CHAPTER II.

HISTORY OF THE THEORY OF HEREDITY.

Requisites of a theory of heredity.—Historical sketch of speculation on heredity—Evolution hypothesis of Bonnet and Haller—Ovists and spermists—Modern embryological research has shown that it is impossible to accept the evolution hypothesis in its original form—Buffon's speculations upon heredity fail to account for variation—Hypothesis of epigenesis—This hypothesis is logically incomplete—The analogy between phylogeny and ontogeny gives no real explanation of the properties of the ovum—Haeckel's plastidule hypothesis—This hypothesis is not logically complete unless it involves the idea of evolution—Jager's hypothesis—Ultimate analysis shows that this is at bottom an evolution hypothesis—No hypothesis of epigenesis is satisfactory—No escape from some form of the evolution hypothesis—This conclusion is accepted by Huxley.

§ 1. *Requisites of a theory of heredity.*

The following list is a brief summary of what seem to me the most important characteristics of the reproductive process in living things:

1. New organisms may be produced by the various forms of asexual generation and from ova.

2. Ova may develop, in certain cases, without fertilization.

3. As a rule the ovum does not develop into a new organism until it has been fertilized by union with a male cell.

4. The ovum and male cell will not unite unless they are derived from organisms with the same or nearly the same systematic affinities.

5. The new organism, whether produced sexually or asexually, is essentially like its ancestors, although it may be quite different from its immediate ancestor, as in cases of alternation.

6. Organisms produced from fertilized ova differ in the following points from those produced asexually:

a. As a rule the development of the egg embryo is indirect, and a more or less complicated metamorphosis *or alternation of generations must be passed through before* the adult form is reached, and the circuitous path thus traversed bears a resemblance to the line of evolution of the species. An organism formed asexually traverses only so much of this path as remains to be traversed by the organism which gives birth to it.

b. Reversion, or the appearance of characteristics not exhibited by the parents, but inherited from remote ancestors, is not at all unusual in egg embryos, but it is more rare in those produced asexually.

c. New variations, or features which are not inherited, *appear continually in organisms produced from fertilized ova*, and they may be transmitted either sexually or asexually to future generations, thus becoming established as hereditary race-characteristics. Hereditary variations are extremely rare in organisms produced asexually.

7. The ovum and the male cell are homologous with each other, and are morphologically equivalent to the other cells of the organism. We must therefore believe that their distinctive properties have been gradually acquired, and that their specialization has been brought about by the action of the same laws as those in accordance with which the *other specializations of the organism* have been produced.

8. Changed conditions do not act directly, but they cause subsequent generations to vary.

9. In the higher animals, where the sexes have long been separated the male is more variable than the female.

10. The result of crossing is not the same when crosses are made reciprocally.

11. The sex of the parent-species affects the degree of *variability of hybrids; and when a hybrid is used as the* father, and either one of the pure parent-species, or a third species, as the mother, the offspring are more variable than when the same hybrid is used as the mother and either pure parent-species or the same third species as the father.

There may perhaps be other requisites which should be included in this list, but I think there can be no doubt that a theory of heredity must recognize and be in harmony with all which are here given.

§ 2. *A sketch of the history of speculation on the theory of heredity.*

The laborious researches of the students of the science of embryology have yielded a rich harvest of valuable facts, and we now know that the process of cell division by which an unspecialized unicellular egg becomes converted into a many-celled, highly-specialized organism bears the closest resemblance to the process of growth or of ordinary cell-multiplication.

We know that all the various forms of reproduction, cell-multiplication, fission, gemmation, conjugation, sexual reproduction, and parthenogenesis, are inter-related in such a way that we must believe that they are different manifestations of the same power, and that they have been evolved one from the other.

We know that direct development, metamorphosis, and alternation of generations are not separated from each other by any hard and fast line, and we know too that the changes through which the embryo passes on its road from the egg to maturity show a wonderful parallelism to the series of changes through which the organism has passed during the history of its evolution from lower forms.

These results are well worth the labor they have cost, and they illustrate, more clearly than any other facts in biology, the common nature of all living things. They do not, however, contribute directly to a clearer insight into the laws of heredity.

Here we are still compelled to go beyond the visible phenomena, and to attempt by the scientific use of the imagination to discover the as yet unseen relations which bind them together.

As we enter upon this subject it will be well to bear in mind the wide difference between the end we have in view—the discovery of the secondary laws of heredity—and the attempt to understand its ultimate cause.

The power to reproduce itself, to impress upon dead inorganic matter its own distinctive properties, is one of the fundamental characteristics of living matter; and while we may hope that increase of knowledge may some day enable us to trace the origin of this power, such an attempt forms no part of our present undertaking.

We shall accept without explanation the fact that living matter does thus reproduce itself, and we shall confine ourselves to the attempt to discover why the egg of a star-fish for instance, reproduces a star-fish, and the egg of a bee a bee; to discover the origin of the differences between the various forms of reproduction, rather than the *cause of what they have in common.*

The phenomena of heredity in the higher animals, as well as the mechanism of ova and male cells through which these phenomena are manifested, have certainly been produced by slow *modification*, through the influence of conditions which are to a great extent open to study. The attempt to trace their origin and significance is not a pure speculation, but a legitimate exercise for the scientific intellect.

As we should expect from the fascinating nature of the subject, there has been no lack of speculation in the past, and various hypotheses have been proposed from time to time to account for the phenomena of heredity. These hypotheses differ greatly among themselves, but they may be roughly classed as epigenesis hypotheses, and evolution hypothesis: the word evolution being here used, of course, in its old sense, as contrasted with epigenesis.

The hypothesis of evolution, pure and simple, as advocated by Bonnet and Haller, is that there is contained in the egg or seed or in the male element a perfect but minute organism, and that the subsequent development of the egg is simply the "evolution" or unfolding of this germ. Up to the end of the last century the prevailing opinion was that each egg contains, in a latent or dormant state, a completely formed organism. The fertilization of the egg was supposed to awaken this dormant germ, to call its latent potential life into activity; and the process of development was regarded as the unfolding and growth of the already fully formed and perfect embryo. The embryo was held to be not produced by, but simply unfolded from the egg, and the act of reproduction was therefore regarded as *eduction* not *production*.

According to Huxley (Encyc. Brit., Art. Evolution) "Bonnet affirms that before fecundation the hen's egg contains an excessively minute but complete chick, and that fecundation and incubation simply cause this germ to absorb nutritious matters, which are deposited in the interstices of the elementary structure of which the miniature chick or germ is made up. The consequence of this intussusceptive growth is the "development" or "evolution" of this germ into the visible bird. Thus an organized individual "is a composite body consisting of the original or elementary parts, and of the matters which have been associated with them by the aid of nutrition," so that if these matters could be extracted from the individual, it would, so to speak, become concentrated in a point, and would thus be restored to its primitive condition of a germ "just as by extracting from a bone the calcareous substance which is the source of its hardness it is reduced to its primitive state of gristle and membrane."

"*Evolution* and *development* are, for Bonnet, synonymous terms; and since, by *evolution* he means simply the expansion of that which was invisible into visibility, he was naturally led to the conclusion, at which Leibnitz had arrived by a different line of reasoning, that no such thing as generation exists in nature. The growth of an organism being simply a process of enlargement, as a particle of dry gelatine may swell up by the intussusception of water, its death is a shrinkage, such as the melted jelly might undergo on desiccation."

Much more anciently the evolution hypothesis found acceptance in a somewhat different form, and the miniature organism was believed to exist in the male element, and to receive from the egg the nourishment needed for its growth and perfect development.

Leeuwenhoek's discovery of the motile spermatozoa of animals was regarded as a new basis for this view, and the "sperm-animalcule" was held to be the perfect and living animal ready for unfolding or evolution, the term "spermatozoon," still retained in scientific nomenclature, being a remnant of this old hypothesis. Leeuwenhoek's discovery inaugurated, in the first half of the last century, the warm dispute between the Animalculists and the Ovists, one side holding that the germ is contained in the egg, and the other that it exists as the seminal animalcule.

It is obvious that, in either form, the evolution theory, as above stated, is logically incomplete, *since it only accounts for a single generation.* Its advocates were therefore compelled to enlarge it, and to assume that, as each organism thus exists, in a perfect form, in *the preceding generation*, each germ must contain, on a still smaller scale, the perfect germs of all subsequent generations. Thus Bonnet held, in his hypothesis of emboitement, "*that all living things proceed from pre-existing germs*, and that these contain, one inclosed within the other, the germs of all future living things; that nothing really *new is produced* in the living world, but that the germs which develop have existed since the beginning of things." (Huxley, Evolution.)

The advocates of the evolution hypothesis appealed to such facts as the presence of a minute plant inside the acorn, or to the butterfly inside the pupa-skin, in support of their views; but the hypothesis, in its crude state, was quickly overthrown by the first discoveries of modern microscopic embryology.

Harvey's studies on the development of the chick, followed by the researches of Wolff, Pander, Von Baer, and the host of embryologists of the last fifty years, show conclusively that the embryo is not unfolded out of, but gradually built up from the egg.

We now know that the eggs of all animals, when they are not complicated by the presence of food, or of peculiar coverings for protection or attachment, are essentially alike in optical structure, and that they are not only like each other, but like the constituent cells of all parts of the body of the organism.

Far from being preformed in the egg, we know that the body is built up gradually, step by step, by repeated cell-division, and that the earlier stages of development do not result in the formation of the parts of the perfect body at all, but that they simply give rise to germ-layers, or tracts of cells out of which organs are gradually formed, and that cells which were at first quite widely separated in the embryo may come at last to enter into the formation of a single organ.

For instance, when the nervous system of a vertebrate first makes its appearance in the embryo, there are no traces of the brain, of the spinal cord, of the nerves or of sense organs. It at first consists of a long group of cells running along the middle line of the body, and presenting no difference from the other cells of its surface. In most cases this elongated group of cells becomes converted into a furrow, and afterwards into a closed tube, the nerve-tube, by the folding together of its edges. The primitive nerve-tube is at first simply a long tube of embryonic cells running along the middle line of the back, and it is a very different thing from the final nervous system of an adult mammal, nor is it in any sense a mammalian nervous system in miniature, for the changes by which it becomes converted into the latter are great and numerous, as well as gradual. Certain parts, such as the eye, are formed only in part from this tract of cells, for the vertebrate eye is the result of the combination of an outgrowth from the embryonic nervous system and an ingrowth from the surface of the head.

The whole history of the nervous system and sense organs is thus seen to directly oppose the view that these organs are present in miniature in the germ.

Still more opposed to the hypothesis of evolution is the remarkable fact that the changes which take place in the developing egg are not such as would lead directly to the formation of the adult animal. In most cases a circuitous or indirect path is followed, and this indirect path leads at first towards the adult form of lower members of the group.

This, the most suggestive fact of modern embryology, may perhaps be made clearer by an illustration.

Let us try to compare the growth of an egg into an adult animal with the growth of some manufactured product in the hands of its maker.

The evolutionist view of the development of an organism may be illustrated by the manufacture of a yarn base-ball. A boy, wishing to make a yarn ball, procures, if possible, a small rubber ball, and winds his yarn onto this until the desired size is reached, the only changes during the growth of the ball being the change of size and of material.

The observed facts of embryology show that the development of an embryo does not take place in any such way as this. It may, however, be illustrated by the growth of a steam-ship in the hands of the builder, who first lays down an indefinite skeleton, and outlines in a vague way the more prominent features, before any of the details are finished. In order to make the illustration perfect, however, we must imagine the builder to commence work upon his steam-ship by laying out the skeleton of a big trireme; we must imagine him to carry this some stages towards completion, and to put into it certain contrivances, such as rowers'-benches, which are of no use in a steam-ship. We must imagine that he then abandons his plan, tears down his benches, and uses the material to make a deck; that he changes the shape and proportions of his hull a little to fit it for sailing instead of rowing, that he puts in masts and spars, and makes everything ready for a ship's rigging; that he then changes the shape of his hull once more; tears out part of his cabin, puts in bulkheads, coal bunkers, and an engine and boiler; shortens his masts, alters his rigging, and finally converts his unfinished ship into a finished steamer.

This is not by any means a forced illustration, but a very fair outline of the development of an animal. In nearly every case we find that the development of the embryo as a whole, or else the development of certain organs, takes place in this roundabout, indirect way, and repeats, usually in an imperfect manner, the structure of a related but lower animal.

As an example, we may refer to the history of the blood-vessels of a mammal. The breathing organs of the lower vertebrates are gills on the sides of the neck, and the venous blood is driven from the heart through a series of branchial arteries to the gills, where it is aerated and conveyed into a series of branchial veins which carry it, not back to the heart, but to the various organs of the body. In a mammal there are no traces of gills at any stage of development; the adult animal breathes by lungs, and the blood which has been aerated in the lungs goes back to the heart before it is distributed throughout the body. Now the early stages in the development of the blood-vessels of a mammal would, if carried out to completion, lead to the *formation of the system found in fishes.*

The mammalian embryo has no gills, but it does have branchial arteries and veins, and its blood at first follows the same course that it follows in a fish. It is plain that the fish-like circulation is not an outline or sketch of that of a mammal; that it is not a necessary stage in the formation of the latter, for the branchial vessels are soon, in part pulled down and destroyed, and in part profoundly modified, in order to conform to the mammalian type.

Cases of this kind are almost universal, and the law of resemblance between the early stages of higher animals and the adult condition of lower animals is a fundamental law of embryology.

It is obvious that the hypothesis of evolution of a perfectly formed germ contained in the egg, is utterly irreconcilable with this law, and we may therefore state with confidence that this hypothesis is refuted by the observed facts of embryology.

We must not forget, however, that there were other less superficial forms of the evolution hypothesis, and that these cannot be disproved so easily.

Buffon, for instance, held that the embryo is built up by the union of organic particles which are given off from every part of the body of the parent, and which, assembling in the sexual secretions, assume in the body of the offspring positions like those which they occupied in the parent. This is essentially an evolution hypothesis, but it is logically complete, since it accounts for the production of successive generations without the necessity for assuming that they were all contained in embryo in the body of a remote ancestor. Microscopic examination cannot overthrow this hypothesis, for a failure to discover these organic particles with any particular magnifying power does not, of course, disprove their existence any more than a failure to see them without a microscope.

Although Buffon's hypothesis does not account for the fact that development is indirect in most cases, that the egg does not build up the adult animal in the simplest way, but takes a roundabout circuit, this fact is not directly opposed to his hypothesis, for we can easily conceive that after an indirect method of development *has been established it might be perpetuated by Buffon's* organic molecules, provided these are given off by the parent organism at all stages of its life, and not simply after it has reached its final form.

There is, however, another class of phenomena of even greater importance—the phenomena of variation.

Buffon's hypothesis accounts for the resemblance between the child and the parents, but we now know that the child is not exactly like its parents or even midway between them, that animals and plants are born with a tendency to vary, that this variation may affect any part of the body, and that by the selection of these congenital variations the most profound changes of hereditary structure may be produced.

The fact of congenital variation is as profound, as universal, and as characteristic of living things as the fact of heredity, and the constant appearance of new variations is as fatal to Buffon's hypothesis of evolution as it is to that of Bonnet.

With the growth of the modern science of morphology these hypotheses have been abandoned and the hypothesis of epigenesis almost universally accepted in their place.

This hypothesis, first brought into notice by the researches of Harvey and Wolff on the development of the chick, has gradually assumed a more definite shape with the progress of embryology, and has been especially modified by the growth of the cell theory.

In its modern form it may, for convenience of discussion, be divided into two parts—a statement of the observed facts, and an explanation of the origin of the phenomena.

So far as it is a statement of facts, it cannot be called an hypothesis, for it simply affirms that the egg is optically an ordinary unspecialized cell; that it gives rise, during the process of segmentation, in a manner which is identical with ordinary growth by cell division, to a number of cells which gradually become specialized for certain functions, and are set apart as the foundations of the various organs of the body; that the repetition of this process gives rise, at last, to the perfect body of the mature animal; that the reproductive elements which are to give rise to the next generation, originate, like all the cells of the body, by cell division during the process of development, and that they are simply cells specialized for the reproductive function as other cells are specialized for other functions. Every one who has the slightest acquaintance with modern biology will accept this statement, not as an hypothesis, but as an observed fact, and will agree that between this and the old evolution hypothesis there can be but one choice.

The old hypothesis of evolution, however, claimed to be something more than a statement of fact, for the presence of the germ within the egg accounted for the wonderful properties of the egg itself.

We are at once compelled to ask, then, how, on the hypothesis of epigenesis, has the egg acquired these properties? If it is simply an unspecialized cell; if, as Gegenbauer states, "the egg is nothing more nor less than a cell; the egg-cell does not differ from other cells in any essential points" (Comp. Anat., Bell's Trans., p. 18), how can the egg of a horse develop into a horse, while another cell, which "does not differ from it in any essential points," develops into a bee or an alligator or an oyster?

Nothing in nature is more marvellous than the development of each egg into its proper organism, and if it is true that the egg which is to give rise to a man differs in no essential point from that which is to give rise to an insect, we may conclude that the mystery is too great to be fathomed by our intelligence, and we may fairly ask what possible explanation can, on this hypothesis, be given of the wonderful properties of the egg.

The answer which has been given, and which seems to have been thought satisfactory by many students, is this:

We know, from a mass of evidence which is constantly and rapidly increasing, and to which each new observation adds cumulative weight, that the various forms of life have been slowly evolved, during long ages, from older and simpler forms; that as we trace back the history of any two animals or plants we find evidence that in the past they had for a common ancestor a species which had not yet acquired the distinctive features of either of them; that a little farther back we trace this species to an ancestor with still wider relationships.

Every day the evidence grows stronger to show that more complete knowledge will ultimately prove that the same thing is true of still larger groups; that families, classes and orders of organisms have been formed in the same way by gradual modification and divergence; that complete knowledge of the ancestry of any organism would lead us back through simpler and simpler forms to a remote unspecialized unicellular ancestral form. It is unnecessary to review in this place the evidence for this conclusion, for the fact that it is fully accepted by those best qualified to judge of its truth, is perfectly familiar to all students.

Now it is said, and the explanation is pretty generally accepted, that since any particular organism, a horse for instance, has been slowly evolved from an ancestral rhizopod, and since the ovum of a horse is homologous with a rhizopod, or is morphologically equivalent to it, we have in the gradual phylogenetic evolution of the horse species from an unicellular ancestor, a satisfactory explanation of the ontogenetic development of the individual horse from an unicellular ovum.

As soon as attention is fairly fixed upon the subject, the weakness of this explanation becomes so evident that I take the liberty of making the following quotation from a well-known authority, in order to show that the explanation has been soberly advanced. In making the extract from Haeckel's writings I am not actuated by a desire to attack his views, for the same idea can be found, expressed pretty definitely, in the works of many other writers, and this particular selection is simply a matter of convenience.

Haeckel says: "Until recently the greatest students of embryology, Wolff, Baer, Remack, Schleiden and the whole school of embryology founded by them, have regarded the science as exclusively the study of individual development. Far otherwise to-day, when the mysteries of the wonderful history of the development of individual organisms no longer face us as an incomprehensible riddle, but have clearly revealed their deep significance: for the changes of form which the germ passes through under our eyes in a short time are, by the law of inheritance, a condensed and shortened repetition of the corresponding changes of form which the ancestors of the organism in question have passed through in the course of many million years. To-day, when we lay a hen's egg in an incubator, and in twenty-one days see the chick break out of it, we no longer gaze in dumb wonder on the marvellous changes which lead from the simple egg to the two-layered gastrula: from this to the worm-like and skulless germ, and from this to later stages which repeat, essentially, the organization of fish, amphibian, reptile, until at last we have a perfect bird. On the contrary, we unravel from this history the corresponding series of ancestral forms, which have led up through the amœba, the gastræa, the worms, the acrania, the fishes, the amphibia and the reptiles to the bird.

"The series of changes in the hen's egg gives us an outline sketch of the series of ancestors. *This ancestral or phylogenetic significance of the phenomena of ontogeny or individual development is up to the present time the only explanation of the latter.*" ("Gesammelte Populäre Vorträge," II., p. 103.) "Any one who accepts the law that individual development is a recapitulation of the evolution of the species *will find it simply natural* that the microcosm of the ontogenetic cell-tree should be the diminutive, and in part distorted, reflection of the macrocosm of the phylogenetic genealogical tree of the species." ("Gesammelte Populäre Vorträge," II., p. 68.)

No one can set too high a value upon the scientific law here expressed—that individual development is a recapitulation of the history of the evolution of the species. It must be regarded as one of the greatest generalizations of modern science, but I do not think it is possible to agree with Haeckel that with its discovery the mystery of individual development has clearly revealed its deep significance, and no longer faces us as a riddle.

It may be true that it is "simply natural" that the egg of a horse should recapitulate the ancestral history of horses, and the egg of a bird the ancestral history of birds, but the statement that this is the case is in no sense an explanation of heredity. For that matter it is "simply natural" that a bird's egg should give rise to a bird, and a horse-ovum to a horse, but no one would accept the statement as an explanation.

We have in the natural selection of variations a true *explanation* of the manner in which an unicellular rhizopod has been slowly and gradually modified by an almost infinite number of slight changes, extending through countless millions of generations, into a bird. The change is one of the most wonderful of the phenomena of nature, but it is in no sense a mystery, for the skill of the breeder may even now, by the employment of the same means, produce similar results, only on a much smaller scale; by the methodical selection of congenital variations an organism may be, in a few generations, slightly modified in any desired direction, and we can fairly and truly affirm that we understand the evolution of birds from their unicellular ancestors; but the resemblance between the evolution of birds from these remote ancestors by natural selection, and the development of an individual bird from an unicellular ovum, is simply an analogy. It is true that it is an analogy of the greatest significance, but we must not lose sight of the fact that the means by which the end is accomplished—the natural selection, through a long series of generations, of congenital variations—is absent in the second case. If the epigenesis hypothesis is true, if the egg is simply, like the rhizopod, an unspecialized cell; if the egg of a bird does not differ from the egg of a star-fish in any essential points, we must acknowledge that the mystery of individual development is not only as yet unsolved, but absolutely insoluble.

The student at the sea-shore may collect at the surface, with his dip-net, three similar transparent spherical eggs. Each of these is, optically, simply a nucleated cell, and each when placed under the microscope will soon be seen to pass through almost exactly the same changes, giving rise by division to a spherical layer of cells. Yet if these three eggs are placed together in a tumbler of water and exposed to identical conditions, one may at last become a star-fish, another a crustacean, and another a vertebrate. Similar things under similar conditions cannot give rise to widely different results, and there seems no escape from the conclusion that these three eggs are not similar, or even essentially alike, but that one of them is a potential star-fish, another a potential crustacean, and a third a potential vertebrate. That there is in each of them a something which separates it very widely from the other two, and determines its future history.

The hypothesis of epigenesis proves, then, on careful analysis to be as unsatisfactory as the speculations of Bonnet and Buffon, and we must acknowledge that we are as yet unable to picture to ourselves the hidden significance of the phenomena of individual development, without returning to some modification of the old evolution hypothesis.

The attempt to escape this necessity, and to hold fast to the hypothesis of epigenesis, has given rise within recent years to much ingenious speculation, and an examination of some of the published papers will help, rather than retard, our argument.

Among these, one of the most ingenious and suggestive is Haeckel's paper, "Ueber die Wellenzeugung der Lebenstheilchen oder die Perigenesis der Plastidule." The following extract ("Gesammelte Populäre Vorträge," II., pp. 66–72) will, I hope, give a sufficiently clear statement of his views:

"In order to penetrate still farther into the mechanics of the biogenetic process, we must descend into the deep obscurity of plastid-life, and search for its true efficient cause in the motion of organic molecules (Plastidule-Bewegung).

"In fine, this question remains to be answered, Are we in a position, by the aid of comparison with analogous phenomena of motion, to form a satisfactory provisional hypothesis regarding the true nature of the plastidule motions which are hidden from our direct observation? Our hypothesis of perigenesis is an attempt to answer this question in the affirmative.

"As we review, from the highest and most comprehensive point of view, *the sum of the* phenomena of organic development, the most general result of our survey is the conclusion that the biogenetic process is a periodic motion, which we can best picture to ourselves as a wave *motion*. *Adhering at* first to facts which are beyond dispute, and which admit of direct observation, we may commence with our own ancestry: either confining ourselves to the so-called historic period, in which *we can pass from man to man* by *direct proof; or* else following, by the methods of anthropogeny, our ancestry still farther back, through the vertebrates to amphioxus, and through the group of invertebrates to the gastræa, *and at last to the* amœba and the moner. In either case the course of development (entwickelungsbewegung) of our series of ancestors can be most simply represented by a wave-line, in which the individual *life* of each *organism answers* to a single wave.

"If now we enlarge our field of view to embrace not simply our own direct ancestry but the whole of our blood-relations, we can make clear by a genealogical tree their relationship to each other. As the history of the evolution of each person is represented by a wave-line, the entire tree will have the form of a branched wave-motion, a ramified undulation. . . .

"A natural system of classification is nothing but a genealogical tree of allied species of organisms, and each branch and twig of the tree corresponds to a greater or smaller group of descendants from a common ancestral form. This community of descent unites all the forms of a class, an order, and so on. Since each class is divided into various orders, each order into several families, each family again into various genera, each genus into a number of species and varieties, there is a similar branching in the wave-motion which is carried from the common ancestral form to the entire group of its descendants; and each undulating branch implants in the same way its individual motion on its various descendants.

"Now the fundamental law of embryology teaches us that this history of the phylogenetic evolution of organisms is mirrored in miniature in the ontogenetic development of each individual. Here the single waves answer to the life of the constituent plastids (cytodes and cells). The cytula, or the first segmentation cell which originates from the fertilized egg, and out of which the many-celled organism is developed, bears the same relation to the various cell-generations which originate from it by division, and which give rise later by specialization of function to the various tissues, that the stem-form of a class or order bears to the various families, genera and species which diverge from it, and which have been differently evolved through adaptation to diversified conditions of existence.

"The ontogenetic 'cell-tree' of the former has exactly the same form as the phylogenetic 'species-tree' of the latter. The developing impulse which in the one case is transferred from the ancestral species to the entire group of species, and in the other case from the ancestral cell to the entire group of cells, assumes in both cases the same form of a branching wave-motion. Any one who accepts the fundamental law of development will find it only natural that the microcosm of the ontogenetic 'cell-tree' should be a diminution, and to some degree distorted reflection of the phylogenetic 'species-tree.'

"As we can only explain and render intelligible a complicated and obscure phenomenon by dividing it into its separate elements, and by the exact analysis of these parts, so it is necessary to penetrate to the ultimate elementary facts of our mechanical theory of development.

"Now the biogenefic process as a whole is the highly compound resultant of the developmental history of all species of organisms. These consist again of the life histories of the individuals, just as the latter are again made up of the histories of the constituent plastids.

"The development of each plastid, however, is in its turn only the product of the active movements of its constituent plastidules. Now we have seen that the developmental impulse of the branches and classes, the orders and families, the genera and species, the individuals and plastids, always and everywhere has for its fundimental characteristic the branched wave-motion. Accordingly the molecular plastidule-motion, which lies at the bottom of all the phenomena of life, can have no other form. We must conclude that this ultimate cause of all the phenomena of life, that the invisible activity of the organic molecules is a branched wave-motion. This true and ultimate *causa efficiens* of the biogenetic process I propose to designate by a single word—*Perigenesis*, the periodic wave-generation of the organic molecules or plastidules.

"This mechanical hypothesis is a true explanation of the process of organic development. . . .

"The designation of this branched wave-motion of the plastidule by the word *perigenesis* or *wave generation* serves to emphasize the distinctive characteristic which separates this *branched* motion from all similar periodic phenomena. This peculiarity depends upon the reproductive power of the plastidule, and this again is brought about by its peculiar atomic composition. This power of reproduction which alone renders possible the multiplication of the plastids is, however, the equivalent of the *memory* (Gedächtness) of the plastidule.

"This brings us to Ewald Hering's ably established view that unconscious memory is the most important characteristic of organized matter, or more properly of the organizing plastidules. Memory is the chief factor in the process of development of organisms. Through the memory of the plastidules the plasson has the power to carry over from generation to generation by inheritance, in continuous periodic motion, its characteristic peculiarities, and to add to these the new experiences which the plastidules have acquired through adaptation in the course of their evolution.

"I have shown that each organic form is the necessary product of two mechanical factors—an inner factor, heredity, and an outer factor, variability, or a power of adaptation.

"By the hypothesis of perigenesis we are able to more sharply define these two fundamental laws of the modification of organisms, for *heredity is the memory of the plastidules: variability their power of perception* (Die

Erblichkeit ist das Gedächtniss der Plastidule, die Variabilität is die Fassungskraft der Plastidule). The one brings about the constancy and the other the diversity of organic forms. In the very simple and persistent forms of life the plastidules have, so to speak, learned nothing and forgotten nothing. In highly perfected and variable organisms the plastidules have both learned and forgotten much."

This somewhat long quotation contains a thorough and exhaustive statement of the perigenesis hypothesis, and it is therefore interesting to notice that its only real claim to recognition as a true *explanation* of the phenomena of heredity is based upon or at least demands the acceptance of some form of the evolution hypothesis.

However great may be the importance of the analogy between the gradual evolution of the species by the specialization of the constituent individuals, and the development of the individual by the specialization of cells, and plastidules, we have already pointed out that it is in no sense an explanation of the latter, since the real cause of the evolution of the species, the selection of congenital variations, is absent.

The only part of Haeckel's hypothesis of perigenesis which has any claim to be considered an explanation of the reproductive power of animals, is the statement that heredity is memory, and variability the acquisition of new experiences. Stated by itself, without explanation, this may seem to those who are unfamiliar with the subject very much like nonsense, for the profound truth upon which it rests is not at all obvious at first sight.

Herbert Spencer has, in his masterly discussion of the nature and distinctive characteristic of life, given us, as the sum and substance of his analysis, the statement that "life is the continuous adjustment between internal relations and external relations." This, like Haeckel's statement that heredity is memory, is not very clear without explanation, but its meaning may perhaps be brought out by an illustration.

If I kick a stone I produce in it certain changes, such as motion, heat, etc.; these changes being directly produced by the kick are simply manifestations of the energy transferred from my foot to the stone. If, instead of a stone, I kick a dog, I produce a similar set of changes, and something more. The experience of the dog and of his ancestors has taught him that such violent attacks are always associated with a disposition to commit still further violence, so, when the dog feels the blow he immediately performs actions which have as their object, escape from or avoidance of the danger which he has not yet experienced, but which he knows to be imminent. These actions are not the effect of the kick, for the energy expended may be hundreds of times greater. Their character is determined, not by any change in the dog, but by the character, the disposition, which he has inherited; and whether he retaliates by an attack on his own part, puts his tail between his legs and runs, or crouches at my feet, his actions are the effect, not of the kick, but of past experience as to the best means of escaping further injury. There is a relation, external to the dog, between the kick and a disposition to injure the dog, and there is within the dog a relation between the sensation of injury and the actions which experience has shown to be the proper ones for escaping further injury.

That which distinguishes the dog from the stone is the power to adjust these internal relations to the external relations, to conform his conduct to the laws of the world around him. The dog, as a living thing, differs from all inorganic bodies, in his power to make this adjustment: so long as he retains this power he lives; his life is a "continuous adjustment between internal relations and external relations." It is plain that this power depends upon experience, but experience depends upon "memory." So we may state, with truth, that in a certain sense, life is memory; and as the power to reproduce its like is characteristic of all living things, we *see that there is in Haeckel's statement a profound* truth.

We know memory, however, only in connection with organization, and if it is true that heredity, the power of an organism to reproduce its like, is simply the memory, by the ovum, of the experience of its ancestors, we must believe that there exists in the ovum an organization of some kind to correspond to each of these past experiences.

We are therefore driven by the hypothesis of perigenesis back from the hypothesis of epigenesis to some form of the old evolution hypothesis, for we cannot conceive that complicated experiences should exist without complicated structure.

We are thus compelled to conclude that, while it undoubtedly expresses a great truth, Haeckel's hypothesis of perigenesis is not a satisfactory and final explanation of the phenomena of reproduction. A satisfactory theory of heredity must explain what it is, in the structure and organization of the ovum, which determines that each ovum should produce its proper organism.

To state that this organization can be expressed in terms of memory, is simply to state the familiar truth that matter and force are different aspects of the same thing; that all problems of matter may be put into the terms of force. The statement does not help us at all to picture to ourselves the essential hidden structure of the egg, the organization upon which its wonderful properties depend.

Jäger has recently brought forward an hypothesis which seems at first sight to be a satisfactory epigenesis. hypothesis, but examination shows that this too, like Haeckel's perigenesis hypothesis, must be turned into an evolution hypothesis before it can be accepted.

The following extract from his paper ("Zur Pangenesis," von Prof. Dr. G. Jäger. *Kosmos* iv. 376. 1879) gives, I believe, a fair statement of his views.

"Each organ and tissue of an animal or plant contains, in the molecules of its albumen at least, a specific *flavor-and-odor-substance* (Duft-und-Würzestoff) which we can easily recognize by our chemical sense, for each organ of an animal has its distinctive flavor. Whenever a full-grown animal experiences hunger, decomposition of albumen takes place in all its organs and tissues, so that their various *flavor-and-odor-substances*, that is their soul-substance (Seelenstoffe), become free, and penetrate to all parts of the body.

"Now, if there exists in any part of the body protoplasm with the power to attract this substance, this protoplasm acquires in this way its *vires formativæ*.

"I have already referred with emphasis to the embryological fact that the formation of the reproductive elements takes place at a very early stage in the embryonic life of an animal, and I have designated this as the reservation of germinal protoplasm. As soon as the embryonal cells of the developing animal have become specialized into ontogenitic and phylogenetic cells, the following will occur. Whenever any decomposition of albumen occurs in the developing organism, from hunger or any other cause, the ontogenetic cell-material which builds up the organism will set free soul-stuff.

"By the law of gaseous diffusion this will not only escape from the body as an *excretion*, but it will also penetrate to the germinal or phylogenetic protoplasm. This process I shall now term soul-reception (Seelenfängerei) in the following sense. The chemical substance which forms *the greater part of the ova and male* cells has lately been called nuclein, since it shows the closest resemblance to the cell-nucleus. The yolk-substance is now regarded, not as vitellin, but egg-nuclein, and the substance of the male cell not *spermatin but* sperm-nuclein. We also know that nuclein consists of albumin, and phosphoric lecithin.

"The question then is the origin of the nuclein in the egg, and the male cell, and this may be answered as follows:

"The reproductive organs do not receive albumen from the body of the mother, since according to the law of Traube, the molecules of a substance which forms a membrane cannot, on account of their size, pass through the pores of that membrane. The germ-cell is an albuminous membrane, and hence it will not allow the passage of albumin molecules.

"It simply *contains the* albumin-nucleus, which re*mains after* the decomposition of the soul-substance, and this is a peptone-like substance which, having lost its soul-substance, has a smaller molecule. It is therefore unspecialized, *or deprived of its soul* (entspesificirt, entseelt), and the process of assimilation in the germ may be termed soul-restoration (Wiederbeseelung). The necessary soul-substance is *supplied* by the decomposition of albumen in the *ontogenetic cell-material*.

"Thus, for example (p. 380), it is known that the reproductive organs of a caterpillar are already formed before it leaves the egg. During its life in the egg, and as a caterpillar, caterpillar-nuclein is formed in its germinal cell-material. During the pupa stage pupa-nuclein is stored up in its reproductive elements, and finally, when it becomes a butterfly, butterfly-nuclein is stored up. The ripe egg and the ripe male cell therefore contain nuclein of three kinds, caterpillar-nuclein, pupa-nuclein, and butterfly-nuclein."

It will be seen that Jäger's hypothesis is, in a certain sense midway between evolution and epigenesis. He holds that at first both the ovum and the male-cell are unspecialized (entseelt); that they exist in the very young embryo as embryonic ova or spermatozoa, and that, as the embryo grows up, the reproductive cells gradually become specialized by the assimilation of soul-stuff, which is thrown off by the decomposition of albumen in various parts of the body of the growing organism, and penetrating to the embryonic ova and spermatozoa is assimilated by them, so that when the animal becomes sexually mature, the cells of its reproductive organs contain all the "soul-stuff" necessary to produce a new organism like the parent.

The statement which I have given is a free translation of Jäger's outline of his theory, and I think it may be regarded as a fair exposition of his views.

A fatal objection to his hypothesis is found in the fact that where a parent gives birth to young before it has reached full maturity and before it has acquired all the characteristics of the species, the young nevertheless inherit these characteristics. The young which are borne by a Cycedomia larva inherit all the characteristics of the full-grown adult insect, and a bull may transmit to female children the good milking qualities of his mother. *It is plain that the child of a beardless boy could not inherit the "soul-stuff" of a beard in the way Jäger imagines, and this fact alone is enough to show that he has not discovered the true secret of heredity.*

We know, too, that reversion, the appearance in the child of the features inherited from a remote ancestor but not shared by its parents, is not at all unusual, and must be regarded as one of the leading characteristics of heredity. It is plain that if the embryonic ovum is, as Jäger states, unspecialized or "de-souled," reversion is inexplicable. Accordingly, when he comes to discuss reversion he makes a fundamental change in his hypothesis, and holds that when the ovum divides, at a very early stage of its development, into two parts, an ontogenetic portion, which gives rise to the new organism, and a phylogenetic portion, which ultimately forms the germinative cells of its reproductive organ, the second part is not unspecialized or "de-souled" at all, but really retains all the characteristics of the ovum which gives rise to it, and is therefore capable, like the ovum, of giving rise to a new organism.

As thus remodelled, I believe, and hope to show in the sequel, that Jäger's hypothesis is a close approximation to the truth, but it is only fair to point out that in its altered form it is not original with Jäger. The author published almost exactly the same view in 1876 ("On a Provisional Hypothesis of Pangenesis," *Proc. Amer. Assn.*, 1876, and *American Naturalist, March*, 1877), and it had been stated as long ago as 1849 by Prof. Owen, in his paper on Parthenogenesis, although this author, in his "Anatomy of Vertebrates," afterwards states that he now believes it to be fundamentally erroneous. It is plain, too, that in its second form Jäger's hypothesis is one of evolution, pure and simple, for the egg is, at no stage of its growth, unspecialized, and it does not require the assimilation of "soul-stuff" in order to develop into an organism.

We must conclude, then, that however satisfactory and accordant with observed fact the hypothesis of epigenesis seems to be at first sight, more careful analysis shows that it is in no sense a true explanation of the phenomenon of development.

The analogy between the evolution of the species from an unicellular ancestor, and the development of the individual from an unicellular egg, is simply an analogy, for the cause of the first phenomenon, the selection of congenital variations, is wanting in the second case, and there is nothing to take its place if it is true that an egg is really, like a rhizopod, an unspecialized cell.

Haeckel's statement that heredity is memory, however true it may be, cannot be accepted as an explanation, for we have no knowledge of the existence of memory apart from organization, and we cannot conceive that an ovum can retain the memory of the past history of its species, unless it possesses a corresponding organization.

Jäger's view that the embryonic ovum is unspecialized, and that its specialization is gradually assimilated during the development of the organism which contains it, fails to account for the phenomena of reversion, and to account for reversion he is compelled to assume that the egg is organized from the time of its origin in the developing egg of the preceding generation.

In each case we are driven to the same conclusion, that the epigenesis hypothesis is inadequate; and we are forced to accept some form of the evolution hypothesis.

This necessity has not escaped the notice of some of our most acute thinkers. Huxley, for example, says

(Encyc. Brit., Art. Evolution), "Harvey's definition of a germ as 'matter potentially alive, and having within itself the tendency to assume a definite living form,' appears to meet all the requirements of modern science. For notwithstanding it might be justly questioned whether a germ is not merely potentially but rather actually alive, though its vital manifestations are reduced to a minimum, the term potential may fairly be used in a sense broad enough to escape the objection. And the qualification of potential has the advantage of reminding us that the great characteristic of the germ is not so much what it is, but what it may under suitable conditions become. "From this point of view the process, which in its superficial aspects is epigenesis, appears in essence to be evolution, . . . and development is merely the expansion of a potential organism or organic preformation according to fixed laws."