BIOLOGICAL LECTURES

DELIVERED AT

THE MARINE BIOLOGICAL LABORATORY

OF WOOD'S HOLL

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PREFATORY NOTE.

When the first volume of these lectures was offered in 1890, their continuance as an annual publication was thought of only as a possibility; it was not promised, nor, indeed, suggested. The usefulness of such lectures had only been tested by a single summer's experience; and, although it was certain that they served a good purpose in the work of the Laboratory, the advisability of publishing them was doubtful. While the reception accorded to the two volumes already issued indicates that it would not now be presumptuous to announce the hope of continuing them, it would be rash to promise this in the present state of uncertainty regarding the future of the Laboratory. The Laboratory is an experiment to test the extent of our need, and the possibility of securing general co-operation. It has furnished a demonstration in both these respects; but it remains to be seen whether this will suffice to bring to it the necessary foundation of a large endowment. Special thanks are due to those who, in reviewing the "Biological Lectures," have called attention to the nature and purpose of this experiment, and to the high importance of the end proposed. The project appeals, not for government support, but to private munificence, and every authoritative confirmation of its merits adds strength to our effort.

The general aim and purpose of these lectures and the place they take in our work have been already defined.[1] Nearly every lecture of the present volume deals with one or other side of the problem of organic development — that problem which has led, and which will most likely ever continue to lead, the biological sciences. The sister sciences dealing with the evolution of the inorganic world are our natural allies and coadjutors, laboring to the same end though in different fields.

[1] Preface to volume II.

Comparison of standpoints must benefit both sides. Cross-fertilization works rejuvenation in theories as in organisms. The biologist may pause to see how the individual vanishes in the abyss of the universal, and how self-determination dissolves in the presence of the physicist's fundamental postulate of inertia. The physicist may find it agreeable from time to time to turn from the Nirvana where self and not-self, rocked in blissful reciprocity of vibration, annul each other, to the world where self asserts itself in organic determinations issuing in purposeful adaptations and conscious intelligent action.

The inexperienced reader may need to be reminded that our standpoints with reference to organic development are not necessarily mechanical for the physicist, and vitalistic for the biologist. Transcendental vitalism has just as little standing on the biological as on the physical side. Indeed, if we were to draw the line between mechanism and vitalism, it would be found, unless I am much mistaken, that there are more physicists than biologists on the side of vitalism. No less a physicist than Lord Kelvin has recently declared that "the influence of animal or vegetable life on matter is infinitely beyond the range of any scientific inquiry hitherto entered on. Its power of directing the motions of moving particles . . . is infinitely different from any possible result of the fortuitous concourse of atoms."[1] This may not be vitalism, but it does not look like mechanism.

It is on the biological side, strange as it may seem, that we meet with extremes of mechanism, equalling, if not exceeding, the discarded errors of vitalism. An epidemic of metaphysical physics seems to be in progress — a sort of *neo-epigenesis*. In place of the *vis essentialis* of the old epigenesis, the new epigenesis sets up as its fetich the *vis impressa*. The new god is preferred to the old because it works from the outside instead of the inside. It represents the sum of external conditions and influences at the present moment, and is proclaimed all-sufficient for building up organisms out of isotropic corpuscles. Previous conditions are not, indeed, quite ignored, for they have resulted in special molecular constitutions called germs, and

[1] *Fortnightly Review*, 1892.

these display peculiar molecular activities known as metabolism, growth, and division. The long past can bring forth only a *molecular* basis; a few hours of the present can supply all, or nearly all, the determinations of the most complex organism. Impotent past, prepotent present. We have no longer any use for the "Ahnengallerie" of phylogeny. Heredity does not explain itself or anything else, and it detracts from the omnipotence and universality of molecular epigenetics. We are no better off for knowing that we have eyes because our ancestors had eyes. If our eyes resemble theirs it is not on account of genealogical connection, but because the molecular germinal basis is developed under similar conditions. The reason this basis becomes an eye rather than an ear or some other organ is wholly due to its position and surroundings, not to any inherent predeterminations. If the material for the eye and the ear could be interchanged in the molecular germ, that which in one place would become eye would in the other place become ear, and *vice versa*. All this is credited to "developmental mechanics," for which we have the highest respect so long as it is really "developmental." But the "mechanics" of "exovates" seems to be peculiarly innocent of any knowledge of nature's experiments.

While biology is certainly indebted to physics for some of its metaphysics, it is to the credit of physics to have made it clear that mechanism, indispensable as are its methods, affords no fundamental explanation of anything. As Karl Pearson has so well said, the mystery of life is "no less or no greater because a dance of organic corpuscles is at bottom a dance of inorganic atoms."[1] What dances and why it dances is not explained by reducing size to the lowest limit of divisibility, and just as little by the assumption of ultra-physical causes. This is no criticism — no disparagement; it is only a confession of ignorance. The ultimate mystery is beyond the reach of both mechanism and vitalism; let pretension be dropped, and approximation to truth will be closer on both sides.

When neo-epigenesis objects to anything previous, if it be above a physical molecule, because what is done must be sub-

[1] *Grammar of Science*, p. 407.

tracted from what remains to be done, the objection has no foundation, for there is no less, and perhaps there is more, mechanism in predetermination than in postdetermination. We may find it difficult to untie the knot of predetermination, or preformation in the sense of preëxisting germs, but are we any wiser for the short-cut of denial? Is our field of exploration reduced by the discovery that germs arise by division of preëxisting germs? Does any one feel it a deprivation that he no longer need search for spontaneous generation among internal parasites? If so, he could still search. It is a strange perversion of fact to imagine that investigation is obstructed by assuming the egg to be more than a molecular aggregate; for it is abundantly evident that the expectation of something more has been a powerful stimulus to recent discoveries in cytology. Were it possible to remove the grounds of expectation, of course the search would come to an end.

The search for ultimate units of organization in the egg — that is, smallest elements capable of organic growth and self-division — has already led directly to the discovery of *mechanism*, where molecular epigenetics had disputed it. The molecule is no doubt universal and very mighty, only perhaps not quite almighty. It is quite conceivable that there should be something at least as far above the molecule as the molecule is above the atom. Indeed there seems to be a considerable number of units actually visible in the cell, which are certainly quite as real as the molecule, and which differ from it in having those fundamental attributes of growth and self-division which appear to be peculiar to every grade of organic life. Every such unit may be reducible by chemical disintegration to molecules, but we should hardly accept that as proof that no organization above molecules preceded the dissolution. There is no warrant for the assertion that life is something different from, and independent of, matter and energy. That is the mistake of vitalism. On the other hand, there is no warrant in decomposition for identifying dead mechanism with living mechanism.

The resolution of organs into tissues, tissues into cells, and cells into smaller units, does not disclose the secret of life, but it does extend our knowledge of organic mechanism. It is strange that experienced and acute biologists[1] should so far misunderstand the spirit and language of cytological research as to imagine that any one expects to explain life and get rid of its mysteries "by imagining a living creature indefinitely divided into minute living parts." Some place the secret of life in the cell, others in smaller units; but no one, so far as I know, has looked upon the unit as anything more than the seat of the mystery.

Just as the final proofs of these lectures reached us, came the lamentable news of the decease of one of the authors of these lectures, our colleague, Professor John A. Ryder of the University of Pennsylvania. Absence of data prevents a full statement.

American biology thus loses one of its ablest representatives, and the Marine Biological Laboratory one of its most valued friends. Those who are familiar with Dr. Ryder's contributions to animal morphology and to the biological questions of the day, and especially those who by close acquaintance came to see the whole-souled integrity of the man, the depth of his loyalty, and the purity of his honor, will deeply deplore his removal and mourn the loss of his genial and inspiring presence.

C. O. WHITMAN.

[1] Mivart. *Harper's New Monthly Magazine*, March, 1895.

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substance", unless it means "practically" or for practical purposes" or "for the purposes of a rational ...ny." But there are many thinkers who are ... in honor, as spokesmen of modern science, ... teach us that every living thing, and everything, ... potential in cosmic nebulosity, and that all ... has come out of it might have been ~~expected~~ foreseen ... had only known enough. For the practical purposes of one with enough knowledge, the cosmic vapor is, from this point of view, "substantially" equivalent to any living thing, or all living things, ~~and~~ or all things in nature. There are, then, many modern men of science, who believe that all things have been, "from the beginning" as we see them ... to be. If the cosmic vapor was "created" or came to be, "in the beginning", then those who are of this opinion ... that all things were created, ~~at~~ the beginning (or came to be in) ... substantially as we now see them to be.
... belief that all things were latent or potential in the cosmic vapor is belief that they were substantially as they are now ... for all the practical purposes of one who knows enough to ... the use of them.
If by "substantially" we mean "in substance" as distinguished from "in accidents" we must mean something by the word "substance" unless it is used in ... as it may be here. If substance means that in which things inhere, or that by which they are supported, or in which they have their being.

FIRST LECTURE.

LIFE FROM A PHYSICAL STANDPOINT.

A. E. DOLBEAR.

I SUPPOSE there is no question about which science concerns itself and everybody has more interest in than this one of the nature of life. Some pretend to think we know nothing about it and never can know anything, others are quite as sure that we know it to be correlated with other forms of force and in some way convertible into them, while a third class may hold an agnostic position, content to wait until knowledge shall grow so as to include the nature of life. Still it may be doubted if there be any thoughtful person who does not hold some sort of a theory about it which he expects will be substantiated, and it is quite certain if any demonstration of the nature of life were to be given to-day, there would be a great multitude of persons who would at once declare they had always so held. This expectancy shows itself in so many ways, that one may be sure that nearly every person has some theory of things, some scheme into which he contrives to fit all kinds of facts. That is to say we can't get along without some sort of philosophy and we make our own if there be none otherwise provided. Even those who pretend to contemn all schematic attempts in knowledge and who mildly reprove such efforts by calling them speculations are easily found to have some pet scheme of their own which finds favor in their eyes.

Now there are speculations and speculations. There is a kind that has been common from the beginning until now, when imagination has full sway with no manner of regard for data or for appropriate facts at all. Such an one was the commonly held view as to the origin of the world and especially of living things, including man. They were created, at their beginning being the same substantially as we see them now to be. There is not and never has been in the history of man any phenomenon that could give warrant to such a hypothesis, yet it has been held and fought for by men now living.

Then there is another kind of speculation that has or tries to have proper data — that shows some respect for experience. Such was the attempt of Robert Chambers in the book called Vestiges of Creation, a book which is deserving of more praise than I have yet seen awarded it, for he undertook to handle such data as were available to him and he discerned dimly the process which all naturalists to-day see clearly. His data were inadequate and could not compel belief, but his attempt as compared with the hypothesis it contended against was as daylight to darkness. It had some experience in its favor; the other had none at all.

Lastly there is a hypothesis derived from the study of groups of appropriate facts, the attempt to find an adequate explanation of all of them, without going beyond the bounds of possible experience, that is, without importing into the phenomena some transcendental conditions. Such is Darwin's Theory of Natural Selection, offered for acceptance as a provisional hypothesis thirty-five years ago. Also fought against stubbornly by naturalists as well as theologians in spite of the plain fact that it was either such a hypothesis or nothing; there was no other competing one that had any standing ground at all, which seems to imply that to some minds it is more rational to entertain an unintelligible hypothesis with no experimental data in its favor, than it is to entertain one that has a considerable body of experimental data for its basis.

Swedenborg taught the nebula hypothesis, but gave no astronomical reasons. Kant developed it, giving philosophical reasons which were not considered to be adequate. Laplace gave mechanical reasons which were adequate, and he who explains that theory to-day gives the reasons of both Kant and Laplace, but he quite ignores Swedenborg. Kepler explained the orbital movements of the planets as due to guiding spirits. Newton explained them by the doctrine of gravitation and dismissed the spirits from service. In his Principia he says he framed no hypotheses ; nevertheless he was a great framer of hypotheses, as for instance the corpuscular theory of light which he worked out, and his theory of a necessary ether which he did not work out. So hypotheses are absolutely needful for guidance in all profitable efforts, and as much so in science as anywhere else. Indeed, what is science if not our correlated experiences? It is interesting to see how men have tried to define it. Buckle says, "Science is a body of generalizations so irrefragably true, that though they may be covered by subsequent generalizations, can never be overthrown by them." Spencer says, "Science is a higher development of common knowledge." Others say, "Science is classified knowledge."

Our experiences of all sorts are the subject matter of science, our interpretation of them is our attempt to be logical, our attempt to be scientific, and a true interpretation of any phenomenon will not be inconsistent with any other truth, that is, it will be consistent with all we know and all we can know, so that any hypothesis that is plainly incompatible with the best we know has no place in science.

So much to clear the way for a proper consideration of life from a scientific standpoint. Some sort of a theory of it is needful for giving direction to research, for if it be a proper subject for investigation the implication is that its explanation will be found to be consistent with what else we know, and if it be not a proper subject, then research is a waste of time. If one assumes that life is some sort of transcendental thing or property not necessarily related to the other things and properties we describe and explain, such an one sets bounds to knowledge on the basis of what he does not know. If on the other hand he is to correlate it with other knowledge, his induction must be wide enough to include all phenomena into which life enters in any degree.

The old theory of a vital force did the former. It assumed that there was in a living thing some sort of an entity capable of directing the functions and that the physical and chemical conditions present were subject to its domination. It made the distinction between a living and a dead thing to consist in the presence of a force radically different from all other forces, which presided for the time in much the same way as Kepler's guiding spirits presided over planetary motions.

We know what the history of such prepossessions has been. A hundred years ago Caloric was thought to be such an imponderable potency, Light was thought to be another, Electricity still a third. Each of these turned out to be no imponderable at all but simply physical properties of matter of the ordinary sort. But the change from the old to the new view in these matters made it needful to change the fundamental ideas concerning matter itself.

The physiologists for a generation have ceased to think of a vital force as different from other forces in the same way as they have ceased to consider light as an emanation. And the consensus of opinion among biologists, if one may judge from a multitude of expressions by them concerning life, is that all the phenomena exhibited by a living thing are finally resolvable into physical and chemical processes.

A vital element peculiar to organisms no more exists than does a vital force working independently of natural and material processes. — *Claus and Sedgwick.*

It must not be supposed that the differences between living and not living matter are such as to justify the assumption that the forces at work in the one are different from those to be met with in the other. — *Huxley.*

Zoölogy, the science which seeks to arrange and discuss the phenomena of animal life and form as the outcome of the operations of the laws of physics and chemistry. — *Lankaster.*

Certain it is that life is a chemical function, says Prof. Stokois, of Amsterdam, and he adds, Is not the chemical function a sort of life?

So vital force as a distinct somewhat invented to account for living phenomena, has now no status anywhere. If it be so, then it is plain that matter has properties which have not been included in its list. If matter has been defined as *inert*, or as *dead* or as *inanimate*, one may have to revise his definition. Is it not plain in an *a priori* way that the phenomena exhibited by living things are to be explained only on the assumptions, first as due to the inherent properties of the matter that exhibits it, *or* to some external agency — not inherent in it, to which the name vital force is just as good as any? and if this has been discarded for seemingly good reason, then there is the other alternative only. But somehow most men who have thought about it have felt loth to adopt this. Is not this the same as saying that there is somehow felt to be a good reason for refusing to adopt it, even in the absence of any proof that it is untrue? I suspect it lies in the common unanalyzed notion into which we have all been schooled, that matter is dead and inert and out of it can come nothing but so-called inorganic phenomena. Along with this has come a relatively new piece of knowledge called the conservation of energy, which asserts that all the forms of energy are transformable and that the sum of their energies is a constant quantity. As no one hitherto has been able to see how vital and physical phenomena are correlated, men have been loth to believe it to be a fact, — a mental position which assumes that before a relation can be logically accepted it must be explained, which is not true. The relation between mechanical energy and electrical energy is very definitely known, yet it has not been explained; but in this question there is no personal equation, no such lively interest in its settlement as in the other. The one has only mechanical interests involved, the other is so much of a sociological question as to threaten war involving church and state. Dr. Barnard, a former president of Columbia College, said concerning a certain debatable statement in science, that if it were true he did not want to know it, and that is the way a large number of persons feel about this question of life in its relation to ordinary matter.

As every one knows, our knowledge of matter has wonderfully increased during the past twenty-five years, and along with this knowledge has come too, the conviction that the older conceptions of its nature and its possibilities cannot possibly be true. It becomes important in a matter of the kind under consideration that one should know what he is entitled to postulate concerning matter and this for the manifest reason that every living thing in our experience consists of a mass of ordinary matter, and we have no experience of any living thing not so embodied. From mammoth to monad there are the same elements combined. Evidences of life are of various sorts, but generally they consist in movements of some kind, which may be locomotive, or such as involve maintenance of functions of nutrition, temperature, and so on, in animals; but in plants of the higher types there is apparently only maintenance of nutrition and reproductive functions. In seeds and eggs, there is somehow the presence of life without any of the obvious evidences. Take a hen's egg for instance. Is it alive, or shall we ask, is it capable of living? Two very different questions. If it be kept at the temperature of 104° for three weeks, the most wonderful transformation takes place, and out of the albuminous mass has grown a thing with curiously adapted organs and endowed with intelligence so it can take care of itself. If on the other hand the same egg had been heated to 150° for five minutes, or cooled to 32°, all possibility of growth would have been stopped. What difference *can* temperature have on life?

What is temperature? Physically it is atomic vibration and is measured by its amplitude. How does atomic vibration affect the conditions of matter? It permits different combinations at different degrees, so one would infer that the egg molecules were chemically disrupted by considerable changes in temperature. But if the egg had other qualities not physico-chemical in nature or necessarily related to them, what becomes of them when there is a change of temperature? Put the same egg away for two or three months, and then it is found to be as unable to grow into a chick as if it had been boiled. What now has taken place — chemical disorganization as before. A grain of corn can stand a much wider range of temperature, and maintain its ability to grow under appropriate conditions of warmth and moisture, and this too for a much longer time, some years; but it slowly deteriorates and in a few years with the best of care it loses — what? its life? Does it really have life until it begins to grow? Let that process once begin and it cannot be arrested. It must continue to go on or it will disintegrate at once. When the proper temperature has once tumbled over the statically arranged molecules of the egg, proper energy for continuing the process must be furnished or the whole structure comes tumbling down and then we say the thing is dead. One may say that heat or temperature did it, but it is better for clearness of vision to see that these terms mean only a kind and rate of motion and nothing else, and then one can understand better how molecular stability depends upon temperature, whether in an egg or in water. Hence in some way life is an affair of atoms and molecules rather than of large and visible masses of them.

How large are the smallest masses that exhibit to the biologist the phenomena of life? Each increase in magnifying power has presented to him still smaller masses having this quality. If one can now see living particles the hundred-thousandth of an inch in diameter, is there any reason for supposing that such a particle is the smallest really living thing? Certainly not. Well then, how much finer may matter itself be divided? There is reason for believing that the atoms of matter such as hydrogen, oxygen, and carbon are approximately the fifty-millionth of an inch in diameter and a mass of matter the hundred-thousandth of an inch in diameter would contain 125,000,000 such atoms. Would one think there would be any probability in the proposition that the *smallest* living thing must contain that number of atoms? If not, then what has the microscope got to say as to what has been called spontaneous generation? There might be millions of living things too small to be seen, having any number of qualities, such as growth, assimilation, reproduction, and so on, and this smallest thing we see be only the last in a long succession of growths and developments. Again if life be not a miraculous endowment, would any one think there could be any probableness in the proposition that the number of molecules and their arrangement *merely* determines the presence or absence of life? Does the number and arrangement of molecules determine whether there shall be gravitation, or elasticity, or temperature among them?

Observation shows no limit to the size of a mass of matter that exhibits the quality called life, and philosophically there is no reason for setting any limit to the size, as one might as well start with a mass the fifty-millionth of an inch in size as with one the hundred-thousandth of an inch. In the absence of any evidence of there being some sort of a physical and chemical hiatus between those limits one is not at liberty even to assume that there is, and if some of the phenomena that come out from aggregates of molecules he is not able to explain satisfactorily, it is safer to enlarge the possible attributes of atoms themselves than to summon a genii who is wholly unaccountable when off duty. But the old theory of matter was that it was absolutely powerless in itself, and that the so-called forces of heat, light, electricity, chemical affinity, and so on, by themselves could bring nothing but disorder, and that arrangements and adaptations required other than such agencies to establish. That this is not so may easily be shown.

Here is the solar system, an orderly body of rotating and revolving globes, the orderly arrangement and motions of which are believed by all astronomers to be due solely to mechanical agencies, gravitation, and the laws of motion. Look at a snow-flake, how beautifully symmetrical in its hexagonal geometry! A difference in temperature of less than one degree determines whether it shall remain a crystal or shall lose its embodiment of form and become a minute drop of water. Here again we meet with temperature — that is vibratory motion as determining not only whether a mass of matter shall exist as a solid or as a fluid, but that it shall exist in a symmetrical form, and not as a hodge-podge of molecules. It is proper to inquire if, in order to produce such an orderly arrangement of molecules it is needful to imagine some extra physical agency in order to account for it. I suppose no one assumes that now, even if he has no conception how the phenomenon can be due to merely physical agency. Such an one has enlarged his concept of the possibilities of matter and is not therefore surprised at the evidences of organizations of that kind. A hundred varieties of stars, or plumes, or feathers, or fern forms are attributed to the properties of molecules without other help. He may not trouble himself to find an explanation, but if he does concern himself to find a mechanical explanation, he needs to know more about atoms and molecules that he may perceive how certain kinds of motions *necessitate orderly arrangment.*

That the atoms of matter have internal vibratory movements is proved, 1st, by their elasticity in the gaseous form ; 2d, by the uniformity of the wave length of light when made incandescent, as shown in the spectrum of a gas, indicating as plainly as can be that the atoms have their regular rates of vibration, an enormous number per second. As the velocity of light is 186,000 miles per second, a wave-length the fifty-thousandth of an inch long implies that atoms that produced it vibrated as many times a second as the fifty-thousandth of an inch is contained in 186,000 miles, something like 600 millions of millions. If one cannot conceive such a number, he is compelled by his arithmetic to believe it represents the truth. But the thing of importance here is to picture to one's self the vibratory motion itself, and here one must have recourse to mechanical models. It may be well to remark that the idea of hard, round, or spherical atoms has been abandoned by physicists as having no probability at all, but whether atoms have one form or another they certainly have these vibratory rates, and one may make his mechanical models in any way that shall not be incompatible with such physical properties as atoms are known to possess.

Within the past 20 years the evidence has been fast accumulating which gives credence to what is known as the vortex ring as being the form of the ultimate atom. The puff of smoke and steam from a locomotive which goes sailing as a ring high in the air, wriggling, vibrating and twisting constantly, but maintaining its ring shape in spite of these, is an example. Such a ring has form, elasticity, momentum, energy, and other physical properties. So if one considers what vibration in such a ring consists in he will have a fair conception of it in an atom. Its diameter lengthens in one direction until its shape is elliptical, *a b* (Fig. 1), then it swings back into an ellipse at right angles to the first, *c d,* and the rate at which this will take place depends upon the size and the degree of rigidity which the ring has. Such vibratory motions constitute the temperature energy of the atom. But it is to be noted that with such kind of motion there are parts of the ring which have a maximum amount of motion and other parts with minimum as at *n*. Suppose, then, that for any reason such atoms should attract each other, say gravitatively, and come together, is it not evident that they could adhere to each other only in certain places, the so-called nodes *n*, of which there are four when the vibrations are of this simplest type? So each such atom would have four points upon its circumference where there could be adhesions. This is the same as saying that so long as such an atom has any temperature its possibilities of combination will be limited to the conditions of its vibratory rate and this will be definite at a given temperature. Such definite combination we call chemical combination, and the combination itself a molecule.

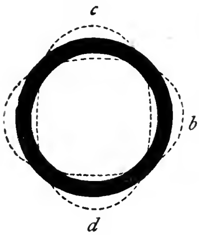

FIG. 1.

Follow out the possibilities of structure with such conditions and one can see how cubes and hexagons result from the positions of the nodes of vibrating bodies, and thus orderly arrangements, as exhibited in crystalline forms, follow, from a simple mechanical process.

Thus consider the rings in the diagram (Fig. 2). The ring 2 touches upon 1 at the node or place of least vibration, and likewise its own nodes correspond in position with those of 1. In like manner rings 3, 4, and 5 are similarly placed, and each individual of the combination could vibrate symmetrically without disturbing its neighbors. This would also leave each one free to swing as upon a hinge upon 1. Imagine then that 5 and 3 should swing upwards from the plane of the page and lean over until they touched over 1. It is plain to see that their nodes would then come together and their

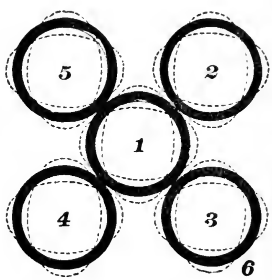

FIG. 2.

individual vibratory rates would in no way be interfered with. If the whole should be turned about so as to be looked at edgewise, it would look like a triangular arrangement (Fig. 3), and half a dozen such would fit together to form a hexagon (Fig. 4), — a form of crystallization very common; for example: water, H_2O; silicon, SiO_2. Again, assume that 2, 3, 4, and 5 should each swing upwards together until their edges touch; they would then form the sides of a cubical box, and, as in the other case, their nodes would be opposite each other, and there would be no interference of vibratory motions. Similar cubes could be added on every side, and a cubic structure built up of any size if the individual rings were of the same size. If some of them were of different size the resulting structure would have some angle of inclination of its sides which would be uniform if the individual parts were similar. If such triangular, cubical or other elementary form be a stable one, as evidently it would be mechanically, one might call it a molecule, but its form would be seen to depend upon its vibratory motions, and if this constituted the temperature of the body, then it would be clear how molecular form depends upon heat.

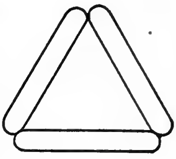
FIG. 3.

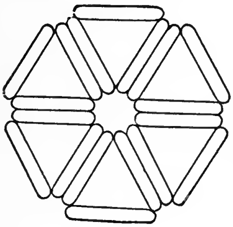
FIG. 4.

Suppose now the amplitude of such motions were to increase, the stability of the combination would necessarily grow less and less until it would be mechanically impossible for any two atoms to remain together. Such increase in amplitude means increase in temperature, and such breaking up of chemical combination by heat is called dissociation. This kind of a process with only details varied in a mechanical way gives an intelligible account of the actions called chemical, and they are in complete accord with that new science which has been developed within the past few years and is known as thermodynamics. Investigations of many sorts have led physicists and chemists to the conclusion that at absolute zero chemical action cannot take place. Indeed, long before that temperature is reached, substances that energetically combine at ordinary temperatures lose all semblance of affinities and cannot be made to unite. Now the point of this chemical disquisition is to make it plain that orderly arrangement and phenomena follow from orderly motions, and one has no need for inventing other agencies when the latter are known to be present, as is true in this case. One may safely postulate that ordinary matter possesses such inherent qualities as enable it to assume geometric forms that depend upon temperature.

But the matter we know possesses other qualities that have to be reckoned with. First it possesses energy even when it is seemingly quiescent. For example when carbon, sulphur and saltpeter are mechanically mixed together, as one might mix sand and salt, we have a mixture that possesses a relatively large amount of energy, which we have not put into it. The mixture simply makes the energy available. A lump of coal might lie around and seem to be as helpless and inert as any stone, but we drive our steam engines with its like and heat our houses, and civilization depends upon it to-day because it is loaded with energy which a furnace makes available. The energy is in it, and if it is not apparent under ordinary circumstances it is evidently not correct to speak of it and reason about it as if it were really inert and dead. One might liken it to a sleeping rather than to a dead man.

What is called the dynamic theory of matter, is an implied denial of inert matter.

A pound of hydrogen and eight pounds of oxygen contain energy enough to wreck a large building. In like manner the substances used for foods are loaded with energy in a shape available for use in living structures, so one has no need to assume some external source of energy for the purposes of any living thing, but this energy resides in the atoms, for molecules are but aggregates of atoms, and there is nothing in molecules which was not before in their constituents. This energy is not all of it, nor any considerable part of it, due to their temperature, that is, it is not to be measured by the temperature, for it is evident that such a structure as I have described is itself an embodiment of energy, for it consists in a rotary movement of something, at an extremely rapid rate.

When a mass of matter is heated and left in space it presently cools by a process called radiation, that is, waves in the ether are produced by the vibratory motions, and the energy is handed over to the ether, which carries it away at an enormous velocity, that of light, but the kind of energy which itself represents it cannot yield up, yet it reacts upon this same ether in another way so as to reduce the pressure about itself; so one might very well consider that half of the energy of the atoms lies in the ether and is exchangeable with it, that is, the atom can apparently call in a supply of energy, from space, for an emergency.

The space about a body, within which it is capable of affecting other bodies without contact with them, is called its field, and there are several different kinds of fields. The gravitation field is as extensive as space, for every particle of matter attracts every other particle, no matter what the distance. In like manner every heated body sends out its radiant energy to other bodies to an indefinite distance, and the bodies on which such radiant energy falls are heated like the first. An electrified body has an electric field, within which other bodies become electrified simply by being present in the space. A magnet has a magnetic field, and iron and some other bodies become sensibly magnetic by being in such magnetic field. Likewise atoms have chemical fields, within which chemical reactions of definite sorts are induced. This field has in some instances been traced in solutions nearly an inch from the body producing it. The effect of this field is similar to that of the others, namely, to bring about chemical reactions, and therefore *molecularly organized products similar to that of the originating body.* A minute crystal of a substance will cause the crystallization of a large mass of the same substance in solution. So that here are other attributes of atoms, in which their conditions and motions bring about similar conditions and motions in distant bodies, by what is called sympathetic action, just as a vibrating tuning-fork will set another tuning-fork vibrating, if the latter has the same pitch, though it be many feet away from the first.

Does it not appear that matter has greater and more wonderful endowments than has been supposed? — loaded with energy, acting sympathetically at a distance upon other bodies and organizing itself into symmetrical forms, through simply mechanical action.

Most of our knowledge of matter and its properties has been derived from study within the past thirty or forty years, and there is no reason for assuming that all are known and appreciated. In every direction, almost, there is good reason for thinking that much will be added, but it is certain that enough is known to quite debar any one at present from dogmatically limiting it. We do not know enough about it to limit it, and what we do know gives no warrant for limits of any sort.

In all this one might well say that such phenomena as you have described might fairly well be true of inorganic matter or what has been held to be non-living nature, and yet leave the peculiar phenomena of living organic matter yet to be explained. And what are the peculiar phenomena that belong to the living thing and not to the non-living? Are they the phenomena of spontaneous movement from place to place? Hardly that. Rub up some gamboge in water and examine the particles in the microscope, and they are seen to be in constant movement like animalcules, and this they keep up. Scatter a few bits of camphor upon water and watch the movements. Each particle swims around upon the surface with surprising velocity, and each one carefully avoids collision with others as if it were alive, and this is kept up until the camphor is disolved or evaporated. A drop of creosote upon a water surface behaves in an equally surprising manner, as do most of the so-called essential oils, each one having some characteristic movements which enable one to identify it by its behavior on a water surface. Some of these are explained as due to evaporation, cohesion, or surface tension, and others to molecular exchanges of energy between the particles and the medium, but these names signify molecular properties and show that it is possible for molecular energy to show itself by just such kinds of movements as living things exhibit.

Hofmeister, of Prague, has shown to a demonstration that all which has hitherto been considered the elective affinity of the living cell can be explained in the most natural manner in the world by its colloid condition and chemical constitution.

Within the past few years several experimenters have been studying the characteristic movements that take place in emulsions of soap, oils, and so on, with the result as announced that they are substantially the same as those seen in amoebiform masses. Pseudopodia are formed and absorptive material in the neighborhood is gathered in, a duplication of the process of feeding and of digestion. Such material has been called artificial protoplasm, and a short account of it will be of interest to those who have not chanced to meet with it. Professors Quincke and Bütschli, of Heidelberg, have perhaps done more in this line than any others, and the latter has published a monograph of 230 pages quarto, with six plates, on such artificial protoplasm.

Quincke found that, if a substance soluble in water be finely powdered and rubbed up with oil and then surrounded with water, that the water diffuses into the oil and makes of it a kind of foam, consisting of minute drops of water closely packed together in oil, and thus presents the appearance of honeycomb structure.

The soluble substance which works best for this preparation is K_2CO_3. Olein oil is generally used, — ordinary oil is useless, — and much pains need be taken in preparing it, but when a minute drop of this properly prepared substance is placed in water or a mixture of equal parts of glycerine and water, it becomes clear and transparent and exhibits changes in shape; streaming movements like those of an amoeba are seen, which are kept up for hours; it throws out processes and withdraws others, and the drop as a whole will change its position.

Up the center of the processes there is a streaming movement to the end of the process, where it spreads out and flows back in a layer next the surface. The movements are influenced by warmth and by electricity, and one who did not know what it was he was looking at would suppose he was seeing an actual amoeba.

Frommann, Klein, and many histologists find that protoplasm consists of a kind of network of less fluid material, the interstices being filled with more fluid material; indeed, such kind of structure is thought to be true of every kind of animal cell. This view is an advance from the older view that protoplasm was wholly structureless and homogeneous. Bütschli, however, on the basis of his experiments and observations, concludes that protoplasm is an emulsion of two fluids, which mechanically presents the honeycomb structure, and that so far the structure is wholly due to the physical and molecular qualities of the substances which exhibit it, and that what was taken to be a network peculiar to a living mass is really only emulsion. He finds it, too, from protozoa to vertebrate. The interfibular substance of muscle which has been taken for network by some observers, Bütschli finds a honeycomb with transverse partitions, and the fibrillated axis cylinder of a nerve has cross strands, indicating this also to be honeycomb. As there are many degrees of fineness possible to such physical structure, it would follow that if there be so called "structureless" protoplasm, it is only apparently so, because the meshes are too fine to be seen.

The honeycomb structure is believed to be an albumen containing some molecules of a fatty acid not miscible with water; the more fluid parts which fill the interstices are watery fluid containing albumen and alkali. Such chemical substances in such close physical relations would necessarily permit such phenomena of movement as are seen in such microscopic masses of living matter. The shorthand explanation is that these are due to surface tension and chemical actions; so both structure and motions are thus reducible to purely physical and chemical terms. The success that has attended the efforts of chemists in synthetic chemistry has emboldened some of them to assert with confidence their belief that every kind of a combination can be artificially produced, and that when the *substance* protoplasm is formed it will possess all the qualities of protoplasm, including life. Now Albumen, $C_{210}H_{330}N_{52}O_{66}S_3$, is very closely related to protoplasm and some kinds seem to be nothing else. Egg Albumen contains 1 sulphur atom for every 70 of carbon, Globulin Albumen 146 and Haemoglobin Albumen 350, or ratios of 1, 2, and 5 — a rather striking fact.

Already albuminoid bodies have been artificially made, but they showed no vital qualities. If Bütschli's experiments signify anything they signify that nothing of the sort should be expected from a substance chemically homogeneous like precipitated albumen, for there is required two differently constituted substances, physically mixed, not chemically combined, and no mere chemical process or chemical product could give such a mixture. It is evident that in a chemically homogeneous mass there can be no occasion for changes of any kind within it, and chemistry alone cannot give us any substance which can give characteristic vital actions.

It is true enough that the materials with which Bütschli has made his observations are not the same as the real substance of living protoplasm, yet they are not so far apart as one at first thought might imagine. Whenever chemical action is taking place, whether fast or slow, these exchanges in the form of energy are likewise taking place, changes from molecular to mechanical motions, from one degree of absorption and conduction of heat to another, from one degree of condensation to another, and so on, and now let one add to these the quality of atoms, referred to a little way back, namely, that their field of action is not limited to a push or pull by contact, but that it acts at a distance from itself in various ways, and one of these is to compel other masses in its neighborhood to assume the same form and condition as itself—that is, the so-called sympathetic action. It can be apprehended that when there is energy being expended in this kind of a way we have a process which is called growth. If the molecules are closely adhesive, as they are in so-called solids, the growth can take place only upon the outer surface, yet even here the growth is limited to the same kind of material as that of the initiating mass; that is to say, a crystal of salt will only annex salt molecules to itself, so, though there be several different substances in a solution capable of crystallizing, each one will select molecules of its own kind, and each crystal is similar in kind and structure throughout. This is a kind of natural selection, inherent in the atoms themselves.

But there is the widest difference in character between the few elements that make up a living thing, from oxygen with communistic instincts to nitrogen with antisocial qualities, and strong individual proclivities. If induced or compelled to associate with other elements, it is ready on the slightest provocation to abandon them and become a free rover. Gunpowder, nitroglycerine, and the fulminates are examples of the qualities of this element to effect disorganization. This element is always one of the constituents of protoplasm, and one might therefore expect it to be unstable and restless, as indeed it is. One of the indications of the rate of activity of any kind in an animal is the rate of elimination of nitrogen. This is emphasized here in order to make it plain first that the origin of movement in a living thing is to be traced to the energy embodied in the chemical combinations, and second, that *particular* movements, or at any rate *some* of them which have been attributed to some directing agency — vital force, or life — are due likewise to harmonic changes of energy inseparable from the atoms themselves.

Movements that result in change of position of the body are called mechanical ; movements that result in the enlargement of the body in one way or another are called growth ; movements that result in the organization of another similar body are called reproduction — and the *similarity* of the second to the first has been attributed to *heredity*, a term expressive of a fact, but embodying no explanation. The conditions in the neighborhood of such growing thing, that react upon it in one way or another, are called its environment ; and this too has been a hazy term, as applicable to one thing as to another ; but in this particular field internal changes necessitate external changes beyond the boundary of the changing body, so as to modify the possible reactions upon it, and in every case it represents but the transformations of energy in the exchange from one kind and amount to another. Here as elsewhere Providence is on the side of the heaviest artillery, and more energy of any given kind always dominates the less.

When a young duckling waddles into the water the first time the action is attributed to instinct. When the terminal of a rootlet leads off in the direction of moisture and nutriment, is it not instinctive too?

In each of the hypotheses devised to account for the phenomena of heredity, from Darwin's Panmixia to Weismann's somatic and ideoplasmic cells, there is an effort to look for the basis of heredity in some peculiar form or composition of matter, which possesses qualities unlike the other kinds of matter with which it is associated. From the physical standpoint one must go farther back than any combination to find the meaning of any combination. If one has abandoned vital force or some equivalent for it, and agrees to rely upon physics and chemistry as his antecedents, there is no good reason why he should expect to get out of a hundred molecules what is not in the individual molecules to begin with. Otherwise he is expecting to get out of his mechanism what is not in it.

But here, so far as the affair is a physical and chemical one, the causes and the conditions of such changes as take place in living organisms are altogether molecular and atomic, and no one has yet seen how to endow a molecule with qualities it does not originally possess; and, so far as present knowledge goes, the way to modify the qualities of a mass of matter is to change its atomic constitution, either in number or arrangement, or both. Each new combination has its peculiar characteristics, because the *field* of any kind of a molecule is the sum of the overlapping fields of its atoms. As the field determines the arrangement of other matter within it, it is plain that any new combination — that is, one having a new atom in it, or an old one displaced in even an accidental way — would build up other molecules like itself out of adjacent unorganized materials, and, as older organizations are necessarily more stable, later atomic acquisitions must be easier lost or sloughed off, and so there would be what is called reversion to earlier type, yet still accounted for on purely physical principles.

As biologists have been able to trace so-called vitality to the smallest particles which can be seen, and have found that no special form of matter is essential as a habitat for it, so physicists have been able in so-called inorganic matter to trace similar characteristics, and so approach the subject from another side. The mineralogists themselves are asking now the question whether the evidence at hand does not warrant the conclusion that matter itself is alive. That can only mean that life is to be considered as an attribute of matter in the same sense as is gravitation or elasticity. To take it there is to go behind even Bütschli's work and conclusions, for such evidently assume that life as manifested in such masses as have been studied is a *resultant* of the physical and chemical action present in the mass, while the other view sees in such structures degrees of complexity depending simply upon complexity of combinations, and that the beginnings of it are to be looked for nowhere else but in the atoms of matter themselves, which view, by the way, would settle the question of what is called spontaneous generation, for matter has always been alive and wherever there is matter there is life, that is, ability to combine, to grow, to reproduce, and these processes go on whenever the environment is suitable for it. With such kind of matter there is neither creation nor destruction of life, only changes in the degree of complexity of it.

But I have before remarked on the fast-accumulating evidence that atoms of matter are vortex rings of ether in the ether, and I would here again like to emphasize this statement, not that it has been proved beyond a peradventure, but 1st, because there is no other theory at all, and 2d, because there is much in favor of it and little or nothing serious against it. I take it that some of you are already adjusting your ideas to such a contingency as is indicated by Dr. Ryder's paper here last summer. He was making vortex rings out of vortex rings, but the ones I mean are fundamental. Now the motions which constitute a vortex ring are known, and some of the qualities that flow from such motions are known. In a frictionless medium like the ether they are persistent, indestructible existences, abiding through all changes, and apparently never changing their physical qualities. The hydrogen that has been combined in rock laid millions of years ago has the same qualities as that derived this instant from disintegrated water; but, whatever those properties are, they are derived from the ether itself by some process we are in absolute ignorance of. It will not do to call ether matter, meaning by it what we mean when we speak of oxygen or carbon, for there is no evidence that such qualities as gravitation or magnetism belong to it.

And if matter be such a form of motion, then the ether must have existed before the atom did, and, as no known form of energy is capable of setting up such a motion in a frictionless medium, it also follows that all this implies some other kind of energy in the universe, different from any in our circle of related energies and outside of them — yea, not necessarily related to them as they are to each other; for 1st, the properties of the ether itself are not to be described by the terms appropriate to matter, and 2d, matter is a form of energy and is therefore itself a *product* of which the ether itself is but one of the factors; so what else may be involved in it one cannot say further than that *something* else must be, and I think this "must" may be written large, even though it quite transcends our ability to make out any of its characteristics. At any rate it is evident that if any such theory of matter as is here presented be true, and if the behavior of matter as we see it in test tube and microscopic slide has been interpreted with any approach to the truth, then it is a much more wonderful thing than the old philosophers thought; its possibilities greatly exceed what could before have been imagined, and if mind itself requires a material habitat then it has in an atom an imperishable living home.

SECOND LECTURE.

A DYNAMICAL HYPOTHESIS OF INHERITANCE.[1]

JOHN A. RYDER.

THE doctrine of the preformation of an organism in the germ is as inconsistent with fact as with the requirements of dynamical theory. The effects of the preconceptions of preformationism have been only too apparent in framing hypotheses of inheritance. The now dominant hypothesis is simply an amplification, in the light of numerous modern facts, of the preformationism of Democritus. He supposed that almost infinitesimally small and very numerous bodies were brought together in the germ from all parts of the body of the parent. These minute representative corpuscles were supposed to have the power to grow, or germinate, at the right time, and in the right order, into the forms of the parts and organs of the new being. In this way it was supposed that the characteristics of the parent were represented in a latent form in the germ, which might grow as a whole, by the simultaneous and successive development of the germinal aggregate composed, so to speak, of excessively minute buds, or rudiments of the organs. In such wise also did the successors of Democritus, namely, Aristotle, Buffon, and Erasmus Darwin, suppose that the inheritance of parental likeness by offspring was to be explained. The later and greater Darwin greatly amplified this hypothesis and proposed, provisionally, to account for the phenomena of inheritance by its help. Conceiving the process somewhat as above supposed, he

[1] It is interesting to note that the views developed in this lecture lead to conclusions in some respects similar to those held by Professor Whitman in his discourse entitled: *The Insufficiency of the Cell-theory of Development*, published in the series of lectures delivered in 1893.

consistently gave to his provisional hypothesis the name of *pangenesis*, since the minute latent buds of the germ were supposed to come from, and thus represent potentially, every part of the bodies of the parents, and possibly of still remoter ancestry.

With the discovery of the presence of germinal substance in multicellular organisms, from the embryonic stages onwards, by Owen, Galton, Jäger, Nussbaum, and others, the theory of continuity of germinal matter came into vogue. Upon this basis Weismann distinguished two kinds of plasma in multicellular beings; namely, the germ-plasm and the body-plasm, and at first assumed that because of this separation the latter could not modify the former, since the fate of the respective sorts of plasma was predetermined by virtue of this separation. The one kind was the mere carrier of the other, and the germ-plasm was immortal because it was produced in each species from a store of it which always existed, either in a latent or palpable form, from the very beginning of development. He seems, however, in recent years, to have admitted that this germ-plasma could be indirectly modified in constitution through the influence of the body-plasm, that bore and enclosed it. Beyond this point Weismann again becomes a preformationist, as truly as Democritus, in that he now conjectures that the supposed innumerable latent buds of the germ, representative of the organs of the future being, are minute masses which he sees as objective realities in the chromosomes of the nuclei of the sex-cells. These chromosomes of the germ he calls "ids" and "idants," according to their condition of sub-division, and supposes them to grow and become divided into "determinants" and "biophors," in the course of embryonic development. To these he ascribes powers little short of miraculous, in that he asserts that these infinitesimal germinal particles grow and divide just at the right time and order, and control development so as to build up anew the arrangement of parts seen in the parent type. This elaborate system of preformationism is bound to produce a reaction, that is already becoming apparent; in fact, it is probable that its very complexity, its many inconsistencies, as well as the numerous subsidiary hypotheses that must be worked out to support it, will be fatal to it as a system.

The path along which the solution of the problem of heredity is to be effected lies in a wholly different direction, namely, in that of the study of the mechanics and dynamics of development, and in the resolute refusal to acknowledge the existence of anything in the nature of preformed organs or of infinitesimal gemmules of any kind whatsoever. Such devices are unnecessary and a hindrance to real progress in the solution of the questions of inheritance. They only serve to divert the attention of the observer from the real phenomena in their totality to a series of subordinate details, as has happened in Weismann's case. All this while he has been watching the results of an epigenetic process, as displayed by an inconceivably complex mechanism in continuous transformation, and out of all of this the most essential thing he has witnessed has been one of the *effects* of the operation of that contrivance, in the mere splitting of chromosomes that are his "ids," "idants," "biophors," etc. The potentiality of the part has been mistaken for that of the whole.

We must dismiss from our minds all imaginary corpuscles as bearers of hereditary powers, except the actual chemical metameric or polymeric molecules of living matter, as built up into ultramicroscopic structures, if we wish to frame an hypothesis of heredity that is in accord with the requirements of dynamical theory. The "discovering" and naming of "ids," "biophors," and "pangenes," time will show to have been about as profitable as sorting snow-flakes with a hot spoon. We must also dismiss the idea that the powers of development are concentrated in some particular part of the germ-cell, nor can we assume the latter to be homogeneous.[1] This we are

[1] The writer finds himself unable to agree with Haacke, if he has properly understood that author's assumption as to the homogeneity or monotonous character of living matter, as set forth in his admirable work *Gestaltung und Vererbung*, 1893. Nor does it appear that anything is gained by the acceptance of Haacke's theory of Gemmaria, that is not easily understood upon the far simpler grounds that will be set forth here, though there is much in the book cited with which epigenesists must agree, aside from the weighty character of its criticisms and its pregnant suggestiveness.

compelled to deny on the ground of the organization of the egg itself. Nor is it possible to deny the reciprocal effects of cells upon each other; the parts are reciprocals of the whole, as the latter is reciprocal to a part. The organism during every phase of its existence is a molecular mechanism of inconceivable complexity, the sole motive force of which is the energy that may be set free by the coördinated transformation of some of its molecules by metabolism. An appeal to anything beyond this and the successive configurations of the molecular system of the germ, as a whole, resulting from the changing dynamical properties of its molecules, as their individual configurations and arrangement change, must end in disappointment. We must either accept such a conclusion or deny that the principle of the conservation of force holds in respect to the behavior of the ultimate molecular constituents of living substance. But to deny that that principle is operative in living creatures is to question direct experimental evidence to the contrary, since Rübner has been able to actually use an organism as a fairly accurate calorimeter.

The initial configuration or mechanical arrangement and successive rearrangements of the molecules of a germ, the addition of new ones by means of growth, plus their chemical and formal transformation as an architecturally self-adjusted aggregate, by means of metabolism, is all that is required in an hypothesis of inheritance. The other properties of living matter, such as its viscosity, free and interfacial surface-tension, osmotic properties, its limit of saturation with water, its segmentation into cells, in short, its organization, must be the result of the operation of forces liberated by its own substance, during its growth by means of metabolism. We cannot exclude external forces and influences, such as chemism, light, heat, electricity, gravity, adhesion, exosmosis, food, water, air, motion, etc., in the operation of such a complex mechanism. It is these agencies that are the operators of the living mechanism, which in its turn makes certain successive responses in a way that is determined within limits by its own antecedent physical structure and consequent dynamical properties. The parts of the whole apparatus are kept in a condition of continuous "moving equilibrium" by external agencies, to borrow a phrase of Mr. Spencer's.

This view, it will be seen, leads to a determinism as absolute as that of the Neo-Darwinists, but upon a wholly different basis. It leads to the denial of the direct mutability of the germ by any means other than the transformation, chemical and structural, through metabolism, of the germinal mechanism. It not only compels us to deny that the germ can be at once so affected by external blows as to transmit changes thus produced hereditarily except under exceptional conditions, as we shall see later. It denies also, by implication, that the cytoplasm can be so modified, except indirectly, or through architectural transformations of its ultramicroscopic structure.

It is also compelled to deny that spontaneous or autogenous characters can either arise or be transmitted without involving the principle of the conservation or correlation of force, since no transformation of such a mechanism can take place without involving forces directly or indirectly exerted by the external world. In short, the energy displayed by a living molecular system from within must be affected by energies coming upon it from without. All characters whatsoever were so acquired, so that the truth is that there are no others to be considered. Characters acquired through the interaction of inner and outer forces are the only ones possible of acquirement.

That through reciprocal integration (fertilization and formation of an oösperm) this rule may have apparent exceptions, through the compounding of two molecular mechanisms of different strengths, dynamically considered, it is impossible to deny in the face of the evidence of breeders. Such exceptions are apparent, however, and not real, as must follow from dynamical theory.

The sorting process, called natural selection, is itself dynamic, and simply expresses the fact that, by an actual operation with a living body of a certain kind, something more than a balancing of forces is involved between internal and external energies whenever a survival occurs. The principles of dynamics therefore apply in all strictness to natural selection.

What it is that makes crosses or hybrids more variable and often more vigorous than inbred forms must also have a dynamic explanation, since there can be no increased activity of metabolic processes without an increased expenditure of energy and an increased rate of molecular transformation.

Variations cannot be spontaneous, as Darwin himself was aware. The only way in which they can be supposed to have arisen is by the blending of molecular dynamical systems of differing initial potential strengths, by the conjugation of sex-cells (reciprocal integration), and by means of variations in the interactions of such resultant systems with their surroundings. This, however, Weismann and his followers deny, though no proof whatever has been offered that such is not the fact. Indeed, it is probable that so long as the ultimate machinery of metabolism is beyond the reach of ocular demonstration, there can be no proof or disproof of the position assumed by the preformationists or Neo-Darwinists. Such proof or disproof is, however, non-essential, since we are forbidden by the first principles of dynamics to assume that transformation of any living physical system whatever can occur without involving some forces or influences that emanate from the external world.[1] The separation and evaluation of the internal and external forces, incident to the manifestation of life, in the present state of our knowledge, and from the very nature of the case, plainly transcends the capacity of present available experimental methods in biology. The discussion as to whether "acquired characters" are inherited can, therefore, have but one outcome, since external forces can never be excluded in considering the life-history of any organism.

Nägeli, in seeking to account for the phenomena of growth,

[1] "Some of the exponents of this [preformation] theory of heredity have attempted to elude the difficulty of placing a whole world of wonders within a body so small and so devoid of structure as a germ, by using the phrase structureless germs (F. Galton, Blood-relationship, *Proc. Roy. Soc.*, 1872). Now one material system can differ from another only in the configuration and motion which it has at a given instant. To explain differences of function and development of a germ without assuming differences of structure is, therefore, to admit that the properties of a germ are not those of a purely material system."— JAMES CLERK-MAXWELL, article Atom, *Encycl. Britan.*, 9th ed., vol. III, p. 42, 1878.

gave us a most ingenious physical hypothesis of the constitution of living matter. This, later on, he modified so as to develop an hypothesis of hereditary transmission. But the micellæ that were representative of the germinal matter of a species he isolated in the form of rows or chains of micellæ traversing the rest of the living substance of the organism, and called it *idioplasm*. Here again the germinal matter was conceived as separate from that forming the rest of the body. Mr. Spencer supposed "that sperm-cells and germ-cells are essentially nothing more than vehicles, in which are contained small groups of the physiological units in a fit state for obeying their proclivity towards the structural arrangement of the species they belong to." These "physiological units" are neither chemical nor morphological in character, according to Mr. Spencer's system, but it is admitted that their properties and powers must be determined in some way by their own constitution, conditions of aggregation, and relation to the outer world. The views of Nägeli and Spencer are akin in certain respects, but they still retain a certain amount of resemblance to the older ones, namely, those hypotheses which assume that the forces of inheritance are lodged in certain very small corpuscles forming part only of the germ or organism. These hypotheses are also dynamical in nature, and have been worked out with the consciousness, in both cases, that the mechanism of inheritance must also be the one through which metabolism operates. Indeed, these two authors seem to be the first to have distinctly recognized the necessity for such a supposition.

Later still, with the advent of the discovery that the male nucleus was fused with the female nucleus during sexual reproduction, it was assumed that the nuclear contents were the only essential material bearers of those hereditary forces that shape the growing germ into the likeness of the parentage. With the development of this idea the name of Weismann is perhaps most closely associated. He has utilized the facts of development, nuclear cleavage, expulsion of polar bodies, halving and subdivision of chromosomes, etc., as the foundation of his hypothesis of inheritance. Its extreme elaboration is its greatest weakness, and in it, no less than in all preceding hypotheses, the theory of a separate category of particles carrying hereditary potentialities again appears.

The one criticism that holds of all these hypotheses is that they are one-sided and ignore a most important set of factors in inheritance, namely, the purely statical ones, or those arising from the mere physical properties of the living matter of the germ viewed as if it were a dead, inert mass, subject to the operation of the reciprocal attraction for one another of its constituent particles. All of these hypotheses, moreover, assume that it is only *some* of the matter of the germ that is concerned in the process of hereditary transmission, and that the remainder may be regarded as passive. The entire germ, on the contrary, or all of it that undergoes development, must be considered as a single whole, made up of a vast number of molecules built up into a mechanism. Such a molecular mechanism, it must be supposed, cannot set free the potential energy of its parts except in a certain determinate order and way, within certain limits, in virtue of the initial physical structure of the whole. If the germ is free to do that, as must happen under proper conditions, as a mechanism, its parts, as they are thus formed by their own metabolism, it may be assumed, will inevitably and nearly recapitulate the ancestral development or that typical of the species. It must do this as a mere dynamical system or mechanism, the condition of which at one phase determines that of the next, and so on, to the completion of development.

In the present state of our knowledge we are not prepared to frame a purely mechanical hypothesis of inheritance that shall answer every requirement, in spite of the fact that no other is possible. Herbert Spencer and Professor Haeckel long ago pointed out that such an hypothesis is a necessity, growing out of the very requirements that must be satisfied in any attempt to coördinate the phenomena of biology with those of the not-living world. The material basis of life is always a chemically and mechanically compounded substance. To the very last molecule, such a body must betray evidence of arrangement or structure of its parts that should make it a mechanism of the utmost complexity and requisite potentiality as a transformer of energy through the mere transposition and rearrangement of such parts. We find indeed that living matter is chemically the most complex and unstable substance known. It is composed largely of carbon, a quadrivalent element that stands alone in its power to combine with itself and at the same time hold in chemical bondage groups of atoms representing other chemical bodies. Such groups are probably held together in great numbers metamerically by the reciprocal or otherwise unsatisfied affinities of the large number of carbon atoms entering into the composition of the proteid molecule. In this way the massive and structurally complex molecule of protoplasm may be supposed to have arisen. We may thus trace the genesis of the peculiarities of living matter to this singular property of the carbon atom. On such a basis we may suppose that the ultimate molecular units are identical with the physiological units, so that their structures may not only determine the nature of the metabolism they can undergo but also be the ultimate units of form or morphological character.

What especially gives color to these suspicions is the extraordinary variety of changes, alteration of properties or powers, and the vast variety of living matter, as represented by the million or more of known distinct living species of organisms. It is as if the permutations, transformations, and the dynamical readjustment of the metameres of the molecules of living matter were the source of its varying potentialities as manifested in its protean changes of specific form and function. That some mechanical, and consequently dynamical interpretation of these transformations may yet be forthcoming is, I take it, distinctly foreshadowed by the advances in the newer theories of stereochemistry developed by LeBel and Van't Hoff. If this is the case we may yet hope for a mechanical and dynamical explanation of the phenomena of life and inheritance. Especially is this true if we further suppose that the large molecules of living plasma are rather feebly held together by a force almost of the nature of cohesion. We may be permitted thus to find an explanation of that phenomenon which is always so characteristic of living matter, namely, the large and relatively fixed amount of water it contains, and also the mobility of its molecules in respect to one another; its jelly-like character at one instant; its fluidity and power of motion at another. It is indeed probable that the amount of water contained in living matter is controlled within certain limits by the forces of cohesion exerted between adjacent molecules against the osmotic pressure or capillary action of water tending to drive them asunder, as supposed by Nägeli, in his hypothesis of micellæ. Such an hypothesis enables us to explain much that is otherwise quite unintelligible in relation to living things. It renders us an explanation of amoeboid motion, of the surface tensions of protoplasm and lastly of metabolism itself through osmosis and the specific characters of the chemical transformations that must take place in each kind of living substance.

Such an hypothesis may also afford us mechanical constructions of atoms, grouped into very large metameric or polymeric molecules of the utmost diversity of powers, capable of undergoing a long series of successive transformations, so as to manifest in the long run, starting with a molecular germinal aggregate, what we call ontogeny or development. These transformations, we must suppose, are effected by the metabolism incident to growth, and moreover, that starting with an initial configuration of a system of molecules, as a mechanical and consequently a dynamical system of determinate powers, in the form of a germ, it cannot undergo any other transformations except such as lead to an approximate recapitulation of the ancestral development or phylogeny. This supposition follows from the rule that must hold of determinate systems of molecules, as well as of systems formed of larger masses, namely, that the initial changes in the configuration of such a complex system must dynamically determine within certain variable limits, under changing conditions, the nature of all of its subsequent transformations, including those due to growth and consequently increased complexity. We thus escape the necessity of invoking certain "proclivities" of physiological units, or the necessity of appealing to the growth and fission of "biophors" or the scattering of "determinants" at the proper times and places in the course of development. We thus escape, too, the mistake of assuming that a part of a germ controls the whole, a proposition that has been so long advocated by one school of biologists that it is astounding that its fallacy has not long since been more generally understood. Such a doctrine is not credible in the face of the fact that we know of no development except that which takes place in intimate association with cytoplasm, which seems to be the principal theater of metabolism and growth. We cannot conceive of the transformations of a germ without considering the metabolism of all its parts, such as nucleus, cytoplasm, centrosomes, archoplasm, chromatin, spindles, astral figures, microsomata, etc. "Tendencies" and "proclivities" are words that have no legitimate place in the discussion of the data of biology any more than they have in natural philosophy or physics. Karyokinesis, now admittedly inseparable in thought from the idea of multicellular development, is a rhythmical process so complex in its dynamical aspects as to some extent lead one unwittingly to underestimate the absolute continuity of the accompanying processes of metabolism. But that is no reason why the importance of nuclear metamorphosis should be exaggerated at the expense of the far more important forces developed by metabolism and growth. In fact the "ids," "idants," etc., of that school of biologists are not causes but mere effects, produced as passing shadows, so to speak, in the operation of the perfectly continuous processes of metabolism incident to development. Reciprocal relations are sustained between nucleus and cytoplasm of such importance that the transformation or fission of the one is impossible without the other.

The so-called "reducing divisions" probably have nothing but a passing and purely adaptive physiological significance in every ontogeny of ova and sperms. The far-fetched and extraordinary teleological significance given by some to the reducing divisions, would lead one to suppose that the clairvoyant wisdom of the original egg that thus first threw out the excess of its ancestral "germ-plasm" in order to save its posterity from harm through the fatality of reversion thus entailed, was greater than anything human, if not god-like. The complete parallelism of the "reducing division" in the sperm and egg has never been established. The comparison of these processes in the two is still only approximate, because in the truly holoblastic egg there is, in some cases, an apparent temporary substitution of the male nucleus for the female, as is shown by the former's assuming a position of equilibrium at the center of the ovum (*Ascaris*), a condition of things that does not and could not occur in the sperm cell.

A still more important contrast is the almost incredible difference of volume of the two kinds of sex-cells of the same species. In man, the ratio of volume of the male cell to the female is as 1 to 3,000 approximately. This extreme contrast of volume is associated with corresponding contrasts in their properties. There can hardly be any doubt that the mature male cell is in a nearly potential or static state of metabolic transformation of its substance, and is characterized by an almost complete want of stored metabolizable reserve material. The egg is in a similar static state, but, on the other hand, contrasts with the male element in that the development of a more or less voluminous mass of reserve material within it has seemingly been also associated with its loss, as a rule, of the power to begin an independent development. The power of the male cell to begin its transformation and growth through metabolism appears to be arrested until it finds the material in which its mere presence will set up transformations. This it must do by in some way setting free and diffusing some of its own molecules osmotically and mechanically through the egg. The substance of the egg appears therefore to be complementary to that of the spermatozoön. The power to set up transformations within the egg leading to the development of a new being is not manifested aside from the presence of the male element except in cases of parthenogenesis. Even the expulsion of the polar cells is not initiated until the stimulus of the presence of the male element is experienced by the egg.

Another contrast is found in the times of the advent of the "reducing division" in the two kinds of sex-cells. In the male cell the "reducing division" occurs earliest, or while it is still in more or less close nutritive relation to the parent; in the egg the "reducing division" or expulsion of polar cells does not occur till the egg is freed, as a rule, from the parent gonad, and generally as a consequence of the stimulating effect of the presence of the male cell. These differences of behavior of the two sorts of sex-cells seem to be correlated with their differences in size.

We may contemplate the sex-cells as molecular mechanisms which, in virtue of their mechanical structure, are rendered capable of controlling the order and manner of rearrangement of their constituent molecules, because of the new successive attractions and repulsions set free, amongst the latter, immediately upon the completion of conjugation. The new forms of metabolism thus initiated enable us to conceive a mechanical theory of fertilization. At any rate, the two sorts of sex-cells are potentially the reciprocals of each other, and their initial or *statical* states cannot begin to set free their energy and thus pass into the successive kinetic states of formal change until the two mechanisms are reciprocally and mechanically integrated into a single one by means of conjugation. The parts of this new single body now act in unison. Even the manner in which the two conjoined molecular mechanisms operate can actually be to some extent traced, as expressed in the complex movements associated with fertilization, the division of the chromosomes and centrosomes. The effect of conjugation is to afford opportunity also for new and various combinations of molecular mechanisms, through the reciprocal integration of pairs of cells having a widely different parentage.

The great size of the egg-cell provides an extensive reserve material, that enables the embryo thus built up usually to reach a relatively great size without entering for a time into competition for food in the struggle for existence. Sexuality is therefore altruistic in nature, since it has led in both plants and animals to the evolution of a condition of endowment, or the storage of potential energy in the germ, so that the latter is the better able to cope with natural conditions. While it may be assumed that sexuality has arisen, in the main, under conditions determined by natural selection, once sexuality was attained, the added power thus accumulated potentially in large germs of double origin enabled the latter the more easily to overcome untoward natural conditions. Natural selection thus becomes altruistic or dotational in that it tends through sexuality to defeat the deadliness of the struggle for existence, just as we may also assert that the theory of superposition to which the mechanical theory of development is committed is also finally altruistic. It may be remarked that the greatest mortality of a species, under the conditions of the struggle for existence, also takes place in the egg and embryonic stages, or before organisms can experience acute pain; so that here again we have a result that must materially ameliorate the pains and penalties of the struggle for life.

These details are, however, of minor import for us just now. The important thing to bear in mind is that all of the forces of development are ultimately metabolic in origin, and that the wonderful order and sequence of events in any given ontogeny arise from the transformation or transposition of the parts of a molecular system, that also thus increases in bulk by the addition of new matter. The steps of this transformation are mechanically conditioned by dynamical laws with as much unerring certainty of sequence as those that control the motions of the heavenly bodies. The consequence of such a view is that we can thus free our minds of all traces of belief in a theory of preformation. The embryo is not and cannot be preformed in the germ, as observation and physiological tests prove; nor is such a preformation necessary if a mechanical hypothesis is adopted.

The egg cannot be isotropic — as follows from observation as well as experiment — in the sense in which the word isotropy is used by physicists of repute. If the egg is a dynamical system it cannot be isotropic or absolutely the same throughout, or along every possible radius from its center, as is proved by its reactions in respect to its surroundings. It may, however, be potentially æolotropic in directions parallel to a certain axis, as experiment has shown by separating the cells that result from segmentation of the egg. Such fragments, if in excess of a certain minimal size, will undergo a larval development of apparently normal character. But this result is fatal to the ordinary corpuscular hypotheses, according to which every future part is represented in the chromosomes by certain hypothetical corpuscular germs. It has, indeed, been shown by Loeb that larval development of portions of an egg can go on whether the division be equal or unequal or in any radius. This seems to indicate that an egg is not necessarily isotropic in the undivided state, but that the moment that separation of its mass has occurred there is a readjustment of the relations and potentialities of its molecules simulating that of the original entire egg. The very definition of isotropy, as given by one author (Lord Kelvin), states that it may be assumed only of a spherical mass of matter whose properties are absolutely the same along every one of the infinite number of radii drawn from its center outward, and, as tested by any means whatsoever, shows that such a condition cannot be assumed, on the ground of observation alone, of any known egg. The condition of the egg we must therefore also assume from its known properties to be æolotropic, or different along every one of the infinite number of radii drawn from its center. When we make this assumption, however, we need not necessarily assume that nucleated fragments that will still develop into larvæ after division of the oösperm, natural or artificial, must be isotropic. They may be æolotropic from the beginning, but in precisely the same way in each case, as a result of the successive cleavages of the germ-mass, by means of planes that cut each other at right angles, as in the diagram Fig. 1, where each of the four segments are precisely alike from the pole *a* to that of *b*. The unlikeness of the pole *a* from *b* is indicated by the stippling. This unlikeness would manifestly be unimpaired by segmentation of the germ into four quadrants by the first two cleavages, as shown in the diagram. The same might hold of octants of the spherical germ. Here the initial æolotropy of the whole egg determines that of its segments; that must therefore become four or eight molecular

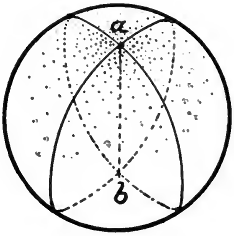

FIG. 1.

mechanisms, each with precisely the same type of potentiality as that of the whole egg. (See concluding note.)

There may, according to the foregoing view, be such a thing as perfect isotropy in every radius lying in a plane cutting the line from *a* to *b* at right angles. This would not, however, be the perfect isotropy of our definition, that we are compelled to accept in the form in which it comes to us from the physicist.

As development proceeds, moreover, we have reason to believe that this æolotropy becomes more and more marked, so that eventually the huge metameric molecules become arranged in definite linear, parallel systems, as in the axis cylinders of nerve cells and in muscular tissue. Here the characteristics of the system become the same in parallel lines, and in any directions at right angles to an axis parallel to these parallel lines of molecules. That is, in certain rectangular directions there is an approximation toward homogeneity. But the completest homogeneity is found to occur in only one direction in parallel lines extending through the mass. This condition we may designate as monotropy. Starting with the extreme æolotropic condition of the germ we must, therefore, assume that as organization becomes more and more complete, in the progress of development, in the specialized systems of tissues and organs, the molecules become more and more definitely monotropic. Therefore they at last become incapable, as dynamical systems, of exhibiting a complex development such as is manifested by a germ, but capable only of manifesting the special physiological functions entailed by their dynamically and mechanically evolved monotropism.

We can now understand why it is that the germinal matter of a species always remains in an æolotropic state. Since germinal matter is always relieved of specialized functions in the body of the parent, it must perforce remain in its primitive condition of germinal potentiality as a molecular mechanism. Since the germ is material that has been produced in excess of the needs of metabolism of the parent body, as supposed by Haeckel and Spencer, it can do no work for that body. The unbroken continuity of the processes of metabolism have provided the conditions for the continuous or interrupted production of germinal matter.

The nearest approach to a condition of continuity of germinal matter is found in the tissue of the "growing points" of plants, where, as in the banana, it has maintained its unabated vigor for probably not less than two thousand years without the help of sexual reproduction. In many organisms the germinal elements must grow and become mature. While in the immature state they do not, for the moment, have the latent potentiality of germs that can, then and there, develop, but may even be destroyed phagocytically, or absorbed by other non-germinal tissues. In still other cases there is no proof that the germinal matter is differentiated, as a complete mechanism, from the first stages of ontogeny onwards, so that the theory of its continuity is not only not always true but is also of small importance. At any rate, it is of far less importance than the fact of continuous metabolism and the gradual advent of monotropism, from a state of germinal æolotropism, effected by the dynamical processes of tissue metamorphosis and specialization.

This development of monotropism cannot take place except through the sorting and grouping of specialized molecules, under the domination of forces the operation of which remains to be discovered in the laws of physiological chemistry and molecular mechanics, and not by an appeal to an unworkable hypothesis that merely covers up our ignorance and impedes our progress by invoking the help of "gemmules" or "biophors" that grow and divide like cells. There is no evidence that will enable us to conceive the growth of the molecules of living matter in this way, since we are now dealing with very complex metameric molecular bodies, the growth and disintegration of which is probably essentially similar to the growth and solution of crystals, during the process of metabolism, with this difference that growth and disintegration go on at the same time in living bodies. We do not even know the real nature of the chemical changes that go on in these molecules and determine their structure. That the forces that do determine this are of a chemical nature, operating under very peculiar conditions, we may be certain. The complexity of these bodies, and their complex relations to one another, give us all the mechanism we need in order to account for the phenomena of heredity.

One-half, or one-quarter, or an uneven part of the oösperm (Loeb) will operate in the same way as the whole. If we accept the dynamical hypothesis here proposed we are relieved of going to the length of the absurdity of assuming that by dividing a germ we multiply its "biophors" as many times by two as we have made divisions, or of postulating "double," or "quadruple determinants." The arithmetical impossibility of multiplying by a process of division is, as we see in this case, too much for any non-dynamical corpuscular hypothesis. Where the division of the germ is unequal, as in some of Loeb's experiments, we should, on the basis of a preformation hypothesis, be compelled to suppose that the "double determinants" were unequally divided.

Regeneration is also to be explained upon the basis of a dynamical theory, as well as polymorphism, alternation of generations, reversion, and so on. We find indeed that it is only the same kind of tissue that will regenerate the same sort after development has advanced a considerable way. Monotropism has been attained by each kind of tissue, and this prevents the production of anything else but the one sort, in each case, after tissue differentiation has proceeded a little way. Polymorphic or metagenetic forms are to be accounted for in the same way as constantly repeated ones. Like the latter they are produced by the operation of a molecular mechanism, the story of the transformations of which is not told off in a single generation but in the course of several distinct ones. Sex itself is thus determined and must in some way depend upon subtle disturbances of the transformation of the molecular mechanism of the germ, the nature of which is still quite unknown to us.

Equally remarkable are the phenomena of heteromorphosis described by Loeb, whose experiments prove that some animals, like most vegetable organisms, may adjust the molecular machinery of their organization in any new direction whatever that may be arbitrarily chosen, so as to realize the continuance by growth of the same morphological result as that which characterized them normally. These experiments would at first thought seem to prove that some organisms were isotropic, but such a conclusion is exceedingly doubtful. It may be that such organisms are, as molecular mechanisms, when subjected to new geotropic and heliotropic conditions, capable of correspondingly new adjustments of their molecular mechanical structure. But this would not be proof of isotropy; only proof of the assumption of a new condition of æolotropy, adjusted in respect to a new axis of reference, that also coincides with some part of the earth's radius prolonged into space. This readjustment of the molecular mechanism may be effected in some way by gravity, as Loeb himself has suspected. It is certainly not due to the control of any lurking "biophors," since it is a purely mechanical readjustment of an ultramicroscopic structure to new conditions which cannot be effected in any other than a mechanical way.

The production of monstrosities also may be explained by a dynamical hypothesis, provided we assume that the forces of ontogeny must operate against the statical equilibrium of the parts of the germ at every step. Especially if we assume in addition, as is borne out by facts, that the æolotropy and consequent recapitulative power of the germinal substance is most marked in certain regions of the embryo. These regions, if their molecular equilibrium be mechanically or otherwise disturbed by division during development, will assert their germinal potentiality and produce an embryo, the relations of which to that already formed alongside of it will be modified by the statical conditions of surface-tension afforded by the adjacent embryo, or the underlying yolk, or by both combined. This is beautifully illustrated by a host of facts. Double toes must have so arisen, as is proved by the direct experiments of Barfurth, some of which I have repeated, as well as by what happens when the toes of an Axolotl are persistently nibbled off by another animal, when duplication may not only take place in the horizontal plane of the foot or hand but also in the vertical one. In this way a number of supernumerary toes may be caused to arise from a single stump, provided the regrowth of the toe be so interfered with as to compel regeneration from two terminal regenerative surfaces instead of one. This must follow from the law demonstrated by Barfurth's experiments, namely, that the regeneration of an organ tends to occur uniformly over and in a direction normal to the regenerating surface. In this way it is possible to mechanically determine the direction in which a regenerated part shall be reproduced by merely making changes in the angular relations of the plane of the regenerating surface to that of the axis of

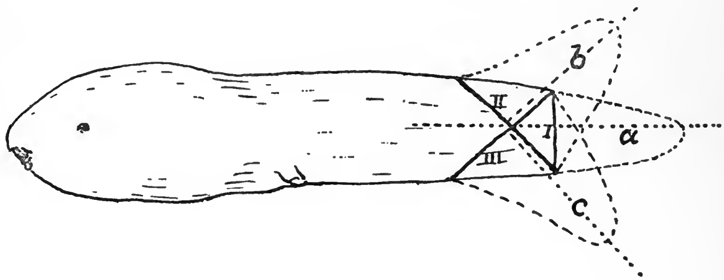

Fig. 2.

the body, as indicated by the diagram in Fig. 2 of the regenerated tail of a tadpole. Here the line I indicates the plane along which the tail has been removed, upon which regeneration will restore the tail straight backward to the dotted area *a*. If the plane of section is along the line II the tail will regenerate upward so as to be restored over the area indicated by the dotted line enclosing *b*. If the plane of section of the tail be along III the tail will be regenerated downward to the dotted line enclosing the area *c*. It is therefore evident that Barfurth's law determines the inclination of the axis of the regenerated part to the body-axis, through the different conditions of surface-tension that must be set up over regenerating surfaces, whenever the inclination of these to the axis of the whole organism is changed.

New equilibria of surface-tension established reciprocally between the cohering but independently developing segments of the oösperm of the sea-urchin, that have been imperfectly separated by mechanical or other means, also cause changes to be produced in the forms of the single larvæ of such coherent groups, and in the spicular skeleton, for the same reason, as is proved by Figs. 23 to 25 given by Professor Loeb.[1] Those figures also illustrate the thesis that the æolotropy of the distinctly developing segments of the egg must be nearly the same, and that component or resultant equipotential surfaces are developed by the interacting molecular machinery of such coherently developing or compound larvæ.

The angular divergence of duplicated tails and toes as well as the axes of monstrous embryos is explained by Barfurth's discovery, taken together with the principle that division of a germ does not change the æolotropy of its segments. If this interpretation is the correct one, the origin of supernumerary digits must be traced back to mechanical disturbances of the processes of ontogeny. The rationale of the manner in which divergent supernumerary toes may be produced is shown in Fig. 3, representing the regenerating toes of the foot of a salamander.

If the toes were cut straight across at the points I, II, III, IIII, the toes would regenerate normally. If, however, the regenerating surfaces were divided into two areas in each case by a line along which regeneration were prevented, two toes would arise from each surface. The angular divergence of the pairs of supernumerary toes thus produced would be measured by the angular inclination to one another of the two areas at the end of each original toe that was thus doubly regenerated. In other words, supernumerary digits are the results directly or indirectly of something akin to mutilations. That such duplications may be produced by mutilations there can be no doubt,

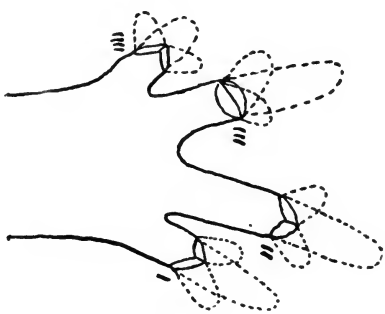

Fig. 3.

[1] *Biological Lectures* (No. III). Delivered at Woods Holl, Mass., in 1893. Ginn & Co., Boston.

and of their transmission by inheritance to offspring there is also no doubt. These facts make it probable at any rate that regeneration of distal parts and the likelihood with which they reappear in duplicate, is due to causes similar or identical in character with those that lead to the production of double monsters, by shaking, mutilation or other physical interference with the normal development of the oösperm. The question of the inheritance of mutilations is consequently far from being concluded as viewed from this new standpoint. Much evidence might be adduced in support of my contention did space allow. The hereditary transmission of such monstrosities as supernumerary digits is well known, and it is a singular fact that it is only the outer digits, *i.e.*, minimus and pollex, or hallux, or those most exposed to the liability of injury during development that are, as a rule, duplicated. If the foregoing view is correct, the origin of supernumerary digits is not always to be ascribed to reversion. It must not be understood, however, that the theory is here defended that mutilations effected after adolescence is reached are likely to be transmitted.

The "mutilations" here referred to are hardly to be regarded as such, but rather as the results of mechanical interference or disturbance of the statical equilibrium of those parts of the developing germ that are duplicated, as we see, in obedience to the principle discovered by Barfurth.

Another dynamical factor in development is so generally ignored that it must be especially referred to here. I now refer to the statical properties of the germinal substance in modifying development. Some of its effects we have already taken note of above. Karyokinesis has been shown by Hertwig to be dominated by the principle that the plane of division of a cell is always at right angles to its greatest dimension, a fact readily verified. The greatest dimension of the cell in turn is also often, if not usually, determined by the conditions of free and interfacial surface-tension manifested between the members of a cellular aggregate composing a segmenting egg. This appears to have a determining effect upon the plan of the cleavage. How far and in what way the remarkable movements of the centrosomes that occur during cleavage, and that have been most exhaustively studied by Professor E. G. Conklin, regulate segmentation, still remains to be determined. There can, however, be but one explanation of such movements, and that must be a mechanical one, but its nature is entirely unknown. Wilson has shown that the conditions of free and interfacial surface-tension in Amphioxus vary in different eggs from some unexplained cause, so that the earlier cleavages of this form also vary to a corresponding and remarkable degree. In other cases surface-tensional forces operate under similar recurring conditions. In the fish-egg I have witnessed the reappearance of the same or similar interplay of statical energies thrice in succession, so as to produce three similar successive sets of formal changes in the egg that are traceable to the action of similar statical agencies. In *A*, Fig. 4, the

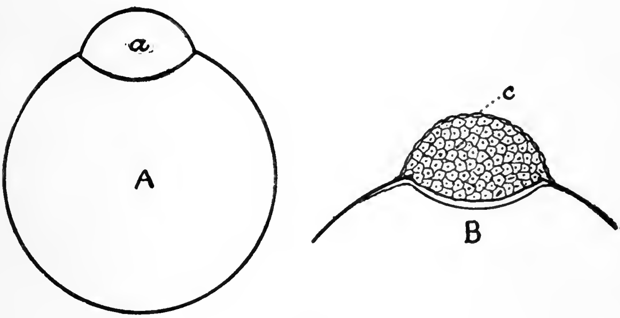

FIG. 4.

germ *a* has assumed a lenticular form of statical equilibrium; after segmentation of the same disk has proceeded some way, as in *B*, the disk, as a cellular aggregate, has again assumed the lenticular form of equilibrium, while the outermost row of cells, *c*, are individually in a similar condition of equilibrium.

These facts are quite sufficient to establish the general truth of the statement that at no stage is the ontogeny of a species exempt from the modifying effect of the surface-tensions of its own plasma acting between the cells as if they were so much viscous dead matter. Such statical effects are not overcome at any stage of the development, or even during the life of any organism. On account of the universal presence and effect of this factor in both the plant and animal worlds, as a modifier of form, we are obliged to consider it as an agent of the first importance in the possible development of the future science of exact dynamical morphology. Its action is so constant an accompaniment of development that the forces of the latter may be divided into the kinetogenetic, or those that develop movement, and the statogenetic, or those that develop rest or equilibria amongst the parts of the germ. The kinetogenetic forces are the consequences of metabolism, but the statogenetic forces, though dependent upon metabolism, are produced as a consequence rather of the interaction of the surface layers of the plasma of the cells, contemplated as if they were small cohering masses of viscous dead matter. These masses are separated, in the organism or germ, by interfacial planes, free and interfacial curved surfaces that are the results of segmentation and growth, and the extent of the areas of which obey a law first pointed out in relation to soap-bubbles by the blind physicist Plateau, who showed that such bubbles tended to form interfacial films and surfaces wherever in contact with each other, of an area that was the minimal consistent with their statical equilibrium.[1] In this connection it may also be remarked that, inasmuch as the cells of a germ or organism are always in statical equilibrium, their surface layers of molecules also always represent complex systems of equipotential surfaces, no matter how intricate the form of the organism may be. Since the equilibria between the molecules of the surface layers of cells can normally be disturbed only by the metabolism incident to physiological activity, it is evident that the figure of the organism must ultimately be ascribed to the action of metabolism or to the functions of the organism as affecting the physical properties of its plasma.

A statical equilibrium in a living cell may be one in which it is not in contact with others at any point on its surface, as in the case of blood-corpuscles or disks. Or a cell may be greatly extended in one direction, as in the case of the axis-

[1] Some interesting applications of the geometrical theory of radical axes and centers also apply here that have never been studied in connection with the phenomena of segmentation.

cylinder of a nerve-cell, owing to very unequal surface-tensions developed in one or more directions so as to draw it out into a condition of equilibrium, in assuming which it acquires a great length. Formal changes in cells, no matter how irregular these may become, must be due to alterations of surface-tension due to molecular transformations at certain points on the surface of globular or polyhedral embryonic cells. The final mature form of a cell is a consequence of the assumption of a statical equilibrium amongst its parts, due to the nature of its metabolism and its consequent molecular structure. The statogenetic factors of development are therefore of just as much importance as the kinetogenetic, or those involving motion. The statical forces that are developed in individual cells also act reciprocally between all of the cells of the organism, so that in this way the effect of statogeny extends throughout the entire organism.

If there were no such statical forces to be overridden by the purely kinetic ones developed by the molecular transformations and consequent motions incident to metabolism, provided the latter, together with assimilation, took place, during development, with great rapidity, the ontogeny of an organism would take place with such swiftness that it could not be successfully studied by embryologists. In other words, ontogeny would take place in the twinkling of an eye, and organisms as large as whales might even mature in an instant, provided the coefficients of viscosity and surface-tension of their plasma were to fall nearly to zero, while assimilation and metabolism proceeded with infinite rapidity.

It follows also from what has preceded that we can now form some idea why apparent rejuvenescence occurs in every ontogeny. Every germ must, for assignable reasons, begin its existence in the original, highly complex, æolotropic condition of the plasma of its species. It must therefore begin its career somewhat in the guise of the mechanically unspecialized plasma of a remote unicellular ancestor. Unlike that ancestor, however, the cells that result from its growth and segmentation cohere until a multicellular aggregate results, the different regions of which fall into certain statical states in relation to one another and to the earth's center, in virtue of the action of the forces of cohesion, friction, gravitation, etc. The different regions of such an aggregate now adjust themselves to the surroundings in such a way that nearly constant effects of light, heat, etc., begin to control or affect the functions of such an aggregate dynamically through its metabolism. Function, thus conditioned, asserts itself under the stress of mechanical adaptation or adjustment that becomes increasingly complex with every advance in ontogeny. Every step in ontogeny becomes mechanically adaptive and determinative of the next. It is thus only that we can understand the wonderful molecular sorting process that goes on in ontogeny, for which others have invoked infinite multitudes of needless "gemmules," "biophors" and "determinants."

It is the whole organism that develops in continuity or coördination; not its nuclei, centrosomes, and asters only. The whole organism, molecularly considered, is as fixed and immutable, within variable limits, as a crystal. Its development, moreover, becomes intelligible only if we contemplate its ontogeny somewhat as we would the growth of a crystal, with the additional supposition that its growth is not conditioned by forces operating along straight lines having a constant angular divergence as in the latter. On the contrary, living matter is capable of developing curved bounding surfaces in consequence of the permanently mobile nature and cohesion of its molecules, that, as a complex dynamical mechanism, can operate so as to tell off the tale of its transformation in but one way, in consequence of the order and way in which the energy of its constituent molecules is set free during ontogeny. Upon the completion of ontogeny a phase is reached in which the income and outgo of metabolism is in equilibrium. The duration of life depends upon the length of time that this equilibrium can be maintained without fatal impairment of the harmonious operation of its mechanism under the stress of the dynamical conditions of life. This may be considered the cause of death, so that the length of the life of the individual is determined by the possible number of harmonious molecular transformations of which its plasma is capable as a mechanism.

The doctrine that cells undergo differentiation in relation to other adjacent cells, or that the destiny of a cell is a function of its position (Driesch), is no doubt true. Nevertheless, we have in organisms machines of such complexity, dynamical potentiality, and power of transformation, that in comparison a study of the theories of crystallography is simplicity itself. In organisms we have the polarities of head and tail, stem and root, right, left, dorsal, and ventral aspects, as definitely marked out as are the relations of the axes of crystals. In the organism, we have diffuse, intussusceptional growth in three dimensions, by means of the osmotic interpolation of new molecules, whereas, in the crystal, growth is superficial, but consequently also tri-dimensional. In the organism the molecules are mobile within limits; in the crystal they are fixed. Nevertheless, we may justly regard organisms as developing after the manner of crystals, but with the power of very gradually varying their forms by means of variation in the structure, forms, and powers of their constituent molecules, in the course of many generations of individuals.

This variation may be directed by the concurrence of a series of natural conditions operating dynamically (natural selection). Or, interbreeding and crossing, with care or under Nature, may unite by means of reciprocal integration — (fertilization) — two molecular mechanisms whose total structure and sum when thus united, as in sexual reproduction, may vary by the mere combination of the two dynamical systems (egg and sperm), differing slightly from one another in potentiality. Finally, adaptive changes may be called forth dynamically in the internal structure of such developing reciprocally integrated systems that must be traced back to changes in the mechanism of metabolism of the parent as well as in the germs it gives off. Such changes produced in the germ must become visible in the effects they produce, as transmitted formal changes exhibited in the course of development.

The tendency or trend of development, however, of a given form must be pretty constant, and controlled within comparatively narrow limits by the initial adult or attained structure. That is, what has been attained must formally affect that which is to be attained in future. This is the idea that underlies the *Vervollkommnungs-Princip*, principle of perfecting, of Nägeli. This view also tacitly recognizes the theory of change of function proposed by Dohrn, as well as the theories of substitution, superposition, and epimorphosis of Kleinenberg, Spencer, and Haacke. Once a condition of stable equilibrium has been reached in the series of transformation of the molecular mechanism represented by the germ, during the development of an organism, we may have what Eimer has called *Genepistasis*, resulting in the fixity or stability of an organic species, under stable conditions.

The cell is a complete organism, but it loses its physiological and morphological autonomy when combined with other cells. We may regard the nucleus, cytoplasm, and centrosome as reciprocally related parts; one of them not much more important than the others. The observed behavior of the centrosome would indicate, as Verworn has held, that it is the important agent in cellular metabolism. If this is true, metabolism has certain centers in the cell to and from which molecular transformations are effected rhythmically in every direction, with the centrosomes as focal points. This view agrees perfectly with the facts, since the rays of the asters may be regarded as the morphological expression of a dynamical process of intermolecular diffusion due to metabolism, as Kölliker has suspected (*Gewebelehre*, 6th ed.).

Such a process would not only serve to alter the surface and interfacial-tensions of the cells during ontogeny, but also vary the osmotic pressure within them. Consequently, we may conceive that all of the phenomena of development, including the appearance and disappearance of cavities within a germ by changing conditions of osmosis, may receive a dynamical explanation. The centrosomes may, moreover, be conceived to lie at the foci of very complex material figures, the boundaries of which are finite equipotential cellular surfaces. These focal points are clearly near or within the nuclei. The equipotential surfaces developed by the sorting or readjusting process that goes on during segmentation in order continually and rhythmically to restore the dynamical equilibrium of the molecular germinal aggregate as a mechanically constructed system during life and development, through growth and metabolism, must maintain the shapes of organisms as we see them. The epigenetic theory of inheritance therefore promises us a secure basis upon which to found a theory of the mechanics of development, as well as a theory of the origin of morphological types. The theory of life may indeed be regarded as having its foundations in cellular, inter- and intra-cellular mechanics and dynamics as conditioned by ontogenetic metabolism. The fact that centrosome, nucleus, and cytoplasm are represented almost coextensively with the presence of life itself is proof that the fundamental machinery of organization must be the same in the principles of its action, no matter how widely its forms may differ from one another.

The theory that the surface layer of molecules of organisms, whether interior or exterior, are in equilibrium also carries with it the idea that the configuration of all organs and organisms are merely the material expression of gradually built up equipotential surfaces. This gives us a far more rational foundation for a theory of general morphology than the hypothesis of gemmaria proposed by Haacke. During growth and metamorphosis these equipotential surfaces undergo formal changes in size and shape, due to the internal processes of molecular transformation or metabolism. But such changes are continuous, and one stage or form passes into the next palpable one through an infinite number of slightly different forms. Examples of such surfaces may be seen in any organism, vegetable or animal, and at any stage of the same. The principle is therefore of universal application.

SUMMARY. — Preformation of any organism in the germ has no foundation in fact.

All that it is possible to account for upon the basis of a theory of preformation may be much more logically and scientifically accounted for upon the ground of dynamical theory. Such a theory must deny the existence of separate corpuscles or gemmules of any sort in the germ, whose business it is to control development. All that is required is the assumption of a determinate ultra-microscopic molecular mechanism, the initial structure of which determines all of its subsequent transformations. The present theory also denies that there is or can be anything passive in the germ that enters into its composition.

A dynamical hypothesis of inheritance is correlated with all the facts of physiology. It is in harmony with the dynamical theory of sex, that sees only in sexuality the means developed by another dynamical process (natural selection) that increases the powers of a compound germ to survive and vary. It is consistent with the facts of morphological super-position, with the dynamical theory of the limit of growth, and duration of life of organic species. It is also consistent with the view that the initial or potential states of the germs of species are those that must result whenever they are relieved from physiological service to the parent organism. The apparent continuity of germ plasm is, in many cases, only an effect of the equilibration of the forces of the organism, and has no further significance. It must also deny any assumed isotropy of the germ as inconsistent with fact. It assumes that the æolotropy of the molecular structure of the germ is followed by a gradually increasing simplification of molecular structure of organs as these are built up. Metabolism is assumed to be the sole agent in effecting the mechanical and dynamical rearrangement or sorting of the molecules into organs during development. Specially endowed corpuscles or "biophors" are not only needless as conditioning form or function, but also out of the question, dynamically considered. No creature can be supposed to have its life or germinal properties associated only with certain corpuscles within it, since we cannot suppose an organized whole dominated by a portion of it; it is not possible, for example, to conceive of individual life except from the entire organism that manifests it. There can be no "biophors" — bearers of life — the whole organism must do that as an indivisible unit. Corpuscular doctrines of inheritance are merely a survival in philosophical hypothesis of a pre-Aristotelian *deus ex machina*. The dynamical hypothesis rejects the *deus ex machina*, but finds a real mechanism in the germ that is an automaton, but that is such only in virtue of its structure and the potential energy stored up within it. Every step in the transformation of such a mechanism is mechanically conditioned within limits by what has preceded it, and which in turn so conditions, within limits, what is to follow, and so on forever through a succession of descendants. The theory of equipotential surfaces, as here applied to organisms, leads to a theory of general morphology that holds of all living forms, and that is at the same time consistent with the facts of development.

EXPLANATORY NOTE TO PARAGRAPH CLOSING AT TOP OF PAGE 38.

It now appears that the statement that the quarters or eighths of an oösperm are to be regarded as "molecular mechanisms of precisely the same type of potentiality" as the whole egg, must be taken with considerable qualification. Loeb (Ueber die Grenzen der Theilbarkeit der Eisubstanz, *Archiv für Ges. Physiologie*, vol. LIX, 1894) has shown that the eggs of echinoderms, if artificially divided, by means of a method of his devising, into quarters or eighths, lose the power of developing beyond the blastula stage. This would appear to indicate that if the egg is subdivided so as to have its parts fall below a certain size, these parts no longer have locked up within them, as molecular mechanisms, as Loeb points out, enough potential energy to transform themselves into completely equipped larvæ. Or, perhaps, the initial æolotropy of the egg does not permit of its subdivision into quarters and eighths without impairing their structure and powers of development.

My own recent experiments have shown that it is possible to incubate for some time the germ of the bird's egg outside of the egg-shell in a covered glass-dish. These experiments also show that restraints to growth developed by the drying of a film of albumen over the germ causes it to be most extraordinarily folded, with many abnormal tumor-like growths from both entoderm and ectoderm, that differ, however, in histological character from the cells of both these layers. These experiments also prove that it is possible to mechanically divide the germ of the warm-blooded Avian type into halves or quarters, and to have these continue to develop for a time.

The converse of the process of mechanical division of the germ we have in Born's remarkable experiments in cutting recently-hatched Amphibian embryos in two, and placing the separated halves again in contact under such conditions as to cause them to grow together, or even to thus graft the half of a larva of one species upon that of another. That such grafting is possible, I can testify, as a result of a repetition of some of the experiments. See Born's paper in *Schlesischen Gesellsch. f. väterländische Cultur: Medicinische Section*, 1894, pp. 13. Supplementing Born's results are Roux's experiments on *cytotropism*, or the reciprocal attraction of isolated blastomeres of Amphibian eggs (*Archiv f. Entwickelungsmechanik*, I, 1894) if brought close together, though at first not in actual contact. There is also some evidence of asexual *caryotropism* as witnessed in the conjugating nuclei of the cells of the intestinal epithelium of land-Isopods (Ryder and Pennington, *Anat. Anzeiger*, 1894).

The experiments of O. Schultze (*Anat. Anzeiger*, Ergänzungsheft zum Bd. IX, pp. 117–132, 1894) by very slowly rotating in a mechanically fixed position the segmenting eggs of Amphibians on a specially constructed clinostat, with the result of disorganizing and killing them, shows that such eggs are not isotropic. His production of double monsters in such ova by disturbing, for a time, their geotropic relations, is also significant, while his conversion of the meroblastic amphibian egg into a holoblastic, evenly segmenting one by merely rotating it through 180° out of its normal geotropic relation, and allowing it to complete its segmentation in an inverted position, proves that the egg can be made structurally homogeneous by mere mechanical means, but at the expense of its power to complete its development. This is further proof that the egg is not isotropic in the sense in which that word is used by natural philosophers.

Since the appearance of the short but important paper by Prof. E. B. Wilson and A. P. Mathews (*Jour. of Morphology*, vol. X, no. 1, 1895), in which they deny the existence of the centrosome, it becomes necessary for me to explain that the word "centrosome" is used in the text in the sense in which they use the expression "attraction spheres." Their discovery that the ovocenter, or attraction sphere of the egg, disappears after the expulsion of the two polar cells in echinoderm eggs, to be replaced by the spermcenter, is of the greatest significance, and may explain the reason why parthenogenetic eggs develop, namely, as a consequence of their retention of an ovocenter. The new facts that these two able workers have disclosed are entirely in harmony with a dynamical theory of fertilization and sex (see p. 34, and farther, of the text).

THIRD LECTURE.

ON THE LIMITS OF DIVISIBILITY OF LIVING MATTER.

JACQUES LOEB.

1. If Physiology is to become a rational science in the same sense in which Physics deserves this name, one of the fundamental problems to be solved is to determine how far the divisibility of living matter goes, and what is the nature of its ultimate elements. On the qualitative side of this question attempts in that line were made simultaneously by Nussbaum and Gruber. Nussbaum found that when he divided an infusorian, only such pieces as contained nuclear substance were able to regenerate the lost parts. "For the preservation of an infusorian, it makes no difference how it is divided; if only the nuclear substance of the piece remains, it regains its original form within twenty-four hours at the most, the length of time required depending upon the temperature." "No growth is possible in a piece which contains no nucleus. But such a piece can retain its contractility — it can move." Among the conclusions at which Nussbaum arrives, the following is of most interest to us: "The cell is not the last physiological unit, although it must remain such for the morphologist. We are, however, not yet able to tell how far the divisibility of a cell goes, and how we can determine the limit theoretically. For the present it will be well not to apply to living matter the notions atom and molecule, which are well defined in Physics and Chemistry. The notion micella, introduced by Nägeli, will also lead to difficulties, as the properties of living matter are based upon both nucleus and protoplasm." "The cell always consists of an aggregate of individuals which are similar one to another in Protozoa." In a very interesting

paper Whitman has shown that from the standpoint of the morphologist it would be equally erroneous to consider the cell as the ultimate unit of living matter.

2. In the experiments of Nussbaum, Gruber, and those who followed them, only the qualitative side of our question has been touched, in so far as they all tried to prove that neither the nucleus without protoplasm nor the protoplasm without nucleus can show phenomena of growth and regeneration.

But there is a quantitative side of the problem, that is to determine the limits of divisibility of living matter and the order of magnitude of the smallest particle that can show all the phenomena of life. Is such a particle of the magnitude of a giant molecule of proteid substance, or of a micella, or a combination of several micellae, or does it approach the magnitude of a cell? If we undertake to get an answer to this question from the egg, we have to determine what is the size of the smallest portion of an egg which, if isolated, is able to undergo normal development. I think we may take it for granted that phenomena of development include all other functions of living matter. Two methods by which the answers to these questions might be obtained presented themselves. The first method depends upon the fact that the ovum is divided by segmentation into a continually increasing number of cells which decrease correspondingly in size. We might isolate a cell in different stages of the segmentation and see what is the last stage from which a single cell can develop into a normal embryo. Such experiments have been made for another purpose by Roux, Chabry, Driesch, Wilson, Hertwig, and others. Driesch found that a single cell from the four-cell stage of a sea-urchin's egg could still develop into a full embryo, but that with one from the eight-cell stage development was apparently no longer possible. But this method is not suited to give us a reliable answer to our question, as we do not yet know whether an isolated cell in the eight-cell stage of an embryo is identical with the eighth part of an ovum before segmentation. It is at least possible that the ovum during segmentation is divided up into cells or regions of chemically diverse materials. It is further possible that the metabolic processes transform the material of the different cleavage cells unequally during segmentation. The consequence might be that an isolated cell of the eight-cell stage could no longer develop into a perfect embryo, while the eighth part of the same ovum before segmentation was potentially able to produce a whole embryo. Therefore the method of isolating a cell of the segmented egg could not be relied upon for our purpose. The second method is one that I described in the Biological Lectures of last year, and is as follows: The eggs of sea-urchins were brought into sea-water that had been diluted by the addition of about one hundred per cent of distilled water. The contents of the egg took up water very rapidly, and the thin membrane of the ovum burst in one or more places. The protoplasm which escaped from the opening thus made assumed the shape of a sphere, and at first remained connected with the protoplasm within the membrane. As soon as the eggs were brought back into normal sea-water they began to segment, segmentation taking place in the extra-ovate as well as in that part of the protoplasm that remained within the membrane. Later on either the extra-ovate and the ovum formed a single blastula, or the extra-ovate and the protoplasm that had remained in the ovum formed two separate segmentation cavities and the egg gave rise to twins. In some cases the twins remained grown together, but more often they became separated. When more than one extra-ovate was formed, three and more embryos would be obtained. It sometimes happened that even when there was only one extra-ovate, crevices would be formed in the substance during segmentation in such a way as to produce more than two embryos. — When the eggs were made to burst before segmentation had taken place, only one nucleus was present, and this was located sometimes inside the ovum, sometimes in the extra-ovate. I showed last year how the nuclear material becomes distributed throughout the whole protoplasm of an ovum which has been made to burst.

3. In these experiments the size of the extra-ovate naturally varies. This being the case, it is evident that these extra-ovates may give the answer to our question as to what is the order of magnitude of the smallest quantity of egg substance

just sufficient to produce a normal embryo (Pluteus). The methods I employed to determine this limit were as follows: I first followed out the development of single small fragments of protoplasm in a drop of sea-water that was protected from evaporation. As such observations are naturally limited to a small number of cases, and as in a single drop development does not, as a rule, go on for more than two days, I based my numerical results upon large cultures kept in larger vessels. From these I ascertained by measurement the ratio of the size of the smallest Plutei to the average size of the Plutei that came from normal eggs of the same culture. By doing this carefully every day and by comparing a great number of cultures, the relative size of the smallest Plutei was determined with a sufficient degree of accuracy. Finally I watched the development of small particles in these cultures. These observations, which I carried on during two months last year, and for about the same length of time this summer, gave results which are very definite, as follows: (1) The smallest normal Plutei had about one-half the linear dimensions of the average Pluteus of a normal egg of the same culture. Their volume, therefore, was about one-eighth of that of a normal Pluteus. (2) Smaller fragments developed into a blastula, but then either stopped developing, or reached the gastrula stage much later than normal pieces. In the best specimens of the latter kind some spicules were deposited, but the organism kept its spherical form, and did not develop into a normal Pluteus. The small embryos that remained in the blastula or gastrula stage were just as lively as the normal Plutei, and lived just as long as these.

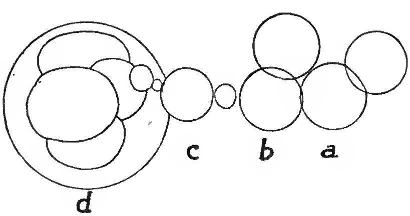

FIG. 1.

Fig. 1 shows the condition of an ovum whose membrane was made to burst before segmentation had taken place. It is divided into twelve cells. The cells *a* and *b* of the extra-ovate developed a few hours later into the blastulae *a* and *b* of Fig. 2. The group *c* of Fig. 1, containing the micromeres, formed an irregular mass of cells *c*, Fig. 2. The protoplasm *d* inside the membrane formed, as usual, one blastula *d*, Fig. 2. The following morning the blastula *d*, Fig. 2, that contained a little more substance than both the blastulae *a* and *b* together, had been transformed into a gastrula, *d*, Fig. 3, while *a* and *b* remained blastulae ; *c* was a mass of detritus. Up to the blastula stage the smaller pieces, as a rule, developed at the same rate as the normal ova, but when the blastula stage was reached, either they stopped developing altogether, or the development went on more slowly. Thus the larger piece *d* went into the gastrula stage, while the smaller pieces *a* and *b* were still in the blastula stage. I do not wish to go into too many details here, as I shall deal with the same phenomena more explicitly at another place. One word may, perhaps, be added concerning such irregular masses of cells as *c*, Fig. 2. They formed, on their outer surface, cilia like normal embryos, and whirled through the water quite as rapidly and lived often as long as normal Plutei, but no differentiation of organs took place. They reminded one of those tumors, the so-called teratomes, which so puzzle pathologists, and which are believed by some to be remnants of embryonic tissue. They appeared, indeed, like free-living teratomes.

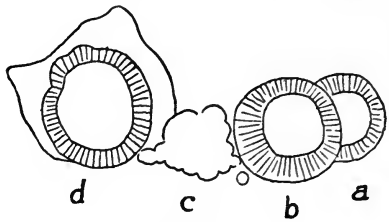

FIG. 2.

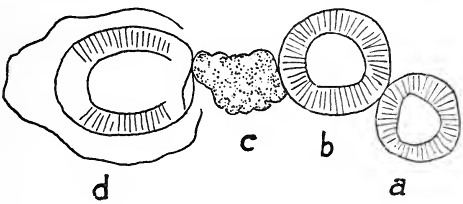

FIG. 3.

4. In all these experiments the smallest Pluteus ever observed was about one-eighth the mass of a Pluteus from a normal egg of the same culture. Before drawing from this fact any conclusion concerning the limits of the divisibility of living substance it is necessary to be sure whether such a Pluteus

originated indeed from a fragment whose mass was not less than one-eighth of the fertilized ovum. As I mentioned before, after the blastula stage is reached the small fragments of an ovum which has been made to burst develop as a rule more slowly than the larger pieces. Now I showed in my "Untersuchungen zur physiologischen Morphologie" that processes of growth and of organization are within certain limits functions of the same variables. Therefore we have reason to believe that small fragments of an egg grow more slowly than larger pieces. If, therefore, in such experiments we find a Pluteus whose volume is only one-eighth that of a normal Pluteus, we may be certain that this small Pluteus comes from a fragment that under no circumstances was less than one-eighth the mass of the normal egg. I will not deny the possibility that a later observer may find still smaller Plutei, but as the number of my experiments is very large I feel pretty confident that the reduction of this limit cannot be considerable.

5. I am not yet able to tell where the limit of divisibility lies, if we require only that the fragments go into the blastula stage. The smallest pieces of protoplasm that I observed segmented if they contained nuclear substance, and so far as I could ascertain most of them reached the blastula stage. Hence the part of an egg able to develop as far as the blastula stage is much smaller than the part necessary to produce a Pluteus. Moreover, it seemed to me that in order that blastulae may become gastrulae the size must reach a certain limit. If this be the case, it is obvious that more substance is necessary for the formation of a gastrula than of a blastula.

6. We are now able to decide a question which does not belong strictly to our subject, namely, whether aside from the mere increase in the number of cells any qualitative differentiation takes place through the first segmentation. As I mentioned above, Driesch found that an isolated cell of the four-cell stage could develop into a Pluteus, but that the same was not possible for a cell of the eight-cell stage. One might conclude from this that such a differentiation in the single cells of the eight-cell stage had taken place that they could produce now only single tissues or parts of a Pluteus, but no longer a whole

Pluteus. It is evident, taking into account the difference in the method of experimentation, that the limit of divisibility determined by Driesch coincides as nearly as could be expected with the limit that we have found. Hence Driesch's and Wilson's experiments do not force us to assume that during the early stages of development qualitative changes take place which prevent a single cell of the eight-cell stage from developing into a complete embryo. But the same fact can be proved in another way. If we let an egg develop normally and bring it into the diluted sea-water as soon as it reaches the eight, sixteen, or thirty-two cell stage, the membrane bursts and part of the contents flow out, just as happens in the unsegmented ovum, only with the difference that the extra-ovate consists of a greater number of cells. In this case also, as in the unsegmented ovum, the development depends upon the quantity of material. Fragments that are larger than one-eighth of the whole ovum may develop into Plutei; smaller fragments will only reach the blastula or gastrula stage. If the early segmentation produced not only an increase in the number of cells but also a definite qualitative differentiation, we should expect that from a small isolated group of cells — say three — from the thirty-two-cell stage there would result an irregular mass of tissue which later on might be transformed by regeneration into a normal embryo. But the embryo is not produced in this way. Such a mass of cells develops directly into a normal blastula and either remains in this stage or is transformed into a gastrula. (This agrees with the results of similar experiments of Driesch.) There is another method of determining whether or not the embryo undergoes differentiation during the early stages of segmentation. If it does, the differentiation must be accompanied by chemical changes. But if chemical changes took place the physiological reactions would change too. I made experiments on fish embryos and found that in the first stages of segmentation such changes do not take place. I made such experiments on sea-urchins also and with the same result.

7. It is clear from the preceding that when it consists partly of nuclear material, a piece of protoplasm from a sea-urchin

egg is able to form a Pluteus provided that its mass is more than one-eighth the mass of the whole egg. Now the question arises, is development a function only of the *mass* or is it also a function of the *orientation* of the protoplasm in the egg? I have shown in a former paper that the adoption of the theory of Sachs leads us to the assumption that there exist in the ovum chemically different substances which are not equally distributed throughout the same. If this were true it might make a difference which part of the protoplasm came under observation in these experiments. But my experiments show that in regard to the possibility of development every part of the protoplasm of the sea-urchin's egg appears to behave as if it were isotropic. This is shown by the following facts: If we rupture an egg the protoplasm flows out from the place where the membrane is torn and the protoplasm that escapes forms an independent embryo, provided the separation is complete. It can further be shown that the place where the membrane bursts bears no relation to the future embryo, or at least to the first plane of cleavage. If we put normal eggs that have just gone into the two-cell stage into diluted sea-water we find that the cleavage plane may have any position in regard to the place where the membrane bursts, as is evident in Figs. 4–7. These figures are drawn by the camera from eggs that were caused to burst after they had reached the two-cell stage. As the extra-ovate develops in all cases in which it is sufficiently large, we must conclude that the protoplasm of the ovum may be considered an isotropic mass, as far as the possibility of its development is concerned.

8. The same is true of the nucleus. In my lecture of last year I showed that the extra-ovate gets as a rule only a small part, say one-fourth of the nucleus, but that this is sufficient to enable it to develop into a normal embryo. Driesch has shown, moreover, by experiments in which the eggs developed under pressure that the nuclei may be considered isotropic as regards their distribution in the cleavage cells. When he brought eggs under one-sided pressure the distribution of the nuclear material took place in a way that was different from what happened under normal conditions. Nevertheless normal

embryos resulted. The same fact can be shown by a method that I published in the *Journal of Morphology*, 1892. If we bring eggs immediately after they have been fertilized into sea-water whose concentration has been sufficiently increased, the nucleus

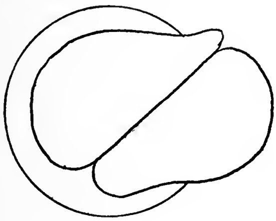

Fig. 4.

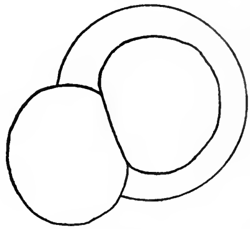

Fig. 5.

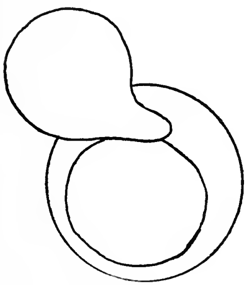

Fig. 6.

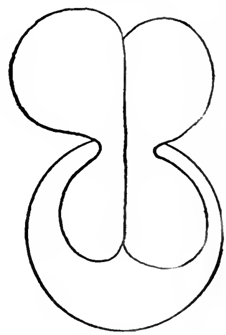

Fig. 7.

begins to segment without any corresponding segmentation of the protoplasm. If the eggs are then brought back into normal sea-water, the protoplasm within from five to twenty minutes divides into as many cleavage spheres as there are preformed nuclei. This year I took up these investigations again with Professor Norman with the same result. Professor Norman found that the nucleus under such conditions continues to segment while the protoplasm does not divide, and that in most cases the segmentation is certainly mitotic.[1]

[1] T. H. Morgan reports in a note in the *Anatomischer Anzeiger* that he has repeated my experiments but obtained different results, namely, that the nucleus does not segment in the concentrated solution, but like the protoplasm goes into the resting stage. If Morgan had made more experiments, or if he had tried the

If the concentration of sea-water is too great, segmentation fails to take place not only in the protoplasm but also in the nucleus. We have thus a very simple method for making the nucleus segment without segmentation of the protoplasm. In each case the distribution of the nucleus is very irregular. Eggs subjected to such treatment are able to develop normally, provided they have not remained too long in the concentrated solution, although the distribution of the nuclear material in the protoplasm is different from what it would be under ordinary circumstances.

9. What idea must we then form concerning the nature of the ultimate units of living substance? As Nussbaum has already shown, it would be erroneous to assume, as elements of living matter, anything analogous to the atom or molecule, for the reason that two substances, nucleus and protoplasm, must be present. We might assume that a combination of two micellae, one of nuclear substance, the other of protoplasm, represents the smallest living element. But our experiments, as well as those of Driesch, show conclusively that the smallest quantity of egg substance that can show all the qualities of living matter is about one-eighth of the mass of an egg in sea-urchins. But why is it that the smallest quantity of living matter required to produce a Pluteus must be considerably larger than the smallest quantity required to produce a blastula or a gastrula? I believe the answer is as follows: The ultimate source of energy of living matter is chemical. Each particle of protoplasm contains or can set free a certain amount of energy that is available for the work of growth and of the other changes of organization. The chemical energy of a piece of the protoplasm of an egg increases with the mass. It is evident that if a blastula is to be transformed into a gastrula and Pluteus an additional amount of work has to be done. Hence, it is clear that a small piece may be able to form a blastula, while it is not able to set free that additional amount of energy that would be required for its transformation into a

effects of a slightly weaker concentration, or if he had used $MgCl_2$ instead of NaCl, the contents of his publication would have been different.

gastrula or a Pluteus. We find somewhat similar phenomena in the processes of regeneration. A piece of the stem of a tubularian hydroid is able to reproduce roots as well as polyps. But it was shown by Miss Bickford in my laboratory, that if the piece cut out of the stem is below a certain size it cannot reproduce all the organs, but only one, namely, the polyp.

But from all this it is clear, too, that the ultimate unit of living matter, in a given species, is not a definite quantity of matter, but that the quantity varies with the functions that we use as a criterion for living matter. If we require that living matter show phenomena of growth and organization, it must consist of protoplasm plus nuclear substance. If we are satisfied with spontaneity or irritability, the ultimate unit is much smaller and qualitatively simpler, since for these manifestations the protoplasm alone is sufficient. However, the units of living matter not only represent a definite quantity of energy, but we have reason to assume that the setting free of this energy is connected with a certain scheme, which may perhaps be the same for all the phenomena of life. If such is the case our further knowledge of the ultimate elements is likely to be dependent upon our understanding of this scheme. A full knowledge of this or these schemes would be a solution of the riddle of life.

FOURTH LECTURE.

THE DIFFERENTIATION OF SPECIES ON THE GALÁPAGOS ISLANDS AND THE ORIGIN OF THE GROUP.

G. BAUR.

The Galápagos Islands form a small archipelago, placed below the Equator about 500 miles west of the coast of South America. When discovered by the Spaniards in the sixteenth century, they were found to be uninhabited. At the end of the seventeenth and during the eighteenth and nineteenth centuries they were often visited by the buccaneers and whalers. Only in 1832 a small colony was established on Charles Island, but soon abandoned; to-day only one island, Chatham, is inhabited.[1] There are five principal islands, eleven smaller ones, and a great number of islets and rocks. Albemarle is the largest, then follow Indefatigable, Narborough, James, Chatham, Charles, Hood, Bindloe, Abingdon, Barrington, Duncan, Tower, Jervis, Wenman, Culpepper, Brattle, Gardner. The whole group is volcanic. The highest mountain (South Albemarle) is 1570 m. high. No volcanic activity has been reported since 1835, but in 1825 a most terrific eruption occurred on Narborough.

Since Darwin's glorious visit in 1835 (September 15–October 20) the Galápagos have been touched at different times for scientific investigation. In 1838 the French frigate "Vénus,"

[1] The Galápagos were discovered the 10th of March, 1535, by the Spaniard Fray Tomas de Berlanga. (Marcos Jiménez de la Espada: Las Islas de los Galápagos y otras más á poniente. Sociedad Geográfica de Madrid, 1892.) In the same paper it is stated that possibly the Inca Tupac Yupangui, the grandfather of the Inca Atahualpa, whom Pizarro so cruelly murdered, discovered the islands. The literature relating to the Galápagos Islands I have published in the *Amer. Nat.*, April, 1891, pp. 320–326.

with Captain Du Petit Thouars, stopped at the islands from the 21st of June to the 15th of July; in 1852 we find the Swedish ship "Eugenie" there, with Dr. Kinberg, the zoölogist and Dr. Anderssen, the botanist; then follows the English ship "Herald," January 6–16, 1846; Dr. Habel from New York, July 22, 1868–January 1, 1869; the Hassler Expedition under Professor L. Agassiz, June 10–19, 1870; the United States Fish Commission steamer "Albatross," April 4–16, 1888; and again with Professor A. Agassiz, March 28–April 4, 1891; the late Mr. C. F. Adams and myself, June 10–September 6, 1891.[1]

It was David Porter, the well-known commodore of the United States frigate "Essex," who for the first time stated (1815) that the different islands of the group contained different races of the gigantic land-tortoises: the same statement is made by Darwin, who says that the colonists on Charles Island were able to tell from the aspect of a tortoise from which special island it came. Similar results were reached by the study of the birds and the flora. These are the words of Darwin:[2]

"I have not as yet noticed by far the most remarkable feature in the natural history of this archipelago; it is, that the different islands to a considerable extent are inhabited by a different set of beings. My attention was first called to this fact by the vice-governor, Mr. Lawson, declaring that the tortoises differed from the different islands, and that he could with certainty tell from which island any one was brought. I did not for some time pay sufficient attention to this statement, and I had already partially mingled together the collections from two of the islands. I never dreamed that islands about fifty or sixty miles apart and most of them in sight of each other, formed of precisely the same rocks, placed under a quite similar climate, rising to a nearly equal height, would have been differently tenanted; but we shall soon see that this is the case. It is the fate of most voyagers, no sooner to discover what is most interesting in any locality, than they are

[1] An account of this expedition is given by me in the *Biol. Centralbl.*, vol. XII, 1892, pp. 221–250.

[2] Darwin, Charles: A Naturalist's Voyage, London, 1845.

hurried from it; but I ought, perhaps, to be thankful that I obtained sufficient materials to establish this most remarkable fact in the distribution of organic beings. . . . My attention was first thoroughly aroused by comparing together the numerous specimens, shot by myself and several other parties on board, of the mocking thrushes, when to my astonishment, I discovered that all those from Charles Island belonged to one species (Mimus trifasciatus); all from Albemarle Island to M. parvulus; and all from James and Chatham islands (between which two other islands are situated as connecting links) belonged to M. melanotis."[1]

In 1890 I examined the specimens of Tropidurus collected by the United States Fish Commission steamer "Albatross," in 1888, on eight islands. The material consisted of 128 specimens. I was not a little astonished to find that nearly every island contained a peculiar race or species of this lizard, and that not a single island contained more than one race or species.[2] Meanwhile Ridgway[3] had studied the birds collected by the "Albatross." He found that Nesomimus had also peculiar species on Hood and Abingdon.

It was this peculiar distribution of the species on the different islands, which convinced me that the Galápagos Islands could not be of volcanic origin, lifted out of the ocean; but that they must have originated through subsidence. Only by such an assumption the harmonic distribution of the fauna could be understood. To secure a better basis for the opinion it was necessary to make very extensive collections on each of the islands and to find out all the details of distribution. During my stay all the islands, with the exception of Narborough, Wenman, and Culpepper, were visited. The result was exactly as had been anticipated.

[1] Mr. Ridgway has shown now that also the specimens from James and Chatham are different.

[2] Baur, G.: Das Variiren der Eidechsen-Gattung Tropidurus auf den Galápagos Inseln. *Biol. Centralbl.*, vol. X, 1890, pp. 475–483.

[3] Ridgway, R.: Birds collected on the Galápagos Islands in 1888. *Proc. Un. St. Nat. Mus.*, vol. XII, 1889, pp. 101–108. — Description of twenty-two new species of birds from the Galápagos Islands. *Proc. Un. St. Nat. Mus.*, vol. XVII, 1894, pp. 357–370.

We may commence with Tropidurus. More than 400 specimens of this lizard were collected. It was found on Indefatigable, James, Jervis, Duncan, Charles, Barrington, Hood, Gardner, Chatham, Bindloe, and Abingdon. On Charles it was exceedingly rare and on Tower no specimen at all was discovered; on Tower it has probably been extinguished by the sea-birds, which are found there in enormous numbers.

Each island possessed only a single species of Tropidurus, all the individuals of one island belonged to *one* species; and nearly every island had its peculiar species or race.

I have counted the number of the scales round the middle of the body in all the specimens and found the following results:—

	Number of Scales.	Average Number.	Number of Specimens Examined.
Indefatigable Island	53–63	57	62
Albemarle "	53–63	57	64
Chatham "	55–65	59	64
James "	59–65	63	64
Jervis "	61–67	63	23
Charles "	59–69	63	6
Barrington "	63–71	67	38
Bindloe "	69–75	71	40
Hood "	69–77	73	61
Gardner "	73–79	75	15
Duncan "	83–89	87	14
Abingdon "	91–101	97	45

The total variation for all forms is 53–101, not less than 48; but in none of the single islands is the variation in the number of scales more than ten. The number ten we find on Indefatigable, Albemarle, Chatham, Charles, Abingdon; the number eight on Barrington, Hood; the number six on James, Jervis, Bindloe, Gardner, Duncan. I do not doubt that in different forms, after an examination of a larger number of specimens, the extension of the variation will be found wider; but probably it will rarely be more than ten. It is interesting to notice that on the larger islands the variation is greater than in the smaller ones.

The number of scales on Indefatigable and Albemarle is the same; but the specimens are at once distinguished by the different coloration. The same is true for Hood and Bindloe; here we have also nearly the same number of scales, but two totally different forms. The specimens from Jervis cannot be distinguished from those of James; the islands are separated only eight kilometers from each other and the water is not very deep between them. The same is true for Gardner and Hood, which are much closer together, and separated by shallow water only. The species from Albemarle, James, and Jervis, Indefatigable, Barrington, and Charles are more closely related to each other than to those of the other islands; the species from Hood, Chatham, Duncan, Bindloe, and Abingdon are more distinct than those of the islands named above.

By comparison of the number of scales it is found that the greatest number of specimens of a certain island possesses a number of scales which agrees with the average number of scales of the specimens of the island. Out of thirty-eight specimens from Barrington, for instance, twenty-one show the number sixty-seven, which number represents the average value; out of thirty-six specimens from James, nineteen have the average number sixty-three, and so on.

These conditions can be shown by a graphic way. The number of scales found in a lizard of a certain island, for instance, Chatham, are placed on a horizontal, the number of cases, corresponding to the different numbers, on a vertical, line; by uniting the points of the vertical lines a curve is produced. All these curves thus constructed ascend to a point, and descend on the other side. The highest point corresponds to the greatest number of cases and also to the mean number of scales.[1]

What has been stated long ago for the tortoises, that they are different on the different islands, is also true for the lizard Tropidurus. We shall now examine the birds in this respect.

The genus Nesomimus has been found on Indefatigable,

[1] Baur, G.: Das Variiren der Eidechsen-Gattung Tropidurus auf den Galápagos Inseln. Festschrift zum siebenzigsten Geburtstage Rudolf Leuckarts. Leipzig, 1892, pp. 259–277.

James, Jervis, Barrington, Charles, Hood, Gardner, Chatham, Bindloe, Abingdon, and Tower. This genus, formerly common on Charles, is now extinct; it has never been seen on Duncan. Mr. Ridgway has studied this genus and found the following: Nearly each island has its peculiar race or species; and there is never more than one race or species found on a single island. On Jervis and James we find the same species, and this can also not be separated from the Indefatigable-bird; on Hood and Gardner we have the same bird; but each one of the other islands shows its own form. This agrees with Tropidurus; Jervis and James have the same Tropidurus and closest to that of Indefatigable; Hood and Gardner have identical forms.

The genus Certhidea was found on Indefatigable, James, Jervis, Barrington, Chatham, Bindloe, Abingdon, and Tower. The specimens on Jervis and James were the same; but each other island showed its peculiar species.

The genus Pyrocephalus was found on Albemarle, Jervis, James, Indefatigable, Charles, Chatham, Bindloe, and Abingdon. On Albermarle (?), Jervis, and James was one species; all the other islands, with the possible exception of Bindloe, had peculiar species.

I could give many more examples, but it will be sufficient to mention only a few.

Phyllodactylus, a genus of the Geckonidae, has been discovered so far on three islands, Chatham, Charles, and Albemarle; on each of these islands it is represented by a peculiar species. Amblyrhynchus, the sea-iguana, is not identical on all the islands, but has developed peculiar races on Tower and Duncan.[1] The genus Schistocerca of the Orthoptera (Acrididae) is the same on the middle islands, but is represented by a peculiar race on the more isolated islands, Chatham, Hood, and Tower.[2]

The following table shows the distribution of these different genera:—

[1] Garman, S.: The Reptiles of the Galápagos Islands. *Bull. Essex Inst.*, vol. XXIV, 1892.

[2] Scudder, Samuel H.: The Orthoptera of the Galápagos Islands. *Bull. Mus. Comp. Zoöl., Harvard College*, vol. XXV, No. 1, 1893.

Table showing the Distribution of some Genera on the Galápagos Islands.

	Albemarle.	Jervis.	James.	Indefatigable.	Duncan.	Barrington.	Charles.	Hood.	Gardner.	Chatham.	Tower.	Bindloe.	Abingdon.
Tropidurus	albemarlensis, Baur.	Jacobii, Baur.		indefatigabilis, Baur.	duncanensis, Baur.	barringtonensis, Baur.	Grayi, (Bell).	delanonis, Baur.		bivittatus, (Peters).	—	Habelii, Steind.	pacificus, Steind.
Nesomimus	parvulus, (Gould).	melanotis, Gould.			—	spec.	trifasciatus, (Gould).	macdonaldi, Ridgw.		adamsi, Ridgw.	baui, Ridgw.	bindloei, Ridgw.	personatus, Ridgw.
Certhidia	albemarli, Ridgw.	olivacea, Gould.		salvini, Ridgw.	—	bifasciata, Ridgw.	—	cinerascens, Ridgw.		luteola, Ridgw.	mentalis, Ridgw.	? fusca, Scl. and Salvin.	fusca, Scl. and Salvin.
Pyrocephalus	nanus, Gould.			intercedens, Ridgw.	—	—	carolensis, Ridgw.	—	—	dubius, Gould.	—	abingdoni, Ridgw.?	abingdoni, Ridgw.
Phyllodactylus	galapagoensis, Pet.	—	—	—	—	—	Baurii, Garm.	—	—	Leei, Cope.	—	—	—
Amblyrhynchus	cristatus, Bell.	cristatus, Bell.			ater, Garm.	cristatus, Bell.	cristatus, Bell.	cristatus ? Bell.		cristatus, Bell.	nanus, Garm.	cristatus, Bell.	
Schistocerca	melanocera, Stål.			melanocera, (Stål.).			melanocera, (Stål.).	literosa punctata, Scudd.		literosa discoidalis Scudd.	literosa hyalina, Scudd.	?	?

What conclusions can we draw from this peculiar distribution? As we have seen, the representatives of each genus on the different islands are very closely related to each other, and certainly have a common origin. The Galápagos Archipelago is comparable to a planetary system.[1] The islands form an harmonic group and so do the planets. The planets at a former period were united with each other, and so must have been the islands. Thus only the harmonic distribution of fauna and flora can be explained. It is this consideration which forced me to establish the doctrine of the continental origin of the Galápagos Islands. We cannot explain the harmonic distribution on the theory of oceanic origin of the group, which so far has been adopted. But let us accept this theory for a moment. There must have been a time, shortly after the islands had been lifted out from the ocean, when not a single land-organism existed on them. By and by stragglers from different regions were landed there, and the islands were peopled. But it is impossible that by these accidental colonists the harmony could be produced which we find there.

Let us now consider the subsidence theory. At a former period these islands were connected with each other, forming a single large island, which itself at a still earlier time was united with the continent, probably with Central America and the West Indies.[2] When this large island was not yet broken up into a series of smaller islands, the number of species must have been very much smaller; probably there was only one species of Nesomimus, of Certhidia, of Tropidurus, of the Land Tortoise, and so on. Through isolation into single islands the peculiar differentiation of the species began; an originally single species was differentiated in many different forms; every, or nearly every, island developed its peculiar races. We still see to-day that islands which are closely to-

[1] "I have said that the Galápagos Archipelago might be called a satellite attached to America, but it should rather be called a group of satellites, physically similar, organically distinct, yet intimately related to each other, and all related on a marked, though much lesser degree, to the great American continent." Darwin: A Naturalist's Voyage, 1845, p. 382.

[2] The discovery of land-birds on Cocos Island, which are intermediate between West Indian and Galápagos forms, is very interesting and important.

gether and not separated by deep water show the same species, like James and Jervis, or Hood and Gardner. The faunas of the larger central islands are again closer related to each other than are the faunas of the more isolated islands, like Tower, Bindloe, Abingdon, Hood, and Charles. The Tortoise of Duncan is closest to the Tortoise from Abingdon; at the same time the Tropidurus of Duncan comes nearest to that of Abingdon. The prevention of intercrossing after the separation of the islands, the time of separation, and the difference in the conditions on the different islands, are the factors which produced the different races. By the subsidence theory every difficulty is explained in the easiest way.

To give further support to my opinion on the continental origin of the Galápagos, I shall now consider the West Indian Islands. That these islands formerly were connected with each other and with Florida, Central America, and also a portion of South America is, I believe, considered to-day an established fact, notwithstanding most of these islands are surrounded by a very deep sea.[1] We even have evidence that this connection still partially existed at a relatively late period; for remains have been discovered of the Edentates Megalonyx on Cuba, of Mastodon on the Bahamas, and of large rodents and deer in caves of Anguilla.

If the West Indian Islands are really the product of the splitting up of a greater area of land, we ought to find the same harmony in the geographical distribution of the fauna, as we found on the Galápagos.

The following table giving the distribution of the species of different genera of birds on some of the islands, speaks for itself; we find exactly the same harmony:[2]—

[1] Suess, Eduard: Die Antillen, in: Das Antlitz der Erde. Wien, 1892. Vol. I, pp. 698–712.

[2] Cory, Charles B.: Catalogue of West Indian Birds. Boston, 1892.

Distribution of some Genera of Birds in the West Indies.

	Cuba.	Hayti.	Jamaica.	Porto Rico.	Guadaloupe.	Dominica.	Martinique.	St. Lucia.	St. Vincent.	Abaco (Baham.).	Grand Cayman.
Amazona	leucocephala, (Linn.).	ventralis, (Müll.).	collaria, (Linn.).	vittata, (Bodd.).	—	augusta, Vig. bongeti, (Bechst.).	—	versicolor, (Müll.).	guildingi, (Vig.).	—	caymanensis, (Linn.).
Todus	multicolor, Gould.	subulatus, Gould.	viridis, Linn.	hypochondriacus, Bryant.	—	—	—	—	—	—	—
Melanerpes	superciliaris, (Temm.).	—	radiolatus, (Wagl.).	portoricensis, (Daud.).	herminieri, (Less.).	—	—	—	—	blakei, Ridgw.	caymanensis, Cory.
Myiarchus	sagræ, Gund.	dominicensis, (Bryant).	stolidus, Gosse. validus, Cab.	antillarum, Bryant.	—	—	sclateri, Lawr.	—	—	—	denigratus, Cory.
Icterus	hypomelas, Bonap.	dominicensis, Linn.	leucopteryx, Wagl.	portoricensis, Bryant.	—	—	bonana, Linn.	laudabilis, Scl.	—	northropi, Allen.	bairdi, Cory.
Myadestes	elizabeth, (Lemb.).	montanus, Cory.	solitarius, Baird.	—	—	dominicanus, Stejn.	genibarbis, Swains.	sanctæluciæ, Stejn.	sibilans, Lawr.	—	—
Cæreba	—	bananivora, (Gmel.).	flaveola, (Linn.).	portoricensis, Bryant.	—	dominicana, Taylor.	martinicana, (Reich.).		atrata, Lawr.	bahamensis, (Reich.).	sharpei, Cory.

Professor Alexander Agassiz[1] has ridiculed the idea of the continental origin of the Galápagos. I have asked him to explain the harmonic distribution of the fauna and flora on the elevation theory.[2] He nor anybody else so far has been able to explain this harmonic distribution by accidental immigration to the islands; which we have to assume of course on that theory.

I do not see any difficulty in accepting the theory of subsidence ; the 1500-fathom line probably embraces Cocos Island and the Galápagos from Central America (Colombia), and 1500 fathoms and more are even admitted now by Wallace[3] as no objection to the continental origin of an island. He says: "All that is necessary to maintain is, that existing continents with their included seas and their surrounding oceanic waters as far as the 1500-fathom, or in some extreme cases, the 2000-fathom line, mark out the areas within which the continental lands of the globe have been built up ; while the oceanic areas beyond the 2000-fathom line have almost certainly been ocean throughout all known geological time." (*Natural Science*, August, 1892.) But even this is, I think, quite arbitrary. There is very little doubt that during the Jurassic Africa was connected with South America, and in this case even 2000 fathoms would be not sufficient. The opinion expressed by Jukes-Brown[4] in the September number of *Natural Science*, 1892, seems to me perfectly sound. He says : "Those who oppose the doctrine of permanence say that the present continents are the outcome of a long series of geographical mutations, and I would add that each phase was an episode in a long process of geographical

[1] Agassiz, Alexander: General sketch of the expedition of the "Albatross," from February to May, 1891. *Bull. Mus. Comp. Zoöl.*, vol. XXIII, No. 1, 1892, pp. 70–74. W. Botting Hemsley also ridicules my idea, quoting Agassiz in a late paper published in *Scientific Progress*. London, vol. I, No. 5, July, 1894, pp. 400, 401, "Insular Floras"; but he also does not try to explain the harmonic distribution.

[2] Baur, G.: Professor Alexander Agassiz on the origin of the Fauna and Flora of the Galápagos Islands. *Science*, vol. XIX, 1892, p. 176.

[3] Wallace, A. Russel: The Permanence of the Great Oceanic Basins. *Nat. Science*, August, 1892, vol. I.

[4] Jukes-Brown, A. J.: The evolution of Oceans and Continents. *Nat. Science*, September, 1892, vol. I, pp. 508–513.

evolution. There is good reason to believe that even in Pliocene time the outlines of the continents were very different from the present, some areas now below the sea being then above it, while other tracts then beneath oceanic waters have since been raised into dry land. We know that Miocene geography differed still more greatly from that of to-day, and it is not therefore unreasonable to suppose that in the Cretaceous period large parts of the modern oceans were land, and large parts of the modern continents were portions of the ocean, the continental connections being totally different from what they are now. In short, the interchange we believe is in the frequent interchange of small portions of oceans and continents till, in the course of time, the accumulated changes have accomplished great geographical mutations."

FIFTH LECTURE.

THE HEREDITARY MECHANISM AND THE SEARCH FOR THE UNKNOWN FACTORS OF EVOLUTION.[1]

HENRY FAIRFIELD OSBORN.

"Disprove Lamarck's principle and we must assume that there is some third factor in Evolution of which we are now ignorant."[2]

Chief among the unknown factors of evolution are the relations which subsist between the various stages of development and the environment.

A STUDY of the recent discussion in the *Contemporary Review* between Spencer and Weismann leads to the conclusion that neither of these acknowledged leaders of biological thought supports his position upon inductive evidence. Each displays his main force in destructive criticism of his opponent; neither presents his case constructively in such a manner as to carry conviction either to his opponent or to others. In short, beneath the surface of fine controversial style we discern these leaders respectively maintaining as finally established, theories which are less grounded upon fact than upon the logical improbabilities of rival theories. Such a conclusion is deeply significant; to my mind it marks a turning point in the history of speculation, for certainly we shall not arrest research with any evolution factor grounded upon logic rather than upon inductive demonstration. A retrograde chapter in the history

[1] This lecture is mainly from an article published by the author, in Merkel u. Bonnet: *Ergebnisse für Anatomie und Entwickelungsgeschichte*, Freiburg, 1894, and partly from a paper before the Biological Section of the British Association for the Advancement of Science: Certain Principles of Progressively Adaptive Variation observed in Fossil Series. *Nature*, August 30, 1894.

[2] Osborn: Are Acquired Variations Inherited? Address before the American Society of Naturalists. *Amer. Naturalist*, February, 1891.

of science would open if we should do so and should accept as established laws which rest so largely upon negative reasoning.

The growing sentiment of the necessity of induction and of inductive evidence is the least conspicuous, but really the most important and lasting outcome of this prolonged discussion. Weismann is the real initiator of this outcoming movement although it has taken a radical direction he neither foresaw nor advocated, for his position is eminently conservative. In fact his first permanent service to Biology is his demand for direct evidence of the Lamarckian principle, which has led to the counter-demand for such evidence of his own Selection principle, which by his own showing, and still more by his own admission in this discussion with Spencer, he is unable to meet. His second permanent service, as Professor Wilson reminds the writer, is that he has brought into the foreground the relation between the hereditary mechanism and evolution.

What have we gained in the controversy of the past decade unless it is closer thinking and this keener appreciation of the necessity for more observation? We carry forth, perhaps, some new and useful working hypotheses as to possible modes of evolution, and a fuller realization of the immense difficulties of the heredity problem — but these are only indirect gains. It is a direct gain that these negative results have led a minority of biologists into a total reaction from speculation and into a generally agnostic temper towards modern theories which is far more healthy and hopeful than the confident spirit of the majority upon either the Neo-Lamarckian or the Neo-Darwinian side. There is no note of progress in the dogmatic assertion that the question is established either as Spencer or as Weismann would have it, unless this assertion can be backed up by proof, and by whom can proof be presented if not by these masters of the subject? The conviction we all reach when we sift wheat from chaff, and bring together from all sources phenomena of different kinds and seek to discern what the exact bearings of these phenomena are, is that we are still on the threshold of the evolution problem, and that the secret is largely tied up with that of vital phenomena in general.

The very wide and positive differences of opinion which prevail are attributable largely to the unnatural divorce of the different branches of biology, to our extreme modern specialization, to our lack of eclecticism in biology. We begin to grasp the magnitude of the problem only when side by side with field and laboratory data are placed paleontological data, as well as anthropological, including the unique facts of human variation and the laws of human inheritance. For in modern embryology certainly the most brilliant discovery is that the physical basis of all inheritance is the same — and growing out of this is the high probability that the laws of heredity are the same in the whole organic world, with no barriers between protozoa and metazoa, or between animals and plants. Both Weismann and Spencer show themselves blind to this nexus of fundamental uniformity when they draw certain lines of division in inheritance where none exist in the visible hereditary mechanism of chromatin and archoplasm. With these discoveries in mind does not Weismann appear as much afield when he maintains that the inheritance of acquired characters is a declining principle in the ascent of life, as Spencer when he maintains that it is a rising principle in the ascent of life?

The first step then towards progress is the straightforward confession of the limits of our knowledge and of our present failure to base either Lamarckism or Neo-Darwinism as universal principles upon induction. The second is the recognition that all our thinking still centers around the five working hypotheses which have thus far been proposed; namely, those of Buffon, Lamarck, St. Hilaire, Darwin, and Nägeli. Modern criticism has highly differentiated, but not essentially altered these hypothetical factors since they were originally conceived. Darwin's 'survival of the fittest' we may alone regard as absolutely demonstrated as a real factor, without committing ourselves as to the 'origin of fitness.' The third step is to recognize that there may be an unknown factor or factors which will cause quite as great surprise as Darwin's. The feeling that there is such first came to the writer in 1890 in considering the want of an explanation for the definite and apparently purposeful character of certain variations.[1] Since then a simi-

[1] *Op. cit.*, 1891.

lar feeling has been voiced by Romanes and others, and quite lately by Scott;[1] but the most extreme expression of it has recently come from Driesch[2] in his implication that there is a factor not only unknown but unknowable!

Theoretically neither of these five hypotheses of the day excludes the others. They may all coöperate. The rôle which each plays, or the fate of each in the history of speculation largely or wholly depends upon the solution of the problem of the transmission or non-transmission of acquired variations and after all that has been written on this question this must be regarded by every impartial observer as still an open one.

We are far from finally testing or dismissing these old factors, but the reaction from speculation upon them is in itself a silent admission that we must reach out for some unknown quantity. If such does exist there is little hope that we shall discover it except by the most laborious research; and while we may predict that conclusive evidence of its existence will be found in morphology, it is safe to add that the fortunate discoverer will be a physiologist.

The Analysis of Variation.

After this introductory survey let us consider as another outcome of the controversy that Variation and the related branch of research, Experimental Evolution, are now in the foreground as the most important and hopeful of the many channels into which the inductive tests of known or unknown factors may be turned. Let us make an honorable exception of those reactionists, such as Bateson[3] and Weldon, who have instituted an exact investigation into the laws of Variation.

How shall the study of Variation be carried on? I totally differ at the outset from Bateson in the standpoint taken in the introduction of his work, that the best method of starting such an investigation is in discarding the analysis which rests upon the experience as well as the more or less speculative basis of

[1] On Variations and Mutations. *Am. Jour. Sc.*, November, 1894.

[2] Analytische Theorie der Organischen Entwickelung. Leipsic, 1894.

[3] W. Bateson: Materials for the Study of Variation. London, 1894.

past research. There is little clear insight to be gained by considering variations *en masse*, and in this lecture I shall put forth some reasons why this is the case as well as some principles which seem to be preliminary to an intelligent collection and arrangement of facts, upon the ground that a mere catalogue of facts will have no result. Variation is to be regarded as one of the two modes or expressions of Heredity, or as the exponent of old hereditary forces developing under new or unstable conditions. It stands in contrast not with Heredity, which includes it, but with Repetition as the exponent of old forces developing under old or stable conditions. Nägeli ten years ago[1] laid stress upon this, as have latterly Weismann, Bateson, Hurst,[2] and others. Nevertheless it is still widely misconceived. Hurst even regards Variation as the oldest phenomenon — an error in the other extreme, for they are rather coincident phenomena — representing the stability or instability of development. The broadest analysis we can make is that variations are divided by three planes — the plane of *time*, the plane of *cause*, and the plane of *fitness*. This raises the three problems to be solved regarding each variation : when did the variation originate ? what caused it to originate ? is it or is it not adaptive ?

The student of heredity, in connection with these three planes of analysis, has then to consider the modes of heredity as complementary or interacting, for as soon as a 'variation' recurs in several generations it is practically a 'repetition,' and the repetition principle is a frequent source of apparent but not real variation or departure in the offspring from parental or race type. This relation becomes clear when we consider variations in man, as seen in anatomy and in Galton's studies of inheritance and expressed in the following table :—

[1] "Vererbung und Veränderung sind, wenn sie nach dem wahren Wesen der Organismen bestimmt werden, nur scheinbare Gegensätze." *Theorie der Abstammungslehre*, p. 541.

[2] Biological Theories. I, The Nature of Heredity. *Natural Science*, vol. I, No. 7, September, 1892. II, The Evolution of Heredity. *Natural Science*, vol. I, No. 8, October, 1892.

HEREDITY.

Repetition.	*Variation.*	
A. Retrogressive to present and past type.	*A.* Neutral both as regards present or future type. Including anomalies and abnormalities which are purely individual phenomena not in the path of evolution.	*B.* Progressive to future type.
(*a*) Repetition of parental type.		(*a*) Ontogenic variation from parental type in one or more characters.
(*b*) Regression to present race type usually in several characters (=Variation from present *parental* type).		(*b*) Ontogenic variation from present race in several characters (=a new sub-type).
(*c*) Reversion to past race type, usually in few or single characters (=Variation from present *race* type).		(*c*) Phylogenic or constant variation towards future race type, in one or more characters, constituting a new 'Variety' (=Repetition of parental type).
Palingenic Variation.		*Cenogenic Variation.*

The most profound gap in time is between 'palingenic variations,' springing from the past history of the individual, and 'cenogenic variations,' which have to do only with present and future history. The former embraces more than reversion. This table gives us only our first impression of this plane of time so lightly regarded by Bateson, if indeed discrimination is possible among data of the kind he has collected. The distinctive import of human anatomy [1] is that a comparison of the past and present habits of the race, or of the uses to which bones and muscles have been and are now being put, opens a possible analysis of variations both as regards their time of origin and as regards their fitness to past, present, or future uses; it is thus an inexhaustible mine for the philosophical study of variation — of which only the upper levels have been worked.[2] Beside the human organism there is no other within

[1] R. Wiedersheim: Bau des Menschen als Zeugniss seiner Vergangenheit. Freiburg, 1887.

[2] H. F. Osborn: Present Problems in Evolution and Heredity. The Cartwright Lectures. I. The Contemporary Evolution of Man, etc. Wm. Wood & Co., New York, 1891.

our reach admitting such exact analysis of variation in the planes of time and fitness. When, again, we connect human anatomy as a field for the study of Variation with Galton's researches, although his emphasis has been chiefly upon the laws of Repetition, we begin to appreciate the far-reaching importance of his inductions. In contrast with those of Weismann they are based upon facts and will stand. In the first volume of these Marine Biological Laboratory lectures I went into some detail to show how Galton bears upon the modern evolution problem, so that here I may briefly recapitulate. He demonstrates two principles : First, that there must be some strong progressive variational tendency in organisms to offset the strongly retrogressive principle of Repetition wherever the neutralizing or swamping effect of natural inter-breeding is in force, as it virtually is for most anatomical characters of the human race. Second, he shows what has not been pointed out in this connection before, that in natural inter-breeding ontogenic or individual variations are conspicuous but in the main temporary, while there is a strong undercurrent of phylogenic variations relatively inconspicuous and permanent. Other evidence supporting this latter principle comes out as we proceed.

What is the value of a distinction between *ontogenic* and *phylogenic* variations? It is this: it sets forth the widely neglected initial problem of the *time of origin of a variation in the life history of the individual.* This is the first step in experimentation upon variation, not only as it will afford crucial evidence as to the factors of Buffon, Lamarck, and of St. Hilaire, which hinge upon the inheritance of acquired variations, but in the coming days of exact research upon Variation in general. Let *ontogenic variation* — a term first used by Brooks, I believe, although I cannot point out where — include all deviations from type which have their cause in any stage of individual development. We are now beginning to fully recognize that the causes of certain kinds of variation actually can be traced to external influences upon certain stages of growth or ontogeny, and that it will be possible ultimately to determine these stages when this matter of time is established by experiment. Let *phylogenic variation* — a term first used by Nägeli[1] — include those departures from type which have become constant hereditary characters in certain phyletic series or even in a few generations. While all phylogenic variations must originate in ontogeny or in some stage of individual development, certainly a very small proportion of the innumerable ontogenic variations which we find in the examination or measurement of any adult individual ever become phylogenic, or constitute more than ripples upon the surface of a tide.

This vital distinction has not been regarded hitherto. The statistics of variation, as compiled by Darwin and lately by Wallace, Weldon, Bateson, and others, do not take into account that among phylogenic variations are others purely ontogenic springing up and disappearing during individual life, owing to causes connected solely with the disturbance of the typical action of the hereditary mechanism during ontogeny. In other words, these writers have without discrimination based upon variations, which may be largely or wholly ontogenic and temporary, the important principles of 'Fortuitous Variation' of Darwin and of 'Discontinuous Variation' of Bateson, whereas it is only the laws of phylogenic variation which are of real bearing upon the problem of evolution. Take as an illustration of this false method the wing measurements of birds given by Wallace. Why may not these be largely cases of purely ontogenic variation due to influences of life habit or to some purely temporary disturbance of the hereditary basis? Above all others, the Neo-Darwinians must reconsider their principle of 'fortuitous variation' which has been based upon data of miscellaneous ontogenic and phylogenic variations, because Neo-Darwinism is essentially and exclusively a theory of the survival of favorable phylogenic variations.

One aspect of the variation problem of to-day may, therefore, be stated thus: What is the cause, nature, and extent of

[1] Die Veränderung, die gewöhnlich der Vererbung gegenüber gestellt wird, steht nicht im Gegensatz zu dieser, sondern zur Constanz. In diesem Sinne heisst eine Veränderung constant, wenn das Gewonnene dauernd behalten, und vergänglich, wenn es bald wieder preisgegeben wird. Die constante oder die *phylogenetische Veränderung* . . . ist eigentlich nichts anderes als die Constitutionsänderung des Idioplasmas. *Theorie der Abstammungslehre*, p. 277.

ontogenic variations in different stages of development, and under what circumstances do ontogenic variations become phylogenic?

This brings us to an analysis of ontogenic variations in the *plane of time* as provisionally expressed in the following table: —

ORIGIN OF VARIATIONS DURING LIFE HISTORY.

A. Ontogenic Variations.	*Theories of Causation.*
(*a*) *Gonagenic*, *i.e.*, those arising in the germ-cells, including the 'Blastogenic' in part of Weismann, the 'Primary Variations' of Emery.	Theoretically connected with pathological, nutritive, chemico-physical, nervous influences, as implied by Kölliker and others, including doubtful phenomena of Xenia and Telegony.
(*b*) *Gamogenic*, *i.e.*, those arising during maturation and fertilization, including the 'Blastogenic' in part of Weismann, 'Secondary,' or 'Weismannian variations' of Emery.	Theoretically connected with influences named above, also with the combination of diverse ancestral characters, 'Amphimixis' of Weismann.
(*c*) *Embryogenic*, *i.e.*, those occurring during early cell division, including the 'Blastogenic' and 'Somatogenic' in part of Weismann.	Theoretically connected with extensive anomalies due to abnormal segmentation and other causes, as observed in the mechanical embryology of Roux, Driesch, Wilson, and others.
(*d*) *Somatogenic*, *i.e.*, those occurring during larval and later development after the formation of the germ-cells.	Connected with reactions between the hereditary developmental forces of the individual and the environment.

B. Phylogenic Variations.

Variations from type, originating in any of the above stages which become hereditary.

The above table illustrates limits which certainly should not be sharply drawn between the successive stages of ontogeny, although intermediate focal points of real distinction must exist. The four terms proposed are not in the sense of the 'blastogenic' and 'somatogenic' of Weismann, for there is no implication of his *petitio principi*, namely, of the separation of the hereditary substance or specific germ-plasm from the body-cells. Even before somatogenic separation has taken place we have little or no reason to believe that all the blastogenic, gonagenic, or gamogenic variations which may have arisen from various causes will become phylogenic.

If we carry our analysis into the '*plane of fitness*' the first point which arises is whether variations are *normal*, including both cenogenic and palingenic variations, or *abnormal,* including teratological and other malformations. The terms 'fortuitous' and 'indefinite' as opposed to 'determinate' and 'definite' may be used apart from any theory, although they have sprung up as distinguishing two opposed views as to the principles of variation. 'Fortuity' strictly implies variation round an average mean, while 'definite' is not the necessary equivalent of adaptive, but simply implies progressive or phylogenic variation in one direction which Waagen and Scott have termed "Mutation." Bateson's terms 'Continuous' and 'Discontinuous' are useful as distinguishing gradual from sudden ontogenic variation.

In general our five working hypotheses as to the factors of evolution are theoretically related to the time stages of Variation as seen in the following table: —

Buffon's	*Ontogenic*	
	a Gonagenic	
	b Gamogenic	
	Allei	
	c Embryogenic	St. Hilaire's
	d Somatogenic	Lamarck's
Darwin's	*Phylogenic*	

I again call attention to the fact that Neo-Darwinism has hitherto presupposed and practically assumed 'fortuitous phylogenic variation' as its basis, for it is solely related with the selection of those ontogenic variations which are also phylogenic. Neo-Lamarckism, on the other hand, is solely connected with inheritable 'somatogenic' variation. Buffon's factor of the 'direct action of the environment' plays upon all four ontogenic stages, and both theoretically and as observed by experiment, produces profound ontogenic variations; the question is, under what circumstances do such ontogenic variations in each of the four stages become phylogenic? This factor would be partly but not wholly set aside by proof that somatogenic variations are not inherited. St. Hilaire's factor of the action of environment upon early stages of development would result in purely fortuitous variations, and, as he himself clearly perceived, would require Selection to give it an adaptive direction. Nägeli's factor, on the other hand, assumes definite but not necessarily adaptive 'phylogenic' variation — his views have been very generally misconceived on these points — and, as he pointed out, his factor would also require Selection to determine which of the definite lines of growth were adaptive.

It seems necessary to thus clearly state the relations of the time stages of variation to each of the five factors, in order to show the decisive bearings our future exact research will have upon them. For example, the proof that variation is either 'definite' or that it is 'adaptive' prior to or independently of Selection, will constitute conclusive disproof not of Darwin's theory but of Neo-Darwinism. The fate of Lamarckism, on the other hand, depends upon the demonstration that phylogenic variation is not only 'definite' and 'adaptive' but that it is anticipated by corresponding somatogenic variation.

A review of recent thought upon the variation problem shows that these life stages are becoming generally recognized. I shall pass by Lamarck's and Darwin's factors which are so thoroughly understood and speak only of the other three.

BUFFON'S FACTOR IN VARIATION.

As regards Buffon's factor, which is the most comprehensive of all, we know that Spencer and Weismann both assumed that the direct action of the environment was primarily a factor of evolution. Weismann first regarded this solely as the protozoan source of Variation, but has recently given it a wider play in the action of environment upon the germ-cells as a cause not of definite variation but of variability. The line of research upon the dynamic action of environment in its influence upon somatogenic variation followed by Hyatt, Dall, and others, is paralleled in the more recent speculation connecting the environment directly with the gonagenic and gamogenic stages, initiated by Virchow,[1] Kölliker,[2]

[1] R. Virchow: Descendenz und Pathologie. *Virchow's Archiv*, CIII, 1886, pp. 1–15, 205–215, 413–437. Ueber den Transformismus. *Archiv f. Anthropologie*, 1889, p. 1.

[2] Kölliker: Das Karyoplasma und die Vererbung. *Zeitschr. f. wissenschaftl.*

Ziegler,[1] Sutton, and others. In a similar vein are the suggestions of Geddes, while those of Gerlach and Ryder direct our attention mainly to mechanical alterations in the embryonic stages of development. Botanists such as Vines, Detmer, and Hoffmann have pointed to the influence of environment upon gonagenic variation. Experiments of a general character resulting principally in embryogenic and somatogenic variation have been recently carried on by Cunningham, Agassiz, and others, as illustrating the direct action of the environment. Followers of Buffon's factor are also more or less identified with Lamarckism. The distinction is mainly expressed in the terms 'otagenic' and 'kinetogenic' of Ryder; for under Buffon's factor the organism is passive, while under Lamarck's it is active. Among others who have supported Buffon's principle are Packard, Eimer, Cunningham, Ryder, and Dall.

This literature and so-called 'evidence' upon Buffon's factor exhibits the greatest confusion of interpretation, and demonstrates that our conceptions first, as regards heredity, second, as regards variation under a changed environment, require thorough recasting.[2] First as regards evolution in relation to heredity. The reversion phenomena as seen in human anatomy wholly set aside Weismann's conception of evolution as the selection of favorable and the elimination of unfavorable hereditary variations; in other words, of selection acting directly upon the germ-plasm. These phenomena indicate rather that the direct process is not one of elimination but of suppression from the later stages of ontogeny, and that only after an enormous interval of time does actual elimination occur. Abnormal nervous conditions such as seen in Anencephaly are accompanied by the revival of a large number of latent characters. In Galton's language, patent characters become latent in the course of evolution.

Zoologie, 1886. Eröffnungsrede der ersten Versammlung der Anatomischen Gesellschaft in Leipzig. *Anat. Anzeiger*, II, 1887.

[1] Ernst Ziegler: Die neuesten Arbeiten über Vererbung und Abstammungslehre und ihre Bedeutung für die Pathologie. Tübingen.

[2] J. T. Cunningham: The Problem of Variation. *Natural Science*, vol. III, pp. 282–287. Also, Researches on the Coloration of the Skins of Flat-Fishes. *Jour. Mar. Biol. Assoc.*, May, 1893. (See also *Trans. Roy. Soc.*, 1892–3.)

In Weismann's language, on the other hand, in explanation of dimorphism in hymenoptera and other types, there are certain sets of biophors corresponding to certain possibilities of adult development. Apply this to the celebrated case of the flat-fishes and the remarkable results recently obtained by Agassiz, Filhol, and Giard in artificially producing more or less symmetrical flat-fishes by retaining the young near the surface. Weismann's interpretation of the evolution of flat-fishes has always been that it was by the selection of asymmetrical and elimination of symmetrical 'determinants.' In the light of these experiments he must now recast this explanation by saying that the flat-fishes have kept in reserve a set of symmetrical 'determinants' since the period when our first record of the asymmetrical type appears or about three million years!

This attack upon the speculations of one writer is a digression. What I really wish to bring out is the necessity of a far more critical analysis of the various kinds of evidence for Buffon's factor. This necessity may be illustrated by the different interpretations of color change in direct response to changed environment.

The most significant experiments upon color are those of Cunningham upon the flat-fishes. He has proved that during the early metamorphosis of young flat-fishes, when pigment is still present on both sides, the action of reflected light does not prevent the disappearance of this pigment upon the side which is turned towards the bottom, so that the color passes rapidly through a retrograde development; but prolonged exposure to the light upon the lower side causes the pigment to *reappear*, and upon its reappearance the pigment spots are in all respects similar to those normally present upon the upper side of the fish. It is very important not to confuse these results, of deep interest as they are, with those obtained where the environment is new in the historic experience of the organism. Experiments upon color, therefore, afford a marked illustration of the necessity of drawing a sharp distinction between cenogenic and palingenic variations. We have, in many cases, been mistaking repetitions of ancient types of structure for newly acquired structures. When the pale *Proteus* is taken from the Austrian caves, placed in the sunlight, and in the course of a month becomes darkly pigmented, there are two interpretations of this pigmentation: either that we have revived a latent character, or that we have created a new character. The latter interpretation can alone be taken as a proof of Buffon's factor when it is found to be followed by hereditary transmission.

Poulton,[1] as a supporter of Neo-Darwinism, takes this view, in reply to Beddard and Bateson, and as an induction from his beautiful and exact experiments upon the coloring of lepidopterous larvae. After producing the most widely various colorings and markings by surrounding the larvae during ontogeny with objects of different colors, he urges that the changes thus directly produced simply revert to adaptations to former conditions of life, in other words, that they are palingenic. Whether this interpretation is correct or not, Poulton proves that, no matter how stable certain hereditary characters may appear to be, repetition in ontogeny depends upon repetition in environment, and that there are wide degrees of ontogenic variations which do not become phylogenic at least in several successive generations.

From many other analogous researches we gather the following principle to which far too little attention has been paid in the study of the phenomena of variation in their bearing upon the factors of evolution: *It is that ontogenic repetition depends largely upon repetition in environment and life habit, while ontogenic variation is connected with variation in environment and life habit.* If the environment be changed to an ancient one, then ontogenic variations tend to regression or reversion (*i.e.*, palingeny) or practically to repetition of an ancient type. It is necessary to state clearly that there is practically conclusive evidence for such a principle, not only in the later stages of development, as in the respiratory metamorphosis of the Amphibia, but extending back to very much earlier stages

[1] E. B. Poulton: Further experiments upon the color-relation between certain lepidopterous larvae, pupae, cocoons, and imagines and their surroundings. *Trans. Ent. Soc.*, pt. IV, p. 293. London, 1892. (Contains a reply to Beddard and Bateson.)

than we have hitherto suspected. Thus a vast amount of evidence which has been brought forward as proof of Buffon's factor, *i.e.*, of the direct action of environment in producing definite and adaptive ontogenic variations is in reality in many cases no proof at all.

Having thus eliminated errors of interpretation, the great question still remains as to what happens when the environment is a wholly new one in the historical experience of the organism. Do the ontogenic variations exhibit a new direction? Is this direction adaptive, *i.e.*, towards progressive adaptation? What relations have such new conditions to the hereditary potencies of the germ-cells?

Out of all actual researches it becomes clear that experimentation can henceforth be separately directed upon the four stages of development, and that it will be possible in some degree to draw such lines of separation. New mechanical and chemical influences can be applied in each stage and withdrawn in the subsequent stages, the difficulty being to reach the extreme point where a profound influence is exerted without interfering with the reproductive functions.

One effect of new environment upon the gonagenic, gamogenic, and embryogenic stages will be *saltation*. Ryder[1] has recently treated this in a most suggestive manner in discussing the origin of Japanese gold-fish. Turning to St. Hilaire's hypothesis, we find he had in mind embryogenic variation mainly traceable to respiratory and chemical changes. Virchow extends the cause of sudden change further back to chemico-physical influences upon the germ-cells. The causes and modes of sudden development arising from whatever ontogenic stage demand the most careful investigation, chiefly in their bearing upon the relation of ontogenic to phylogenic variation. Galton has discussed the subject objectively under the head of 'Stability of Sports,' and Emery, under the head of 'Primary Variations,' has supported Galton's observation that such salta-

[1] The inheritance of modifications due to disturbance of the early stages of development, especially in the Japanese domesticated races of gold-carp. *Proc. Acad. Nat. Sc. Phila.*, 1893, p. 75.

tions often exhibit a strong capacity for inheritance. Bateson reaches in the conclusion of his work a modified form of St. Hilaire's factor of saltatory evolution, and believes that species have largely originated by 'discontinuity' of variation or the sudden accession of new characters from unknown causes, concluding that all inquiry into the causes of variation is premature. The materials he has brought together are of the greatest value, and he has already been able to throw in doubt many current beliefs, such as that variability is greater in domestic than in wild animals. His interpretation of these materials is, as we have seen, weakened, so far as it bears on our search for the evolution factors, by the fact that from the nature of most of his evidence he cannot discriminate between ontogenic and phylogenic variation: moreover, he discards any attempt to discriminate between palingenic and cenogenic variations. This lack of analysis leads him into what appears to be an entirely erroneous induction, for the principle of discontinuity is opposed by strong evidence for continuous and definite phylogenic variation as observed in actual phyletic series.

Nägeli's Factor and Phylogenic Variation.

Nägeli's factor[1] introduces us to an entirely distinct territory — to the opposite extreme from saltation. It is one we can no longer set aside as transcendental because of the strong likeness it bears at first sight to the internal perfecting principle of Aristotle. It is supported in a guarded manner by Kölliker and Ziegler. It contains the large element of truth that the trend of variation and hence of evolution is predestined by the constitution of the organism; that is, granted a certain hereditary constitution and an environment favoring its development, this development will exhibit certain definite directions, which when reaching a survival value will be acted upon by selection. I have recently[2] described as the '*potential of similar varia-*

[1] C. v. Nägeli: Mechanisch-physiologische Theorie der Abstammungslehre. München und Leipzig, 1884.

[2] Rise of the Mammalia in North America. *Stud. Biol. Dept. Columbia College*, vol. I, No. 2, September, 1893.

tion' an evolution principle which seems to be well supported by palaeontological evidence. It is this: while the environment and the activity of the organism may supply the stimuli in some manner unknown to us, definite tendencies of variation spring from certain very remote ancestral causes; for example, in the middle Miocene the molar teeth of the horse and the rhinoceros began to exhibit similar variations; when these are traced back to the embryonic and also to the ancestral stages of tooth development of an early geological period, we discover that the six cusps of the Eocene crown, repeated to-day in the embryonic development of the jaw, were also the centers of phylogenic variation; these centers seem to have predetermined at what points certain new structures would appear after these two lines of ungulates had been separated by an immense interval of time. In other words, upper Miocene variation was conditioned by the structure of a lower Eocene ancestral type.

This is the proper place to recall a kindred conception of Variation which has been in the minds of many, and has been clearly formulated it appears by Waagen. It is of Variation so inconspicuous and so slight that it can only be recognized as such when we place side by side two individuals separated by a long series of generations.[1] Mark the contrast with the extreme of St. Hilaire's saltatory evolution; or again, the contrast with Darwin's and Weismann's conception of Variations, not, it is true, of a saltatory character, but as sufficiently important and conspicuous to become factors in the survival of the organism. This conception of 'phylogenic variation,' as we have seen, is consistent with the application of Galton's principles to human evolution, but it finds its strongest support in palaeontology, and is the unconscious motive of dissent on the part of all palaeontologists, so far as I know their opinions, independently working in all parts of the world, to the fortuitous Variation and Selection theory.

[1] This was brought out by the writer in his Oxford paper. See *Nature*, August 30, 1894, p. 435. It has recently been independently stated with great clearness by Scott in his article Variations and Mutations. *American Journal of Science*, November, 1894. Scott, following Waagen, revives the term 'mutation' for what Nägeli has termed 'phylogenic variation.'

Our palaeontological series are unique in being phyletic series. They exhibit no evidences of fortuity in the main lines of evolution. New structures arise by infinitesimal beginnings at definite points. In their first stages they have no 'utilitarian' or 'survival' value. They increase in size in successive generations until they reach a stage of usefulness. In many cases they first rise at points which have been in maximum use, thus appearing to support the kinetogenesis theory. In extensive fossil series we also find evidence of anomalous or neutral variations, such as Bateson has brought together, but these are aside from the main lines of evolution. They present no evidence for the Neo-Darwinian principle of the accumulation of adaptive variations out of the fortuitous play around a mean of adaptive and inadaptive characters, but they present strong evidence of the Darwinian principle of the survival of the fittest. The main trend of evolution is direct and definite throughout, according to certain unknown laws and not according to fortuity. This principle of progressive adaptation may be regarded as inductively established by careful studies of the evolution of the teeth and the skeleton. Its bearing upon Lamarck's factor of the transmission of somatogenic variation was pointed out by myself in 1889; it does not positively demonstrate Lamarck's factor because it leaves open the possible working of some other factor at present unknown, and Lamarck's factor is also inadequate; but it positively sets aside Darwin's factor as *universal* in the origin of adaptations and as a consequence 'the all-sufficiency of Natural Selection.' If Lamarck's factor is disproved, in other ways, it leaves us *in vacuo* so far as a working hypothesis is concerned.

The conclusions which Hyatt, Dall, Williams, Buckman, Lang, and Würtemberger have reached among invertebrates are independently paralleled by those of Cope, Ryder, Baur, Scott,[1] the writer, and many other morphologists. The same general philosophical interpretation of evolution is now independently announced from an entirely different field of work by Driesch. We may waive our applications of these facts to theories, but let us not turn our backs to the facts themselves!

[1] W. B. Scott: On Some of the Factors in the Evolution of the Mammalia. *Journ. of Morphology*, vol. V, 1891, p. 378.

The Outlook for Induction.

The problem just raised is the main one. No longer misled by palingenic variation under revival of an ancient environment, let us set ourselves rigidly to the analysis and investigation of the responses of the organism to new environment, in all four stages of development. Are these responses adaptive? Is there a teleological mechanism in living matter as Pflüger[1] has expressed it? Is this mechanism in the adult reflected in the germ?

One most hopeful outlook is in Experimental Evolution. Bacon in his *Nova Atlantis* three centuries ago projected an institute for such experiments, which when it finally materializes should be known as the Baconian Institute. The late Mr. Romanes proposed to establish such a station at Oxford, and went so far as to institute an important series of private experiments, which were unfortunately interrupted by his death. What we wish to ascertain is, whether new ontogenic variations become phylogenic, and how much time this requires.

The conditions of a crucial experiment may be stated as follows: An organism A, with an environment or habit A, is transferred to environment or habit B, and after one or more generations exhibits variations B; this organism is then retransferred to environment or habit A, and if it still exhibits, even for a single generation, or transitorily, any of the variations B, the experiment is a demonstration of the inheritance of ontogenic variations. These are virtually the conditions rightly demanded by Neo-Darwinians for an absolute demonstration, either of Lamarck's or Buffon's principle of the inheritance of embryogenic or somatogenic variation. There is no record that such conditions have as yet been fulfilled, for hitherto organisms have been simply retained in a new environment, and the profound modifications which are exhibited may simply be the exponents of an hereditary mechanism acting under the influence of new forces. Such experiments will probably require an extended period of time, for we learn from palaeontology, as well as from palingenic variation,

[1] Pflüger: Die teleologischen Mechanik der lebenden Natur. Bonn, 1877.

that phylogenic inheritance is extremely slow in a state of nature.

It is desirable to establish non-infectious experimentation involving the conditions named above, mainly as a test of Lamarck's factor. Varigny has also proposed a crucial experimental series mainly upon Buffon's factor. His volume upon *Experimental Evolution* is an invaluable review, especially of French researches in experimental transformism. Much of this is in the line brought together some years ago by Semper in his *Animal Life*. Varigny draws a valid distinction between morphological variation and physiological variation, including under the latter internal chemical and constitutional differences which are not displayed in structure but must underlie all reactions. Under the head of what I have called Gonagenic Variation, the author discusses the work of Gautier[1] upon the influence of previous fertilization in plants as well as upon the chemistry of plants in connection with color variation. He adds to the observations of Yung and Born other studies upon sex determination. He describes the experimental teratogeny or embryonic variation of Dareste, Fallou, and later observers.

Throughout Varigny's volume it is nevertheless evident that none of the studies upon Ontogenic Variation hitherto have been specifically directed to the vital problem, as they must be in the future. Varigny makes a useful suggestion as to the importance of imitating natural conditions in experimental work, but he fails to emphasize the importance of the tests set forth above in order to ascertain whether the acquired modifications have actually been impressed upon the hereditary mechanism or merely upon the various stages of ontogeny.

The general conclusion we reach from a survey of the whole field is, that for Buffon's and Lamarck's factors we have no theory of Heredity, while the original Darwin factor, or Neo-Darwinism, offers an inadequate explanation of Evolution. If acquired variations are transmitted, there must be therefore

[1] Armand Gautier: Du Mécanisme de la Variation des Êtres vivants. (Hommage à Monsieur Chevreul à l'Occasion de son Centennaire. F. Alcan. Paris. 1886.)

some unknown principle in Heredity; if they are not transmitted, there must be some unknown factor in Evolution.

As regards Selection, we find more than the theoretical objections advanced by Spencer and others. Neo-Darwinism centers upon the principles of fortuitous variation, utility, and selection as universal. In complete fossil series it is demonstrated that these three principles, however important, are not universal. Certain new adaptive structures arise gradually, according to certain definite laws, and not by fortuity.

Lamarck's and Buffon's factors afford at present only a partial explanation of these definite phylogenic variations, even if the transmission of acquired variations be granted. Nägeli's factor of certain constitutional lines of variation finds considerable verification in fossil series as a principle of determinate variation, but not as a general internal perfecting tendency. St. Hilaire's factor of occasional saltatory evolution by sudden modification of the hereditary mechanism is established, but not as yet understood, although we are perhaps approaching an explanation through experimental embryology.

Our standpoint towards Variation in relation to all the Factors requires thorough reconsideration. The Darwinian law of Fortuity and the Buffon law of the direct action of Environment, have hitherto been inductions from variations which may be largely ontogenic and transitory. They both require confirmation on data of phylogenic variation. As for Lamarck's factor, the evidence seems to be conclusive that somatogenic variation is largely adaptive; but it remains to be proved that phylogenic variations as observed in human anatomy and in palaeontology are invariably anticipated by corresponding changes in the individual, in other words, that the definite current of variation is guided by the inheritance of individual reactions.

Another consideration is, that individual Variation may play a far less conspicuous rôle than we have assigned to it; in other words, that many of the most important changes in successive generations are so gradual as to be entirely inconspicuous in a single generation.

Our conception of the mechanism or physical basis of

Heredity is also to be made much clearer by a series of experiments directed to palingenic variation, in order to ascertain how far the revival of an ancient environment arouses latent hereditary forces. The experiments already well advanced by Cunningham, Agassiz, and Poulton indicate that *progressive inheritance is rather a process of substitution of certain characters and potentialities than the actual elimination implied by Weismann.*

My last word is, that we are entering the threshold of the Evolution problem, instead of standing within the portals. The hardest tasks lie before us, not behind us, and their solution will carry us well into the twentieth century.

SIXTH LECTURE.

THE EMBRYOLOGICAL CRITERION OF HOMOLOGY.

EDMUND B. WILSON.

THE word homology is at present generally employed to denote two widely different kinds of morphological likeness. One of these is the similarity between corresponding parts of *different individuals* (hence equivalent to the "special homology" of Owen), and this we regard as a result of the descent of those individuals from a common ancestor; such a resemblance may, therefore, be designated as a *genetic homology*. The other is the similarity between corresponding or repeated parts in the *same* individual (including the "serial homology" of Owen, or homodynamy of Bronn, and the "homonomy" of Haeckel); this may be called *meristic homology*, adopting the convenient word recently introduced by Bateson. We shall here deal only with genetic homologies (which form the groundwork of all systems of classification), and especially shall attempt to consider the criteria employed in their determination as they appear in the light of recent advances in embryology.

I.

As originally defined by Owen, genetic (*i.e.*, "special") homology was based entirely upon anatomical data. It was a morphological correspondence in the "relative position and connexions" of parts without regard to their mode of development; indeed Owen expressly repudiated that "loose use" of the word to denote similarity of development of which he accused Geoffroy St. Hilaire and the German anatomists.

With the development of the "biogenetic law" or recapitulation theory as a corollary to the general theory of evolution the matter appeared in a different light. For if ontogeny be in truth a repetition or record of phylogeny, then the embryological development must furnish the highest criterion of homology, since community of phyletic origin (homology) becomes synonymous with community of ontogenetic origin.

Now, although no one believes that ontogeny is actually a true and complete record of phylogeny, it is nevertheless surprising to observe to what an extent the embryological criterion has superseded the anatomical, and how deeply rooted the ontogenetic conception of homology has become, notwithstanding all that has been written about "falsification of the record," cenogenesis, secondary and adaptive modification, and the like. Even the greatest of naturalists has tacitly allowed it to pass; for in the glossary of the Origin of Species (drawn up by Mr. Dallas but approved by Darwin) homology is defined as: "That relation between parts which results from their development from corresponding embryonic parts, either in different animals, as in the case of the arm of man, the fore-leg of a quadruped, and the wing of a bird, or in the same individual, as in the case of the fore and hind limbs in quadrupeds, and the segments or rings and their appendages of which the body of a worm, a centipede, etc., is composed." It appears in the writings of many eminent contemporary morphologists and has crept into some of our best dictionaries. I cite a single example of each: "On the other hand, the point of fundamental importance in the comparison of two or several organs is their origin from equivalent parts of the embryo." "Hence in the comparison of two or more embryonic organs we must rely not so much upon their later development as on their first origin."[1] The *Century Dictionary* has it thus: Homology is "that relation of parts which results from their development from corresponding embryonic parts. Homology in this sense implies genetic relationship, and consequently morphological likeness or affinity"—*i.e.*, the morphological likeness is an inference from the mode of ontogeny!

[1] Rabl: Theorie des Mesoderms, I. *Morph. Jahrb.*, XV, 1889, p. 229.

It is not to be supposed that the authors of these and similar statements (which might be almost indefinitely multiplied) hold an erroneous view of homology. The citations are given merely to show how intimately the conception of homology has become associated with the embryological data — how prominent a place has been assigned to the embryological as distinguished from the anatomical criterion for its determination. And, yet, it must be evident to any candid observer not only that the embryological method is open to criticism but that the whole fabric of morphology, so far as it rests upon embryological evidence, stands in urgent need of reconstruction. For twenty years embryological research has been largely dominated by the recapitulation theory; and unquestionably this theory has illuminated many dark places and has solved many a perplexing problem that without its aid might have remained a standing riddle to the pure anatomist. But while fully recognizing the real and substantial fruits of that theory, we should not close our eyes to the undeniable fact that it, like many another fruitful theory, has been pushed beyond its legitimate limits. It is largely to an overweening confidence in the value of the embryological evidence that we owe the vast number of the elaborate hypothetical phylogenies which confront the modern student in such bewildering confusion. The inquiries of such a student regarding the origin of any of the great primary types of animals involve him in a labyrinth of speculation and hypothesis in which he seeks in vain for conclusions of even approximate certainty. Was the ancestral vertebrate most nearly like an annelid, an arachnid, a crustacean, a nemertean, or a tunicate? Who shall say whether annelids arose from platodes, from medusæ, from actinian-like forms, from "Trochozoa," or from something else? It is not surprising that morphology can give no certain answer to these questions, for they are complex and difficult and must necessarily be attacked by means of inference and hypothesis. It is, however, a just ground of reproach to morphologists that their science should be burdened with such a mass of phylogenetic speculations and hypotheses, many of them mutually exclusive, in the absence of any well-defined standard of value by which to estimate their relative probability. The truth is that the search after suggestive working hypotheses in embryological morphology has too often led to a wild speculation unworthy of the name of science; and it would be small wonder if the modern student, especially after a training in the methods of more exact sciences, should regard the whole phylogenetic aspect of morphology as a kind of speculative pedantry unworthy of serious attention. There can be no doubt, I think, that this state of things is leading to a distaste for morphological investigation of the type represented, for instance, by Balfour and his school, while the brilliant discoveries of the cytologists and experimentalists, supplemented by speculations of the Weismannian type, have set up a new tendency that gathers in force from day to day.

No candid morphologist can deny that the responsibility for the present degradation of pure morphology must on the whole be laid at the door of speculative embryology, and is the result of too exclusive and undiscriminating a faith in the embryological criterion of homology and the recapitulation theory. It is no wonder that a strong reaction against that theory has set in, — that faith in the embryological record is giving way to skepticism and indifference. There is a strong suspicion that the embryological method has somehow failed, and there are even some morphologists who seem almost ready to abandon the entire recapitulation theory. That theory has always had its critics, but the present movement against it may conveniently be dated from Gegenbaur's paper on "Ontogeny and Anatomy," published five years since. In a very moderate and reasonable spirit the author protests against too exclusive a faith in the embryological record, insisting that ontogeny is not the exclusive or even the main source of evidence regarding descent. "But if we are compelled to admit that cenogenetic characters are intermingled with palingenetic, then we cannot regard ontogeny as a pure source of evidence regarding phyletic relationships. Ontogeny, accordingly, becomes a field in which an active imagination may have full scope for its dangerous play, but in which positive results are by no means everywhere to be attained. To attain such results the palingenetic and the ontogenetic[1] phenomena must be sifted apart — an operation that requires more than one critical *granum salis!* On what ground shall this critique be based? Assuredly not by way of a *circulus vitiosus* on the ontogeny again; for if cenogenetic characters are present in one case, who will guarantee that a second case, used for a comparison with the first, does not likewise appear in a cenogenetic disguise? If it once be admitted that not everything in development is palingenetic, that not every ontogenetic fact can be accepted, so to speak, at its face value ('als bare Münze'), it follows that nothing in ontogeny is immediately available for the critique of embryological development. This conclusion cannot be escaped. The necessary critique must be drawn from another source."[2] This source is, namely, the facts of comparative anatomy.

The force of this passage cannot be disputed, and it has led the way in a revolt against the recapitulation theory which has assumed formidable dimensions, especially in England, where within the year one leading morphologist has declared that "von Baer's law falls to the ground," and another has asserted that "the embryological method has failed in so far as the attempt has been made to extend the general proposition (von Baer's law) to particular questions of descent." Most of the protests against the theory have thus far been directed against the view that particular larval or embryonic forms (Trochophore, Nauplius, etc.) can in the totality of their organization be regarded as representatives of ancestral types, even after allowing for a considerable amount of "secondary" (cenogenetic) modification. As far, however, as particular parts or organs are concerned, it is still generally assumed that a safe basis of comparison is to be found in the origin of these parts from particular regions (germ-layers, etc.) of the embryo; and thus the embryological criterion of homology is still, on the whole, accepted. It is just here, however, that some of the most startling contradictions have recently come to light; and to certain of these attention will now be called.

By way of introduction we may first inquire, what is meant by the "embryological origin" of a part or organ. Origin

[1] *Cenogenetic* obviously intended. [2] *Morph. Jahrb.*, XV, p. 5.

with respect to what? The events of ontogenesis may conveniently (though quite arbitrarily) be divided into four series of stages, viz., (1) cleavage-stages, (2) gastrular stages (including the *formation* of the germ-layers as distinguished from their further *differentiation*), (3) embryonic (differentiation of the germ-layers, early organ-formation), and (4) larval (the free immature stages). These stages, of course, overlap more or less, and a special larval stage often does not exist. Which, now, of these periods shall be taken as a starting-point? This question may best be viewed from an historical standpoint. The early embryologists, chief among them von Baer, were impressed mainly with the embryonic and larval stages; and it was the study of these stages that led von Baer to the enunciation of his celebrated law. It was the same stages, again, that were taken years afterwards by Agassiz, Bronn, Darwin, and Fritz Müller as the basis of the recapitulation theory; and they have always formed the basis of popular exposition, which has worn threadbare the subject of gills and gill-slits, visceral and vascular arches, notochord, tails, and teeth. Similarities in development are here not only clear and striking, but obviously have some palingenetic meeting, since they give irresistible evidence of ancestral reminiscence. But embryologists did not stop here. Huxley's brilliant comparison between the layers of the embryo and those of the coelenterate body, and the ultimate demonstration of the universality of the germ-layers, pushed the basis of comparison back into the gastrular stages, and the germ-layers came to be taken as the real starting-point in the embryological study of homology. Meanwhile, however, it was found that the "mesoblast" shows so many contradictions in its mode of origin, that by common consent it was regarded as of subordinate value. Thus the primary germ-layers, ectoblast and entoblast, came to be regarded — are perhaps still generally regarded — as the ultimate standard for the comparison of one form with another; and the embryological criterion became in the long run a question of similar relations to the primary germ-layers. "In every case homologies between organs must be reduced to similar relations to the two layers of the coelenterate body (due allowance being made for possible processes of substitution). Ectoderm and entoderm are the original bases of all tissues and organs (with the probable exception of the germ-cells) in the Coelenterata: the same holds true of the ectoderm and entoderm of embryonic forms." [1] Justification for this implicit trust in the primary germ-layers as a fixed and absolute standard of comparison was sought, on the one hand, in the supposed constancy of their relation to corresponding adult parts (ectoblast always giving rise to nervous structures, entoblast to the digestive epithelium, etc.), on the other hand, in their alleged homology to the layers of the diblastic ancestral type (that "mageres Thiergespenst" the Gastraea of Haeckel, etc.) from which all other forms have descended.

The final steps in this direction were the attempts to determine the origin of parts even in the pregastrular or cleavage stages by tracing out the cell-lineage or cytogeny — *i.e.*, the derivation of particular parts from individual blastomeres of the segmenting ova. This method, which for a time seemed to give brilliant promise, took as a starting-point the unsegmented ovum; and thus exhausted the possibilities of observation.

It is plain from the foregoing analysis that the phrase "similarity of embryological origin" is used with great latitude, sometimes denoting merely a similar relation to well-differentiated larval or embryonic parts (*e.g.*, parts derived from the skeleton of the first visceral arch); sometimes a similar mode of origin with direct regard to the germ-layers (ventral nerve-cord of annelids and arthropods); sometimes a similar relation to the cleavage-stages (products of the neuroblasts in leeches and chaetopods).

It may be shown, in the first place, that not one of these stages can *in itself* be taken as a fixed standard of homology. Let us first consider the larval and embryonic stages, which may be conveniently considered together. It is a familiar fact that parts which closely agree in the adult, and are undoubtedly homologous, often differ widely in larval or embryonic origin either in mode of formation or in position, or in both. Innumerable cases will suggest themselves to any em-

[1] Kleinenberg: Lopadorhynchus, p. 18.

bryologist of hollow organs that arise either by invagination or by delamination; of paired organs that arise from either single or paired foundations, and *vice versa*. No one is disposed to question the homology of the spinal cord of a teleost with that of a shark on the ground that the one arises as a solid cord, the other as an infolded tube. The stomodæum of *Lopadorhynchus* is undoubtedly homologous with that of *Lumbricus*, though the one appears as a paired, the other as a single median structure. The ventral nerve-cord of *Polygordius* is certainly homologous with that of *Lumbricus*, though the former appears as a median unpaired thickening of ectoblast while the latter arises by the concrescence of two widely separated halves. A very striking example of this kind is afforded by the development of *Balanoglossus*. In *B. Kowalevskii* the third pair of body-cavities arise as archenteric pouches (Bateson); in the Bahaman form, as shown by Morgan,[1] these same cavities are formed, not as pouches, but by the aggregation of scattered mesenchyme cells of unknown origin. Such cases show that the particular *modus operandi* by which a structure arises in the larva gives in itself no certain standard of morphological value. Position is equally untrustworthy, for in numberless cases homologous parts differ in this respect, for example, the heart of mammals and birds, the mesoblast-bands of leeches and oligochaetes (which are at right angles to those of many polychaetes), the nerve-cords of *Polygordius* and *Lumbricus*, as already cited. Any embryologist could cite scores of cases of homologous parts that arise in some cases at or near their final position, in other cases far removed from it, so that very extensive growth is necessary to transport them thither.

Let us now examine briefly the gastrular stages, that is, the origin of parts with respect to the germ-layers. Until very recently the primary germ-layers have been — and with justice — regarded as the most constant and trustworthy basis of comparison; and so constant is the connection between them and the adult organs (*e.g.*, between ectoblast and nervous system) that it is difficult not to regard this connection as a fixed

[1] *Journ. Morph.*, IX, 1894.

or even necessary one. Morphologists can, however, no longer close their eyes to the fact that the primary germ-layers do not have that fixed and absolute value that has so long been attributed to them. This is shown by contradictions both in the origin and in the fate of the germ-layers. It has long been recognized that the primary layers are not, as Haeckel originally endeavored to maintain, always differentiated by the same process. On the contrary, there are many processes, some of which differ radically from the very beginning of development, such as the multipolar delamination of *Geryonia* as compared with the embolic invagination of *Amphioxus* or *Echinus*. It is true that here, as elsewhere, a nearly complete series of intermediate forms exists; but this does not affect the truth of the general proposition or remove the difficulty. Despite these differences of origin, however, the primary germ-layers have been generally regarded as homologous; for they are considered as homologous with the respective layers of the Coelenterata (in which the primitive diblastic condition has been retained), a homology which has persisted through all the transformations of the higher types, and through all the secondary modifications of the process of gastrulation.

But even this faith is being shaken, since it is becoming more and more clearly apparent, both on general and on special grounds, that even in a prospective sense the inner and outer layers of the diblastic embryo do not always have the same value. Balfour recognized this truth on the general ground that their relation to the "mesoblast" is not always the same, and later researches have, I think, abundantly confirmed his view. As I have elsewhere urged, we certainly cannot regard the layers of the diblastic embryo of *Lopadorhynchus* as the precise homologues of those of *Amphioxus*, when in the former case it is the outer layer and in the latter case the inner layer that is to give rise to the entire mesoblast.[1]

[1] A curious example of the lengths to which embryologists are driven in the attempt to meet this difficulty is shown in Lwoff's recent attempt to show that the mesoblast and chorda of *Amphioxus* are derived from the outer layer. My own observations on this point (in Amphioxus) differ widely from Lwoff's in the matter of fact; but even by accepting his conception of the gastrulation we do not escape the contradiction.

It is when we turn to more special evidence, however, that we discover how much caution is necessary in our treatment of the germ-layers. The most striking of this evidence is afforded by the extraordinary contradiction between the egg-development and bud-development in certain animals, of which I select the Tunicata as the best known example and one which, through the courtesy of Dr. Hjort, I have myself had an opportunity to examine critically. In the egg-development of Tunicata, in all known cases, the atrial chamber is derived as a pair of ectoblastic pouches invaginated from the exterior, and the nerve-ganglion is as usual derived from the dorsal ectoblast. In the bud-development the history is totally different. In all cases the bud arises a two-layered vesicle of which

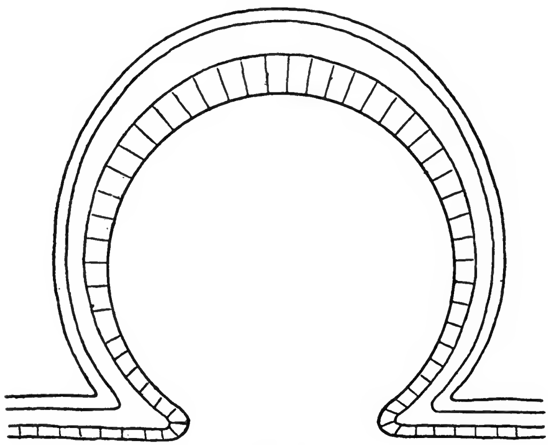

DIAGRAM I.

Very young diblastic tunicate bud. The outer layer always arises from the parental ectoderm. The inner layer arises from the entoderm (epicardium or pharyngeal wall) in *Clavelina*, *Perophora*, *Didemnum*, etc., from the ectoderm (atrial wall) in *Botryllus*.

the outer wall is continuous with the parental ectoblast. The inner wall shows a surprising contrast in different forms. In one series, represented by *Perophora*, *Didemnum*, *Clavelina*, and some others, the inner vesicle is derived from the parental entoderm, viz., from the wall of the branchial sac. In *Botryllus*, on the contrary, there is not the least doubt that it arises from the wall of the atrial chamber, that is, from what was originally ectoblast. In both cases the later history is the same.[1] The inner vesicle, namely, divides into three sacs, of which two give rise to the atrial chamber of the bud, while the third (median) forms the alimentary canal and *from its dorsal wall arises the ganglion.*

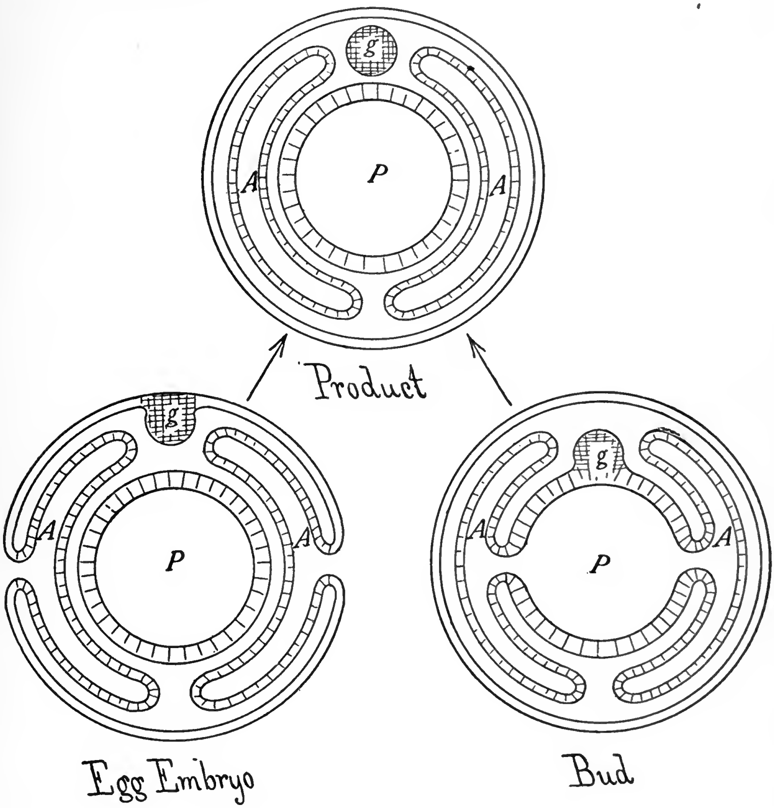

DIAGRAM II.

Bud-development contrasted with egg-development in the compound tunicates. *P*, the inner sac; *A*, atrial chamber; *g*, ganglion. The figures are purely diagrammatic.

From whatever point of view we regard this case we are confronted with a fatal dilemma. Thus, in the case of *Botryllus*, if we regard the inner and outer layers of the bud as corre-

[1] See Hjort, *Mitth. Zool. St. Naples*, X, 1893; and *Anat. Anz.*, X, 1894.

sponding respectively with those of the gastrula, then both atrial chamber and ganglion arise from entoblast. If, on the other hand, we consider both these layers as ectoblast (on account of their origin) then the alimentary canal of the bud arises from that layer. Should it hereafter be shown that the atrial chamber of *Botryllus* arises in the egg-development from the entoblast, the difficulty regarding the ganglion would remain as great as ever. If with Hjort we say that the layers of the bud are not germ-layers "in the ordinary sense," we do no more than restate the problem.

Analogous contradictions have recently been observed in the asexual reproduction and regeneration of worms. In these cases, as a rule, the new parts are derived from the corresponding parts of the old body and in accordance with the demands of the germ-layer theory. In the regeneration of the tail of *Lumbriculus*, for example, Miss Randolph has shown[1] that the new tail is derived from a mass of cells which have nearly the same arrangement of germ-layers as in the egg-embryo and are derived from the corresponding layers of the old body. The later researches of v. Wagner and Schmidt seem, however, to show that in this same animal both proctodaeum and stomodaeum are regenerated from the *entoblast* instead of arising from the ectoblast, as in the egg-embryo. In the Rhabdocoelous genera *Microstoma* and *Stenostoma* the new pharynx is regenerated (in the process of asexual division) from the *mesoderm* (parenchyma) as shown by the concurrent researches of v. Wagner and Ott, while in the egg-embryo (of the related genus *Mesostoma*) it is invaginated from the *ectoblast*.

It is plain that in such cases of asexual development as these the developmental test of homology breaks down more or less completely; for parts that are undoubtedly homologous (ganglion of the egg-embryo and bud-embryo of *Botryllus*, *etc.*) differ totally in mode of origin even with respect to the germ-layers. It may be urged that in regeneration and agamogenesis, development is condensed and abbreviated so as no longer to repeat the phyletic development, and this is no

[1] *Journ. Morph.*, VII, 1892.

doubt true. This explanation contains, however, a fatal admission ; for if secondary modification may go so far as completely to destroy the typical relations between the germ-layers and the parts of the adult, then those relations are not of an essential or necessary character, and we cannot assume that the germ-layers have any *fixed* morphological value, even in the gastrula.

Let us finally consider the study of cell-lineage or cytogeny. The contradictions here reach a climax. In some cases, it is true, there is a really marvelous agreement in the cytogeny of related forms (annelids, gasteropods), so that adult homologies are accurately foreshadowed by cell-homologies, even in the earliest cleavage-stages. But as we extend the comparison extraordinary contradictions arise. Lilly has recently shown that the lamellibranch *Unio* agrees very precisely with the gasteropod *Crepidula* (Conklin) up to a certain point, but then shows a sudden and at present inexplicable departure in the origin of the larval mesenchyme. The cephalopod suddenly presents us with a totally different type of cleavage in which no homologies whatever can be drawn between the individual blastomeres and those of other mollusks or of annelids. In another direction we find (in the Polyclade) a cleavage very closely resembling the annelid type in form, yet the individual blastomeres have from the very start an entirely different morphological value.

II.

The puzzling facts reviewed in the foregoing brief survey leave no escape from the conclusion that embryological development does not in itself afford at present any absolute criterion whatever for the determination of homology. Homology is not established through precise equivalence of origin nor is it excluded by total divergence ; and this statement holds true for all the stages of development, though on the whole the later stages seem to show a closer agreement than the earlier. But it does not by any means follow that the embryological method has therefore failed and must be abandoned as a means of investigating homologies. The most skeptical critic of the recapitulation theory cannot deny that the embryological evidence is often of the clearest and most convincing character. What is needed is a more trustworthy basis of interpretation; and until this has been established the embryological method must be employed with the greatest caution. At the present time we do not apparently possess the data necessary to establish such a basis, but certain principles are becoming evident and some of these I shall endeavor to consider.

The very statement that homologous parts differ in embryological origin itself implies some higher standard of homology that outweighs that of development. What is that standard? Obviously it is the standard of Owen, viz., *the structure and structural relations of the developed organ;* it is the standard of comparative anatomy. It is this criterion that we employ, for instance, in the identification of the ganglion of the *Botryllus* bud, the stomodaeum of the regenerating *Lumbriculus*, the primary mesoblast-cells of the polyclade or annelid, the neural cell-cords of the leech or earth-worm, or the posterior body-cavities of Tornaria. In all these cases — and they might be indefinitely multiplied — *it is the prospective and not the retrospective aspect of development that is decisive.* This is shown most clearly in the case of the germ-layers and the cleavage-stages. In the latter case embryonic origin and position are utterly valueless apart from developmental destiny. In all these cases homology is determined *not by origin, but by fate.* And thus we are brought to a point of view directly opposed to that which on the whole is, I believe, the prevalent one — to the view, namely, that *we must primarily take anatomy as the key to embryology, and not the reverse. Comparative anatomy, not comparative embryology, is the primary standard for the study of homologies, and hence of genealogical descent.*

There are, of course, many special exceptions to this statement, yet I believe on the whole that it is from this point of departure that the renovation and reconstruction of embryological morphology must be carried out. The practical bearings of this conclusion cannot be discussed without some consideration of the general nature of development; and the present divergence of opinion on this subject is so great that it will be necessary to define to some extent my own position. I hold, in common with many others, that the ovum is a body composed of a specifically organized substance which may conveniently be called *germ-plasm* or *idioplasm* (for the present purpose we need not inquire whether the idioplasm is contained in the nucleus, in the cytoplasm, or in both). Upon an appropriate stimulus (fertilization, etc.) and under certain definite conditions, the idioplasmic organization gradually transforms itself (during the "ontogeny") into another form of organization, namely, that of the multicellular adult body. The egg-organization, no less than that of the adult, must in every species possess a definite and specific character, for the eggs of different species developing under identical external conditions give rise each to its own appropriate form. Adult homologies must be potentially represented in the idioplasm; for by no process of casuistry can we escape the fact that every adult character is in some manner involved in the constitution of the idioplasm. But is it, then, necessary to assume that every such character is represented by a definite part or region in the idioplasm — that the germ-plasm is, for instance, a microcosm of biophores, determinants, etc., as Weismann assumes, or that there is a predetermined region of the egg-substance for every adult part? According to such a view adult homologies, being represented by homologies between corresponding parts or regions of the germ-plasm, would be really as complete and definite in eggs as in adults.

I, for one, cannot regard such a view either as logically necessary or as in accordance with known facts. Our ignorance of the internal constitution of the germ-plasm is so great that we may well be cautious in setting up definite hypotheses regarding its nature; but the facts of regeneration, of heteromorphosis, of the development of isolated blastomeres are, I believe, fatal to any strictly conceived theory of germinal localization. I believe that facts point on the whole to the conclusion that the idioplasmic organization may be far simpler than that of the adult; that ontogeny is not merely the transformation of one kind of organization into another, but involves beyond that a steady increase of complexity, owing partly to the interaction of the developing organism with its environment, partly to the multiplication and interaction of its own parts. If this view be correct adult homologies need not necessarily preëxist in the form of egg-homologies but *may be created as the ontogeny progresses.*

How such a process is possible may be illustrated by one or two cases. Loeb has shown that the color pattern in the yolk-sac of a fish-embryo (*Fundulus*) is not in itself predetermined, but depends on the distribution of the blood-vessels. The pigment-cells are at first uniformly distributed, but upon the establishment of the circulation of the yolk-sac they migrate towards the vessels (probably, as Loeb suggests, attracted by a chemical substance in the blood) and thus give rise to a definite pattern. Graf has recently shown,[1] in like manner, that the color-patterns of leeches are not in themselves inherited but depend upon the arrangement of the muscle-fibres, between which the amoeboid pigment-cells wander. In either of these cases the assumption of a special set of "determinants," etc., for the color pattern, is absurd.

A third illustration, of the most instructive kind, is the case of the ciliated arms of the *Pluteus* larva of sea-urchins which has been carefully studied and discussed by Herbst.[2] As is well-known, these organs are definite in form and number and have a characteristic arrangement; and no one would question that the arms of the various species may be homologized with one another. Each arm contains a calcareous axis or spicular skeleton, and in the developing larva the arm grows out as the axis is formed. If now the larvae be made to develop in water containing no calcareous matter (Pouchet and Chabry) or in water containing a small excess of potassium chloride (Herbst) no spicules are formed *and in consequence no arms are produced.* Thus arises a larva (Diagram III) closely similar in general appearance to a *Tornaria.* In this case it is quite unnecessary to suppose that the ectoderm inherits any tendency to produce a definite number of arms in a particular position. The for-

[1] Reported at the meeting of the Am. Morphological Society in December, 1894.

[2] *Zeit. wiss. Zool.*, LV.

mation of the arms may be only incidental to the production of the spicules, and we need only assume in the ectoderm a general power of growth which is exerted at particular points under stimulus acting at those points. In this case the necessary condition of development is a certain internal stimulus (formation of spicules). This stimulus, itself, however, is directly dependent on external conditions (the chemical environment), and hence the formation of the arms is determined both by internal and external conditions.

Accurately determined cases like these are at present far from common, though some others might be mentioned.

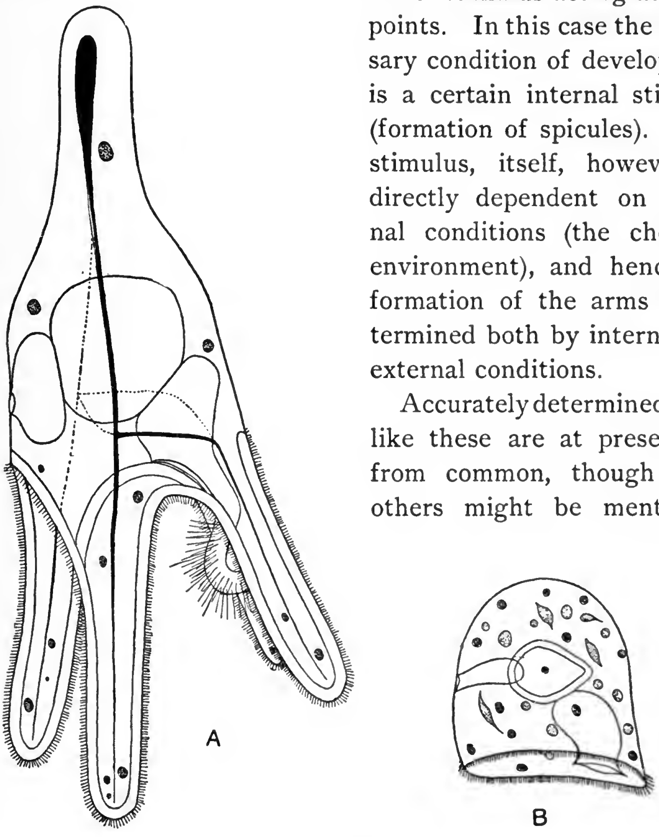

DIAGRAM III.

A. — Normal *Pluteus* of *Strongylocentrotus lividus*, from the side.
B. — "Potassium-larva" of *Sphærechinus granuluris* at a stage corresponding with the last (after Herbst).

But even a single such case opens the way to a rational conception of epigenesis; for it enables us in a measure to comprehend how a single property of the germ-plasm may involve a whole train or cluster of events in development — how, in the words of Herbert Spencer, development involves a multiplication of effects, each differentiation tending to become the parent of new differentiations. This conception does not in any manner set aside the necessity of assuming, for each species of animal, a specifically organized germ-plasm, nor does it conflict with the fact that the egg-substance may even show a certain amount of regional differentiation before development begins. It does, however, greatly simplify our view of the germ-plasm, and removes it in a measure from that inaccessible and mysterious region where Weismann and his followers would place it. These cases reveal, furthermore, the vital part played in development by environmental conditions. We perceive that our attention has been focused so closely upon the germ-plasm regarded as the substratum of inheritance and development as to obscure our view of the essential relation in which it stands to the conditions under which development takes place. In other words our point of view has been too largely morphological while the physiological aspect of development has been thrown into the background.

Recent writers in embryology, foremost among them Driesch, Hertwig, Loeb, and Herbst, have, however, clearly perceived the vital importance of the conditions of development in distinction to the innate tendencies of the germ-plasm, and Driesch especially has published an elaborate theory of development in which full recognition is accorded to the physiological aspect of the question. The germ of this theory is contained in the writings of Wilhelm His, and the views of this profound and philosophical embryologist are of immense importance because of the abundant fruit they have borne in the works of the experimental morphologists. His resolves the work of the ontogeny into two factors. The first of these is the "law of growth" (Wachsthumsgesetz) that is inherent in the germ-plasm or idioplasm (Keimstoff) and represents the essential element of inheritance; the second comprises the conditions under which that "law" operates (such as the shape and size of the egg, distribution of yolk, pressure of membranes, nature of the surrounding medium, and the like). Every event in the development may therefore be conceived as the product of these two factors. Thus, the various foldings by which the body of the embryo vertebrate is formed are produced by definite distribution of horizontal growth in the blastoderm in connection with mechanical limitations which oppose its lateral extension.

A conception essentially similar to this, though elaborated with far greater detail and subtlety, lies at the foundation of Driesch's and Hertwig's theories of development; and similar views appear in the writings of Nägeli, Vöchting, and many others. In Driesch's writings, which in some respects appear to express most adequately the present aspect of the problem (though few, probably, will accept his more extreme views), we find every step in development regarded as a *physiological reaction* of the idioplasm (*i.e.*, an "Auslösung") to the conditions of its environment, internal or external, existing at the time. The nature of the reaction (*i.e.*, of any particular phenomenon in the development) depends always upon the two factors recognized by His, viz., primarily upon the nature of the idioplasm, which is predetermined, and secondarily upon the conditions existing at the moment of the reaction. These conditions are in part external to the embryo (chemical composition of the surrounding medium, temperature, pressure of membranes, osmotic relations, and the like), in part internal (effects of food-yolk, surface-tensions, chemical differences, mutual pressure of cells, and no doubt a multitude of unknown physiological relations between the developing parts), the latter being progressively created by the activity of the idioplasm itself.[1]

We may now return from this digression to a consideration of the question of homology. It is clear, according to the view just outlined, that development may be altered in two ways, viz., either by congenital changes in the idioplasm (which must in a greater or less degree involve correlated changes in the internal conditions), or by changes in the external conditions under which the idioplasm operates; and it is this fact that renders it so difficult, in the present state of our knowl-

[1] Hertwig's Zeit- und Streitfragen der Biologie (received during the preparation of the MS. of this lecture) gives an extremely clear and suggestive discussion of a theory of development similar in many respects to that here outlined.

edge, to frame any satisfactory definition of homology on an embryological basis.

His himself has attempted such a definition in the following words: "From a physiological point of view definite systems or organs are morphologically equivalent when they arise from the same foundation (aus einer gegebenen Anlage) under the same conditions."[1] Such a correspondence constitutes, according to His, a "complete homology" in Gegenbaur's sense. If, however, the conditions (Formbedingungen) be not identical, then arises a partial correspondence equivalent to the "incomplete homology" of Gegenbaur.

This definition is obviously true as far as it goes; but a little consideration of the facts of normal and experimental embryology show that it is so defective as to be practically worthless. For, in the first place, it demands that completely homologous parts shall be identical in normal development, which is by no means always the case (witness the ganglion of *Botryllus* in the bud-embryo and in the egg-embryo, or the summer and winter eggs of Cladocera, or the different species of *Balanoglossus* or of *Peripatus*). A particularly striking case of this kind is that of the crustacean *Alpheus* (as described by Brooks and Herrick), a single species of which has three different modes of development in three localities, although the adults do not perceptibly differ, and two of these modes are widely dissimilar, involving the whole character of the metamorphosis. It seems impossible to explain this case except under the view that the differences of development result from corresponding differences in the surrounding conditions. In the second place, the conditions of development at particular stages may be artificially altered (so that, for instance, an egg is compelled to undergo a mode of cleavage totally unlike the normal) without in the least degree altering the final outcome of the ontogeny.

Such cases make it certain that changed conditions *may* profoundly alter the mode of development without perceptibly affecting the end-result (though in many cases the end-result is affected also, as in the case of polymorphic insects, etc.).

[1] *Arch. Anat. u. Phys.*, 1887, p. 438.

They indicate, farther, that the ontogenetic stages are plastic, capable of modification, in a far higher degree than has hitherto been supposed; and they point towards the conclusion that the events of ontogeny are essentially adaptive, and that *the persistence of ancestral reminiscences in development or of similarities in the development of homologous parts is in some way connected with the persistence of ancestral conditions of development.* We are still too ignorant of the nature of these conditions to make much use of this conclusion, but the way of further investigation is pointed out by two recently enunciated principles. The first of these has recently been stated by Adam Sedgwick, who, arguing along very different lines from those I have followed, concludes that "the tendency in embryonic development is to directness and abbreviation; that ancestral stages of structure are only retained in larval stages in so far as they are useful; and that their appearance in the embryonic (foetal) stages is owing to 'the absorption of a larval or immature free stage into embryonic life,' where they become 'functionless,' and therefore largely removed from the direct action of natural selection." This is undoubtedly a true explanation as far as the larval stages are concerned, and in a measure, no doubt, applies to the embryonic stages. It leaves out of account, however, a second principle which was enunciated by Kleinenberg (1886), namely, that although embryonic ancestral stages may be functionless so far as the external environment of development is concerned, they are still functional in the sense of forming a more or less necessary part of the mechanism of development, — *i.e.*, as a preparation for organs that succeed them in the ontogeny, as, for example, cartilage precedes bone, or a tubular heart forms the foundation for a chambered one. "From this point of view many rudimentary organs appear in a different light. Their obstinate reappearance throughout long phylogenetic series would be hard to understand were they really no more than reminiscences of bygone and forgotten stages. Their significance in the processes of individual development may in truth be far greater than is generally recognized. When in the course of the phylogeny they have played their part as intermediary organs (*Vermittel-*

ungsorgane) they assume the same function in the ontogeny. Through the stimulus or by the aid of these organs, now become rudimentary, the permanent parts of the embryo appear and are guided in their development; when these have attained a certain degree of independence, the intermediary organ, having played its part, may be placed upon the retired list."[1]

This principle is unquestionably of fundamental importance; and it remains true whether or not we accept the doctrine of "substitution," with which it was connected by Kleinenberg. It is thus that I would interpret, for example, the gastrula stage of development. The diblastic embryo is a necessary stage in the formation of a complex multicellular body of which the most fundamental characteristic is the differentiation of an internal part devoted in the main to the functions of nutrition from an external part which serves as a protection and as the medium of communication with the environment. In a broad sense, therefore, the diblastic embryo does represent an ancestral phase such as still exists in the lower metazoa, *but only by virtue of the persistence of the original functional contrast between the inner and outer parts.* For if the diblastic embryo be simply an inheritance from the ancestral type ("Gastraea," etc.), why has not its ancestral mode of origin likewise persisted "by inheritance," and why should it arise by processes (invagination, delamination, etc.) so widely diverse?

We are still too ignorant of the nature and distribution of the forces at work in development, and so of the causal connection between the successive stages of ontogeny, to determine how far this principle can be applied. But it seems clear that when once a particular train of events has been established in the ontogeny, it must form, as it were, a path of least resistance along which the idioplasmic transformation will continue to proceed until definite causes operate to divert it into a new path. Only upon such a view can we form any conception of the physiological meaning of recapitulation in the case of functionless ancestral stages. And it is equally clear that we cannot successfully analyze the morphological aspect of development

[1] Kleinenberg: Lopadorhynchus, p. 223.

without further knowledge of its physiological aspect. I believe that until this knowledge is forthcoming the embryological criterion of homology must remain of relatively small value, and be held in subordination to the anatomical.

The all-important need of embryology at the present day is the study of embryonic physiology. In this direction experimental embryology has opened the way to an apparently unlimited field of research; and there is reason to hope that here, as in the physical sciences, the study of phenomena under artificially modified and simplified conditions, will give us a deeper insight into the more complex conditions existing in nature. The greatest fault of embryology has been the tendency to explain any and every operation of development as merely the result of "inheritance," overlooking the vital point that every such operation must have some physiological meaning for the individual development, hard though it may be to discover. We have still but the most rudimentary notion of what the physiological conditions of development are, and how they operate, but they must be thoroughly investigated before the reform of embryological morphology can be carried out, and here experimental embryology and physiological morphology must lead the way. But, on the other hand, it is no less essential not to neglect the study of phenomena where nature is the experimenter. While it is true that the normal operations of development are essentially physiological problems, we must, nevertheless, not lose sight of the cardinal fact that the organization of the idioplasm, which is at the bottom of every such operation, is *an inheritance from the past.* The idioplasm of every species has arisen through the modification of a preëxisting idioplasm, and every response that it gives to stimulus is an expression of its past history. Hence, we need not despair of ultimate success in the attempt to decipher the meaning of the embryological record, and to find in ontogeny a real criterion of homology; and it is here that we find encouragement, were any needed, not to relax our efforts to investigate the normal phenomena of comparative embryology on the largest scale, and down to the minutest detail. I do not belong to those who, impressed by the rich fruits and still greater promise of the experimental method, regard the past achievements of comparative morphology as labor lost, and look forward with indifference to its future. If its present methods are defective, they must be reformed; but the great body of facts it has accumulated, and will accumulate hereafter, will always form the very framework of biological science.

SEVENTH LECTURE.

CELL-DIVISION AND DEVELOPMENT.

J. PLAYFAIR McMURRICH.

WITHIN the last few years the science of embryology has undergone a remarkable development, especially along two lines. In earlier years the dominant idea was a phylogenetic one, embryologists seeking to discover from the individual development facts which might contribute to the formulation of a correct phylogeny for the species or group under consideration. They were content accordingly to carry the ontogeny back to the formation of the primary germ-layers, that is, back to a stage supposed to represent an ancestral diploblastic ancestor, the Gastraea; for still earlier stages a brief statement as to whether the gastrulation was embolic or epibolic or that the segmentation was total, regular or irregular, centrolecithal or meroblastic, being considered sufficient for the most part. Not but that there were striking exceptions to this prevailing indifference regarding the details of cleavage, and these have borne fruit in the awakening of embryologists to the importance of tracing out the cell-lineage of organs and of gaining thereby a deeper insight into the phenomena of differentiation, the line of research which is so characteristic of recent embryology, and which forms one of the paths along which the science has progressed. Concomitant with this new departure, which may be termed the cytogenetic method of embryology, in contrast to the phylogenetic, came the development of the science of experimental or physiological embryology, from which so many important deductions concerning the fundamental constitution of the ovum have resulted.

Both cytogenetic and experimental embryology have had to deal more especially with the earliest stages of development and with the factors which govern the histological differentiation of the ovum; and inasmuch as both these phenomena, in those ova which have been most carefully studied, are associated with a cleavage of the ovum into spherules standing in definite relation to one another, inquiry has naturally been aroused as to the laws or forces which determine the relation which one cleavage plane shall bear to another. The cytogenetic method has revealed the fact that in the ova of any one species, under normal conditions, the relations of the cleavage planes to one another in the earlier stages vary only to a slight degree, while the experimental method, on the other hand, has shown that, under abnormal conditions, these relations may be completely changed, and that in certain cases the cleavage may even be temporarily suppressed, the nuclei only undergoing division. External conditions, such as pressure, may then interfere with the normal direction of the cleavage planes, but what determines these normal directions?

Zoölogists, however, have not been the first to consider this problem, the earliest attempts at its solution having been made by botanists, the greater definiteness of the vegetable cell-wall and the relative lateness of tissue-differentiation in plants rendering the study of the problem apparently simpler than it seems to be in the case of animal tissues; and in addition it is noteworthy that the tendency to reduce the phenomena of life to chemical and physical causes has been more marked in the case of students of vegetable physiology, due perhaps to the greater complexity of the vital phenomena exhibited by animals.

A most suggestive discussion of the question has been given by Sachs, the famous Wurzburg botanist, in a series of important papers, the gist of his conclusions being, however, contained in his lectures on vegetable physiology. He points out in the first place a fact too often lost sight of by zoölogists, that there is a decided distinction between growth and cell-division. In the animal kingdom the two phenomena are as a rule somewhat intimately related, though a little consideration will show that in it examples are to be found comparable to the cases among plants which have led Sachs to this important deduction. Sachs recalls the cases of such algae as *Caulerpa,* in which an organism of considerable size, differentiated into root-, stem-, and leaf-like portions, is presented, the whole, nevertheless, consisting of but a single cell, just as a unicellular Infusorian may reach a size considerably greater than that of many multicellular Rotifera, and may show also a very decided differentiation of tissue. The most conclusive case bearing upon the idea is, however, that of the alga *Stypocaulon,* a portion of which is represented in Fig. 1. Here one finds in the terminal part of the largest branch a distinct indication of branching, and it may be noticed that the terminal portion of the branch is equal in size to the lower portion. In other words, this terminal part of the branch has reached its full growth and yet it has undergone no cell-division. Growth is in this case accordingly independent of cell-division, and the converse is likewise true, for in the older portion of the plant, *in which growth has ceased,* cell-division occurs.

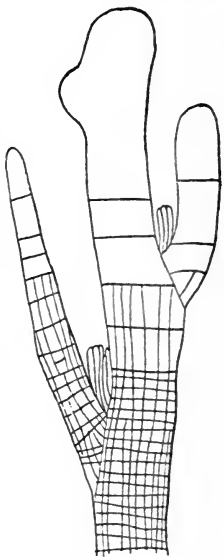

FIG. 1. (After Sachs.)

The form of the plant, accordingly, since form is dependent on the mode of growth, is not determined by the cell-division; but, on the other hand, it seems that, to a certain extent at least, the mode of cell-division is determined by the form, an idea which has been admirably expressed by DeBary in the aphorism, "Die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen." A simple example of this thesis is furnished, according to Sachs, by the pollen mother-cells of the orchid *Neottia.* These cells vary in shape considerably, and the mode of their division into the four pollen grains to which each gives rise, varies according to the shape. Thus where the mother-cell is circular and discoidal it divides into four cells lying in a single plane (Fig. 2, *A*); where it possesses an oval form two cleavage planes divide it into two parts, a third plane at right angles to the first two dividing the middle cell (Fig. 2, *B*); where it is club-shaped the arrangement of the division planes is that shown in Fig. 2, *C*; and, finally, not to multiply examples, where it has a tetrahedral form the four resulting cells are also arranged in a tetrahedral manner (Fig. 2, *D*).

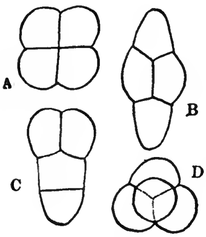

Fig. 2. (After Sachs.)

We have, then, as the first thesis that the direction and arrangement of the cleavage planes is dependent, to some extent at least, upon the form of the original mass. To this Sachs adds two other theses to the effect that there is a tendency for cells to be equally divided, and that successive cleavage planes tend to be arranged at right angles to those which precede them. These three theses may be grouped together and spoken of as Sachs' law of right-angled division.

Let us now, following Sachs' example, apply this law to a comparatively simple case, noting the result with the view to observing if it agrees with what is actually found in Nature. For this purpose Sachs chooses a disc of protoplasm with an elliptical outline (Fig. 3) which is to undergo division only at right angles to the surface, *i.e.*, only in two planes. The first two divisions will naturally correspond with the longer and shorter axes of the ellipse, and will divide it into four segments. To carry out the law the succeeding divisions will necessarily fall into two series; in the first place there will be a series of cleavage planes which form ellipses (p, p) confocal with one another and with the periphery of the original elliptical disc of protoplasm, and secondly, crossing these there will be two series of planes (a, A, a), each of which consists of a number of confocal hyperbolas arranged around one of the foci (f) of the original ellipse. Sachs

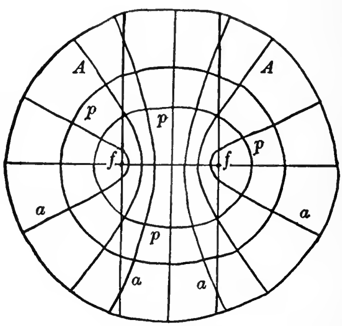

Fig. 3. (After Sachs.)

terms the confocal ellipses the *periclines*, and the hyperbolas *anticlines*, the division of the protoplasmic disc being produced by an alternation of these two kinds of cleavage planes. The result of this mode of division is a number of cells arranged in definite curves, each cell belonging to two curves which cross one another at right angles, one of the curves being portion of an ellipse while the other is portion of an hyperbola. The periclines and anticlines, in other words, form what geometricians term orthogonal trajectories, and if Sachs' law be valid we must expect to discover in plant and animal tissues indications of the occurrence of these trajectories.

We do not, it is true, find either in plants or animals a mathematical regularity of the periclines and anticlines, but an examination of plant embryos, or even of adult individuals of some of the simple plants, shows unmistakable indications of their existence. For instance, in Fig. 4 is shown a specimen of the alga *Melobesia*, in which the periclines and anticlines, though modified by the fan-like form characteristic of the species, nevertheless are clearly recognizable, and, so far as animals are concerned, orthogonal trajectories are to be found in the early stages of some of the Crustacea,[1] where the ectodermal cells form a single layer lying on the surface of the yolk, as in the naupliar region of the embryo of the Crayfish. The general form of the embryo here, as in *Melobesia*, modifies the arrangement somewhat, and is a factor which must be taken into consideration.

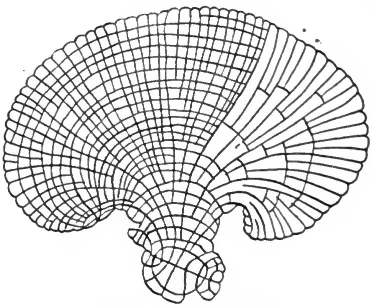

FIG. 4. (After Sachs.)

If, for instance, instead of an elliptical disc, which is not infrequent in plant forms, a circular one had been taken as a basis on which to estimate the arrangement of the division-planes under Sachs' law, then there being but a single focus, all the anticlines would pass through that focus, and, furthermore, if a

[1] H. Reichenbach: Studien zur Entwickelungsgeschichte des Flusskrebses. *Abhandl. Senckenbg. Naturf. Gesellsch.*, XIV, 1886.

sphere had been the form chosen, the anticlines would have been meridional planes and the periclines equatorial, the typical cleavage of a hololecithal animal ovum by two meridional planes followed by an equatorial, being in perfect harmony with Sachs' law.

Let us now leave for a time further consideration of this law and consider briefly another one also formulated by a botanist, Berthold,[1] and known as the law of minimal contact surfaces. If air be driven through water to which a considerable amount of albumen has been added, a froth is produced, the globules composing it flattening against one another so as to give an appearance resembling closely that presented by the parenchymatous tissues of plants. The forces which determine this pseudocellular formation, as it has been termed, have been investigated principally by the physicist Plateau, who discovered the law of minimal contact surfaces, which Berthold has applied to cases of true cell-formation. This law is to the effect that the lamellae which separate the various air particles arrange themselves so that the sum of the surface-areas which they form, shall, under the given conditions, be a minimum. The force to which this result is due is that known as surface tension.

Berthold examined the arrangement of the division-planes in certain plant tissues with reference to this law, and found that it held good, and also pointed out that the movements or rearrangement of cells, which frequently take place after division is completed, especially in animal ova in which definite and firm cell-walls are wanting, is explicable under the same law. The division of any two cells takes place in a plane which is determined by the law acting on these particular cells, but this plane need not be that which is called for when the entire mass of cells is taken into account, and therefore a rearrangement is necessary. There seems to be little room for doubt but that this law of minimal contact surfaces acts in the determination of the arrangement of cleavage-planes, and we have thus two factors which enter into the question, or rather four, since Sachs' law involves three distinct factors.

[1] G. Berthold: Studien über Protoplasmamechanik. Leipzig, 1886.

It may be pointed out that these two laws are very different fundamentally, since that adopted by Berthold is based on the action of extrinsic causes, while Sachs' seems to depend rather on the interaction of intrinsic forces. It seems probable, however, that Sachs' law is to be brought into correlation with the principle which, according to Hertwig,[1] governs the direction of the karyokinetic spindle. It is a well-known fact that the division of the cytoplasm stands usually in intimate relation to the karyokinetic phenomena, though not invariably, since karyokinesis may occur and result in nuclear division without an accompanying division of the cytoplasm. The two phenomena are, however, as a rule associated, and it is to be noted that Hertwig has shown that in an ovum subjected to pressure the spindle forms with its longer axis at right angles to the line of pressure, *i.e.*, in the direction of least resistance. The same result has been obtained by Driesch[2] in his experimental studies on Echinoid eggs, polar pressure applied to these eggs converting the third cleavage, which normally is equatorial, into a meridional one, an oblong plate composed of eight cells lying in the same plane being the result. It is interesting to note, in passing, that a similar arrangement of the cells in the eight-celled stage is normally found in the ova of Teleosts, and is due to the pressure produced by the large yolk-mass, as is shown by Morgan's[3] experiment of puncturing the egg-membrane and allowing a certain amount of the yolk to escape, whereupon the third cleavage became meridional as in normal Echinoid ova.

It is possible, then, that both the laws already defined may be due to the action of extrinsic forces, but it must be remembered that these laws do not account for all the phenomena shown in the formation of cleavage-planes, and that there are numerous cases which cannot be brought into harmony with them. Thus it is well known to every embryologist that cells, even when destitute of yolk, do not by any means divide

[1] Hertwig: Welchen Einfluss übt die Schwerkraft auf die Theilung der Zellen? Jena, 1884.

[2] H. Driesch: Entwicklungs-mechanische Studien, III–VI. *Zeitschr. für wissensch. Zool.*, LV, 1892.

[3] T. H. Morgan: Experimental Studies on Teleost Eggs. *Anat. Anz.*, VIII, 1893.

equally, — in all cases of teloblastic growth, for instance, the division of the teloblasts being unequal ; and, indeed, the phenomena presented by teloblastic growth stand apparently in such marked contrast to what might be expected from the operation of the factors included in Sachs' law that a brief consideration of them will not be out of place here, and for example's sake the case of teloblastic growth seen in the embryo of an Isopod Crustacean may be considered.

In an Isopod embryo, such as that of *Asellus*, two well-marked regions can be distinguished. Anteriorly there is recognizable a somewhat heart-shaped region whose ectoderm shows more or less distinctly the orthogonal trajectories already referred to, and which, as the later development shows, is that portion of the embryo which corresponds to the Nauplius larva, which is of such frequent occurrence in the life-histories of the lower Crustacea, but which does not exist as a free-swimming stage in the Isopods, there being in these forms a marked condensation of the development. Behind this naupliar region one finds the ectodermal cells arranged in remarkably definite longitudinal rows, varying in number from about twenty-two to twenty-five, and on tracing them back towards the hind end of the embryo each one will be found to terminate in a single large cell which is known as a teloblast (Fig. 11, *et*). It is by the continued division of these teloblasts that the cell-rows are formed ; in a very young embryo the teloblasts are situated at the posterior end of the naupliar region, the metanaupliar region, as it is termed, being unrepresented at this stage, and if successive stages be examined it will be found that first of all spindles form in the teloblasts with their long axes parallel with the longitudinal axis of the embryo, and situated slightly in front of the centers of their cells, the result being that a transverse row of cells is divided off from the teloblasts by a process of unequal division. Later spindles again form in the teloblasts, and another transverse row of cells is interposed between the teloblasts and the row previously formed, and so the process goes on, the teloblasts being gradually forced backwards over the surface of the yolk as the transverse rows increase in number.

This, then, is what is meant by teloblastic growth, and it will have been noticed from the description that the division of the teloblasts is not a division into equal parts, and that the successive division planes are not at right angles but parallel to one another. The arrangement of the cells may, however, be reduced to an accordance with the principle of orthogonal trajectories, the metanaupliar region being regarded as a quadrangular superficies, in which case the trajectories would be straight lines cutting one another at right angles, and it may be presumed that the exception to the third factor of Sachs' law is only apparent. In fact, if this factor be defined as a tendency for the cells to divide so as to be arranged in orthogonal trajectories, the exception no longer exists, there being, then, no necessity for successive rectangular divisions. The divisions by which the row of teloblasts is formed originally may be regarded as one set of trajectories which are formed once and for all, the other set of trajectories being produced by successive divisions.

There is still left, however, the exception to equal divisions, and in addition it may be pointed out that teloblastic division forms an exception to Hertwig's law since the successive spindles form not at right angles, but parallel to the lines of pressure, as it has been pointed out that the teloblasts are being continually forced backward over the surface of the yolk and are, therefore, subject to a pressure acting on them in an antero-posterior direction. It does not, indeed, seem possible to account for the peculiarities of teloblastic growth on any of the mechanical hypotheses at present at our disposal. Sachs' law, even if modified as suggested, and the law of minimal surface areas, while explaining the arrangement of the cells, do not explain why this arrangement should have been brought about by teloblastic division, since it might have been accomplished by a succession of rectangular divisions. It seems in the Crustacea to be a provision for the rapid growth of the metanaupliar region of the body, and at present it must be conceded that our knowledge of cell-mechanics is too superficial to permit of an explanation of it on a purely mechanical basis.

We have, so far, been dealing with cases in which distinct cleavage planes are developed, and have very largely confined our attention to the planes themselves. It must be recognized, however, that on account of the intimate relation usually existing between karyokinesis and cytoplasmic division, the arrangement of the cleavage planes stands, to some extent at any rate, in relation to the direction in which the karyokinetic spindle lies, and we may carry our inquiries a little further and seek to determine the cause of the positions assumed by the spindles. Berthold's law, of course, refers only to the arrangement of the cleavage planes; granting the division of the cell in any direction, the flattening which its surface undergoes, or the shifting which it itself undergoes, is governed by the law of minimal contact surfaces, and this depends on the forces which we term surface tension. Now it is clear that Berthold's law affects only the form and, within narrow limits, the position which a cell may possess; it does not necessarily affect the plane in which that cell may divide. On the other hand, Sachs' law attempts to define the direction which the spindle shall occupy, the plane in which the division shall occur, and, therefore, has a much deeper significance. It formulates a certain number of the factors which influence the direction of the division planes, the most important of these factors being that of form. It has been shown, however, that exceptions occur to one at least of the factors, and even so far as the factor of form is concerned, it is readily seen that it is not all-sufficient to explain variations which occur in the cleavage of ova having a similar form. Thus it does not explain why the spherical yolkless ovum of an Ascidian should have a bilateral cleavage, as shown by van Beneden and Julin,[1] while the apparently similar ovum of an Echinoderm should undergo what may be termed a radial cleavage; we must go deeper, and add to the factor of form that of the constitution of the cell. But even this hardly suffices, for we can hardly imagine that different ova from a single individual can differ very greatly in their

[1] E. van Beneden and C. Julin: La segmentation chez les Ascidiens et ses rapports avec l'organisation de la larve. *Arch. de Biol.*, V, 1894.

constitution, chemical or physical, and yet, as E. B. Wilson[1] has shown, the cleavage of different ova of *Amphioxus* may vary considerably, being in some cases radial, in others "spiral," and in others even bilateral. The factors laid down by Sachs represent only some of those which govern cell-cleavage.

In this connection mention may be made of a set of phenomena, first, I believe, pointed out by Rauber,[2] who groups them together as instances of what he terms segment attraction, without, however, essaying to explain how this attraction is effected. An excellent example of this phenomenon is afforded by the segmenting egg of the Squid, *Loligo*, according to the account given by Watasé.[3] In this egg, which undergoes what may be termed a meroblastic segmentation, the first cleavage plane corresponds with the median longitudinal plane of the adult animal, the egg being thus divided at the first cleavage into a right and left half. The second cleavage is at right angles to the first, while the third, represented by two planes, is practically parallel with the first. As a result of these cleavages the protoplasmic pole of the egg presents the appearance shown in Fig. 5, and possesses, as may readily be seen, a well-marked bilateral symmetry. In the succeeding divisions the segment attraction becomes marked, peculiarities affecting a cell or a group of cells at one side of the blastoderm being repeated in the corresponding cell or group of cells of the opposite side, even though a number of cells not showing the peculiarities intervene. A concrete example of this phenomenon, which Watasé speaks of as analogous variation on the two sides of the blastoderm, may be given. In an ovum

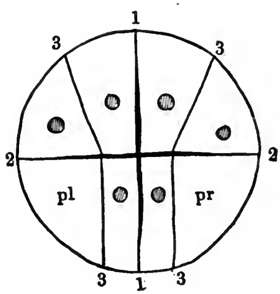

FIG. 5. (After Watasé.)

[1] E. B. Wilson: Amphioxus, and the Mosaic Theory of Development. *Journ. Morph.*, VIII, 1893.

[2] A. Rauber: Neue Grundlage zur Kenntniss der Zelle. *Morph. Jahrb.*, VIII, 1883.

[3] S. Watase: Studies on Cephalopods. I. Cleavage of the Ovum. *Journ. Morph.*, IV, 1891.

which had reached the stage represented in Fig. 5, one cell, that designated *pr* in the figure, was found to show an abnormal karyokinetic spindle, a triaster, indicating a simultaneous division of the nucleus into three parts, being present, and in the corresponding cell of the other half of the blastoderm, *pl*, the same abnormality occurred. This is simply one out of several cases which could be given and may suffice to illustrate what is meant by segment attraction. This name suggests an interaction of certain cells of the blastoderm upon one another, a sort of telepathy as it were, but what the nature of the interaction may be, indeed, whether it is in reality an interaction in the strict sense of the term or not, it is quite beyond our present power to determine.

There has been a tendency, most marked, perhaps, among the experimental embryologists to reduce the direction of the cleavage planes, that is, the direction of the karyokinetic spindles, to the action of causes acting from without the cell, pressure and gravity being the forces most frequently brought forward as explanations. Let us consider what takes place in cases where there is apparently no chance for the operation of pressure. Such a case is offered by the developing ova of the Isopod Crustacea, in which the segmentation follows the typical centrolecithal method. The egg of the marine Asellid *Jaera*, to use this form for illustration, shows very near the center the nucleus surrounded by a stellate mass of cytoplasm, and upon the outside there is a thin layer of protoplasm, which close observation will show to be united with the central nucleus-containing mass by a delicate network of protoplasmic filaments, the granules of yolk, which are quite abundant, lying in the meshes of the network. When this egg segments one finds that the division of the nucleus is accompanied by the division of the central mass of protoplasm only, the peripheral protoplasm and the network showing no indication of the cleavage. And this process may be repeated again and again, so that eventually there will be found distributed through the mass of the ovum sixteen nuclei, each with a distinct mass of cytoplasm surrounding it, every one of these masses being united with its fellows and with the undivided peripheral protoplasm by means of the protoplasmic network. The egg at this stage is to be regarded as a multinucleate cell or, as such a structure is usually termed, a syncytium. Now it will readily be seen that in such a case as this the spindles, lying as they do in the center of the undividing mass of the egg, are protected to a very great extent from external influences and especially from mutual pressure, since the mass of protoplasm surrounding each one is in connection with that surrounding any of the others only by the filaments of the network.

What, then, as to the directions which the karyokinetic spindles assume? Do they arrange themselves as they should for perfectly rectangular divisions or do they present in some cases special directions? These questions may be answered by a consideration of the directions assumed by the spindles occurring during the first three cleavages, and for convenience the cleavage will be spoken of as affecting only the nucleus, though it must be remembered that the mass of protoplasm surrounding each nucleus is also affected by it.

The first cleavage produces two nuclei, the spindles lying at right angles to that one which produces the second polar globule. The second cleavage produces four nuclei, the spindles being directed at right angles to that of the first cleavage, and up to this point the process is in harmony with the third factor of Sachs' law. At the close of the second cleavage a peculiar rearrangement of nuclei occurs, two of them, which come from the same spherule of the preceding stage, rotating through an arc of 90° so that the line joining them lies in a plane at right angles to that in which the line joining the other pair lies (Fig. 6). I speak of a rotation through 90° of one of the pairs of nuclei;

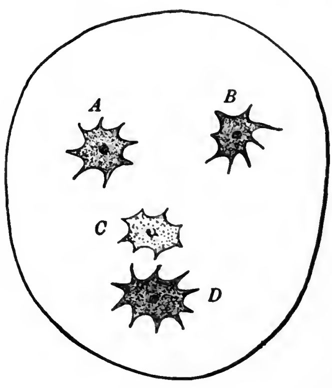

FIG. 6.

this is merely for convenience, since it is quite possible that both pairs may rotate in opposite directions through arcs of 45°, in which case the same final arrangement would result. This is an interesting phenomenon, since it shows that the re-arrangement of cells after cleavage is completed may take place independently of the law of minimal contact surfaces, and that, though this law may suffice to account for the re-arrangement in some cases, yet in others some other force is the efficient cause.

At the next cleavage two of the nuclei divide at right angles to the plane of the preceding division, as does also a third one, though its division plane is also at right angles to those of the other two. So far the cleavage follows the rule of rectangular division, but the fourth nucleus has its spindle arranged practically at an angle of 45° to those of all the other nuclei. The result of this division is shown in Fig. 7, in which one finds at one extremity of the somewhat oval egg a circle of four nuclei *A*, *A′*, *B*, *B′*, which are derived from the nuclei *A* and *B* of Fig. 6, while at the other extremity is a single nucleus *D*, and between it and the circle of four is a circle of three nuclei *C*, *C′*, and *D′*. What determines the peculiar direction of the spindle of the nucleus *D* of the preceding stage? It is not in accordance with the law of rectangular division, nor can it be determined by the principle of least resistance, for if this principle acts, a similar arrangement at both extremities of the ovum should be found. We are not, I believe, yet in a position to determine the ultimate cause of this division, but perhaps some clew to its significance may be obtained by carrying the development on a stage or two.

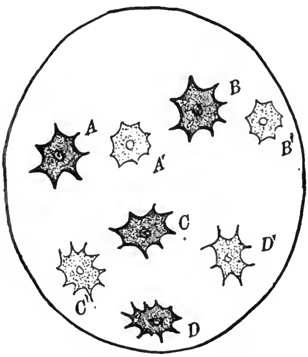

FIG. 7.

Let us examine the stage in which thirty-two nuclei are present. At this stage several marked peculiarities are to be seen. In the first place there is a striking differentiation of the protoplasmic masses which surround the nuclei, an appearance such as is represented in Fig. 8 being produced. At one pole of the ovum four nuclei (*vi*) are seen with only a very slight amount of protoplasm surrounding them, so that when stained with haematoxylin they stand out very clearly on the white yolk; these nuclei have resulted from the division of the nucleus *D* of the stage represented in Fig. 7, and when followed in later stage will be found to sink into the yolk and become the vitellophags of the embryo, still later, as will be shown in a paper shortly to appear, giving rise to certain mesodermal structures. Surrounding the area occupied by these vitellophags, is a circle of twelve nuclei (*me*) whose surrounding protoplasm stains very deeply, being thus in marked contrast to the vitellophags; these cells and their descendants later concentrate on the ventral surface of the embryo, and give rise to a mass of cells from which the endoderm and so much of the mesoderm as is not represented by the vitellophags will be formed. Finally, scattered over the rest of the ovum are sixteen nuclei (*ec*), whose protoplasm, though distinctly visible, does not stain so deeply as that of the mesendodermal nuclei, and which give rise later to the ectoderm of the embryo.

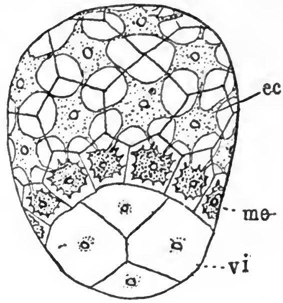

FIG. 8.

In the second place it will be seen that a cleavage of the yolk has supervened, the entire surface of the egg being divided into hexagonal or pentagonal areas, in the center of each one of which is one of the nuclei. This yolk cleavage is, however, superficial, as can be seen from Fig. 9, which represents a section of an ovum in the stage under consideration. From this section it will be seen that the nuclei and their surrounding protoplasm have now reached the surface of the yolk; in fact,

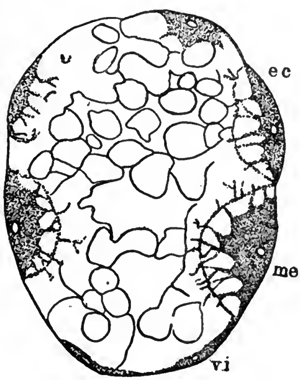

FIG. 9.

in each stage of the cleavage the nuclei assume a position nearer the surface and further away from the central position which the original segmentation nucleus occupied. We can speak of a centrifugal migration taking place, and incidentally it may be pointed out how inappropriate are both the terms centrolecithal and superficial which are usually applied to this method of cleavage. In the earliest stage it is the nucleus and its protoplasm which is central, and it is only in the later stages that the cleavage can be said to be superficial, and that the ovum can strictly be termed centrolecithal.

Thirdly, and this is an important point, the ovum is still a syncytium. In surface views one can readily see, especially in connection with the ectoderm cells, rays extending from the protoplasm surrounding each nucleus towards the lines which mark the cell boundaries, and in many cases the rays of adjoining cells meet at the cell boundary, strongly suggesting a protoplasmic continuity. That this actually occurs is clearly shown by sections, which reveal the nature of the lines which form the cell boundaries. Thus, in one of the mesendoderm cells (*me*) of Fig. 9 one can readily perceive the rays extending from the protoplasmic mass to the boundary of the cell, from which again rays extend further into the central yolk mass. The cell boundary cuts off only a slight amount of the superficial yolk, the greater portion of this constituent of the ovum being destitute of protoplasm except for the scattered filaments which extend into it from the cell boundary, and the fact of the occurrence of these filaments, as well as the staining properties of the boundary wall, show that it is protoplasmic in character. It seems certain, when the results obtained from surface views and from sections are combined, that every cell of the ovum is organically united with its neighbors, and that the entire ovum is a syncytium.

As stated, this is a highly important fact, since we see from it that a separation of the protoplasm into distinct spherules, such as presumably occurs in cases of total segmentation, is not necessary in order that histological differentiation may occur. Indeed, such an idea might have been derived from what we know of forms like the Infusoria, in which, notwithstanding the fact that they are unicellular, differentiation of the protoplasm into myophanes, for example, occurs. How far organic continuity obtains between the spherules in cases of total cleavage is something upon which we have as yet but little information, but in typical cases of centrolecithal cleavage there seems to be little question of its existence. It may be pointed out, however, that in the practically alecithal ovum of *Peripatus capensis* the syncytial condition exists according to the observations of Adam Sedgwick,[1] and it is interesting to note that the ova of this form show indications of having lost a considerable amount of yolk in correspondence with their intra-uterine method of development, the ancestral species of *Peripatus* having probably possessed an ovum provided with a considerable amount of yolk and resembling somewhat the ovum of *P. Novae-Zealandiae* which undergoes a centrolecithal segmentation.

Of course the comparison of the syncytial ovum of *Jaera* with an Infusorian is not perfectly just, since the Infusorian possesses but a single nucleus, and the differentiation seen in the *Jaera* ovum might be ascribed to influences exerted by each nucleus on the protoplasm in its immediate vicinity. What the nature of this influence may be, whether or not it even exists, is a question at present without an answer, but a case may be mentioned which seems to me to point very clearly to the probability of a cytoplasmic differentiation occurring independently of any direct nuclear influence. The case I refer to is presented by the developing ova of the terrestrial Isopods, *Porcellio* and *Armadillidium*. In the unsegmented stage these ova resemble in all structural peculiarities those of *Jaera*, differing only in their greater size. One finds in them the central nucleus surrounded by a mass of protoplasm which is joined by a network with a peripheral protoplasmic layer, which up to the stage in which four nuclei are formed, is uniformly distributed over the entire surface. Now it must be premised that in the later stages of *Jaera* there is a concentration of the cells towards one surface of the ovum,

[1] A. Sedgwick: The Development of the Cape Species of Peripatus. *Quart. Journ. Micr. Sci.*, XXVI, 1886.

which will eventually become the ventral surface of the embryo, concomitantly with this concentration the outlines of the naupliar region of the embryo being formed. In *Porcellio* and *Armadillidium* a similar concentration occurs, but in these forms the development of the naupliar region of the embryo is retarded, and one finds at an early stage a layer of cells closely aggregated together at one portion of the surface of the ovum, a few scattered cells being distributed over the rest of it. This aggregation of cells may be termed the blastoderm.

To return now to the phenomenon to which I wish to call attention. At the conclusion of the second division of the nucleus in *Porcellio*, one finds that the peripheral protoplasm is no longer uniformly distributed over the surface of the ovum, but there has been a concentration of a large amount of it to one portion of the surface (Fig. 10). The nuclei are still imbedded in the yolk, and only after several divisions do they complete their centrifugal migration, entering the peripheral protoplasm and forming with it the blastoderm. At the period at which the concentration of the peripheral protoplasm occurs the nuclei are separated from it by equal and considerable distances, being united with it, however, by the protoplasmic network, and it is difficult to perceive how any of them could be able to influence the peripheral cytoplasm in such a way as to produce the concentration. It seems rather that we have to do with an independent action of the cytoplasm, which precociously prepares for the formation of the blastoderm.

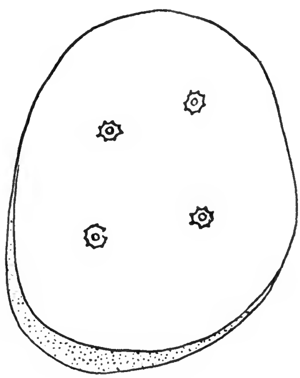

FIG. 10.

We are now, I believe, in a position to appreciate the significance of the peculiar direction of the spindle of the nucleus D of the ovum of *Jaera*, a significance which is indicated by what has been said regarding the aggregation of the peripheral protoplasm of *Porcellio*. Both phenomena are simply precocious preparations for a differentiation which will later become pronounced; they refer to the final form of the embryo, and are instances of Sachs' law that growth determines division and not division growth. Each stage of the development appears to stand in relation not only to what has preceded it, but to what is to succeed it, and is a link in a chain one end of which is lost in the obscurity of the past while the other stretches forward into the future. We must, I believe, recognize the fact so forcibly discussed by Dr. Whitman in his lecture on the *Inadequacy of the Cell-Theory of Development* and so clearly shown by centrolecithal ova, that in embryological development the differentiation which occurs is a differentiation of the entire organism and not of the constituent parts or cells of which it is composed; physiologically, if not morphologically, every organism is a syncytium, and future theories of heredity must take this into consideration.

From what has been said so far it will, I think, be evident that while the direction of the cleavage spindles and the arrangement of the boundary planes between adjacent cells may in some cases be explained by the action of simple mechanical laws, many of the peculiarities seen in animal ova cannot be thus accounted for. I do not mean to assert that the causative force which produces these peculiarities is at all different from the forces with which we are already familiar; I do not mean to say that there is a special *vis vitae* differing in its nature from the physical and chemical forces which are already known to us; but the actions and interactions of these forces are far too complicated for us to obtain even a faint conception of them, even as the chemical composition of protoplasm itself is too complex for us to understand its exact nature and its synthesis. What conception can we form of the forces which cause the aggregation of the peripheral protoplasm of *Porcellio* for instance? It may be spoken of as a precocious segregation of the cytoplasm of the blastoderm, but can we picture to ourselves the dynamic interactions which bring about this segregation? We have a resultant here which we cannot yet analyse into the constituent forces.

And with regard to the later processes of development a mechanical explanation is even more difficult. For instance, I have already described to you the teloblastic growth of the metanaupliar region of the Isopod embryo, in so far as the ectoderm is concerned in it, but careful observation will show that the mesoderm also participates in this mode of growth. Lying below the ectodermal teloblasts or ectoblasts, as they may be termed, one may see, as is shown in Fig. 11, a row of

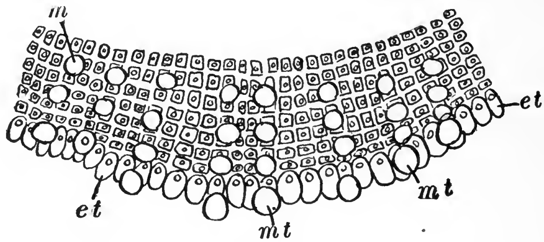

FIG. 11.

eight mesoblasts (*mt*), and in embryos of the proper age in front of these may be seen a number of rows (*m*), also consisting of eight cells, which have been budded off from the mesoblasts. The mesoblastic rows are separated from one another by intervals corresponding to a single row of ectodermal cells, and it must therefore be concluded that the ectoblasts divide twice as frequently as the mesoblasts. By tracing on the development it will be found that each mesoblastic row corresponds to a metamere of the adult animal, the mesoblasts themselves forming the mesoderm of the terminal metamere or telson. Now there are in the metanaupliar region of an Isopod two maxillary, one maxillipedal, seven thoracic, and six abdominal metameres, in all, together with the telson, seventeen metameres. Since the mesoderm of each of these metameres is developed from the products of a single division of the mesoblasts, and since the mesoblasts themselves develop into the mesoderm of the telson, it is evident that the mesoblasts must divide in a teloblastic manner just sixteen times, and no more and no less; otherwise there would be an extra metamere, or else a missing one in the adult animal.

The constancy of the number of metameres in the Isopods and their allies is remarkable, and I know of no recorded cases of variation in this respect in the group. One teloblastic division more than is proper would produce a monstrosity, yet through thousands of generations and thousands of individuals the number of divisions is just sixteen! Can we imagine the physical forces which determine this most remarkable regularity? It is, again, the final result which determines the division, but to say that, does not carry us far enough. There are intrinsic forces at work far too complicated for our understanding at present, and to speak of the phenomenon as produced by physical causes conveys an idea to our minds but little more definite than that which we get by speaking of a vital force.

We have heard a great deal lately concerning cell-dynamics, and the reduction of all vital phenomena to the action of molecular forces. I wish in conclusion to sound a note of warning to younger students of Biology, lest they be carried away by the apparent simplicity of such theories. I have endeavored to show that none of the mechanical theories so far proposed will account for the arrangement of the cleavage spindles in certain ova, and that our knowledge of the fundamental properties of protoplasm is too scant to enable us to formulate any scheme of molecular interaction sufficient to account for the phenomena of development. It is not to be inferred, of course, that because we cannot do this at present it never will be done. On the contrary, all investigations looking toward a complete knowledge of the molecular constitution of protoplasm, and of the forces at work in it, — for it is not only extrinsic forces which must be considered, — all such investigations are most worthy of encouragement.

What is to be protested against, however, is the tendency to overlook the intrinsic forces, which are of far greater importance than the extrinsic. They may, it is true, be largely of the same nature as the forces which act from without, but they require study, for yet we know practically nothing concerning them. To ascribe vital phenomena at present to the action of molecular forces is to recall the speculations of the classical philosophers who found in the primary elements, earth, fire, air, and water, and their attributes, all the materials for a cosmogony. We must adopt an analytic method in dealing with this question, and not a synthetic one, and must trace each phenomenon down to its ultimate causes before we can begin to build up dynamical hypotheses. To start the building up now is a "Looking Backwards"; it is building the superstructure before our foundations are ready. Let us begin with our foundation, let us build slowly and firmly, and the time will come when we can erect our superstructure in the full assurance that it will stand secure.

Since the above pages were written I have had an opportunity of reading an interesting paper by His,[1] in which he discusses the application of mechanical forces to an explanation of the form assumed by vertebrate embryos. He demonstrates experimentally the conditions which govern the formation of folds, such as that formed at the posterior edge of the blastoderm of a shark's ovum at the beginning of the concrescence phenomenon, and which represents the first formation of the medullary groove, or those which we term the head and tail folds, and which separate the embryo from the yolk anteriorly and posteriorly. Given the proper conditions, these folds may be explained on mechanical principles, but it is the development of these necessary antecedent conditions that is the important point. There must be differences in the thickness of various portions of the blastodermic area. There must be a greater accumulation or a greater compactness of the cells at one portion than at another, and these variations cannot at present be explained on purely physical bases. The thickening of the embryonic region of the blastoderm and of the germ-ring can only be regarded as a preparation for what is later to develop, and the cell migrations and the formation and dissolution of cell-layers, which His describes, allow no mechanical explanation at present.

His takes, it seems to me, the correct position when he states "so viel ist sicher, dass sich bei der Bildung der Keimschichten vitale Processe mit rein mechanischen combinieren, und dass es auch hier nicht angeht, mit einigen schablonenhaften Vorstellungen der vorhandenen Probleme Herr zu werden." The

[1] W. His: Ueber mechanische Grundvorgänge thierischer Formenbildung. *Archiv für Anat. u. Phys. Anat. Abth.*, 1894.

information we possess shows us a combination of mechanical with what we may term vital forces in the phenomena of Biology: we must guard against being carried away by the apparently beautifully simple explanations of the upholders of the physical school, and at the same time we must recognize the contentions of the Vitalists. Bunge,[1] an ardent supporter of the latter school, writing in 1889, says: "Je eingehender, vielseitiger, gründlicher wir die Lebenserscheinungen zu erforschen streben, desto mehr kommen wir zur Einsicht, dass Vorgänge, die wir bereits geglaubt hatten physikalisch und chemisch erklären zu können, weit verwickelterer Natur sind und vorläufig jeder mechanischen Erklärung spotten." This represents the ideas of the extreme Vitalistic school, and between it and the extreme mechanical views a median ground, represented by the quotation which I have made from His, exists. In the light of recent investigations in cell-mechanics we must prepare ourselves for the extension of the application of mechanical principles, but for the present we will do well to follow the advice given by Phoebus to the headstrong Phaëthon: "*In medio tutissimus ibis.*"

[1] G. Bunge: Lehrbuch der physiologischen und pathologischen Chemie. Leipzig, 1889.

EIGHTH LECTURE.

THE PROBLEMS, METHODS, AND SCOPE OF DEVELOPMENTAL MECHANICS.

An Introduction to the "Archiv für Entwickelungsmechanik der Organismen."

WILHELM ROUX.

[Translated from the German by WILLIAM MORTON WHEELER.][1]

I. *The Problems of Developmental Mechanics.*

DEVELOPMENTAL mechanics or causal morphology of organisms, to the service of which these "Archives" are devoted, *is the doctrine of the causes of organic forms, and hence the doctrine of the causes of the origin, maintenance, and involution (Rückbildung) of these forms.*

Internal and external *form* represents the most essential attribute of the organism in so far as form conditions the *special manifestation* of life, to which the genesis of this form itself in turn appertains.

The term "mechanics of development," to designate the causal doctrine of this whole subject, is employed in accordance with the principle *a potiori fit denominatio*, for the *evolution* of organic form comprises the main processes and implies the principal problems of organic formative operations.

[1] The translation of this philosophical essay has been attended with not a few difficulties. Besides the difficulties resulting from the great compactness of Professor Roux's style, there are others, not the least of which are the great conciseness of meaning with which all the terms are used, and the often very delicate qualifications of the leading ideas in the various paragraphs and sentences. I believe that I have rendered the ideas truthfully in the main, but I fear that it has been at the expense of a somewhat forced and unnatural construction in many of my sentences. — W. M. W.

In accordance with Spinoza's and Kant's definition of mechanism, every phenomenon underlying causality is designated as a *mechanical phenomenon;* hence the science of the same may be called mechanics. Since only phenomena underlying causality are capable of investigation, and hence alone may be made the subject of an *exact science,* and since the production of *form* constitutes the essential feature of development, it is quite permissible to call the science of the causes of form developmental mechanics.

Since, moreover, physics and chemistry reduce all phenomena, even those which appear to be most diverse, *e.g.,* magnetic, electrical, optical, and chemical phenomena, to movements of parts, or attempt such a reduction, the older more restricted concept of mechanics in the physicist's sense as the causal doctrine of the movements of masses, has been extended to coincide with the philosophical concept of mechanism, comprising as it does all causally conditioned phenomena, so that the words "developmental mechanics" agree with the more recent concepts of physics and chemistry, and may be taken to designate the doctrine of all formative phenomena.

Inasmuch as we call the *causes* of every phenomenon *forces* or *energies,* we may designate as the general problem of developmental mechanics *the ascertainment of the formative forces or energies.* In so far, however, as forces or energies are only known to us by their *effects, i.e.,* every kind of force by its specific *mode of operating,* the problem may be defined as the *ascertainment of the formative modi operandi.*

In accordance with this statement, a *general,* not quantitative, but in the first instance, merely *qualitative causal explanation* will always consist in tracing back a particular phenomenon to *modi operandi of more general validity, i.e.,* to such as operate *constantly,* also in many other processes, and hence under the same conditions, at all times and in all places, and in the same manner. Such modes of operating may be called "constants of operation" ("Wirkungsbeständigkeiten").

These constant modi operandi which follow from the properties of the components and hence of necessity, — these so-called *uniformities of nature,* — are usually called "*natural laws.*"

Accepting this latter term, the task of developmental mechanics would be the reduction of the formative processes of development to the natural laws which underlie them.

It is, however, preferable, at least in those cases to which the expression *constant mode of operating* is more applicable, to employ this phrase instead of the term *natural law*, which is based upon anthropomorphic conceptions of nature. It behooves us, especially when entering on a new and extensive field of investigation, beset with quite special difficulties, to call *the thing to be sought by its own name*, instead of employing an expression which is foreign to its nature.

Since, moreover, all the *modi operandi* underlying causality, and hence all *modi operandi* which may become the subject of our investigation, are "constant or uniform," this adjective may generally be omitted, and it is sufficient to say simply *modi operandi*, instead of natural laws. Instead of the "law" of the refraction of light we may also speak of the *modus operandi* of refraction; instead of the "laws" of functional adaptation let us say the *modi operandi* of functional adaptation, *e.g.*, of the muscles. This designation at the same time renders impossible in Biology one widespread, incorrect usage of the term "law," viz., the use of the term to designate *facts* or *results* instead of *operations*, as, for instance, in the current expression "Bell's law." When we attempt to use, instead, Bell's *modus operandi*, it becomes at once apparent that this term is inapplicable to the "fact" of the motor nature of the anterior, and the (supposed) purely sensory nature of the posterior nerve-roots.

If, furthermore, we define *the general task of developmental mechanics* so that it shall include the fewest mysterious concepts, and hence in a way which is simplest and most compatible with the immediate method of procedure, *we must reduce the processes of organic formation to the fewest and simplest modi operandi*. This, of course, implies that for each of these modes the *simplest expression* is to be sought.

All *operating*, and hence also its product, all *operation*, has at least two causes or components, since in last analysis nothing can change its condition of itself.

Development is a change and must, therefore, always depend on several components, and hence on *combinations of causes or energies.* More accurately speaking, we understand by development the *production of multiformity.* The latter results from every operation, from every combination of energies, at least during and for a short time after the duration of the operation ; and its origin depends on the *unequal distribution* of energy during its transmission, *e.g.*, in pressure on a body, in heating or electrifying an object, in the radiation of light-rays, etc. It is, therefore, unnecessary *in principle* to postulate *specific energies of development;* this, however, does not preclude a possible participation at the same time of special components, as, *e.g.*, the energies of growth, in producing *formative* diversity during particular phases of organic development.

Organic development consists in the production of perceptible, *typically constituted* diversity. If we look aside in this place from the conditions of perception (1), *typical combinations of causes or energies are indispensable to the origin of "typical diversity."* For the specifically *constituted* nature of this diversity, specific *form-producing combinations of causes are required,* and these represent the just-mentioned "formative components." Now if these formative components be forthcoming in a perfectly typical manner, in kind, magnitude, and arrangement, it is self-evident that in the absence of disturbance from without, the constructive diversity produced by these components must be perfectly typical.

Accordingly, in any given case, we must trace back each individual formative process to the special combination of energies by which it is conditioned, or, in other words, to its *modi operandi;* and each of these *modi operandi* must be ascertained with respect to *place, time, direction, magnitude,* and *quality.* Or, inversely, we may endeavor to determine *in the individual structure the special part which is performed by every modus operandi known to participate in the development of the organism.*

These *modi operandi*, to which we reduce organic formative processes, and hence also the energies which condition them, may be identical with those which underlie inorganic or physico-chemical processes.

Since it is not the task of the biologist, as such, to investigate and to subject the components of *inorganic* phenomena to an analysis further than that undertaken by physicists and chemists, we may accept these components as given, and may designate them, so far as they are concerned in organic operations, as "SIMPLE COMPONENTS," no matter how problematic their nature may be, and even if sooner or later they should be still further dissociated by physicists and chemists. When this is accomplished, we shall make use of these further, still simpler components.

Besides the endeavor to ascertain such "simple components," the lines of research in developmental mechanics must from the start be guided by the conviction that *organic structure is mainly due to the operation of components which at present are so complicated as to exceed the limits of our observation.* For these I have suggested the term "COMPLEX COMPONENTS" (2). Although according to our immediate conception of the matter, even these components depend in the last instance on inorganic *modi operandi*, nevertheless *the complexity of their composition lends them attributes which often differ so widely from those of inorganic modi operandi* that they are not only very *dissimilar* but even *appear to contradict* in part the functions of these same inorganic *modi operandi.* This is the case with the non-exosmosis of salts from living fish-eggs in water, the non-desiccation of small living insects in the sunlight; whereas after death, these organisms, in the former instance suffer diosmosis, in the latter desiccation; another instance is the pouring of a glandular secretion into a cavity which is under higher pressure than that which obtains in the blood capillaries of the gland. These processes show that in the former instances the salt or the water is not in a free state, but fixed and operant (beschäftigt), whereas in the last instance we are dealing with specific active functions carried out with commensurate expense of energy on the part of the epithelial cells.

It must, therefore, be our next most important task to ascertain these components, *which, though complex, are nevertheless* *alike constant and always alike operant under like conditions, i.e.*, to reduce organic formation to such *modi operandi* as are constant, albeit in themselves not understood.

Every "complex component" thus represents merely the effect, the resultant of inappreciable individual effects. From such complex components result most of the formative processes which we perceive; it is our task, therefore, to analyze the chaos of internal operations into the least possible number of such *modi operandi.*

In the first place the elementary cell-functions are such "COMPLEX COMPONENTS": *assimilation, dissimilation* (katabolism) the *self-movement* of the cell in general, the *self-division* of the cell as a definite coördination of self-movements; to these we may add the *typical formal self-constructivity* and the *qualitative self-differentiation* of the cell as still more highly complicated effects.

On the other hand, the *growth in mass* of cells probably represents only the resultants of simultaneously occurring processes of assimilation and dissimilation; and the same may hold good with reference to external pressure when the cell *decreases in mass. Local growth*, however, besides depending on a growth in mass of the cells of a given area may also depend on the immigration of cells, and hence on other complex components, such as *chemiotropism* and *cytotropism* (3). On the other hand, exclusively "*dimensional growth*" (4) of an area may depend on the active metamorphosis of cells. Further complex components which also determine the direction of movements in unicellular or multicellular organisms are *galvano-, helio-, hydro-*, and *thigmotropism.*

The *directive effect of the "form"* of the cleavage-cell prior to its histological differentiation *on the position of the nuclear spindle*, viz., the adjusting of the spindle to coincide with the longest axis that can be drawn through the center of mass of the protoplasm (5); *the trophic effect of functional stimuli* (to which all the extraordinarily diverse phenomena of functional adaptation are reducible) (6); *the trophic effect of ganglion cells on their nerve-fibres* and corresponding end-organs — all these are further complex components which are already established, and through which many formations are attained. The *effect of increased blood-supply* on the increase of connective tissue in the affected parts is another instance.

These complex components seem relatively simple in comparison with others which must be postulated before we can begin the analysis of many structures.

As an example of these the following may be formulated, if only provisionally; for if we never have the courage to begin we shall never escape from our ignorance.

The cells of all tubular and acinous glands have a *bipolar* differentiation ; they have a *basal surface* which serves to take up nutriment from the adjoining capillaries, and opposite this a *secreting surface ;* both surfaces are separated by the *whole* diameter of the cell ; the remaining surfaces are merely *surfaces of contact* with the neighboring cells. Metabolism is carried on in the direction of the axis uniting the polar surfaces, which direction is usually that of the greatest dimension.

The arrangement of the cells in lobules in the fully developed mammalian liver, which is a *reticular gland* with the narrowest possible meshes, viz., meshes only the breadth of a single cell in diameter, causes the cells to be *multipolar* in the above sense, for each cell has several nutriment-absorbing and several secreting surfaces. The secreting and nutriment-absorbing surfaces are removed from one another by only *half* the cell-diameter. The lobular structure composed of these cells represents, so far as its form is concerned, merely a cast of the interstices between the meshes of the network of tubular blood capillaries.

Inasmuch as the lobular structure, molded as it is on the blood capillaries, presupposes the small-meshed reticular type and this in turn the multipolarity of the liver cells, we may regard as the *primitive* factor in all these deviations from the tubular type of other glands, the change in the polarity of the liver cells, and we may say accordingly : The transformation of the tubular type, which is also present at first in the mammalian liver, into the definitive lobular type is the consequence of the differential change of the original bipolar nature of the liver cells to a multipolar nature, or ; *the multipolar differenti-*

ation of the liver cells conditions or effects the transformation of these cells from the tubular to the lobular type, whereby the lobule for purposes of best nutrition accommodates itself intimately to the tubular blood-capillaries.

All these fixed "constant *modi operandi*" of organic formative processes must be still further determined with respect to their place and the time, direction, and extent of their participation in the special structures of organisms, and with respect to their mode of operating.

In the first place we shall have to ascertain a great number of such constant *modi operandi,* and all of these must then be further decomposed into simpler and more widely distributed complex components. In this undertaking it will probably be frequently possible *to disentangle a simple component from among the complex components.*

The immediate result of this undertaking, as in every analysis, will be complication instead of simplification, since apparently simple processes will often be separated into two or more components. The simplifying effect of the analysis will only appear after it has been extended to *many* processes with the result of repeatedly finding the *same* components.

This simplifying effect is already apparent: all the extremely diverse structures of multicellular organisms may be traced back to the few *modi operandi* of cell-growth, of cell-evanescence (Zellenschwund), cell-division, cell-migration, active cell-formation, cell-elimination, and the qualitative metamorphosis of cells; certainly, in appearance at least, a very simple derivation. But the infinitely more difficult problem remains not only to ascertain the special rôle which each of these processes performs in the individual structure, but also to decompose these complex components themselves into more and more subordinate components.

And notwithstanding such apparent simplicity, the formative causes in each higher aggregation of living units may differ in part from the formative causes of a lower order, as, *e.g.*, formative modes which belong to the independently existing lower units, such as the Protista, may be absent in the higher state of aggregation from the corresponding units, viz., the cells of a multicellular organism; while at the same time, new effects are produced which are peculiar to the *higher unit* in question and which would naturally depend on the *reciprocal* operations of the lower constituents. After *ascertaining the formative functions of each such unit*, the *modi operandi* on which these functions depend must be established by themselves; this holds good in the case of the *lowest independent parts* of the cell (7): the *isoplassons, autokineons, automerizons, idioplassons*, and the parts which they constitute, *the nucleus, centrosome*, and *protoplasm*. It also holds good in the case of the entire cells themselves, of the tissues, organs, and the organism which is composed of the latter.

Inasmuch as *each* of these vital units of different orders is distinguished by its individual functions, whenever such a unit coöperates with an "external" factor, we are often interested only in the behavior of the unit and we call this its *reaction*. In a *complete* estimate of the phenomena we should, of course, have to take cognizance of the way in which the external, or more correctly speaking, "other" factor is affected, especially when this happens to be also a living part.

Thus we speak of the *formative reactions* of cells, tissues, organs, or of the whole organism which these go to make up, *e.g.*, of the influence of increased functional stimuli on bones through the activity of the muscles, etc.

Besides the *modi operandi* or energies of *development*, the *modi operandi* or energies of the *maintenance* and of the *involution* of organic forms and their bearers must be investigated by themselves, although it is probable that *maintenance often represents merely the equilibration of diverse components which are also active and formative during development;* and that during subsequent *involution* this *equilibrium is upset by altering, destructive components*. Besides searching for such conditions we must, on the other hand, seek to determine whether *each of these phases has not formative modi operandi peculiar to itself*.

Furthermore, in accordance with the double course of development, viz., the *phyletic* and *ontogenetic*, developmental mechanics must look for the causes, or *modi operandi*, of each of these two courses; hence an *ontogenetic* and a *phylogenetic developmental mechanics* are to be perfected.

Since the object of the developmental mechanics of *ontogeny* is the investigation of phenomena which are hurried through rapidly in present time, it will, of course, yield greater results than phylogenetic developmental mechanics, the phenomena of which belong in great measure to the past, and, so far as they occur at present, must be carried on with extreme slowness. But in consequence of the intimate causal connections existing between the two, many of the conclusions drawn from the investigation of ontogeny will also throw light on phylogenetic processes; moreover, phylogeny, even within the limits of its present occurrence, is not entirely inaccessible to investigation; many a causal connection may be ascertained by means of *experiment*, as has already been shown in the case of artificial selection.

The components with which the doctrine of phylogenesis has hitherto exclusively dealt, viz., *variation* (adaptation) and *heredity*, are still more complicated than the above-mentioned complex components. Nevertheless, this distinction at the same time represents the reduction of extremely diverse phenomena to two, albeit in their special *modi operandi* exceedingly variable, and hence not "constant" or "uniform," components. The word "variation" is to a much greater degree even than the word "heredity" a *collective term* for *results* which are in a certain sense uniform, but which may depend on very diverse *modi operandi*. Hence developmental mechanics has before it the further task of searching out, first, the various constant sub-components of the effects so named, and, second, the causes of these effects.

In this direction, too, encouraging attempts have been made. While Darwin's *doctrine of natural selection* represents only *collective causes* (Aufspeicherungsursachen) of *given* characters on the basis of the survival, — non-extermination, — of the fittest, the new *doctrine of mechanomorphoses* of Julius v. Sachs (8) is already giving us an insight into actually operant, and hence immediate formative causes, — into the formative *modi operandi* of the prehistoric life of organisms.

II. *Methods of Investigation in Developmental Mechanics.*

The causal method of investigation, κατ' ἐξοχὴν, is *experiment.* This statement holds good of the mechanics of development more than of any other line of causal investigation, as will be apparent from the following considerations:

The formative operations occurring in the organism are hidden from sight; we cannot see the ganglion cells of the anterior cornua influencing the development of the muscles, nor increased activity stimulating the growth of organs, nor the substances secreted by cells exerting a chemiotropic attraction on other cells; indeed, it is not even possible to observe directly that pressure is exerted by cells during growth, nor the passive alterations in the form of parts on which such pressure is exerted. All these operations can only be inferred.

The ascertainment of these operant conditions is, moreover, made still more difficult because the really formative *activity* is carried on so rapidly, as compared with any visible changes, that even in the production of considerable transformations the efficient causes, the *antecedent is*, according to His (9), *almost always in advance of the effect*, or consequence, *by a differential;* even in eventually resulting passive deformations the nature of the processes cannot be ascertained by removing the pressing parts because the form resulting from the pressure has in every case already settled into *internal equilibrium* and lacks only a minimum of adaptation; for after the removal of the pressing parts a passively deformed structure does not return to its original form, as does a bent rubber tube after the cessation of the bending forces.

Since, moreover, during the normal development of an individual there are always *many changes taking place simultaneously*, we can only conclude from observation of these changes that the *ensemble* of former changes is or may be the cause of the changes which follow; *but we are not in a position to conclude on what preceding change each single ultimate change depends.*

In accordance with the aphorism: two phenomena which always occur together are causally connected, we can, it is true, deduce *from comparative observations on normal phenomena*, without recourse to experiment, many *modi operandi* which obtain among the parts; and these *modi operandi* will have the greater probability the greater and *more varied* the materials of observation.

In this way Balfour (10) deduced the fact that the eggs of sharks, bony fishes, and birds undergo only a partial segmentation from the inhibitory effects on division of the great amount of yolk accumulated in the eggs of these animals.

Nevertheless such conclusions never yield "complete" certainty because the observed connection of the phenomena need not be a direct one, but may depend on the effects of a third unknown component, or components. For the organic processes of the *typical* or normal development of organisms are so incomprehensibly manifold and enigmatical that, particularly in the beginnings of *exact causal investigations*, we can never deny with assurance the existence of such a common third component or other components; and the less because in every case only a small part of the secondary or tertiary phenomena fall within the limits of our observation, while all the primary phenomena of organic formation are concealed from our view. *Hence, modi operandi may be "ascertained" by means of comparative observations on normal phenomena, but they cannot be "proved."*

This must always be borne in mind; we can never regard such effects as are concluded from mere observation of typical normal phenomena as perfectly certain; *we must endeavor to obtain direct proofs of these effects.*

It has been shown that in the early cleavage of many eggs the directions of the division-planes follow one another in definite sequence. Bearing in mind that the nuclear spindle lies normally at right angles to the division-plane of the cell, the common result of the directions of these first divisions with reference to the *shape* of the cells in corresponding periods of time, is this: in these first divisions the nuclear spindles place themselves in the *longest* axis which can be drawn through the center of mass of the protoplasm. Starting with this statement, it is possible to conclude deductively as to the sequence of the first planes of cleavage. At the same time, this statement is *not certain* so long as it cannot be proved *directly;* for the same typical sequences of division in normal development might be brought about by other, albeit, perhaps, *much more complicated,* but, nevertheless, *typical* operations. More than by a hundred further agreements with the rule in *normal* phenomena, the approximate truth of the above statement was proved by a single experiment, in which by pressing the eggs till they assumed an abnormal form, the sequence of the planes during the early cleavage departed from the normal, but even in this condition the nuclear spindle came to lie in the above-mentioned greater axis. At the same time it was shown, however, that in rare cases the nuclear spindle places itself in the *smallest* axis which can be drawn through the center of mass of the protoplasm, a fact which points at the same time to the operation of *several* factors in the determination of this directive influence (5).

Among biologists there is a tendency derived from the inorganic sciences, *to regard the hypothetical deductions which appear to us to be the "simplest," as having the greatest probability for the very reason that they seem so simple.*

Although much has been done on this assumption, and unfortunately must be done, and although much that is true has already been brought to light, nevertheless this method must always be applied with great reserve to normal biological phenomena, for deeper knowledge shows us that *we have not yet a sufficient insight into the actual mechanisms of development to venture an opinion as to what may be easiest and simplest for these same mechanisms.*

Thus we suppose that we are really simplifying matters when, *e.g.*, we attribute in consequence of functional adaptation many typical and purposive forms to the self-constructive effects of use. The correctness of this *principle* and of its application in many cases has long been capable of direct proof. Nevertheless, we observe that many structures which might be the result of this principle, *e.g.*, the form of joints, the functional structure of the gut, are already established before there is an opportunity for them to exercise their definitive functions. Hence some other mode must operate in producing these structures, a mode, which, it would seem, depends rather on *independently* inherited and *typically* formative forces in individual organs. This latter formative mode appears to us more difficult than the former for the very reason that it requires a whole series of *independent, typically localized individual formations* for the building up of a single structure. But that *this formative mode must in reality be carried out with very great ease* is shown by the difference in the rich and beautiful pattern of birds' plumage in closely allied species, although in every such plumage every feather, characterized as it is by its position on the body and its relation to the other feathers, must have its own typical pattern, differing from that of neighboring feathers in a typical manner.

"*Certainty*" in causal deduction *can only come from experiment*, either from "*artificial*" or from "*nature's*" *experiment*, such as *variation, monstrosity*, or other *pathological phenomena;* this certainty, however, is only to be obtained by adhering to various precautions which are often difficult to follow.

In an experiment performed under the most favorable conditions, only *one* of the components known to us is or will be changed, and through the results of this change we apprehend those phenomena which are connected with this component.

In practice, however, matters are not so simple; for in organic objects even after artificial, analytical experiment we often experience the greatest difficulty in tracing back the effects to their *true* causes; in the first place we are obliged to repeat the experiment often in order to obtain *constant results* and then it must be *modified in various ways* in order that we may be able to determine the true causes. This is because the conditions are so complicated that we do not know the primarily altered components even by means of artificial interference, since, when we suppose we have succeeded in changing only a single component, *accidental* external or internal conditions or unintentional *collateral effects* of our own interference have already affected several components. Only when we are perfectly sure that in reality no other than the single component which we intended to change is affected, are we in a position to draw a definite causal conclusion from a *single* experiment.

This conviction or insight will only rarely be obtained from experiments on organisms. Hence it so often happens that when we believe we have experimented under the very same conditions and in the same manner as on a former occasion, we nevertheless obtain different results. So long as we do not arrive at the same result, at least after several repetitions of the same experiment, we must not permit ourselves to draw any conclusion whatsoever. And now that we are in the first stages of our investigations, without having any survey of the *modi operandi* which may occur, it will often be necessary *to use as many methods as possible in experimenting on the same subject;* and only when these different experiments point to the same causal connection should we assume that this is the true one.

With the aid of such experiments we are in a position on the one hand to test the relationships which are *determined* by comparative study of the normal forms, and on the other hand to obtain — yes, to extort — an answer to newly arising questions.

Before we can establish the *causal modi operandi according to their qualities,* we must *first determine the parts between which formative operations take place, i.e.,* we must determine the "*locality*" of the formative operations. With reference to the *single circumscribed structure or part,* this means that we must ascertain whether the causes of its formation lie within itself or whether external influences are necessary to its formation.

The rôle which the different causes that take part in a formation play in its production may be a very unequal one.

Inasmuch as some singular notions and terminology have gone abroad concerning *causes of different dignity,* it seems proper in this place to go somewhat into details for the sake of paving the way towards greater uniformity of opinion.

All the components whose *temporary* and *local coincidence* is necessary to produce a certain effect, constitute in their totality the "*whole cause*" of the effect. Of these components we often call those with the commencement of which the effect *begins* (*i.e.*, the last preceding *event*), the *cause* of the effect, while the components which were previously and continuously present (*i.e.*, the *permanent facts*), are known as the *preëxisting conditions*. This is, however, an arbitrary distinction, and one which is detrimental to our quest for *complete* knowledge. The essential point is this: *All the components* of an effect must exist *beforehand*, but they need not all "*begin*" immediately before.

It seemed to me useful, in order to further the special aims which we have in view, to introduce a different distinction of cause and preëxisting condition, although this distinction, too, is somewhat arbitrary.

I have called such components "CAUSES," or, better, "SPECIFIC CAUSES," "SPECIFIC COMPONENTS" of a *process of organic formation*, as condition the "*specific nature*" *of the process*, while the other components which are equally essential to the starting in of the phenomena, but which, like heat and oxygen, do not determine the character of the formation, were called "PREËXISTING CONDITIONS," "INDIFFERENT CAUSES," or "INDIFFERENT COMPONENTS" (11).

If our endeavors be directed not to the *qualitative* cause of the phenomenon but only to the cause of the *place*, *time*, or *magnitude* of the same, we must designate as "*specific*" *causes of these circumstances* those causes which condition the given circumstance.

The theory of this unequal participation of the components in conditioning the *specific nature of the resultant* requires further elaboration.

Starting with the view of the different functions of the components of the same process and consequently with a preference for the components which condition the specific nature of the phenomenon investigated, I have designated as "SELF-DIFFERENTIATION" *of the circumscribed or presumably circumscribed structure or part*, that change, whose specific causes (in the sense just defined) lie within the formal structure or part itself; and this expression would be employed even when the admission of energy from without, in the form of heat, oxygen, etc., is necessary. In order to distinguish the two cases the term "COMPLETE SELF-DIFFERENTIATION" was employed when *all* the components lie within the formed part itself, while "INCOMPLETE SELF-DIFFERENTIATION" obtains when the accession of energy from without is required, in so far as this energy represents only the preëxisting condition of the formative operation in the sense above accepted; but since, nevertheless, the accession of energy from without in the form of heat, light, gaseous, and liquid nutriment, is in varying quantity necessary to the development of the eggs of different animals, but does not determine whether an egg is to develop into a chick, a frog, or a fish, or whether the lung is to be laid down at a particular spot in the embryo, *the development of the egg would be more accurately designated as "incomplete self-differentiation."*

As was set forth above, self-differentiation in the strict dynamical and analytical sense, can, of course, have no existence, since every change in a phenomenon must depend on reciprocal operations. Since the concept "self-differentiation" is, accordingly, not processual but merely topographical, implying something with regard to the *locality* of the causes of the formative process, whenever it is employed, the particular circumscribed structure to which it refers must be mentioned.

"DEPENDENT DIFFERENTIATION" is a change in which one or more of the components that condition the specific formation, operate from without on the circumscribed or presumably circumscribed part to be formed; and "PASSIVE DIFFERENTIATION" occurs when all of the components of the respective formative process of a given part operate from without, as, *e.g.*, in the modeling of a figure in clay or wax.

Self-differentiation and dependent differentiation may occur in the most varied combination either simultaneously or successively.

Thus the normal formation of skeletal structures like the tibia is very probably partially due to self-differentiation, because, presumably apart from external influences, there arises from the given Anlage-material a rather long skeletal structure with a thickening at its proximal end; but in other respects this formation is due to dependent differentiation, since the finer details of structure, like the surfaces of the joints and the three-sided shape of the diaphysis, are conditioned by the operations of neighboring parts.

The segmentation of the common arborescent glands into lobules appears to be conditioned by the formative operations of the epithelia and hence of the specific parts, and, so far as this is true, the segmentation is a *self-differentiation of the glandular substance.* In the liver, however, which is a reticular gland, the normal size and form of the lobules and also the lobular segmentation itself appears to be conditioned by the blood-vessels — on the one hand by the requisite length of the capillaries, and on the other by the peculiarity in the ramification of the portal vein, which during its growth develops *dichotomic* branches in its capillary network. Hence *the acinous segmentation of the liver parenchyma represents a differentiation of the glandular substance depending on the vascular system.*

After, or at the same time as the actual ascertainment of such "*local*" *conditions of the formative causes*, we shall endeavor to look for factors which condition the *magnitude* and *direction* of the formative processes; simultaneously, or even before this, we may be able to ascertain also the *time* when many of these formations are reduced to a *norm*, as, *e.g.*, the *time* when the *direction* of the median sagittal plane of the embryo is determined; for it is not necessary that these formative conditions be first conditioned when the ultimate forms first become visible.

On the contrary, in the perfectly normal, *i.e.*, *perfectly typical*, course of the individual development, all the typical structures must at the very latest be in some way conditioned in the fertilized egg, either *implicite* in their earliest components, or *explicite* in already visible Anlagen. Nevertheless, we must assume that there is really no such thing as *perfectly* typical development (12), but that in every individual development greater or less disturbances take place, which are compensated by the putting into action of regulating mechanisms. Accurately speaking, therefore, we should only have to determine in respect of time, *within what preceding developmental phases structures which are not visible till sometime afterward can no longer be varied by disturbing influences;* and in respect of form, *what* preceding visible or invisible structures condition every formation that is later observable, as, *e.g.*, in the case of the median sagittal plane of the embryo which is *normally* conditioned by the first cleavage plane, and this in turn by the axis of the copulation of the male and female pronuclei.

Ultimately we shall attempt to get at the *causal modi operandi*, by attempting to ascertain their *quality*, and to trace out the more general *modi operandi*, of the combination of which a given effect is itself only a special case.

For all this *analytical* experiment gives us ample opportunity. By isolating, transposing, destroying, weakening, stimulating, false union, passive deformation, changing the diet and the functional size of the parts of eggs, embryos, or more developed organisms, by the application of unaccustomed agencies like light, heat, electricity, and by the withdrawal of customary influences, we may be able *to ascertain a great many formative operations in the parts of organisms.* Thus we may, perhaps, determine the possible influence of the muscles in the formation of the joints and sockets by cutting the sinews of the biceps and triceps brachii in very young animals and sewing them on again with transposed insertions; by cutting out transverse wedge-shaped pieces from the longer bones and feeding with madder, it may be possible to learn something of the processes of functional adaptation in the structure of the bones and hence of their immediate relations.

By such artificial interference we shall in the first place be able to establish the occurrence of dependent differentiation and hence of differentiating reciprocal effects in *such* parts as are far enough removed from one another to be isolated by the crude means at our disposal, without their vitality being destroyed by the harmful vicinity of the wounded region.

Even now several results seem to show that during the course of *normal* development, the "specific causes" of many differentiations lie almost entirely within the altered parts, even in very small parts, so that, therefore, areas of independent differentiation may at an early stage comprise a single or only a few cells. The investigation of such narrowly localized processes of differentiation is attended with much greater difficulties; and since, moreover, *the fundamental formative processes*, viz., assimilation, growth, self-movement, and the qualitative differentiation of cells take place altogether or, at least, in the first instance within the province of the invisibly minute, it will be necessary, in order to clear up these fundamental processes, *to make as much or even more use of hypotheses, as physicists and chemists are compelled to do* when they cope with the fundamental processes of their respective sciences. And just as in these sciences, we shall have to regard those assumptions as approximating most nearly to the truth which explain the most facts and permit of the successful prediction of new facts; and *ceteris paribus* we shall prefer that explanation which appears to be the "simplest," not forgetting, however, that we may easily fall into error on this point for the reasons above set forth.

Experiment on living beings is quite peculiar and apt to be misleading, in that in many cases, like *mutilations* and certain *disturbances of the arrangement* of parts with respect to one another, conditions arise in which the organism does not react with the formative mechanisms of *direct or normal development*, but with the regulative and regenerative mechanisms of *indirect development, or regeneration* (13).

Indirect development runs its course in great measure under the *regulating reciprocal activities of many*, or, as in the case of great defects and disturbances in lower animals, for a time at least, of *all* parts of the organism; it differs essentially in this respect from the *direct or typical development* of the fertilized ovum, which goes on in the absence of any interference, or even for a short time after the cessation of the interference, and often completes its course with extreme *self-differentiation* of circumscribed parts. (*Within* these, of course, the changes depend on the *reciprocal operations of the parts*.)

The modi operandi of each of these two varieties of development must be investigated.

In the setting to work of the mechanisms of *indirect* development lies, however, *one of the greatest hindrances to the investigation of normal formative modes* of direct development.

In those low organisms in which regeneration steps in promptly after *mutilation* or after *disturbance in the arrangement* of parts, the value of the experiment is much lessened when it is intended for the investigation of the *normal* methods of development. On the other hand, the higher organisms are more advantageous in that their regulatory mechanisms, especially during the later stages of development, are much weaker in their manifestation and in part much more difficult to call into activity, *i.e.*, they set in much later after the disturbing influence than they do in lower animals.

This favorable circumstance enables us to investigate exhaustibly by means of experiment the processes of normal development in the organisms which rank next to ourselves.

Owing to the fact that these two typically different kinds of development, as well as the rôle they play in the reactions of animals subjected to experiment, have not been kept distinct heretofore by most experimenters, recent experimental investigation has been productive of more confusion than enlightenment; quite apart from the fact that the observations themselves leave much to be desired in point of accuracy and completeness, perhaps for the reason that we do not yet sufficiently appreciate how much more expenditure of patient observation is required in experimental investigation than in current descriptive embryological investigation. In the latter we are already sufficiently advanced to be able to recognize the different developmental stages, and we often know when the stage of immediate interest will make its appearance; whereas unusual experimental interference may *at any time bring forth something new*, so that in order to follow up the subject it is often necessary to observe continuously, or at least frequently, by day and night.

We must not conceal from ourselves the fact that the causal investigation of organisms is one of the most difficult, if not the most difficult, problem which the human intellect has attempted to solve, and that this investigation, like every causal science, can never reach completeness, since every new cause ascertained only gives rise to fresh questions regarding the cause of this cause.

Inasmuch as many of its problems are nearly or quite insoluble by means of experimental investigation, *developmental mechanics must needs, so far as possible, seek to utilize for its own ends, all the kinds and ways of causal investigation of organisms and the results thereby attained*, and not cast aside as useless any biological discipline in silly conceit. Developmental mechanics should, moreover, cultivate the analysis of formative processes into constant "complex components" to a greater extent, if anything, than the ascertainment of simple components.

This conception of the methods of investigation *first* to be undertaken in developmental mechanics differs essentially from the views of many contemporaneous workers in the same field, who believe that descriptive and comparative anatomy as well as embryological investigation are of little value to developmental mechanics. This opinion is held by authors who see the *present* task of developmental mechanics in the immediate reduction of organic formative processes to purely inorganic, physico-chemical components (14).

If, however, we limit ourselves to that which is *possible* at present, we can regard *this* task only as a *final goal*, which for the present, and even for some time to come, we shall approach in a *direct* path only at a relatively slow pace; still we are not to cease in our endeavors "to reduce the formative forces of the animal body to the general forces or vital tendencies of the world as a whole," as K. E. von Baer has said (15).

It is evidently advantageous, and will be productive of much important information, if we endeavor to reproduce *synthetically* in an inorganic way *structures, forms, and processes which resemble as closely as possible*, or are the same as those of the organic world. This has been done by G. Berthold, Errera, and more recently, and with marked success, by O. Bütschli.

Were we, however, to follow this as the *only* method of procedure, and, in accordance therewith, to attempt the investigation only of those processes which resolve themselves at once into simple components, or from which at least such components may at once be *split off*, we should very soon reach a limit at which we should be brought to a standstill; for the majority of organic processes are far too complicated in their conditioning to admit of immediate reduction to physico-chemical *modi operandi*. And even in cases where it is claimed that such a reduction has been brought about, it appears that the part which the simple components contribute to the formation in question, as compared with that of the coöperant complex components, has been considerably overestimated.

If we would advance without interruption, we shall have to be content for many years to come with an analysis into complex components.

While thus in some quarters the possibility of a physical explanation, so far as it is attainable at present, is considerably overestimated, it appears that in another quarter our possible attainments in this direction are, on the whole, essentially underestimated, so that organic structure is claimed to be incapable of any explanation, and only to be deduced teleologically.

We may be easily misled to such a metaphysical conclusion by the facts of regeneration, and also by the observations recently made by Driesch on the origin of normally formed products after *extreme* interference during the early development, viz., during the cleavage stages. Although these processes actually do produce the impression that mechanical operations are inadequate, and that the purpose of bringing about the typical form as a whole must step in actively, still we are bound not to entertain such a supposition, at least with our present limited insight, *till every other possibility has been with certainty excluded*. This is at present by no means the case. For in regeneration there is still extant a portion of the typical whole, a portion, moreover, in which the *whole itself* may be supposed to be contained *implicite* in the form of germ-plasm, and hence in an undeveloped condition; this regeneration-plasma being called into activity, may, thereupon, restore the whole *explicite*. *From this source* is brought forth again the *typical* form, after its kind, and, what is worthy of special consideration, often in a somewhat *defective* manner. The problem is not, therefore, one of a peculiar nature, nor one which involves a leading principle, but refers solely to the *special process whereby* the normal form is restored. The same holds good also with respect to the manifestations of the postulated regenerative-plasma in cases where development is disturbed during the cleavage stages.

The continuity of typical formation, the continuity of the typically developed and undeveloped material of formation is, therefore, not interrupted by these irregular processes, and, no matter how difficult it may be to form a conception of the details of the phenomena, *there is still no urgent reason for assuming a metaphysical process.*

"*Incidit in Scyllam, qui vult vitare Charybdim*" is particularly applicable to the investigator in the field of developmental mechanics. The *too simply mechanical* and the *metaphysical conception* represent the Scylla and the Charybdis, to steer one's course between which is indeed a difficult task, a task which few have hitherto accomplished. It cannot, however, be denied that the seductiveness of the latter views has been increasing with the increase in our knowledge.

The *least productive method* of carrying on developmental mechanics is to start out in the very beginnings of exact investigation from the limited number of facts at our disposal, and to pour forth numerous and long-winded essays on the length to which our understanding can go in this field and on the rôles which opposing formative principles play during developmental processes.

It is true that in order to understand the problems before us it was necessary to elucidate more clearly the old contrasts between Evolution and Epigenesis, but this was not for the purpose of producing endless theoretical disquisitions, but *with the aim of establishing a basis for exact investigation* (16). Still we must regard as useful the attempt to bring together all the facts which were supposed to support each of the possible views. Continued discussion, however, and the premature expression and maintenance of final one-sided opinions on these still unknown conditions, can only injure the reputation of our immature investigation along causal lines, and withdraw the few who have devoted themselves to the subject from more productive activity.

III. *The Relations of Developmental Mechanics to the Other Biological Disciplines.*

The branches of Biology hitherto recognized, viz., descriptive *zoölogy*, *anatomy*, *embryology*, and *physiology*, represent the essential prerequisites of developmental mechanics, for it is they that teach us the facts in forms and processes, the causal explanation of the latter being the province of the discipline we are discussing.

Because they depend on comparison of structure, anatomy and embryology are also productive of causal information to the extent that such comparison can take the place of experiment.

This substitution cannot be a complete one for the logical reasons presented above. Nevertheless, *comparative anatomy and comparative embryology are the means of ascertaining many causal relations* between the parts of organisms, and these relations, in so far as they rest on a sufficient mass of observations, lack only the direct proof of artificial or natural experiment to become certainty. *In so far as these disciplines reveal causal information, they are themselves developmental mechanics,* and inasmuch as they do and have done this to a very great extent, they represent disciplines which are only historically separated from developmental mechanics.

The new character which these causal investigations have acquired in recent times, and will continue to acquire, is the use of *analytical* experiment, together with the endeavor to collect together all causal information, and to raise causal investigation to the dignity of a principal aim, — an aim in itself.

Thus phylogenetic and ontogenetic developmental mechanics receive from the older branches of biology besides their problems much causal information, and still more guidance to such information. *The methods with which this knowledge has been acquired will continue to be necessary to developmental mechanics even in future,* since many causal problems are scarcely accessible to experimental investigation, and since, moreover, the correct interpretation of the results of experiment is often fraught with such difficulty, that every possible aid from other sources must be utilized.

Still developmental mechanics will be of more or less service to these morphological disciplines in return for what it is continually receiving from them.

It will open the eyes of the descriptive observer to many structural relations hitherto overlooked; structures which have been scarcely appreciated will acquire a deeper significance; many a problem arising from descriptive study and incapable of solution through observation on normal phenomena will be elucidated, and the causal deductions of these sciences will be corrected or established on a firmer basis. Thus the doctrine of the *transposition of cells* during embryonic formation — a doctrine which has of late been greatly expanded by His — will be *proved* to be correct only by experiment, and tested as to the extent to which it is claimed to obtain, and traced back to its causes. In like manner our ideas derived from comparison of different *phases of cell-division* require direct experimental proof, or confirmation and extension with respect to the immediate causal interrelations of these processes. It was only through causal observation that life was infused into the dead facts of corrosion anatomy, when the *laws which govern the ramification of blood-vessels* were discovered.

Comparative anatomy will be able to receive a great deal of assistance from developmental mechanics, especially *in extending the problems with which it deals.* As comparative anatomy endeavors to ascertain the genetic connection, the "Stammbaum" of organisms, it is itself essentially a causal science. It analyzes structures into the two components, *variation* and *heredity.* It is true that both of these, as understood in comparative anatomy, are general formative principles, but, in the first place, they are of much greater diversity than the complex components given above as illustrations, and in the second place, they are not uniform, *i.e.*, not always constant in their modes of operating.

Heredity is a constant principle, always *operating* in the same way, only in so far as it depends, according to Weismann and others, on the continuity and variations of the *germ-plasm*, and hence on *assimilation*. When we are dealing besides with the inheritance of somatogenic, or so-called acquired characters, the same word is used to designate *modi operandi* of a totally different nature.

The concept *variation* (adaptation) comprises so many different operations that Haeckel has established for them a whole series of "laws" (19). Both heredity and variation, however, are in urgent need of causal explanation, *i.e.*, of analysis into their uniformly operant components. This analysis is one of the tasks of developmental mechanics. This is true also of *cœnogenesis* and of the so-called "*fundamental law of biogenesis*."

The hypotheses which *comparative anatomy*, like every other science, continually employs, *have essentially the character of developmental mechanics.*

As this fact does not seem to be sufficiently well known, a few illustrations may be adduced here.

Gegenbaur rejects the homology of the ventral nerve-cord with the spinal cord (20) mainly for the reason that he regards the *difference in the respective "positions"* of the two organs as much more important than the *agreement* of their occurrence throughout the whole length of the animal, their metameric segmentation, similarity of ramification, and composition of the same form-elements. This opinion rests upon the assumption that in phylogeny an organ may more easily arise *anew* and independently of a preëxisting organ with which it has in common the same biological constituents, essentially the same distribution, the same segmentation, and the same function, than that the latter organ should have changed its *position* to such an extent, viz., from the ventral to the dorsal side of the animal.[1]

As will be seen, this assumption is purely one of developmental mechanics and was certainly a bold hypothesis in the state of developmental mechanics at that time; and although we do not doubt its truth in this particular case, Gegenbaur

[1] I have taken the liberty of correcting an obvious *lapsus calami* in this sentence. — W. M. W.

himself would hardly regard it as true *in general*, but only in respect of such axial organs as would have to shift their position through an angle of 180° to the opposite side of the body.

The morphological inequality of the upper lobes of both human lungs assumed by Aeby (21) — an inequality which he deduces from the fact that the bronchus from the right side takes an eparterial, that of the left, a hyparterial course, so that the left lung lacks an equivalent of the right upper lobe — also rests upon the developmental mechanical assumption that the relations of *position* of the air-passage to the blood-passage are essentially more constant, *i.e.*, may vary with less facility than the *shape* of the portions of the lung to which these two passages lead. This assumption, though doubtful, is supported by the fact — also of a developmental mechanical nature — that the lung has little shape of its own, but adapts its form largely to its environment.

The fundamental law propounded by Wiedersheim (22) as the result of extensive comparative investigation, "that the impulse to the development of the appendicular skeleton in vertebrates always starts from the periphery, and that the central (girdle) portions are only secondarily developed under the formative influence of the free appendages," is, as will be seen, also of a purely developmental mechanical nature, and requires further developmental mechanical substantiation and analysis. This is also the case with the important conception of imitative homology, or parhomology, introduced by Fürbringer (23).

Although these examples have been adduced without special selection, they nevertheless show clearly how comparative anatomy is continually assigning problems to developmental mechanics by making that science acquainted with new operations, and how, on the other hand, developmental mechanics, by devoting itself to the solution of these problems, is becoming the continuation and at the same time the mainstay of comparative anatomy.

As long as comparative anatomy attempted to establish only the *main course* of development in the animal kingdom, following in a general way the continuous development of forms only through the *classes* of each type, comparison of different forms showed that essentially and unequivocally the same course of progressive development is followed by nearly all systems of organs. But in further approximations of a higher degree, viz., in tracing that development through the orders, families, genera, and species, even to the individual, so many incongruities in the development of organ systems and organs made their appearance, that comparative anatomy has been compelled to call in the assistance of quite a number of developmental mechanical hypotheses, for the correctness of which only experimental tests can give complete security.

Even the *appreciation of "essential" or "unessential" agreements or differences*, an appreciation which is continually necessary in the phylogenetic explanation of comparative observations on form, *in ultimate analysis always shows itself to be of a developmental mechanical character.*

Since developmental mechanics, perhaps for some time to come, or at least in the beginning, will pursue its own course, it would be encouraging if comparative anatomists would themselves resort to experimentation for the purpose of solving, so far as possible in a short time, the problems in which they are interested, *e.g.*, the continually recurring main question, as to what are actually — not in a formal, but in a developmental sense — "*slight*" or "*easy*" *variations;* whether *the number* of organs may be *increased* "easily" (*i.e.*, by a simple interference and hence by a correspondingly slight accident), as perhaps by the passive infolding of a somite, by the splitting of a shoot, or by linear pressure on the same in a direction contrary to its direction of growth, and further, in case these attempts are successful, whether or not such newly formed organs at once attain to the full differentiation of the former ones; further, whether, inversely, a *decrease in the number* of organs may be "easily" brought about, perhaps by inhibiting a normal infolding or constriction or by compression and resulting concrescence; whether in these cases according to the earlier or later stage of development, during which such interference is applied, the united parts may at once become perfectly simple or still retain traces of their double origin, etc.

Of course these would not be *hereditary* changes; on which account, the essential results of these experiments could only be utilized in explaining *individual* variations with reference to their representing "reversions" or "monstrosities." Hence it would be of greater importance to ascertain to what extent after artificial *local* changes in an embryo, changes make their appearance in other organs — no matter whether these bear functional correlations to the affected regions or not — since in the case of the same primary or inherited change the secondary changes would then also be "inherited." Moreover, by raising animals that are born without fore limbs or have been deprived of them, it may be possible to ascertain to what extent such animals, being compelled from the first to adopt a method of locomotion, like jumping, which is foreign to their species, are nevertheless able by direct adaptation to this mode of progression, to develop the requisite proportions in the length of the skeletal parts and in the size of the lever-arms of the muscles, and whether in these respects Lamarck's theory is confirmed or refuted.

In the introduction to his *Morphologisches Jahrbuch* Carl Gegenbaur gave expression to the following words full of insight: "Indeed the time will come when morphology, too, will be conscious of the mutability of its aims and aspirations and when other problems and methods will take the place of those with which we busy ourselves at present." This new end is that of developmental mechanics — the investigation of the causes of the forms of organisms.

But it will be a long time before it takes the place of "the aim" of morphology. In the sense of the comparative anatomist, this can only come about when this science has reached the measure of its possible perfection. In the last instance both tendencies have the same aim and it is through *coöperation* that an approach to this aim will be most facilitated.

We must also define our position with respect to *Physiology*. This science in its fullest sense embraces *all the functions of life*. Developmental mechanics represents an integral part of this science, and after it has reached its development it will be the largest and most essential part. But alongside of human and animal physiology as it is almost exclusively carried on by its representatives at present, under the stress of immediate questions; alongside of this science which treats of the maintenance-function of parts already established, usually to the exclusion of the formative functions of maintenance; alongside of the residual "*science of the mere keeping a-going of the living machine*," whereby the functions most difficult of comprehension, viz., those of the construction, formation, and the maintenance of that which is formed, remain unheeded and uninvestigated — the science of the causes of this formative activity constitutes an essentially independent branch.

Since, however, the performance of a function, even in already developed organs, has a *formative effect* in consequence of "*functional adaptation*" to magnitudes of function which have been increased for a considerable time beyond the common mean, or depressed below it, this *doctrine of mere machine-activity* is of importance to developmental mechanics, and many of the results of its investigation may be of service to the latter, so that we must also remain in close touch with this kind of physiology. But quite as great or even greater will be the assistance which later on this physiology will receive from an insight into the causes of the formation and maintenance of structure.

Since in plant life the *formative functions* greatly predominate over the *functions of maintenance* (Betriebsfunctionen), owing to the absence of the nervous and muscular systems and sense organs, and since, moreover, plants are more easily accessible to experiment than animal organisms, *plant physiology* has been spared the onesidedness which exists in animal physiology; thanks to the investigations of such men as Julius v. Sachs, Wiesner, Pfeffer, Strasburger, Berthold, de Vries, Voechting, Klebs, and others, it has already become in a great measure developmental mechanics in the full sense of the word, and has far outstripped the developmental mechanics of animal organisms.

The causal tendency of Phytomorphology was considerably advanced by the fact that *plant forms*, being fixed to a particular spot and hence much more exposed to external influences and to these in part in constant directions, *are influenced even in their typical morphology to a great extent by "external" factors, whereas the "typical" structure of animals, which are capable of active locomotion, is in great measure independent of external formative influences* and consists, apart from certain functions of superficial parts, in self-differentiation. It is, however, much more difficult to understand the *internal* than the external factors and the reactions to the same.

In *sessile* animals J. Loeb (24) has recently discovered differentiating effects of gravity on the organism, like those observed in plants. For example an inverted piece of a hydroid polyp will produce *roots* at its *lower* and *shoots* at its *upper* end. But we must be careful not to extend this occurrence to other animals, as has already been done, thus ignoring the causal implication in the sessile mode of life, and ascribing in all animals a differentiating effect to gravity, especially when irreproachable experiments have already proved the opposite in the case of other animals.

Of particularly great importance to developmental mechanics, are, furthermore, many of the results of the PATHOLOGICAL SCIENCES.

Looking aside from the cases in which *immediate death* is brought about by a sudden stopping or disturbance of the functions which are necessary to keep the machine going, we observe in every *primary disturbance*, no matter how it may be caused, *secondary changes* intervening, which even though they be *merely functional* at first, nevertheless gradually lead to *formative* changes.

In this manner these secondary formative changes give us evidence of formative interrelations, formative modi operandi of parts one upon another, an understanding of which is essential to our purpose.

But even here, as in the effect of an experiment, we must first ascertain whether these pathologically formative *modi operandi* enable us to draw any conclusions whatever with respect to *normal* operations, or whether under *abnormal* conditions abnormal modes of reaction may also occur, and hence processes which do not occur at all in normal phenomena.

To sum up the results of observation in the pathology of the *higher vertebrates*, we may say that pathology is essentially the doctrine of phenomena which are in themselves normal, but which manifest themselves in the wrong place, at the wrong time, or in the wrong magnitude or direction; for all pathological *processes*, a few *kinds of decay* (like amyloid and waxy degeneration) excepted, also occur as normal phenomena.

Hence there do not occur in the pathological conditions of these animals any *modi operandi which are foreign to normal development or any new substantive or even productively formative modi operandi;* and hence in case of secondary changes pathology has only to investigate the way in which the organism makes use of its normal modes of formation and reaction during or after disturbances of the normal conditions.

Of course these results of pathology hold good also of *artificial* experiments. *We are able to conclude*, therefore, from the reactions which take place after experimental or pathological changes *as to the modi operandi which also occur under normal conditions*, but which operate normally with different intensity and at a different time.

On the other hand, whenever regeneration of destroyed parts occurs, the mechanisms of *indirect* development are put into activity. These were referred to above.

Here we are concerned with the *secondary changes of other parts*, which following upon primary disturbance are either themselves disturbances; in this case they indicate that the primarily affected part is necessary to the maintenance or development of the secondarily affected part, and hence in some way participates in its production, thus exercising a "trophic" influence upon it.[1]

Such conditions follow from the secondary atrophy of the sensory or motor nuclei of the brain and spinal cord when their respective peripheral end-organs are removed soon after birth, and inversely from the aplasia of the muscles after destruction of the motor ganglion cells of the anterior cornua in infantile paralysis; from the degeneration of the nerves when they are separated from their respective ganglion cells, etc.

[1] There is only one alternative mentioned in this sentence, the other clause having been omitted. — W. M. W.

The following conditions point to *still more enigmatical connections:* the disturbance in the development of the brain in congenital defect of both suprarenals, the origin of cretinism and myxœdema after complete extirpation of the thyroid, the default in development of the secondary sexual characters, such as the female habitus, the female mammæ, the male habitus, the beard, the male voice after extirpation of the sexual glands; other cases are unilateral visual atrophy, symmetrical gangrene of the toes and fingers, etc.

In an extensive series of other cases, primary disturbance or destruction of one part is followed by a *compensatory hypertrophy* of other parts of the same kind, which take on the function of the disturbed parts. On such manifestations of *functional adaptation* mainly depends — regeneration being insignificant in man — the very important principle of the *equalization of disturbances* after pathological changes, a principle which has of late been thoroughly studied in all its bearings by Nothnagel (25).

Of a contrary nature is the enigmatical compensatory hypertrophy of *non-functioning organs, e.g.*, of the milk-glands of young animals.

Besides such trophic and functional correlations, many *other formative correlations* make their appearance during pathological processes. A *mechanical equilibrium of parts* under normal conditions is indicated by disturbances like the bending outwards of the teeth when the tongue is abnormally large, the triangular shape assumed by the previously round tibia when the muscles of the leg are developed, and the return to the rounded contour with the atrophy of the muscles in spinal infantile paralysis, the hypertrophy of the interstitial connective tissue following the atrophy of the specific tissues of organs, the proliferation of the pavement epithelium of the outer surface of the body into cavities like those of the nose, mammary glands, ureters, and bladder, which are normally lined with a different epithelium; or the proliferation of the vaginal epithelium into the uterus.

To the same category belong the *formative reactions to well known external influences, i.e.*, influences coming from without the parts affected ; the formation of bones in connective tissue that has been subjected to mechanical impact ("Reit-" and "Exercierknochen") ; occasional progressive ossifications like *leontiasis ossea* after a single injury; further, the formation of giant cells around dead or dying parts (around foreign bodies), around bones which are no longer supplied with nutriment, or which have become disarticulated, the formation of blisters under skin which has been subjected to repeated pressure or displacement, the formation of the placenta materna on any part of the peritoneum in extra-uterine pregnancy, the formation of new capillaries from those already existing in consequence of an increased demand for nutrition, even when this demand is occasioned by the presence of a body foreign to the particular region (metastatic tumor), together with an increase in size in the afferent and efferent vessels of the region, etc.

The fact that transplanted pieces of skin, like artificial noses, gradually acquire connections with the sensory pathways, indicates that the sensory nerves continue to send out processes in all directions till every region is supplied from one, or normally from two sensory branches ; this is evidence, at the same time, of a peculiar touch which the parts supplied with sensory nerves keep with one another or with the sensory nerves of neighboring parts.

The ends of broken bones which are not bound together and hence movable on each other, gradually develop a joint with the circumjacent connective tissue. Since the normal joints are laid down and developed without any movement of the kind, this pseudarthrosis corresponds only to the *further development* of an already formed normal joint in adaptation to an individual requirement.

Peculiar properties of life are evinced furthermore by the hypertrophy of connective tissue and young epiphysial cartilage or bone in stoppage-hyperæmia, whereas, in contradistinction to this, the specifically functional portions of glands, muscles, and of the central nervous system, are injured by such hyperæmia ; further, the tendency of like parts to grow together in synophthalmia, etc. Many authors will be inclined to include here the formation and retention of bones in places protected from pressure (in reality only apparently thus protected) like the arachnoidea, dura-mater, in the atrophied eyeball.

The property of self-maintenance or self-differentiation of parts is evinced by the development of very minute detached portions of tumors which may be carried anywhere by the blood current and grow to be secondary tumors of the same morphological character as the primary tumor; the development of sporadic masses of gray brain-substance; the retention of the normal structure in abstricted pieces of the retina lying outside the eye; the formation of hair and teeth in dermoid cysts; the teratomata; the healing over of transplanted skin, bones, eyeballs, etc.

To these examples of the *important developmental mechanical results of pathological research* should be added further those cases of aberrations from the normal which accrue from a study of *monsters*, and the lesser deviations designated as *varieties*.

Besides the varieties which may fall under the observation of anatomists, there are a great number of these "*experiments of nature*" to which especially *pathological anatomists* and *clinicians* have access.

It would, therefore, be most serviceable and advantageous to developmental mechanics if those investigators to whom such phenomena present themselves were more mindful than they have been heretofore of *the importance of these facts in ascertaining normal formative causes*, and if they would for this reason endeavor to collect *all the formative modi operandi of which there is evidence, together with more accurate data concerning their magnitude and time relations, their mode of operating, their connections, and remoter causes.*

It is probably best to begin with an attempt *to formulate concisely* every such phenomenon as a *modus operandi.* Such an attempt shows at once the unsatisfactory condition of our present knowledge, and there follows as a matter of course the necessity of rendering this knowledge more complete.

The same purpose would be served by many observations which pathologists might make during experimentation undertaken with other aims in view. Thus, *e.g.*, in experiments on the effects of hunger, protracted fever, chronic poisoning, or of any other chronic disturbance like paralysis, etc., *a useful extermination of cells*, hitherto unnoticed by pathologists, always takes place — an extermination, the magnitude and extent of which depends upon the still unknown magnitude of *qualitative* variations among the like cells of a single organ. Under such circumstances the cells which happen to be least able to resist the noxious influences must *ceteris paribus* be the first to perish, and for this very reason after these cells have been supplanted by the offspring of qualitatively more resistent cells, the whole organism, or in the case of local affections, the organ in question, must have become better able to resist these particular noxious influences. (This does not exclude the possibility that in special cases the resistance may be at the same time diminished by other factors.) *By means of hunger, e.g., the organism is transformed by a process of selection into a saving machine*, because those cells which require much nutriment will be the first to starve. Such an *internal selection* must also occur among the *variations* in nourishment and activity during the course of *normal* vital processes, but to a considerably less extent and in a manner more difficult to determine ; hence we may expect that these conditions will be first elucidated in pathological cases of a grosser character.

Since, moreover, pathologists, representing as they do the science of phenomena which are to a considerable extent normal though occurring under abnormal conditions, take a real interest in learning to comprehend normal modes of formation, it will probably be the case in future more often than at present, that these investigators will experiment with the express purpose of ascertaining and analyzing normal modes of formation. This has already been done with success by surgeons in the case of the *modi operandi* of bone-formation.

The "Archiv für Entwickelungsmechanik" will be glad to welcome every such contribution from clinicians and comparative anatomists.

The advantage that will accrue in the first instance to developmental mechanics from such contributions will revert to the service of the clinical disciplines, when once the *modi operandi* of formation and maintenance and their causal relations shall be to a considerable extent understood. For in this way we shall acquire a deeper insight into pathological changes and at the same time a foundation for a therapeutics scientific in the true sense of the word and based upon adequate understanding.

Just as developmental mechanics utilizes for its own purposes all methods which may be productive of causal understanding and all biological disciplines, so does it embrace as its field of investigation all living things, from the lowest Protista to the highest animal and vegetable organisms.

Accordingly *these Archives will accept causal essays on all biological subjects*, but as it does not propose to compete on their own special grounds with periodicals devoted to special subjects, *only those biological papers will be included which directly pursue a causal aim and for which the material has been collected and elaborated with this end in view.*

Descriptive papers, however, containing only occasional suppositions of a causal nature, or even apodictic assertions without any attempt to support these assumptions by comparison of the different pertinent facts, fall outside the scope of these Archives. But it may be suggested to such authors as desire their causal remarks to be preserved, to send their papers to the editor, with an indication of the passages in question, so that attention may be called to them incidentally, perhaps in the form of an essay.

Papers of a comparative anatomical nature which reduce the forms of organisms exclusively to the factors of variation and heredity, without attempting any *further analysis* of these "inconstant" complex components, also lie outside the territory covered by our Archives, since such preliminary analysis together with the ascertainment of descent, properly belongs to the field of comparative anatomy.

It is much to be wished that in concluding *every contribution* which appears in these Archives, *the causal results be concisely summarized.* Although such a summary can at most have only a provisional value, it is nevertheless of great assistance to the author, who is thus compelled to reduce his views to the conciseness of brief expression, to the reader who is thus enabled to see the results in a definite form, and to the future investigator, who thus finds a clearly circumscribed starting-point, and is in a better position to express the differences to which his own observations may lead him.

It is a matter of long experience that truth is only born in the conflict of opinions. If this maxim has proved itself to be correct in the descriptive sciences, how much more applicable will it be to a science which treats of causes!

Accordingly, the better to serve truth, the Archives will furnish space for the most conflicting opinions, provided they be supported by a *basis of observation.*

But *one* limitation is to be wished for in the approaching struggle, and it will be the endeavor of the editor to attain it in these Archives: the maintaining of a respectful tone even towards those who hold very different opinions. The ascertainment of truth, for which we are all seeking, is not furthered but retarded by the expression of personal feelings. Sufficient space will always be allotted to a proper treatment of differences and to remarks on priority.

The more vehement the struggle waged for the truth between different contentions, the more rapidly, generally speaking, shall we approach the lofty and distant goal of our ambition.

The specific processes of life are bound to the form and structure of its substrata. Hence *developmental mechanics* as the science of the causes of these formations will sometime constitute *the common basis of all other biological disciplines* and, *in continual symbiosis with these,* play a prominent part in the solutions of the problems of life.

At present opinions on the subject of developmental mechanics are much divided. While several biologists regard attempts in this direction as little more than the hobby of a few authors, and others are of the opinion that "so small a field" cannot pretend to maintain a publication of its own, the other conviction is already gaining ground that developmental mechanics is destined to become a science that will interest all the other biological disciplines.

That such will be the case is evinced in the most encouraging manner by the list of collaborators of these Archives — a list in which all the great departments of biology are represented. Besides these many other prominent investigators have expressed their interest and sympathy in the new tendency and in its organ. In this place I would again express my gratitude to all of these gentlemen.

INNSBRUCK, August, 1894.

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NINTH LECTURE.

THE ORGANIZATION OF BOTANICAL MUSEUMS FOR SCHOOLS, COLLEGES, AND UNIVERSITIES.

PROF. J. M. MACFARLANE.

EVERY teacher of botany must have experienced the difficulty at times, of presenting to a class a series of natural specimens illustrating some problem in the science. Dried plants are practically useless for such a purpose, as the process of drying involves crushing and displacement of parts that are often highly instructive. Even were our most active period of teaching to embrace the summer months — which is the rare exception — it is impossible to obtain at any one time all those stages of growth in a species or in genera that may be desired for comparison. The question naturally arises as to whether this state of things can be remedied. The writer believes that it can, and now proposes to outline means by which the remedy can be obtained.

It is universally conceded that a well-arranged museum of comparative zoölogy is an invaluable aid to the study of animal forms in class-room and laboratory, particularly if care has been taken to display dissections as well as entire specimens. It will be my endeavor now to show that the same holds true for the study of plants. But it may be well to remind you here that till within the past few years a botanical museum was supposed to be a collection of gums, resins, oils, sugars, fibres, woods, fruits, and seeds, varied occasionally by hats, shoes, musical or other instruments, manufactured from vegetable products, and all arranged according to some approved system of classification. Such a collection could appropriately be called a museum of economic botany, and in its own place has been proved to possess high utility; but it is practically valueless for illustration of the facts of the science as set forth in modern botanical literature.

A teaching botanical museum then, is a present-day necessity for our educational institutions. The following practical directions epitomize the experience gained by the writer in organizing such. They have been brought together owing to numerous requests having been made by teachers for guidance in the matter. Already the example set in one of our universities has been followed in several schools with the happiest results. It seemed fitting, moreover, that the subject should be presented before such an audience as this, which includes representative teachers from the educational centers of the States and Canada.

The animating idea, then, in working out the subject should be to obtain in permanent form specimens that will retain their natural outline, relationship, and structure. Here it may be stated that, in the great majority of cases, the natural color of the object is entirely removed owing to the mode of treatment. This may seem, on first thought, to be an undesirable result; but with widening experience the conclusion will be reached, by teacher and student alike, that instead of a necessary evil it is a real gain. A pure bleached specimen often reveals details that had been overlooked in specimens when decked in all their wealth of color.

The subject can best be treated under the following heads: (*a*) requisites for the work; (*b*) selection of objects; (*c*) preparation of objects; (*d*) finishing of preparations; (*e*) arrangement of preparations; (*f*) description of preparations; (*g*) some of the results obtained.

(*a*) *Requisites for the work.* — The first and most important consideration here is the type of glass jar that experience has proved to be the best as combining many commendable points. All things considered, three sizes of a pure blown-glass bottle, with short, straight shoulder, answer best. The sizes are $3 \times 6\frac{1}{2}$ inches, $3\frac{1}{2} \times 7\frac{1}{2}$ inches, and $3\frac{3}{4} \times 11\frac{1}{2}$ inches, while their average cost per gross, with fitted corks, is $15, $24, and

$36. It is essential that the corks be of good quality and free from holes or fissures, as the sequel will explain. The bottle also should be free from warps or flaws, and should have a neat, sharply-rounded collar, as in Fig. 3.

The preservative fluid that has alone proved suitable for nearly all specimens is commercial alcohol of 93 % to 95 % strength. Its advantages are many. It quickly hardens, and therefore retains in position all plant parts that can readily be permeated by it; and this applies to most objects. It bleaches uniformly, as a rule. Its cost is reasonable when purchased by an institution, while it is a clean and harmless liquid to use along with metal instruments.

As already indicated, it rapidly discharges plant colors in most instances, but there are some striking exceptions: thus, the violet-blue color of the petals in some *Ranunculaceae*, *Boraginaceae*, and *Compositae* is either retained in its original intensity, or is only slightly discharged. So also with such scarlets as that exhibited by the macrosporangial coat of *Cycas revoluta*. But no matter what the subsequent change may be, the specimen, after being arranged in alcohol, should at once be placed in direct sunlight to effect the discharge of chlorophyll and other coloring matters.

Two pairs of long fine forceps are needed for dissection of flower, fruit, and seed parts, or for displaying properly the organs of cryptogams. Alike for dissection and for placing of parts when the specimen has been dropped into alcohol, two needles in long handles will prove useful. A pair of rather strong scissors for neat removal of a specimen from a plant, also fine-pointed scissors for dissection, are essential. For flower, fruit, and seed sections a sharp razor is indispensable, but for rougher purposes, a pocket-knife will suit. For sections of hard fruits like those of palms, a fine rotary or hand-saw should be employed, and the surface then polished.

Not unfrequently, as will be pointed out later, it is desirable to place two or three specimens alongside each other in a common jar for comparison. Thus I have arranged, side by side, three inflorescences of our native pickerel weed (*Pontederia cordata*) to show its trimorphic condition. To retain the inflorescences in position short lengths of fine glass wire were passed through the axis of each at different levels. A stock, therefore, of such glass wire of varying thickness should always be at hand.

For setting out dissected parts separately, pure plate mica, white silk thread, a few fine needles, and ribbon pins are requisite. Equipped with the above, the botanist is ready for nearly every object that presents itself.

(*b*) *Selection of objects.* — The judicious selection of an object is of supreme importance, and cannot be left to the discrimination of any ordinary laboratory worker. It requires the best judgment of the skilled botanist. By this we mean that, while any one can gather a specimen and place it in a jar of alcohol, only the expert can select such an example as will epitomize details, and thus give permanent value to it as a museum object worthy of study. In choosing each specimen, then, the aim should be to learn how much can be judiciously displayed and how many points advantageously shown; for a multiplicity of detail may only bewilder the student. This notwithstanding, the amount of information that a well-selected specimen can convey is astonishing. Take, for example, this preparation of Larkspur (*Delphinium Ajacis*) gathered three days ago from a garden near by. On looking round the bed I found, that of the plants in bloom, only one had a good flowering branch — that now shown — which deserved preservation. But an intelligent study of it is instructive. The lowermost flowers have withered, but each has left a maturing follicle, which in one example has been cut transversely, in another longitudinally, to expose the rows of sporangia or ovules. Of the six that are in bloom, four have been left entire; but the others have been cut in longitudinal and transverse section, so that the shape and relationship of sepals, petals, stamens, and carpel are evident. The uppermost flowers illustrate how the floral leaves are folded in bud.

Look again at this specimen of *Vitis Labrusca*. From numerous flowering shoots that seemed all equally good, that now shown was selected. The lowermost axis is tendriliform and has clasped an oak twig; the next above is in part tendriliform, in part flower-bearing; the uppermost is an inflorescence only. Here, then, morphological modification for physiological work is graphically presented. But, small though on first sight the flower parts appear to be, the organs of each are quite evident, and appropriately displayed on one side are three flowers just pushing off their cap-shaped corollas.

Here is a terminal shoot of the common woodbine (*Lonicera grata*, Fig. 1).[1] Three days ago it was gathered and placed in alcohol at 12.30 P.M., but had it been intended as a permanent specimen, it would have been collected at 7.30 to 8.00 P.M. The reason is, that while the one now shown illustrates well the floral relations of irregular Caprifoliads, at the time stated it further shows the earliest stage in the process of flower pollination by moths. But even this deserves study from that standpoint.

FIG. 1.

It may be necessary for some forms that not only careful selection but special treatment be resorted to. A case in point is the Corpse plant (*Monotropa uniflora*) that is saprophytic, and abundant in the woods of the Eastern States. The two specimens exhibited were selected four days ago. Both are instructive as showing some of the buds and open flowers with

[1] The author's best thanks are due to his students, Lily and Howard Wells, for the accompanying illustrations.

deflexed stalks, some erect and recently pollinated, others considerably elongated and maturing fruit. Both specimens were dug up surrounded by a large mass of soil. They were washed clean under a strong water jet. The dense coralloid mass of humus or saprophytic roots was thus exposed (Fig. 2). One of the sickly looking masses was at once dropped into an alcohol jar; the other was boiled in water for ten minutes, allowed to dry slightly, and thereafter placed in alcohol. The former is now black and unsightly. Owing to changes in the tannin cells through boiling, the latter has retained its pure, white appearance.

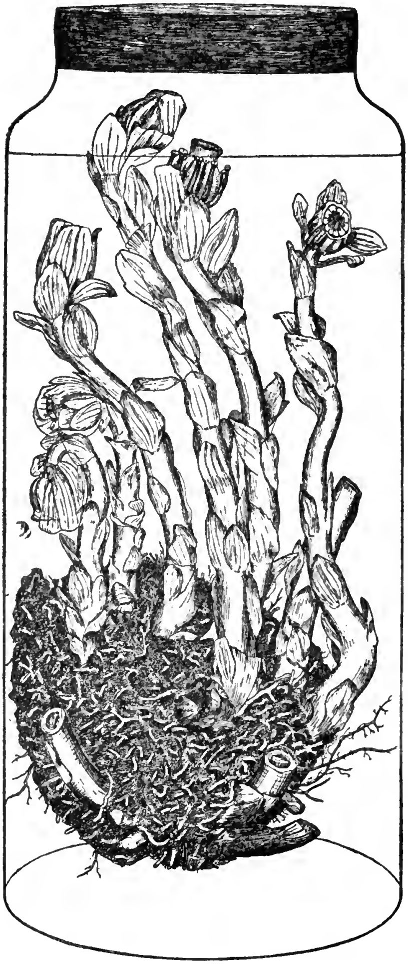

Fig. 2.

Root parasites, again, like *Gerardia*, *Comandra*, etc., should be similarly dug up and treated in the laboratory. As the soil is washed away by the strong water jet, the root-suckers of the parasite are exposed singly or in clusters attached to the host-root. Much more might be said on the spermaphytes or seed-plants, but the "cryptogams" claim a fair share of attention, and can yield fine results. A series of specimens placed side by side to illustrate the oöphyte, and stages in the developing sporophyte of our common Hair-moss (*Polytrichum commune*), forms a natural picture that excels the best diagram or model. These can either be arranged in jars in groups of three or four by the aid of glass threads, or can be fixed on sheet mica in the manner that will shortly be explained.

The Fungi give excellent opportunities for the display of selective skill. Take, for example, the Stinkhorn (*Phallus impudicus*), or the False Puffball (Fig. 3). To show merely the spore-bearing portion and a small bit of mycelium gives a poor idea of the plant, compared with that got by bringing a large sod into the laboratory, washing the soil from the copiously-branched mycelium and laying bare the young hypogeal spore receptacles in all stages of development. But few objects are more telling than a good piece of decaying bark covered with the reticulate, golden-yellow plasmodium of "Flowers of Tan" (*Aethalium septicum*); for whether we view the organism as plant or animal, it carries an impression at all times to the student that nothing else can so well do. In alcohol it retains much of its richness of coloring.

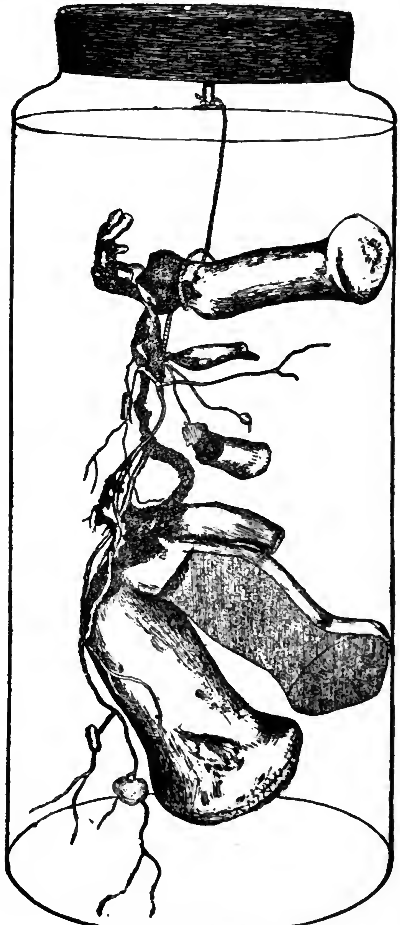

Fig. 3.

(*c*) *Preparation of objects.* — By this we mean the setting out of certain selected specimens in a manner that will best display the points that should be emphasized. Of many such it may be said that, previous to being placed in alcohol, trimming and dissection of parts is absolutely necessary. Take, for illustration, the fine example of Corpse plant (Fig. 2) already referred to. By aid of scissors several of the flowering stalks have been neatly cut away, in order the better to show those that remain. Of these one has had its maturing fruit cut transversely, another longitudinally. But even here we do not stop; for, taking advantage of the original large size of the plant, we have it cut in half, and the interwoven humus roots are thus exposed.

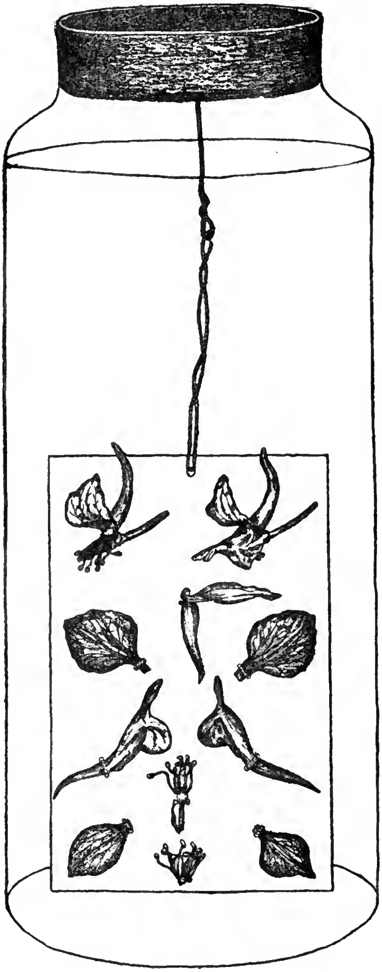

Fig. 4.

Suppose, again, we wish to set out in two bottles staminate and pistillate branches of the maiden-hair tree (*Ginkgo biloba*), or, as shown here, of the Honey-Locust (*Gleditschia triacanthos*). To expose the inflorescences properly, most or all of the leaves should be removed to a greater or less extent; though the retention of the petioles is important, from their morphological relation.

Still more elaborate preparation may be desirable. For example, to represent the growth-phases of seedlings, an excellent plan is to tie these side by side on a sheet of mica with white silk thread passed through small holes in the sheet. In this way the relative development of primary, secondary, or adventitious roots, the time of appearance on these of root tubercles in leguminous species, the swelling up of root or stem as a storing center in other plants, can all be illustrated. But skill and patience alike can be displayed over flower parts, and once set out, these remain as a natural picture that greatly excels the best drawing. Here (Fig. 4) are flower dissections of the Larkspur already referred to, which become to the student a permanent record of his laboratory work. The irregular and petaloid calyx with its spurred member, the irregular, reduced, and partially united corolla, the hypogynous stamens and their protandrous phases of maturing, the monocarpellary pistil and its relation to other parts, are all demonstrated.

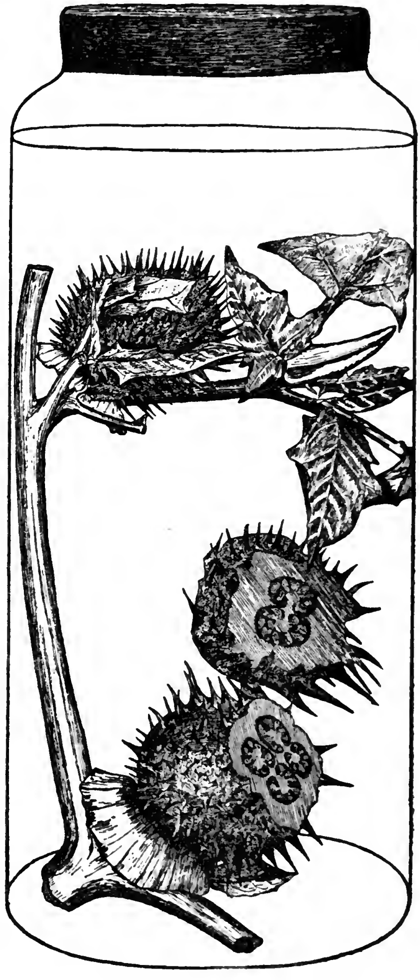

FIG. 5.

Or take a small capitulum of the sunflower. In addition to half of a sliced capitulum being displayed in one jar, in another can be suspended a mica sheet with dissections. These might consist of an entire and sectioned ligulate floret, a tubular floret in the latest bud stage, another in the expanded staminate stage, still another in the pistillate stage, and one in longitudinal section. They can all be neatly tied on by silk thread; but a preferable method would be to attach them with some transparent cement that would not alter in or be dissolved by alcohol. Such a cement is still a desideratum with me.

Considerable ingenuity can likewise be displayed over fruits and seeds. Witness, for example, this preparation of the Thornapple (Fig. 5) as an illustration of the former group; while entire and sectioned seeds, as well as the contained embryo of seeds like the bean, ash, maple, oak, beech, etc., can often be serially displayed to advantage.

A good many objects, especially cryptogamic ones, should be displayed in mass as well as singly. As a case in point we might cite a tuft of fern prothallia that has grown on a tenacious soil, and which may probably show all stages of maturation in the oöphyte and seedling sporophyte. Such a tuft would inevitably fall to pieces if placed in alcohol directly when gathered; but if imbedded in a black-pigmented matrix of plaster of Paris, the prothallia when bleached stand out in fine relief. Antheridial and archegonial tufts of various mosses and of *Marchantia* can be similarly treated.

(*d*) *Finishing of preparations.*—When a green plant is placed in alcohol and exposed, as already recommended, to bright sunlight, the discharge of color is rapid, but the specimen should be exposed for several days. Where plants contain tannin compounds, however, a few drops of dilute hydrochloric acid should be added to the alcohol, otherwise the object will assume a dirty brown color. When the specimen is decolorized, the discolored liquid should be carefully poured out, or drawn off by a siphon, as the object has been made extremely brittle. Pure distilled alcohol should then be added, and the preparation put aside on a rather large table along with others that are ready to be sealed up. After the waste alcohol has accumulated for a time it can be passed through a still, and a clear, sparkling liquid is then obtained that is even superior to new alcohol.

Probably no step in the process of preservation requires more attention than the sealing of the jars. It is a truly difficult matter to obtain a cement which will resist alcohol. Six years of trial incline me to recommend the following: Four parts of plaster of Paris, one part of glue, and one-fortieth part of red lead, intimately mixed together when the glue is melted and hot. Previous to its application the cork of the bottle should have been pressed home till its upper surface is one-sixteenth inch below the top of the neck, and its lower surface slightly above the alcohol. At this time care should be taken not to disturb the bottle so as to wet the cork till the cement has been applied and has hardened for one or two days. Filtration of the alcohol along the junction of cork and bottle, with the formation of an alcohol film on its upper surface, is fatal to success. When applied the cement should be rather dense in consistence, and, by aid of a spatula, should be spread evenly over the cork, and be arched over from the bottle edge. If left undisturbed, the whole will have hardened, in from two to four days, into a hard and tenacious mass. Its surface can then be sand-papered over; or, if a flaw or crack has appeared, some of the surrounding cement should be cut out, and a fresh application should be given, so as to fill up the deficiency and cover anew the entire cement surface. Finally, on a large turn-table, two successive coats of deep blue enamel paint (this, as experience will demonstrate, is the color that best accords with nearly all specimens) can be applied over the cement and neck of the bottle to just beneath the lower level of the cork.

(*e*) *Arrangement of preparations.* — When properly set out and classified the real value of museum preparations becomes evident. For this end three distinct but correlative departments should be developed, (1) the morphologico-physiological, (2) the taxonomic, (3) the pathological. This will mean at times, either the duplicating of specimens or of reference descriptions, but the results attained are such as to justify us in saying that museum organization should be the great educational advance of the near future. Let us see how we might proceed here. Under the first department, series of seedlings can be set out to illustrate modes of germination and relation to environment; or series of axes for upright growth, for storing, for climbing, for twining, for defense, and for assimilation; or series of leaves that are analogously modified as the last; or series of flowers that illustrate relation of parts to each other, their modes of insertion, their shape, their adaptation to environmental agents; or series of fruits that demonstrate dehiscence or consistency, modes of dissemination, etc. — these and many others that might be named indicate possible lines of arrangement. The principle is equally applicable to the cryptogams.

In the second or taxonomic collection, the central idea inspiring the whole should be to dispose types of species or genera so that these will link together and illustrate each other, at the same time that they represent in natural relation a family or order. Details can be worked out here that will suggest themselves to any reflecting mind. Under the third department more has already been done than under either of the former, but great possible advances are still in the future. A series of preparations of the black-knot fungus (*Plowrightia morbosa*), and of others whose life rôle is simpler or more complex; a series of the flowering parasites and their relation to host; all the life forms of gall insects and the appropriate gall formed by each species or life-phase of a species, — such are a few of the biological problems that can be graphically and permanently illustrated.

All who have had to do with the arrangement of museum specimens know that the lighting of a museum building is a prime consideration. Where the smaller details of floral structure are to be traced, the placing of the jars in some badly lighted room is tantamount to the concealment of knowledge. But, granting that the lighting is all that could be desired, the eye can often be helped by a specimen being arranged against an appropriate background, a black one, for example, in the case of all bleached preparations.

Finally, it cannot be too strongly emphasized that such specimens should not be handled loosely, or passed round in a class-room. Equally important is it that in the original selection and disposition of a plant in a jar, care should be exercised to have every feature displayed toward one side of the jar, so as to obviate the necessity of its being turned round. This can readily be done in nearly every case.

(*f*) *Description of preparations.* — After each jar has been assigned to its proper place, there remains the work of description. This should not, as in most museums of the past, be a bare statement of the species and order to which the specimen belongs, but be so elaborated as to guide the observer to an intelligent appreciation of the features that the specimen presents.

To all teachers I would say, enlist the sympathies of your students by asking those who have the draughtsman's faculty, to sketch one drawing each month as a regular class exercise, for which credit will be given. The teacher should select a certain jar for a student, indicate the various details that are shown when the object is placed in a certain position, and leave it with him to work out an illustration. When finished the teacher can append to the drawing short reference descriptions, and when returned to the museum shelf it will ever after be a source of instruction — a silent lecture to those who follow.

In a few years a pretty large collection can thus be artistically described. By the subscription of each draughtsman's name to his design, a record will accumulate of the quality of each year's classwork, while the teacher, each time that he inspects the collection, will live over again the intercourse he had with his students.

Short reference can now be made to the cost of such collections, and their practical educational value. We will accept it that all public institutions receive duty-free alcohol at about 60 c. per gallon, and that the cost of the three sizes of jar is approximately that given in the earlier part of this paper. For the average high school a collection of one gross small size, two gross medium size, and a half gross large size would suffice. The entire cost would be about $250. For a college, where the teaching is rather more varied and advanced, a set of one thousand jars would cost about $500. A university collection should be so rich and capable of extension as to constantly represent and keep abreast of every new departure in the science.

(*g*) *Some of the results obtained.* — We claim for the system as now outlined many valuable results. It compels on the part of teacher and student alike a closer intimacy with living plants than has hitherto been attained on the average. It enables the teacher to draw the student's attention to the natural form of plants at all seasons of the year. It presents ample scope for the exercise of mental, manipulative, and artistic ingenuity. It stimulates the comparative method of observation and study, while it presents the idea of function at every turn as a factor that is molding and modifying types to a degree that we scarcely as yet realize. It is, proverbially, a hazardous and ungrateful task to forecast the future. Nevertheless, we venture to predict that the formation of botanical museums on the plan now sketched, in all the higher institutions of learning, would do much to advance the science of Botany, and commend it in our system of education as a living science of living things.

TENTH LECTURE.

EVOLUTION AND EPIGENESIS.

C. O. WHITMAN.

"Die Physiologie ist keine Wissenschaft, wenn nicht durch die innige Verbindung mit der Philosophie." — JOH. MÜLLER, *Physiologie d. Gesichtssinnes*, p. 36.

It is well from time to time to take account of stock even in such intangible things as theories may appear to be; it is only in this way that we can measure the progress made in the interpretation of facts. Theory without fact is phantasy; but fact without theory is chaos. Divorced, both are useless; united, they are equally essential and fruitful. The father of modern embryology, Karl Ernst von Baer, modestly described his great work on "The Evolution of Animals" (1828) as "*Beobachtung* und *Reflexion*" — Observation and Reflection; and a similar motto adorns the title-page of Goethe's "Zur Morphologie" (1817). The words are: "*Erfahrung, Betrachtung, Folgerung*" — Experience, Reflexion, Inference.

Fact-gathering and theory-making are both prime functions of the investigator. Mutual service is the principle which ties them together. This point was strongly put by Huxley in his review of the cell-theory, in 1853:

"In so complex a science as that which relates to living beings, accurate and diligent empirical observation, though the best of things so far as it goes, will not take us very far, and the mere accumulation of facts without generalization and classification is as great an error intellectually as, hygienically, would be the attempt to strengthen by accumulating nourishment without due attention to the primal *viae*, the result in each case being chiefly giddiness and confusion in the head." [1]

[1] *British and Foreign Medico-Chirurgical Review*, vol. XII, p. 291.

As William Whewell has well said in one of his "aphorisms concerning science," —

"The distinction of *Fact* and *Theory* is only relative. Events and phenomena, considered as particulars which may be colligated by Induction, are *Facts;* considered as generalities already obtained by colligation of other Facts, they are *Theories.* The same event or phenomenon is a Fact or a Theory, according as it is considered as standing on one side or the other of the Inductive Bracket."[1]

The truth of this aphorism is quite as pertinent to-day as when it was written in 1840. The notion that what is visible is "fact," and that what lies beyond vision is "theory," has not been fully outgrown even among men of science. Those who presume to act as Levites in charge of the ark of "fact," should beware of blundering into a distinction that places most of our knowledge to the credit of "theory." There is, indeed, "a mask of theory over the whole face of nature, if it be *theory* to infer more than we *see.*" (Whewell.)

The claim has been made that epigenesis stands for "fact" and evolution for "theory." One author, with Wolff's "*Theory* of Generation" on his lips, affirms that "epigenesis is a statement of morphological (!) fact ; it is not, and *does not pretend to be, an explanation of those facts.*"[2] What would the earlier prophets of epigenesis have exclaimed at such apostasy? No "theory" in the περὶ ζῴων γενέσεως? None in the "*Exercitationes de Generatione Animalium,*" or the "*Additamenta*"? None in the "*Theoria Generationis*"? Would it not be a little nearer the "fact" to say that Bonnet and Haller did not pretend to explain generation? Was not Wolff quite right when he complained, —

"*Qui igitur systemata praedelineationis tradunt, generationem non explicant, sed, eam non dari, affirmant*"? Was there no "pretension" in the "*vis corporis essentialis*" of Wolff? in the "*vis productrix*" of Needham? in the "*impressio idealis*" of Harvey? or in the "ψυχική ἀρχή" of Aristotle? Who were the authors of those "*mechanical explanations*" of de-

[1] *Phil. Ind. Sc.*, p. xli.

[2] G. C. Bourne, *Science Progress*, April, 1894, p. 108–109.

velopment which drove Bonnet and Haller to the other extreme? Who reproached the "evolutionists" for having adopted an hypothesis that excluded explanation with miracle? Who are to-day elaborating mechanical theories of development? Who undertake to refer the polarity of the egg to such mechanics as "geocentric differentiation," or to some wholly accidental circumstance in fecundation? Who claimed to have found the long-sought *vis directrix* in gravity, and by the force of his brilliant example, started an avalanche of theories from which no delivery is yet in sight? Is the doctrine of "directive stimuli" less theoretical than that of determinants? Is the epigenesis of so-called "dynamic evolution" conspicuously free from theory?

The claim to a monopoly of fact is obviously a pure epigenetic origination deserving notice only because it reflects an arrogance which seems to be epidemic, though generally held in more insidious reserve.

Oscar Hertwig proceeds with more cautious circumspection, and with a clearer perception of the fundamental differences between the old and the new theories of development; but he labors with ingenuity to show that epigenesis opens the door to investigation while evolution offers the dangerous "*Ruhekissen*" to our desires for a causal explanation of development. Hertwig concludes his able essay on "Präformation oder Epigenese?" with the following grave indictment:

"The doctrine of determinants has thrown back the mystery, which we might hope at least partially to resolve by investigation of the properties of visible forms, into an invisible region where there is absolutely no point of attack for research. Thus by its very nature it remains unfruitful for research, to which it can offer no possible way of advance. In this respect it resembles its predecessor, the preformation theory of the 18th century."[1]

Had not the doctrine of determinants already proved a most powerful stimulus to research, and had not Hertwig himself conceded the principle of determinants, at least for such characters as can be realized in the cell for itself (p. 84), his indict-

[1] *Zeit- und Streitfragen der Biologie*, 1894, p. 137. Cf. pp. 11, 12.

ment might have appeared more serious. As it is, however, the attempt to identify epigenesis with the interests of research is scarcely more successful than Bourne's effort to credit it with a monopoly of "fact." An author who can accept the hypothesis of "Intracellular Pangenesis"[1] of Hugo de Vries and the theory of migrating pangen-determinants, is not so far from the perilous "Ruhekissen."[2]

Hertwig[3] is no less emphatic than Bourne[4] in asserting that His, Weismann, and others occupy the standpoint of the old evolution. Bourne, persevering with his thesis, *epigenesis a fact, not a theory*, declares that "the evolutionary theories which have lately been put forward are not, therefore, of the nature of a general statement of fact, but are assumptions made in order to explain the causes of observed phenomena; *they are dependent upon reason, not on observation*" (p. 114). Both Hertwig and Bourne point out some fundamental distinctions between the old and the new evolution, and yet they assert that there is an essential likeness of standpoints. To some extent this comparison of standpoints has been sanc-

[1] *Die Zelle und die Gewebe*, 1892, p. 287.

[2] "From our standpoint also," says Hertwig, "we require for the explanation of the development-process in different species of organisms *different kinds of germ-substance with an extremely high organization*, by virtue of which they react in a specific manner (*i.e.*, in a manner corresponding to their kind), and in the finest way, to all external and internal stimuli." (*Zeit- und Streitfragen*, p. 131.)

To make the concession somewhat stronger, Hertwig indorses the following from Nägeli: "Egg-cells just as well as fully developed organisms possess all the essential characters, and organisms differ from one another as egg-cells, not less than in the developed condition. In the hen's egg the species is contained as completely as in the hen, and the hen's egg is as different from the frog's egg as the hen from the frog."

[3] Referring to Weismann, Hertwig remarks: "Somit wären wir denn in etwas veränderter Weise auf dem Standpunkt der Evolutionisten des vorigen Jahrhunderts angelangt, nach welchem der Keim das ausserordentlich kleine Miniaturbild des ausgebildeten Geschöpfes sein soll" (*Zeit- und Streitfragen*, p. 10). Of His he says: "Am meisten hat His das Problem der Entwickelung im Sinne der älteren Evolutionstheorie in mehreren entwickelungsgeschichtlichen Schriften zu lösen gesucht" (*Aeltere und Neuere Entw.-Theorien*, p. 16).

[4] Bourne (*Science Progress*, April, p. 107) says: "It is certainly a striking fact that the most minute and elaborate researches of the last few years have led the course of biological speculation back to the point of view of Haller and Bonnet in the 18th century, and have threatened to discredit altogether the opposite doctrine of epigenesis."

tioned by Huxley, Brooks, Roux, Weismann, and others. I am of the opinion that such comparison, especially as handled by Bourne and Hertwig, is unwarranted and decidedly misleading. It is the chief purpose of this and the two following lectures to elucidate the more essential distinctions between our standpoints and theories of development, and thus to remove some misconceptions which have become rife.

I should perhaps say at the outset that I have no theory of development either to announce or to defend. It is of more importance just now to have well-defined standpoints and clear ideas of guiding principles. The foundations at least must be made secure before we can profitably undertake to elaborate the superstructure. The corner-stone on which most theories of development now rest — the assumption that the germ-plasm is exclusively contained in the nuclear chromosomes — may not be so secure as some imagine. Let that stone be upset, and what would become of all the hypotheses erected on migrating pangens and disintegrating determinants? The centrosome question has yet to be settled, and a much deeper insight into the nature of protoplasmic structure is required before we can safely locate the seat of heredity. The possibility — not to say probability — that *the egg is from the beginning of its existence as an individual cell definitely oriented*, has as yet received but little attention. Many difficult questions are involved which can only be settled after the most exhaustive analysis of its structure and the most careful examination of its entire history. It is not enough to catch a fact here and there, in this or that species; the whole series of phenomena must be studied genetically, and in as many forms as possible. It often happens that we have to snatch facts as opportunity brings them within reach, regardless perhaps of their connections; but so long as they stand isolated, they are unsafe pegs to hang theories upon. Examples abound on this one question of the orientation of the egg, and the mention of "*isotropism*" will recall more than one windfall of premature speculations.

As we have seen in the case of Bourne and Hertwig, who represent fairly well the more moderate epigenesis of to-day, the problem of development presents itself in the form of an alternative — one choice between two contradictory extremes. It is epigenesis *or* evolution, with no middle ground for Bourne, and with only a minimum for Hertwig. Hertwig accepts determinants in homœopathic doses — just enough to fix the characters of individual cells, but not enough to affect cell-complexes.[1] Bourne, with fully as much loyalty to epigenesis as to "fact," holds that the truth lies on the side of epigenesis, and epigenesis, be it noted, as understood by Harvey and Wolff. As Bourne echoes prevalent sentiment in a somewhat emphatic form, it may be well to note his words:

"The subsequent history of the oösperm," he says, "that is, of the ovum after it is impregnated, is an *absolute demonstration of epigenesis in the sense in which it was understood by Harvey and Caspar Friedrich Wolff.*" Notwithstanding this high degree of certainty, we are told that "there is some reason to fear that, unless a protest is raised, *the failure of the attempts to form hypotheses explaining the causes of developmental phenomena, on epigenetic grounds* [no pretension ?] *will discredit the doctrine of epigenesis as a statement of the observed facts of development.*"

There is no doubt some danger that "the doctrine of epigenesis," as understood by Harvey and Wolff, can hardly be accepted even as a statement of the "facts" of development. But facts easy of "absolute demonstration" are fairly safe, however much the epigenesis of past centuries may have to be revised in order to accord with the results of recent work.

Mr. Bourne's criticisms[2] of what he calls evolutionary views do not concern us here further than as they reflect current misconceptions, which tend to obscure fundamental principles.

[1] Herbert Spencer (*Weismannism Once More, Postcript*, p. 24) exposes the weak point in a single remark: "*To this it may be replied that the ability to form the appropriate cell-complexes, itself depends upon the constitutional units contained in the cells.*" "Constitutional units" Mr. Spencer offers as a substitute for "physiological units."

[2] Those directed against "The Inadequacy of the Cell-theory of Development" are largely the result of misunderstanding, which may be trusted to correct itself.

Are Bourne, Hertwig, and others putting the question correctly in the form of the old dilemma? Are we bound to accept either horn? Was not the antagonism of the epigenesis and evolution of last century due, in part, to errors in both directions? and has it not become quite certain that, as there was error, so there was truth, on both sides? Does not Mr. Mivart [1] state the situation correctly when he says, — "The idea of evolution, *as now understood*, far from being antagonistic, is complementary, to that of epigenesis"? Roux, although among the first to suggest that present issues remind of the old, now protests against Hertwig's alternative — "preformation or epigenesis" — and defines our task to be "to determine the actual share of each of the two [2] formative principles in individual development." Even Hertwig, though a zealous apostle of the gospel of epigenesis, claims that his view seeks "to extract from the doctrines of epigenesis and evolution, what is good and serviceable in each." Weismann, while declaring himself an "evolutionist," makes large allowance for epigenesis, as his Romanes Lecture makes abundantly evident.

The drift of opinion, as it seems to me, is neither back to the standpoint of Harvey and Wolff, nor to that of Bonnet and Haller, but towards a new standpoint, which seeks to avoid the errors, and blend the truth, of the old hypotheses.

The use of the same name for different things is always liable to lead to confusion, and perhaps some of the latest contentions on questions of development have been obscured in this way. Evolution, standing at first as the antitheton of epigenesis, has come down to us as a synonym for it, and is now a popular term — a sort of omnium-gatherum — for all extant views of development. It claims alike the two great antagonistic factions in the biological world, the Lamarckians and the Weismannians, and repudiates only the creation hypothesis, the very doctrine on which it originally rested.

Views have multiplied, and the necessity for definition finds

[1] *Science Progress*, August.

[2] "Den wirklichen Antheil jedes der beiden Gestaltungsprincipien an der individuellen Entwickelung zu ermitteln." *Gött. gel. Anz.*, No. 9, 1894.

new meanings for old words. One calls himself an evolutionist (in a modern sense) because he is not an epigenesist in the old sense; another declares adherence to epigenesis in order to emphasize the fact that he is not an evolutionist of the old school; and still another, discovering analogies in both directions, accepts both terms for what he can extract from them.

The term evolution seems to have come to stay, and the stanchest epigenesists of our day are known of all the world as evolutionists. This title indefeasible will cling to such men as Darwin, Wallace, Huxley, and Spencer. To define the evolution of to-day as a contradiction of epigenesis is, indeed, a step backward in our vocabulary, and one which, at first sight, might be misunderstood as a return to views long ago abandoned. In this deceptive appearance the controversialist finds a convenient *ad captandum* argument. As a matter of fact, no such return is anywhere visible. I do not deny that analogies may be found between the new views and the old, but a closer examination will show, if I am not mistaken, that we are moving steadily forward, not encroaching upon, but extending, the ground already conceded to epigenesis.

It has become perfectly clear, however, that epigenesis, as now understood, does not cover the whole field. Only the old epigenesis, if we except a few eccentric views of later date which have had no influence, ever pretended to start the development of organisms from the level of inorganic matter. No entelechy equal to that task has yet been discovered. Spontaneous generation, xenogenesis, and the like, are epigenetics of historical interest mainly. So far, the old epigenesis has suffered curtailment, if you choose to so regard it.

The indubitable fact on which we now build is no bit of inorganic homogeneity, into which organization is to be sprung by a coagulating principle, or cooked in by a *calidum innatum*, or wrought out by a spinning archaeus, but the *ready-formed, living germ, with an organization cut directly from a preëxisting, parental organization of the same kind.*

The essential thing here is, not simply continuity of germ-substance of the same chemico-physical constitution, but *actual identity of germ-organization with stirp-organization.*

When we speak of the *organization* of the germ as "cut directly from a preëxisting parental organization of the same kind," we are not thinking of the definitive organization which belongs to the fully formed organism, but of that primary organization which belongs to the protoplasm itself. We are so accustomed to connect the idea of organization with the anatomical organs of the adult, that we are apt to forget that there is a primary organization which underlies every anatomical organ. The germ has this primary organization; it is therefore an *organism*, and as such may dominate its own development. The "fallacy" which Mr. Bourne finds in my use of the word organism is entirely of his own making. "It is not conceivable," says Mr. Bourne, "that the organism, that is the *final aggregate of parts* which have been successively formed, dominates the formation of parts without which it has no existence" (p. 122). Who, before Mr. Bourne, ever suggested such a "fallacy"?

Our present inability to grasp the mechanics of this organization and diagrammatize its ultimate elements may detract from its importance in the eyes of observers who are accustomed to find the goal of mental repose in the cell; but to those who have more thoughtfully scanned the gap between the cell and the physical molecule, intra-cellular organization will not appear to be a piece of empty speculation. The metaphysical bugbear of *emboîtement, ad infinitum*, is an old and discredited acquaintance. We have seen too many grades of organic units disincased to be frightened at the necessity of venturing beyond the cell-wall.

Let this "organization" stand for no more than our neo-epigenesists freely concede, namely, that *original constitution of the germ, which predetermines its type of development and the form which ultimately distinguishes it from other species developing under like external conditions,*—let it stand for nothing more than that, and obviously the standpoint rises to an altitude scarcely dreamed of in the philosophy of Harvey and Wolff. The difference is not merely one of degree; the prime contention of the old epigenesis, that the organism begins as an entirely *new* formation, is repudiated. What remains, and what everybody accepts, is, that the definitive organs arise by progressive differentiation, rather than as expansions of parts predelineated in a miniature organism. With Harvey we may say, that in the egg, "no part of the future offspring exists *de facto*, but all parts inhere *in potentia*" (Ex. XXVI). But we do not mean it quite as he meant it. We mean it with a reservation not anticipated in his theory — a reservation which is at once the foundation, and the essence, of the modern doctrine of *homogenesis*, as contradistinguished from *agenesis*, or *abiogenesis*, and *xenogenesis*.

Continuity of organization is indeed a species of preformation, but it is a preformation which no one will now deny, who accepts the fact reached over so many battle-grounds, that *germs are not produced epigenetically, but by division of preëxisting germs*. "It is certain," says Huxley, "that the germ is not merely a body in which life is dormant or potential, but that *it is itself simply a detached portion of the substance of a preëxisting living body*" ("Evolution in Biology," *Darwiniana Essays*, II, p. 198). To this extent we are all preformationists, *nolens volens*.

We are no longer in the position of the philosophers of last century, who were still totally blind to the central fact of modern biology — *the law of genetic continuity*, first neatly embodied in Virchow's formula: *omnis cellula e cellula*, but since extended to every order of vital unit within the cell, and raised to the full dignity of a general law by the final abandonment of the hypothesis of spontaneous generation.

The law of genetic continuity is to the biologist what the law of conservation of energy is to the physicist. It abolishes the miracle of original creation. It sets the individual up, not as a separately made instrument, but as a vital link in a continuous series of developments. It gives heredity a rational basis, — reduces it to a formula that accords with the physical law. It enables us to see what before could not be divined, that preformation involves no miraculous intervention of a supernatural agency. It enables us to view germs, not as *de novo* creations, but as complex products, embodiments of work previously done. It puts in a clear light the fact that *organization* can be, and actually is, directly transmitted. It shows us how the whole organic world hangs on the power of growth and self-division in its primordial units. It teaches us that the germ may stand for two things, which the old philosophy held to be irreconcilable : namely, something *already* accomplished as well as something yet to be accomplished.

The "something" with which development begins was sadly underestimated in the old epigenesis, and as sadly overestimated in the old evolution. Think of Harvey protesting that it is a mistake to look for any such thing as "*prepared matter*" in the egg (Ex. XLIV), and insisting that even his "*antegenial colliquamentum*" could not *preëxist*, but must come into existence *after* the egg, as a result of decoctive liquefaction of the albumen (Ex. XVI). And, at the other extreme, see Bonnet and Haller denying generation altogether, claiming that all the essential (organic) parts of the adult organism preëxist ready-formed in the germ, and that development means nothing but expansion of the organs by the infiltration of matter wholly foreign to them.

The two views missed the mark by over-shots in contrary directions. The one claimed too much preformation; the other too much post-formation. Both were equally blind to the law of genetic continuity, and so the choice lay between the mechanical difficulties of formation *de novo* and the bald fatalities of *emboîtement*. It was the option of Scylla or Charybdis.

There is some analogy with our present position, but it must not be mistaken for anything more than a superficial resemblance. Our present difficulties do not arise in consequence of a return to the old position, but rather as the result of its abandonment, and a general advance that enables us to approach the problem from a much higher level. Organic development is still an unsolved problem, but it is a problem which rides the crest of one of the most revolutionary waves that has ever deluged human philosophy. We have but too lately experienced the shock and heard the reverberations of the tidal advance in every direction, not to realize how profoundly changed is our whole position. What is development? is a question as old as human inquiry; but does sameness in the *form* of the question indicate identity of standpoints? Embryology, histology, cytology, and all the sciences that are now dealing with this question, are of comparatively recent origin, mainly growths of the last fifty years. It would be a little strange if all this work had merely increased our knowledge of details, and left us drifting back to the issues as they stood one or more centuries ago. But that is practically what we are told by some who rise to champion the epigenesis of Harvey and Wolff. That is the "*circuitus theoreticus*" discovered by Mr. Bourne. The discovery assuredly deserves embalmment by the side of Harvey's solution of the "*circuitus gallinaceus*": "Quodnam eorum fit prius ovum-ne, an gallina? *Quippe hac naturâ prior exstitit, illud autem tempore*" (Ex. XXVIII). It has been left to an "epigenesist" of our day to revive this old riddle of Plutarch, and try to palm it off as a sample of modern evolution.

When we find Harvey gravely discussing such questions and offering such verbal somersaults as solutions, are we reminded of progress or of retrogression in standpoints? And when this "*circuitus gallinaceus*" is brought forward as an evidence that there must be a "*vis enthea*" in our common poultry which sustains this perpetual "revolution from fowl to egg and from egg back to fowl," does it suggest modern evolution, or the kindred notions of Wolff and Blumenbach? When the first step in preparation for development is pictured as a reduction of a portion of the albumen to "a more spirituous and better digested fluid," under the influence of a "*calidum innatum*," directed by Divinity; and when the egg is defined as a "*primordium vegetale*," which may come from living parents, but which may also arise spontaneously and from putrefaction,— by a sort of accidental parentage, — are we led back to Aristotle, or forward to present views?

As Robert Willis has well said, Harvey wrote his work on generation in "the harness of Aristotle," and with "the bit of Fabricius between his teeth." Nearly everything that is usually appealed to in his work in illustration of the principles of epigenesis may be credited to the Stagirite. Whatever adumbration of the law of genetic continuity (homogenesis), as now understood, is to be found in the *Exercitationes*, may be traced to the same source of inspiration. The significance of that beautiful aphorism so often ascribed to Harvey, — *omne vivum ex ovo,* — hangs on the definition of its last word. As defined by Harvey the whole idea shrinks to the doctrine of Aristotle. It falls far behind Redi's formula, *omne vivum ex vivo,* which still did not exclude xenogenesis and syngenesis. In order to put modern notions into the expression, we have to read the old "primordium" out, and read in its place everything implied in the latest revisions of the germ theory.

Banish the tradition of spontaneous generation, the metaphysical relics of "vital spirits," "ingenerate heat," "final causes," "generative contagion," "immaterial form," such extravagant analogies as that of "uterine conception to mental conception," such concoctions as "antegenial moisture," and other "fabulae" confessed and unconfessed, — banish the whole phantasmagoria, and then read "ovum" in all the light of Redi's formula, the cell doctrine, Virchow's formula, Gegenbaur's researches on the egg, and all the corollaries supplied by recent cytological work, and Harvey's dictum comes forth transfigured into truth empyreal, no longer a vague generalization, exceeding in no way what Aristotle had already maintained.[1]

Harvey grasped some details of development that had escaped both Aristotle and Fabricius; but his *philosophy* of

[1] Harvey concludes the sixty-third exercise with the following from Aristotle: "*All living creatures, whether they swim, or walk, or fly, and whether they come into the world with the form of an animal or of an egg, are engendered in the same way.*"

Harvey identifies the "seed," the "egg," the "conception," and the spontaneous "primordium," on the ground that they all agree in containing the "matter out of which and the efficient cause by which whatsoever is produced is made." "Let us, therefore, say that that which is called primordium among things arising spontaneously, and seed among plants, is an egg among oviparous animals; *i.e.*, a *certain corporeal substance, from which, through the motions and efficacy of an internal principle,* a plant or an animal of one description or another is produced; but the prime conception in viviparous animals is of the same precise nature, a fact which we have found approved both by sense and reason" (Ex. LXIII).

Aristotle did not insist that his "spontaneous foam-vesicle" must be called an egg; but he did insist that it was fundamentally the same, inasmuch as it represented both the "matter" and the "efficient." Harvey's assertion that "all animals are in some sort produced from eggs," is a fair summary only of what Aristotle affirmed of the "conception," the "egg," and the "worm" (*De Gen. Anim.*, lib. III, cap. IX).

epigenesis surpassed that of Aristotle only in metaphysical extravagance.[1]

That part of Harvey's theory which affirms that the parts of the future organism do not preëxist as such, but make their appearance in due order of succession, and which is so often cited as the essence of epigenesis, was all clearly stated by Aristotle. No one, so far as I am aware, now thinks of disputing that point. In fact, we are obliged to go much farther than Harvey in this direction, for we cannot say with him that this mode of development holds only of "*perfectiora animalia sanguinea*" (Ex. XLV), but must claim that it is equally true of all those forms he excepted under "*metamorphosis*."

The distinction which Harvey made between epigenesis and metamorphosis shows us precisely what he regarded as the most essential thing in generation. To his mind development by epigenesis was the only "*proprie dicta generatio*"; and for the reason that *it required no preëxisting "prepared material." "Nulla iis immediata materia praeexistens adest"* (Ex. XLV, p. 124). The "immaterial conception," the "divine idea," must preëxist as "*impetum faciens.*" "Not only is there a soul or vital principle present in the vegetative part, but even before this there is inherent mind, foresight, and understanding, which from the very commencement to the being and perfect formation of the chick, dispose and order and take up all things

[1] "Let it then be admitted as a matter of certainty," says Harvey, "that the embryo is produced by *contagion*. But a great difficulty immediately arises, when we ask: In what way is this contagion the author of so great work? . . . How, I ask, does a nonentity act? How does a thing which is not in contact fashion another thing like itself? . . . What is it in generation which, in virtue of a momentary contact — nay, not even of contact, save through several media — forms the parts of the chick from the egg by *epigenesis?*" (Ex. XLIX).

This "contagion" is the *calidum innatum*, which has its seat in the blood. This is the "vegetative soul, the prime efficient cause of all generation, which moves by no *acquired* faculty which might be designated by the title of skill or foresight, as in our undertakings; but operates in conformity with determinate laws like fate or special commandments. . . . It is equally manifest that *this agent, existing in every egg and seed, is so imbued with the qualities of the parents, that it builds up the offspring in their likeness, not its own.*" The solution of this grand mystery is found, if we assume "the conception of the uterus to be of the same nature as the conceptions of the brain, and *fecundity to be acquired in the same way as knowledge*" (Ex. L).

requisite, molding them in the new being, with consummate art, into the form and likeness of its parents" (Ex. LVII).

Harvey does not evade the question for which epigenesis itself is responsible; namely, how is development set in motion and directed? "*Quomodo omnia ex univoco fiant? quo pacto scil. idem semper idem progeneret?*" (*De Conceptione*, p. 298.) That was to him, as it still is to us, the grand question. It was here that epigenesis found its *ultima Thule*, beyond which all was "nonentity," "contagion by non-contingents," "*species sine materia*," "*cujus gratia*," etc. The theory vanished in a void. There was no getting over it, and no escape from it. Like begets like, and yet there is a vacuum between them and absolutely nothing to fill it except immaterial "*exemplaria*." "Seeing nothing left," says Harvey, "I have devised this fable (p. 297) . . . preferring a fanciful opinion to none at all" (p. 298).

No shadow of reproach falls on the immortal discoverer of the circulation of the blood for inventing such a fable and winding up with syllogisms in its support. Two and a half centuries ago, that was the best that could be expected even from a genius that is now deservedly esteemed as a sort of divinity in Embryology as well as in Physiology. But it is a matter of some interest to us that the old epigenesis found its logical end invariably in some fatal fabula, the purpose of which was — in its last analysis — to cover a void of its own creation. A train of orderly appearances is to be accounted for. The nearer we get to the original germ, the more obscure become the phenomena. Heterogeneity sinks gradually out of sight, and the inference is that it terminates in homogeneity. But how is homogeneity "cooked" into heterogeneity? Epigenesis is cornered. Seeing how difficult it is to epigenesize something out of nothing, it invokes spiritual agencies and vital forces and assigns them the task. There arise the mystical host, — "vegetative soul," "psychic heat," "ingenerate heat," "*vis plastica*," "*vis enthea*," "*vis essentialis*," "*nisus formativus*," and all the other "nonentities" devised before and since Harvey's day. Aristotle, Harvey, Wolff, and Blumenbach, all traversed the same problem and landed in the same pitfall. They all faced the question of preformation, and discovering no natural way by which the germ could come ready-made, they insisted that the germ must start anew every time and from the pit of material homogeneity, acquiring everything under the guidance of hyperphysical agencies, assisted by the accident of external conditions.

It is most instructive to recall with what persistence this dogma of *formless homogeneity* maintained itself, ever on the alert to challenge the most distant suggestion of anything that pointed to reconciliation with its old foe, preformation.[1]

While the epigenesist of the old school could not tolerate even so much as a "quasi-preformation" of any description, the epigenesist of to-day has become so familiar with the reality of preëxistent germs that he now comes forward claiming that the ovum actually represents "*a highly complex organization.*"

What then is the standpoint? Is it that of preformation or of post-formation, or of some higher ground, reconciling both aspects of the subject? The answer has already been anticipated. Our position involves the old standpoints, but not as they stood in antagonistic separation, but as they stand in union after a century's revision and amendment. Both preformation and post-formation, as now understood, enter into every theory of development. Taking the words in their old sense, we should have to abandon both. We cannot affirm that the parts of the adult organism are preformed as such; we can only say that of the germ, as something which is not produced epigenetically, but comes ready-made. Neither can we affirm that development is post-formation independent of any predetermining organization.

The old conceptions thus revised furnish the basis for an entirely new standpoint. The question is no longer whether *all* is preformation or *all* post-formation; it is rather this:

[1] "Wenn hingegen andre, um die Evolutionshypothese mit der Lehre von der allmählichen Bildung zu vereinbaren, zwar zugeben, dass der Zeugungstoff nicht präformirt sei, aber doch meinen, dass er dessen ungeachtet einen Keim enthalte, der dennoch was anders sei, *als ungeformter Zeugungstoff*, so sind das unbestimmte, leere Ausdrücke. Wenigstens geht mir es dann mit solchen *Quasi-Keimen*, wie dem Cicero mit dem *quasi corpus* des Gottes der Epicuräer, wovon er sagt: '*Corpus* quid sit intelligo: *quasi corpus* quid sit, nullo prorsus modo intelligo.'" Blumenbach: *Handbuch der Naturgeschichte*, 1830, p. 12.

How far is post-formation to be explained as the result of pre-formation, and how far as the result of external influences? That is a very different thing from the old dispute as to whether there was any such thing as generation. That contention has been settled beyond recall, and the deeper problems involved in generation now engage attention. The question does not now turn on either of the old hinges, but on what factors determine the type of development. Instead of asking, are all the parts predelineated? we ask, how are they delineated? Instead of referring development to a *deus ex machinâ*, or accident, we ask, what is the mechanism of the germ which enables it under suitable conditions to grow, divide, differentiate, and reproduce all the complicated details of its own species? We see that every form presented in development issues as the *product* of what has gone before and as the *foundation* of what is yet to come. Retrospectively, it is a "determinate," prospectively, it is a "determinant." It is at once consequent and antecedent, reflecting something pre-existent and anticipating something post-existent. In one direction it illustrates the axiom *ex nihilo nil fit;* in the other, the axiom, *nil fit ad nihilum.* Whether we search in this direction or that, and whether within or without, it is to catch the causal relations of the phenomena. We may differ as to what the determinants are and where they are, but all agree that they are to be found out as nearly as possible.

Now, what is our chief difference in this regard? It seems to be, that some look for the determinants mainly within the germ, while others search for them mainly in external influences. No one identifies determinants with future organs. Both sides maintain that the organs of the developed form have to be made, and that they must be made in orderly succession, as epigenesis affirms. Both sides recognize the germ as something determined, and as determining something. Both sides claim ultimate units of organization within the germ, and both agree that external influences are responsible, to some degree, for what results.

Our difference, then, is not one of mutual contradictions, each excluding the other, but one of mutual concessions, diverging only as we estimate the two classes of complementary causes unequally. The *intra* and the *extra* do not exclude each other but coexist and coöperate from beginning to end of development.

I do not forget that there is an important distinction to be kept in mind between the internal and the external factors. Within the germ we have *formed* elements acting in *organized* unison towards a definite end — that end being prescribed, not teleologically, but constitutionally, as the fruit of all that inheritance has preserved of ancestral progress. Without, we have the conditions and influences of a boundless environment — ether, air, water, earth, gravity, solar heat, light, and all the rest. Some of these fluctuate from moment to moment, or rise and fall periodically, while others appear to be absolutely constant. They comprise food, conditions, and stimuli. Broadly considered, they are common to all germs. They do not act organically; that is, they are not coördinated and directed to specific ends. It is the germ that does all the measuring, weighing, selecting, transmuting, distributing, coordinating. All germs grow and multiply at the expense of external conditions and influences; and so the internal and external are forever interchanging.

While we distinguish between the *formed* and the *unformed*, we do not set one against the other as absolutely distinct and inconvertible. On the contrary we insist that interchange is of the essence of organic phenomena, and thus our position contradicts the central idea of the old evolution, and at the same time supplies epigenesis something more substantial to build upon than spontaneity and spiritual agencies.

Our difference is no longer measured by the distinction made between the formed and the unformed, but by inequalities of emphasis which we apportion to the two sets of factors. Our present standpoints differ from the old far more than from each other. In some respects the extreme views of to-day reverse the extremes of last century. The old evolution, denying the possibility of generation, was compelled to maintain that *whatever development adds to the organism comes from external sources.* Monstrosities and hybrid forms were explained in a grossly mechanical way that might excite the envy of an ultra-epigenesist. On the other hand the old epigenesis, instead of appealing to external mechanical influences as dominating development, invoked "ingenerate heat," "vital force," "spirits," etc., as agencies, operating from within.

The chief analogy between the old and the new evolution, — which holds for epigenesis as well, only in a less degree, — lies in what correspondence there is between *predetermination* and *preformation*. It seems to be believed by some that these two things are essentially one and the same ; or at least that they differ only as the more and the less of the same thing. That is a mistake which the controversialist in epigenetics is particularly prone to make. He protests that this predetermination is only the old preformation thinly disguised, and that it really involves all the absurdities of *emboîtement*. Grant that the evolutionist claims too much organization or architecture in the germ ; how does this "*too much*" differ from the *less* on which epigenesis builds ? Certainly not in kind. Carry the "too much" to any excess exemplified in recent theories, and it never loses its identity with the approved "less"; and never comes any nearer the old idea of preformation. However extensively the features of the adult organism may be predetermined, they are never predelineated. Predelineation views organization as completed; predetermination implies just the contrary, setting the completion always at the end of a histogenetic building-process.

It seems to be forgotten that determination from within may proceed quite as epigenetically as determination from without. From the old standpoints even Weismann's doctrine of determinants would appear to be extravagant epigenesis. A theory which begins with the claim that the entire body of the germ outside the nucleus is isotropic, and starts developmental differentiation with biophores emanating from the nucleus, and generating new organizations at every step, — such a theory certainly is wanting in none of the cardinal virtues ascribed to epigenesis. The scheme is the acme of discontinuity in development, for it builds not only *de novo*, but keeps on rebuilding, organizing, and reorganizing to the end.

Why then call it "evolution"? Evidently not to recall the defunct ideas of Bonnet, but to better define a new distinction which has come into prominence largely as the result of Weismann's own work.

No one, as it seems to me, has defined the issue with which we are now confronted more tersely than Mr. Mivart, when, in opposition to Bourne, he declares that "the term evolution may be employed as it has been, to denote that the successive formation of parts not previously existent is due *not to their imposition from without, but to their generation from within.*"

This statement compasses the whole situation: "the successive formation of parts not previously existent," represents the accepted verdict on the old issue, and the expressions, "imposition from without," and "generation from within" define the new issue, which lies wholly this side of the old, as shown in the Spencer-Weismann controversy.[1]

[1] Spencer: "Every organism tends to become adapted to its conditions of life; and *all the structures of a species, accustomed through multitudinous generations to the climate, food, and various influences of its locality, are moulded into harmonious coöperation favorable to life in that locality: the result being that in the development of each young individual, the tendencies conspire to produce the fit organization.*" (*Contemporary Review*, Feb., 1893. Reprint, p. 36.)

"The structure of any organism is a product of the almost infinite series of actions and reactions to which all ancestral organisms have been exposed." (*Principles of Biology*, I, p. 199.)

Weismann: "Not only degenerations of parts, but even the harmonious and efficacious metamorphosis of many coöperative parts can proceed without any concurrence of the transmission of acquired characters." (*Contemporary Review*, Sept., 1893, p. 314.)

"*The offspring owes its origin to a peculiar substance of extremely complicated structure*, viz., *the germ-plasm. This substance can never be formed anew; it can only grow, multiply, and be transmitted from one generation to another.* My theory might therefore well be denominated *blasto-genesis* — or origin from germ-plasm, in contradistinction to Darwin's theory of *pangenesis* — or origin from all parts of the body." (The Germ-Plasm. *Contemporary Science Series*, 1893, p. xiii.)

ELEVENTH LECTURE.

BONNET'S THEORY OF EVOLUTION.

A SYSTEM OF NEGATIONS.

C. O. WHITMAN.

"Truth emerges sooner from error than from confusion." — BACON.

THOSE who imagine that they see in recent theories of development a renascence of Bonnet's evolution, must be well aware, one would suppose, of the fundamental distinctions between the old and the new standpoints. Yet some of the advocates of epigenesis maintain that these distinctions vanish when we compare Bonnet's latest views with those now held by evolutionists. This claim has often been repeated of late, and I am aware that it is backed by eminent authorities, for whom we all have the very highest respect, and with whom I should not venture to differ, except for reasons that seem indubitable.

If Bonnet's theory of evolution had in it a truth of such vitality that it can rise, phœnix-like, from the ashes of its supposed demolition ; or, to state it in a more conventional form, if our theories of development are carrying us back to the standpoint reached by the evolutionists of last century, it is a matter of more than historical interest. The issues that now lead embryological research are involved. Our ideas of development, the landmarks already passed, the cardinal points in our present horizon, our tendencies are all brought under the rubrics of comparison. Any mistake here must obscure the general situation in just those points where it most needs to be clearly defined.

Our chief concern is with standpoints. Compared with them, theories are of little consequence. The standpoint sets the limits to our horizon, and so determines the reach and range of vision. It is the vantage-ground of progress, the conquest of laborious research, of which one might say, as Johannes Müller once said of his own work: "*Es klebt Blut an der Arbeit.*" We have to deal, then, with a question of moment, and one which presents, in addition to its inherent difficulties, the obstacles raised by prejudgment. Let us try to clear the ground a little, so as to get into closer touch with the question.

One fact orients the whole field. It is the fact that we now build upon two broad truths which found their negation in the old theories of development, namely, *heredity* and *generation.* It may sound a little paradoxical, but it is true, that the two theories of last century not only contradicted each other, but also denied the very truths they came to explain. Evolution was the absolute negation of both heredity and generation, while epigenesis upheld generation, but denied organic continuity, the essential foundation of heredity. Let us make no mistake on this point, for it is fundamental and decisive as regards standpoints.

Both Bonnet and Haller boldly denied the possibility of generation. Why? For the obvious reason that generation meant epigenesis. There was no middle ground. If by any possibility anything of an organic nature could be referred to epigenesis, the miracle of creation would be reduced to the level of an every-day occurrence. The backbone of the argument for *original* preformation would go to pieces if a single vertebra could arise epigenetically. Not so much as a supernumerary digit, or a monstrous organ of any description, troublesome as such things were to the preformationist, could be allowed to pass to the credit of epigenesis. Allow that a single organ can be formed anew, and the whole edifice of preformation would be irretrievably undermined. Bonnet saw the bearings and the perils of his theory, and he did all that ingenuity could do to guard the central idea against hostile attacks.

What that central idea was, and how the fate of the whole theory hung upon it, Bonnet makes clear in one of his earlier writings. Referring to the principles advanced in relation to the development of the mule, Bonnet makes the following remarks, "prophetic of the event" already fulfilled on his own head:

"They [the principles] will always rest on *the importance of the preëxistence of the germ to fecundation. I admit, then, that if the falsity of this observation should ever be demonstrated, the edifice I have attempted to erect on that basis, would be as ruinous as those I have undertaken to destroy.* Such is the natural fate which threatens analytical works; if we can but destroy the fundamental principle, and detach the main link from the chain, the whole work will be little more than a series of propositions which are more or less erroneous, and it can be looked upon in no other light than as a mere romance.[1]

That "the *preëxistence of the germ to fecundation*" meant to Bonnet the preëxistence of a *completely formed* organism, and hence the denial of generation, is expressly stated in a previous paragraph. "Mais si le germe préexiste à la fécondation, s'il n'est pas *engendré;* si des parties qui ne paraissaient point du tout exister *existaient réellement*, n'est-il pas fort probable que l'organe de la voix du mulet n'est pas engendré non plus?" (*Ibid.*, p. 57.)

Such is the burden of the argument throughout. Indeed, no one doubts that Bonnet *began* with a preformation so complete as to exclude generation, and that this idea was the center around which the whole of his philosophy at first revolved. Did he ever abandon the idea, or modify it in such a way as to nullify the original distinction between his doctrine and epigenesis? Did he knowingly, or by any inadvertence, ever once drop the bars to epigenesis? If he did, then there may be some truth in the current opinion that the new evolution is a revival of the old idea as it was finally left by Bonnet. If he did not, either directly or by implication, then there can be no foundation for such an opinion. I believe this opinion is erroneous, and that it leads to confusion that is wholly mischievous. I find myself thus in conflict with a number of recent writers, and among them a no less revered authority than Professor Huxley.

What Professor Huxley has said on this point must be care-

[1] Preface to his *Contemplation of Nature* (1764); finally published as *Tableau des Considérations*, as an introduction to the *Palingénésie Philosophique*, Art. XII, p. 62 (1783).

fully noted, as I suspect that some writers have taken his words in a sense that somewhat betters the instruction.

After pointing out that the hypothesis of *emboîtement* is to be carefully distinguished from the hypothesis of evolution of a germ containing in miniature all the organs of the adult, Huxley makes the following statements: "While holding firmly by the former, Bonnet more or less modified the latter in his later writings, and, at length *he admits that a 'germ' need not be an actual miniature of the organism; but that it may be merely an 'original preformation' capable of producing the latter.*

"But, thus defined, the germ is neither more nor less than the '*particula genitalis*' of Aristotle, or the '*primordium vegetale*' or 'ovum' of Harvey; and the 'evolution' of such a germ would not be distinguishable from 'epigenesis.'" [1]

Observe that Huxley does not here authorize the opinion that evolutionists are reviving the objectionable features of Bonnet's system. There is no suggestion of a retrograde movement on the part of embryologists. Indeed, it is very clear that Huxley saw in modern embryology the verification of the main contention of epigenesis, and the repudiation of both of Bonnet's hypotheses. But while claiming for epigenesis a complete victory over the doctrine of evolution as understood in the eighteenth century, Huxley takes care not to sanction the idea that epigenesis contains the whole truth. In fact, he makes a suggestion that, to my mind, outshines "the divination of genius" ascribed to Harvey. The words already "proved a prophecy" are the following:

"*It is not impossible that, when the analysis of the process of development is carried still further, and the origin of the molecular components of the physically gross, though sensibly minute, bodies which we term germs is traced, the theory of development will approach more nearly to metamorphosis than to epigenesis.*" (*Ibid.*, p. 283.)

The movement here anticipated is not in the direction of the old evolution, but towards a view which represents the residual truth of both "epigenesis" and "metamorphosis."

[1] Article Evolution, *Encycl. Brit.*, p. 745; Darwiniana Essays, 1893, p. 193.

That part of the old epigenesis which started the germ as "*a sort of living precipitate*" *in a clear fluid* ("colliquamentum"), is of course set aside, and along with it the absurdities of Bonnet's idea of metamorphosis (change of external form without change of structure or substance).

In place of these errors are put the ready-made germ, with a structure received from the parent organism, impregnation by fusion of two germs, and development by a process of division. Evolution is viewed as "a course of progressive differentiation" — "a succession of changes of the form, structure and functions of the germ by which it passes, step by step, from an extreme simplicity, or relative homogeneity of visible structure, to a greater or less degree of complexity or heterogeneity." (*Ibid.*, p. 199.)

"From this point of view," says Huxley, "the process which in its *superficial aspect* is epigenesis, appears *in essence* to be evolution *in the modified sense adopted in Bonnet's later writings*; and development is merely the expansion of a potential organism, or 'original preformation,' according to fixed laws." (*Ibid.*, p. 204.)

The position here so concisely sketched in 1878, is the one toward which opinion seems to be drifting. But while the philosophy is clear, the identification of it, or any part of it, with Bonnet's later views is, I believe, unwarranted by anything contained in Bonnet's writings. The comparison, if it be inadmissible, is all the more unfortunate for the sanction of an authority so universally respected. It has been taken for considerable more than its author would probably approve; for some have construed it against epigenesis, and others against evolution.

We should have no fault to find with the comparison if it were true, as Huxley seems to have supposed, that Bonnet finally adopted a definition of the germ which dropped the chief distinction between evolution and epigenesis, as understood in his time. I do not find any such inconsistency between Bonnet's earlier and later definitions, and it is very certain that Bonnet never made any concession which, to his understanding, weakened in the least degree his idea of preformation. Is it probable that he tripped on so fundamental a matter without knowing it? Is it not more probable that Prof. Huxley has put an interpretation upon his words which he would have most emphatically disputed? Is not the suicidal concession imputed to Bonnet, after all, merely an inference to which his words were liable, only when isolated from the context and construed to the mind of the reader rather than to the intention of the author?

Although the words "evolution in the modified sense adopted in Bonnet's later writings," might suggest, if they do not distinctly imply, that Bonnet finally resigned himself to a view hardly distinguishable from epigenesis; still I am inclined to think that Huxley only intended to hold Bonnet responsible for a definition, himself alone responsible for the conclusion supposed to be involved in it.

Primary Hypotheses of Bonnet's Theory.

We might appeal at once to Bonnet's definitions of germs; but it will be better, I think, to consider first the general principles and bearings of the theory as a whole, reserving the definitions to be examined in the light of the ideas underlying them. Let us see what were the primary hypotheses of Bonnet's system of philosophy. Huxley has already pointed out the distinction to be kept in mind between *emboîtement* and *preformation.* These two hypotheses do not stand alone, however, neither are they of equal importance. Preformation, as I have already said, was the central idea — the very heart of the whole system of hypotheses — just that part, in fact, on the maintenance of which hung the life and use of all the other parts, and which was, therefore, most carefully guarded. Other parts could be modified, supplemented, or even wholly abandoned, if need be; but whatever the changes adopted, they were always measured to the necessity of keeping the preformation idea inviolate.

The doctrine of *emboîtement,* although regarded by Bonnet as "one of the greatest triumphs of the mind over the senses," and although filling a very conspicuous place in his speculation, was yet only an auxiliary hypothesis, to be used or laid aside at convenience. Its prominence as a butt of ridicule has thrown its companion hypothesis quite into oblivion. I refer to the hypothesis of "the *dissemination of germs*," which Bonnet always held in reserve for emergencies not provided for in "*emboîtement*." This hypothesis underlies no inconsiderable part of Bonnet's philosophy, and figures prominently in his ideas of regeneration and propagation by buds and slips. The more important modifications of views on the germ are connected with this same hypothesis.

We have, therefore, to recognize three primary parts in Bonnet's theory, namely, *preformation* (of the adult organism with all its essential parts), *emboîtement* and *dissemination*, and to bear in mind that the first stood as principal, the second and third as ancillaries. The latter, as employed by Bonnet, had no use or meaning, except to affirm and sustain the former. Holding firmly to *emboîtement* and dissemination and abandoning preformation would be a monstrous self-stultification. To this it may be replied that no one has charged Bonnet with complete abandonment of the idea of preformation, but only with a modification of his definition of the germ. But a modification that reduced "evolution" to a point where it could no longer be distinguished from "epigenesis" (if the old epigenesis is meant), would seem to fall but little short of complete surrender.

Preformation.

The whole question turns on what preformation meant to Bonnet. Preformation may stand for ideas that are quite distinct, or even antagonistic. As understood generally by the evolutionists of the eighteenth century, it was *the negation of all new formation.* It was the dogma of *original creation*, according to which all real formation was completed at the beginning of the world. The creative power was believed to have acted once for all, and to have since taken "Ferien," as Burdach expresses it. This was *syngenesis* versus *epigenesis*, *original* formation of all at one time in opposition to *new* formation all the time. This conception of preformation, which characterized the old evolution, has lost all scientific standing. So far the triumph of epigenesis has been complete, as all admit.

But the word preformation still has its use in an entirely different sense. We speak of the germ as the preformed foundation of the organism to which it gives rise, meaning, not that the adult form is already outlined in all its parts, but that the initial stage alone exists prior to, and different from, the stages that are to follow. In this sense preformation stands in no contradiction with postformation or epigenesis, for both are complementary phases of one development. Development begins with a minimum of preformation and increases this by every increment of postformation, until both the *pre* and the *post* are abrogated in complete formation.

The further we examine the new idea of preformation, the clearer it becomes that it differs *toto coelo* from the old notion. It does not allow that even the minimum of preformation with which development begins was an original creation. The germ is a preformation and at the same time a new formation. Germs are continually forming as the result of growth and self-division. The new germs are the preëxisting germs enlarged and divided. How the original ancestral germs arose we do not know. We find no evidence of spontaneous generation, but it does not accord with what we know to suppose that they were originally just what they are to-day. As all later stages of development are variable, we see no reason for supposing the initial stages invariable. In fact, germs must have varied, or the evolution of organisms is a myth. But the simplest germs we know grow and multiply by self-division. They do not arise agenetically like crystals, and we do not see how germs could be so simplified as to arise by chemico-physical combinations. The simplest term of the developmental series presupposes the coexistence of the fundamental powers of growth and self-division as absolutely indispensable conditions of heredity and variation. Yet we do not fall back on the rejected hypothesis of original creation. If there ever was a time when no organic elements of the nature of germs existed — and of this we are by no means sure — then we feel warranted in assuming that they came into existence at a stage in the evolution of the cosmos when conditions were somewhat different from those now obtaining, and that they came by the same great highway by which all things come and go — the highway of natural law.

Observe how complete the revolution in ideas. The old preformation affirmed syngenesis and denied epigenesis; the new preformation affirms epigenesis and denies syngenesis. I do not assert that the present idea of preformation affirms all the extravagances that have usurped the name epigenesis; but I do claim that, as now generally understood, it denies the very thing it formerly stood for, syngenesis, and presupposes and advocates the very thing it formerly opposed, generation in the sense of epigenesis. Not only is postformation, which is all there is left of the old epigenesis, maintained, but it is claimed to take place both from within and without.[1]

More than that, everything that preformation now stands for is regarded as the product of phyletic generation — as the heritage of all past epigenesis.

Is it strange that preformation now rests on the very principles it was originally supposed to exclude? No stranger certainly than that the old evolution should die as an idea and live as a name for the antithetical idea of epigenesis. Such changes are not rare, and when comparing the doctrines of development in the eighteenth century with those of to-day, we have to be on guard against concluding from identity of names to identity of ideas. If names could be relied upon for the identification of ideas, it would be easy to make Bonnet the father of the dominant ideas of modern evolution. Bonnet held to continuity in the scale of life, but how different is continuity in *grades* from continuity in *generation* of organisms? Bonnet uses the expression "*genealogical tree*" to describe a branching community of polyps. But would any one accuse modern phylogenists, who make use of the same expression, of

[1] The present idea of preformation opposes only that one-sided epigenesis that has lately come into vogue, which insists that all true epigenesis is from without, and that all generation from within must bear the name "evolution." That is an important distinction, setting off the extreme Lamarckian school, but it is modern and not essential to the idea of true generation.

reverting to Bonnet's conception, into which the idea of genetic affinity did not and could not enter? The expression "*cellular tissue*" also occurs in Bonnet's writings, but I have never heard it intimated that Schleiden and Schwann were thus forestalled. If further illustrations were needed to show that community of vocabulary does not always imply community of ideas, an appropriate one is found in Kant's definition of epigenesis as "*generic preformation*,"[1] and another in Burdach's "*epigenetic preformation*."[2]

Bonnet's Position.

Having seen that preformation may stand for extremes as wide apart as the doctrine of specific creation and that of modern evolution, we will try to ascertain Bonnet's position. That he began with the first extreme is undisputed; that he could have held both extremes at the same time is impossible; that he must have abandoned the first if he ever reached, or approximated, the second, is self-evident.

We are generally told that the germ, as first defined by Bonnet, was supposed to be an exact image, or, to use Huxley's words, "*an actual miniature of the organism.*" Although Bonnet's language sometimes appears, at first sight, to indicate such likeness of form, it is made clear from numerous statements that it cannot bear that interpretation. In fact, exact form-resemblance was positively denied. In those earlier meditations upon germs, recorded in the first eight chapters of the *Corps Organisés*, we find already the suggestion that the germ state differs from the developed state, approaching the form and nature of a liquid globule (Chap. IV, Art. 57). In Chap. IX of the same work, but written about twelve years later (1759), Bonnet points with evident pride to the fact that

[1] Since the power of reproduction is given in the organization of the race, it may be said that in the first parents all future generations preëxisted dynamically.

[2] Differing from syngenetic preformation in not being *original*. Called "epigenetic" to indicate that the germs arise in the parent organism, at *different times*, but always *before* sexual concurrence. In the old theories of generation *prae* and *post* generally related to the prime act of reproduction. Preformation was always *complete;* postformation, *gradual*.

he has nothing to change in his earlier views, and again dwells on the contrasts between the earlier and the later stages in respect to form and consistency (Arts. 143, 146, 154), cautioning the reader, however, against supposing that the germ ever represents a fluid in the strict sense of the word.[1] In the last chapter of the work, which deals with the formation of monsters, Bonnet says that the germ of the chick differs from the foetus so greatly in form, proportions, and arrangement of parts that, if we could see it enlarged just as it is, we should not be able to recognize it as a chick.[2]

It is thus made quite certain that Bonnet did not regard the germ as an exact photographic image of the adult form, and that idea must be put entirely aside if we would see just what is strictly essential in his conception of preformation.

The essential thing, as we shall see, was the preëxistence of the organism with all its parts completely formed, though not definitively shaped. Development could not form anything new, but it could modify shape and proportions very considerably. The ears, for example, in the germ of the horse, were supposed to preëxist as actual ears, but in what shape and proportions Bonnet never undertook to say. *All his theory required was that they should be present as perfect original creations, admitting of no differentiation or modification in their essential nature.* They must have shape, but not the particular shape presented in the adult state. The Creator had so designed

[1] "On se tromperait si l'on pensait que le germe est originairement un véritable fluide. Les fluides ne sont pas organisés; le germe l'est, et l'a été dès le commencement. Lorsqu'il s'offre à nous sous l'apparence trompeuse d'un fluide, il a des vaisseaux, et ces vaisseaux s'acquittent de leurs fonctions essentielles. Ils sont donc solides; mais leur délicatesse extrême paraît les rapprocher de la fluidité" (Art. 154).

[2] Tandis que le poulet est encore dans l'état de germe, toutes ses parties ont des formes, des proportions, des situations qui diffèrent extrêmement de celles que l'évolution leur fera revêtir. Cela va au point, que si nous pouvions voir ce germe en grand, tel qu'il est en petit, il nous serait impossible de la reconnaître pour un poulet. On n'a pour s'en convaincre, qu'à relire l'Art. 146. Le poulet étendu alors en ligne droite, ne présente, comme le ver spermatique, qu'une grosse tête et une queue effilée, qui renferme les ébauches du tronc et des extrémités. . . . Enfin, toutes les parties du germe ne se développent pas à la fois et uniformément." (Part II, Chap. VIII, Art. 351, p. 508. Tableau prefixed to Palingénésie, Art. 15, pp. 67, 68.)

them that, under normal conditions of development, they would expand into the form peculiar to the species. Slight variations of those conditions in the first stages might enlarge these organs to the dimensions exhibited in the mule, or transform them to monstrous shapes, or even prevent their unfolding at all.

In organs conceived as infinitesimal "organic points," shape, size, proportions, signified nothing. Preëxistence of everything truly organic was the all-essential thing. Preëxistence, precluding all generation and regeneration, reducing all metamorphosis to simple change of external form, leaving no place for growth, differentiation, heredity, variation, or multiplication of individuals or species, — that was the preformation contended for by Bonnet. To be sure, Bonnet had much to say about fertilization, assimilation, growth, heredity, and other general phenomena of development; but every one of these things was treated as extra-organic, and as purely mechanical means for expanding, without increasing, the original organic framework. All these things appear to go on; but our senses deceive us. They cannot go on at all, according to Bonnet. A mask of falsehood obscures the whole face of nature. Development is a complete illusion; for what appears to arise only emerges from a state of invisibility to one of visibility.

"It is not necessary to suppose," says Bonnet, "that the germ has all the features which characterize the mother as an individual. The germ bears the original imprint of the species, and not that of the individuality. It is on a small scale a man, a horse, a bull, *etc.*, but it is not a certain man, a certain horse, a certain bull, *etc.* *All germs are contemporaneous in the system of evolution, they do not communicate to one another their features, their distinctive characters.* I do not say that all those of the same species are exactly alike. I see nothing identical in nature; and without recourse to the principle of *indiscernibles*, it is very clear that all germs of the same species do not come to develop in the same womb, at the same time, in the same place, in the same climate, in a word, under the same conditions. . . . Such are many of the causes of variation." (*Corps Organ.*, II, Chap. VII, Art. 338, pp. 462, 463.)

But none of these causes of "variation" strike deep enough to change the essential foundation of the organism. Variations disguise the organism, without effecting any real change in its essential parts. "The soil, cultivation, and other special conditions, may influence the proportions and certain characters, so as to make it difficult to recognize the species. Here will be a dwarf, there a giant. Do not allow yourself to be imposed upon thereby; bring them both to close examination, and you will be able to discover the species in the midst of these deceptive appearances. The forms may likewise change, and disguise the species still more; redouble your attention, and you will recognize the disguise." (*Contemplation*, I, Part VII, Chap. XII, p. 295.)

We meet with this idea of the immutability of species at every turn, in both the earlier and later writings of Bonnet. In the eighth chapter of the *Corps Organisés* (p. 90) we read: "Nature is assuredly admirable in the conservation of individuals; but she is especially so in the conservation of species. . . . No change, no alteration, perfect identity. Species maintain themselves victoriously over the elements, over time, over death, and the term of their duration is unknown."

In the same chapter (p. 89) Bonnet says: "We cannot doubt that the species which existed at the beginning of the world, were no less numerous than those which exist to-day. The diversity and the multitude of combinations, perhaps also the diversity of climates and of foods, have given rise to new species or to intermediate individuals. These individuals uniting in their turn, the shades have multiplied, and in multiplying become less noticeable. The pear-tree among plants, the common fowl among birds, the dog among quadrupeds furnish striking examples of this truth."

Here Bonnet speaks in language befitting modern evolution of "new species," the very thing so positively denied. This manner of self-contradiction is habitual, and there is not the least inconsistency in it. Bonnet describes *appearances*, and he expects the reader to remember, what he has so often repeated, that appearances are deceptive. In many instances he uses the language of modern evolutionary doctrines without having any conception of them, and carrying always ideas that contradict them.

Bonnet's Preformation an Incorrigible Negation.

This preformation theory, contradicting appearances at every point, seemed to Bonnet and many other eminent men of the eighteenth century to magnify the glory of the Creator. To us it seems to be scepticism towards all nature, crystallized into a colossal system of inflexible negations, each involving the others, and all involved in one capital negation: NO ESSENTIAL CHANGE IN THE ORGANIC UNIVERSE.

The discovery of a single flaw in this all-embracing negative would put the whole theory in the light of a "romance," as Bonnet himself repeatedly declared. In one of the last of the many supplementary notes to the final revision of the *Corps Organisés* (1779), Bonnet reaffirms this negative as a fundamental principle to which he had always firmly adhered. The note begins with the following warning from Haller: "Observe that it is very dangerous to concede the formation of a finger by accident. If a finger may thus form itself, then a hand, an arm, a man, will do the same." To this Bonnet replied: "You are right; I have insisted upon that point a hundred times. I came to that conclusion long before you, when you supposed it possible for *une glu se figer et s'organiser*, and when epigenesis pleased you most. (*Corps Organ.*, Art. 155.) But observe, in your turn, that I have never attributed the *formation* of the least thing to *accident*. I have always conceded and maintained the preformation of everything that is truly *organic*. M. de Mairan made the same remark to me as yourself, and he received the same response. His objections against the sixth finger relate only to the graft of Lemery. I have not appealed to ingraftment; I have merely questioned if accidental causes might not have separated one or more fingers while they were yet in a gelatinous or nearly fluid state. In a word, — *and can I repeat it too often?* — I have never conceded anything but simple modifications of preformed parts, except certain cases of grafts or accidental separations." (*Corps Organ.*, p. 543.)

Such was Bonnet's testimony in 1778, while engaged in the final revision of his works, over thirty years after putting his first meditations on generation into manuscript (1747), and about ten years after concluding his system of philosophy in the first edition of the *Palingénésie Philosophique* (1769). It was his testimony after a prolonged consideration of that greatest of stumbling-blocks to the evolutionist, the *propagation of* *monsters.* Although finally forced to admit that sex-digitism could be transmitted by either sex (p. 536), Bonnet maintained his position as firmly as ever, only hesitating to pronounce decisively between the hypothesis of originally monstrous germs and that of accidental causes. On this point he could close his volume with, "*fiat lux*"; but on the main thesis, — *all preformation, no generation,* — he had chained himself irrevocably, and left no possible escape.

The same incorrigible negation meets us in Haller's dictum: "*Nulla adeo est epigenesis.*" To Bonnet it remained to the end the alpha and omega of philosophy and the sheet-anchor of religious faith. Let one example suffice:

"A true philosopher," says Bonnet, "would not undertake to explain mechanically the formation of a head, an arm, however simple might be the structure of this head or this arm. In the most simple organic structure there are still so many relations; these relations are so varied, so direct; all the parts are so intimately connected, so dependent on one another, so coöperative to the same end, that they could not be conceived of as having been formed one after the other and arranged successively, like the molecules of a salt or a crystal. A sound philosophy has eyes that discover in every organized body the ineffaceable imprint of a work done at a single stroke, and which is the expression of that Adorable Will that said, '*Let organic bodies be, and they were.*' They were from the beginning, and their first appearance is what we very improperly call *generation, birth.*" (*Contemplation,* Part IX, Chap. I, p. 2.)

After wrestling with all the perplexing questions presented in Hydra; after accounting for sex as a means of diversifying the unity of the *beau physique,* and sexual reproduction as a device for expanding the germ and preserving regularity of specific form; after reconciling the existence of varieties with the permanence of species; after contending that a mule is a disguised horse and a hinny a disguised ass, and that the sterility of hybrids is to be regarded as fertility kept dormant by lack of adequate means to unfold; after reducing all heredity to likeness of original, contemporaneous, and independent creations, unfolding under similar conditions; after elaborating a scheme of "natural evolution" broad enough to take in any number of cosmic revolutions, and provide for the ultimate perfection of every organism as an immortal being; — in a word, after setting "Ferien" to all creative activity, Bonnet resolutely undertook to devise a scheme that would keep the holiday repose forever inviolable. With a zeal never daunted, and an ingenuity seldom baffled, never defeated, he piled mountain upon mountain of negation, rolling Ossa on Olympus and Pelion upon Ossa, until the whole organic world seemed to be completely buried under a stupendous mass of negations, blending in one infinite negation — NO CHANGE.

TWELFTH LECTURE.

THE PALINGENESIA[1] AND THE GERM DOCTRINE OF BONNET.

C. O. WHITMAN.

"Toutes les pièces de l'univers sont donc contemporaines. La Volonté Efficace a réalisé par un seul acte tout ce qui pouvait l'être. Elle ne crée plus; mais Elle conserve, et cette conservation sera, si l'on veut, une Création continuée." — *Palingénésie*, Part VI, Chap. II, p. 181.

If our examination of the principles and general bearings of the doctrine of preformation has been successful, we have the key to Bonnet's whole philosophy, and are so far prepared to deal intelligently with his definitions of germs and his ideas of "natural evolution," or "*Palingénésie*," as he called it. We have fulfilled just that condition upon which Bonnet himself insisted, when he requested the reader of his *Palingénésie Philosophique*[2] to accord him the favor of reserving judgment until after having read the work and "*reflected a little upon the nature of the principles, their logical dependence, the consequences of those principles, and the harmony of the whole.*"

It might look like a waste of time to examine further a system of ideas dominated throughout by the dogma of creation, or preformation; but we are not dealing with the system as an isolated thing, for its own sake alone. It appeals to our in-

[1] Πάλιν = again, repeated, and γένεσις = birth, generation. As defined by Haeckel, *palingenesis* signifies *original development* in distinction from *cenogenesis, modified development.* Palingenesia, as used by Bonnet, does not mean actual *re-creation*, but *renaissance, resurrection*, or "*natural evolution*" of organisms pre-existing in the germ state.

[2] Bonnet speaks of this work as "a sort of supplement" to three earlier works: (1) "L'Essai Analytique sur les Facultés de l'Ame" (1760), (2) "Les Considérations sur les Corps Organisés" (1762), and (3) "La Contemplation de la Nature" (1764–65).

terest chiefly as exhibiting an instructive stage in the development of our conceptions of organic phenomena, and as helping to define the antithetical standpoint of to-day.

A system of philosophy supported by such men as Malpighi, Swammerdam, Leeuwenhoeck, Leibnitz, Bonnet, Haller, and Cuvier; supposed to have been modified in the hands of its chief expounder until at last it ceased to differ essentially from epigenesis; and frequently referred to as the precursor of ideas now engaging the attention of many eminent biologists — such a system, whatever its intrinsic merits, cannot be devoid of interest to those who realize that the present is born of the past — of the false as well as the true.

Bonnet's Writings.

As we have to follow "the march of ideas" in Bonnet's works in order to note the modifications introduced, it may save some confusion if we acquaint ourselves with the historical order of the writings to be consulted.

Bonnet's meditations upon germs and the phenomena of development cover a period of about thirty-five years, extending from his earliest philosophical composition, in 1747, to the latest revision in 1783. *Les Œuvres d'Histoire Naturelle et de Philosophie de Charles Bonnet* were collected at Neufchâtel, in 1779–83, in eight vols., 4°; and in 18 vols., 8°. It is to the complete quarto edition that my references are made.[1]

[1] To the first volume of this edition is prefixed a list of Bonnet's writings, from which seven memoirs published in the *Recueil des Savants Étrangers*, and ten memoirs published in Rozier's *Journal de Physique* (1774–1777), are omitted.

LIST OF WORKS.

CHARLES BONNET (1720–1793).

I. *Traité d'Insectologie*, 2 vols., 8°, Paris, 1745; last ed. 1779.

II. *Recherches de l'Usage des Feuilles*, 4°, Göttingen and Leyden, 1754. Edition of 1779 contains the memoirs published in the *Recueil des Savants Étrangers*.

III. *Considérations sur les Corps Organisés*, 2 vols., 8°, Amsterdam, 1762; reprinted 1768, revised 1779.

IV. *Contemplation de la Nature*, 2 vols., 8°, Amsterdam, 1764–65; reprinted 1769, revised 1781.

The *Corps Organisés*, the *Contemplation*, and the *Palingénésie* are the three works of chief interest to us.

The first outline of Bonnet's theory was laid down in manuscript in 1747–1749 (?), as an introduction to the *Contemplation.* It was detached from this work and published in 1762, as the first eight chapters of the *Corps Organisés.* The 7th and 8th chapters are mainly devoted to an examination of Buffon's views, and appear to have been written immediately after the second volume of Buffon's *Histoire Naturelle* fell into the author's hands, presumably in 1749. The composition of the rest of the *Corps Organisés* was begun in September, 1759, immediately after the completion of the *Essai Analytique,* and shortly after the appearance of Haller's memoirs on the development of the chick (1758), and completed in 1762. The body of the work is thus separated from the introductory chapters by an interval of from twelve to fifteen years. Nearly twenty years later (1779) the third and final edition was published, containing many supplementary observations in the form of footnotes, together with numerous references, inserted for the benefit of the reader who might wish to consult what the author had written at different times and places on special subjects.

Bonnet warns the reader (Preface, p. xvi) not to judge this work by the first eight chapters, which he describes (footnote, p. 29) as "only a feeble outline drawn with a hand little

V. *Écrits sur divers Sujets d'Histoire Naturelle,* 1781. Contains Memoir on Germs, memoirs published in Rozier's Journal, and new memoirs on Bees, Regeneration in the Snail and the Salamander, and (in Part II) Letters to Spallanzani and to others.

VI. *Essai Analytique sur les Facultés de l'Ame,* 4°, Copenhagen, 1760; reprinted in 8°, 1769; revised 1782.

VII. *Palingénésie Philosophique,* 2 vols., 8°, Geneva, 1769; reprinted 1770, revised 1783. Contains as an introduction the *Analyse abrégée de l'Essai Analytique,* the *Tableau des Considérations,* and the *Application des Principes Psychologiques.*

VIII. *Essai de Psychologie et Écrits Divers,* 1783. This Essai appeared first at Leyden in 1754. It is followed by *Principes Philosophiques sur la Cause Première, Leibnitz sur la Survivance de l'Animal* and other topics, *Bornes Naturelles de nos Connaissances, Remarques sur la Liberté, Observations sur les Miracles, l'Origine du Mal, Philalèthe,* etc.

assured." His theory and the "march" of his ideas may be understood, so he tells us (Preface, p. xv), by consulting Chap. XII of Part I, and Chaps. I, II, VII, VIII, of Part II. For his doctrine of germs he refers (p. 29) to Chap. I of Part II; to Chap. VIII of Part VII of the *Contemplation*, and Chaps. I and II of Part IX of the same work; and to Part X of the *Palingénésie*.

As a further aid to the understanding of the *Corps Organisés*, Bonnet has given a résumé of the whole work, which first appeared as an introduction to the *Contemplation* (1764), but which, in the collected edition of his works, is prefixed to the *Palingénésie*, under the title of *Le Tableau des Considérations*. Without these various guides, which Bonnet's ever-mindful regard for the reader has supplied, it would not be easy to get the historical perspective of this single work.

Bonnet's views are presented in a more popular form in the *Contemplation*, which was composed long before the *Corps Organisés* was begun, although not published until 1764. The revision of this work, consisting in the addition of many new chapters and extensive footnotes, occupied over two years, and resulted in the edition of 1781. In Parts VII and IX (*vid.* Pref., p. xii) we find views presented which belong to the same early period as the first eight chapters of the *Corps Organisés*, corrected and supplemented by the author's later reflections. The theory as developed here is a good introduction to the reading of the *Corps Organisés*.

The *Palingénésie* followed in 1769, completing Bonnet's system of speculation, and forming a sort of general supplement to the *Essai Analitique*, the *Corps Organisés*, and the *Contemplation*. The revised edition of this work appeared in 1783. Among the later writings dealing with germs are the "*Mémoire sur les Germes* (1773), and the second *Mémoire sur la Reproduction des Membres de la Salamandre aquatique* (1778), published originally in Rozier's *Journal*, and reproduced in Vol. V of the complete works. The views contained in these memoirs are given at length in Part X of the *Palingénésie*, which stands as the chief authority for Bonnet's final convictions on evolution.

Fortunately Bonnet's revisions were made in footnotes, distinguishable from the original footnotes by a double obelisk, and in chapters marked as "new." The original text has thus been preserved, so that the reader may often see on the same page the earliest ideas and their latest modifications.

First Meditations.[1]

For Bonnet's first reflections on germs, we turn to the first *eight* chapters of the *Corps Organisés*. It is worthy of note that the word *preformation* does not occur in these chapters. We find such expressions as, "*exist originally*," "*exist already*," "*exist before their birth*," "*preëxist*." The word "preëxist" occurs three times,[2] and elsewhere in this work it seems to be preferred to preformation. The word "miniature" occurs twice.[3]

The idea of an exact image is suggested by such expressions as "*dessiné en miniature*"; but, as we have before seen,[4] Bonnet has left us no excuse for any mistake on this point. In the third chapter (p. 15) the germ is defined as follows: "The germ is called an outline or a sketch of the organism. That idea may not be sufficiently precise. Either we must undertake to explain the formation of the organs mechanically — what sound philosophy finds to be above its powers — or we must admit that the germ actually contains epitomized all the parts essential to the plant or animal which it represents.

"The principal difference between the germ and the developed animal is, that the first is composed of *elementary particles* alone, and that the meshes which they form are as narrow as possible; while, in the second, the elementary particles are joined to an infinite number of other particles which

[1] "J'ai donné dans les huit premiers chapitres du livre des *Corps Organisés* mes premières méditations sur la génération et sur le développement." (*Paling.*, p. 205.)

[2] (1) "Germes préexistants" (p. 20). (2) "Développement de parties préexistantes" (p. 22). (3) "Le germe préexiste dans la femelle à la fécondation" (footnote, p. 88).

[3] (1) "According to the idea which I have given of the germ, it is an animal, so to speak, *in miniature*; it has all the parts *très en petit* which the animals of its species have *en grand*" (p. 23). (2) "I have imagined that the horse is designed *in miniature*" (p. 86).

[4] Previous Lecture, pp. 234–37.

nutrition has associated with them, and the meshes of the simple fibres are enlarged as much as the nature and arrangement of their principles will admit."

Recapitulating, and at the same time reaffirming with some changes, the ideas contained in these chapters (*Paling.*, Part VII, Chap. IV, p. 205), Bonnet says:

"I was still young when I engaged in those reflections, and I pursued my aim by the glimmer of the facts which I had collected and which I compared. The discoveries of Haller on the chick had not then been made, and it is principally those discoveries which have furnished me the most exact knowledge, and which, confirming several of my early ideas, have impelled me to penetrate farther into one of the most profound mysteries of nature.

"*I at first assumed, as a fundamental principle, that nothing was generated;* that everything was originally preformed, and that what we call generation was but the simple development of what preëxisted under an invisible form and *more or less different from that which becomes manifest to our senses.*

"I postulated that all organized bodies derived their origin from a germ which contained *très en petit* the elements of all the organic parts.

"I conceived the elements of the germ as the *primordial foundation,* on which the nutritive molecules went to work to increase in every direction the dimensions of the parts.

"I pictured the germ as a network, the elements of which formed the meshes. The nutritive molecules, incorporating themselves into these meshes, tended to enlarge them; and the ease with which the elements glided over one another permitted them to yield more or less to the secret force that drove the molecules into the meshes and tended to open them. . . .

"I thus excluded every new formation, admitting only the mediate or immediate effects of a preëstablished organism, and endeavoring to show how it could suffice for everything.

"Strictly speaking, I said (Art. 83, pp. 47, 48), the elements [inorganic] do not form organic bodies; they only develop them, and this is accomplished by nutrition. The primitive organization of the germs determines the arrangement which the nourishing atoms must take in order to become parts of the organic whole.

"An inorganic solid is a piece of mosaic or unconnected parts. An organic solid is a fabric formed by the interweaving of various threads. The elementary fibres with their meshes are the warp of the stuff; the nourishing atoms which insinuate themselves into these meshes are the woof. These comparisons, however, should not be carried too far.

"On these principles, which seemed to me more philosophical than those that had been held before me, I came to regard death as a sort of *envelopment*, and the resurrection as a second development incomparably more rapid than the first.

"This is the simple and clear way in which I conceived the thing: I considered the organic whole, attained to its full growth, as a composite of original or elementary parts and of foreign substances which nutrition had associated with them during the entire course of life.

"I imagined that decomposition, which follows death, extracted, so to speak, from the organic whole those foreign substances which nutrition had associated with the constituent, primitive, and indestructible parts of this whole; that during this extraction these parts tended to approach one another more and more, and to take *new forms, new relative positions, new arrangements;* in a word, to return to the primitive state of the germ and thus concentrate themselves in a point.

"On this little hypothesis, which seemed wholly my own [the similar "envelopment" hypothesis of Leibnitz was unknown to Bonnet at first], I explained quite felicitously, as it then appeared, and *in a purely physical way*, the so consoling and philosophical dogma of the resurrection. It sufficed me for this to suppose that there were *natural* causes, arranged originally by the benevolent Author of our being, and designed to effect the rapid development of this organic whole concealed under the invisible form of a germ, and thus preserved by Infinite Wisdom for the day of this great manifestation."

Thus according to Bonnet's earlier notions, death simply reverses the process of evolution — marks the end of de-velopment and the beginning of en-velopment. The shuffling off of this mortal coil is a restoration to the state of pure immortal "essentials." Returned to its original state, the germ might undergo a second development (*Essai Analyt.*, p. 362); and thus a theory of generation supplied a theory of the resurrection.

The "essentials" are inconceivably minute "elementary particles," supposed to represent on an infinitesimal scale the entire "organic" foundation of the future plant or animal. They are imperishable, gaining nothing by development, losing nothing by death and decomposition. The whole difference in bulk between the germ and the developed organism is made up of non-essential, inorganic matter. Think of the shadowy tenuity of a framework such as these "organic points" must be imagined to represent in a state of maximum distension, with their interstices stuffed with foreign matter.

There is nothing in the whole scheme implying photographic likeness of form between the germ and the fully expanded organism. No two stages in development need be characterized by the same form. It was only necessary to assume that the series would terminate in the form proper to the species, provided the conditions of development were normal. Supply the germ of the horse with proper nourishment and it will become a typical horse ; vary the nutritive fluid that first penetrates it in certain definite relations, and the series may end in a mule.

The theory was fully equal to all emergencies in the way of form variation, as is more clearly seen in Bonnet's "conjectures upon the second population of the earth" (*Paling.*, pp. 184–187). He imagines a "first world" reduced to chaos, out of which the present world arose as a renewal.

"Should I abuse the freedom of conjecture," he asks, "were I to say that the plants and animals of to-day have arisen by a sort of *natural evolution* from the organized beings that peopled the first world, which came directly from the hands of the Creator? . . . *They were probably very different then from what they are to-day. They were as much so as the first world differs from the one we inhabit. We have no means of judging* *of those differences, and perhaps the most skilful naturalist of the first world would have failed to recognize our plants and animals.*"

"*Envelopment*" *Renounced.*

Singularly enough Bonnet at first overlooked an obvious and fatal objection to his theory of the resurrection. Its discovery led to the speedy abandonment of the "envelopment" idea, and to the introduction of a new hypothesis that greatly added to the complexity of his doctrine of germs. This was the greatest change which Bonnet's system of speculation underwent. His brief account of it runs as follows:

"One salient objection, of which I had not at first thought, came to destroy in a moment this whole system, which had begun to please me greatly, it was that derived from men who have been mutilated — who have lost the head, a leg, an arm, *etc.* How could these men be resuscitated with the members that their germ would no longer have? How could they be made to recover this head in which I had located the seat of personality?

"There remained to me, indeed, the resource of supposing that the germ in question inclosed another head prepared by Divine Prescience. But this head would have held another soul; it would have constituted another personality, and the important point was to preserve the personality of the first individual.

"I did not hesitate an instant, then, to abandon an hypothesis which I should have been able to sustain only with the aid of suppositions that would have clashed more or less with probability. Nature is so simple in her ways that an hypothesis loses in probability in proportion as it becomes complicated." (*Paling.*, p. 208.)

"*Metamorphosis*" *the Secret of the Resurrection.*

The theory of "development" remained as originally conceived, and the difficulty about the resurrection was disposed of by assuming that there is a soul-bearing, indestructible germ lodged somewhere in the brain,[1] which carries the personality, and which is destined to develop into the "spiritual body" of the next world.

The adoption of this view added greatly to the complexity of Bonnet's system of germs; but the change was merely an extension of his original basis, and did not necessitate the sacrifice of a single principle of "evolution." It simply doubled the number of germs to be evolved in order to escape the objection to re-evolving decapitated or otherwise mutilated germs.

Bonnet's speculations were all inspired by his faith in the doctrine of a future life. How to invent a scheme that should make the resurrection look credible — that was the chief concern. Although a devout believer in miracles, Bonnet proceeded on the principle that "God would not multiply miracles unnecessarily" (*Essai Analyt.*, p. 353). "If nature has placed the germ of the butterfly in the caterpillar, and in the seed the germ of the plant that is to arise from it, why would she not be able to place in the human body the germ of the body which is to succeed it?

"It is then possible that the seat of the soul actually incloses the germ of that glorious and incorruptible body of which Revelation speaks. It is even probable that it incloses it; for it is at least probable that God only makes exceptions to the laws of nature when secondary causes do not suffice by themselves to fulfil the ends of his wisdom.

"Revelation itself appears to suggest the idea which I have proposed on the seat of the soul, by the beautiful and philosophical comparison of *the seed sown in the earth.* It seems to remind us thereby of general laws and to suggest that the resurrection will only be the effect of those laws. Man is the seed sown in the earth; the envelope of the seed perishes, and from its interior comes forth a plant, very different from this envelope, which will bear fruit in eternity.

. . . "I have to show here how we are to conceive the development of this small germ concealed in the seat of the soul, or, what comes to the same thing, how the resurrection takes place.

[1] *Contemplation*, Part IV, Chap. XIII, and *Essai Analytique*, Chap. XXIV.

"A sound philosophy teaches us to think that there is no true generation in nature, and that the bodies which appear to be generated are only developed, since they exist already fully formed *en petit* in the germs . . .

"As in the case of the animal germ, so the spiritual germ can only be developed by the action of substance which is analogous to it. If this germ is of a nature analogous to that of fire or of light, then it will be a matter analogous to fire or light which will cause its development . . . and this will be done in *un clin d'œil*." (*Essai Analyt.*, pp. 358, 359, 361, 362.)

Thus Bonnet works out a theory which brings the resurrection into an "*order of events purely natural*," and provides for the preservation of the personality by "*une préordination physique*."[1] Death is no longer an "*envelopment*," but "a preparation for a sort of *metamorphosis*" (p. 351). The "*corps terrestre*" is to be shed and the "*corps humain*," bearing the soul, set free, with a new form, new organs, more perfect senses.

The ancient doctrine of metempsychosis is completely outdone in this scheme; for the soul is from the beginning inseparably linked to the body which is destined to be its final abode, and in leaping from one state to the next, all it has to do is to leave behind the body that has served its purpose and develop another from the germ coming next in order of *emboîtement*.

"*Palingénésie*" or "*Évolution Naturelle.*"

This idea of metamorphosis opened the way to a further extension of the doctrine of preformation. If one such metamorphosis as that conceived for the resurrection could be provided for, why not two, three, or more? It was easy to extend the idea to plants and animals and thus account for the repeopling of the earth after any number of revolutions. The basis was broad enough for a scheme embracing the whole animate world, past, present, and future; and even for a succession of worlds, all peopled with the same beings, but each representing a higher state of existence than the preceding.

[1] *Essai Analyt.*, p. 353.

Let us assume with Bonnet three revolutions.[1] The "first world" came directly from the hands of the Creator; the second was inaugurated, after a night of chaos, by the Mosaic creation; and the third is to be introduced with the resurrection. In accordance herewith, the theory supposes three germs for each individual soul, incased one within another, in the order in which they are to be developed, with the soul lodged in the innermost germ. The external germ came to development in the first or pre-Adamic world, and perished, leaving the soul with the two remaining germs uninjured, but incapable of another development until the second and present order of things was instituted. The new conditions appearing with the dawn of the present state were adapted to awaken the second germ to development, but not the third. The undeveloped germ, the real seat of the soul, is supposed to sustain certain close relations with the present body, by virtue of which it receives from without lasting impressions on its seat of memory. "These impressions constitute *the physical foundation of the personality of the animal.* It is through them that the future state will preserve more or less connection with the past state, and that the animal will be able to perceive the increase of its happiness or of its perfection."[2]

The third and last germ, variously called "the germ of restitution," "the little ethereal machine" of the soul, "small body," "principle of reparation," "primitive corpuscle," *etc.*, is composed of indestructible elements analogous to fire, ether, light, or electricity. It represents an organism of a higher order than the preceding ones, with many new and more exquisite senses.

When the present body sloughs off, the "germ of restitution" is set free, but remains torpid until, at the resurrection, by the sudden inflow of matter analogous to itself, its "evolution" will be achieved "in the twinkling of an eye." This final development is called "a *grand metamorphosis.*"

Bonnet's "natural evolution" is, in fact, only a succession of "metamorphoses." The germ emerges to each new state as a complete organism, after deliverance from the envelope of

[1] *Palingénésie*, p. 187. [2] *Loc. cit.*, p. 124.

its dormant state, as a butterfly deserts its chrysalis and soars to new life.

But why does Bonnet call such evolution *natural?* Had he in mind anything comparable with the modern idea of development, as a natural course of progressive differentiation? Most certainly not, for this whole scheme of palingenesia was built upon the same old negation, *no generation.*

This strange conception of a "mixed being," consisting of one soul and three bodies, strikes one as the most unnatural exaggeration of the unnatural. What more stupendous miracle could be imagined than this trinity of germs, each awaiting the reduction of the earth to chaos or ashes for its turn to unfold, and each and all presided over by a single soul! What strange revolutions planned for this soul; what fiery ordeals for its intervals of slumber; what grand metamorphoses to be triumphantly concluded in perfection and eternity!

What is "natural" about all this? Was not all "evolution" of preformed beings regarded as "natural"? What exception could there be? Bonnet was thinking of the Mosaic creation, which he was trying to explain, not as an immediate act of the Creator, but as a fulfilment, in a purely mechanical way, of events already arranged for by the creation completed at the beginning of the pre-Adamic world. Bonnet was anxious to keep his theory free from even a shadow of contamination with epigenesis[1]; hence he insisted that there had been but one "creation." All the rest, Mosaic creation and resurrection, were "natural," *i.e.*, parts of the machinery of nature previously consummated.

[1] "It would be the greatest absurdity," says Bonnet, "to suppose that in the first formation of animals, God commenced [after the manner of epigenesis] by creating the heart, then the lungs, then the brain, *etc.* I do not think it would be less absurd to suppose that in the formation of the universe, God began by creating a planet, then a sun, then another planet, *etc.* . . . I will not affirm that at the first instant of Creation all the heavenly bodies were arranged in relation to one another precisely as they are to-day. That primitive arrangement may have undergone many changes by a *natural* series of the movements of those bodies and of the combination of their forces. But Divine Wisdom foresaw and approved those changes, as it foresaw and approved an almost infinite number of modifications which arise from the structure or primitive organization of the beings belonging to each world." (*Paling.*, pp. 180–181.)

Bonnet brings forward the phases of development in the chick as helping us to form some idea of the "revolutions" through which organisms are carried by this "natural evolution." The comparison is of interest to us in two ways: First, it shows that Bonnet did not regard the germ as a facsimile of the adult; and secondly, it reminds us of the parallel which modern embryology traces between the development of the individual and that of the race — between the ontogenetic and the phylogenetic series. The phases of the chick are first briefly sketched:

"It is not without astonishment that we behold the strange revolutions which the chick undergoes from the time when it begins to be visible to the time when it shows its true form. I shall not redescribe those revolutions here. It is sufficient to remind the reader that when the chick begins to be visible, it appears under a form which resembles closely that of a very small worm. Its head is large, and to this head is attached a sort of tapering appendage. It is in this appendage, so like the tail of a small worm, that the trunk and limbs of the animal are contained. The whole is extended in a straight line and is motionless. . . .

. . . "*The different successive phases under which the chick shows itself, enable us to form an idea of the different revolutions which organized bodies have to undergo in order to reach this last form by which they are known to us.* . . .

"*All this helps us to conceive the new forms which animals will take in that future state to which I conjecture they are called.* This small organic body, by which their soul is actually bound to the grosser body, incloses already, infinitely small, the elements of all the parts which will compose that new body under which the animal will appear in its future state.

"The causes which will effect this revolution of our globe, of which the Apostle speaks, will be able at the same time to effect the more or less accelerated development of all the animals concentrated into those organic points which I might call *germs of restitution.*" (*Paling.*, Part I, Chap. IV, pp. 125, 126.)

These are some of Bonnet's latest statements; and as yet we discover no surrender, no advances even, towards epigenesis. Indeed, the main intent of this "natural evolution" was to shut every possible avenue to epigenesis, and make one creation responsible for the whole machinery of the universe. Creation once and for all, instantaneous, perfect; the universe and all it contains, one harmonious machine operating "naturally," that is, turning out just as many "evolutions" and "revolutions" as were originally designed and spoken into existence — that was Bonnet's creed — his religion, his philosophy, his science.

Idea of Progress.

This scheme of "natural evolution," which excludes all progress, as we understand it, yet provides for the elevation and perfection of all living organisms. Progress, however, meant to Bonnet only *the unfolding of successively higher grades of germs.* The soul-bearing germ, representing the highest grade of perfection, was placed at the center of the germ trinity, so that it would "naturally" come to development last. Bonnet does not fix any limit to the number of germs originally appointed to each individual; he only sets the minimum at three.

"This same progression" (*i.e.*, gradation), says Bonnet, "which we discover to-day among the different orders of organized beings, will be seen, without doubt, in the future state of our globe; but it will follow other proportions which will be determined by the degree of perfectibility of each species. *Man, transported then to another abode better suited to the eminence of his faculties, will leave to the monkey or to the elephant that first place which he occupied among the animals of our planet. In that universal restitution of the animals, the Newtons and the Leibnitzes may be found among the monkeys and the elephants; the Perraults and the Vaubans among the beavers, etc.*

"The lowest species, as the oysters, the polyps, *etc.*, will be to the highest species of that new hierarchy as the birds and quadrupeds are to man in the present hierarchy.

"Perhaps there will be a continued progress, more or less slow, of all species towards a higher perfection, such that all degrees of the scale will be continually changing in a constant and determined order: I mean that the mutability of each degree will always have its reason in the degree that shall have immediately preceded it." (*Paling.*, pp. 149–150.)

Of the animal, Bonnet says, — "Not only will its actual senses be perfected, but possibly it may acquire new senses, and with them new principles of life and action. Its perceptions and its operations will be multiplied and diversified to an unknown degree (*ibid.*, p. 146).

Adopting the Leibnitzian idea of an ascending scale of beings, and applying the theory of "natural evolution," Bonnet conceived it possible for plants to rise to the state of animals.

"If the being of the plant has been attached to an incorruptible germ, that germ may contain, like that of an animal, the elements of new organs, which will perfect, develop, and ennoble the faculties of that being. I cannot say to what degree it will rise in the scale of animality; it is enough for me to perceive the possibility of such elevation, and through it an increase of beauty in the organic realm" (*ibid.*, p. 160).

This great scale, extending below the lowest plant to the simplest substance of the inorganic world, and above man to celestial beings, terminating in Divinity itself, — this regular gradation in the perfection of beings, presented with the talent of Bonnet, formed, as Cuvier remarked, "an enchanting picture which was destined to win many minds and have many partisans."

The coincidences discoverable between Bonnet's ideas of development and those of to-day are for the most part of a deceptive nature. Likeness of subject and likeness of vocabulary present many seductive parallels, but they vanish the moment we go below the surface. His statements may be positive, truthful, and beautiful in *form*, and yet negative, false, and grotesque in the assumptions which they veil. Often his words counterfeit the language of modern evolution; but what monstrous travesties they disclose on closer examination!

There is "natural evolution," the most unnatural negation of evolution; "progress" that discloses nothing but a succession of preformed hierarchies; a "law of continuity" that vanishes in the mist of fine grades, without any bond of connection whatever; a "metamorphosis" that conceals one preformation under another; a "palingenesis" that denies all genesis, and agrees with modern palingenesis only in etymology; a "genealogy" of contemporaneous beings; "heredity" that transmits nothing; "births," "evolutions," and "revolutions" that bring nothing new, and so on through all the negations that a fertile genius could invent against the intrusion of epigenesis.

Perhaps you are puzzled to understand how a sane mind could ever have been led to devise such a scheme and accept it as a partial solution of the great mystery of life. If so, you will not be less puzzled to understand how any one, who has reflected upon the subject, could ever assert, either that Bonnet advanced to our standpoint, or that we are returning to his.

Reason for Rejecting Epigenesis.

Unaccountable as it may seem, Bonnet had better reasons for his conclusions than we have for confusing them with present conceptions. Bonnet accepted preformation only to escape what seemed to him a greater miracle. To suppose that men and other organisms are forming anew every day, that such marvels of structure and purposeful adaptations can suddenly come into existence of themselves, seemed to him not only to contradict Revelation but also to be incompatible with sound philosophy. The mechanical explanations offered by the epigenesists were so obviously absurd that there seemed to be no refuge except in the dogma of creation. Bonnet never claimed that his own theory was satisfactory; but only that it was less unsatisfactory than epigenesis appeared to be. Towards the end of the third chapter of his early writing (*Corps Organ.*, p. 20), he says, — "All that I have said upon generation may be taken for a romance if you like. I am myself strongly disposed to regard it from the same point of view. I feel that I have only imperfectly satisfied the phenomena. But I will ask if other hypotheses are found to be more satisfactory. On this point I have two observations to make.

"First, I could not abandon so beautiful a theory as that of *preëxistent germs*, to accept purely mechanical explanations.

"Secondly, it seems to me that we should try to investigate more thoroughly the manner in which development goes on before seeking to discover how generation takes place."

In 1759, Caspar Friedrich Wolff, then a young man, came forward with his *Theory of Generation*, a powerful defence of epigenesis; but his work could avail little against such an authority as Albert von Haller, whose studies on the development of the chick had converted him from epigenesis to preformation. Bonnet was confirmed in his early convictions by Haller's results and conclusions, and henceforth devoted himself with increased assurance and zeal to the amplification of the doctrine of preformation.

The old objection to epigenesis, often reiterated and expatiated upon, is strongly stated in the *Tableau des Considérations* (Art. 14, pp. 64–66):

"If organized bodies are not preformed, then they must be formed every day, in virtue of the laws of a special mechanics. Now, I beg you to tell me what mechanics will preside over the formation of a brain, a heart, a lung, and so many other organs?

"I do not yet make the difficulty strong enough: it consists not alone in making such or such an organ, itself composed of many different parts, form mechanically; it consists chiefly in accounting, through the laws of mechanics alone, for that multitude of varied relations which bind so closely together all the organic parts, and in virtue of which they all coöperate to the same general end; that is, to form that unity called an animal, that organic whole which lives, grows, feels, moves, maintains, and propagates itself.

"Observe that the brain implies the heart, and that the heart, in its turn, implies the brain. The brain and the heart imply the nerves, the arteries, and the veins. The animal nourishes itself; — the organs of circulation imply also those of nutrition. The animal moves; — the organs of movement imply those of sensation. The animal propagates itself; — the organs of generation suppose also those of nutrition, of circulation, of sensation, of movement. We must not keep to generalities here · we must enter into details, into the minutest details.

"When we regard the animal merely from a general point of view, we are not sufficiently struck by the difficulty, one might rather say the impossibility, of all mechanical solutions.

"I do not demand that the human body, this masterpiece of nature, be taken as the starting-point; one may start from the body of a vile insect. I only ask one favor of those who are fond of mechanical explanations; this is, that they will cast a glance at the wonders produced by the graver of the celebrated Lyonet. They will not behold without profound astonishment those four thousand muscles employed in the construction of a caterpillar, their admirable coördination, and that of the tracheae, which is no less admirable. And I am fain to persuade myself they will then feel that a whole so marvelously composed and yet so harmonious, so essentially one, cannot have been formed, like a watch, of related pieces, or by the ingraining of an infinitude of diverse molecules united by successive apposition. They will admit, I hope, that such a whole bears the indelible imprint of a work done at a single stroke.

"What is the use, indeed, of putting one's soul to torture in seeking mechanical solutions, which do not satisfy the case, while there are very decisive facts that seem to lead us as by the hand to the preëxistence of germs? I do not pretend to pronounce judgment on the ways the Creator has chosen for bringing divers organic wholes into existence; I limit myself to saying that, in the actual state of our knowledge of the physical world, we do not discover any rational way of explaining mechanically the formation of an animal, or even the least organ.

"I therefore think it more consonant with sound philosophy, because it is more consonant with facts, to admit, as at least highly probable, that organized bodies preëxisted from the beginning."

This *Tableau*, appearing for the first time in 1764 as a preface to the *Contemplation*, stands about midway between the first and the last of Bonnet's writings; but as it presents the earlier views as confirmed by the studies and reflections of his maturer years, and as it was finally placed at the head of the *Palingénésie*, and left in the final revision without correction on the points here considered, it may be said to span the whole course of his speculation and to stand as an authoritative certificate of steadfast adherence to the doctrine of preformation. Far from holding less firmly to this doctrine, Bonnet's faith outgrew the early lack of confidence which could speak of the theory as a "romance," and comes forth at the conclusion of the *Palingénésie* proclaiming that the "enchanting system" already puts us in possession of the very substance of things hoped for.

The Doctrine of Germs.

After thus vindicating his preference of the single miracle of preformation to the endless miracle of epigenesis, Bonnet continues the *Tableau* with a remark upon the signification of the word germ, which recalls the passage cited by Huxley to show that Bonnet finally admitted that "a germ need not be an actual miniature of the organism, but that it may be merely an 'original preformation' capable of producing the latter."

The remark is as follows: "*J'ajoute ici que j'entends en général par le mot de germe toute préordination, toute préformation de parties capable par elle-même de déterminer l'existence d'un Plante ou d'un Animal*" (p. 68).

If we allow to Bonnet "the right to be his own interpreter," and read his remark in accord with what he has told us about the "luminous principle of preordination" (p. 56), we shall find it difficult to construe the definition as a modification in favor of the doctrine he has just pronounced impossible and absurd. Taking the statement, not for what it was intended, but for what it might mean, coming from a writer of to-day, it would not be difficult to read into it ideas suggestive of theories now in the field. But if it is our purpose to find Bonnet's meaning, not our own, we must interpret his definitions from his standpoint just as we did his "natural evolution," his "palingenesia," and other expressions counterfeiting the current phraseology of to-day.

The date, place, and connection of the remark are all such as to make it certain that Bonnet was still holding as firmly as ever to the doctrine of preformation. In fact, his very next words are:

"I have, therefore, tried to apply the luminous and fertile principle of the preordination of beings to animal reproductions of every kind." Then, after briefly recounting the application of his principles to regeneration, buds, and grafts, he again reminds us that "we should not imagine that all the parts of an organized body are precisely the same, *en petit*, in the germ as they appear, *en grand*, in the developed whole.

"I have shown, according to the new discoveries upon the chick, that in the germ all the parts, both external and internal, have forms, proportions, a consistency, and an arrangement which differ extremely from those which they will have later." This is followed by the remark that the germ is understood to cover "*every preordination, every preformation of parts capable by itself of determining the existence of a plant or an animal.*"

Setting aside the connotations supplied by Bonnet's theory, and ignoring the intent inspiring the whole work, these words might not offend orthodox epigenesists of our times. If such license is inadmissible, then it will not do to impute to Bonnet any radical change of views, and we may confidently expect to find an interpretation consistent with his continued adherence to the doctrine of original preformation or syngenesis.

Starting with a "feeble sketch" in his youth, Bonnet devoted the rest of his life to trying to show that the doctrine of germs and the "law of evolution" might be extended to the whole organic creation. He encountered many difficulties, was doubtful at first, and suspicious that his theory might prove to be a "romance," and was on the point of abandoning the whole scheme after reading Buffon's theory; but Haller's work and encouragement gave him confidence, which carried him buoyant over multiplying obstacles, and brought him to the conclusion of his Paligenesia exulting in the triumph of his imagination over facts.

The theory was essentially anthropocentric, holding all things to have been teleologically ordained, with the resurrection and the future life as chief consideration. Man's destiny was assured by putting his soul into an ethereal corpuscle, and that was the main thing. But animals develop, move, feel, and show some intelligence. Would not Infinite Benevolence include them in its provisions for man? And if them, then why not plants, since all organisms seem to form one immense *scala coeli*. If one round of the celestial ladder can be advanced, the others should follow, that no gaps break the harmonious continuity.

The thought was pleasing, and reason seemed to demand that the theory should be of universal application. It would not do to set up original creation for one organism, and allow the rest to come by epigenesis. As well leave the whole to epigenesis as the formation of the simplest organic element.

Although insisting from first to last on the universality of the principle, *no generation*, Bonnet never claimed to be able to apply his theory satisfactorily to all cases. He frankly acknowledges his inability to do this in the case of microscopic organisms; but, while confessing to ignorance of the laws of their evolution, he does not surrender them to epigenesis.

On this point, and in connection with difficulties presented in Hydra, Bonnet remarks as follows:

"I have repeated more than once that we transfer too confidently to the lowest species the ideas of animal existence which we derive from the higher ones. If we reflect more deeply on the immense diversity that prevails in the universe, we shall understand how absurd it is thus to confine nature within the narrow circle of our feeble conceptions. *I declare, therefore, that all the foregoing exposition of the various kinds of organic preformations relates chiefly to the species which are best known to us, or on which we have been able to make the most exact and continuous observations.* I confess to ignorance of the laws which determine the evolution of that multitude of microscopic beings, of which the best lenses hardly teach us more than the existence, and which belong to another world, which I would call the world of the invisible." (*Paling.*, Part X, Chap. VII, p. 279.)

THE DIFFICULTY WITH HYDRA.

Bonnet struggled hard in the attempt to apply the doctrine of germs and the theory of evolution to Hydra. The celebrated experiments of Trembley presented most formidable difficulties, and they seemed to threaten the most precious article of his creed — the immortality of the soul — for the sake of which a germ trinity had been devised.

Could the personality of such a divisible creature be caged in a triple-germ case, such as seemed to fit man and "the species which are best known to us"? Bonnet did not affirm positively that animals have souls; but he regarded it as probable. Assuming that they have a soul, it must be immaterial and indivisible. "The soul of Hydra will also be indivisible. We do not then divide this soul, when we divide the Hydra; but we thus render it possible for certain germs to develop. . . . As many new persons will be formed as new individual wholes are developed." All this is according to principles laid down in Chap. III of the *Corps Organisés* (*Tableau*, p. 70).

Bonnet gives the results of Trembley's observations on Hydra in the first part of the *Corps Organisés* (Chap. XI), but postpones his "*essai d'explication*" until the second chapter of the second part, in order to bring analogous facts, found among plants and worms, to bear on the difficulty.

"My readers," says Bonnet, "who will take the trouble to follow my steps and to reflect upon my ideas, will conclude with me that the facts concur in establishing the great principle of the preëxistence of germs. *They will not consider themselves obliged to abandon it in view of the wonders that the history of polyps reveals to us; but they will prefer to seek with me the reconciliation of those strange facts with the law of evolution.* I shall not force these facts to come and range themselves under this law; I shall confine myself to comparing them to analogous facts that are evidently subject to it, and where I do not see a satisfactory solution I shall say so; I shall try never to confound the doubtful with the probable, and the confession of my ignorance will not cost me a great effort. We are still only at the beginning of things; why should a philosopher blush not to be able to explain everything? There are a thousand instances where an '*I know nothing about it*' is worth more than a presumptuous attempt. . . .

"The polyp is then an organic whole, of which each part, each molecule, each atom, tends continually to produce. It is, so to say, all ovary, all germs. In cutting a polyp into pieces, the nourishing fluid that would have been employed in the growth of the whole, or put to other uses, is turned to the profit of the germs concealed in each portion." (*Corps Organ.*, p. 252–3.)

To this is appended an important footnote, which shows that the chief modification in the definition of a germ had reference to Hydra solely:

"I beg the reader to make use here of the remark on which I have strongly insisted in Chap. I of Part IX of the *Contemplation de la Nature;* to wit, that it is not necessary to limit the meaning of the word germ to denote *an organic corpuscle which actually incloses, on a very small scale, all the parts that characterize the species; but this signification must be extended to every organic preformation from which an animal may result as from its immediate principle.* It should suffice to the end proposed in this work that the laws of multiplication are always constant, although very different in the different orders of animals."

Concluding, he says:

"If we do not wish to have recourse to purely mechanical explanations, which experience does not justify and which good philosophy condemns, we must think that *the polyp is, so to speak, formed by the repetition of an infinity of small polyps,* which only await favorable conditions to come forth."

This is supplemented by the following footnote:

"I should not wish this statement, *that the polyp is formed by the repetition of an infinity of small polyps,* pressed too far. . . . *When we are dealing with the polyp, the word germ must be taken in its widest sense; that is, for every organic preordination of the skin of the polyp-mother from which a little polyp* *may result as from its immediate principle.* The young of polyps do not originate precisely like the shoots of a tree; they are not enclosed at first, like those, in a bud, which gradually increases in size and then opens, disclosing all the parts of the new production folded over one another. Nothing like this is observed at the first appearance of the shoot of a polyp. It seems to be only a protuberance, or simple continuation of the skin of its mother. *But it is quite indifferent to the philosophy which we seek to establish in this work, whether the young polyp springs from a germ properly so called, or whether it originates from a secret preorganization of certain parts of the polyp-mother.*" (*Corps Organ.*, p. 271.)

These footnotes are among the very latest writings of Bonnet, and they are especially important as showing precisely what organism he had in mind in his modified definition of the germ, and how closely his first conclusions with reference to Hydra agree with his latest.

Bonnet was compelled, as we have seen, to make an exception of microscopic organisms, conceding that they might not arise from proper germs or eggs; and he finally allowed that Hydra might also be so far an exception among animals as to arise from *a secret preorganization*, "an organic preordination" or "preformation," doubtfully entitled to be called a "proper germ."

It was not necessary to suppose — so Bonnet seems to have reasoned — that the Hydra-bud was a germ containing the animal as perfectly framed as the plant in the seed or the chick in the egg; but it was necessary to assume that it was an *original creation*, so fashioned that it would evolve, *without any new formation*, into the perfect animal. Just where the soul-bearing element was located, did not matter. It was sufficient to have shown that "the phenomena of its reproduction did not militate the least in the world against the doctrine of the *immateriality* of the soul." (*Tableau*, p. 71.)

But has not the definition of the germ, as modified for Hydra, brought us to the very verge of epigenesis, and does it not disclose a fatal inconsistency that sinks the whole speculative fabric below the dignity of a "romance"?

If the Hydra-bud need not necessarily contain "*all* the parts that characterize the species," what does it contain? What is this "secret preorganization" if not a subterfuge to cover defeat and retreat? Where are we to find the promised "reconciliation of those wonders revealed in the history of the polyps with the law of evolution"?

But Bonnet goes on unaware of any inconsistency or concession that admits epigenesis. Was he blind to the consequences involved in his definition of the germ? Or was the definition perfectly consistent with preformation, excluding still, as completely as ever, every possibility of a really new formation? For a final and decisive answer to these questions, we must turn to Part X of the *Palingénésie*; for this is the source of the evidence adduced to show that Bonnet modified the hypothesis of evolution, by defining the germ in such a way that its development would not be distinguishable from epigenesis.

Varieties of Germs.

According to Bonnet's earlier notions, all germs were supposed to be germs of whole organisms; no germs of parts were admitted.[1] Regeneration of lost parts was referred, not to partial germs, but to partial development of complete germs, which were supposed to be scattered[2] throughout the organ-

[1] "Je ne pense pas qu'on veuille admettre des germes particuliers pour chaque organe, et multiplier ainsi les êtres inutilement." (*Corps Organisés*, Chap. IV, p. 24.)

[2] "The hypothesis of germs dispersed through all parts of nature furnishes a spectacle not less interesting, though of an entirely different kind. Every organized body presents itself to me under the image of a little earth, where I perceive in miniature all the sorts of plants and animals that appear on the surface of our globe. An oak seems to me composed of plants, of insects, of shell-fishes, of reptiles, of fishes, of birds, of quadrupeds, and even of men. I behold ascending in the roots of this oak, together with the juices designed for its nourishment, innumerable legions of germs. I see them circulate in the different vessels and then lodge in the thickening of their membranes, to extend them in every way. I observe them ranging themselves side by side or intertwining with one another, forming thus tiny edifices, which recall to my mind those strange monuments that American superstition once reared in honor of its gods, and which were constructed solely of the heads of animals sacrificed for that purpose. The winds, the rains, the heat, the cold, etc., beating in turn on the oak, finally triumph over its force and its vigor. I see the structure crumble, and become a heap of dust. Then the

ism, and to be capable of developing as wholes, or only to the extent of replacing parts lost by the containing whole.

Further reflection seemed to make it necessary to admit germs of organs, or "dissimilarity of germs in the same individual." The consolation was that preformation was not endangered,[1] and the consequence was a multiplication of germs

little organized beings which entered into its composition, superior to all these assaults, are set at liberty and disperse in all directions. Continuing to follow them, I see them soon enter into other organic compounds, and become successively fly, snail, serpent, carp, nightingale, horse, etc. What shall I say then? The air, the water, the earth, appear to me to be only a mass of germs, only a vast organic whole.

"Struck with astonishment at the sight of this perpetual circulation of germs, and these immense riches which have been stored in reserve in all bodies, I contemplate with delight this wonderful economy. I behold the ages pile themselves one on the other, the generations accumulate like the waves of the sea, without the number of germs used to produce them sensibly diminishing the organic mass that they compose.

"The last point of view under which I have just presented the system of germs would seem to approximate much to the system of organic molecules if I had not defined what I understand by germs, and if I had not indicated the manner in which they may be conceived as entering into bodies." (*l. c.* p. 76.)

[1] "Whether regeneration depends on germs that contain precisely what is to be repaired, or whether it depends on germs that contain an entire animal, and of which only a part develops exactly similar to that which has been removed, *it amounts to the same thing; it is never a generation, properly so called; it is the simple evolution of what was already engendered.* So many positive facts that I have collected in this work concur so plainly in establishing this great principle that he must have the strongest predilection for new ideas who could undertake to combat it." (*l. c.* p. 243.)

"Now that I have reflected more on the matter, I see no objection to supposing, in these sorts of worms, germs of anterior and germs of posterior parts. This hypothesis appears to me at least open to fewer difficulties than that of the obliteration of a part of the germ. If we concede particular germs for the production of the teeth, why should we refuse to concede them for the production of parts that are much more composite, and the formation of which is still more irreconcilable with mechanical explanations?

"An observation taken from vegetables seems to confirm this diversity of germs in the same individual. The seed, which effects the natural multiplication of the vegetable, incloses an entire plant . . . . A bud, on the contrary, incloses only the plumule . . . . The roots arise as little eminences which seem to perform the office of buds. Such a bud contains only the radicles. There are therefore, in the vegetable, germs of plumules and germs of radicles, as there are those that contain at once both plumule and radicle.

"In the worms that multiply by budding, germs that contain only anterior or posterior parts may be compared to vegetable germs that contain only plumules or radicles. Germs destined to effect the natural multiplication of the worm may likewise be compared to germs contained in seeds." (*l. c.* p. 241–2.)

to any number of possible reproductions. "I admit then," says Bonnet, "as many primitive, descending orders of elements as there are possible reproductions: for, as I have often repeated, *I know of no mechanics capable of actually forming the least fiber.*" (*Paling.*, p. 271.)

This concession might, at first sight, appear to lead in the direction of epigenesis; but, in reality, it is the same old negation multiplied to the utmost limit of organic elements. These elements are no more numerous and no less preformed, when conceived as individual germs, constituting a divisible whole, than when conceived as *continuous parts* of an indivisible whole. From Bonnet's standpoint, the innovation signified nothing but subdivision, the total amount of preformation remaining practically the same as before. The germs reserved for regeneration were simply cut to just the dimensions of the losses which they were preordained to replace. The simplification in this direction Bonnet modestly credited, not to his own ingenuity, but to Infinite Prescience.

Germs of Parts and of Wholes.

This extension of the doctrine of germs brought some confusing distinctions in classification. It became necessary to distinguish between germs of "little wholes" (parts) and germs of "great wholes" (organisms); and among the former, the simpler terms were held to be hardly worthy of the name of germ. These could be called "constituent parts," or "elements," or, if preferred, "germs," although they were "not *proper* germs."

Here we come upon a distinction that serves to clear up the obscurity respecting germs defined as "preordinations" and "secret preorganizations," which were spoken of as not complete enough to be called "proper germs."

But if a germ lacks anything of completeness, can it be completed by pure evolution without any epigenesis? That depends upon what we mean by "incomplete." If all the parts are actually present, and in an order so preordained that they will fall into the adult adjustment as they expand, then there is no new formation. The evolution is free from the slightest taint of epigenesis. Changes in *form*, *arrangement*, and *con-*

sistency were never denied, not even in the development of the germs of the higher animals. If, on the other hand, all parts are not present, if some are yet to be added as new formations, by the operation of natural laws, then the completion of the germ will mean epigenesis.

Evolution Unchanged.

Which view did Bonnet take? Chap. IV, Part X, of the *Palingénésie* supplies an answer, which removes any doubt as to Bonnet's continued adherence to the doctrine of preformation, and at the same time clears him from the imputation of having surrendered unwittingly to epigenesis.

The chapter in full:

(1) "It is by the aid of such principles that I attempt to account for the regeneration of a *similar* organic whole. But when it is a question of explaining the reproduction of a *dissimilar* organic whole, it seems to me that I am under philosophic obligation to assume that this whole preëxisted in a germ *properly so called*, in which it was completely designed on a very small scale. I assume, then, that a tail, a leg, preëxisted originally under the form of a germ, in the great organic whole in which they were appointed to develop. I consider this whole as a piece of ground, and these germs as seeds sown in this ground, and kept against the future needs of the organized being.

(2) "Thus I should be led to think that there are at least four principal kinds of organic preformation. The first kind is that which determines the regeneration of *similar* composites, for example, a bark, a skin, a muscle, etc. I say that, strictly speaking, *these sorts of composites do not preëxist in a germ which exactly represents them in a reduced size, but they are formed by the development and interlacement of a multitude of slender gelatinous filaments that belong to the old whole which nourishes and makes them expand in every direction. These filaments are not properly germs of bark, germs of skin, etc., but they are small constituent parts or elements of a bark, a skin, etc., which does not yet exist, and which will owe its existence to the complete evolution and to the close union of all the filaments.*

If, nevertheless, we preferred to regard as a germ each of these filaments taken by itself, this would be a germ improperly so called; for it would *contain only similar particles, and would represent, so to speak, only itself. It would be to the new bark or the new skin, in some sense, what unity is to number.* This is what I meant to express above when I designated the principles of these filaments by the term organic points. *There are, perhaps, in certain animals of the lowest classes, for example in polyps, organs of so simple a structure that nature succeeds in forming them in such a way. It cannot be said, exactly speaking, that these organs preëxisted all formed in the animal; but it must be said that the organic elements from which they were to result existed originally in the animal, and that their evolution is the natural effect of the derivation of the juices, etc.*

(3) "According to these principles, each similar part, each fiber, each fibril, carries in itself the sources of reparation relative to the various losses that may happen to it. What an idea this manner of regarding an organic whole gives us of the excellence of the work and the intelligence of the Worker!

(4) "Moreover, as we have seen above, each fiber, each fibril, must necessarily be organized with so marvelous an art as to assimilate the nourishing juices in a direct relation to its particular structure and its peculiar functions; *otherwise the fiber or the fibril would change structure in developing, and would no longer be able to discharge the functions to which it is destined. Its primitive organization is therefore such that it separates, prepares, and arranges the nutritive molecules in such a manner that ordinarily no essential change occurs in its mechanism or in its working.*"

When in paragraph 2d Bonnet says of the bark or skin, that "it does not yet exist," he evidently means that it does exist in the state of organic elements, though not yet in the state known as "bark" or "skin." This state is reached, not by epigenesis, but by "*complete evolution* and the close union of all the filaments."

So in the case of Hydra, the organs may be of such a simple nature that they do not need to preëxist "all formed"; that is, with all their elements *arranged precisely* as they will be in their expanded state. The "elements" themselves, however, were *all* supposed to preëxist, and their development to be "evolution" in the same old sense.

It becomes clear, then, what Bonnet meant when he said:

"I will not affirm that the buds which produce polyps are themselves polyps *in miniature* concealed under the skin of the parent; but I will affirm that there are in the skin of the parent certain particles which have been pre-organized in such a way that a young polyp results from their development." (*Tableau*, p. 68.)

And, again, when he says of the germ:

"This word will therefore denote not only an organized body reduced in size, but also every species of original preformation from which an organic whole can result as from its immediate principle." (*Paling.*, p. 267.)

Paragraph 4th shows how faithfully Bonnet guarded the principle of preformation, insisting that the "fiber" and the "fibril" must be organized to such perfection as to exclude "*change of structure*" or "*function*." And how are these various kinds of germs, proper and improper, supposed to develop? Clearly, and beyond all question, by the same old process of evolution: that is, by expanding without "*essential change*."

No amount of subdivision of germs could endanger this theory of preformation. So long as the "elements" could not be multiplied, or changed in their essential nature, Bonnet could say, as he did say, "*It amounts to the same thing: it is never a generation, properly speaking; it is the simple evolution of what was already engendered.*"

We leave Bonnet, then, at the end where we found him at the beginning, with "no essential change" in his position; but with his "romance" more fully evoluted; his faith in the principle "*nulla est epigenesis*" confirmed; his loyalty to the theory of evolution tested and attested; and his hope for an eternity of *palingenesia* raised to a pitch that seemed to yield him the beatitude of actual possession. There was triumphal exultation as well as fervid piety in the exhortation with which Bonnet concluded his philosophical writings:

"*Saisissez la vie éternelle.*"

Having covered the whole ground of revealed religion with "natural religion"; having shown that one instantaneous creation would suffice to complete the universe; that science, philosophy, and religion agree in excluding any new formation in the organic world; that development simply unfolds what was originally infolded, without change of structure or function; that death has no sting, the grave no victory; that the distance between the created and the Uncreated, the finite and the Infinite, is infinite, so that there can be a "*Flux perpétuel*" towards Supreme Perfection without ever reaching it;—in a word, having shown how "reason" can triumph over the senses, Bonnet becomes enrapt over the "ravishing system," sees time ended, eternity begun, the kingdom of Heaven disclosed, and the crown of unfading glory already upon his head. The vision closes, and the "end" is a vignette symbolizing the "grand metamorphosis."

We have seen that the old and the new evolution are based upon antithetical conceptions, which exclude each other at every point. Both deal with the same subject-matter, but from standpoints so radically incongruous as to shut out every possibility of convergence in principles. There is parallelism, but only of opposite extremes; analogy, but no homology of ideas; parity of hypothesis, but no fundamental coincidence.

Bonnet's theory was a negation wrapped in negations to a depth that was absolutely hermetic to positive reality. It is conceivable that this negation might be stripped of every investing envelope, but no "metamorphosis" of coats could ever modify its fundamental character. In the very nature of the case, it precluded any real advance towards the modern standpoint. If the old evolution did not, and could not, advance to the new, the progress of the new will never lessen the distance from the old.

The old evolution was the greatest error that ever obstructed the progress of our knowledge of development. If our examination has helped to clear the mist that obscured important distinctions, we have not labored wholly in vain.

THIRTEENTH LECTURE.

ORIGIN OF THE CENTROSOME.

S. WATASÉ.

If we judge the significance of any biological discovery by the amount of new literature which it has called into existence, the discovery of the centrosome must be considered as one of the most important events in the history of the cell-theory.

A glance at the cytological literature of the present day will show to what a large extent the attention of biologists is being devoted to the elucidation of this structure. Indeed, as has been truly observed, if there is one feature by which the cytological literature of the present may be distinguished from that of some years past, it lies chiefly in the fuller recognition given to this structure. Robert Brown's discovery of the nucleus in the plant cell paved the way to the formulation of the cell-doctrine by Schleiden and Schwann, who made the nucleus ("cytoblast") the soul of their famous theory. The discovery of *corpuscules centraux* by E. van Beneden in the animal cell, or *centrosomes*, as they have been subsequently called by Boveri, has led to an activity unparalleled in the recent history of the cell doctrine. Professor Flemming's remark that the discovery of the centrosome marks as important an epoch in the history of biological science as did the discovery of the nucleus, seems certainly justified.

The questions naturally arise, — What is the centrosome? Is it a unique organ of the cell equal in importance to the nucleus or the cytoplasm, as claimed by the discoverer? Does it occur in every cell? What is the exact part which the centrosome takes in the division of the nucleus? What part does it play in the process of fecundation? What bearing has this new organ of the cell upon the phenomena of heredity?

Such are some of the questions that are being asked on every side. But it is evident that there are certain problems which must take precedence of others. Such, for example, is the question relating to the mode of its development in the cell. And it is along this line that the inquiries have of late been most active. It is to this subject that I propose to invite your attention.

So far as I have been able to gather, no less than seven different hypotheses have been proposed in regard to the nature and origin of this structure. This is neither the place nor the occasion, however, to enter into any critical examination of technical details. Suffice it to say, that these divers hypotheses may be reduced to two fundamental forms, which are mutually exclusive of each other.

According to the one view (1), the centrosome is a permanent or ultimate organ of the cell, an organ *sui generis*, and coexistent with other ultimate organs of the cell, as the nucleus and the cytoplasm.

According to the other view (2), the centrosome is a derivative structure, arising by the modification of some preëxisting element in the cell, as the chromosome, "nucleolus," or the cytoplasm.

I repeat, that these two views are mutually exclusive; because, if the centrosome is considered to be a permanent organ of the cell, that is to say, if it always originates from a preexisting centrosome, obviously it cannot be considered as a derivative from another structure. If, on the other hand, it can be maintained that it is a derived structure, it can neither be called a permanent nor an ultimate organ of the cell.

Thus, from the nature of the case, no middle ground is possible. It is rare that an investigator is confronted with alternatives so sharply contrasted; nor does he often meet with an issue that can be brought to so sharp a focus. For, if it could be shown by the examination of cell-structure that there exists any element which has a close affinity to, or identity with, the centrosome, its claim as a unique organ must fall to the ground. Only utter failure to identify the centrosome with any other element in the cell could justify the adoption of the theory that it is a unique organ.

Investigators who have studied this subject have generally selected cells in which the centrosome appeared in a most conspicuous form; and naturally, as the main object at first was to demonstrate its existence. It is interesting to notice that the permanent-organ theory of the centrosome had its first origin among those who studied the structure in its most conspicuously developed form, as in the egg of *Ascaris*.

But the possibility of discovering the affinity of the centrosome to any other cell-constituent is rendered all the more difficult, as long as our attention is directed only to those cells in which this organ has reached its highest development. From the standpoint of the derivation theory, however, such extreme cases are just the ones to be avoided, for the theory presupposes an element in the cell which may be directly compared

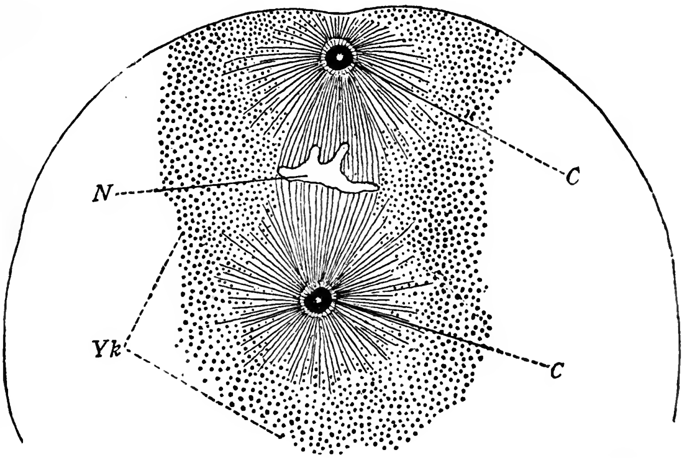

Fig. 1. — *The egg of Unio complanata.* *C*, centrosome: *N*, nucleus, chromosomes not represented: *Yk*, yolk-granules. The centrosome is spherical in shape.

with it; and it stands to reason that, if such an element really exists, it cannot be a very conspicuous structure, or otherwise the theory of the centrosome as a unique organ would never have been proposed.

These considerations, then, suggest inquiries along two lines:

(1) Inquiries into different forms of the centrosome and its structural correlations with functions of cells in which it occurs.

(2) To see if, among the hitherto recognized elements in the cell, there is any structure which shows affinity to or identity with the centrosome.

Whatever conclusion may be reached as to the value of two rival forms of theories, it seems pretty certain that the existence of the centrosome and its aster is closely correlated with the phenomena of definite movements of the protoplasm.

Thus, in the caryokinetic process of the cell, which is pre-eminently a phenomenon of protoplasmic motion, the centrosome or its equivalent is invariably present (Fig. 1). In the leucocyte, which has a highly developed power of protoplasmic motion, the aster and its centrosome are well developed (Fig. 2). In the pigment cell, in which motor phenomena are well known, the centrosome and its aster find their most remarkable development (Fig. 3). In some pigment cells with circular outlines, the aster with its centrosome assumes an ordinary stellate form. In elongated pigment cells, the centrosome, instead of assuming a spherical shape, is elongated or rod-like, with a fringe of cytoplasmic filaments proceeding from it (Fig. 4, *b*). In still another form of the pigment cell, the centrosome assumes neither the spherical nor the rod-like shape, but exhibits an extensive network conforming to the general shape of the cell (Fig. 5, *C*).

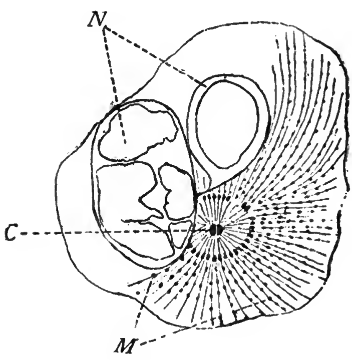

Fig. 2.—The *leucocyte* of Salamander, showing the radial system of cytoplasmic filaments (aster), and the distribution of the microsome (*M*). *C*, centrosome; *N*, nucleus. —(After Martin Heidenhain.)

On the other hand, in fixed cells with no power of definite movement, such as gland cells or cartilage cells, we have no evidence of the existence, either of the centrosome or of the aster, in any part of the cell. If such cells are artificially injured in some way, however, they may begin to multiply by the process of caryokinetic division, when the centrosome makes its appear-

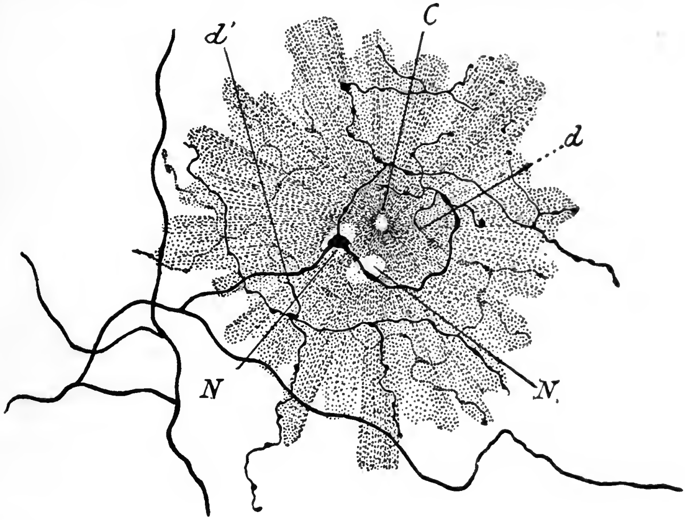

Fig. 3. — *The pigment cell of Esox lucius,* showing the clear centrosome area C: NN, nuclei. By the application of Golgi's method, as modified by Cajal, the nerve endings are well brought out. The cell is innervated on both sides of its surface. At d, d', the nerve filaments on one side are seen boring through the whole thickness of the cell and innervating the other side. — (After E. Ballowitz.)

ance, and takes an active part in the separation of the chromatic elements. The division over, the cell assumes a quiescent state once more, and we no longer recognize a centrosome or a radial arrangement of the cytoplasmic threads.

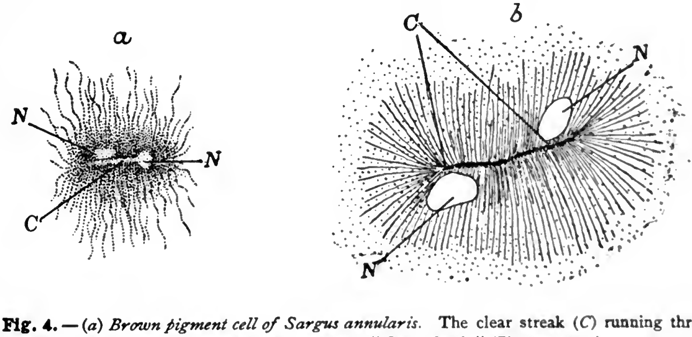

Fig. 4. — (*a*) *Brown pigment cell of Sargus annularis.* The clear streak (C) running through the length of the cell is the elongated centrosome or " Centralstab " (Zimmermann).

(*b*) *Yellow pigment cell of Sargus annularis.* C, the rod-like centrosome, with parallel fibrils proceeding from it. N, the nucleus. — (After K. W. Zimmermann.)

In this connection, it is interesting to notice a structure closely similar to the aster, as described by Grenacher, Greeff, Schulze, and Sasaki in different forms of unicellular organisms (Fig. 6). The peripheral pseudopodia are connected with the cytoplasmic filaments, which converge and meet at the center of the organism, thus forming a huge aster whose fibrils extend through the whole organism. If we suppose, however, that the individual fibrils of the aster in a leucocyte (Fig. 2), or in

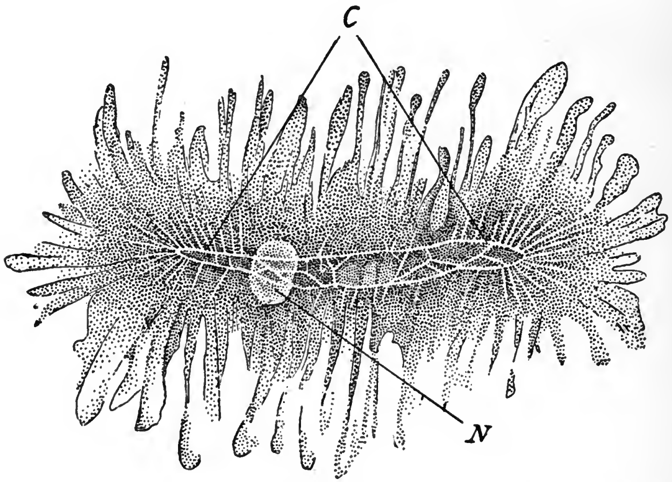

Fig. 5. — *Brown pigment cell from the pectoral fin of Blennis trigoides* (larva), showing the reticular centrosome (*C*), — the "Centralnetz." — (After Zimmermann.)

a pigment cell, extend beyond the general outline of the cell-boundary, we shall get the appearance presented by the unicellular organism with a large aster whose rays extend through and beyond the mass of the entire organism, as represented in Fig. 6.

The absence of the centrosome and the aster in a stationary cell, or in cells which show no trace of "nuclear motion" or caryokinesis, and their invariable presence in cells which show some kind of definite movement, make it tolerably certain, then, that they are intimately correlated with the movement of the protoplasm.

This general observation naturally leads us to consider the mechanism of motion in the muscle cell, in order to see if it can in any way be brought into harmony with the structure and function of the aster.

A striated muscle cell reduced to its simplest form may be

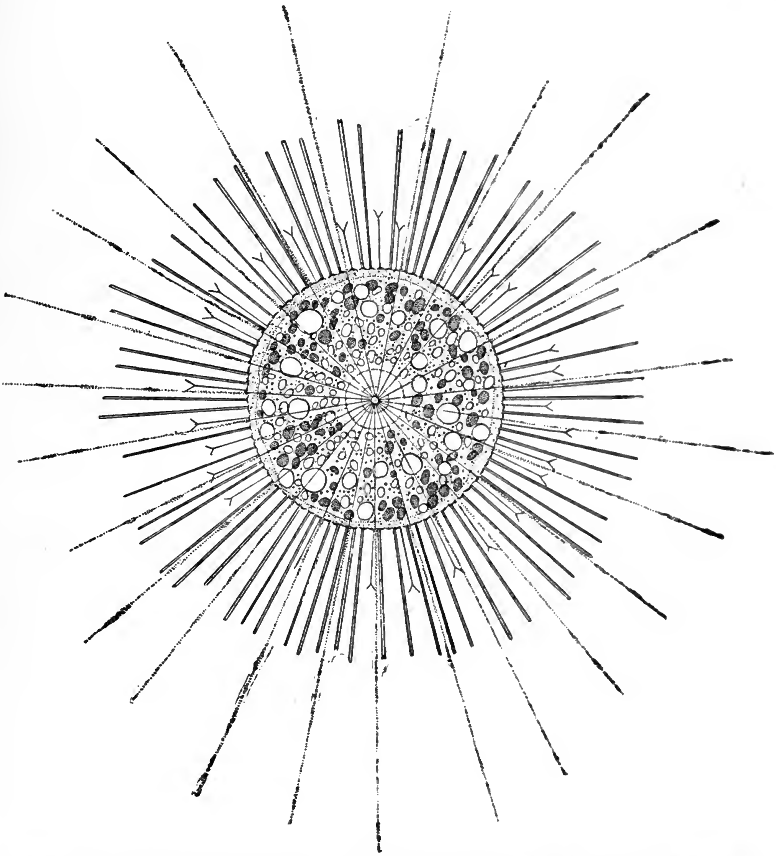

Fig. 6. — *Acanthocystis turfacea*, with an aster-like structure in the center of the body, with its rays forming the axial filaments of the pseudopodia. — (After Richard Greeff.)

diagrammatically represented as in Fig. 7. A part of the cell is occupied by undifferentiated granular protoplasm — the *sarcoplasm* (*s*) — and the rest of the cytoplasm is converted into a series of contractile filaments arranged in parallel rows, thus forming the *myoplasm* of the muscle cell (*m*). Each filament has varicosities which receive different names according to their position. These varicosities are deeply stainable, and have different optical properties from the connecting filamentous portion. When contraction sets in, the varicosities on both sides of the intermediate zone (*Z*, Fig. 7) increase in bulk

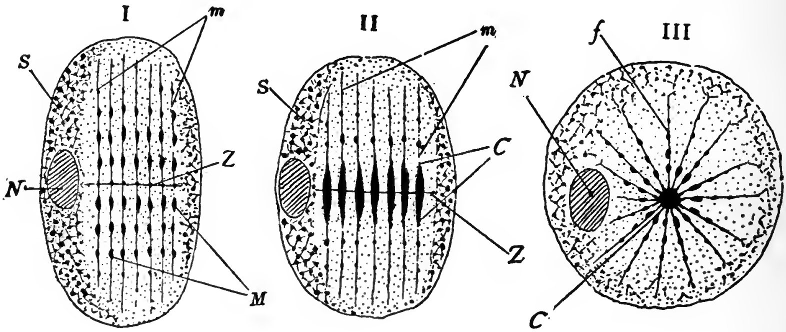

Fig. 7.—(I) *A schematic representation of the muscle cell.* *N*, nucleus; *s*, sarcoplasm; *m*, myoplasm; *M*, microsome of the filament; *Z*, Zwischenscheibe, or Krause's membrane.

(II) The same in a state of contraction. *C*, the contraction band.

(III) Diagram showing the possible mode of formation of the centrosome by the convergence of the fibrils (*f*) into one common focus. *N*, nucleus; *C*, centrosome.

at the expense of intervening filamentous substance, and at the maximum state of contraction a thick, new zone is formed as the result of such a process, giving rise to what is known as the contraction band (*C*, Fig. 7, II). This contraction band has the same chemical and physical property as the ordinary thickenings or varicosities of the fibrils, only much more massive and conspicuous, being formed by the fusion of several varicosities on both sides of the intermediate zone (*Z*).

When the relaxation of the muscle sets in, this contraction band resolves itself into a series of smaller varicosities distributed along the fibrils (Fig. 7, I).

The contraction of the muscle cell means, therefore, the formation of more stainable substance at the expense of less stainable protoplasmic filaments; and the expansion of the muscle means just the reverse of this process, viz., the conversion of the deeply stainable varicosities into the less stainable filamentous substance.

Now, coming back to our original subject, the aster, we notice that, so far as we can judge by the use of staining reagents, the varicosities in the muscle fibrils and those in the aster filaments are identical. Only in the muscle the size and arrangement of the thickenings are somewhat more regular than those in the aster filament.

As has been already stated, the contractile filaments in the muscle cell are arranged with perfect regularity, and are *parallel with one another*, passing through a common plane, — "the Krause's membrane," or "*Z*." Suppose these fibrils, instead of running parallel with one another, *converge* into one common center (*C*, Fig. 7, III). The central ends of the fibrils, instead of forming an elongated contraction band in the middle plane of the cell, will then form a contraction sphere in the center of it. In other words, the contraction sphere in the center of the radial fibrils will be the centrosome; and the varicosities along the fibrils will correspond to the varicosities of the muscle fibrils, and the whole system will constitute the aster. In the muscle cell, the fibrils being arranged side by side, their contraction and expansion result in the shortening and lengthening of the whole cell along the longitudinal axis. In the aster-bearing cell the contraction and expansion of the fibrils will result in the movement of the cell-mass along the radii of the aster. The principle involved in both cases is identical; the difference in results is due to the dissimilar arrangement of the cytoplasmic filaments.

Such thickenings (*M*, Fig. 7) in the cytoplasmic fibrils are called *cytomicrosomes;* when such cytomicrosomes attain a more or less conspicuous dimension, or several of them fuse into a common mass in the center of the aster, they give rise to the *centrosome;* when several microsomes belonging to the parallel fibrils are arranged along the common plane, as in a muscle cell, in the state of contraction, they give rise to what is known as the *contraction band* (*C*). The case of a pigment cell, in which the centrosome appears as a linear rod (Fig. 4, *b*), suggests a close parallel to this contraction band.

But the centrosome once formed in the center of the aster, unlike the contraction band of the muscle cell, is apt to persist for a long time; further, it seems to undergo some chemical changes in certain cases, as is shown by the staining reagent, which is slightly different from that of the ordinary microsome of the cytoplasm. Moreover, the centrosome may sever its connection with the radial rays, as indicated by the formation of a clear space around it, and finally, the centrosome may become wholly bereft of its rays, and stands alone naked in the general mass of the cytoplasm. But these are secondary phenomena which come into play after the centrosome has once been definitely formed. Too much emphasis laid on these secondary features, which are induced after the centrosome has once been formed, is liable to lead one to lose sight of the primary process which is directly concerned in its formation.

As I have maintained elsewhere, a satisfactory solution of the problem of the centrosome depends on the explanation of the relation existing between the cytomicrosomes and their connecting cytoplasmic filaments. If the preceding interpretation of the origin of the centrosome is true, it seems that the substance of the cytoplasmic filament and that of its microsome stand in genetic relationship, exactly in the same way as that which takes place in the contraction and expansion of the muscle fibrils. In short, the history of the filament and its microsome runs in a cycle. The microsome may be converted into the filament under one condition, and the filament in turn, under another condition, may give rise to a microsome at the expense of its material. They may, therefore, be considered as two alternating phases of one and the same cytoplasmic substance.

If this view be a true one, the centrosome is simply a modified portion of the cytoplasm, and not a permanent organ. According to this view, the centrosome is no more a permanent organ of the cell than is the contraction band in the striated muscle cell. Only the centrosome once formed in the focal point of the several fibrils, as has been already stated, is apt to be more persistent than the contraction band.

And further, just as the contraction band can go back to the state of original filamentous substance during the expansion of the muscle cell, so the centrosome can give rise to the cytoplasmic filament, as may be seen in the caryokinetic process in certain cells, where the clear, smooth, cytoplasmic filaments are seen coming out from the centrosome. This is particularly well seen in those cases where the centrosome rests directly on the surface of the nuclear membrane (Fig. 8). The new fibrils which proceed from the centrosome press on the nuclear membrane or break through it, and eventually form the spindle of the caryokinetic figure.

The same interpretation may be applied to those cases where the centrosome divides at some distance from the nucleus (Fig. 9). Each daughter centrosome spins out the cytoplasmic filaments, forming a small spindle between them. Thus the formation of the centrosome by the ends of the aster fibrils,

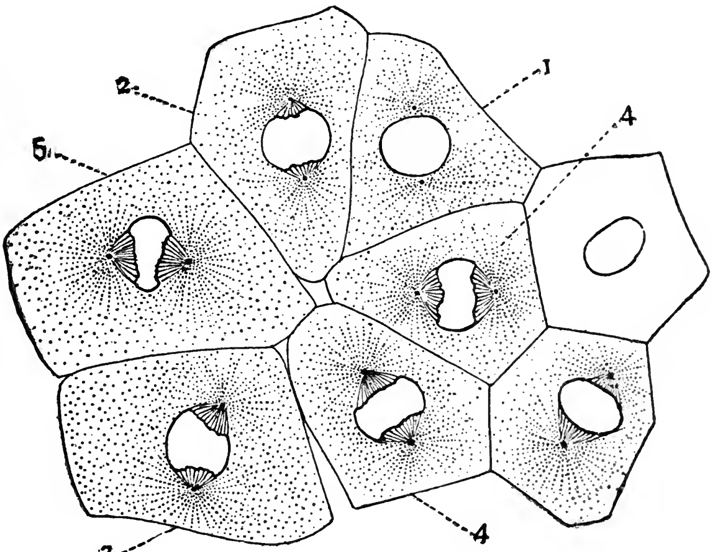

Fig. 8. — *Blastomeres from the central portion of the blastodisc of Loligo.* The segments 1, 2, 3, 4, 5, etc., show different stages in the formation of the spindle fibrils from the centrosome.

and the production of the group of filaments from the centrosome, are phenomena parallel with those seen in the thread and varicosities in the striated muscle cell during the alternating phases of contraction and expansion.

Viewed in this way, the function of the aster and centrosome falls under two heads:—

(1) By the radial arrangement of the cytoplasmic filaments, and the consequent condensation of the cytoplasmic substance in a definite place, the cell is able to produce the filaments in

any desired part, as is seen in the formation of the caryokinetic spindle, for the separation of the chromosomes. The aster, from this point of view, may be considered as a physiological device for concentrating the cytoplasmic substance in a form which can be spun out again into filaments in the direction which will produce a definite physiological effect.

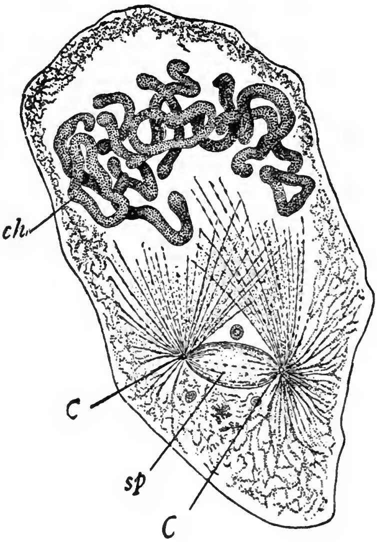

Fig. 9. — *The spermatocyte of Salamander*, showing the formation of a small spindle (*sp*) between the two centrosomes, *CC*; *ch*, chromosome. — (After Hermann.)

(2) The second function of the aster and the centrosome is quite different. I refer to the function of the aster in the pigment cell and its like. The centrosome in such cases becomes the incidental product, due to the fusion of the proximal ends of the aster fibrils. It is the fibril itself, however, that is chiefly utilized in such cells. By the lengthening and shortening of the fibril the shape and apparent size of the cell are changed, which is the essential characteristic of a pigment cell.

Thus, it appears probable that the two parts of the radial system of the cell, by which I mean the compound structure composed of the centrosome and its peripheral rays, have different functions in different cells. In cells dividing caryokinetically the centrosome is chiefly utilized, and in pigment-cells and their like, the peripheral rays. In all cases the centrosome and ray-like fibrils are the modification of the cytoplasm, but the uses to which the two respective parts are put are quite different. The view that the centrosomal portion of the radial system is chiefly utilized in the caryokinetic division of the nucleus is further rendered probable by the existence of free centrosomes at the poles of the spindle, without any visible rays around them.

The question will be asked that, if the centrosome be a purely cytoplasmic structure, is there any instance in which this mode of origin can be directly observed?

It is not difficult to observe, in sections of certain cells, that whenever three or more cytoplasmic fibrils meet at a common point, we find a microsome at the point of their junction. From this miniature aster to the normal aster with a more or less conspicuous centrosome, the transition is a gradual one. I have seen in the egg of *Macrobdella* a series of thirteen asters ranging from the miniature aster, with the microsome in its center, to the normal aster with a veritable centrosome.

Reinke's recent observation shows a similar series. He divides the aster into three kinds. The aster of the normal caryokinetic figure he calls the *primary mechanic center* of the cell (Fig. 10, 1); the next smaller aster he calls the *secondary mechanic center* (2); while to the smallest radial structure of the cytoplasm, with a small microsome in its center, he gives the name of *tertiary mechanic center* (3).

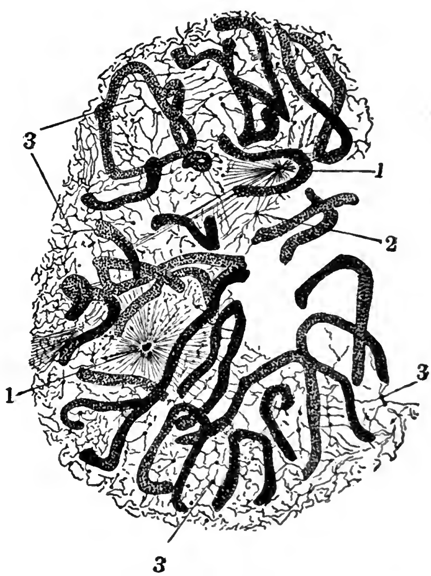

Fig. 10. — *The connective tissue cell of Salamander larva.* (*1*) the centrosome, or the primary mechanic center; (*2*), the secondary mechanic center; (*3*), the tertiary mechanic center. — (After Reinke.)

In view of such examples, of which many more might be given, it is difficult to maintain that the centrosome, with its sphere, is the unique organ. The difference between the primary and tertiary asters, as of the centrosome and the microsome, is simply the difference of magnitude, and therefore a difference in degree of development, and not in the kind of material of which they are composed.

There is one important fact which, at first sight, appears to militate against the view that the centrosome is cytoplasmic in its origin. I refer to the observation that the centrosome originates inside the nucleus in some cells. Of course, as I have stated elsewhere, when the centrosome originates inside the nuclear membrane, it may be said to be derived from the "nucleus"; when it originates outside of the nuclear membrane, it may be said to be "cytoplasmic" in origin. Such a distinction is a purely nominal one, however, from my standpoint, and I believe the general statement that all centrosomes are cytoplasmic in their origin is fundamentally a correct one. Confusion only arises when we do not keep in mind the fact that the cytoplasmic net-work, in the substance of which the microsome and centrosome arise, exists on both sides of the nuclear membrane, and the structure known as "nucleus" contains, besides the chromosomes, a certain quantity of the cytoplasmic substance in it. Such intranuclear cytoplasm passes under the name of *linin.* The mere fact, therefore, that the centrosome originates inside the nucleus does not show that it is derived from the chromosome, which, though essential, is but one of the nuclear constituents.

As to the often repeated statement that the centrosome is derived from the "nucleolus," it will become more valuable when the nature and origin of such "nucleolus" are more clearly given.

It can no longer be doubted that in certain cases the centrosome first assumes its visible form inside the nucleus, from which it emerges into the cell-body through the nuclear membrane. It will not be going too far when I suggest that such a centrosome is probably formed by the intranuclear cytoplasm in the same manner as the centrosome outside the nuclear membrane. Is not some "nucleolus," which is said to give rise to the centrosome in certain cases, the centrosome itself, formed by the intranuclear cytoplasm also?

But, whatever view one may take in regard to the nature of the centrosome, one thing is clear, viz., that the centrosomes offer a great deal of structural difference in different cells. In one cell it may assume a spherical shape composed of deeply staining material; in another cell this sphere is represented by a greater or less number of discrete granules which bear the closest resemblance to the ordinary microsome of the cytoplasm; in still another, it assumes the shape of a linear rod, reminding one of the contraction band of the striated muscle cell. In a pigment cell the centrosome may even assume the reticular framework, consisting of strands of deeply staining cytoplasmic material. Indeed, to use the term centrosome in the sense it was originally intended, appears hardly appropriate to cover all these cases. And any one who attempts to explain the nature of the centrosome must not confine himself to the consideration of the spherical type, with which we are now most familiar, but must take in all other forms under some common point of view.

On the derivation theory, as explained in the present paper, such polymorphism of the centrosome is full of significance. If, as explained already, the centrosome is the modified cytoplasm, which takes divers shapes in correlation with some definite motion of the protoplasm, such diversity of its forms in different cells is not at all surprising. They are the structures which originated independently in different cells, but having been evolved in correlation with the same function in all cases, careful researches disclose some curious similarity even amidst the features of great anatomical divergence.

On this derivation theory, also, the absence of the centrosome in the *fixed* cell becomes intelligible. If, as has been already pointed out, such fixed cells show any decided phenomena of intracellular movement as caryokinesis, the centrosome is again reconstructed from the ordinary cytoplasm; the division over, the rearrangement of the cytoplasm comes in, and even the centrosome, though a more persistent structure than the spindle, becomes eventually merged in the general cytoplasm of the "resting" cell.

If this view seems to detract from the dignity which the centrosome would have as a permanent organ of the cell, it may be said, on the other hand, to emphasize a certain endowment of the cytoplasm which has not been fully recognized in connection with the problem of the origin of the centrosome.