintained and its steady locomotion effected. Such highly instructive organisms have to be looked upon as

forming one single so-called pseudopodium, through the apex of which a renewed flow of hyaline material is ever maintained. In this manner only is its steady locomotion accomplished. The true mode of amoeboid locomotion is here visibly demonstrated, and all other attempted explanations of genuine amoeboid locomotion will be found erroneous.

Since twenty-five years, 1879, "St. Thomas' Hospital Reports," I have urged in English and German* periodicals this explanation of amoeboid locomotion as part of my interpretation of vital motility. I was surprised that, so far as I am aware, not before nineteen years had elapsed was it corroborated. Rhumbler published 1898 observations, which led him to explain amoeboid locomotion in the same manner.

The same occurrence, which leads in its unimpeded fulfillment to continuous locomotion, takes partly place in every pseudopodium emitted by amoeboid beings. The substance forming the pseudopodium would keep pushing out into space if a sufficient supply of expanding material

*1881, *Plueger Archiv*, p. 502-3, I said: "Bei dem in Fig. I dargestellten Moner wird es mit einem Blick übersichtlich, dass der lebendigen Bewegung ein chemischer Cyklus von Zersetzung und Wiederherstellung zu Grunde liegt. Es flieszt der morphologisch unorganisirte Körper, unter Beibehaltung seiner ovoiden Gestalt, kontinuierlich in der Richtung seiner Längsachse in den Raum hinaus. Es musz demnach das überaus lehrreiche Protoplasma-individuum als ein einziger, durch die ganze Körpermasse geformter Fortsatz aufgefasst werden; ein Fortsatz durch dessen Spitze stets neugebildete, sich streckende Substanz hervorbringt. Man sieht deutlich wie diese vollkommen hyaline Substanz aus einer granulirten matrix hervorgeht und sich nach Vorwärts zu Bahn bricht; wie sie dann überwältigt von äussern Einflüssen zur Ruhe kommt; alsbald jedoch von neuem hyalinen Stoff durchbrochen und bei Seite geschoben wird; wo sie verdichtet und langsam schrumpfend die Wände des fließenden Körpers bildet, um zuletzt nach hinten zu als granulirte Substanz wieder in den aufsteigenden Theil des chemischen Kreislaufs einzutreten. Da aus der hyalinen Substanz durch Berührung mit dem Medium, durch funktionelle Zersetzung, schrumpfende und granulirte Substanz wird; da ferner aus der im inneren des Protoplasma-körpers geborgenen granulirten Substanz wieder hyaline sich streckend Substanz in stetigem Fluss hervorgeht; so ist es klar, dass diese hyaline Substanz das Produkt der chemischen und funktionellen Wiederherstellung ist. Der durch äussere Einflüsse oder sogenannte Reize disintegrierte Protoplasma-körper vervollständigt sich wieder durch innere Mittel."

1882, "*Jenaische Zeitschrift für Naturwissenschaft*," p. 679: "Hier besteht das ganze Individuum aus einem einzigen stest erneuerten Fortsatz, und das stetige Vorwärtsfließen solcher amoeboiden Wesen wird allein dadurch zu Stande gebracht, dass unaufhörlich neugeformte, hyaline Substanz sich nach vorn zu durch die Spitze des Fortsatzes hervorbringt. Es wird dadurch die an der Berührungsfläche mit dem Medium zersetzte und schrumpfende Substanz bei Seite geschoben und neuer Raum zur Weiterbewegung durch den frisch hervorbrechenden, sich streckenden Stoff gewonnen. Das sich auf diese Weise vorwärts bewegendes Protoplasma-individuum erhält, durch die vorn sich ereignende funktionelle Zersetzung, zugleich auch eine festere, schrumpfende Umhüllung. Das hüllenbildende Protoplasma, welches am Entstehungsort noch hyalin est, wird seitwärts geschoben und auf seinem Wege nach hinten zu immer mehr granulirt. Bereits seitlich, aber zumeist am hinteren Ende wird diese Hüllensubstanz als granulirter Stoff wieder dem inneren aufsteigenden und regenerirenden Strom einverleibt. Dieser Strom, der von hinten nach vorn zu stetig an Geschwindigkeit zunimmt, wird von der granulirten, fließenden Matrix gebildet, die den Hauptinhalt des Protoplasma-körpers ausmacht und aus deren vorderem Ende man die hyaline Substanz als Spitze des ganzen Wesens oder Fortsatzes hervorbrechen sieht."

were continuously furnished. Failing this supply its prolonged exposure to the stimulating influences of the medium causes profound disintegration and consequent contraction. This is demonstrated by certain amoeba that generally emit numbers of pseudopodia, which singly expand and contract. The amoeba remains during such variformed activity either stationary, or moves quite irregularly by means of its body being dragged along in the wake of one or the other of its expanding or contracting pseudopodia. At times, however, such amoeba come to form one single pseudopodium involving their entire substance, in which case they move straight along, head foremost, through space, exactly like the ovoid being above described. I have depicted such an amoeba in Pflueger's Archiv, Vol. XXV, Fig. IX. I have also seen Arcella Ebby and Difflugia pyriformis move at times straight along in the same manner.

The phenomena of vital motility prove conclusively that protoplasm is a unitary substance, all parts of which are interdependently bound together through what is called chemical affinity, and its vital manifestations are, consequently, due to chemical processes. The living substance being, moreover, a chemically cumulating substance, is therewith of different chemical constitution in its sundry ascending parts, though forming altogether a unitary whole. Best manifest in such amoeboid beings as form one continuously flowing pseudopodium, the living substance is seen to assume by dint of its vital activities, and its interactions with the medium, a bipolar and bilateral shape. These intimate constitutional properties of the living substance sufficiently account for the hitherto mysterious phenomena of "polarity" and "bilaterality" found to exist in plants and animals. They receive here their scientific explanation by recognizing that the living substance necessarily assumes a bipolar and bilateral form as a consequence of its all-involving cycle of chemical activities induced by its relations to the stimulating influences of the medium.

In 1880 I expressed these fundamental biological facts, which I had discovered during my protoplasmic investigations, in the following terms: "The protoplasmic projection, with its chemically cumulating substance, highest at the apex, next high at the circumference, and with its direct dependence on the digesting substance, constitutes the primitive zooid, the veritable animal unit. All essential divisions and directions of organization are predetermined and foreshadowed in its molecular constitution and activity. The entoderm and ectoderm, the longitudinal axis with its cephalic and acephalic pole; the transverse axes, that remain equal when the animal does not creep; but that get distinguished in size and import through the establishment of a dorso-ventral differentiation, when the animal does creep; all these fundamental tendencies of organization are contained in the specific flow of the living substance, and are invariably expressed in the shape of a protoplasmic projection." Mind, "The unity of the organic individual."

This interpretation of the primitive, formative factors of organiza-

polarity



tion advanced on the strength of my observations of the vital manifestations of Protozoa, have been lately confirmed by Morgan as an inevitable conclusion from manifold, most instructive results yielded by experimental regeneration and experimental ontogeny. Morgan asserts that "there can not be much doubt that both the polarity and the bilaterality of the egg or of a piece of the egg, belong fundamentally to the same class of phenomena, and we are forced to the supposition that they are inherent peculiarities of the living substance." "Regeneration," p. 248.

I may add that the interpretation of vital phenomena here given and found to result from the cumulative reintegration of the living substance as a whole, necessarily following its normal or abnormal disintegration; that this interpretation yields, as will be shown in the section on organization, the master key to the unlocking of the otherwise impenetrable phenomena of ontogeny, regeneration, and organic shaping in general.

Protoplasm is a collective name, and not a substance of definite chemical composition, such as other analyzable organic substances. As living substance it is by no means, as sometimes supposed, of the same chemical constitution in different protoplasmic beings. On the contrary, it is precisely the difference of chemical constitution which underlies the multifold and profound differences of such beings, structurally and functionally. The difference of chemical constitution evinces itself morphologically in the definite configuration which each of the numerous kinds of protoplasmic beings assumes; and functionally in the more or less rapid reintegration of the functionally deteriorated substance. The higher the chemical constitution, the quicker the functional restitution.

With regard to amœboid beings, close observation and comparison of many kinds, reveals that the alternate expansion and contraction of their pseudopodia is not merely a casually induced phenomenon, nor merely a means of moving and seizing nutritive material; but that it constitutes the most essential and central manifestation of their vitality. An expanding, explosive substance is thereby offered to the stimulating influences of the medium, resulting in more or less profound disintegration by its clash with the same, whereupon the intrinsic restitutive forces gain the ascendancy, and a renewed wave of expansion beats against the functionally disintegrating influences. In sundry ways, with slower or quicker pulsations, all forms of amœboid beings display in ever reiterated sequence the same see-saw motion of alternate expansion and retraction. There are amœboid beings, such as the *Heliozoa*, that push out long and slender pseudopodia, which quickly stagnate through and through, whilst others, such as reticulate *Rhizopods*, push out just as long and slender pseudopodia, that appear, on the contrary, vividly active by means of the rapid play of reintegrating and disintegrating pulses, aided by the coalescence of joining pseudopodia. There are again amœba which push out irregularly shaped, lobular pseudopodia, consisting mostly of hyaline substance, whilst others push out long,

cylindric or conic pseudopodia, consisting mostly of granular material. All these differences of form and consistency, and many more, are due to differences in the chemical constitution of the living substance.

Like form and function depend on like chemical constitution; unlike form and function on unlike chemical constitution of the protoplasmic individuals. But in all kinds of amœboid beings functional disintegration and reintegration of their substance underlies their vital motility; and, indeed, their entire vital activity. Without functional disintegration protoplasm would not be a living substance, but just as little would it be a living substance without functional reintegration. It is to this two-fold, seemingly antagonistic, yet really compensative activity that it owes its vitality, by which it is so strikingly distinguished from lifeless matter.

The living substance is, then, quite essentially a substance which has the power to reintegrate itself after suffering deterioration. Its normal function consists, in fact, in the harmonized play of disintegration and reintegration; definite reintegrating pulses responding to definite disintegrating pulses. All ectodermic interactions with the medium take place under such functional pulsations. Vital function consists in specific reactive responses of the living substance to definite incitements emanating from its environment.

What has been positively ascertained regarding the agencies that actuate vital motility, reveals, then, unmistakably, that a protoplasmic being is a unitary individual or organism, whose entire living substance is formed and maintained by a cycle of out and out interdependent chemical activities. Disintegrating changes of its exposed surface involve reintegration, not only of the surface substance, but necessarily also in consequence of it, reintegration of the entire substance forming the unitary individual. The protoplasmic individual is, in fact, a chemical whole, all of whose constituent parts and elements form integrant, and nowise mere aggregated components. The identity of the whole, the identity of the entire protoplasmic individual, indispensable to its existence as a unitary being, can be maintained only by its complete reintegration following whatever deterioration it may suffer, normal or abnormal, functional or otherwise.

The intrinsic power of the protoplasmic individual to restore its identity as a whole when externally encroached upon is, as already stated, the most fundamental formative influence in the life of organic beings. The living substance, by its signal power of maintaining its identity, under change: its power of identically reshaping its organization when impaired: by this power of reintegrating itself to full identity it becomes the natural and naturalistic substance par excellence, the real prototype of what in philosophical conception is regarded as the essence and nature of that which constitutes substantiality. For it alone in our world renders possible that a body may undergo changes, displaying sundry modifications, properties, attributes, and whatever modes of

activity, and yet withal remain identical. The living substance is in this sense the only substance we have, or can have, any knowledge of.

Protoplasm is often looked upon as a mere mixture of various organic substances, which in combination, or singly, are believed to be the bearers of vital properties. But no kind of statical substance can be alive, or be the bearer of vital properties. Life consists essentially in the ever sustained chemical and dynamical play of the organism with its medium. In a publication of 1882 I said:* “As regards the chemical composition of the living substance, how could it ever be possible to ascertain the same? No analysis of such a synthetic unity, of a substance that is throughout in constant chemical flux, can throw any light on vital motility, which is the immediate mass-manifestation of the indivisible, self-rounded play between the continually reintegrated protoplasm, and its as continual disintegration by the influences of the medium.” Recently Johannes Reinke, who has assiduously labored to ascertain the chemical constitution of protoplasm, has emphatically arrived at the same conclusion. He says: “Dead protoplasm is no longer real protoplasm, just as little as a watch ground to powder continues to be a watch.” He, therefore, likewise looks upon the protoplasmic individual as an indiscernibly organized whole, whose structure he therewith holds to be the “dominant” agency in functional activity.

By close observation of visible occurrences we have, I think, succeeded in gaining some positive, not merely hypothetical, insight into the real nature of the living substance, and of that which constitutes its vitality; an insight far more profound and instructive than any aggregational theory has ever afforded. We have discovered the ways and means by which the peculiar chemical substance, called protoplasm, comes to be alive; and have found that it is a living substance only by dint of the cycle of chemical activities by which it is constituted and maintained during its interaction with the medium.

ASSIMILATION.

The fundamental process of alternate disintegration and reintegration, which gives rise to vital motility, involves, as indispensable adjuncts, nutrition and depuration. On the one hand it necessitates appropriation, preparation and assimilation of complemental material fit for recomposition; on the other hand oxydation and elimination of waste products of decomposition.

Food serves essentially as restitutive material, and not as is often asserted, as fuel which is supplying from outside by force of its oxydation the moving energy, which sets an otherwise immobile machinery going. In 1870 (*Centralblatt für die Med. Wiss.* No. 11), the present writer published observations on the living muscles of locusts, which induced him to conclude, in opposition to the generally accepted views of Julius Robert Mayer, that the contraction of muscular fibres is not

**Jenaische Zeitschrift für Naturwissenschaft.* vol. XVIII, p. 680.

simply mediated by a machine-like construction of the same, but that chemical changes in the constitution of the muscular substance itself causes its contraction. "From these observations, I think, I may conclude, that in the muscular fibre its contraction is not mediated by any kind of machinery, but that changes in the chemical constitution of the muscular substance itself are the cause of the entire process of contraction." In 1881, in an article in Pfluger's *Archiv. Zur Lehre von der Muskelkontraktion.* after two entire years of further observation, I ventured to advance a new interpretation of muscular contraction, in which I laid stress on the positive, reintegrative, expansive phase of muscular activity, as compensation of the negative, disintegrative, contractive phase, which latter remains still the only one physiologically acknowledged. These observations made nutrition or the functional use of food, and oxydation or reduction of organic substances, appear in an entirely different light. The office of nutrition was recognized as having essentially to supply and prepare assimilative material fit to reintegrate the functionally deteriorated substance. And the office of oxydation evinced itself as having essentially to reduce the eliminable products or waste substances of functional disintegration.

The assimilation of nutritive material consists in the power of the living substance to fill the chemical gap caused by functional disintegration. This direct conclusion from observable facts scientifically explains in what nutrition really consists, and shows how assimilation is rendered possible. The force which compels assimilation by causing lifeless matter to be incorporated in the living substance, and to become itself thereby vitalized; this vitalizing force consists in the avidity of functionally deteriorated protoplasm to reconstitute its chemical integrity.

The current hypotheses of individuated molecular units have turned vital assimilation into an inscrutable mystery. Under their sway it remains utterly unintelligible how lifeless outside matter can possibly be converted into swarms of vitalized and vitalizing molecules, of which organisms are then supposed to be built up. The untenability of such aggregational theories have been here sufficiently exposed. It has been found that without a correct understanding of assimilation, and therewith of organic growth, neither self-division, nor other modes of reproduction can be scientifically explained. For assimilation and growth are processes upon which organic reproduction in all its forms is altogether dependent. We have now positively recognized that assimilation, or the vital and organic incorporation of nutritive material consists nowise in a mysterious new formation of vital units, either by spontaneous generation, or by the self-division of already existing units; but that it is simply a result of chemical reintegration of the living substance by means of combination with complemental material. Of course, in a general way it is taken for granted that organs repair the waste they suffer during functional activity. But by what means such organic restitution is effected has hitherto remained in the dark.

It is instructive to elucidate the process of assimilation by tracing it

in different kinds of amœboid beings. By watching the slender, seemingly deadened pseudopodia of Heliozoa, we see all manner of stray stuff drift between their rays. Among the particles of foreign matter coming in contact with the far-reaching pseudopodia, only a few are specifically attracted and retained; evidently through what is called chemical affinity. By combination with many such minute particles the sharp outlines of the pseudopodia become gradually serrated. Their substance is undergoing progressive restitution through chemical union with the foreign complementary material. It is, in fact, seen gradually to remelt and contract. Several rays in this state are often seen to meet and to coalesce, acting upon one another as complementary material. Contracting more and more they eventually form together a globule, which is drawn into the body of the protoplasmic individual, there to constitute a nutritive corpuscle. At times some large body, fit for food, gets entangled between the rays, which on contact with it rapidly dissolve, coalescing around it, so as to form a large globule inclosing the foreign body, eventually to be drawn into the protoplasmic individual to serve there as nutritive material. Nutritive corpuscles of this kind are found, as is well known, in most "fluent" protoplasmic beings. They have the function of preparing assimilable material fit to reintegrate the living substance after functional deterioration. This preparation of assimilable material is effected in the nutritive corpuscle by chemical interaction between the enveloping protoplasm and the nutritive material.

In these stellar protozoa the rays become so deeply deteriorated as to remain exteriorized and deadened until redeemed to life by direct combination with complementary material. The preparation of assimilative material becomes in this instance a function of every pseudopodic ray. The substance of each ray melts under direct union with externally supplied material, and elaborates then the complementary substance for reintegration of the entire being, enabling it to emit new rays.

In more highly developed amœboid beings the process of direct external reintegration of the pseudopodia, exclusively by means of immediate union with foreign material, is transformed into a process of indirect reintegration from within. The nutritive corpuscles, formed by partial assimilation of food material on the part of one portion of the amœboid substance, are lodged in the interior of the protoplasmic individual, and elaborate there the assimilable material for the complete reintegration of other portions of the protoplasm. In this manner one portion of the living substance comes to prepare assimilative material for the restitution of the other portion, which in consequence is enabled to assume exclusively the dynamical interaction with the medium. A digesting portion of the common protoplasm becomes thus subservient to a moving portion. And this means that the internal substance, or what in higher organisms is called the entoderm, has the function of furnishing restitutive material for the substance that is brought into

immediate interaction with the dynamically stimulating influences of the medium.

The protoplasmic individual becomes thus a being with a two-fold, almost bipolar relation to the medium. At its outer surface it carries on what may be called the dynamical interaction with its environment, suffering thereby disintegration. In its interior it carries on the digestion of nutritive material furnished by the medium, whereby reintegration is effected. This evident subserviency of the internal digesting substance to the externally active substance of living beings is pregnant with important developmental consequences. For it is extremely probable that the incessantly maintained interaction of the chemically cumulating substance of the organism with the divers and definitely stimulating influences of the medium; that this ceaseless reciprocal play leads to the gradual functional attunement of diverse parts of its surface to the diverse modes of stimulation, and therewith to structural elaboration and structural differentiation. This adaptive process would then necessarily involve corresponding adaptation of the entire individual, consisting, as it does throughout of a chemically integral substance.

We actually find the different surface structures of organisms respectively attuned in their functional activities to different corresponding modes of external stimulation. Such specific attunement must have been somehow brought about during phyletic evolution. And, surely, it is more likely that it has been wrought by constant interaction of the living substance with the externally stimulating influences, in which its most essential and culminating vital function actually consists; more likely to have been wrought in this way, than by accidentally useful nutritive variations of composition having been offered for random selection to haphazard contingencies arising during the struggle for existence; whatever helpful adaptive assistance this may have rendered.

Results of botanical investigation point to this formative and developmental dependence of the living substance on its interaction with the sundry influences of the environment. The plant stands in more immediate dependence on its medium than the animal. For its sundry organs evolve to a considerable extent in dependence on the same stimuli, with which they will eventually remain in functional interaction.

Considering that the functional activity of the entire organism takes altogether place in more or less direct interaction with outside agencies, and in more or less important relations to the same; considering, furthermore, that the interaction of their surface structures or ectodermic organs with the sundry stimulating influences of the medium constitutes their culminating activity, to which all other functions are subservient; considering all this, it lies near to conclude that in this very activity is to be found the fundamental and most essential formative and developmental process. Nutrition having proved to be essentially complementary restitution of a preformed, most specific constitution of the living substance, it can not possibly take a leading part in organic evolution, as is generally believed.

Inferences regarding phyletic agencies are, however, apt to stray more or less widely from what has really occurred. To avoid false expectations and wasted labor it is well not to forget that the organic individual, together with its environment, are conjointly revealed to our perception chiefly in the symbolical medium of our visual space. We perceive thus definite forms representing on the one hand the organism, and on the other its environment. And from direct or compared changes in our field of vision we conclude that the changes in the organism have been induced by corresponding changes in the environment. We distinguish hereby, by dint of established experience, between chemical composition and activity, and purely physical or mechanical composition and activity. And in the case of the organism and its environment, we rightly conclude that the observed changes wrought in the organism are chemical changes induced during cetodermic activity by interaction with the physical incitements emanating from the environment. But we know as little the intimate nature of what in our perception appears as chemical substance, as we know by what means physical agents are empowered to induce changes in the constitution of bodies. We symbolically perceive the results without being able to form adequate conceptions of the real nature of the activities, or of the actuating agents at work. Though we know for certain that the living substance has, and steadfastly maintains, a most specific chemical constitution, we are explaining its vital phenomena only symbolically, principally in terms of visual perception. The adaptation of the structures of the organism to the functions, which they exercise in relation to external conditions, consists evidently in the chemical elaboration of the living substance into functionally adapted structures, which are perceived as out and out organized forms.

Assimilation is the consummation of the nutritive process. And the vitality of the substance composing living beings, with all its principal manifestations, such as irritability, motility, growth, regeneration and ontogenetic evolution, must all remain enigmatical, so long as the true nature of the assimilative process is not understood. The transformation of lifeless into living substance underlies all vital function. And this conversion of lifeless into living substance consists, as has been shown, simply in complemental assimilation of nutritive material, by means of which the living substance is reintegrated, after it has suffered disintegration. It does not consist, as generally accepted, in the new-formation of vital units. The restitutive process, actuated by the intrinsic affinity and avidity of functionally deteriorated protoplasm towards nutritively complemental material, renders alone possible the vital reaction, the motility, the growth, the regeneration, and the reproduction of organic beings, together with the maintenance of their structural and functional identity.

Such sweeping generalizing from the vital phenomena of beings low in the scale of organic evolution to the vital phenomena of organisms in general, may appear overbold and unjustified to many, perhaps to most investigators. But we are dealing here with the observable processes

which give rise to the essential vital properties of the living substance, of which all organisms are admittedly composed. These properties, which constitute protoplasm the one living substance in nature, and which are, in fact, the essential vital properties of all organisms, reveal themselves intelligibly in the morphologically uncomplicated and transparent forms of amœboid beings. Here the sundry vital functions are not morphologically specialized in intricately organized structures, and to all appearance separately confined in definitely formed organs, but are still interdependently fluent to our view. And this allows their mutual relations and activities in the service of the organic whole to be satisfactorily ascertained and scientifically explained.

DEPURATION.

To complete our understanding of the cycle of chemical activities that constitutes vitality, we have to give a moment's attention to depuration, the other indispensable adjunct to vital activity besides nutrition, and well nigh its opposite, though interdependently connected with it. During functional activity, during its functional interaction with the medium, the living substance becomes to some extent deteriorated. The effete products of this functional deterioration have to be eliminated, in order to keep the living substance undefiled and unimpeded in its activity. This is one of the occasions for depuration. Moreover, the process of nutrition, during its elaboration of assimilable material, gives likewise rise to the formation of effete products, which have also to be eliminated. This is the second occasion for depuration. The functionally severed particles of organic substance are seized upon by oxygen and reduced to eliminable elements.

There are, therefore, two different regions, and two different occasions, where and when depuration takes place; the first, where what may be called the dynamical play with the medium occurs; and the second, where the nutritive processes are at work. The former we may designate "dynamical," the latter "nutritive" depuration. In Protozoa these functions are in most cases visibly performed by depurative vesicles, which gather and eliminate the oxydized and fluidized waste products. In amœboid beings the depurative vesicles, or so-called vacuoles, indiscriminately arise more or less numerous where and whenever needed. In ciliated Infusoria, however, they become definitely localized, and constitute then regularly functioning organs. In some, as in the Vorticellidæ, one single pulsating vacuole ministers normally both to dynamical and to nutritive depuration. In others, as in Paramœcidæ, a vacuole in the oral region ministers to dynamic depuration, and another in the aboral region to nutritive depuration.

In *Actinophrys sol*, when the animalcule has first been made to shrink, the formation and eventually the definite localization of the depurative vacuole can be observed. This interesting localization of an organ in the making, I have described in the *St. Thomas Hospital Reports*, 1879.

Besides the two modes of fluid depuration occurring in Sarcodina,

solid particles of undigestible nutritive material, and particles derived from deteriorated protoplasm, are eliminated by being bodily crushed out of the vital cycle.

Depuration brings the protoplasmic individual into a third direct relation of interaction with the medium, and especially with its atmospheric oxygen.

The living substance stands thus in three different direct and vital modes of dependence upon its medium. Its vitality is conditioned and actuated by the three different processes of interaction which arise from these three modes of dependence. First, the stimulating process which specifically incites the ectodermic or dynamical functions; second, the nutritive process which furnishes the complemental material for reintegration; and third, the depurative process which necessitates the absorption of atmospheric oxygen. These vitally indispensable modes of interaction presuppose an intimately pre-established harmony between every structure and function of the organism and the conditioning and actuating factors of the medium. This proves that fundamental adaptation of the organism to its medium is coeval with life itself at every stage of its evolution, as Gustav Wolff has pointed out in his masterly polemic against adaptation by means of natural selection.

GROWTH AND REPRODUCTION.

The general conditions which give rise and which sustain the vital activity of the substance composing living beings, involving motility, nutrition and depuration, have in their essential characteristics been considered. There remains unexplained the growth and the reproduction of organic individuals.

After having gained an insight into the process of assimilation, indispensably connected with reintegration of the living substance, that which essentially constitutes organic growth becomes almost self-evident. Growth, when manifested to its full extent, consists evidently in the power of a fragment of the living substance derived from an adult organism to reintegrate itself, so as to reproduce the complete adult form. In ordinary functional disintegration the identity of the adult organism is quite obviously restored by means of complemental reintegration through assimilation of nutritive material. The deeper the disintegration penetrates, the larger the specific chemical gap to be complementally filled. The disintegrated living substance forms thus a more or less disequibrated chemical fragment of its former self, endowed with the power of reintegrating or regenerating under suitable conditions. This power of fragments of organism to reconstitute the entire individual is most strikingly evidenced by parts of the living substance artificially severed from organic individuals. Trembly's experiments on the regenerative power of sweet water polyps, published as early as 1714, and Reaumur's experiments chiefly on earthworms, published in 1742, which experiments were repeated and extended by other investigators, remained more a source of wonderment than of scientific

enlightenment. Not until Gruber's researches on "the artificial division of Infusoria," 1884-5, and M. Mussbaum's investigations of "spontaneous and artificial division," 1884, and on "the divisibility of the living substance," 1886, was there a new fruitful impetus given to the attempt at scientifically explaining this astonishing process of organic reintegration. Wonderful and most instructive results have since been experimentally attained in this field of research by a number of investigators; an account of which, with much original matter has been lately given in Morgan's excellent work on "Regeneration." It is becoming more and more certain that this power of fragments, detached from organic beings, to regenerate the entire adult form from which they are derived; that this regenerative power is one of the most fundamental properties of the living substance.

As to the relative smallness of fragments capable of regenerating the entire organism, Lillie found that fragments of the substance of *Stentor*, measuring only 1-27 of the volume of the adult infusorium, retain still the power to regenerate the entire individual. And still more decisive in this respect was the great discovery that single blastomeres, and even mere small fragments of egg-plasm possess the power to reproduce the complete embryo. As early as 1870 Haeckel observed that pieces of the segmented egg of *Medusæ* were capable of regenerating complete animals. O. and R. Hertwig, Boveri, Driesch, Morgan and others found that single blastomeres, or pieces of egg-plasm of sea-urchins reproduce the entire embryo. Wilson showed that similar results can be obtained with *Amphioxus*; Herlitzka with salamanders; Zoja with jellyfish; Morgan with fish, etc.

It is certain, then, that even small fragments of the substance composing protoplasmic individuals of highly complex structure, and even fragments of their egg or germ-plasm, have power to reintegrate, regenerate, or reproduce the entire structure and form of the organism from which they are derived. This process of gradual reintegration is evidently genuine organic growth. Consequently, organic growth does not consist in the new formation and aggregation of multitudes of separate vital units, but quite essentially in the power of fragments of the living substance to reintegrate, regenerate, or reproduce the entire protoplasmic individual from which they are derived.*

On the strength of numerous instructively varied experiments on artificially induced regeneration, and considering that even small fragments of egg-plasm are capable of reproducing the entire embryo, it is, I think, not far-fetched to conclude that normal reproduction is like-

*"Da nun das Ziel des normalen Wachstums zanz dasselbe ist, nämlich die Herstellung eines vollständigen Individuums, so ist im Wesentlichen Wachstum die Erreichung einer bestimmten chemischen Vollendung der lebendigen Substanz, vermittelt Wiedervervollständigung eines funktionell abgetrennten Fragments derselben." *Jenaische Zeitschrift für Naturwissenschaft*, XVIII, p. 699, 1882. In this neglected article all essential observations and explanations concerning vitality and organization here again brought forward will be found clearly and explicitly recorded.

wise a process of reintegration, due to the same restitutive power inherent in chemical fragments derived from adult organisms, and here called reproductive germs. If a minute fragment artificially and necessarily more or less clumsily severed from the egg of an Echinoderm has power to reproduce so complex and specific a structure and form as that of a pluteus; and a small irregular slice of the substance of Stentor power to reproduce the definitely formed and organized Infusorium, it is, surely, no very bold leap in the dark to conclude that the infinitely more refined methods of organic development have succeeded in normally detaching from the living substance of ever so highly constituted organisms more or less minute germinal fragments, which as such retain the power to reproduce the structure and form of the adult organism from which they are derived.

Germes of all kinds may then rightly be looked upon as chemical fragments or radicals, which by means of complementary assimilation of nutritive material gradually grow to adult stature, reproducing thereby the structure and form of the organism from which they originated. In 1880 I expressed this fundamental biological fact in the following terms: "Any portion of the unitary protoplasm of an organic individual, and especially its so-called germs, have to be considered in the strictest sense of the term, chemical radicals. You remove from a chemical compound a part of its integrant atoms; it is no longer saturated, but represents a chemically disequilibrated residue with combining powers corresponding to the severed atoms. Whenever occasion offers the radical will become resaturated; it will in fact reconstitute itself, will restore the integrity of the compound which it radically represents. Surely it is this admitted chemical occurrence which underlies the vital phenomena of growth, repair and reproduction." ("The Unity of the Organic Individual" *Mind* V., pp. 465-489.)

The results of experimental regeneration and experimental ontogeny; the latter dating from Pflueger's experiments on the eggs of frogs, 1883, and extended since by numerous observers; these results closely corroborate the views forced upon me by the study of primitive protoplasmic individuals, as will be fully explained in the section on "Organization."

By watching the sundry modes of reproduction of various kinds of Protozoa a pretty clear insight into the intimate workings of the process may be obtained. Self-division into two equally formed and organized halves; an occurrence wholly unintelligible to aggregational and mechanical theories, consists really in a most elaborate process of complete reintegration. It starts from two independent centers of reproduction, arising within the substance of the protoplasmic being. It is in no way connected with overgrowth as usually asserted; for it may occur at different stages of ontogenetic evolution. It is caused by conditions that are obstructing the unitary cycle of chemical activities which constitutes the protoplasmic individual; or it is caused by conditions favoring otherwise the independent formative activity of parts of the living

substance. Each independent center of reproduction begins then separately to exercise its power of reintegration, tending thereby to reconstruct the entire adult form. To effect this it uses substance derived from the dividing individual itself, and also prepared nutritive material. And failing the supply of nutritive material it assimilates so much of the protoplasmic substance as it can draw to its share.

By watching the self-division of quiescent Infusoria, such as that of *Epistylis*, or still better that of *Colpoda cucullus*, the out and out transformation of the protoplasm by force of an elaborate process of reconstitution from independent centers of activity can be readily ascertained. I have observed in 27 *Colpoda*-spheres simultaneously under view their respective division in two, four, five, six, and seven new individuals. Mitotic centrosomes are evidently such independent centers of reproduction and the astrospheres the visible signs of the reproductive activity.

Buds, external and internal, and spores and germs of all kinds, constitute chemical fragments of the organism from which they are detached, centers of reproduction awaiting favorable conditions of the medium to begin their regenerative or reproductive activity. The notion that all kinds of reproductive plasms are essentially chemical fragments of the organism from which they originated, is by no means a mere hypothetical assumption, such as that to which the purely hypothetical units of Darwin, Haeckel, De Vries, Naegeli, Weismann, etc., owe their existence. It is, indeed, hardly more than a direct interpretation of observable facts. For we actually witness that fragments of organic beings, and even fragments of their egg-plasm do reproduce the organic form, from which they are derived. That these fragments are of a specific chemical nature, endowed with most specific chemical affinities which are being satisfied or saturated during reintegration, regeneration or reproduction; this their definite chemical consistency follows from the living substance being itself an out and out specific chemical substance, forming as such an integrant whole, and exercising its functional activities, its motility, assimilation and depuration, by force of chemical reintegration following functional disintegration. The chemical bond which constitutes protoplasm being ruptured, it loses at once all its vital properties, and is as Reinke forcibly expresses it no more real protoplasm, than a watch ground to powder is a real watch. Consequently reproductive fragments of all kinds, in order to consist of real protoplasm or living substance, and not of dead matter, must necessarily partake of the chemical nature of the protoplasmic individual from which they are derived. They must be specific chemical fragments. And the power of reintegrating itself being the central vital property of the protoplasmic individual, its reproductive germ, to be endowed with vitality, must likewise be endowed with reintegrative power. Growth and reproduction consist, then, in the reintegration of a chemical fragment, so as to reproduce the organism from which the fragment was detached.



GENERAL REMARKS.

It has been shown in this section that a definite cycle of chemical activities constitutes protoplasm a living substance; that its interaction with the stimulating influences of the medium, taking place at its chemically highest region, is its culminating function, to which all other functions are subservient; and that this state of things necessarily involves nutrition or restitutive assimilation on the one hand, and on the other hand deuration or elimination of waste products.

Howsoever intricately differentiated into organs, tissues and components of tissues an organism may appear to sight, its structures are nevertheless out and out the visible substratum of this manifoldly related and yet indiscerptible cycle of activities which constitutes the vitality and governs the organization of all living beings. It inseparably underlies the structural unity of the organic individual in all its varied forms of appearance.

Although since Descartes' purely mechanical views, and then especially since atomic mechanics have guided the interpretation of vital phenomena, many prominent biologists have, notwithstanding, felt compelled to assume, as help in their scientific explanations; a special vital force or agency operative in vital phenomena. The existence of such a special vital force Lotze first successfully combated in his celebrated article in Wagner's *Handwoerterbuch der Physiologie*. He clearly showed that that which had been called a "vital force" is a mere metaphysical fiction. And though thoughtful observers such as Johannes Muller, Claude Bernard, Liebig and even Virchow still adhered to the belief that something transcending physical forces is operative in vital manifestations, the sway of atomic mechanics overruled until quite lately all attempts to introduce into biology modes of activity additional to such as are merely mechanical.

The insufficiency of the purely mechanical interperation of natural phenomena in general and of vital phenomena in particular, was forced upon the present writer during his protoplasmic researches, and insisted upon in various publications for the last twenty-five years. In its relation to biology I have expressed this need of a more profound view perhaps most concisely in Pflueger's *Archiv*, 1881, v. xxv, p. 534, of which I give a translation: "The power of regeneration is in all cases the mechanically unaccountable energy of protoplasm to chemically reintegrate itself. Consequently its actuating energics and even the mechanical capacity for work on the part of animal organisms, does not admit the application of exact physical methods. We have here before us as source of energy an explosive substance, which is ever restituting itself, and whose power of reintegration, grounded in endless phyletic elaboration, stands therefore in no direct mechanical relation to its environment. Neither the complemental restitution, nor the effects of stimulation, are here mechanically transparent. They are, on the contrary, to be looked

upon as processes in sharp contrast to modes of mechanical energy-concatenations."

The organized living substance is not, as has been so generally taught, a mere machine actuated by externally transmitted energy; but it is itself the very source of specific modes of energy, differing altogether from the mere mechanical kind. Its functional reintegration is not due to mechanically transmitted modes of motion; but to its phyletically inwrought power of regenerating its own specifically efficient integrity. And its functional reactions on external stimulation are nowise the equivalently converted energy of the stimulating influences; but an intrinsic response of its own generically accumulated wealth of organized power, qualitatively and quantitatively incommensurable with the stimulating energy, which merely arouses to action its indwelling potentialities.

When I first expressed this view, the introduction of other than purely mechanical modes of energy, and especially of hypermechanical vitalistic modes, was considered scientific heresy, not deserving serious attention. Principally through the persistent efforts of Ernst Mach, other modes of activity or manifestations of energy, than the purely mechanical, are now allowed to play a part in the actuation of natural phenomena, even of the physical kind. In keeping with this more comprehensive view, and with manifold biological results and considerations recently arrived at, thoughtful investigators, among whom Driesch is most prominent and outspoken, have under various guises been led to make again use of vitalistic modes of interpretation. They have become aware that vital phenomena are actuated by specific energies of their own, and not by mechanically transmitted modes of motion.

In this connection Eugen Albrecht in his "Vorfragen der Biologie" 1899, says: "All vital hypotheses mentioned testify, by dint of their mere existence that beyond the physico-chemical analysis there must lie problems, uncertainties, which we feel without being able to express them in current mechanical terms. It seems to me that in all these vitalistic attempts a hitherto unsolved question makes itself more or less distinctly discernible; a question which in its full import does not occur and can not occur to the rigorous mechanist, which, however, perhaps constitutes the essential ground and real object of the contention. I mean the problem of the living form."

The power of the living substance, and therewith of organisms composed of it; the power to reintegrate or regenerate its structure and form, underlies all other vital manifestations. It insures the maintenance of the identity of organic beings, without which neither their structures nor functions could retain any permanency; but would from moment to moment degenerate toward complete dissolution. The reintegration of living individuals, after functional or abnormal deterioration is an unmistakably observable vital manifestation, which obviously indicates that the organic individual is an integrant whole. And it evidently constitutes a mode of energy not operative in inorganic nature; energy being defined as the capacity of performing work. Its specific

nature is evidenced here by the peculiar work it is performing; the work of chemically reintegrating the structure and form of organic beings, whose modes of reaction are mechanically unaccountable. It may therefore confidently be looked upon as vital and formative energy without losing its character as essentially a chemical process. A chemical fragment of the living substance represents a phyletically accumulated store of most specific potential energy. There is here no abrupt introduction of some transcendent kind of force or energy imposed from outside upon the chemical substance composing organic beings, and believed to mould and to vitalize their structures. The living substance is by force of its own chemical composition structurally organized, and by force of its cycle of chemical activities vitalized. Vital energy arises here naturally and intrinsically from the chemical constitution of the substance composing organic beings, and is displayed in consequence of their functional interaction with the influences of the medium. It is obvious that the maintenance of the definite structure of protoplasmic individuals is the work of this formative and vitalizing energy. The definite chemical constitution of the living substance evinces itself to our spatial vision as a definitely organized form.

If we, furthermore, ask what in reality constitutes chemical composition with its specific modes of qualitative reaction, we have to confess that this question transcends as yet the limits of our knowledge. Suffice it to say, that, whatever theory may be advanced with regard to the ultimate constitution of what is called matter, chemical constitution is clearly recognized as a mode of composition, differing from mere physical aggregation of equal molecules by forming integrant bodily units, of which all component elements are interdependently bound together by a specific bond which is figuratively called chemical affinity. And it is certain that the qualitative modes of reaction of such chemical compounds, which in organic beings give rise to such striking phenomena; that these specific modes of reaction are mechanically incalculable. Driesch conceives them as "intensive manifoldness," because they have their being, not in a spatially mechanical arrangement of parts, which could react on stimulation only in one single definite manner; but subsist in a hypermechanical, superspatial, vital sphere, which admits of manifoldly complex modes of reaction on the part of one and the same spatially visible substance.

ORGANIZATION

INTRODUCTION.

The interpretation of vital phenomena given in the former section rests not on hypothetical assumptions, but on the direct observation of visible and always verifiable manifestations. Its principal outcome, besides the scientific explanation of vitality, consists in having established the fact that the organism is essentially an indiscerptible whole, and not an assemblage of autonomous elementary units; that all its parts are integrant and not mere aggregated constituents; that its structure and form can nowise be explained as the result of a coming together and marshaling of a multitude of separate beings, nor its functions as the automatically co-operative activity of a host of elementary units. Form, structure and function are, on the contrary, the work of a self-rounded cycle of interdependent chemical activities, which constitutes the unitary individual's vitality or life.

Organisms are avowedly protoplasmic individuals, products of the phyletic elaboration of the living substance, of which they are all composed. It has been shown that all essential vital phenomena: irritability, specific reaction, motility, assimilation, growth and reproduction, naturally result from the power of the living substance to restitute itself to full integrity or identity when functionally disintegrated, and also to an astonishing degree when artificially fragmented. The maintenance and reconstitution of the integrity or identity of the organism as a whole is the essential conjoint work of all vital functions.

It has been proved by many striking examples, that artificial fragments, not only of so-called unicellular organisms, but also of highly complex "multicellular" organisms, have the power to restitute or regenerate the specific structure and form of the adult individual from which they are derived. And it has been here clearly demonstrated that this power of fragments to reconstruct the whole is due to their being specific chemical fragments endowed with the faculty of regenerating themselves by complemental assimilation of nutritive material, or even by transformation of their own substance, so as eventually to reform the typical whole of which they are a fragment. And it has also been shown that the living substance is a chemically cumulating substance which involves the formation of the axes of organic individuals; their basal and apical "polarity," their oral and aboral pole, their bilaterality, and transverse axial distinctions; fundamental vital properties hitherto altogether enigmatic.

No aggregational theory of reproduction, even when formulated by

polarity

the most eminent biological investigators has proved logically tenable in its explanatory assumptions. And even when these are granted, no such theory has or can efficiently explain the fundamental phenomena of vitality, motility, assimilation, growth and reproduction.

THE UNITY OF THE ORGANIC INDIVIDUAL.

Visible appearances to the contrary, undeniable facts are forcing investigators to look upon the morphological configuration of so-called multicellular organisms, as the functionally specified structure of a unitary protoplasmic whole. And more and more is it becoming evident that no aggregation of separate units can, save by miraculous intervention, arrange themselves in space so as to form and actuate the interdependent organs and functions of the complex organism.*

Leading botanists have already acknowledged the unity of the organic individual. Strasburger in his inaugural address as rector of his university, 1891, p. 16, says: Until recently it was accepted that there existed no communication between the plasma of plant-cells. It had to be asked how under such conditions is the co-operation of the sundry cells in the service of the organism as a whole at all possible, and how can the plant as a unitary being be thus formed. The problem found its solution in the discovery that the plasma of the different cells is connected by protoplasmic filaments. These traverse from cell to cell and cause thus the living substance of a plant to be continuous. The plant, therefore, like the animal, constitutes a unitary living organism." Pfeffer "*Die Entwicklung*" 1895, arrives at the conclusion that: "All cells are correlated pieces of the whole uninterruptedly connected protoplasmic body." And Vines in his address as President of the Botanical Section of the British Association, 1900, feels justified in declaring: "The general and perhaps universal continuity of the protoplasm in cellular plants has been established. Hence the body is no longer regarded as an aggregate of cells, but as a more or less septated mass of protoplasm."

It now devolves upon zoologists to harmonize the apparent multicellular structure of animals with their real indiscernible unity. Here also the continuous consistency of the protoplasmic structure is evinced by established, and by newly forming, protoplasmic bridges ensuring the vital intercommunication of the contents of cells. According to the observations of H. Sedgwick Quart. *Journal of Micr., Science*, v, xxvi, 1886, all cells are during ontogenetic evolution as well as during adult life in protoplasmic intercommunication. Frommann in the article "*Zelle*," *Real-Encyclopædie der Gesamten Neilkunde*, 1890, sums up the then attained knowledge regarding cells in the following words: "We can no longer, as was formerly the case, regard the body as being

*See "*Mind*," January, 1880, "The Dependence of Quality on Specific Energies," a paper written to oppose Lewes' and Wundt's theory of "Functional Indifference," and wherein is proved the impossibility of autonomous units to combine their efficiencies without a combining medium.

formed by a mere conglomerate of cells, completely separated from one another by membranes and having independent lives. There exist, on the contrary, in the tissues and organs such numerous connections between equal and disparate cells, that it is entirely justifiable to regard the body as a unitary mass of living substance, as a synplasm." Even Haacke, an out and out aggregationist and mechanician, by admitting in his "Gestaltung and Vererbung," 1893, p. 124, that "every cell of the organism is directly or indirectly connected with all the rest by protoplasmic bridges" virtually acknowledges the unity of the living substance composing the organic individual. It would seem that zoologists are as much justified as botanists to conclude from the continuity of the living substance: "the unity of the organic individual," in opposition to its formation out of autonomous cells. But other stringent proofs of the unity of the animal organism are at the command of zoologists.

Recent experiments on ontogenetic potentialities of fragments of egg-plasm and on the extent and efficiency of regeneration in general, have broken further decisive ground towards the establishment of the essential unity of animal organization. Roux, although himself an aggregationist, has as early as 1885 drawn the logical conclusion that "if the germ does not contain definitely preformed germinal particles, then differentiation must be dependent on the influence of the whole of the embryo upon its sundry parts.*" Roux's own pregnant experiment, performed 1888, resulting in the formation of half-embryos, from one of the two blastomeres, when the sister-blastomere had been killed, involved unbeknown to him, the "influence of the whole of the embryo upon its sundry parts," and it involved, moreover, irresistibly, the complete overthrow of the cell-theory. For the two blastomeres proved by this decisive experiment to be, not what according to the cell-theory they would have to be, namely equal daughter-cells formed by the self-division of an elementary mother-cell; but, on the contrary, they proved to be the potential embodiment of the complementary halves of one and the same organism to be ontogenetically evolved. It follows that all further stages of segmentation can not be anything in the remotest degree resembling the multiplication by self-division of autonomous cellular beings; but that they represent the visible segregation of strictly complementary parts of a predetermined whole in the course of being evolved. This is not a hypothetical assumption, but a positively observed fact.

Pflueger's results gained by experiments with the eggs of frogs, published in his *Archiv* 1883, and formulated in his theory of the "Isotropie des Eiplasmas," led to similar conclusions. They proved that, though the different constituent elements of the egg-plasm are made to change their relative positions, a perfectly formed embryo is nevertheless produced. And, even if it is true as Born seems to have shown, that no

*Einleitung zu den Beiträgen der Entwicklungsmechanik des Embryo. *Zeitschrift für Biologie*, 1885.

intermixture of the pigmented and the non-pigmented plasm takes place, but only rotation within the egg-shell; still, as different parts of the egg-plasm are found to be able to exchange their ontogenetic potentialities with regard to the evolution of the whole embryo, differentiation must be somehow dependent on the influence of the whole on its parts. This being the case, structural differentiations can not possibly be preformed in the egg-plasm as specific germinal units. All portions of the egg-plasm seemed here to be of equivalent potency as regards the reproduction of the embryo. And, of course, in this case differentiation must be somehow dependent on the influence of the whole upon its parts.

As these experiments of Pflueger were essentially confirmed by R. and O. Hertwig, Roux, Driesch, Boveri and others, it is obvious that these investigators were thereby logically compelled, not only to acknowledge the influence of the prospective whole on its evolving parts; but they were also logically compelled to relinquish the aggregational theory of specifically preformed germinal units. Roux, by confining the reproductive substance to nuclear plasm, evaded the biological consequences involved in Pflueger's experiments. O. Hertwig admitted that the whole exerts a formative influence on its parts, but nevertheless adhered to the opinion that differentiations of embryonic structures are performed in definite particles of egg-plasm. Driesch, on the other hand, soon came fully to recognize the weighty negative and positive consequences involved in the equal prospective potency of different parts of the egg-plasm. He repeatedly declared, that not only as regards form, but also functionally is the adult organism reproduced from the egg as a unitary whole. This view of the potential integrity of ontogenetic evolution, whereby all its structural differentiations, and all its progressive stages, are subservient to the predetermined aim of reproducing the whole adult organism; this view follows indeed logically from the discovery of the equal "prospective potentiality" of different parts of the egg-plasm; the potentiality here of each such part being able to reproduce the entire structure and form of the embryo. The recognition of this power of fragments to reproduce the whole is, of course, of paramount importance to the science of life, as fully explained in the former section. It is the real formative power in all ontogenetic evolution and in all regeneration, and in fact a fundamental property of the living substance. As a result of his experiments on regeneration Eugen Schultz arrived at the same conclusion. He says: "Regeneration is a primary property of living beings." "Upon the original capacity of regeneration depends the evolution of the embryo." *Biol-Centralblatt*, v. xxii, Jan. 15.

The entire drift of Morgan's admirable work on "Regeneration" tends to establish the unity of the organic individual, and the subordinate part cells are playing in ontogenetic evolution. His observation that the diminished number of cells in fragments of the blastula has no influence on the power of the fragments to regenerate the entire embryo,

affords sufficient proof that cells, as such, are not the essential agents in ontogenetic evolution. And he finds himself compelled to conclude, "that the organism is not the sum total of the actions and interactions of its cells; but has a structure of its own independent of the cells." Whitman, 1893, published a paper, *Journ. of Morph.*, viii, "On the inadequacy of the Cell-Theory of Development." And a number of other investigators have likewise arrived, more or less positively, at the conception that the construction of the whole is, in the words of Driesch, "the clearly recognized goal of the entire process of development."

The recognition that the whole is potentially predetermined even in fragments of egg-plasm excludes the possibility of its multifold structural differentiations being represented in the germ-plasm each by a separate germinal unit, and consequently of its being constructed by an aggregation of autonomous cellular beings. The present writer has on the strength of his protoplasmic researches strenuously opposed the cell-theory, and advocated the unity of the organic individual for the last twenty-five years in a number of publications. I concluded my articles entitled "The Unity of the Organic Individual," *Mind*, 1880, with the following sentence: "To contradistinguish the theory of organization here briefly expounded from the prevailing cell-theory I call it the theory of Specification; specification of a single protoplasmic unit into definite areas of disparate stimulation; not association of a number of elementary organisms for the purpose of dividing among themselves a hypostasised physiological labor."*

But here the question naturally arises, how the whole, which is not actually present, which in fact is not yet in existence can possibly exert a preponderantly directive influence upon the evolution of the germ-plasm. The ancient puzzle of the priority of the whole over its parts, so fateful in philosophical discussions of the conceptual order, and popularly expressed in the riddle: "What is first in existence, the hen or the egg?" This profound puzzle, philosophically as well as biologically, finds its solution by recognizing that the germ-plasm is not an aggregate of separate and disparate units, nor anything like an elementary organism; but that all reproductive plasm is really a chemical fragment of the whole from which it is derived, endowed as such, by force of its indwelling most specific affinities, with the power of regenerating it by means of gradual reintegration. The germ-cell far from being an elementary organism, is, on the contrary, the potential embodiment of all phyletic elaboration.

Without this chemico-vital conception, scientifically justified by actual observation and definite experimental results, thoughtful investigators will find themselves inevitably driven to vitalism of the *deus ex machina* kind; for it is certain that vital phenomena are hypermechanical and specifically vital. Of course, it has always to be borne in mind that

*See also "The Dependence of Quality on Specific Energies," *"Mind,"* January, 1880, and "Are We Cell Aggregates?" *"Mind,"* January, 1882.

what we call "chemical" is a name for a definite set of phenomena expressed in terms of sensorial affections, and mostly in those of visual space-manifestations; in fact in terms of visual consciousness.

ORGANIC DIFFERENTIATION.

It has to be asked: How do organisms come to be at all constituted and structurally differentiated as they are actually found to be?

In order to gain a scientific understanding of the conditions that give rise to the shaping and definite organic differentiation of protoplasmic individuals, it will be best to have recourse again to primitive forms of life, where all vital activities take place in visible and transparent unity. Here we find certain amœboid beings, whose living substance forms, as explained in the former section, one single, self-rounded pseudopodium or process, "exhibiting no trace of morphologically established organization; but forming nevertheless an organism composed of all the essential appurtenances of complex vitality." "The entire chemical cycle constituting the organism and its vitality is here observable. It is distinctly perceived how the complex chemical circuit gives rise to the definite location of all the chief differentiations found in advanced organization." ("The elementary functions and the primitive organization of protoplasm." St. Thomas' Hospital Reports, 1879.)

It will be seen that the attempt was there made to attack the problem recently pointed out by Driesch as only vitalistically interpretable; the problem of the interdependent localization of the differentiated tissues that constitute the unitary organism. Driesch clearly recognized the impossibility of solving it mechanically by mere juxtaposition of separate units, or dynamically by the influence of external stimulation. When venturing a solution of this obscure problem on the evidence afforded by the study of Protozoa; other evidence then lacking, I was well aware that on such meager grounds the interpretation given would appear highly fanciful. I formulated the problem in the following terms: "Why, then, is the morphological unit (*Paramœcium aurelia*) constructed such as it is? Why is it thus shaped? Why has it an oral and an aboral pole, an integument, a contractil layer, a digesting substance, etc." Conscious of the boldness of proposing such an inquiry, I added: "These are questions that sound strange indeed, almost as emanating from the school of Schelling or Oken; yet it will presently be seen how completely justified they are from a strictly scientific point of view." ("The Unity of the Organic Individual," *Mind*, No. xx, 1880.)

Now that with the help of experimental ontogeny and experimental regeneration investigators have penetrated more deeply than before the secrets of vitality and organization, it may be hoped that, assisted by this new light, the interpretation of these fundamental biological phenomena, reached long ago, and reiterated in English and German periodicals, will no longer be overlooked. It will be found in essential

agreement with the results recently attained on entirely different lines of research, and will, moreover, contribute to render them intelligible.

First let us face the problem of the specific interdependent localization of the principal tissues and organs of organic individuals. As regards this highly important question concerning the structural localization and unity of composition of living animal beings, I will quote the solution I ventured to advance as applied to inferior organism. This solution will be found to flow naturally from the constitution and the activities of the living substance, as explained in the former section. The quotation is again from *Mind*, No. xx, 1880. "Here is a clear-cut protoplasmic ovoid flowing evenly along, straight across the field of the microscope. We will not let it slide by without closely scrutinizing its activities; for, after closely examining them, it will seem as if this morphologically undifferentiated organism had been made on purpose to reveal to us the secret of tissue-formation. It embodies all the essential traits of organization, but organization not yet structurally fixed. Like our *Paramœcium* it also maintains a definite shape. It is bilaterally symmetrical. It has an oral and an aboral pole, an incipient integument and contractil layer, a digesting substance, a depurative vesicle peculiarly situated. It takes food in only in front, retains it until digested in the center of the body, and eventually evacuates the residue at the aboral pole. There can be no doubt it constitutes a complete organism with definitely determined positions of all its parts. Yet it can be readily ascertained that it consists, nevertheless, of nothing but a fluent mass of molecularly coherent protoplasm. We have here before us a single unit of living substance, fluent through and through, and exhibiting, notwithstanding, a strictly localized distribution of organic divisions and functions: we have before us a living vortex, maintaining itself, and advancing head-foremost through space." "All the differently functioning regions of our vital vortex gain their peculiarities merely from the special position which they occupy in the chemical cycle that constitutes protoplasm. We have here, indeed, essentially one and the same substance performing all the sundry organic offices; but it is by no means one and the same substance in one and the same state of efficiency. It is a complex chemical circuit that gives rise to the definite location of all the chief differentiations of the organism: and it is the same substance at the different stages of this its chemical circuit, which by means of its specifically changing relations, becomes in turn the seat of all the main performances of vitality." "The fundamental features of organization assumed by the living substance are the result of the same chemical cycle by which this very substance is itself formed and sustained." At the time this view was advanced such a protoplasmic individual was believed to be throughout composed of an aggregate of equal molecules; and each part of it was held to be indifferently capable of performing all vital functions.

Visibly the living substance, when assuming the shape of a single protoplasmic process or pseudopodium, forms then by force of its chemi-



ally cumulating reintegration and its definite relations to the medium, a self-rounded organism, performing all essential vital functions in interaction with the medium, and having the functional differentiations and localizations of organic structure determined in consequence of it. The problem of structural differentiation and localization can therefore not be statically solved, having regard only to the morphological juxtaposition and conjectured interactions of separately formed parts. Under such a supposition the formative agencies remain hopelessly unintelligible. For organic shaping can nowise naturally result from a mosaic-like arrangement of separate units. It is obviously a unitary dynamic process, whose indivisible vital activity involves the construction of the organism as a whole. It evinces, as Driesch would say, the autonomy of vital phenomena.

The living substance has to be looked upon as a chemically cumulating vortex, whose foremost and highest region comes into active contact with the surrounding medium, suffering thereby functional disintegration; and whose basal substance, in the case under consideration, enters into direct assimilative relations of reintegration with nutritive material. The continuously evolving living substance increases in chemical complexity the further it gets advanced from the region where nutriment is directly elaborated. The foremost and outermost regions of the organism, its apex and circumference, are, in consequence, the chemically highest portions of the protoplasmic unit. Its headmost portion represents, in fact, the consummation of all the vital labor performed within the organism. And the outer surface constitutes a chemically graduated substance, of which each succeeding zone is different in quality and responsive reaction from the one preceding it in position.

In the former section it was found, as repeatedly stated, that what was called the dynamical interaction with the medium, constitutes the highest function of the protoplasmic individual, and that it necessarily involves nutrition and depuration, which three indivisible processes underly their vitality and govern their organization. This being demonstrably the case in lower forms of life, it is by no means visionary, or too bold a stretch of scientific imagination to look upon the complex configuration of Metazoa as the visible structural elaboration of these three indivisible vital activities: functional interaction with the sundry dynamical influences of the medium inciting the gradual development of ectodermic structures; interaction with the nutritive material resulting in the development of entodermic structures; and corresponding structural development of depurative organs taking place in direct or indirect interaction with atmospheric oxygen; the entire organic development being essentially induced and controlled by the dynamical life of outside relations carried on by the ectodermic structures, by which motor activities play a prominent part.

The problem of structural differentiation and localization in its general features finds its solution in these results arrived at by the study

of protoplasmic individuals of a low order of development. The laborious task remains to apply it in detail to successively higher forms of life, whereby accurate inferences from comparative anatomy and comparative ontogeny may possibly yield the desired knowledge; for, of course, the problem is at the bottom one of phyletic evolution.

Not to overrate the kind of information we have been here gathering from directly observable phenomena, it is well to remind ourselves here again that chemical constitution with its specific configurations and most specific modes of reaction is a creative datum transcending scientific explanation. We can not explain why and how a complex of simple elements of a few well known inorganic substances come to be endowed with the potential power of forming by intricate modes of combination with one another an innumerable host of complex organic substances, each specifically distinguished from others, often by astonishingly different properties, as is strikingly exemplified by the hydrocarbons. It stands to reason that the infinitely more complex and manifold constitution of what is collectively called protoplasm or the living substance, phyletically elaborated during ages upon ages of interaction with the various influences of the medium; it stands to reason that this phyletic substance will display correspondingly complex and developed modes of specific reaction. The combining and reacting potencies of what we perceive as protoplasm are intrinsic properties of its chemical constitution, though incited to activity, and influenced in taking special developmental directions by the interacting agencies of the medium. To add to our explanatory perplexities we have, furthermore, to acknowledge that all these wonders of chemical constitution and reaction are only symbolically revealed in terms of our own sensorial perception, and especially of our visual awareness. However, the relation of consciousness to perceptible nature is an epistemological problem only to be indicated, but not discussed in this biological treatise.

GERM-PLASM AND ITS ORGANIZATION.

From numerous and varied experiments with eggs of Echinidæ Driesch felt justified in concluding that egg-plasm possesses normally the character of an organization; but that, after disturbances had upset the normally organized arrangement, every not too minute portion or amount of egg-plasm retained, nevertheless, the power to reproduce the complete, though proportionally reduced form of the embryo. It follows therefrom, in opposition to the theory of a preformed mosaic of definite germinal units, that not only "segmentation mosaic need not be mosaic of potentialities," but also that distinct potentialities do not inhere in specific germinal units. This astonishing discovery is of utmost importance to the science of life. It carries with it the strongest proof of the utter futility of trying to explain vital phenomena in accordance with purely mechanical principles. And it reveals also the inept superficiality of the mere mechanistic view of organization. It renders certain, on the other hand, that not only germs as a whole, but

also fragments of germs, are endowed with an intrinsic formative power capable of reconstituting specific tissues and forms, which are organized down to their minutest component parts, and throughout alive to their innermost core. This formative and vitalizing feat on the part of small fragments of germ-plasm surpasses incommensurably anything that mere mechanical actuation can possibly accomplish, and mere mechanical arrangement can bring about.

It has been shown that only by recognizing reproductive plasm to be in every instance a specific chemical fragment of a specific chemical whole, can we gain a scientific insight into this most wonderful of all occurrences in perceptible nature; the faithful reproduction of a definitely predetermined and intricately constructed organism from a minute bit of morphologically all but homegenous plasm.

By means of ontogenetic experiments of the same kind, it was also found that the nucleus, to which the entire formative potency had been ascribed, does not really play any leading part in this formative process. This conclusion is likewise of great importance to a right understanding of ontogenetic processes. It may have been considered strange, that in the section on "Vitality" no notice was taken of the nucleus, which is still considered by many observers to be of paramount importance in the actuation of vital phenomena. The discussion of the part it is taking in vital processes has, however, been intentionally reserved for this and other pertinent occasions. The study of the self-division of certain Protozoa forced upon the present writer, likewise the conclusion that the nucleus is playing only a subordinate part in vital and formative processes. In reference to the distinctly visible, clearly outlined nucleus of gigantic amœba, I remarked in the *Jenasche Vierteljahrsschrift für Naturwissenschaft*, 1882, p. 689: "As a self-rounded, sharply outlined granular body the nucleus of the amœba is pushed and rolled from place to place during the creature's changing movements, and is forced now in front, now behind, and again into any other position." "No formative organic process determines for it from moment to moment its specific position and form. It is not an integrant constituent of the continuous cycle of activities to which the life of protoplasm owes its existence. It is a persistently established accessory organ, whose general function is not yet ascertained, but which presumably consists in the absorption of oxygen."

Sundry experiments performed since the above was written seem to confirm the conjecture that the function of the nucleus is intimately connected with the indispensable process of oxydation. To this conclusion Loeb has arrived, as explained in the *Archiv für Entwicklungs-Mechanic*, 1899, p. 689. Pieces of non-nucleated living substance quickly disintegrate, while pieces containing oxygen-absorbing chlorophyll retain their vitality for a long time. The fact that blood-corpuseles are absorbers of oxygen seemed to me also to favor the conjecture I had formed. For blood-corpuseles originate from nuclei detached from the epithelium of lymphatic glands and form kindred kinds

of epithelium. Neither white nor red blood-corpuscles are autonomous cellular beings, and as such really independently alive. The amoeboid motions of the white corpuscles are not genuine vital motions. To this conclusion I arrived long ago on the strength of numerous observations and experiments.* This may suffice at present to characterize my view of the functional import of the nucleus. As to the specific role attributed to it in mitotic division, it will be examined when fertilization comes to be discussed.

The principal ontogenetic results gained by experiments with the eggs of many kinds of organic beings, and no doubt essentially applicable to ontogenetic evolution in general, can, I think, be deduced from the recognition of the cardinal fact, the egg-plasm is a chemical fragment of the organism from which it is derived. A chemical fragment of the egg-plasm must necessarily possess a definite chemical constitution, an intimate "molecular" organization, which strictly predetermines the structure of the progressive stages of ontogenetic evolution, or, what is the same thing, the stages of its chemical reintegration. But this definite normal constitution of the egg-plasm as a whole, when upset or disrupted, its complete living substance, or parts of it, suffering thereby additional disintegration, necessarily falls—as has been shown to be the case with the disintegrated protoplasm in general—into different chemical equilibration, forming thus a new and different chem-

*In a paper read before the Royal Society of London, December 20, 1866, I showed that the nuclei of various kinds of epithelium furnished under different conditions what were known as white bloodcorpuscles, granulative corpuscles, mucous corpuscles, and puscorpuscles. And on the strength of these and other observations I said in "Mind," No. XX, p. 486: "As regards the autonomous vitality of organic elements, the white bloodcorpuscles have had chief stress laid on them. The white bloodcorpuscles of which red bloodcorpuscles are transformations, perform amoeboid movements. What more striking proof of the separate vitality of each single cell could be found, than the display of motility on the part of its protoplasm? Nevertheless these movements are not vital movements, but merely the effect of a chemical metamorphosis of protoplasm. Young infusoria under unfavorable conditions are sometimes unable to maintain their surface-equilibration. They are then transformed into amoeboid beings, the substance of which gradually declines in molecular constitution till, at last, all activity ceases. A white bloodcorpuscle forms originally an integral part of an organic tissue. It is then detached from it, and left to attain chemical equilibration in a new and constantly changing medium. In some annelids the inner surface of the entoderm, the surface forming one of the walls of the perivisceral cavity, is seen during digestion to become densely crowded with large refractive granules. Irregular flakes composed of such granules held together by a viscid hyaline protoplasm, detach themselves and float about in the perivisceral cavity, constituting primitive bloodcorpuscles, and displaying amoeboid movements. This I have watched numbers of times." "The bloodcorpuscle does not maintain its structural integrity, on the contrary, it is transformed from a lymph-corpuscle into a red bloodcorpuscle, and, after having spent its store of chemical efficacy, is soon eliminated as effete matter. Its amoeboid movements are not due to any vital play with the medium, but are simply movements accompanying its career of chemical transformation. In pus-corpuscles even the myeline-nature of the projections can be sometimes detected with the help of the polariscope. The most perfect movements of the kind I have ever witnessed were displayed by pus artificially derived from the epithelium of an eye macerated in serum for forty-eight hours at a temperature of 96 F.

ical fragment. And this is also found to be capable of reintegrating in its own way the structure and form of the embryo as a whole. The new fragment possesses no longer the same organic arrangement of the egg-plasm as a whole; but, being of a lower chemical order, it takes up the work of reintegrating the embryo at a less differentiated stage of its structural reconstitution than had been the case with the normal egg-plasm.

This hypothetical interpretation, unlike the fanciful conception of aggregational and mechanical views, flows consistently from the ascertained nature of the living substance, as explained in the former section. It is confirmed by the different stages of chemical or structural development found established in the egg-plasm of different organisms. In some organisms their egg-plasm consists of a less disintegrated or rather higher integrated fragment than in others, and represents therefore a more advanced and firmer stage of structural development or "maturation," evincing itself in a more definitely and solidly differentiated organization, or so-called mosaic-like arrangement.

The interpretation here ventured of these striking and most instructive ontogenetic phenomena, revealed by means of experiments with egg-plasms, is signally corroborated by Morgan's experiment with the substance of the living half blastomere of the egg of frogs, whose adjoining partner had been killed. Left in its normal position the living blastomere developed into a half-embryo. By disturbing the "molecular" or structural arrangement of its substance through reversion of the egg, it developed an entire embryo of reduced size. Here the blastomere possesses obviously at first a definite unilateral organization, derived from the bilateral organization of the egg-plasm as a whole. Its definite chemical constitution, representing only one-half of a normally established ontogenetic germ, being upset, its living substance becoming thereby further disintegrated, retains nevertheless its character of being a fragment of the entire organism of which it is derived, and reintegrates itself as such, not to a half, but to an entire embryo. It forms a new germ at a lower chemical level, involving potentially complete formative potency. Even small artificially severed portions of egg-plasm, at different stages of its ontogenetic evolution, retain the power of reproducing not the mere structure of the plasm from which they were immediately severed, but the structure and form of the entire embryo; and their living substance must therefore reconstitute itself a chemical fragment of the entire organism, of which it then proves to be a reproductive germ.

In a general way it may be asserted, that the higher the stage of chemical integration, or ontogenetic evolution the egg-plasm represents in relation to the whole embryo it is destined to reproduce, and also the higher the organism of which it is derived stands in the scale of animal development, the less readily will fragments of such egg-plasm, or fragments of such organisms reconstitute themselves into totipotent germs. In order that fragments may become totipotent, their living substance

has first chemically to reorder itself, so as to form a germ representing an initial stage of ontogenetic evolution. This reduction of artificial fragments to germinal totipotence occurs more readily when they are derived from lower stages of ontogenetic and phylogenetic evolution. In Infusoria, during the process of their self-division, the formation of two exceedingly minute totipotent germs or centers of reproduction, and the gradual reintegration therefrom of complete adult organisms, can be observed from beginning to end.

The more developed the organism from which the fragment is derived, the more it is found to resist reduction into ontogenetic totipotence. And the more will it possess only the power of regenerating the part or the tissue of which it is an immediate fragment. Fragments of highly developed tissues, or even of entire organs, when left attached after almost complete loss or extirpation of the respective tissue or organ, may reproduce or regenerate the same. An extreme instance of this circumscribed and localized regenerative power in an animal high in the scale of development is afforded by the remarkable regenerative processes observed in Triton. Gus. Wolff's startling discovery of the regeneration of the lens from the iris, and of the injured iris itself, not from the injured surface, but by a deep-seated formative process, may possibly find their explanation in such localized and partial regenerative potency. In certain worms such localized and partial regeneration is plainly exemplified when, for instance, whole segments with all their tissues are regeneratively intercalated; or, in other cases, when after partial resection some internal organ is regenerated. Yet, though localized and partial, these regenerated tissues or organs are incorporated as integrant constituents of the entire organism. The formative process is still under the control of the whole. It may be conjectured as highly probable that this power of localized regeneration is a phenomenon indicative of such localized germinative processes occurring normally during the ontogenetic evolution of separate tissues, complicating thereby the epigenetic process, without interfering with the general predetermined tendency of reproducing the organism as a formative whole. And it may possibly also help to account for the reduced size of reproduced structures and forms, when only a reduced amount of assimilative material is given for chemical reintegration.

Normal germ-plasm is never derived from highly differentiated tissues, never from muscles, nerves or sensory organs. This fact sufficiently refutes, if such refutation were necessary, the fanciful notion of some biologists, that the successively differentiated cell-generations of ontogenetic evolution represent "alternate generations."

As regards the definitely discernible structural differentiations of the evolving germ-plasm, they start into perceptible existence more or less early and more or less distinctly, probably in proportion as the germ-plasm is representing a higher or lower stage of ontogenetic elaboration or "maturation," and in proportion as the adult organism in the course of reproduction is itself of a higher or lower order in the scale of

phyletic evolution, and in proportion, moreover, as the embryo represents a more or less advanced stage towards the complete reproduction of the adult organism. The germ-plasm itself must at every stage of its evolution necessarily possess a more or less complex chemical organization in proportion as it is derived from a more or less complexly developed organism.

To our vision ontogenetic evolution assumes the aspect of a process giving rise to different definitely grouped parts of the evolving substance, and it takes a definitely regulated course within the portion of our field of vision occupied by the developing substance. Our conclusions regarding the specific potencies actuating these visible changes have to be inferred from what we see arising here and there within the sphere of the evolving plasm. However accurate our observations and descriptions of such spatial changes may be, it is clear that the inferences and interpretations based upon them, regarding the agencies actuating the changes, and also regarding the interdependence of the changes seen to take place in different parts of the evolving plasm; that these inferences and interpretations are of a different explanatory order from that of mere description. To the extremely difficult solution of these ontogenetic questions of special potencies, and causal dependence of localized changes, experimental ontology is supplying the most efficient and instructive means.

But it must not be forgotten, that the final, predetermined result and outcome of all the divers and complex changes is the exact reproduction of the adult organism from which the germ-plasm was derived. The sundry divers changes form part of one and the same ontogenetic process. Or as Driesch more specifically expresses it: "Despite relative self-differentiations something unitary is achieved." The entire ontogenetic evolution which we see running its course in space and time with such intricate formative manifestations is essentially a unitary process, predetermined in its minutest details in the specific chemical constitution and in the chemical potencies of the germ-plasm; attaining its final goal in the definite organization of the reproduced adult organism as an indiscrptible whole. There is here at work no sort of struggle for supremacy of separate elementary units, and no automatic co-operation of the same. From its initial stage to its completion the ontogenetic process consists in the harmonious, gradual reintegration of a specific chemical fragment under complemental assimilation, until it has effected the reconstitution of the whole of which it is a fragment; and which whole is then visually revealed to us as the complex adult organism.

If a morphologically undifferentiated fragment of the egg of a frog can reproduce an entire, highly differentiated, embryo, it is almost self-evident, that, in what may be rightly called the chemical constitution of the egg-plasm, must lie the power to evolve the eminently complex structure and form of the adult frog; that, therefore, this eminently complex structure and form represents to us the perceptible out-

come of the chemical evolution; that, in fact, the structure and form of organisms is the perceptible manifestation of a unitary, though marvelously complex, composition and activity, scientifically expressible in terms of chemical experience.

In the section on Vitality it has been shown that the living substance, out of which all organisms are formed, owes its vitality to a process of alternate disintegration and reintegration, involving all essential vital functions. It has been furthermore shown, that the fundamental structural and functional differentiations of animal beings originate through the very same cycle of chemical activities, which imparts to the compound called protoplasm its vitality, and causes it to be a living substance. And it has long been known that minute artificial fragments of so-called unicellular organisms, whose undeniably unbroken continuity of living substance is evidently of chemical consistency; that such chemical fragments have power to reintegrate the highly complex structure and form of certain Protozoa, which process we can watch in its fluently coherent operation. Considering all these facts it certainly lies near to conclude, without overstepping the limits of scientifically justified inference, that organic beings, consisting as they do of phyletically elaborated living substance, and possessing whatever complexity of structure and form, are likewise essentially chemical wholes, ontogenetically reproducible from chemical fragments.

Confronted by the results of experimental ontogeny and experimental regeneration, the inference is inevitable, that the reproductive germs or fragments must either possess as such intrinsic formative powers of their own; or that, on the contrary, they are merely the vehicle and raw material of a formative power not inherent in themselves, but moulding and evolving them from out a transcendent order of existence into the nevertheless predetermined structure and form of the organism from which they were derived. The first inference, that of inherent formative power, becomes scientifically intelligible when the germs or fragments are recognized as being specific chemical fragments of a specific chemical whole. Though what we call chemical composition, activity and affinity are terms for efficiencies, which are only symbolically revealed as sensorial phenomena within our individual consciousness, scientific explanation consists in gaining an understanding of what is thus symbolically revealed. The alternate inference, that of a transcendent moulding and evolving power, is incommensurable with scientific thought. It transfers ontogenetic and regenerative actuation to a wholly hypothetical sphere of existence and efficiency, whose doings are superimposed upon the visibly evolving substance, which can serve it then only as inert raw-material. It is obvious that this means the assumption of a vital force of the old metaphysical kind.

In accordance with the views here advocated a few words concerning the vexed contention of evolution versus epigenesis may not be out of place. Ontogenetic evolution, the evolution of a germ into an adult organism, may rightly be called evolution in the strict sense of the term,

in so far as the constitution of the adult organism is rigorously predetermined in the chemical constitution of the germ. But the adult organism is nowise structurally pre-established in the germ in the sense of Bonnet, Haller, Roux, Weismann, and their more or less faithful followers; nowise in the sense of the old and new theory of structural pre-formation. It is not as Roux declares the merging into visibility of latent pre-existing differences. It is the merging into visibility of newly arising differences. Ontogenetic development takes place through such epigenesis as advocated by Wolff and Baer; epigenesis, namely, in the sense that morphological structures merge into visible existence as out and out new formations, one stage of structural development serving as foundation for the next stage. The development of the germ into an adult organism is chemically evolutionary, but structurally or morphologically epigenetic. In ontogenetic evolution the successive stages of chemical reintegration, though evolutionally predetermined, represents a formative process by which the structures of the adult organism are newly reproduced.

True phyletic genesis consists in the complete new formation of what is being for the first time produced, and not merely generically reproduced. Creative increments of organic development give here rise to progressively higher forms of beings, and the corresponding reproductive potentialities of their germs are newly acquired, and represent not merely a pre-existing fund of previously established dispositions.

SEGMENTATION.

The disentanglement of the factors that condition the segmentation of the germ-plasm, and therewith the normal "prospective import" of the successive blastomeres, is no easy task. To rightly attack the problem one has above all to discard the misleading notion, that what we have here before us as an egg represents anything in the remotest degree resembling a cell, or elementary organism, as scientifically defined. The germ-plasm is nowise an autonomous elementary organism, which multiplies by self-division. Its divisions are essentially a manifestation of unfolding potentialities, in which all ensuing formative evolution is rigorously predetermined. An egg-cell, instead of being an autonomous elementary organism, represents, on the contrary, the potential concentration of all the accumulated results of phyletic elaboration. This should be quite obvious without further discussion, though, strange to say, most zoologists still adhere out of traditional prejudice to the cell-theory, which has come to be highly obstructive to biological progress.

But how do the two first blastomeres come each potentially to represent one entire half-embryo? It has been shown that the living substance in its earliest formative manifestation, as an amoeboid projection, or so-called pseudopodium, assumes by force of its intrinsic constitution and its vital motility a symmetrically bilateral form. And when the entire living substance of an amoeboid being comes to constitute one single

such projection or pseudopodium steadily maintained, it clearly represents a bipolar and bilateral organism. How then does it happen that in its higher stages of development this unitary bilateral constitution of the living substance becomes divided during ontogenetic evolution into two unilateral, but still interdependent halves? Here one is led to assume, that in the course of phyletic elaboration the two lateral halves of the living substance, though composing a continuous whole, have each undergone more or less independent structural development, having necessarily been separately, but under the same conditions, exposed to the same stimulating influences of the medium, with which they have stood, and are still standing in a relation of functional interaction. The separate structural elaboration of each unilateral half has here evidently come to constitute the most fundamental organic differentiation retained in the chemical organization of the germ-plasm, expressing itself ontogenetically in the segregation of the two first blastomeres, of which each possesses then separately the power of further self-differentiation.

Bichat already recognized the bilateral duplication of organs as the essential characteristic of what he called the animal life, which is the life of the dynamical outside relations structurally embodied in the ectodermic organs. Numerous observations and experiments prove that the germ-plasm is bilaterally organized even before fertilization. Watase found that the egg of the *Loligo pealii* discloses already before fertilization a bilaterally symmetrical arrangement of its substance, which determines the direction of the first segmentation, and the axis of the embryo. The plasm of the egg of most insects is visibly bilaterally arranged. In annelides and mollusks the egg-plasm has likewise before fertilization a visible bilateral arrangement, which determines the direction of the first segmentation. Driesch showed by experiments with the eggs of *Echinus* that they possess a bilateral structure before fertilization, which after fertilization determined the direction of the segmentation, and which in consequence is not due to the influence of the spermatozoon as had been asserted by some investigators. R. Hertwig, Morgan, Loeb and others by inducing through chemical means unfertilized eggs to undergo normal evolution, proved thereby the original bilateral structure of the egg-plasm.

It is of paramount importance, as already stated, to recognize that the first two blastomeres can nowise be regarded as the autonomous offspring of a self-dividing elementary organism, as demanded by the cell-theory. Self-division produces here no equal sister-cells; equal to each other, and equal to the mother-cell. On the contrary, self-division divides here a whole into two complementary halves, each representing only one lateral half of the "germ-cell" in a somewhat more advanced stage of ontogenetic evolution. They each possess laterally corresponding ontogenetic potentialities, representing complementary halves of the organism to be reproduced. The two primary blastomeres segregated during ontogenetic evolution from an undivided whole, are destined conjointly to reproduce in the course of ontogeny by one and the same



developmental process, the unitary, indiscerptible organism of which they are complementary parts. As halves of a common whole, they can certainly not be autonomous, elementary beings, the offspring of an elementary mother-cell.

This simple consideration contains, it must be again insisted upon as of utmost importance, inevasively the complete refutation of the cell-theory. For it is of the essence of this theory that an elementary mother-cell propagates by fissiparous division, autonomous lineal offspring of the same kind. Instead of this, all successive divisions of the egg-plasm prove to be divers interdependent, complementary parts of a strictly predetermined whole. There could be no more thorough-going disparity than here obtains between the generally accepted cell-theory and the real state of things, as unmistakably revealed by experimental ontogeny. Of whatever nature and import the more or less distinct cellular divisions of the organism may be, they are certainly not the autonomous lineal progeny of an elementary cellular being, which the cell-theory declares them to be. At every step of our biological interpretation we have found the cell-theory obscuring, instead of elucidating the scientific explanation of observable facts.

On further segmentation it seems that the two different germinal layers, the ectodermic and the entodermic substance become plasmatically and germinally segregated. The organism to be evolved from the two primary germinal layers, as they are called, stands constitutionally in opposite relations to the surrounding medium. The ectoderm represents mainly the structures that minister to the life of active outside relations, the life that carries on the functional play with the dynamical influences of the medium. Entodermic plasm, on the other hand, evolves the organs of the so-called vegetative life, which enters into direct interaction with the nutritive material furnished by the medium, and elaborates assimilable pabulum for functional restitution. Here also both layers, though more or less distinctly divided from each other, evolve their structures conjointly in subservience of the unitary purpose of reproducing the indiscerptible adult organism.

As to subsequent stages of segmentation, they would seem, to judge from final results, to segregate the plasm destined to evolve the separate metameres, of which the organism is composed. Each mereme represents an original zooid, which contains a complete structural organization of its own, retaining it ontogenetically, though blended more or less intimately with the unitary organization of the complex individual to be reproduced as the final aim of the entire reproductive process.

The division into the prospective metamera would then be followed by the parallel evolution of the sundry structures found respectively to form part of them. And as regards nutritive and depurative organs they would all along concomitantly evolve in constant harmony with ectodermic organs.

The obvious inference from all these ontogenetic phenomena is, that every stage and division of the eminently complex evolution, however

separately disposed and circumscribed its spatial manifestations may appear to our vision, that it all forms, nevertheless, from start to finish, a unitary ontogenetic process, every phase of which is integrantly connected with every other.

FORMATIVE STIMULATION.

The specific stimuli or inciting agencies that act as inducing causes in the development of the succeeding stages of ontogenetic evolution, and which have been so diligently sought for, now in external, now in internal conditions; these inciting causes are actually found in the immediate conditions which give rise to gradual reintegration, and therewith to ontogenetic evolution. The presence, namely, of specifically assimilable material coming in contact with the living substance, at whatever stage of its disintegration, germination or fragmentation, naturally and necessarily acts as a specific formative stimulus, calling into activity the inherent power of reintegration through complemental assimilation. Reciprocal chemical attraction between the assimilating vital fragment and the assimilable material, due to their complemental affinity are here evidently the actuating agencies. This interpretation flows consistently and harmoniously from the general vital properties of protoplasm, as explained in the former section. The power of complemental reintegration after more or less profound disintegration is that which essentially constitutes protoplasm a living substance.

By having gained the scientific understanding that assimilation is a process of reintegration on the part of the unitary living substance, and not a new formation of elementary units, it becomes clear that the presence of assimilable or complemental material will act upon fragments of the living substance as a specific and adequate stimulus or inciting cause whereby reintegration is effected. No need here of any other specific stimuli, provided the conditions of the general medium are otherwise normal and favorable.

In higher organisms morphological appearances mask to a great extent the unitary formative process. To gain a clear idea of the far-reaching commotion of the chemical activity and its concomitant mass-movements during ontogenetic evolution, one need only closely watch the phenomena occurring, for instance, within the spherical plasm of a self-dividing Colpoda. The process, though primarily one of self-division, involves the ontogenetic evolution of a new generation of individuals from germs derived from the parent organism. Here two and often four and more separate germinal centers start into existence within the spherical plasm, and around each the reintegrating work takes its course. It consists evidently in an extremely complex process of chemical assimilation and elaboration. For more or less vivid commotion of granules; more or less extensive mass-movements of plasm, with concomitant formation of larger or smaller depurative vesicles, more or less rapidly arising, dwindling and reforming, testify to the intimate chemical nature of the occurrence. The unitary substance of the plasmatic sphere is under-

going transformation through and through, resulting eventually in its self-division. Each germinal center attracts, stage by stage, of its ontogenetic evolution, the requisite complemental material from the general plasmatic fund, until each developing germ has become an entire self-rounded organism, separated from the rest, not by any membrane, but by its own chemical constitution as an individuated whole. In each individuated unit a lively formative process continues its work, often involving the rotation of their entire substance. They then glide round and round one another, the direction of the rotation becoming at times reversed, and at times ceasing altogether, whilst all along the internal motion of granules at different places, and the formation of depurative vesicles, afford proof that the formative commotion is due to chemical activity. Suddenly the adjoining individuals, now fully organized, separate and dart away, each to pursue life on its own account. In this case the separating individuals do not finally break through an inclosing membrane, as is the case in some other infusoria. No trace of a membrane inclosing the plasmatic sphere is visible during the formative process, and no trace of such a membrane is left after the individuals have separated. This interesting fact would seem to justify the inference that chemical taxis holds the segregated units together until diminishing in power with their increasing structural organization its attraction ceases at last altogether, allowing the completely individualized units to sever their connection. I have observed on other occasions similar manifestations of chemotaxis in operation between protoplasmic individuals, which I was led to ascribe to complemental chemical affinity between the attracted beings.

Now, is it not likely that in Metazoa similar ontogenetic commotions and mass-movement, involving the shifting of certain substances and the wandering of certain "cells" to different positions; may not these seeming attractions from a distance be due to essentially the same kind of chemical elaboration and assimilation, as directly witnessed in our Colpoda?

FERTILIZATION.

It has been found that the unfertilized egg-plasm is already bilaterally organized, and also that artificial conditions can incite it to parthenogenetic self-evolution, whereby it undergoes the same normal segmentation as it would have undergone after spermatic fertilization. This being so, what kind of specific influence on ontogenetic evolution has the fertilization of the egg? The intrusion of the spermatozoon can, of course, not be regarded as a mere incitement, which simply sets going the self-evolution of the egg-plasm, as has been actually believed by some biologists.

The spermatozoon contains evidently as complete an endowment of ontogenetic efficiencies as the egg itself. The bisexual adult organism proves clearly to be a product attained by the intimate blending of male and female germ-plasm. How, then, does the germ-plasm of the sperm-

atozoon manage to become materially and potentially unified with the germ-plasm of the egg, without upsetting the intimate specific potential constitution and bilateral arrangement possessed by the egg-plasm before fertilization, which determines the formative course of ontogenetic evolution? This question gives expression to the most central and essential problem of bisexual ontogenetic evolution. And it may be regarded as the stronghold of those who believe nuclear plasm to be the sole and real germ-plasm. For the head of the spermatozoon is undeniably of nuclear origin and consistency. It represents in fact a complete nucleus. Now, if the nuclear head really carries with it all male ontogenetic potentialities, and if the nucleus of the egg, with which it combines, contains on its side all female ontogenetic potentialities, then, despite all contrary considerations, there is no escaping the conclusion that the rest of the fertilized egg-plasm can be only indifferent raw-material at the service of the ontogenetically evolving nuclear plasm. And in this case the alleged organization and bilateral constitution of the non-nuclear egg-plasm could be of no ontogenetic consequence.

Hence to avoid this dilemma more felt than recognized, we have the elaborate theories of diversely endowed and diversely aggregated formative units, assumed to compose the minute speck of nuclear plasm, nay, to compose the much more minute chromosome. To these hypothetical, ultra-microscopical elements would then fall the stupendous task of structurally reproducing from out their invisible retreat the comparatively enormous bulk of the adult organism. For, as just stated, under the assumption of formative chromatic elements it is logically inadmissible to attribute to somatic plasm any other office than that of supplying constructive raw-material to the chromatic germs. They alone would have to construct the adult organism, out and out, by means of their own self-divisions or spontaneous multiplications, which proliferation would have to occur at an inconceivably prodigious rate, resulting in an organism consisting of nothing but chromatic units, miraculously aggregated so as to constitute the tissues and the form of the adult organism, and to actuate its many interdependent functions.

It is true, the visible specific divisions and sections of chromosomes, with their definite, numerically regulated distribution, and their specific mode of deployment, afford a tempting ground-work whereupon to erect theories of heredity and ontogeny. But the nuclear, aggregational hypothesis of vital and ontogenetic potencies possessed singly by an incredible host of invisible elementary units; such an hypothesis is directly contradicted by the very nature of the living substance out of which all organisms are formed. And it is refuted by the non-participation of the nucleus in all essential vital manifestations and formative processes. The distinctly circumscribed nucleus of some *amœba*, for instance, take, as already stated, no active part in the vital manifestations of the immensely larger bulk of non-nuclear plasm, nor in its formative phenomena. The cycle of chemical activities which gives rise to the vital-

ity and formation of protoplasm, is operative solely in the non-nuclear substance, and the nucleus itself performs only an accessory function in the vitalizing and formative process, however indispensable this accessory function may be. The nucleus can here, consequently, nowise be regarded as the exclusive bearer of vital and formative efficiencies.

In Metazoa the nuclear chromatin divides into exactly equal parts, while the "cells," into which it equally enters, divide into heterogeneous progeny. The chromatic substance is therefore not accountable for the cellular differentiations. The hypothesis of the qualitatively unequal division of chromatic plasm, which underlies Roux's and Weismann's view of heredity and ontogeny, and which is seemingly supported by the formation of half-embryos from each of the two first blastomeres. This view is sufficiently disposed of by the repeatedly and amply confirmed demonstration of the ontogenetic totipotence of the plasm of each blastomere. As the same nucleus is here present in both cases, in the formation of the half-embryo, and in the formation of the whole embryo by one and the same reproductive plasm, it is evident that the formative efficiency resides, not in the nuclear, but in the non-nuclear plasm. This is likewise proved in Morgan's experiment with the eggs of frogs, which, after one of the two blastomeres had been killed, the living blastomere formed whole embryos when the position of the egg had been reversed, but half-embryos when left in position. Here also the nucleus is in both cases the same, and can, therefore, have no direct influence on the formative process.

Driesch showed that a normally formed embryo is produced where during segmentation the nuclei of the blastomeres are by means of pressure shifted into entirely different positions in the aggregate mass of protoplasm. This likewise proves that the nucleus exerts no formative influence upon ontogenetic evolution. Non-nucleated pieces of the fertilized blastula of Echinidæ have been found to develop into plutei. This is a further striking confirmation of the passive part played by the nucleus in ontogenetic evolution. Townsend found that non-nucleated plasm is capable of forming in plants a cell-wall when it is merely connected with a nucleated cell by a filament of protoplasm passing through the wall of this cell. This also shows that the non-nuclear plasm is the real formative agent.

Moreover, it has to be insisted upon as essential in making way for a correct interpretation of ontogenetic evolution, that even if the continuity and immortality of chromatic plasm as exclusive bearer of the formative potency be for argument's sake, granted, then the entire adult organism, in every one of its structurally differentiated parts, would really consist of nothing but self-multiplied chromatic units. For somatic plasm, despite the assumed self-multiplication of its own constituent units or biophores, would nevertheless only serve as building material, or rather only as so much nutritive material, to the formative units or biophores of the chromosomes, which would then as such constitute the entire organism. The special group of chromatic germinal

units, called "determinants" by Weismann, whose biophores are supposed at the right moment and at the exact stage of development to scatter among the somatic biophors as formative germs, and to determine the specific differentiation of the cellular substance; these determining biophores could accomplish this wonderful feat only by assimilating the indifferent biophores of the somatic or morpho-plasm, using them for their own self-multiplication, or in plain words by bodily devouring them.* The sole alternative here would be, that the formative influences of the chromatic germs is due to an inscrutable, wholly magical power, by which they determine the structural differentiations by their mere presence and contact. To endow in this manner mere hypothetical beings with an all-efficient, utterly mysterious power is clearly to beg the entire question.

As early as 1861 Lionel Beal advanced a nuclear theory of structural formation, and bravely drew its consistent conclusions. Relying on tincture of carmine as his principal means of research, he came to look upon all somatic structure as formed of lifeless substance secreted and fabricated by nuclear plasm as exclusive life-bearer and formative agent. And he did not shrink to declare even muscle and nerve to be such lifeless fabricates. This monstrous conclusion proves once more to what extreme positions false premises will blindly drive, not only conceptual philosophers, but also close observers of natural phenomena.

The refutation of the nuclear germ-plasm theory flows, indeed, directly from the nature of the living substance, and its visible vital manifestations. Yet, despite all these weighty considerations, based on actual facts, if the nuclear head of the spermatozoon can be proved to be the real and exclusive bearer of the male characteristics, then no ever so plausible an array of objections could invalidate the conclusion, that it is after all the nuclear plasm which is endowed with specific formative powers, governing and directing ontogenetic evolution.

Highly instructive observations of Boveri, and also of Wilson and Mathews, confirmed by many other investigators, prove that it is not the nuclear head of the spermatozoon which is the real bearer of the formative potencies, but its medial portion known to be of non-nuclear origin and import. As early as 1888 Boveri** described an occurrence that took place in an egg of *Echinus*, which of itself affords strong evidence that the non-nuclear, medial part of the spermatozoon is its real actively formative constituent. Here the medial part, in which the two centrosomes had formed, became completely severed from the nuclear head, proceeding with the astropheres far in advance on its course into the interior of the egg. And though no union of the spermatie nucleus with the nucleus of the egg occurred, the segmentation of the egg-plasm began to take its normal course. The spermatie nucleus, which event-

*See "Molecular Theories of Organic Reproduction," *Pro. Texas Acad. Science*, 1895.

**"Zellenstudien," *January, 1888*, "Über Partielle Befruchtung Sitz, Ber. Ges-Morph. Phys. B 4, München.

ually became inclosed in one of the blastomeres, coalesced with its nucleus. Segmentation was thus nowise influenced by the non-participation of the spermatic nucleus, and the non-nuclear portion of the spermatozoon proved to be here the active agent in the bisexual ontogenetic process. Similar occurrences were witnessed by Teichmann (a). And numerous observations have confirmed in many classes of animals that the formatively active portion of the spermatozoon, the portion in which the centrosomes arise, and around which the astrospheres form, is the medial, non-nuclear portion. This agrees entirely with the fact, that in mitotic division in general the process starts and is actively governed by extra-nuclear centrosomes.

Important to the contention here dwelt upon is the observation of Wilson & Mathews (b) and others, confirmed as occurring in all classes of animals examined; the observation, namely, that after entrance into the egg the spermatozoon turns completely round, so that the head comes to face the circumference of the egg, whilst its base or medial portion develops under granular commotion the centrosomes with their astrospheres, and penetrates in this position under constant activity into the interior of the egg-plasm, proving thereby that the non-nuclear, medial portion of the spermatozoon is the real bearer of vital and formative activities. R. Hertwig, v. Erlanger and others have come to the conclusion that the medial part of the spermatozoon and the developed centrosomes have to be considered as essentially identical in substance. And this really means that the formative process starting around the centrosomes involves the entire medial plasm, while it is gradually involving all non-nuclear egg-plasm, and finally also all nuclear plasm.

The experiments on segmentation and development of artificially fertilized portions of egg-plasms initiated by R. and O. Hertwig and continued by Boveri, Morgan, Ziegler, Delage and others go likewise to show that the centrosomes have power without the aid of the nucleus to actuate and control the process which gives rise to segmentation. Boveri found, moreover, the non-nuclear portions of the egg-plasm of *Echinus* in which a spermatozoon had penetrated undergo segmentation solely under the influence of the activity of the centrosomes without the aid of nuclear chromatic substance whatever. And Ziegler* observed that in a normally fertilized egg the entire nuclear substance of both united nuclei remained confined in one of the blastomeres, whilst in the other blastomere there remained only the corresponding centrosome with its astrosphere. Thereupon further segmentation took place

a. Ueber Furchung Befruchteter Seeigeleier ohne Betheiligung des Spermakerns," *Jenaische Zeitschrift für Naturwissenschaft*, B. 37, 1902.

b. "Maturation, fertilization and polarity in the Echinoderm egg. *Journ. Morph.*, V, 1895.

*Furchung ohne Chromosomen. *Arch für Enter. Mech* B, 1898. Living far away from any public biological library, I have not been in a position to verify all quotations from the original papers, but relied in many of them on Korschelt and Heider's splendid "Lehrbuch," 1893.

in the non-nucleated blastomere without the presence, and therefore without the aid of any nuclear or chromatic substance.

All these manifold and numerous observations and experiments go to prove that the non-nuclear plasm is the real bearer of the vital activities and potentialities.

Conclusions drawn from appearances found in fixed and tinted specimens, however instructive, are apt to lead investigators to interpret flowing vital phenomena morphologically and mechanically, instead of looking upon them as specific chemical processes, of which the changing morphological appearances are incidental, though definitely disposed, perceptible expressions. Of course, it is from these visible appearances that we have to infer what is really happening. But we have to be careful to regard them simply as mass-manifestations of a process at work among the intimate, ultra-visible constituents of the vitally changing substance. The entire organism, in all its living parts, down to the very core, is in constant vital commotion, and represents essentially a synthetic chemical laboratory in ceaseless activity. It is not, as has been long believed, essentially a mechanical apparatus, whose wheel-work is made to run by the burning of food-material.

This caution of not mistaking morphological appearances for stable machine-like structures, or for static chemical compounds, has to be especially borne in mind in interpreting the process of mitotic division, and above all that of fertilization and its accompanying morphological appearances. Here it is safe again to rely in great measure on what can be so readily and so clearly observed in the self-division of suitable Infusoria, the purport of which is likewise the ontogenetic evolution or reproduction of new individuals. I have in a general way described the morphological signs of the exceedingly complex chemical activity at work during the comparatively elementary case of reproduction taking place in Colpoda. In the reproduction of highly complex organisms we have to expect, even in parthenogenetic, and all the more in bisexual reproduction, correspondingly complex manifestations of the ontogenetic process. But here also reproduction of the adult organism can start only from germs, which are specific chemical fragments of the organism from which they are derived, and which they are destined to reproduce. This, I think, has been sufficiently proved, and seems indeed quite obvious.

Now as regards what really happens during fertilization in Metazoa, starting with fully matured male and female germ-plasm, and leaving out of consideration the preceding phenomena of their maturation, I believe that Boveri's observations and views, supplemented by those of Wilson, and confirmed by a great number of investigators, as applying to many kinds of animals; that these views can be taken as a solid foundation for the understanding of what really occurs during fertilization.

After the matured spermatozoon has entered the matured egg, we know for certain that the egg-plasm itself has a definitely organized, bilateral structure; and we know that it is the medial, non-nuclear portion of the spermatozoon which is the active agent in fertilization. We

know, furthermore, that after fertilization has been accomplished the fertilized egg-plasm is found to be again bilaterally organized, and on its way to divide into two unilateral halves, represented by the two first blastomeres. The final result of the entire ontogenetic process proves that an intimate interblending of male and female germ-plasms has been somehow achieved during fertilization. When and how does this interblending of the two plasms take place?

The medial part of the spermatozoon in contact with natural egg-plasms is seen to divide, and to form two centrosomes from which the fertilizing activity starts, manifesting itself in granular commotion and formation of atrospheres extending more and more deeply into the egg-plasm, involving more and more of it in the bisexual transformation. The matured egg-plasm proving at the beginning of the process to be bilaterally organized, it is not far-fetched to conjecture that the sperm-plasm, embodied in the matured medial part of the spermatozoon is likewise bilaterally organized; and that its division into two centrosomes is really a division into the unilateral halves. This, indeed, becomes finally evident, as the result of the fertilizing transformation; and concomitant blending of female with male plasm, which takes place around the centrosomes of the medial portion of the spermatozoon; as this result proves to be actually the formation of the two first bisexual and unilateral blastomeres.

Centrosomes have always to be considered germinal centers, and the formative activity around them as one of gradual reintegration towards the reproduction of the adult organism. Centrosomes may arise in protoplasmic beings under whatever conditions go to favor the origination of new formative centers; and they may dissolve again when their substance becomes assimilated by stronger formative activities than their own. This has been proved by various experiments, such as those of Morgan after the application of solutions of salt. In normal formative processes, however, the number and localization of centrosomes is definitely predetermined.

It remains still unexplained how the definitely organized egg-plasm can come to be intimately interblended with male-plasm, as is the case in bisexual reproduction. How can a definitely organized structure blend with another definitely organized structure without both losing their definite organization? This is a problem inexplicable by any mechanical and aggregational theory. It has been shown that all attempts in that direction have necessarily failed, and that we are face to face with a specific vital activity, which would have remained utterly enigmatic had not experimental ontogeny furnished us with data that essentially assist its understanding. For it has been experimentally proved that the definite bilateral organization of egg-plasm being upset, all parts or fragments of it become totipotent germs, capable of reproducing entire embryos. In fertilization it is egg-plasm that has become totipotent in all its parts after its bilateral organization has been upset by the influence of the spermatozoon; it is this totipotent plasm that enters into

the bisexually restitutive process, started and governed by the two centrosomes of the sperm-plasm, At each stage of its evolution the sperm-plasm assimilates congruous egg-plasm, the process ending in the formation of the two bisexual and unilaterally potential blastomeres.

The interpretation of fertilization here offered flows likewise consistently from the nature of the living substance, as positively demonstrated in the first section. It has to be added, that, as in normal and artificial parthenogenesis, the two first blastomeres form around germinal centrosomes arising within egg-plasm, it seems that even in some cases of fertilization the egg-plasm takes the lead in the bisexually blending and reproductive process. This appears to have been the case in Wheeler's observation of what takes place during fertilization of *Myzostoma*. And it may possibly happen more frequently than at present supposed. If this were found to be the case, it might suggest a scientific explanation of sex-determination. Indeed there is no theoretical objection to egg-plasm-activity taking at times the lead in the process of fertilization and ontogenetic evolution, as it is otherwise so readily induced to do so in parthenogenetic self-evolution. Though this suggestion is supported by various experiences, of course only direct observation can have weight in the decision of such a question.

In every case of ontogenetic segmentation the nucleus itself remains passive, and is drawn into the formative activity by non-nuclear plasm. The chromosomes, the only enduring constituents of the nuclear plasm, are, however, bearers of an indispensable function, though not of formative import. As already suggested, it is likely connected with the vital process of oxydation, which suggestion is supported by the blood-corpuscles being of nuclear origin.

THE PROBLEM OF THE LIVING FORM.

The blending of two or more Protozoa into a proportionately enlarged individual without disturbance of the specific structure of the species, is a fact of nature readily observable. This occurrence proves that the specific form of protoplasmic beings is not directly dependent on the amount of substance entering into it. Driesch succeeded in bringing about the union of two segmented eggs of *Echinus*, and obtained perfect single individuals. Zur Strassen obtained giant embryos of *Ascaris* formed by the fusion of two eggs. The remarkable results of experiments attained by grafting point to the fact, that the more or less intimate blending or coalescence of the living substance of different individuals is dependent on specific complemental affinity attaching to the chemical constitution of the substance of the coalescing organisms or fragments of the same.

The highly significant fact, that organic form and structure is not directly dependent on the amount of formative material entering into their constitution, is most strikingly revealed in the production of complete embryonic forms from almost any fragment of egg-plasm, which

though proportionately reduced in size, resemble in all essential structural details the normal embryo.

It has been here demonstrated that the organic form in all its structural details is the visible expression of the specific chemical constitution of the living substance composing it. Consequently, in the intricacies of this chemical constitution has to be sought the explanation of the phenomena under consideration. The potency of a chemical fragment to develop into a full-sized embryo, when supplied with sufficient complementary material; or, failing this supply, the potency to transform its own substance into a proportionately-sized embryo; this potency of fragments to reconstruct the complete typical embryo out of whatever amount of formative material is available, seems to indicate that each definite link in the chemical structure underlying the specific form of an organism is a subordinate formative division, which has power separately to increase in bulk or grow to adult stature in proportion as it is supplied with nutrition or complementary material. And this supposition seems to be corroborated by the mosaic-like morphological divisions, which make their appearance during ontogenetic evolution. And corroborated also by the separate regenerative power of such mosaic-like divisions, or structural provinces.

In normal ontogeny the blastomeres of each stage of segmentation have to be regarded as the merging into morphological visibility of latent dispositions in the chemical structure of the germ-plasms during its process of gradual reintegration. Each blastomere contains then potentially all structures to be eventually evolved from it. Each successive segmental division or segregation curtails and distributes thus the potential areas of reproduction, confining them to specific portions of the evolving substance. And when, at last, such formative morphological subdivisions have reached their climax, and have conjointly reproduced the adult organism; then it is found that such morphological areas may still possess more or less separate reproductive potentiality, as evidenced by manifold phenomena of regeneration. And the less highly differentiated such morphological areas have come to be, the more reproductive potentiality do they generally retain.

In this light it becomes irrefragably certain that in "multicellular" organisms the divers "cells" that compose their specific tissues are as direct derivatives of progressive segmentation, not autonomous lineal descendants of an elementary mother-cell; but very obviously definite morphological subdivisions, arising during progressive ontogenetic evolution as complementary constituents of a predetermined whole. And as such they may likewise retain reproductive potentiality of their own; may undergo mitotic division, or may even as epithelial "cells" reproduce highly complex structures.

That which is visibly revealed as vital organization in all its minutely differentiated and functionally interdependent structures proves to be the morphological manifestation of what our scientific experience teaches us to regard as specific chemical and specific vital potencies.

The chemical potencies evince themselves as forming unitary bodies, all of whose constituent parts, though consisting of heterogeneous elements known to enter into their composition, are, nevertheless, somehow intimately blended so as to form integrant and not merely aggregated components of the same. They evince themselves, furthermore, in displaying specific modes of action and reaction nowise deducible as combined mechanical effects of the spatial arrangement and modes of motion of the component elements. The chemical body acts and reacts as a specific whole; not simply in one definite mechanically quantitative manner; but in manifold peculiar and diverse qualitative ways.

The specific vital potencies evince themselves, above all, in the power of certain such phyletically elaborate chemical wholes to reintegrate themselves, after partial disintegration, through assimilation of complementary material. The integrity, and therewith the identity of the organic being as a whole, is thereby preserved, despite functional and other modes of deterioration. Every part of an organism is a complementary fragment of the whole, and not merely an aggregated component. Germs of all kinds are such fragments, endowed with the power of reintegrating or regenerating the whole of which they are fragments. This reproduction of the whole organism as final aim of the ontogenetic process, resulting, moreover, in its complete adaptation to the medium with which it is to enter into manifold modes of interaction; this striking and undeniably purposeful evolution towards a predetermined end serves as prototype for the conception of teleology in nature, or of so-called final causes. Such strange constructive aiming at the attainment of something whose future existence and constitution are strictly predetermined, yet only potentially present, has ever been one of the principal puzzles of philosophy and natural science. It finds its explanation solely in biological conditions, and exclusively applies to the same.*

*"We are confronted by the much-vexed, yet still open problem, how different units come to be constitutionally destined to enter into interdependent relations so as aimfully to form an organically efficient whole." "This consideration of innate reciprocal dependence in the constitution of a larger whole involves the entire teleological riddle; the puzzle, namely, how the integral constitution of a whole, eventually to be formed, can possibly act as a so-called final cause, act as the chief determining cause of the nature, disposition and function of the constituent units that enter into its formation.

Kant sought to argue away teleology in nature by declaring it to be a peculiar mode of our conception of a certain order of things. He held that every occurrence in nature being strictly dependent on immediate or so-called efficient causation, final causes could not possibly enter into the system of nature. And recently, much in the way of Empedocles of old, natural selection has been believed more particularly to reduce all seeming teleology in nature to mechanical or, at least, to efficient causation. In fact, the principal aim of our present scientific interpretation of nature is to attribute all its occurrences to adequate mechanical causation.

Natural science, when it interprets organization as resulting thus simply from the peculiar rearrangement of so many pre-existing material units moved by so much pre-existing energy, misses in its explanation all that is most essential to an adequate understanding of the case. The fact here overlooked, the essential fact, is that in the process of organic development new modes of aim-



ful energy, manifest in specific modes of vital reaction of the organism in relation to its medium, come creatively into existence. All that is most characteristic of vital organization and its activity, all that constitutes its specific nature, merges thus newly produced into being, resulting from potencies not previously realized. This amounts not altogether to a creation out of nothing; but it is a coming into existence of efficiencies previously non-existent.

It is evident, explain it as we may—a living being in relation to its organic and inorganic environment is found to be out and out teleologically developed. Its organization is preconcertedly constituted for life in a specific medium. And the development of an organism from a reproductive germ is obviously teleologically predetermined by the nature of the organism to be developed therefrom. The exact plan of the whole being, eventually to be formed as a product of nature, enters here somehow as a final cause in its reproduction." This was written seventeen years ago in an article in which I aimed to prove the radical difference obtaining between the so-called social organism and the actual vital organism. "International Journal of Ethics," Vol. VIII, pp. 58, 59, 1887.

EDMUND MONTGOMERY.

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