B. Prevailing Views on the Bearers of Hereditary Characters

CHAPTER II

THE SIGNIFICANCE OF THE CHEMICAL MOLECULES OF THE PROTOPLASM WITH REFERENCE TO THE THEORY OF HEREDITY

§ *1. Introduction*

According to our present conception of all nature, the wonderful phenomena of heredity must have a material basis, and this basis can be no other than the living protoplasm. Every cell originates through the division of one that already exists; the living substance of the mother-cell is distributed among the individual daughter-cells and passes into them with all its hereditary qualities. Microscopic investigation of the cell-body and the art of the breeder, so far apart from each other until recently, come nearer and nearer to working hand in hand. And it is only through the co-operation of these two great lines of human thought that we can succeed in establishing the basis for a theory of heredity.

Chemistry teaches us that living protoplasm, like any other substance, must be built up of chemical molecules, and that a final explanation of the phenomena of life can be reached only when we shall succeed in deriving the processes in protoplasm from the grouping of its molecules, and from the composition of the latter out of their atoms.

We are still, however, very far from this goal. The chemists study chiefly pure bodies, that is, such as are built up from like molecules; but protoplasm is evidently a mixture of numerous, if not of almost countless different chemical compounds. And by far the most of these latter have been, even chemically, only very incompletely investigated.

Of course, this consideration must not keep us from utilizing the great truths of chemistry in the explanation of life processes. Haeckel, and many other investigators after him, have pointed out the great significance, for such an explanation, of the power of carbon to combine in the most varied relations with other elements. "This, in its way, unique property of carbon we must designate as the basis of all pecularities of the so-called organic compounds."[1] The differences, which occur in the growth of organic and inorganic individuals, are due to the more complex chemical composition and the power of imbibition of many carbon-compounds,[2] *et cetera.*

In chemistry also this importance of carbon has been emphasized. In his *Views on Organic Chemistry,* van't Hoff[3] says: "From the chemical properties of carbon it appears that this element is able, with the help of two or three others, to form the numberless bodies which are necessary for the manifold needs of a living being; from their almost equal tendency to combine with hydrogen and oxygen, follows the capacity of the carbon-compounds to be adapted alternately for processes of reduction and of oxydation as the simultaneous existence of a vegetable and an animal kingdom requires." And, after a discussion of the influence of temperature on the change of the chemical property of carbon, he continues: "Therefore, one does not go too far in assuming that the existence of the vegetable and animal world is the enor-

[1]Haeckel, E. *Generelle Morpholgie.* **1:** 121. Berlin. 1886.

[2]Loc. cit. p. 166, and Haeckel, E. *Die Perigenesis der Plastidule.* p. 34. 1876.

[3]Van't Hoff. *Ansichten über die organische Chemie.* **1:** 26. 1878.

mous expression of the chemical properties which the carbon-atom has at the temperature of our earth."

Furthermore if we take into consideration the numberless isomers, which especially the more complicated compounds of carbon, such as protein bodies, can form, according to the present chemical theories, there can hardly be any doubt that we shall some day succeed in reducing the hereditary characters of all organisms to chemical differences of their protoplasmic basis.[4]

But, much as such general considerations may help to further our need for a uniform conception of all nature, they are still far from serving us, especially at the present time, as a basis for a theory of heredity.

Experimental physiology of plants and animals has succeeded in reducing many of the processes of life to the chemical effects of the involved compounds, to repeat them in part outside of the organism, but in part also to demonstrate the fact that their behavior in the living body is ruled by the general laws of chemistry. Into an understanding of the processes of breathing, nutrition, and metabolism we have been initiated in a simply astonishing manner by numerous investigators, and the purely mechanical manifestations of energy which accompany growth and motion have also, in great part, been analyzed and reduced to general laws. But the chief discovery of these studies is that two kinds of processes occur in the living body. In the first place, those that are separable from living substance, and can therefore be artificially imitated, or even exactly duplicated. In the second place, those that are inseparable from that substratum, and which indeed find their existence in the

[4]Cf. Haeckel, E. *Generelle Morphologie.* **1:** 277, and Sagiura, Shigetaké. *Nature* **27**: 103. 1882.

processes of life of that very substratum. The former processes are purely physical or chemical; in a word, they are aplasmatic processes; the latter ones we must designate as plasmatic; that is, as taking place in the molecules of the living protoplasm itself. The former belong to physiological chemistry and physics, the latter form the proper subject of physiology. But toward an understanding of the latter we have taken only the first steps.

It is neither by general considerations, nor on an experimental basis, that we can penetrate, at the present moment, into the relations between the qualities of the chemical molecules of the protoplasm and the phenomena of heredity. It can therefore be only a matter of trying, by means of hypotheses, to get an insight into these relations.

It is evident that we are justified in making such an attempt. This right is very generally acknowledged, for several prominent investigators have published their views on this subject. Some have even made their hypotheses accessible to the critical consideration of others by working out logically the consequences arising therefrom. And certainly, no one can doubt for a moment that these hypotheses, much as they differ at present, have aroused scientific interest in these questions.

The directions which these hypotheses take can, I believe, be summarized under three heads. Some authors go directly back to the chemical composition of protoplasm and seek to derive the life-processes from it. Others again assume that the chemical molecules are combined into larger, but still invisibly small organic units, and regard these units as the real bearers of heredity. Some of them imagine that these units always represent the whole specific character, and that therefore the individual bearers of heredity in the same cell, with the exception of insignificant differences, are alike. Finally, there is the directly opposite opinion of those investigators who assume a special kind of material bearer for every individual hereditary character; and according to whom, therefore, protoplasm is built up of numberless unlike hypothetical units.

It is these three different principles that we will subject to a thorough comparative examination in this and the two following chapters. Before doing so, however, we must first critically consider the relation between protein substances and protoplasm.

§ 2. *Protoplasm and Protein*

Lately the conceptions of protoplasm and protein have been confused by many authors.[5] This has led to the hypothetical, and in no way justified assumption of a living protein.[6] This usage has exercised its influence, even on the theory of heredity, and for this reason it should not remain unmentioned here. Without this confusion, the view which regards the chemical molecule of protoplasm as the bearer of the hereditary characters would probably never have met with any favor.

Protein is a chemical, protoplasm a morphological concept. Chemistry is able to produce many pure proteins, while the nature of protoplasm is conditioned by its very heterogenous composition. Many protein bodies can pass into solution, but nobody will ever think it possible to obtain a solution of protoplasm in a test-tube.

[5]Haeckel refers to protoplasm as a protein body: *Generelle Morphologie.* **1:** 278.

[6]A term proposed by Pflüger. *Arch. Ges. Physiol.* **10:** 251. 1875. *Tr.*

Protein bodies are indeed products of life, but not the bearers thereof; they do not offer us, in the chemical laboratory, any essentially different quantities than the other more complicated compounds. Protoplasm, however, is the bearer of life; it is distinguished from all chemical substances by its power of assimilation and of reproduction. The nature of these two processes will undoubtedly be recognized some day, but up to the present time they are still in complete darkness, and even the boldest minds have not yet succeeded in lifting even as much as a corner of the veil that covers them.

The designation of protoplasm as a protein body, or as a mixture of such bodies, is based upon chemical analyses and micro-chemical reactions. The latter undoubtedly betray the quite common presence of protein in protoplasm. But the explanation of this fact is obvious. Protein can very well be dissolved in the water of imbibition of protoplasm, since it can be proven to occur frequently in solution in the cell-sap. It is even not improbable that, in killing the protoplasts, protein bodies are frequently formed. But, in order to be able to assert that protoplasm and protein are identical, it ought at least to be demonstrated that protein-reactions are lacking neither in any protoplasm nor in any individual organ thereof. But such does not, by any means, appear to be the case.[7] Nucleus, trophoplast, and nucleo-plasm, have, it is true, never been observed without protein, in well nourished cells; but, whether the wall of the vacuoles and the plasma-membrane are structures that contain protein, *is still very questionable.*[8]

Chemical analyses have, without doubt, brought to

[7]Cf. Zacharias, E. *Bot. Zeit.* **4**: 209. 1883.
[8]Cf. *Jahrb. Wiss. Bot.* **14**: 512. 1883.

light important conclusions concerning many compounds developed from protoplasm. But whether those compounds were present, as such, in the living protoplasm, or have only developed after death, or through the influence of reagents, as products of decomposition, is another question.

The chief point for the theory of heredity is, however, that protoplasm always offers us certain historical characters besides physical and chemical properties. It is to these that it owes its peculiarity. A synthetic composition of protein bodies is no longer regarded by anybody as an impossibility; but whether we shall ever succeed in obtaining living protoplasm in any other than the phylogenetic way, will probably remain for a long time a matter of well-founded doubt.

The historical characters demand a molecular structure of such complicated nature that the chemistry of the present time fails us entirely in our attempts at an explanation. For the present, therefore, theory must be content to accept the idea that protoplasm is composed of morphological units. These, of course, must themselves be built up from chemical molecules, and among the latter the protein bodies must play an important rôle. To conclude from this fact, however, that protoplasm itself is a protein body, seems not at all justified.

Those invisible morphological units are of a hypothetical nature and we will not follow up this subject any further in this connection. I only wished to show how this consideration also, leads us to that assumption of pangens, with which we shall have to deal in the last two chapters of this section.

§ 3. *Elsberg's Plastidules*

The most thorough attempts to explain the phenomena of heredity by the qualities of the molecules of living matter were made by Louis Elsberg and Ernst Haeckel. Elsberg, who called the cells plastids, chose for the component particles the name of plastid-molecule or, abbreviated, plastidule.[9] Haeckel considered this expression a brief and suitable designation for the polysyllable protoplasm-molecule,[10] and secured general consideration for the term in his "Perigenesis of the Plastidule."[11]

According to Elsberg, living matter consists entirely of plastidules which multiply in such a manner, through nutrition, assimilation, and growth, that new molecules with the same characters as those present, are constantly developed. At each cell-division these are transmitted to the daughter-cells. The resemblance of children to their parents, grand-parents, and ancestors is explained in a simple manner by saying that they are essentially built up of the same kind of plastidules, which they have inherited from their ancestors. All individuals of one species consist, on the whole, and apart from incidental varieties, of the same plastidules; every species, however, contains the plastidules of its whole ancestry, and consists therefore, of as many different plastidules as there were different species in this ancestry. The differences between individual species are conferred by their

[9]Elsberg, Louis. Regeneration, or The Preservation of Organic Molecules: a Contribution to the Doctrine of Evolution. *Proc. Amer. Assoc. Adv. Sci.* **23:** 1874; and Elsberg, Louis. On the Plastidule Hypothesis. *Ibid.* Buffalo Meeting, August, 1876. **25:** 178. 1877.

[10]Haeckel, E. *Jenaische Zeits. Med. Naturw.* **7:** 536. 1873.

[11]Haeckel, E. *Die Peregenesis der Plastidule.* p. 35. Berlin, 1876.

descent, and are, therefore, materially based on the differences of the plastidules. Systematic affinity depends upon the possession of the same plastidules, systematic differences on the presence of different molecules in addition to the bulk of those that are alike.

Haeckel, who, in his "Generelle Morphologie," had not yet considered the significance of the molecule for the theory of heredity,[12] has further carried out Elsberg's train of thought[13] in his above mentioned monograph. "The sum total of physical and chemical processes, called life, is evidently conditioned in the last instance by the molecular structure of the plasson."[14] In the non-nucleated plasson (or protoplast) the plastidules are everywhere uniform; in the nucleated ones they are differentiated in such a manner that a distinction must be made between plasmodules and coccodules (nucleo-molecules). The differentiation of the organism into organs, and the division of labor thereby achieved, Haeckel attributes to a division of labor of the plastidules, for in this way they are segregated more or less, and thus produce the various kinds of protoplasm. Fertilization consists in the fusion of two protoplasts which have developed in different directions through a far-reaching differentiation of their plastidules.[15]

We will limit ourselves to this part of the theory of

[12]Only in a general way does Haeckel point here to the significance of "the numerous and minute differences in the atomic constitution of the protein-compounds, which form the plasma of the plastids." *Gen. Morphol.* **1:** 277.

[13]Elsberg later *(Proc. Amer. Assoc. Adv. Sci.* **25:** 178. 1877.) insisted that he had been misunderstood and misinterpreted by Haeckel in the monograph above referred to. *Tr.*

[14]*Perigenesis.* p. 34.

[15]*Loc. cit.* p. 52.

the plastidules, and not enter into the speculations on the undulating motion of these particules. But, in critically discussing that part, we can emphasize here the fact that the theory is composed of two hypotheses:

1. Protoplasm is made up of numerous small units, which are the bearers of the hereditary characters.
2. These units are to be regarded as identical with molecules.

The first of these two hypotheses has obviously very great advantages. It explains the fundamental phenomena of heredity in a simple manner, and especially accounts sufficiently for the independence and miscibility of the individual hereditary characters. It is identical with the first law of Darwin's pangenesis, as we shall see more in detail in the third Chapter. We shall, therefore, put off a more thorough discussion, especially as Elsberg wrote a few years later than Darwin, and in not nearly as clear a manner.

Let us now turn to a criticism of the second thesis. Elsberg never expresses himself clearly about the identity of his plastidule with chemical molecules. He defines them as the smallest particles of a cell in which the hereditary characters lie hidden.[16] These particles must be larger than the molecules of the ordinary protein bodies; this follows from their much more complicated character. Haeckel, however, devotes a detailed discussion to this identity.[17] "The plastidules possess, first of all, every quality which physics ascribes generally to the hypothetical molecules, or combined atoms. Consequently each plastidule cannot be analyzed any further into smaller plastidules, but only into its component atoms. . . ."

[16]Elsberg. *loc. cit.* p. 9.
[17]Perigenesis *loc. cit.* pp. 35-36.

As long as we are concerned only with the explanations of the chemical processes in cell-life, this hypothesis is certainly highly satisfactory. The production of various compounds, as for example, the red coloring matter of a flower, can be imagined as a function of definite molecules of the protoplasm, more or less in the same manner as the action of enzymes or chemical ferments. Even the secretion of cellulose one might try to explain thus by analogy. As soon, however, as we have to do with morphological processes, this hypothesis fails us entirely, because the frequently attempted comparison with the formation of crystals furnishes only a remote similarity. The hypothesis is quite useless when applied to that peculiar attribute of life, growth through assimilation. It is obvious that any attempt to explain life-processes from the properties of chemical molecules must consider this phenomenon first of all. But in the great realm of the lifeless there is no analogy for it. Chemical molecules do not grow in such a way as to separate later into two molecules which are like the original one. They *do not assimilate, and in this sense they are not capable* of independent multiplication. They do not possess any qualities at all from which one could at present hypothetically explain a growth through assimilation.

Here lies the great difficulty of the plastidule hypothesis. Indeed, Haeckel says, "Besides the general physical properties, which modern physics and chemistry ascribe to the molecules of matter in general, plastidules possess some special attributes which are exclusively their own, and these are, quite generally speaking, the life-attributes which, according to the present conception, distinguish the living from the dead, the organic from the inorganic." But it is easily understood that by such an ancillary hypothesis the meaning of the hypothesis as a whole is changed. For, with the same right, one might say that the plastidules are not molecules at all, in the sense of physics, but are distinguished from them by their very life-properties.

It would be easy further to criticise the plastidule-hypothesis in the same direction. It leads to pure speculation. According to Haeckel, we must attribute sensation and will power to atoms.[18] The plastidules possess memory, according to his theory; this faculty is lacking in all other molecules.[19] We shall not discuss, either, the wave motion of the plastidule.

What is of interest to us, is to show that any attempt, at the present time to reduce life-phenomena to the properties of the molecules of living matter, is, to say the least, premature. We must either limit ourselves, with Elsberg, to such deductions as can be derived from Darwin's gemmule-hypothesis, or be compelled to resort everywhere to ancillary hypotheses, in place of explanations. If we choose the first method, we arrive naturally at the assumption of invisible units, of a higher order than the molecules of chemistry, and of such a complicated composition that every one of them must be made up of a large number of chemical molecules. To these units we must attribute growth and multiplication as qualities which so far cannot be explained. In a like inexplicable manner we must further assume that they are the material substratum for hereditary characters. Leaving this part unexplained, we can clear up many other things. But in that case we cannot revert to the molecules of protoplasm.

[18]Haeckel *loc. cit.* p. 38.
[19]*Loc. cit.* p. 40.

Therefore the material bearers of hereditary characters cannot be identical with the molecules of chemistry; they must be conceived of as units, built up from the latter, much larger than they, and yet invisibly small.

It does not seem to me correct to apply the name molecule, or living molecule, to these units. This appellation must lead to confusions and misunderstandings, and I suppose it is employed only from lack of a simple designation. As such a term, the name "pangen," proposed in the Introduction (p. 7), may be adopted.

Chapter III

THE HYPOTHETICAL BEARERS OF SPECIFIC CHARACTERS

§ 4. *Introduction*

The majority of investigators assume that the material bearers of hereditary characters are units, each of which is built up of numerous chemical molecules, and is altogether a structure of another order than the latter.

Growth through assimilation, and multiplication by division are always assumed for them. For this reason, as Darwin has already said, they are rather to be placed in a class with the smallest known organisms, than with the real molecules. An explanation of these properties is not attempted; they are simply accepted as a fact. Neither does the theory of heredity require such an explanation; it can, for the time being, be reserved as a problem for a later theory of life.

A second assumption in regard to the nature of those hypothetical units is still needed; namely, one concerning their relation to the hereditary characters. As to the manner in which the latter are determined by the structure of the bearers no suppositions are yet made, for the theory of heredity does not, for the present, need this elaboration. The only question is, whether the units are the bearers of all the specific attributes, or of the individual hereditary characters only. Spencer and Weismann are the chief representatives of the first view, Darwin's pangenesis assumes the latter.

We have now critically to compare these various opinions. In doing so the chief question is in how far the hypotheses themselves, as they have just been described, and without further ancillary hypotheses, can lead to an explanation of the phenomena of heredity.

§ 5. *Spencer's Physiological Units*

In his famous system of Synthetic Philosophy, Herbert Spencer attempted, probably for the first time, to formulate a material conception of heredity. His Principles of Biology, which form the second and third volume of that system, appeared in 1864 and 1867, therefore before the publication of Darwin's pangenesis (1868). His train of thought is essentially as follows:

Bud-formation from leaves, et cetera, teaches us that the living particles of these organs possess the power of reproduction, which is also shown in animals by the restoration of lost members. Now these particles cannot be the cells themselves, because some cells can also replace lost parts. Just as little can they be chemical molecules, because these are much too simply constructed for an explanation of all the morphological differences. They must, therefore, be units of intermediate size, invisibly small, but composed of numerous molecules. Spencer[20] calls them *physiological units*.

Every one of these units represents the entire specific character; slight dissimilarities in their structure cause the differences between allied species (p. 183).

Spencer finds it difficult to explain fertilization. There is no sense in it unless there is some kind of difference between the two groups of physiological units.

[20]Spencer, H. *Principles of Biology.* Ed. 2. 1: 180-183.

This makes him assume that the units of different individuals are slightly dissimilar. From this it follows that in the child the two kinds of units of both parents are mixed, in the grandchild the four different units of the grandparents, and so on. In this way one would arrive at just the opposite of what was at first assumed, namely, the similarity of all units in the same individual (pp. 253, 254, and 267).

To escape this difficulty Spencer points to hybrids. In these the physiological units of two species are mixed. The hybrids are liable to be inconstant in the following generations, and to revert to the parental forms. Therefore the unlike physiological units oppose a mixture, they repulse each other, and try each, by excluding the dissimilar kind, to form the whole individual (p. 268). In the same manner the unlike physiological units exclude each other in normal fertilization, and in this way uniformity within the individual is sufficiently assured.

The physiological units multiply at the expense of the nutrient material (p. 254) and thus produce, as a rule, new units that are quite alike. Under the influence of external circumstances, however, they sometimes undergo slight changes during the process of their multiplication, and this is the cause of their variability (p. 287). Through fertilization, however, the balance thus disturbed is regained (p. 289).

On this basis heredity is easily explained; it is founded on the fact that the child receives from father and mother the material units that go to make up its characters. Strong resemblance of the child to one of its two parents is due to the predominance of the respective physiological units; atavism depends upon the presence of units inherited from some given ancestor. Many other phenomena are explained by Spencer in a similarly simple manner.

Spencer's theory has, without doubt, the advantages of a clear and concise system. But it does not take into account the train of thought developed in our first section. On the basis of those general considerations, therefore, the theory is insufficient. Especially can it not explain in a satisfactory manner the differentiation of organs, and any attempt to bring it into accord with this process would prove its fundamental inadequacy. Since the same thing is likewise true of Weismann's theory of the ancestral plasms I refer the reader, in regard to it, to the conclusion of the next Section.

§ 6. *Weismann's Ancestral Plasms*

In a series of thoughtful writings during the last decade, August Weismann has aroused the general interest of the scientific public in the principles of heredity. In doing so, he used, as a basis, the most recent achievements in the domain of cell-theory and the process of fertilization.

Proceeding from the conviction that the development of children from material particles of their parents is the cause of heredity, and that the solution of the great mystery is, in truth, to be looked for in the molecular structure of the protoplasm, he tries to form a definite conception of this structure. He begins by saying that, in lower organisms, which do not possess a sexual differentiation, the germ-plasm of each individual must still be completely uniform. During fertilization, however, a mixing of the two parental germ-plasms must take place, and thus in the child there are mixed two, in the grand-child four kinds of germ-plasms.[21] In the children of the first sexually produced generation there will be only one-half of the original amount of the two kinds of germ-plasm, in the grand-children only one quarter. In every succeeding generation the germ-plasm will consequently consist of a larger number of unlike units, the so-called ancestral plasms. But this can only continue until the number of the ancestral plasms has reached that of the smallest units of the entire hereditary substance. These units, originally quite alike, are so no more, but each possesses the tendency to transmit, under given conditions, to the new organism, the totality of the characteristics of the respective ancestors.

If now sexual propagation takes place in a species with this kind of compound germ-plasm, (and all living, sexually differentiated species must obviously have reached this stage long ago), a further multiplication of the ancestral plasms within the germ-plasm can no longer continue. Therefore the number of the ancestral plasms must be reduced from time to time. In the separation of the polar bodies from the egg before fertilization, he sees a process, the result of which is just this reduction.[22]

This reduction in the egg of the number of hereditary particles, as Weismann calls them, is obviously a necessary consequence of the original assumption of the uniformity of the germ-plasm. It is very instructive that two such prominent thinkers as Spencer and Weismann, starting from the same hypothesis, have arrived at an ancillary hypothesis which is intrinsically the same. One may well conclude from this that whoever does not wish

[21]Weismann, A. *Ueber die Zahl der Richtungskörper,* p. 30. 1887.

[22]*Loc. cit.* p. 32 ff.

to accept the ancillary hypothesis must also give up the principle of the uniformity of the germ-plasm.

Weismann has connected his theory in a clear way with the results of cell-study. He assumes that the nucleus dominates and determines the nature of its cell, and also that, for all functions of the cell, the material bearers of the hereditary characters must be situated in the nucleus. He assumes further that these bearers are arranged in rows on the chromatin-thread of the nucleus, and points out how, with this assumption, all the hereditary characters are divided through the longitudinal splitting of the nuclear skein, and how they are distributed among the two daughter-cells.

On the basis of these and similar conceptions, he also treats the question concerning the cause of the differences between the single organs of an individual. It is clear that this question forms a great difficulty of the theory. For the assumption of the ancestral plasms, every one of which represents all the characters of the individual, can, of itself, not serve as an answer, especially in connection with the thesis just mentioned, that the nature of the nucleus determines the character of its cell.

Let us see what ancillary hypothesis Weismann uses. The theory of heredity demands that, on the germ-tracks,[23] the completeness of the germ-plasm be preserved, for every egg-cell and every bud contain, on the whole, the same hereditary elements as the germ-cells of the previous generation. In all the sequences of generations of cells, which lead from one egg-cell to the germ-cells that come next in order, (and these are the germ-tracks), the germ-plasm must therefore remain the same. In all other cells, however, which do not belong to the organs capable

[23]Cf. Part II, A. p. 79.

of reproduction, this, according to Weismann, need not be the case. On the contrary, from the one-sided differentiation of these cells, he believes that there is a corresponding reduction of their germ-plasm. Every somatic cell receives, at the time of its origination, only those hereditary elements which will be needed by itself and its descendents.

Against this assumption objections have been raised from different sides, and some of them we shall describe in detail in the Section on cellular pedigrees. Here, however, we must enter into the principal phase of the question, namely, the relation of the ancillary hypotheses to the main principle of the author.

That principle is the assumption of units, of which every one is capable of reproducing all, or at least nearly all, hereditary characters of the species. There is supposed to be, for each individual, only one hereditary substance, only one material bearer of the hereditary tendencies.[24] To be sure, this is composed of ancestral plasms which differ only slightly. A check must necessarily be put to an excessive accumulation of various hereditary tendencies by some kind of an arrangement. But, as we have seen in our first section, the differentiation of the organs demands the divisibility of the units of the germplasm, and this in exactly the same high degree that the differences of the individual organs and cells of an organism reach themselves. In the somatic cells the germplasm must therefore gradually become divided into those components, and hence, these are the bearers of the individual hereditary characters.

Let us continue to build a few moments longer on this conclusion, without reference to the chief assumption. In

[24] *Ueber die Zahl der Richtungskörper*, p. 29.

that case the germ-plasm must evidently consist, everywhere, of these same components, and, in the lowest organisms, in which fertilization does not take place, as well as in the germ-cells of the higher plants and animals, we must assume, as the material basis of heredity, numerous material bearers, which correspond to the individual hereditary characters, and are not inseparably united. This assumption, however, makes that of the ancestral plasms completely superfluous. Thus it is easily seen that the whole ancillary hypothesis regarding an occasional numerical reduction of the ancestral plasms may fail.

In a word: In a consideration of the differentiation of organs, Weismann's theory of itself leads to the quite opposite assumption of individual material bearers for the individual hereditary characters.

§ 7. *Nägeli's Idioplasm*

In his mechanico-physiological theory of descent, Nägeli, a few years ago, advanced the concept of the idioplasm[25] In distinction to the other protoplasms, it is the bearer of the hereditary qualities. A factor *(anlage)* representing every perceptible character, is present in it; in every individual of the same species, even in every organ of a plant, it has a slightly different composition. It is not limited to the nucleus, but runs through the entire protoplast as a strand with many windings. All cross-sections of this strand are alike, each one containing every hereditary tendency. That is why, in cell-division, the daughter-cells, with their part of the strand, are also endowed with all the hereditary factors.

The nature of the idioplasm is determined by its mole-

[25]Nägeli, C. von. *Mechanisch-physiologische Theorie der Abstammungslehre.* pp. 21-31. 1884.

cular composition, and especially by the arrangement of its smallest particles. These are combined in hosts, which again are united into units of a higher order. The latter represent the primordia of the cells, tissue-systems, and organs. The idioplasm is a rather solid substance, in which the smallest particles do not undergo any shifting *through the* forces at work *in the living* organism, for it is precisely the mutual arrangement of the molecules that determines the nature of the hereditary factors.

The characteristics, organs, adaptations, and functions, which are all perceptible to us only in a very composite form, are, in the idioplasm, resolved into their real elements. These elements are obviously the individual hereditary factors, through the manifold changing combinations of which the visible characters originate. These elements themselves are not strongly emphasized by Nägeli; he lays greater stress on the fact that their properties are conditioned by their molecular structure, and that they themselves, by their mutual association with each other, again build up the entire idioplasm.

No definite conclusions can be drawn from the theory in regard to the arrangement of the elements in the idioplasm, nor in regard to the question of how the idioplasm develops its factors; here a wide field is still open to hypotheses.[26] In general, however, the definite mutual arrangement of the elements forms the chief points in which Nägeli differs from his predecessors. Neither Spencer nor Weismann enter into this question, and Darwin's pangenesis supposes a relatively loose combination of those elements, which does not hinder a mutual penetrating and mixing. The question as to how the idioplasmic strands of the two parents unite during fertilization is also

[26]*Loc. cit.* p. 68.

only briefly mentioned by Nägeli,[27] and the whole presentation of this subject shows what great difficulties the hypotheses of the solid composition of the idioplasm encounters.

Nägeli's theory tells us as little as any other theory about growth through assimilation and the multiplication of the material bearers of heredity. That the properties of those elements are determined by their molecular structure is just as little an advantage of his theory; it is a conclusion derived from our most general conceptions, which can be applied with the same right to the hypothetical units of every theory of heredity. But how that molecular structure explains the hereditary factors, we, of course, learn as little here as by any other theory. It is a weak point of Nägeli's work that these hitherto unexplained facts are not clearly designated as such, and that the common basis of the various theories is not simply mentioned as such.

§ 8. *General Considerations*

To my mind the above briefly sketched theories clearly prove that the fundamental thought of pangenesis, that is, of different material bearers for the individual hereditary characters cannot be avoided. Spencer, who wrote before Darwin, did not have this thought, and it was impossible for him to give a satisfactory explanation of the differentiation of organs. Weismann's theory, as we have already seen, led its originator himself in that direction, and forced him to admit, more or less clearly, a divisibility of the germ-plasm in this sense. And Nägeli's idioplasm is, on the whole, built up from those elements.

The more carefully we look into these theories in de-

[27]*Loc. cit.* pp. 215-220.

tail, the more we shall find that their efficiency lies in that implicitly made assumption, while their difficulties arise mostly through the other hypotheses. If, for the present, we consider the material bearers of the individual characters, out of which we must imagine the physiological units, the ancestral plasms, and the idioplasm to be composed, as their elements, then the assumption of such elements is in itself sufficient to explain the fact of heredity. The prevailing resemblance of children to one of the parents, and the phenomena of atavism become thereby comprehensible without any further assumptions.

The consequence which Spencer and Weismann emphasize as a necessity of their theory, namely the reduction of the number of units, (which, according to the former, results through mutual repulsion, according to *the latter, through the polar bodies), is a difficulty which arises from the union of the "elements," assumed by both* thinkers, and not from the assumption of the elements themselves. If we discard the grouping of the elements into units or ancestral plasms, such a reduction becomes quite superfluous, because the individual elements can arrange themselves, after the fertilization in the egg, in a similar manner as previously in the egg and in the sperm-cell. And the phenomena of so-called specific atavism, in which species preserve latent characteristics which they have inherited from their ancestors, as, for example, the *Primula acaulis caulescens,* show that latent characters need not be thrown off, but may be preserved through thousands of generations. In the idioplasm the firm union of the "elements" is most strongly worked out, and it is precisely in that point that every attempt fails to make the theory harmonize with the phenomena of fertilization and hybridization. For these processes teach us that hereditary factors are miscible, but the idioplasmic strands are not.

Variability teaches us that individual factors may considerably increase, independently from others, and, on the other hand, may almost completely disappear. And in the formation of species this possibility has been utilized to the highest degree. In the solid union of the idioplasm such a behavior of the individual "elements" might be made extremely difficult, if not quite impossible.

We cannot, therefore, maintain the solid union of the "elements" into physiological units, ancestral plasms, or idioplasm. This leads, not only in the cases mentioned, but almost everywhere, to contradictions with the facts, or at least to superfluous assumptions. But it is just on this union that the originators of these theories have laid the greatest stress, while they have nowhere emphasized, as an independent assumption, the conception of the "elements," and have not considered that as a thing apart from their other hypotheses.

As soon as we do away with this union, the kernel of all theories is the same as that of pangenesis, as has already been mentioned at the beginning of this Section.

Chapter IV

THE HYPOTHETICAL BEARERS OF THE INDIVIDUAL HEREDITARY CHARACTERS

§ 9. *Introduction*

The views on the nature of heredity expressed in the first Section lead us to the conviction that hereditary characters must be units, independent to a higher degree, and combined in nature in the most varied groupings.

On the other hand, a critical survey of the theories so far discussed induced us to perceive in all of them a more or less clearly defined kernel, which assumes material bearers for the individual hereditary characters. To shell this kernel was our task, and it had its justification in those views. While the solution of the problem was hitherto achieved with difficulty, this very nucleus is as clear as day in Darwin's *pangenesis*.

The assumption of different material bearers for the individual hereditary characters was worked out for the first time by Darwin. The great phenomena of nature which demand this assumption, and of which I could make only a hasty sketch in the first Section, were clearly comprehended and brought together in a masterful manner by him. The entire work on "The Variation of Animals and Plants" amounts, so to speak, to establishing the foundation of this fundamental idea, which he has then worked out and tried to harmonize with contradictory experiences.

It is remarkable that Darwin, with a modesty that puts us to shame, presents this fundamental thought as a current opinion, and not as his own discovery. He even hoped to be able to identify his idea with Spencer's theory.[28] But so little did this view prevail that his critics have separated it only in a few instances from the ancillary hypotheses, and most of them have rejected the fundamental thought, together with these secondary assumptions. But let us proceed to analyze Darwin's theory.

§ 10. *Darwin's Pangenesis*[29]

As already mentioned in the Introduction, the so-called provisional hypothesis of pangenesis consists, in my opinion, of the two following parts:

I. In the cells there are numberless particles which differ from each other, and represent the individual cells, organs, functions and qualities of the whole individual.

These particles are much larger than the chemical molecules, and smaller than the smallest known organisms;[30] yet they are for the most part comparable to the latter, because, like them, they can divide and multiply through nutrition and growth.

They can remain latent through countless generations, and then multiply only relatively slowly, and at some later time they may again become active and develop apparently lost characters (atavism).

They are transmitted, during cell-division, to the daughter-cells: this is the ordinary process of heredity.

II. In addition to this, the cells of the organism, at every stage of development, throw off such particles,

[28]Darwin, C. *The Variation of Animals and Plants.* **2**: 371, note.

[29]I have already brought together the most important parts of this paragraph in the Introduction (pp. 3-7); but a repetition cannot be easily avoided.

[30]Darwin, C. *loc. cit.* **2**: 372.

which are conducted to the germ-cells and transmit to them those characters which the respective cells may have acquired during their development.

These two parts must be considered separately. They deserve this the more as their significance has been so far generally misunderstood.

The hypothetical particles Darwin called "gemmules," on account of the analogy mentioned in the first proposition. This is a poorly chosen term, which has contributed much toward the raising of insurmountable objections to his theory. It has led many readers to imagine that they were preformed germs (*Keimchen*); a conception which does not in the least correspond to that of Darwin. On the contrary, one would have to say, according to the second proposition, that they originated only after the acquisition of certain characters, or, at the most, simultaneously with them. But we will not enter any further into this question.

The greatest number of investigators, in their criticisms, have considered the second proposition only. When pangenesis is mentioned, only this hypothesis is usually meant. The whole theory is identified with this second assumption, and the transportation of the gemmules is regarded as the chief point.[31]

I admit that, on a superficial reading, that chapter might easily create such an impression. But when it is read several times attentively, the transportation-hypothesis is lost sight of, while the fundamental idea, which is stated in the first proposition, becomes predominant.

This is partly due to the difficulty of familiarizing one's self immediately with the great thoughts of the

[31]Darwin distinctly calls it "The chief assumption." *The Variation of Animals and Plants.* **2**: 384. New York. 1900. *Tr.*

gifted investigator, partly also to the circumstance, already mentioned, that Darwin himself represents the first proposition as a matter of course and generally known, and presents only the second one as his own hypothesis.[32]

The assumption of the transportation of gemmules, which was, especially for plants, very greatly limited by Darwin himself, has been denied so frequently, and with so much ingenuity that it would be superfluous to criticise it any further here. Especially to Weismann is the credit due of showing how little it is demanded by well known facts and tested experience. The cases collected by Darwin, which seemed to require it,[33] were exceptions, and their trustworthiness has been strongly shaken by Weismann.[34] I believe I need only cite here the works of this investigator.[35]

Freed from the hypothesis of the transmission of gemmules, pangenesis now appears to us in the purest form. It is the assumption of special material bearers for the various hereditary characters. It is true that Darwin does not always express himself clearly as to what he calls *one* hereditary character, and occasionally

[32]In his letters also, he lays the greatest stress on this part. Cf. *Life and Letters of Charles Darwin.* **3**: 72-120. (**2**: 264. New York. 1901.)

[33]The well-known experiments of Brown-Séquard, which are so frequently quoted as supporting the theory of the heredity of acquired characters, were regarded by Darwin himself as opposing his hypothesis of the transportation of gemmules. Cf. Darwin. *The Variation of Animals and Plants.* **2**: 392.

[34]Weismann, A. *Ueber die Vererbung.* 1883; also *Die Bedeutung der sexuellen Fortpflanzung für die Selektionstheorie.* p. 93, etc. 1886.

[35]The so-called graft-hybrids, and the remarks on the influence of the male element on the parts surrounding the germ, give no proof, to my mind, of the necessity of an assumption of transmission. Cf. Part II, D, § 5, p. 207.

small groups of characteristics, or of certain morphological units, are probably regarded as such. This, however, lies in the incompleteness of our knowledge, which, in certain cases, does not, even now, allow us to carry through the principle, even though it is quite clear to our author. Every character which can vary independently from others, must, according to him, be dependent on a special material bearer.[36]

In what manner these hypothetical bearers are combined in the cells, Darwin has not explained. He only emphasizes that each of them can multiply independently from the others, although, as the phenomena of variability teach us, this multiplication frequently takes place simultaneously in small groups of bearers.

In the Introduction I have mentioned the reasons which induce me to reject the name "gemmule." It is, in everybody's mind, too closely connected with the transmission hypothesis. I may be allowed to christen the hypothetical bearers of the individual hereditary predispositions by a new name, and call them pangens.[37]

§ *11. Critical Considerations*

Among the critics of Darwin, Hanstein deserves to be named first, because no other has given as clear and correct an appreciation of pangenesis as he, nor explained in such a distinct manner the conclusions to which it leads. Unfortunately, owing to his particular turn of mind, Hanstein[38] had to discard these conclusions, and with them the whole theory.

[36]Darwin. *Loc. cit.* 2nd Ed. **2**: 378. 1875.

[37]Cf. Introduction, p. 7.

[38]Hanstein, J. Beiträge zur allgemeinen Morphologie der Pflanzen. *Bot. Abhandl.* **4**: 1882.

Hanstein, with good reason, first rejects the name gemmule, and calls the Darwinian units mikroplasts, or archiplasts. And since he denies the transmission hypothesis, he concludes from pangenesis:[39] "One ought even to make the hypothesis, that every cell of the entire plant-body, at its very origin, is endowed by its mother-cells with every kind of archiplast."[40] The correctness of this conclusion will probably now be admitted by all readers as a necessary consequence of the assumption of archiplasts, as these are indeed transmitted from one generation to the other in the egg- and sperm-cells.[41]

Hanstein's objections I may here pass over. They are based chiefly on his conviction that it is unavoidable to assume a special power of nature for organisms.[42]

Weismann, in his work on heredity (1883. p. 16), has expressed himself against the assumption of different bearers of the individual hereditary characters. According to him, this conception does not show how these "molecules" are to stay together in exactly those combinations in which they exist in the germ-plasm of the respective species. Without doubt this is the main difficulty, and the fact that it has been the most important cause of the establishment of the theories discussed in the preceding chapter, shows what weight it carries.

But this difficulty is no objection. It is true that it cannot be explained how the individual pangens may be held together. But the more recent investigations on nuclear division have given us an insight into extremely complicated processes, the object of which is evidently an

[39] *Loc. cit.* p. 219.

[40] *Loc. cit.* p. 223.

[41] *Loc. cit.* p. 219.

[42] *Loc. cit.* p. 225.

equitable distribution of hereditary characters among the two daughter-cells. It is not to be thought that to-day we already stand at the end of our investigations concerning the nucleus. On the contrary, the great discoveries which have been made up to the present time awaken within us the hope that many more complex processes within the nucleus, and of which we have not, as yet, the slightest inkling, will some time be discovered. The fact that we do not know how the hypothetical pangens are held together is in harmony with this statement. But this question does not need to be solved by auxiliary hypotheses. It is simply to be reserved for further study of the phenomena within the protoplasts and their nuclei.

An objection frequently urged is the necessity of assuming such a large number of different pangens.[43] Apparently the assumption of bearers of the whole specific character is indeed much simpler. In that case only one hypothetical unit is required for each species. However, if we do not limit ourselves to the consideration of one species, but extend our view over the whole world of organisms, this objection breaks down, as has already been said in the first Section; for we then have to assume as many units as there are and have been species, and their number thus becomes increased without limits. But Darwin's units recur, most of them, in numerous plants or animals, many in almost all of them, and a relatively small number of such hypothetical pangens is sufficient to explain, through the most varied possible groupings, all the differences between species. On the whole, then, the assumption of pangens is the simplest that can be made, and this is obviously a great advantage.

[43]Cf. Weismann, *Die Bedeutung der sexuellen Fortpflanzung.* p. 102 seq. 1886.

I think I can omit here a further comparison of the doctrine of pangenesis with the theories established by other investigators. Substantially it is contained in my criticism of those views, and besides it will follow from the working out of the fundamental thought in the succeeding paragraphs.

§ *12.* *Conclusion*

The considerations of the first division of this Part, and the critical explanations of the second division, have led us to recognize, as unavoidable, a hypothesis of the material basis of hereditary characters. It is, in a certain sense, a postulate at which everybody must more or less surely arrive who thinks upon these questions, and which we have always been able to trace as the kernel of the best theories of inheritance.

Let us conclude now by presenting this hypothesis in the most simple manner possible, and by indicating the most important explanations which it is able to give us without ancillary hypotheses.

In the first Division we arrived at the conclusion that hereditary qualities are independent units, from the numerous and various groupings of which specific characters originate. Each of these units can vary independently from the others; each one can of itself become the object of experimental treatment in our culture experiments.

Hereditary characters are connected with living matter, and heredity depends on the fact that children originate from a material part of their parents. The visible characteristics of organisms are determined by the invisible characters of the living matter. In this living substance we assume special material bearers for the individual hereditary characters. This is the fundamental thought of Darwin's pangenesis, at which almost all later investigators arrived more or less clearly. At least, the critical discussion of their opinions leads, in the end, to this postulate. Whether we speak of the molecules of the protoplasm, or of the germ-plasm and idioplasm, as bearers of the entire specific character; or whether we place in the foreground the phenomena of hereditary; or, again, whether, like Sachs and Godlewski, we use as a basis the processes of growth and regeneration,[44] we always finally end by assuming different bearers of the inherited attributes. But we reach this conclusion in the most certain and clear manner if, following Darwin's example, we regard the whole world of organisms from the most general point of view possible.

According to the hypothesis concerning their nature, these units have been given different names. For the one adopted by me I have chosen the name, pangen.

These pangens do not each represent a morphological member of the organism, a cell or a part of a cell, but each a special hereditary character. These can be recognized by each being able to vary independently from the others. Their study opens a very promising field to experimental investigation.

The pangens are not chemical molecules, but morphological structures, each built up of numerous molecules. They are the life-units, the characters of which can be explained in an historical way only.

We must simply look for the chief life-attributes in them, without being able to explain them. We must therefore assume that they assimilate and take nourish-

[44]Sachs, J. Stoff und Form der Pflanzenorgane. *Arbeit. Bot. Instit. Würzburg.* **2:** 452. 1880. Godlewski, E. *Bot. Centralb.* **34:** 82. 1888.

met and thereby grow, and then multiply by division, two new pangens, like the original one, usually originating at each cleavage. Deviations from this rule form a starting point for the origin of varieties and species.

At each cell-division every kind of pangen present is, as a rule, transmitted to the two daughter-cells. What combination of circumstances is the condition of this, and what relation is established by the practically uniform multiplication of the various pangens of an individual, we do not know.

The pangens, in smaller and larger groups must stand in such a relation to each other that the members of one group, as a rule, become active at the same time.[45]

All these conclusions follow naturally when we try to connect the fundamental thought with the known phenomena of heredity and variability.

The whole import of this fundamental idea will, I believe, be made most clear by briefly grouping now the most important advantages of the hypothesis in answering some great biological questions. For entire large groups of phenomena are made comprehensible to us in a simple manner, and this without any ancillary hypothesis, by a mere consideration of the ever changing relative quantities in which the pangens must occur, according to the nature and age of the cells. In the main these advantages have already been pointed out by Darwin.

According to Darwin's idea, the phenomena of heredity evidently depend on the fact that the living matter of the child is built up of the same pangens as those of its parents. If the pangens of the father predominate in the germ, the child will resemble him more than the

[45]Darwin called these groups "compound gemmules.' *Loc. cit.* **2**: 366. New York. 1900.

mother, if only certain pangens of the father prevail, then this resemblance will be limited to single characteristics. If certain pangens are fewer in number than others, then the character represented by them is only slightly developed; if they are very few, the character becomes latent. If external conditions cause later a relatively great increase of such pangens, the previously latent character reappears, and we observe a case of atavism. If certain pangens entirely cease multiplying, the respective character is definitely lost, but this seems to occur very rarely.

In the protoplasm, or at least in the nuclei, of the egg- and sperm-cells, as well as in that of all buds, all the pangens of the respective species are represented; every kind of pangen in a definite number. Predominating characters correspond to numerous pangens, slightly developed attributes to less numerous ones.

The differentiation of the organs must be due to the fact that individual pangens or groups of them develop more vigorously than others. The more a certain group predominates, the more pronounced becomes the character of the respective cell. Connected with this is the fact that external influences may frequently alter the character of an organ in its earliest youth, but that this becomes more difficult the more advanced it is in its development, i. e., the more strongly definite pangens are already predominating.

The regeneration of detached members, the restoration of smaller lost parts of tissues, and the closing up of wounds are evidently due to the fact that the pangens of the lost parts are not limited to these parts, but that all cells capable of reproduction contain all the pangens necessary thereto.

Some pangens represent characters which usually develop only in quite definite organs. If these happen to predominate in the wrong place we get the phenomena of metamorphosis.[46] If, for example, the pangens which determine the peculiarities of the petals develop in the bracts the petalody of the bracts takes place.

Other pangens represent qualities which may appear in many or in all members of the plant. And therein lies doubtless the reason that such characters are so very often equally strongly or feebly developed in all of those members. Thus the red coloring matter of the white-flowered varieties of red species is most frequently also lacking in the stem and foliage, and plants with variegated leaves not infrequently bear variegated fruit.

Phenomena of correlative variability, when not of purely historical nature, i. e., if not originated by simultaneous accumulation of two independent qualities, find their explanation in the union of the pangens into groups.

Systematic relationship is based on the possession of like pangens. The number of identical pangens in two species is the true measure of their relationship. The work of the systematist should be to make the application of this measure possible experimentally, by finding the limits of the individual hereditary characters. Systematic difference is due to the possession of unlike pangens.

According to pangenesis, there may be two kinds of variability. These are differentiated in the following manner by Darwin.[47] In the first place the pangens present may vary in their relative number, some may increase, others may decrease or disappear almost entirely,

[46]Darwin, C. *Loc. cit.* **2**: 387.
[47]*Loc. cit.* p. 390.

some that have long been inactive may resume activity, and finally the grouping of the individual pangens may possibly change. All of these processes will amply explain a strongly fluctuating variability.

In the second place some pangens may change their nature more or less in their successive divisions or, in other words, new kinds of pangens may develop from those already existing. And when the new pangens, perhaps in the course of several generations, gradually increase to such an extent that they can become active, new characters must manifest themselves in the organism.

In a word: An altered numerical relation of the pangens already present, and the formation of new kinds of *pangens must form the two main factors of variability.*[48] *Unfortunately we have not yet succeeded in analyzing* the observed variations so far as to be able to determine the share of each of those factors. But it is clear that the former kind is more likely to determine the individual differences and the numberless small, almost daily variations and monstrosities, while the second one has chiefly to produce those variations on which depends the gradually increasing differentiation of the entire animal and vegetable world.

This conception of phylogenetic variability indicates that the pangens, too, must have their pedigrees which correspond to the pedigrees of the respective characteristics. At every advance in the pedigree of the species one or more new kinds of pangens must have developed from those present. In the lowest organisms, therefore, the pangens themselves become relatively simple, and not

[48]In a note to the translator, the author says: "That sentence has since become the basis of the experiments described in my '*Mutationstheorie.*'" *Tr.*

very different from each other. With increasing differentiation they must themselves have become more complicated, and gradually more unlike each other.

But the farther we get away from the facts the more likely we are to get lost in false speculations. My object was only to place the fundamental idea of Darwin's pangenesis in the right light. I hope I have succeeded in this.