

MINOT (C.S.)

ON HEREDITY AND REJUVENATION.

BY

CHARLES SEDGWICK MINOT.

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BY CHARLES SEDGWICK MINOT.²

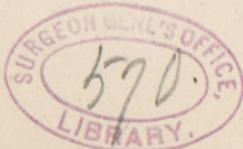
The subject of this article is presented under the following sections :

- I. The Formative Force of Organisms.
- II. The Conception of Death.
- III. A Comparison of Larva and Embryo.
- IV. Concluding Remarks.

The first section is not new, but a reproduction without change, of an article published in *Science*, July 3d, 1885. As this article has not become generally known, and yet is an essential link in the chain of reasoning, I venture to repeat it. Though written in 1885, I consider that to-day it is still sufficient to disprove Weismann's theory of germ plasm. Weismann has not considered this article, otherwise, from my point of view, he could not have maintained his theory.

¹ This article is translated from one which appeared in the *Biologisches Centralblatt*, Vol. XV, Page 571, August 1st, 1895. A few trifling changes have been made in the text. An abstract of the article was read before the American Association for the Advancement of Science, at its recent Springfield meeting.

² Professor in the Harvard Medical School.



The views which I then defended have been recently brought forward in almost parallel form, and without essential additions, by O. Hertwig (*Zeit-und Streitfragen der Biologie*, I, Heft, D. 32-53) as arguments against the views of Weismann.

The second section is also directed against Weismann, for it attempts to replace his conception of death by one more exact.

The third section is intended to make the significance of rejuvenation clear, and at the same time, by a comparison of larvæ and embryos, to demonstrate a law of heredity which has not been hitherto recognized.

THE FORMATIVE FORCE OF ORGANISMS.

The assertion is safe, that the majority of biologists incline at present to explain the forming of an organism out of its germ upon mechanical principles. The prevalent conception is that the forces of the ovum are so disposed that the evolution of the adult organism is the mechanical result of the predetermined interplay of those forces. The object of the present article is to point out that this conception is inadequate, and must be at least supplemented, if not replaced, by another view, namely, that the formative force is a generally diffused tendency, so that all parts inherently tend to complete by their own growth and modification the whole organism—a fact which finds a legitimate hypothetical expression in Darwin's Doctrine of pangenesis. The nature of the view here advanced will become clearer upon consideration of the evidence upon which it is based, and which is adduced below. The evidence that the formative force is diffused through all parts falls under three heads: 1. The process of regeneration in unicellular and multicellular bionts; 2. The phenomena of the duplication of parts; 3. All forms of organic reproduction. Let us briefly consider these categories.

1. *Regeneration.*—All living organisms have, to a greater or less degree, the ability to repair injuries; indeed, we must regard the power of regeneration as coextensive with life, but

the capacity varies enormously in the different species. In man the power is very small, though more extensive than is generally realized. Among Annelids are species, the individuals of which may be divided in two, and each piece can regenerate all that is needed to render it a complete worm. We sometimes see a small fragment of a plant, a single switch of a willow, for instance, regenerate an entire tree, roots, trunk, branches, leaves, flowers, and all. In the last instance a few cells possess a latent formative force, which we recognize by its effects, but cannot explain. We perceive, therefore, that each individual has, as it were, a scheme or plan of its organization to which it strives to conform. As long as it actually does so, the cells perform their routine functions; but when an injury destroys or removes some portion, then the remaining cells strive to conform again to the complete scheme, and to add the missing fragment. The act of regeneration of lost parts strikes the imagination almost as an intelligent pursuit by the tissues of an ideal purpose.

Our knowledge of the regeneration power has recently received important extensions through the noteworthy experiments of Nussbaum³ and Gruber,⁴ who have demonstrated, independently, the possibility of dividing unicellular animals so that each piece will regenerate the missing parts. In this manner the number of individuals can be artificially multiplied. For example: Nussbaum divided a well-isolated *Oxytricha* into two equal parts, either transversely or longitudinally, and found that the edges of the cut became soon surrounded with new cilia. Although some of the substance of the body, or even a nucleus, was lost through the operation yet, by the following day, the two parts converted themselves into complete animals with four nuclei and nucleoli (*Nebenkerne*) and the characteristic ciliary apparatus. "The head piece has formed a new hind end; the right half, a new left half." The

³ M. Nussbaum, *Ueber spontane und kunstliche Zellteilung*, Sitzungsber. d. neiderrh. Ges. f. Nat. u. Heilkunde, Bonn, 15, Dez., 1884.

⁴ A. Gruber, *Ueber kunstliche Teilung bei Infusorien*, Biol. Centralblatt, Bd. IV, No. 23, 717--722.

newformed duplicate Infusoria multiplied subsequently by spontaneous division. From one *Oxytrachia* cut in two, Nussbaum succeeded in raising ten normal animalcules, which subsequently all encysted. After an unequal division, the parts are both still capable of regeneration, but parts without a nucleus did not survive, which suggests that the formative energy is in some way bound up with the nucleus. But nucleate pieces may break down. Thus, all attempts at artificial multiplication of the multinucleate *Opalina* failed, although the division of *Actinosphærium* had been successfully made by Eichhorn as long ago as in the last century. *Pelomyxa palustris* has been successfully divided by Greef, and *Myastrum radians* by Haeckel.

Gruber (*l. c.*, p. 718) describes his experiments with *Stentor*: "If one divides a *Stentor* transversely through the middle, and isolates the two parts, one finds on the cut surface of the hind part, after about twelve hours, a complete peristomial field with the large cilia and buccal spiral newly formed. On the other hand, the piece on which the old mouth is situated has elongated itself backwards, and attached itself in the manner peculiar to these Infusoria. If one has made a longitudinal section, so that the peristome is cut in two, then the peristomes both complete themselves and the lateral wounds heal over. I have repeatedly separated, by transection, pieces considerably less than half of the original *Stentor*, and these have also regenerated themselves to complete animals." Gruber, too, observed that artificially divided Infusoria were capable of subsequent spontaneous multiplication. If the section is not very deep, there may arise double monsters; but here, just as in spontaneous divisions, as long as there remains an organic connecting band, the two parts act as one individual, showing that the nervous actions are not restricted to determined paths. Gruber also adds that two divided pieces may be reunited if brought together quickly enough. The observation thus briefly announced is of such extreme interest and importance that the publication of the full details of the experiment will be eagerly awaited. Gruber adds that at present we can-

not go much beyond the proof of existence, to a high degree, of the regenerative capacity in unicellular organisms. He also makes the significant observation that in the Protozoa, we have to do foremost with changes of function; in the Metazoa, with growth also.

2. *Duplication of parts.*—In these anomalies we find an organ which, although an extra member, yet still conforms to the type of the species. For example: a frog is found with three posterior limbs; dissection proves the third leg to agree anatomically with the typical organization of the frog's hind leg. In determining the importance to be attributed to this evidence, it should be remembered, on the one hand, that these instances are by no means unusual; on the other, that the agreement with the normal structure is not uniform.

3. *Asexual reproduction.*—When a species multiplies by fission of any kind, we must assume that each part, after division, possesses the formative tendency, since we see it build up what is necessary so complete the typical organization of the individual. Again: a bud of a hydroid or polyzoon, although comprising only a small part of the body, is equally endowed with this uncomprehended faculty. In pseudova we reach the extreme limit; in aphid, for example, the parent gives off a single cell, the capacity of which, to produce a perfect and complicated individual, fully equals the like capacity of a hydroid bud or of half a worm.

The evidence forces us to the conclusion that the formative force or cause is not merely the original disposition of the forces and substances of the ovum, but that *to each portion of the organism is given*: 1. *The pattern of the whole organism*; 2. *The partial or complete power to reproduce the pattern.* The italicized formula is, of course, a very crude scientific statement, but it is the best which has occurred to me. The formative force, then, is a diffused tendency. The very vagueness of the expression serves to emphasize our ignorance concerning the real nature of the force. In this connection, I venture to insist upon the fact that we know little or nothing concerning any of the fundamental properties of life, because I think the

lesson of our ignorance has not been learned by biologists. We encounter, not infrequently, the assertion that life is nothing but a series of physical phenomena; or, on the other hand, what is less fashionable science just now, that life is due to a special vital force. Such assertions are thoroughly unscientific; most of them are entirely, the remainder nearly worthless. Of what seems to me the prerequisites to be fulfilled before a general theory of life is advanced, I have written elsewhere.⁵

II. CONCEPTION OF DEATH.

My thesis reads: There are two forms of death. These are *first*, the death of the single cells; *second*, the death of multicellular organisms. Death in the one case is not homologous with death in the other.

Weismann assumed the complete homology of the two forms of death. Without this assumption, his hypothesis of the immortality of unicellular organisms falls to the ground and with it falls the entire superstructure of his speculations upon germ plasm. Oscar Hertwig (*Zeit und Streitfragen*, Heft 1) has already expounded, very clearly, the dependence of the theory of germ plasm upon the hypothesis of unicellular immortality; it would, therefore, be superfluous to discuss it here.

The conception of the biological problem of death, to which I still hold, was formed several years before Weismann's first publication, which appeared in 1882, with the title, "*Ueber die Dauer des Lebens*." He has further defended his view in his article, "*Ueber Leben und Tod*" (1884), and has steadfastly adhered to it since. In the years 1877-1879 I published my theoretical interpretation of the problem.⁶ This interpretation became the starting point of elaborate special investigations, by which I endeavored to advance the solution of the problem and, in fact, observation and experiment have confirmed the

⁵ C. S. Minot, *On the conditions to be filled by a theory of life*, Proc. Amer. Assoc. Adv. Sc., XXVIII, 411.

⁶ Proc. Boston Soc. Nat. Hist., XIX, 167; XX, 190.

original thesis.⁷ Moreover, in an especial short article I have directed attention to the fact that Weismann has not considered the essential issue of the problem. The difficulties pointed out still remain, and, according to my conviction, cannot be removed. Weismann passes these difficulties by and carries out his speculations without first securing a basis for them. His method is illustrated by the following quotation: "I have, perhaps, not to regret that I cannot here discuss the article referred to (Minot's Article in *Science*, Vol. IV, p. 398); nevertheless, almost all objections which are there made to my views are answered in the present paper." (Weismann, *Zur Frage nach der Unsterblichkeit der Einzelligen*, Biol. Centralbl., IV, 690, Nachschrift). I have studied the paper with conscientious care and cannot admit that the objections have been answered. On the contrary, I maintain now, as formerly, the judgment: "He misses the real problem." For this reason I hold it to be unnecessary to discuss the details of Weisman's exposition, because—if I am right—he has not considered the actual problem of death at all. "He misses the real problem." The following reasoning leads to this decision: Protozoa and Metazoa consist of successive generations of cells; in the former the cells separate; in the latter they remain united; the death of a Protozoa is the annihilation of a cell, but the death of a Metazoon is the dissolution of the union of cells. Such a dissolution is the result of time, that is to say, of the period necessary to the natural duration of life, and we call it, therefore, "*natural death*." Moreover, we know that natural death is brought about by gradual changes in the cells until, at last, certain cells, which are essential to the preservation of the whole, cease their functions. Death, therefore, is a consequence of changes which progress slowly through successive generations of cells. These changes cause senescence, the end of which is given by death. If we wish to know whether death, in the sense of natural death, properly so called, occurs in Protozoa or not, we must first pos-

⁷ *Journal of Physiology*, XII, and *Proc. A. A. A. S.*, XXXIX, (1890).

sess some mark or sign, by which we can determine the occurrence or absence of senescence in unicellular organisms:

Around this point the whole discussion revolves. Certainly a simpler and more certain conclusion could hardly be drawn than that the death of a Metazoon is not identical, *i. e.*, homologous with the death of a single cell. Weismann tacitly assumed precisely this homology, and bases his whole argument on it. In all his writings upon this subject, he regards the death of a Protozoon as immediately comparable with the death of a Metazoon. If we seek from Weismann for the foundation of this view we shall have only our labor for our pains. Starting from this view Weismann comes to the strictly logical conclusion that the Protozoa are immortal. This is a paradox! In fact, if one compares death in the two cases, from Weismann's standpoint, then we must assume a difference in the causes of death, and conclude that the cause in the case of the Protozoa is external only, while in the Metazoa it is internal only, for, of course, we may leave out of account the accidental deaths of Metazoa. If we approach the problem from this side, we encounter the following principal question: Does death from inner causes occur in Protozoa? Weismann gives a negative answer to this question, with his assertion that unicellular organisms are immortal. The assertion remains, but the proof of the assertion is lacking. In order to justify the assertion, it must be demonstrated that there does not occur in Protozoa a true senescence, showing itself gradually through successive generations of cells. Has Weismann furnished this demonstration? Certainly not. He has, strictly speaking, not discussed the subject. It is clear that we must first determine whether natural death from senescence occurs in Protozoa or not, before we can pass to a scientific discussion of the asserted immortality of unicellular beings. The problem cannot be otherwise apprehended. Weismann has not thus conceived it, therefore the judgment stands against him: *he misses the real problem.*

Senescence has been hitherto little investigated; for many years I have been studying it experimentally and have tried

to determine its exact course. My paper, "Senescence and Rejuvenation," affords evidence of new facts proven by these experiments. I believe I have thus won the right to oppose my view to the pure speculations of Weismann.

(To be continued.)

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By C. W. STODOLSKY

III. A COMPARISON OF FERTILE AND INFERTILE

It has long been known that animals develop according to two types appearing in their younger stages without distinction of sex. The larvae had either the male and female characters or the female characters on the body, do not have a sex. They are nourished by the yolk accumulated in the parent. There is of course no sexual dimorphism between the two classes; nevertheless a general comparison between them establishes several conditions which show veridicality upon some recent biological hypotheses. First of all it must be remarked that the larval development has been a continuous one and that the embryonic development has been evolved later. Conditions are also to be noted which are not reported for this reason. In the lower animals we assume that the male and female characters are developed in the embryo and remain all their lives. In the higher animals, however, the male and female characters are developed in the embryo and remain all their lives. In the higher animals, however, the male and female characters are developed in the embryo and remain all their lives.

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(Continued from page 9.)

III. A COMPARISON OF LARVA AND EMBRYO.⁸

It has long been known that animals develop according to two types, appearing in their younger stages, either as larvæ or as embryos. The larvæ lead a free life and must obtain their own food. Embryos, on the contrary, do not lead a free life and are nourished by the yolk accumulated in the parent ovum. There is, of course, no absolute demarcation between the two classes; nevertheless, a general comparison between them establishes several conclusions which throw valuable light upon some recent biological hypothesis.

First of all, it must be remarked that the larval development is primitive, and that the embryonic development has been evolved later. Geologists are able to present two principal supports for this assertion: 1. In the lower animals we encounter only larvæ, never embryos; sponges, colenterates, echinoderms and worms, all pass through the early stages of

⁸ Read before the Amer. Soc. of Morphologists, December, 1893.

their ontogeny as larvæ. It would, therefore, be superfluous to linger for the defense of a view which is already accepted by all biologists. 2. The embryonic development depends on the presence of yolk. Now we have learned that the yolk has developed very gradually and in all the lower animals appears only in small quantities. It was not until the increase of yolk material had become enormous, as, for example, in the meroblastic vertebrates, that we find the development completely embryonic in type. With the increase of the yolk comes the gradual transition from larval to embryonic development. Since the embryo is dependent on the yolk, and since the yolk exists only in the higher forms in sufficient quantity, it follows that fully typical embryos can occur exclusively in the higher (later developed) animal types.

The fact that larvæ represent the primitive forms of development, obliges us to conclude that the correctness of Weismann's theory of the continuity of germ plasma can be tested better in larvæ than in embryos, since in embryos the relations have undergone profound modifications by secondary changes, which in this connection might easily deceive us.

I do not venture to assert that I know what the present form of Weismann's continuity theory may be; I hold, however, the exact form of this much discussed theory to be non-essential, because, according to my conviction, the theory can in no form be brought into agreement with our present knowledge. Nussbaum founded the theory, and opened the way along which we certainly hope to make great advance. Let me acknowledge the great value and the strictly scientific character of Nussbaum's work; doing this not merely because I esteem it, but also because the unjust attempt has been made to diminish his claim. Nussbaum⁹ thought that the germ cells are *direct* descendants of the fertilized ovum, keeping the germinating power, while the rest of the cells developed from the egg are transformed into the tissue of the body. He brought forward several facts which could be interpreted in favor of his theory. By this theory the whole problem of her-

⁹ M. Nussbaum, Zur Differenzierung des Geschlechts im Tierreich, Arch. f. Mikrosk. Anatomie, XVIII, 1--121, (1880).

edity and development was stated in an entirely new form. Since this publication of Nussbaum's we are seeking for the explanation of the germinating power, and the propagation of this power; formerly we sought for the causes of the inheritance of parental parts. The difference may be illustrated by the following example. Before Nussbaum we were ruled by Darwin's conception of Pangenesis, and we investigated accordingly for the agency by which the eye of the father reproduced itself in the child. Since Nussbaum we leave Pangenesis behind—it belongs henceforth to the past—and try to determine how the germinal substance behaves, and especially in what way it is perpetuated from the ovum through the following developmental stages, so that it is finally still present for the creation of the next generation. It is the conception of the continuity of the germinal substance which we prize so highly, and owe to Nussbaum.

Larvæ teach us that it cannot be special cells which affect this continuity. In fact, we find the organs of larval life fully differentiated before any sexual organs are recognizable, and indeed, in the majority of known larvæ we cannot recognize even the rudiments of the sexual glands. On the contrary, we find in larvæ unmistakably differentiated locomotive apparatus, such as cilia and often muscle fibres, a digestive canal, sensory organs, and, in many cases, also special excretory organs, and yet, only in a very few and exceptional cases can we distinguish the cells which belong to the future sexual glands. Thus, in regard to the primitive or larval type of development, we cannot say that the germ cells are constantly separated from the somatic cells during the segmentation of the ovum, but must rather draw precisely the opposite conclusion, namely, that the germ cells belong to the tissues which arise latest. We often meet many tissues in larvæ at a time when there is still no indication of germ cells. We find the same relations in embryos also, since in them the principal tissues become recognizable before germ cells are present. This fact was well established for vertebrates many years ago. It is characteristic of Weismann that he long defended the continuity of germ cells, in defiance of the facts. He has since

given up this wrong view and put in its place his hypothesis of the continuity of germ plasm. Of Nussbaum's conceptions, Weismann has left out the fruitful part, and has sown broadcast those ideas which were incapable of fruitful development. He has attempted to defend his notion of the difference between the elements of the embryo destined for the construction of the body, on the one hand, and those elements destined for sexual propagation on the other. Now, since the sexual cells usually develop from somatic cells, he was forced to assume that there is a mysterious substance which he names "*Keim-plasma*." This substance is supposed to store itself in the body by some secret way, to separate itself at command from the histogenic plasm, to appear unchanged and ready to be the exclusive agent of hereditary transmission.

Nussbaum furnished the conception of the continuity of germinal substance, which appears to be of immeasurable importance for the scientific investigation of the phenomena of heredity. But this continuity holds for all cells which arise from the fertilized ovum, as explained in the first section of this article. We must, therefore, seek for the causes of the differentiation of cells, that is to say, for the causes of the production of nerve cells, muscle cells, gland cells, etc, *and* of the production of germ cells.

I will now try to make clear the significance of the comparison between larvæ and embryos for the interpretation of germ cells. This calls for a short digression.

In the course of my investigations on "*Senescence and Rejuvenation*," of which only the first part has been published (*Journal of Physiology*, xii, 97), I learned that as cells become older there occurs an increase of the protoplasm in proportion to the nucleus, and I further succeeded in proving, as an essential process in reproduction, the formation of cells with comparatively little protoplasm. Further, it was found probable that a rapid multiplication of cells is only then possible when the cells have small protoplasmatic bodies (*Proc. A. A. A. S.*, XXXIX (1890)). We, therefore, have learned that the power of development depends on a special condition of the cell. By these facts I have been led directly to the following hypothesis:

The development of an organism does not depend on a substance stored in special cells, but on a special condition (stage) of organization. As a corollary of this hypothesis may be given this conclusion: *Germ plasm, in Weismann's sense, does not exist.*

According to my view, every part inherits from the germ, and every part of the animal body, as well as its germ cells, possesses the multiplying morphogenetic force, the action of which, however, is inhibited to the condition of the parts themselves. What this condition may be is not yet exactly known, but this much we do know, that the morphogenetic force is found in full activity in cells with little protoplasm. It is indeed highly probable that the slight development of protoplasm in proportion to the nucleus is an unavoidable condition of morphogenesis, or in other words, of the action of heredity. In fact we see that the first processes of development—as I have elsewhere explained (Proc. A. A. A. S., XIX)—show in the most varied cases a remarkable uniformity, for they always accomplish the production of cells with little protoplasm. Compare, in this respect, the vegetation points of plants, the root buds of slips, the budding zones of Annelids, the germinal layers of vertebrates, etc. The condition which allows the morphogenetic or hereditary force to act, arises under differing conditions, of which the fertilization of the ovum is one only.

Weismann tries to make comprehensible to us this one case, that of the fertilized ovum, by a special explanation which is available for no other case. Oscar Hertwig has recently (*Zeit und Streitfragen*, Heft I) clearly shown that Weismann's explanation is a speculative assumption, which can only be saved from rejection by numerous and often selfcontradictory additional assumptions. As I fully agree with Hertwig's criticism, I need only refer to his essay.

We will return to our proper theme. The next point is to determine whether there is a difference in the condition of the cells, as, regards their capacity for development, between larvæ, on the one hand, and embryos on the other. It can be proved that this is the case, by the following considerations. So far as we yet know, it is chiefly two factors which inhibit

development: *first*, the increase of protoplasm; *second*, the progress of organization, i. e., of differentiation.

As I was about to close this article, I received through the kindness of the author, Nussbaum's address on differation, in which he has defended essentially the same views as those which I hold. Such an agreement is of great value to me.

Now we know that larvæ are animal forms which have to obtain their own food and to protect themselves against enemies, and therefore are provided with differentiated tissues. Embryos, on the contrary, take their nutriment simply from the ovum, and the cells continue for a long time, developing and multiplying, while the protoplasm of the single cells increases very slightly, and *the beginning of the differentiation proper is correspondingly postponed*. I believe that we here have to deal with causal relations. From the actual relations just described, I conclude that the most essential difference hitherto known between larvæ and embryos, is to be found in the differing lengths of the period of multiplication of undifferentiated cells. In consequence of the shorter duration of the period in larvæ they have a much smaller total number of undifferentiated cells than embryos, or reversely expressed, embryos are much better equipped with material for the construction of the adult body, than are larvæ. As already stated, embryos are produced by the higher animals. This fact finds its explanation in the relations just described, because the increased number of undifferentiated, or so called embryonic cells, is precisely the necessary preliminary condition of the greater complexity of the differentiation by which the animal becomes more highly organized.

For the sake of clearness I have put aside all complications which might come in to play. It goes without saying, that the relations, in many respects, are by no means simple, nevertheless, the main conclusion above given seems a secure gain.

I therefore interpret the embryo as a device to render possible the increase of undifferentiated cells, and consequently a higher ultimate organization. The origin of this device is conditioned by a supply of food independent of the embryo.

From our present standpoint it is a matter of indifference whether the independent food supply comes from the yolk or from the uterus, however important the difference may be from other points of view.

It is to be further noted that our interpretation of the significance of the embryo is also opposed to Weismann's theory of germ plasm, because it emphasizes the importance of the *condition* as opposed to the assumption of a germinal substance or plasm. This road also leads to the conclusion reached above by other ways, the conclusion, namely: Reproduction involves rejuvenation, and rejuvenation is characterized by the production of cells with little, and that little not differentiated, protoplasm. Since rejuvenated cells arise by asexual as well as by sexual reproduction, since they appear in much greater numbers in embryos than in larvæ, and since they may be interpolated, as in the pupæ of butterflies, in the midst of the development of an individual, we must admit that the hereditary impulse (*vererbende Kraft*) is distributed in very different cells and is probably distributed equally through all cells. Hertwig has reached the same conclusion, with which Weismann's theory of germ plasm cannot be made to agree.

As Weismann has neglected the problem of rejuvenation, he has necessarily often gone astray in his discussion of phenomena in which rejuvenation plays the principal role. One is astonished at the slight attention bestowed on rejuvenation when one recalls that it is the central problem of all questions of heredity treated by him.

Rejuvenation is one of the principal phenomena of life, and the rejuvenated condition of the cell is probably an unavoidable preliminary of heredity. We know that at least one *anatomical* sign of the rejuvenated condition is to be found in the preponderance of the nucleus in proportion to the protoplasm; a second *anatomical* sign is found in the structure of the protoplasm, which, in young cells always remains without differentiation. The chief *physiological* sign of rejuvenation in cells which we as yet know is the power of rapid multiplication. Thus, we see, in case of sexual rejuvenation, that the

development of the fertilized ovum begins with an excessive proliferation of the nuclei, by which numerous cells are created, each with little protoplasm. Histogenetic differentiation begins later. The asexual rejuvenation has a similar course, but needs more thorough investigation.

Now differentiation is the sign of inheritance, and this morphological inheritance cannot develop itself fully until the senescence of the cells becomes recognizable by the growth of their protoplasm. On the other hand, we see complete inheritance develop itself, after preceeding rejuvenation. Accordingly we gain two conceptions: *first*, the hereditary impulse belongs to the inherent and constant properties of cells in general; *second*, the activity of their impulse may be inhibited by the condition of the cells. My view may be expressed in the following way: Somatic cells are simply cells in which the activity of the hereditary impulse is inhibited in consequence of their senescence, or, in other words, differentiation; but under suitable conditions the somatic cells may pass over into the rejuvenated stage, and thereupon develop the most complete hereditary possibilities.

The importance of rejuvenation must also be recognized when we consider the phylogenetic origin of single organs. Let us take a simple example. We may safely assume that the ancestors of mammals possessed a smooth skin, and that the covering of hairs is a new acquisition. Each hair is the product of a local growth. If we investigate the germ of a hair, we find that it consists of rejuvenated cells, that is to say, of cells with little protoplasm, or, as we are accustomed to say, of the embryonic type. Thus the formation of hairs depends on numerous centers of rejuvenation. In the multiplication of striped muscle fibres we find the agents to be the muscle buds, which are small, protoplasmatic structures, with relatively numerous nuclei. If we observe a developing gland, let us say a pancreas or a sweat gland, we find the rudiment to consist of rejuvenated cells; the cells multiply rapidly, and after the organ has its essential form, the histogenetic differentiation begins. It would be easy to multiply such examples a thousandfold.

The consideration of the role of rejuvenation in the origin of organs leads us to the theory of POST-SELECTION (*Nachauslese*). The theory is by no means new, but I wish to emphasize its far reaching importance. The preceding discussion teaches us to divide the origin of a new morphological part into two stages. The first stage is the development of the rudiment (*Anlage*) by multiplication of the cells. The second stage is characterized by the gradual differentiation of the cells, by which they become capable of their ultimate functions. Especially in embryos is the difference in time very marked between the formation and the differentiation of the "*Anlage*." Now it is evident that the undifferentiated "*Anlage*" is not useful, but becomes useful later. The formation and conservation of the "*Anlage*," therefore, are due to selection, working, not directly upon the "*Anlage*," but indirectly through preservation of the fully developed organ. The conception advanced is very simple and appears to me a necessary consequence of our knowledge. For the conception itself there has been hitherto no definite term, I propose, therefore, to call it "*Post-selection*" (in German, "*Nachauslese*"). To avoid possible misunderstanding, I give another example of post-selection. A parasitic wasp lays its egg in a certain caterpillar; the mother wasp gains no advantage, natural selection does not touch her, but only her progeny, the wasp larva. Nevertheless, the survival of the fittest rules.

In conclusion, I should like to direct the reader's attention to a problem which, so far as I am acquainted with the literature of biology, has been left almost unconsidered. This present translation enables me to insert a qualification of the preceding sentence, which ought to have been inserted in the original article, namely, that the problem has been the subject of important discussions by Hyatt, Cope and a very few others among paleontologists. I am glad to be able to refer to the article by Professor Hyatt, (see *Jan. Naturalist*) and presents the paleontological theory of the loss of ancestral characteristics. The problem above referred to is the *problem of lost characteristics*, which seems to me one of the fundamental problems of the doctrine of evolution, because we cannot un-

derstand the development of the higher organisms until this problem is solved. Everybody is writing about the origin of new organs, and we take lively pleasure in discussions about acquired characteristics. But if we consider the circumstances closely, we recognize that the loss of ancestral characteristics almost equals in importance the acquisition of new characteristics for the formation of new species. We assume that man had fishlike ancestors, and we strengthen ourselves in this belief by the comparison so often made between the human embryo, on the one side, and the adult fish on the other. But if the comparison be impartial we are forced to admit that nearly everything which is most characteristic of the fish is conspicuously lacking in the human embryo. Taking the embryo at the stage when the gill clefts have their maximum development, we find the following relations: the body is not straight but coiled up, and this coiling up is indispensable, in order to bring about the proper distribution of the human nerves, blood vessels, and so forth; the gill clefts are closed; gills are wanting; the digestive canal has no glands; the epidermis has no scales; the chorda dorsalis does not form a large axis of the body, but is a minute string of cells. In short, the *Biogenetisches Grundgesetz* (Recapitulation theory or von Baer's law, according to Adam Sedgwick) is scarcely half true. I have previously defended this conclusion at a meeting of the American Society of Morphologists, in December, 1893. Subsequently, but independently, Adam Sedgwick has reached a similar conclusion, see his paper "*On the Law of Development, etc.*" (Quart. Jour. Micros. Sci., XXXVI, 35). Were it not, as above implied, that the departures from the fish type are in great excess, there would be no embryo at all, and consequently no man, for the adult form is a consequence of the embryonic. The embryo is the mechanical cause of the adult body. How has the disappearance of the ancestral fish characteristics been effected? The question remains unanswered. It will, perhaps, be replied "through disuse" or "through panmixia." But "disuse" is merely a name, not an explanation of the phenomena. Panmixia is an hypothesis erected on nothing. In fact, this hypothesis as-

sumes that the majority of variations fall below the value maintained by natural selection, and consequently that when the influence of natural selection is eliminated (as in disuse), the mere variation will bring the traits concerned to disappearance. It marks Weismann's style of thought to find that he has entirely omitted to determine whether his assumption was correct, and nevertheless in his book, "The Germ Plasm," presents panmixia as an established law. As a matter of fact, the statistics of variations which we already have, show that his assumption is erroneous, and that it is equally probable that mere variation will magnify a characteristic as it is that it will diminish it.

Let us return to the embryo. The following hypothesis may be advanced :

The loss of ancestral characteristics in the embryo is due to post-selection, the cells being kept in a rejuvenated stage, in order that they may afterwards accomplish new differentiations.

This conclusion follows directly from the preceding considerations, and, therefore, needs no further defense.

IV. CONCLUDING REMARKS.

The views presented in the preceding sections are intimately connected one with another and collectively determine our conception of the process of heredity. The conception concerns only the process and not the essential character or cause of heredity. According to my view, heredity exists in all cells, but its display is inhibited by organization of the living substance, and can be complete only in embryonic cells; embryonic cells arise under very various conditions. That which is novel in this theory is the significance attributed to embryonic cells. Embryonic cells I prefer to designate as rejuvenated cells.

The theory above presented is an unavoidable consequence of the facts known, and stands in absolute contradiction with Weismann's theory of the germ plasm.

I have read with the greatest conscientiousness every article hitherto published by Weismann, which deals with his theories of heredity. My final impression from this study is that

the "*Theory of Germ Plasm*" corresponds to the personal inclinations of its author and is in no sense a logical deduction won by the collation of facts. The assumption of a difference between germ plasm and histogenic plasm explains nothing. Even according to Weismann's own exposition it explains nothing, for the supposed phenomena which the assumption is said to explain, according to Weismann, do not exist. According to him, the circumstances are the following: The phenomena due to the germ plasm do not occur in somatic cells, therefore they have a different plasm, namely, histogenic; further, these phenomena do occur in somatic cells, therefore, they have germ plasm. Attention must be directed also, and explicitly, to the fact that Weismann offers no *observations* to support his fundamental assumption. His theory is mystical to an extreme degree. In Weismann's book, "*The Germ plasm*," one finds one hypothesis after another in order to support his tottering first hypothesis—germ plasm and histogenic plasm are special and separate substances. I demand of Weismann that he lay aside *all his hypotheses*, and present to us solely the *facts*, which support his theory of germ plasm. Then he will learn, as other investigators have already learned, that his hypothesis has been built up without sufficient foundation.

Let an investigator enquire for a possibility of testing the existence of the "Ids," "Biophors," "Determinants," etc., asserted by Weismann, and he will discover that the whole fabric is woven by speculative imagination. Confirmation of his ideas has, strictly speaking, not been attempted by Weismann. Indeed, confirmation is altogether impossible, for his conceptions are far beyond the limits of present human means of investigation.

It is time to finally discard a theory which leads astray and which, although it arose without scientific justification, is again and again pushed to the front by its promulgator. It is a scientific duty to take an unhesitating stand against Weismann's theory, for only so can it become known that those who have specially occupied themselves with the problem of heredity reject Weismann's theory of germ plasm unconditionally.

APPENDIX.

THE THEORY OF PANPLASM.

It appears desirable that the modern theory of heredity should be designated by a brief and appropriate name, and accordingly I propose the term "*Panplasm*," and that the theory be called "The Theory of Panplasm." By panplasm will be understood the physical basis of hereditary transmission, which is supposed to be distributed through all cells, and which accounts for the phenomena of sexual reproduction, regeneration and asexual reproduction. Panplasm is not a collection of gemmules or biophors. The term "panplasm" was first used by me at a meeting of the Society of Arts, in Boston, November 14, 1895.

On another occasion I hope to discuss the theories of pan-genesis and panplasm in their historical aspects.

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