C. The Functions of the Nuclei

CHAPTER I

FERTILIZATION

§ 1. *Historical Introduction*

The first author who described the nucleus as the organ of heredity was Ernst Haeckel. In the second volume of his "*Generelle Morphologie der Organismen*,"[1] he established this conception, founding it especially on the behavior of the nucleus during cell-division. For him the "inner nucleus has the work of transmitting the hereditary characters, the outer plasm has the part of adaptation, accommodation or adjustment to the conditions of the outer world." And just as the nucleus plays its principal rôle in propagation, so is nutrition the chief task of the plasma. In the lowest, non-nucleated organisms the two functions are not yet separated.

For almost ten years this prophetic utterance remained without noticeable effect on the progress of cell-anatomy and the theory of fertilization. It was only when Oscar Hertwig discovered that in fertilization the spermatozoids copulate with the nucleus of the egg-cells that Haeckel's idea became the starting-point for a new line of investigation.[2] Hertwig first observed this fact in the eggs of the Echinidæ.

R. Hertwig, Fol, Selenka, Flemming, and others, have lent their support to this opinion by further investigations,

[1] pp. 287-289. 1886.

[2] Hertwig, O. Beiträge zur Kenntnis der Bildung, Befruchtung und Theilung des thierischen Eies, *Morphol. Jahrb.* 1: 347. 1875.

and in consequence of this it is quite generally recognized at present in zoölogical science.

In the field of botany Strasburger has the merit, by investigations of many years' duration, of having definitely proved the theory that fertilization consists essentially in the union of the nuclei. His first studies on the fertilization of the conifers, and later on the same process in the angiosperms[3] now form the foundation of this part of our knowledge.

The other organs of the protoplasts take no part in fertilization during copulation. And since, in spite of this, the derivatives of the fertilized egg-cell possess later the characteristics of both parents, it is clear that a transmission to them of the hereditary characters from the fertilized nucleus must take place. This transmission, however, has, at least so far, eluded observation. But many facts, even outside the scope of the theory of fertilization, speak in favor of its existence.

It is my intention to put together in this Section, as completely as possible, all the facts that might throw any light on the nature of this transmission. The prevailing conception regards this process as a dynamic one, while my hypothesis of intracellular pangenesis assumes a transport of material particles as bearers of the hereditary characters. Therefore it is a question of ascertaining which of these two conceptions is best supported by the material available for observation.

[3]Strasburger, E. *Ueber Befruchtung und Zelltheilung,* 1878. *Neue Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen,* 1884.

CHAPTER II

FERTILIZATION (continued.)

§ 2. *The Conjugation of the Zygosporeae*

The behavior of the chlorophyll-band of Spirogyra during conjugation is very instructive. De Bary[4] has already observed that in many species having one spiral the two chlorophyll-bands of the conjugating cells join their ends in such a way that they form a continuous ribbon. For the one-spiraled species, *S. Weberi,* however, Overton has quite recently described and figured how the band of the maternal cell splits in the middle during conjugation, and how the paternal band then inserts itself between the two halves and attaches itself to their ends.[5] Later, owing to the considerable swelling of the pyrenoids, as well as to other processes, the windings of the band gradually become more indistinct, and finally, in the zygospore, quite indistinguishable, until they reappear again during its germination.[6]

These data are quite sufficient to give us an idea of the derivation of the chlorophyll-bands of the young germ-plant. We assume, as a result of the above mentioned investigations, that the chlorophyll-band of the germinating zygospore consists of the bands of the two sexual cells which are joined by their ends in one way or an-

[4]De Bary. *Die Conjugaten.* p. 3.

[5]Overton, C. E. *Ber. Deut. Bot.* **5**: 70. Taf. IV. 1888.

[6]See also on this subject Klebahn. *Ber. Deut. Bot. Ges.* **6**: 163. 1888.

other.[7] What will happen to these first parts of the band at the first divisions of the young plant? Evidently, in the case described by de Bary, the first cell-division will, by cutting the band through in the middle, give the maternal half to one daughter-cell and the paternal half to the other. In *S. Weberi* the two subsequent divisions will do this; the middle cells of the four-celled thread will then bear the paternal, the two end-cells, the maternal band.

The result of this speculation is, that, for the individual cells of a one-spiraled Spirogyra-thread, it makes no difference whether they get their chlorophyll-band from the father or from the mother. However, there is no doubt but that all the bands of the young plant possess, later, the same hereditary characters, even though there were individual differences between father and mother. We must therefore assume that they necessarily got these from the nucleus, after fertilization. If we attribute to the process of conjugation any significance at all for the active hereditary characters, and do not wish to restrict its effect, through all generations, to the nuclei, we are evidently compelled to accept this assumption.

But in this case the necessity of a transmission of the hereditary characters from the fertilized nucleus to the other organs of the protoplasts, lies before us in a simple illustration.

We will generalize this theory, and say that in the entire plant world it is indifferent for the new individual whether, with the exception of the nucleus, it gets the organs of its protoplasts from the father or the mother.

[7]In other cases the chlorophyll-band of the male cell is disorganized and resorbed. Cf. Chmielevsky. V. Eine Notiz über das Verhalten der Chlorophyllbänder in den Zygoten der Spirogyraarten. *Bot. Zeit.* **48**: 773. 1890.

But the nucleus must be from both. The facts to be discussed in the two following Sections, teach us that, in fertilization proper, the other organs come from the mother only. But this is simply to be regarded as a special adaptation.

The chromatophores of the other Zygosporeæ, examined with this end in view, behave essentially similarly to those of *Spirogyra.* They touch one another *(Epithemia),* or do not unite *(Zygnema* and many others), but they never conjugate in the true sense of the word.[8] At the first divisions of the zygospore, the paternal and maternal chlorophyll grains must therefore always be distributed to the individual cells of the thread.

Schmitz, who was probably the first to observe the conjugation of the nuclei in the Zygosporeæ, and who studied carefully the above mentioned behavior of the chromatophores, demonstrated in a clear manner that, in these cases also "the essential point is only the union of the nucleus of the male cell with the nucleus of the female cell."[9] And the facts which have been discovered later have fully confirmed this statement.

§ 3. *Fertilization in Cryptogams*

Schmitz, in his important monograph on the chromatophores of the algæ, has comprehensively demonstrated that these structures which, at each vegetative cell-division, are transmitted from the mother-cell to its daughter-cells, are usually entirely lacking in the spermatozoids.[10] The egg-cells, however, always possess these

[8]Schmitz. *Die Chromatophoren der Algen,* p. 128. See also Overton and Klebahn, *loc. cit.*

[9]*Loc. cit.* p. 128. note 2.

[10]Schmitz, *loc. cit.* p. 120 ff.

organs. After fertilization they multiply by division, and thus form the chromatophores of the new individual. In regard to this point the organization of the protoplasts is therefore inherited directly from the mother and not from the father.

Let us now see, how the other members of the protoplast, with the exception of the nucleus, behave. To all appearances the spermatozoids possess neither vacuoles nor chromatic bodies, and hence the condition is the same for the former as for the latter.

According to the best recent investigations, the spermatozoids do not originate, as some authors previously assumed, from the nucleus only of the mother-cell, but the rest of the plasma also takes part in their formation. It is true that the nucleus forms the bulk of the body of the male reproductive cell. Schacht has already voiced the theory, on the basis of his observations and those of others, "that the nucleus takes a very active part in the formation of the spermatozoid and in a certain way blends into it."[11] He declares further that, in this process, the granular contents of the mother-cell disappear. This transformation of the nucleus, although denied by prominent investigators[12] at the beginning of the more recent researches, is now generally recognized as the most important part of the whole process.

Outside the nucleus there lies, in the spermatozoids, the limiting membrane, which protects this organ against external influences, and, in a certain way, serves as the little boat that carries it to its destination. The distinc-

[11]Schacht. *Die Spermatozoiden* p. 35. 1864.

[12]Comp. e. g. Sachs, *Lehrbuch,* 4. Auflage, p. 303; and Strasburger, *Zellbildung und Zelltheilung,* III Aufl. p. 94; also *Bot. Zeit.* **39:** 847, 848. 1881.

tion of these two parts we owe chiefly to Zacharias, who thoroughly investigated the micro-chemical reactions of the male reproductive cells, and pointed out repeatedly the different behavior of their external and internal parts.[13] The nuclein especially forms the chemical characteristic for the substance of the nuclei. Fluids which easily dissolve and extract this substance remove only the inner part of the spermatozoids and leave the outer layer and the cilia in general undissolved. In return the cilia dissolve in pepsin, and do not, therefore, consist of nuclein.[14] According to Campbell, also, the cilia of the spermatozoids are not developed from the nucleus, but from the cytoplasm of the mother-cell.[15]

But, during fertilization evidently the nucleus alone plays a part. The deep penetration of the entire spermatozoid into the egg-cells teaches that there is no probability of a conjugation of its outer layer with that of the egg-cell. More likely do this organ and the cilia disappear within the egg-cell, without playing any noteworthy rôle therein.

Exceptionally the spermatozoids possess small chromatophores which, perhaps, they may need on the way to the egg-cell, either for taking the right direction, or for other purposes. An example is found in *Fucus,* where Schmitz proved that they arise by division from the chromatophores of the mother-cell.[16] But no observation teaches that they play any rôle in fertilization.

Phylogenetically, the spermatozoids of the algæ have

[13]Zacharias. *Bot. Zeit.* 1881-1888.

[14]Zacharias, E. Ueber die Spermatozoiden. *Bot. Zeit.* **39:** 828, 836, 850. 1881.

[15]Campbell, D. H. Zur Entwickelungsgeschichte der Spermatozoiden. *Ber. Deut. Bot. Ges.* **5:** 120. 1887.

[16]Schmitz, *loc. cit.* p. 122.

doubtless originated from conjugating swarm-spores. In time they have gradually lost their chromatic bodies, and probably also their vacuoles. For the disappearance of the former Schmitz describes a number of intermediate steps. May I be allowed to quote the following sentences from his important treatment of this subject:[17] "Sometimes, especially where the difference of the two kinds of sexual cells is not yet very considerable, the spermatozoids act exactly like the isogametes, and like these retain the chromatophores unchanged (e. g., in *Scytosiphon lomentarium*). As that difference becomes greater, however, the chromatophores of the male cells show a distinct tendency to disappear, and especially does their coloring become less intense *(Bryopsis)*."

This comparative study bridges the chasm lying between conjugation and fertilization, which is no doubt chiefly due to the fact that, in the latter, the organization of the protoplasts is inherited morphologically from the mother only, while in the former, in some cells, the inheritance is from the mother, in others from the father. But, on the other hand, the above mentioned phylogenetic consideration leads to the conviction that the outer layer of the spermatozoids has the same significance and the same origin as that of the swarm-spores, and is just as indispensable.

§ *4. Fertilization in Phanerogams*

In the seed-bearing plants, also, the organization of the protoplasts is directly inherited from the egg-cell alone. From the pollen-tube only the nucleus penetrates into the latter; other parts, even if they should be necessary for the transportation of the nucleus and should ac-

[17]*Loc. cit.* p. 121.

company it, do not play any rôle in the true process of fertilization.

Everybody is acquainted with the valuable investigations of Strasburger in this field which, since 1878, have repeatedly treated this point and have completely proven the above mentioned theories. It would be superfluous to redescribe them here, or to enumerate their confirmations by other investigators.

How the nuclei unite during fertilization is a question which is very far from having been satisfactorily answered. Furthermore, differences predominate here which are at least very striking. According to Strasburger, not only do the nuclear skeins fuse, but also the nuclear vacuoles, and hence the nuclear sap.[18] According to van Beneden, the nuclear skeins of the male and the female cells in *Ascaris megalocephala* arrange themselves side by side and form the segmentation nucleus.[19] They seem to unite at their ends, thus forming a single nuclear thread, in which, therefore, only juxtaposition takes place, and not a mutual penetration of their elements. But while, in animals, according to the available data, fusion does take place during the state when the chromosomes are arranged in the form of a star, it is seen to occur in the plants in the state of rest. Whether this difference really exists, and how the nuclear threads generally unite, are questions which have to be more thoroughly investigated.[20]

It is significant that the number of the chromosomes, according to Strasburger's most recent investigations, has

[18]Strasburger. *Ueber Kern- und Zelltheilung,* p. 230. Jena. 1888.

[19]Van Beneden, E. *Recherches sur la maturation de l' oeuf.* 1883.

[20]Strasburger. *Ueber Kern- und Zelltheilung.* p. 240. Jena. 1888.

also been found to be constant in plants in the generative-cells of every species, being the same for the male cells as for the female. Sometimes it is the same for large groups of plants as, e. g., for the Orchidaceæ 16; in the Liliaceæ it varies[21] between 8, 12, 16 and 24. For *Ascaris megalocephala* it is 2, for *A. lumbricoides* 24. Obviously this number does not have any systematic significance or stand in any relation to the hereditary characters.

However, from a continued investigation in this field, we may expect important disclosures on the question as to which parts of the nucleus are the real bearers of the latent hereditary characters. For the present the evidence is in favor of the assumption that they are to be looked for in the chromosomes.[22] For the further working out of the theory of heredity this is, without doubt, of the highest interest; for our hypothesis, however, a decision is not absolutely necessary.

[21]Strasburger. *Loc. cit.* pp. 239, 242.
[22]Roux, *Ueber die Bedeutung der Kernfiguren,* 1883.

Chapter III

THE TRANSMISSION OF HEREDITARY CHARACTERS FROM THE NUCLEI TO THE OTHER ORGANS OF THE PROTOPLASTS

§ 5. *The Hypothesis of Transmission*

The question of a transmission of hereditary characters from the nuclei to the other organs of the protoplasts has been repeatedly raised in the foregoing sections. But, if we review all the facts combined in the preceding chapter, and in this, the necessity of the assumption of such transmission is forced upon us.

The protoplasts of the plant possess a visible organization, which, at every cell-division, is transmitted by division of the individual organs, directly from the mother-cell to its daughter-cells. The heredity is here a visible and not a latent one. But the individual organs are ontogenetically independent from each other; they originate only through the division of such as are already present. And even if, in the course of development, they adapt themselves to various functions and, in doing so, receive other names, and although their origin in individual cases is not yet cleared up, so much is, on the whole, certain, that the nucleus, the chromatophores, the vacuoles and the granular plasm, and probably also the limiting membrane, are primary organs which never arise from each other, but only multiply side by side.

Each of these primary organs possesses a complement of characters and potentialities which, together, form the character of the species. These qualities can either be seen directly under the microscope, or they betray their presence by definite functions. That the hereditary characters lie in the respective organs of the protoplasts can hardly be doubted. But whether they also lie thus in cells where they are present only in the latent condition is not disclosed by the processes of vegetative propagation.

Here the process of fertilization serves as a clue. Hybrids teach, and daily observations on man confirm the fact that children, on an average, receive their characteristics, to the same extent, from both parents. But the fertilized egg-cell receives its organs from the mother only, while from the father only the sperm-nucleus conjugates with the nucleus of the egg-cell. All the hereditary characters of the father must therefore be transmitted in the nucleus, as potentialities in a latent state. And before they can become active in the other organs of the protoplast, they must evidently be transported to the latter ones from the nucleus. This transmission is therefore a hypothesis, the assumption of which may well be regarded as a necessity at the present state of our knowledge.

May I be allowed to illustrate this transmission by a few examples. I take them from hybrids, because here the relations lie most clearly and convincingly before us, and I chose the colors of the flowers because they are easily observed.

Let us first take the red color of flowers. *Phaseolus multiflorous* has red flowers, *Phaseolus vulgaris nanus* white ones. By pollinating the latter with the pollen of the former there came about several times, in 1886, in my own cultures, a hybrid seed. This does not deviate externally from the normal seed of its mother-plant, but it develops into a plant which is similar to the twining *P. multiflorous,* but remains smaller than the latter. The flowers of the hybrid are of a pale red, being a tint midway between the two parents, as I had the opportunity of convincing myself personally. The red coloring matter is found in solution in the vacuoles of the cells of the petals.

The ability of the vacuoles to form the red erythrophyll comes from the father, in this instance. But the vacuoles of the hybrid originate morphologically from those of the mother. The power of producing erythrophyll must therefore have been transmitted in a latent condition in the sperm-nucleus of the father to the nucleus of the egg-cell, and must have been communicated sooner or later to the vacuoles of the hybrid.

The same thing is taught by many other hybrids, as, for example, *Digitalis lutea* ♀ × *purpurea* ♂, *Linaria vulgaris* ♀ × *purpurea* ♂, *Linaria genistaefolia* ♀ × *purpurea* ♂, *et cetera.*[23]

The yellow color of the flowers behaves in the same way. *Digitalis lutea-purpurea* forms the best illustration. The two forms *D. purpurea* ♀ × *lutea* ♂ and *D. lutea* ♀ × *purpurea* ♂ are quite alike, with the exception of some slight variations in the color of the flowers.[24] Naudin gives an illustration of the hybrid; the flower has a pure yellow color in one cluster, while in the other one, yellow is mixed with pale red.[25] Of the two mentioned hybrids of the *Linaria* I do not find any record of the reciprocal forms.

[23]Cf. Focke, *Die Pflanzenmischlinge,* pp. 311, 315, and other passages.

[24]Focke, *loc. cit.* p. 315.

[25]Naudin. Nouvelles recherches sur l'hybridité. *Nouvelles Archives du Muséum d'histore naturelle de Paris.* p. 95, Pl. 2. 1869.

Like the qualities of the vacuoles, those of the chromatophores must be communicated to the hybrid during hybridization, in a latent condition in the pollen-nucleus of the father. As an instance I mention *Raphanus sativus* ♀ × *Brassica oleracea* ♂, *Medicago sativa* ♀ × *falcata* ♂, *Geum album* ♀ × *urbanum* ♂, *Verbascum phoeniceum* ♀ × *blattaria* ♂.[26]

Similar instances can be found in great number in the abundant literature on hybridization-experiments. But science greatly needs a comprehensive miscroscopic study of hybrids in relation to the anatomical structure of their parents.[27]

Still more forcibly and more generally do we feel the necessity for the assumption of a transmission, when we observe the hybrids in the second and following generations. Almost always, when cultivated in a sufficiently great number, some of them revert to the grand-mother, others to the grand-father. The latter ones are so similar that they could be easily confounded with the grandfather. This teaches us that in hybridization, all the characters of the father pass on to the hybrid, where they are present in the latent state only, but that they become active again in some of its children. All the organs of the protoplasts must therefore be able to draw their active characters from the nucleus.

In the hybrid, however, the characters of father and mother are equally represented. Especially are both hy-

[26]These instances are from Focke, where more can easily be found. I regret to say that I had no opportunity of controlling the nature of the yellow coloring matter.

[27]The "Comparison of the Minute Structure of Plant Hybrids with that of their Parents, and its Bearing on Biological Problems," by J. M. MacFarlane (*Trans. Roy. Soc. Edinburgh,* **37**: 203. 1892) is still practically the only investigation in this field. *Tr.*

brids produced by two species, in which the one species will function at one time as the father and at another time as the mother, with few exceptions, essentially alike. There is no ground for the assumption that the hereditary characters, latent in the egg-cell and in the spermatozoid, are inherited in a fundamentally different manner from the father than from the mother. And thus we arrive at the conclusion that the latter, too, must lie in the nucleus, and are not distributed over the individual organs of the egg-cell.

Hence the nuclei are the bearers of the latent hereditary characters. In order to become active, the greater part of these characters,[28] at least, must pass from the nuclei into the other organs of the protoplasts

§ 6. *Observations on the Influence of the Nucleus in the Cell*

Even the first investigators of this organ realized that the nucleus plays a prominent rôle in the life of the cell. They have given expression to this conviction in the name itself. And, although later the supposed absence of the nucleus in large groups among the Thallophytes gave rise to a doubt as to the correctness of this opinion,[29] it has been entirely removed by more recent investigations.

At first it was impossible to form any idea as to the nature of that rôle. The investigators mentioned in the first chapter of this Section, Haeckel, Hertwig, Flemming, Strasburger, and others, were the first to teach us to regard the nucleus as the real organ of heredity. And even in these later years there are some authors who

[28]The characters that regulate nuclear division, are probably active in the nuclei themselves.

[29]Cf. Brücke, *Sitzungsber. Akad. Wiss.* Wien. 1861.

still, in opposition to Haeckel's positive assurance, regard the nucleus as an organ of nutrition, ascribing to it an influence on the formation of protein, starch, or other products of assimilation.

Owing to the influence of the above named investigators, attention has been directed, in recent years, more and more to the nucleus. In consequence of this, a series of observations have been made and published, which speak in favor of the fact that the nucleus, although not self-active, still exercises a very great influence on the most important processes in cell-life. On the whole, the conditions observed must, without doubt, be reduced to this, that the hereditary characters, as long as they are latent, are stored up in the nucleus, and become active only in the other organs of the protoplasts. But it must not be forgotten that, in individual cases, there may be a special correlation between nucleus and protoplasm, which must be attributed to specific adaptations, and not to general laws. In the individual case it will usually be very difficult to decide between these two possibilities.

First, I shall describe some of the conditions emphasized already by the older investigators. In young cells the nucleus lies in the middle of the cell. With the increasing size of the vacuoles, when the protoplasm reaches the so-called foamy state, it remains in that position and is connected with all the parts of the peripheral plasm by bands and strands radiating from it by the shortest lines. This familiar picture, and the considerable size of the nucleus in young cells, may have been the first reasons for attributing special importance to this organ. The nucleus does not grow correspondingly with the increasing growth of the cells. It becomes relatively smaller, and the fusion of the vacuoles forces it out of its central position. Ordinarily, it does not take any definite position after this, but is moved around in the cell by the currents of the granular plasm. As Hanstein describes it, the nucleus traverses a long and very tortuous way within a few hours, and sails in all directions throughout its whole domain, "as if to inspect it everywhere."[30] Everything argues for the assumption that the activity of the entire protoplast is under the regulating influence of the nucleus.[31]

Besides the general behavior of the nuclei the investigations of Tangl, Haberlandt, Korschelt, and others, have made us acquainted in recent years with a special relation of the nuclei to individual processes in cell-life.

Tangl observed bulb-scales of *Allium Cepa,* which had been recently wounded, for example, the day before.[32] He saw that near the wound-surface the nuclei are not, as otherwise, irregularly distributed over the cells, but that they had gone to that side of their cells which was nearest to the wound. With them the granular plasm was also accumulated on those walls. The shorter the distance from the wound, the more pronounced was the phenomenon, but as far away as about 0.5 mm. it could still be distinctly seen. These conditions probably indicate that the process of regeneration which the wounds usually cause proceed here, under the influence of the nuclei.

Haberlandt studied the position of the nucleus during this process in a great number of cases in which the cells of the higher plants show a more vigorous local growth

[30]Hanstein, *Das Protoplasma.* **1**: 165. 1880.

[31]Cf. Strasburger. *Neue Untersuchungen.* p. 125. 1884.

[32]Tangl, E. Zur Lehre von der Continuität des Protoplasmas im Pflanzengewebe. *Sitzb. Math.-Naturw. Cl. Akad. Wiss. Wien.* **90**: 10. 1884.

in some definite part of their circumferences.[33] He did so partly where, through localized surface growth, the shape of the cells changes, partly where unilateral thickenings of the membranes, or a definite wall sculpture are started. And although, owing to the abundance of individual phenomena, a rule without exceptions could not be expected, he found, on the whole, that the nucleus most frequently turns to where growth is strongest, and remains longest where the latter continues longest.

According to Korschelt, the same rule is valid, in a general way, for the animal cell.[34] With chiefly unilateral or local activity of the cells, this investigator succeeded, in a number of cases, in observing for the nucleus a definite position which was as near as possible to the place where this process was going on. Frequently, when the distance is more considerable, the nucleus is connected with such favored places by bands and accumulations of protoplasm.

Where the nucleus does not betray its influence on the processes in the protoplasm by a change of position, it does so frequently by a definite arrangement of the latter around the nucleus. The accumulation of the amyloplasts in the immediate vicinity of the nucleus, as is frequently observed in young cells, has been ascribed by various investigators to the influence of the nucleus on their activity.[35] Pringsheim has demonstrated that, in

[33]Haberlandt, G. *Ueber die Beziehungen zwischen Funktion und Lage des Zellkernes.* 1887.

[34]Korschelt, E. G. Haberlandt, Ueber die Beziehungen zwischen Funktion und Lage des Zellkerns bei Pflanzen, Jena, 1887, nebst einigen Mitteilungen. *Biol. Cent.* **8**: 110. 1888.

[35]Cf. e. g. Strasburger, *Ueber Kern und Zelltheilung,* p. 195. 1888. Schimper, A.F.W. Untersuchungen über die Chlorophyllkörper, und die ihnen homologen Gebilde. *Jahrb. Wiss. Bot.* **16**: 1. 1885. Haberlandt, G. Die Chlorophyllkörper der Selaginellen. *Flora.* **71**: 291. 1888.

the cells of *Spirogyra,* the threads which radiate from the nuclear cavity attach themselves especially to the pyrenoids of the chlorophyll bands, and by ramifying, frequently connect several of them directly with the nucleus.[36] In cell-formation in those embryo-sacs where the new cells arise in a peripheral layer, after the formation of numerous nuclei, Strasburger has repeatedly described radiated figures which unite the nuclei, and which are present, not only between the two daughter-cells of a mother-cell, but also are placed between the nuclei that are not so closely related to each other. The repeated studies of this investigator certainly remove all doubt of the fact that along these rays some influence from the nuclei makes itself felt during cell-division.[37]

The multinuclear nature of the coeloblasts, discovered and carefully studied especially by Schmitz,[38] also argues for the great importance of the nucleus. As a rule, here the nuclei do not lie in the moving part of the granular plasm, but in its resting layers. They are arranged evenly at almost equal distances from each other, and are mostly small and so numerous, that every detached piece, if indeed not too small to remain alive, probably always contains one or more nuclei. All parts of the protoplasts can evidently be directly influenced by them.

Following the observations on uninjured cells, the investigations on injured protoplasts must lastly be discussed. Schmitz has already drawn attention to the fact that the extruded protoplasmic balls of *Vaucheria* and other Siphonocladiaceae, are enabled to form a new cell-

[36]Pringsheim, N. Ueber Lichtwirkung und Chlorophyll Function in der Pflanze. *Jahrb. Wiss. Bot.* **12**: 304. 1881.

[37]Cf. e. g. Strasburger, E. *Bot. Praktikum,* 1 Aufl. p. 610.

[38]Schmitz. Die vielkernigen Zellen der *Siphonocladiaceen. Festschr. Naturf. Ges.* Halle. 1879.

membrane and to regenerate into new vital individuals only when they possess one or several nuclei.[39] This must not be understood to mean that the nucleus is the only condition. The chromatophores and the other organs of the other protoplasts must also be present, but the significance of these for growth and nutrition is of such a nature that their indispensability may be regarded as a matter of course. Nussbaum and Gruber have later proven through extensive experiments in the division of protozoa, that here too the fractional parts of the protoplasts can regenerate completely only when the nucleus, at least, is not lacking.[40]

The experiments of Klebs on the culture of plasmolysed cells are also important.[41] I take from them what follows: If cells of *Zygnema* and *Oedogonium* are plasmolysed in a 10% solution of glucose, the contents of the longer cells not infrequently divide into two or more pieces, which, joined at first by thin threads, later separate entirely from each other. If the threads are now grown in light in this solution, the contracted protoplasts surround themselves with a new cell-wall, which gradually increases in thickness. Sooner or later they begin to grow and divide, and in so doing, break through the old cell-membrane. But in those cells where the contents are split into two or more parts, of which, of course, only one can get the nucleus, only this latter part forms a new cell membrane; the non-nucleated pieces

[39] *Loc. cit.* p. 34.

[40] Nussbaum, Ueber die Theilbarkeit der lebenden Materie, Archiv Mikr. Anatomie. 1886. Gruber, A. Ueber Künstliche Theilung bei Infusorien. *Biol. Cent.* **4**: 717. 1885; *Ber. Naturf. Ges.*, Freiburg i-B. 1886.

[41] Klebs, G. Ueber das Wachsthum Plasmolysirter Zellen. *Bot. Cent.* **28**: 156. 1886; *Arbeiten Bot. Instituts.* Tübingen. **2**: 565. 1888.

can, it is true, produce starch and nourish themselves, but they are not able to grow.

In order to get more information on the rôle of the nucleus a method would evidently be needed, which would allow us *to kill the nucleus without injuring the cell body.* Perhaps this end could be attained by making use of the method suggested by Pringsheim, of partially killing the cells in the focal point of a lens.[42] By selecting a lens that makes it possible to strike a single point of the cell, it could be focused on the nucleus with a dim light, and then a brief exposure to the direct rays of the sun might produce the desired result in some of the cells. I therefore warmly recommend this method for further elaboration in this direction.

In reviewing the results of the investigations that have been discussed, we see that the nuclei have an influence on the activity of the other members of the protoplast. They exercise this influence only as long as the respective members remain in the most intimate protoplasmic connection with them, preferably at the shortest possible distance, or otherwise by direct plasma-bands.

[42]Pringsheim, N. *Jahrb. Wiss. Bot.* **12**: 331. 1881.

D. The Hypothesis of Intracellular Pangenesis

Chapter I

PANGENS IN THE NUCLEUS AND CYTOPLASM

§ 1. *Introduction*

We shall now try to connect with each other the conclusions to which the critical survey of previous theories of heredity, in the first Part, and the review of the present state of the cell theory, in the second Part, have lead us.

The result of the first Part was that the comparative consideration of the world of organisms, from the broadest standpoint, compels us to regard specific characters as being composed of innumerable, more or less independent factors, of which by far the most recur in various, and many in extremely numerous species. The almost unbounded variety of living and extinct organisms is thus reduced to the numerous different combinations which a comparatively small number of factors makes possible. These factors are the individual hereditary characters, which, indeed, most frequently, are extremely difficult to recognize as such in the intricate sum total of the phenomena, but which, however, since every one of them can vary independently from the others, may, in many cases, be subjected separately to experimental treatment.

These hereditary characters must be grounded in living matter; every vegetative germ-cell, every fertilized egg-cell must potentially contain within itself all the factors that go to make up the characters of the respective species. The visible phenomena of heredity are hence the expressions of the characters of minutest invisible particles, concealed in that living matter. And we must, indeed, in order to be able to account for all the phenomena, assume special particles for every hereditary character. I designate these units, pangens.

These pangens, invisibly small, yet of quite another order than the chemical molecules, and each of them composed of innumerable such molecules, must grow and multiply, and must be capable of distributing themselves by means of ordinary cell-division, over all or at least nearly all cells of the organism. They are either inactive (latent), or active, but they can multiply in both states. Predominantly inactive in the cells of the germ-tracks, they usually develop their highest activity in the somatic cells. And this in such a way, that, in higher organisms, not all the pangens of any given cell probably ever become active, but in every cell one or more of the groups of pangens dominates and impresses its character on the cell.

Fertilization consists in a fusion of nuclei. The offspring receives from the father only that which was contained in the nucleus of the sperm. All the hereditary characters must therefore be represented in the nuclei by their respective pangens. Nuclei, therefore, are to be regarded as the reservoirs of hereditary characters.

In the nucleus, however, by far the most of the characters remain latent all through life. They become active only in the other organs of the protoplast. Haeckel has already said "that the nucleus within had to take care of the transmission of the hereditary characters, and the surrounding plasm, of the adjustmment, accommodation, or adaptation to environmental conditions." (Cf. p. 169).

Therefore, a transmission of the hereditary characters from the nucleus to the cytoplasm[1] must in some way take place here, and the observations communicated in the previous Section furnish important arguments for the correctness of this deduction.

These are the conclusions that, to my mind, are fully justified by the facts at hand. The assumption of pangens is a hypothesis that seems to me indispensable at our present state of knowledge. To my mind it is absolutely necessary for the explanation of the allied relations of organisms, provided that this explanation is attempted on a material basis.

I shall leave now these general considerations, and attempt to describe how I picture to myself the relation of the pangens to the phenomena of cell-life. I am perfectly aware of the fact that the working out of a hypothesis to its extreme consequences leads only too easily to erroneous conclusions, and is of value for science only when leading to definite problems that can be solved experimentally. I shall therefore limit myself to only one hypothesis, which, it seems to me, recommends itself by its simplicity. This hypothesis, with the deductions resulting directly from it, will form the subject of this last section.

The hypothesis reads as follows: *All living protoplasm consists of pangens; they form the only living elements in it.*

§ *2.* *All Protoplasm Composed of Pangens*

From Hertwig's renowned discovery, some investigators have inferred that only the nucleus is the bearer of hereditary characters; that they are entirely restricted

[1]By cytoplasm I mean all the protoplasm except the nucleus.

to it. To my mind this is a much too far-reaching deduction, and without justification. The fusion of the nuclei during fertilization is evidence only that all the hereditary characters must be represented in the nucleus, but this fact does not decide that they cannot be present, in addition, in the cytoplasm.

The organs of the fertilized egg-cell are still the same as those of the unfertilized; the young plant has inherited from the mother its chromatophores and vacuoles as such. In the long succession of cell-divisions which are started by the fertilized egg-cell, those organs, multiplying steadily by division, are transmitted each time to the daughter-cells. They have, so to speak, their independent pedigree in addition to that of the nucleus. There is, therefore, an additional heredity outside the nucleus.

The smallest morphological particles, out of which the chromatophores are built up, must evidently possess the power of multiplying independently, otherwise neither the growth nor the repeated divisions of these structures could be explained. In this respect these particles are obviously similar to the pangens of the nucleus. The power of producing chlorophyll must be present in a latent state in certain pangens of the nucleus; it is also inactive in the smallest particles of the chromatophores, in the higher plants, as long as the respective members are in darkness, and becomes active only on exposure to light.

We shall therefore either have to assume chlorophyll-pangens in the nucleus, and special chlorophyll-forming particles in the chromatophores, or identify the two, and imagine that those hypothetical units are inactive in the nucleus, and become active only when they pass on to the chromatophores. The second assumption is obviously the simpler one; for the first requires, for every function, two kinds of units, which multiply by growth and division, and which must stand in such mutual relationship that the units in the chromatophore can function only in the manner prescribed by the respective pangens in the nucleus.

Precisely the same argument can also be used for the other characters of the chromatophores, and for the other organs of the protoplasts, in a word, for all hereditary characters.

Let us consider the question from the standpoint of the theory of descent. In the first, as yet non-nucleated organisms, we must also, as a matter of course, regard the individual characters as being connected with pangens. But here the latter must evidently lie in the protoplasm. And, as soon as differentiation advanced so far that not all qualities had to be active at the same time, active and latent pangens must in these simple protoplasts, have lain side by side and intermingled. According to age and external circumstances, at one time some, at another time other pangens would enter into activity. Here it would be quite superfluous to assume, for each function, two kinds of units, on the one hand latent pangens, merely having charge of heredity, and on the other hand, particles which might express the latent characters. The assumption that the same pangens can be either active or latent according to circumstances, is evidently much simpler for these lower organisms.

It can hardly be doubted that protoplasm consists of most minute particles which are able to multiply independently. This is indeed the real attribute of life. And it also seems to me clear that we should regard only these particles as life-units, and everything else, such as protein, glucose, and salts, present only in the water of imbibition, as secondary to them. How these particles are constituted, whether they themselves contain water of imbibition, or not, and how the visible characters are conditioned by their structure, we do not know; much less are we acquainted with their manner of dividing and multiplying. Apart from these difficulties, which adhere to any theory, the assumption that these particles are identical with the bearers of the hereditary traits, is obviously the simplest one that can be made with regard to the structure of living matter.

From this point of view, the origination of the nucleus in the phylogenetic differentiation of the lowest organisms, appears to us as an extremely practical division of labor. Hitherto, the active and the inactive pangens were lying everywhere in the protoplasm, side by side and intermingled. And the higher the differentiation that had been reached, the greater would be the number of diverse pangens, in the same protoplast; and the greater, also, would have to be the number of the latent among the active ones. The latter would thereby be distributed over a relatively large space, and the efficiency of the whole must therefore suffer. By the formation of the nucleus this situation could be changed. In the latter the inactive pangens would be accumulated and stored; the active ones could come nearer each other.

Let us further elaborate the picture. As soon as the moment arrived for certain pangens, which until then had been inactive, to be set into activity, they would obviously pass from the nucleus into the cytoplasm. But in so doing they would retain their characters, and especially their power to grow and multiply. Only a few like pangens would therefore have to leave the nucleus every time in order, by further multiplication, to impress the characters of which they are the bearers, on a given part of the cytoplasm. This process would repeat itself at every change of function of a protoplast; every time new pangens would leave the nucleus in order to become active. In this way the whole cytoplasm would soon consist of pangens drawn from the nucleus, and of their descendants.

§ 3. *Active and Inactive Pangens*

Darwin has already emphasized the fact that the transmission of a character and its development, even though they frequently occur conjointly, are yet distinct powers.[2] This point, derived from the phenomena of atavism, has attained great significance in cell-theory through the discovery of the function of the cell-nucleus. The function of the nucleus is transmission, that of the cytoplasm, development.

Former theories assumed a complete contrast between nucleus and cytoplasm, imagining hereditary characters to be limited to the former, and seeing in the rest of the protoplasm only a passive substratum, by means of which the nuclei do their work. Thus the nucleus became the essential part of the cell; not only did it dominate, but also completely determine the functions. But the experiments of Nussbaum, Gruber, Klebs, and others have taught that non-nucleated fractional parts of lower organisms are also able to exercise certain functions. Especially do they seem to possess the power of continuing later those functions in which they were already engaged before being detached. Hence, the influence

[2]Darwin, *The Variation of Animals and Plants.* **2**: 381. New York. 1900.

of the nucleus, for such functions at least, need not be continuous; if the functions have once been exercised they can continue later without the cooperation of the nucleus.*

The simplest explanation of this lies obviously in our assumption that nucleus and cytoplasm are both built up from the same pangens, with this difference, only, that in the nucleus every kind of pangen of the given species is represented, while in the remainder of the protoplasm of each cell essentially only those are present which shall attain their power of activity in it. In the nucleus most of them are inactive, that is, they only multiply. Naturally there must be also some active pangens in the nucleus, as, for example, those that carry out the intricate process of nuclear division; but this does not affect the main point. In the organs of the protoplast the pangens can continue their multiplication, and, to all appearances, they probably always begin here with a relatively great increase in number. With that they can here remain active or inactive for a shorter or longer period; or they may be active and inactive by turns. Some become active at their arrival, others later, some independently from external conditions, others again only as a reaction to definite stimuli that start their activity.

The most remarkable processes that take place in the interior of the nucleus during nuclear division are quite in harmony with the assumption of pangens. Most investigators regard the chromatic thread as the morpho-

*Godlewski's experiment, in which non-nucleated portions of sea-urchin's eggs were fertilized by the spermatozoa of a crinoid, is now well known. The resulting larvae manifested only maternal characters. In the fifth edition of his *"Allgemeine Physiologie,"* Jena, 1909, Verworn cites this experiment as establishing beyond doubt the fact that hereditary substance is not entirely confined to the nucleus. *Tr.*

logical place where the material bearers of the hereditary qualities are stored.* This thread would, therefore, consist of pangens united into smaller and larger groups, and it shows, in its thickest portions a distinct structure of special particles strung together. We can entirely agree with the opinion of Roux, where he sees, in the longitudinal splitting of the nuclear skein, the visible part of the separation of the maternal factors into the two halves destined for the two daughter cells.[3] This conception is in most complete harmony with pangenesis.

§ *4. The Transportation of Pangens*

Our hypothesis that all protoplasm consists of pangens, led us to the conclusion that all kinds of pangens are represented in the nucleus. Here, most of them are inactive, while in the remainder of the protoplasm, they can become active. From this it follows that, from time to time, pangens are transported from the nucleus to the other organs of the protoplast.

I am quite aware that, with most readers, this deduction will prove the chief difficulty against my view. The pangens are invisible, therefore their transportation eludes observation. It is true that the experiments of Nussbaum, Gruber, and Klebs, discussed in the preceding Sections, prove that, on cutting off the opportunity of transportation, the functions of the protoplast are very greatly restricted, but there is here a possibility of many other influences being at work. Therefore I should here like to emphasize the fact that, by rejecting my hypothe-

*Cf. the Translator's Preface, p. viii.

[3]Roux. *Ueber die Bedeutung der Kerntheilungsfiguren.* Leipzig. 1883.

sis, one does not arrive at a satisfactory view of the relation between nucleus and cytoplasm.

If my hypothesis is rejected and the prevailing conception concerning the contrast between nucleus and cytoplasm is followed, we can imagine the effect of the nucleus to be either dynamic or enzymatic.

Strasburger represents the first view. According to him, the reciprocal action between the nucleus and the cytoplasm is a dynamic one, meaning that it takes place without transmission of substance.[5] For this investigator has never been able to discover, in his extensive studies, a transmission of visible particles. "From the nucleus, molecular excitations are transmitted to the surrounding cytoplasm which dominate, on the one hand, the processes of metabolism in the cell, and on the other hand, give a definite character, peculiar to the species, to the growth of the cytoplasm, which depends on nutrition." As long as it is a question of general insight only, this assumption is sufficient, but as soon as attention is directed to individual processes, we meet with insurmountable difficulties. Morphological phenomena are indeed far from having been sufficiently analyzed to allow a true understanding, but in the meantime we can turn to the much simpler chemical processes.

Let us select an example. It is an hereditary character of by far the greatest number of plants to produce malic acid for the purpose of preserving their turgor, and to store it in their cell-sap, most frequently in connection with inorganic bases. We cannot imagine the secretion

[5]Strasburger, E. *Neue Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen,* p. 111. 1884. See also Weismann, A., *Die Kontinuität des Keimplasmas als Grundlage einer Theorie der Vererbung,* p. 28. 1885. Cf. Translator's Preface, p. viii.

of this acid otherwise, than by means of definite particles, which have this power, owing to their molecular constitution, and which might best be likened to enzymes.

There is no difficulty in assuming that these particles become active only when they are made so by molecular excitations from the nucleus, and I do not doubt that such co-relations frequently occur. But the difficulty lies in the question as to whence the cytoplasm gets these particles. Because, obviously, the power of forming malic acid cannot be communicated by those excitations to any kind of substratum. Such excitations can only set free a function, and only that can be set free which is already present potentially. Whence then originate the malic acid formers of the cytoplasm?

This question is not answered by the dynamic theory. But, as previously stated, hybrids teach us that similar paternal characters can be inherited from the father, and therefore be transmitted in a latent state in the sperm-nucleus. Hence the producers of the malic acid must, themselves, be derived from the nuclei. They are simply the active states of the malic acid pangens that are inactive in the nucleus. And the same must evidently hold, in a similar manner, of all the other hereditary factors.

In this way, we arrive at the assumption previously made, that the pangens of the cytoplasm originate from the nuclei.

Haberlandt has pointed out the possibility of an enzymatic influence of the nucleus on the cytoplasm. The significance of peculiar positions of the nucleus, observed by this investigator, in the vicinity of the place of most vigorous cell-activity, remains, according to him, the same, "if that influence should be *not* a dynamic, but a material one, and if, consequently, a diffusion of certain chemical compounds, secreted by the nucleus, should take place through the plasm to the place of growth. The effectiveness of these substances would doubtless be dependent on the degree of cencentration of their solution, and this in such a way that the cytoplasm would react to them only at a certain concentration."[6]

But in order to react in a definite manner on the substance secreted by the nucleus, the cytoplasm must already possess the requisite characters. Starch will react to a secretion of diastase, but not all kinds of substratum will do so. Thus the assumption of enzymatic effects demands the presence, in the cytoplasm, of hereditary characters, which have been taken from the nucleus.

Therefore, no matter how strange the assumption of a transmission of pangens from the nucleus to the cytoplasm may appear at first glance, we arrive by the most various ways of reasoning at a recognition of its correctness.

An important question is that of the time when this transportation chiefly occurs. A comparative consideration of the various forms of variability will in the end, it is hoped, furnish the necessary material for its answer; in the mean time we may assume it as probable that immediately after fertilization, as well as during or after every cell-division, such a transportation takes place. Hybrids, and those variations that affect in a similar manner all the members of a plant, argue in favor of the first point, and for the other, the previously discussed phenomena of dichogeny, where during the earliest youth of an organ its later nature can be determined by external influences. When, for instance, the terminal bud of a rhizome grows prematurely and turns into an upward

[6]Haberlandt, G. *Ueber die Beziehungen zwischen Function und Lage des Zellkernes*, p. 14, note. 1887.

shoot, or the primordium of a transformed leaf becomes a normal leaf, we may assume that other pangens have been given up by the nucleus, than would have been the case without artificial interference. Therefore, in that youthful state, the normal delivery cannot yet have come to an end. When grown cells are stimulated to form callus or wound-cork or, as in Begonia, to produce *de novo* entire plantlets, it is to be supposed that the pangens that thereby become active must first be aroused from their latent state.

The transportation of pangens, and their conveyance to the proper places, demands quite special arrangements, the existence of which many a reader will hardly venture to suspect. But who would have dared, ten years ago, to assume the remarkably complicated structure of the nucleus? We must be as sparing as possible with our hypotheses, but on the other hand we must not be blind to the fact that since Mohl's time, the investigation of the structure of the protoplast has disclosed more and more differentiations, and that, most likely, we are still far from the end.

To my mind the currents in the protoplasm form one arrangement for the purpose of this transmission. Everybody knows how they take place in youthful cells at paths that radiate from the nucleus, and more recent investigations have taught how they frequently connect the places of greatest activity directly with the nucleus.

A few years ago the conviction that these little currents are a quite common peculiarity of plant-cells, was far from being prevalent. The phenomenon was imagined to be limited to a number of instances. Hanstein has already pointed out how little this view was justified,[7] and Velten has proven the presence of currents in all plants

[7]Hanstein, *Das Protoplasma,* p. 155. 1880.

examined with this point in view.[8] In the Botanische Zeitung for 1885, I have furnished proof that mechanical contrivances are not sufficient for the transmission of the assimilated nutrient matter in plants, and that, of the processes known up to date, it can only be accomplished by the currents of the protoplasm.[9]

In this connection I have carefully verified Velten's statement, and have confirmed the quite common existence of currents in vigorously living plants.[10]

The mechanical possibility of a transmission of pangens is, therefore, sufficiently assured for all plant-cells. Only one difficulty has yet to be overcome. Following the precedence of Hofmeister, it was generally assumed that the currents in the cells begin only at the end of the meristematic period, and that, until that time, the granular plasm is in a state of rest. Now the meristematic period is not only that in which the cells originate, but also that in which their later character is chiefly determined. Hence it is in this very period that we must place the most important part of the transportation of the pangens.

But Hofmeister's statement was based on insufficient observations. A subsequent investigation by Went, with the more modern methods, led to a quite different result.[11] The movements are indeed slow, and one examination will often not disclose them. But if the observation of

[8]Velten, W. Ueber die Verbreitung der Protoplasmabewegungen im Pflanzenreiche. *Bot. Zeit.* **30**: 645. 1872.

[9]Vries, H. de. Ueber die Bedeutung der Circulation und der Rotation des Protoplasma für den Stofftransport in der Pflanze. *Bot. Zeit.* **43**: 1. 1885.

[10]Over het algemeen voorkomen van circulatie en rotatie in de weepelcellen der planten, *Maandbl. v. Natuurw.* No. 6. 1884. Cf. *ibid.* No. 4, 1886, and *Bot. Zeit.* **43**: 1, 17. 1885.

[11]Went, F. A. F. C. Die Vermehrung der Normalen Vacuolen durch Theilung. *Jahrb. Wiss. Bot.* **19**: 329. 1888.

the same object is continued for hours under favorable life-conditions, there will be noticed all kinds of displacements, which put the presence of slow currents beyond a doubt.

From this side, therefore, no difficulty stands in the way of the assumption that the transmission of the pangens in plant-cells is accomplished by the currents of the granular plasm. In the domain of animal physiology we are far from possessing the necessary knowledge of the currents of the protoplasm. But then the difficulties of investigating are here considerably greater than in the plant-world.

§ 5. *Comparison with Darwin's Transportation-Hypothesis*

Possibly to some readers there will appear to be a great similarity between the assumption of a transmission of pangens from the nucleus to the other organs of the protoplast, as described in the previous paragraphs, and Darwin's hypothesis of the transportation of gemmules. However, this agreement is only apparent and not real. The two hypotheses are fundamentally different throughout.

Darwin assumed a transportation of gemmules through the entire body; my view requires only a movement within the narrow limits of an individual cell. But this is not the chief difference. In the gemmule-theory, the particles that are separated from a cell or a member can again enter new cells, especially the germ-cells, and thus endow them with new hereditary factors. Not only can the latter then reach their development in the given germ-cell, but they can also be transmitted to all its descendents. To this end, however, they must, according to the present state of cell-anatomy and of the study of fertilization, be received into the nuclei. The hypothesis of intracellular pangenesis obviously does not make such an assumption; the pangens that have once left the nucleus do not have to return to it, neither into the nucleus of the same cell, nor into that of any other.

It is true that, with our present anatomical knowledge, the possibility of a transmission of pangens from one cell to another cannot be denied. The researches of Tangl, Russow, and many other investigators on the direct connections of the protoplasts of neighboring cells by means of the delicate pore canals of the pits, even indicate the path on which such a passage might eventually take place. In the latex vessels the currents of protoplasm are undoubtedly not limited to the individual constituent cells, the current continuing without regard to the former cell-limits. This is especially the case with the mass-movement after injuries, and probably also with the proper movements of the granular plasm in the normal state. If we assume that all living protoplasm consists of pangens, their passage from one cell to another cannot be denied here. But this phenomenon is obviously of no importance for the theory of heredity. Similar considerations could be made for other cases of cell-fusions, or symplasts.

The mode of origin of the secondary pores of the Florideæ, discovered by Kolderup-Rosenvinge,[12] is also worthy of note. The cortical cells, e. g., of *Polysiphonia,* divide in the usual manner with preceding nuclear division. But one part contains almost the entire protoplast and the other but a small corner at its base. The

[12]Kolderup-Rosenvinge, L. Sur la formation des pores secondaires chez les Polysiphonia. *Botanisk Tidsskrift.* **17**: 10. 1888.

wall arising between the two halves forms a primary pit. At that place the wall between the separated corner and the underlying cell is dissolved, and contact being thus established between the two protoplasts, they fuse. The old poreless cross-wall is thus replaced by a new one that contains a pore. But the interesting point for our purpose is the circumstance that the underlying cell has now received a nucleus from its upper neighbor. It has two nuclei, and later it becomes multi-nuclear by nuclear divisions. For all those who regard the nucleus as the bearer of the herditary endowment, a transmission of the latter here takes place from one cell to another. But obviously again without any significance for the theory of heredity.

The possibility of a transmission of material bearers of hereditary characters from one cell to another can therefore not be denied. Further investigations will, without doubt, bring to light other facts that can be utilized for the same purpose. And that here and there, in plants, processes take place in a similar way, which stand in direct relation to heredity can, of course, not be denied *a priori.*

But it is quite another question whether such a transmission occurs commonly, and plays an important rôle in the transmission of hereditary characters in the whole plant and animal world.

Anatomical facts alone are not sufficient to answer this question. From them, only the possibility of a transmission can be deduced or, more correctly speaking, the conclusion that our present knowledge does not furnish any reasons which would make that transmission appear impossible. It may be that such a thing will be discovered later. But it is not likely that anybody will think it is therefore permissible to infer the actual occurrence of a general intercellular transmission of the bearers of hereditary properties.

Hence, the answer to the question must be looked for in a quite different field. The theory of heredity must tell us whether there are facts for the explanation of which the assumption of an intercellular transmission is indispensable.

To my mind, this is not the case, as I have already stated in the Introduction. I have there referred to Weismann's writings, which contain copious demonstrations that all observations which so far seemed to demand such an assumption, could in reality have been explained as well, and in most cases better, without them.

Especially should the so-called heredity of acquired characters be mentioned here. I have previously, in another place, drawn attention to the fact that in many cases we have here to deal with malformations.[13] If we limit the meaning of that expression to the variations which have arisen on the somatic tracks, and ask whether these can be transmitted to the germ-tracks of the organism, then the question has a clear meaning. In that case we can join Weismann in quietly answering, no. But, if we also call such characters as may have originated on the germ-tracks acquired, the question is no longer of any significance for the problem which occupies us here.[14]

In botany graft-hybrids and xenia are mentioned as

[13]"Over steriele Mais-planten," *Jaarboek v. h. Vlaamsch kruidk. Genootschap,* Bd. 1. Gent. 1889.

[14]The conception of germ-tracks and somatic tracks in the sense developed in the first Section of this second Part may contribute much, in this connection, to help the mutual understanding. See also e. g., in regard to Eimer's discussions, his work: *Die Entstehung der Arten auf Grund von Vererben erworbener Eigenschaften.* Theil 1. 1888.

arguments for an intercellular transmission of hereditary qualities. But both groups of phenomena are much in need of being critically investigated before they can be reliably employed in this way. The transmission of the hereditary characters of the crown-graft to its stock[15] has, to my mind, never been scientifically proven, and never will be, as long as new experiments are not made, in which the variations of the stock itself, are thoroughly studied and have become well known. Because, until then, the possibility is not excluded that this variability of the stock itself forms the most important factor in the phenomena that have been observed.

The cases where the pollen is supposed to have transmitted hereditary characters outside the fertilized egg-cell and the embryo issuing from it, to the tissues of the maternal fruit, have been carefully arranged by Focke under the name xenia.[16] And his review shows plainly that here one has to deal with exceptional cases which have never yet been thoroughly studied and sufficiently controlled.[17] And I think that, without a control, based on critical examination, these data cannot be given that far-reaching significance that would make them the

[15]Cf. the critical summary of the material for observation bearing on this point, by H. Lindemuth, Uber Vegetative Bastarderzeugung durch Impfung. *Landw. Jahrb.* **7**: 887. 1878.

[16]Focke, *Die Pflanzenmischlinge*, pp. 510-518. 1881. [See also, Webber, H. J. Xenia, or the immediate effect of pollen on Maize. *U. S. Dept. Agr. Div. Veg. Physiol. Pathol. Bull.* 22. Sept. 12, 1900; Correns, C. Untersuchungen über die Xenien bei Zea Mays. *Ber. Deut. Bot. Ges.* **17**: 410. 1899. *Tr.*]

[17]The best known instance of Xenia, that of corn, has since been shown to be of a different nature, consisting in the hybridization of the endosperm in the process of double fertilization. See de Vries, Sur la fécondation hybride de l'albumen. *Compt. Rendus Acad. Sci.*, Paris, **129**: 973. 1899, and Sur la fécondation hybride de l' endosperme chez le Mais. *Revue générale de Botanique.* **11**: 129. 1900.

bases for an assumption of an actual intercellular transmission of hereditary qualities.

The facts of heredity so far known, do not, to my mind, make the assumption of an intercellular transmission of pangens necessary. When the pangens have once left the nucleus they do not need the power of penetrating back into that nor into any other nucleus. The pedigree of the pangens lies in the nuclei, and its protoplasmic side-branchings all end blindly, although often only after many cell-divisions.

I believe that the passage of the pangens from the nuclei is a necessary conclusion of our present knowledge concerning the physiological significance of the nuclei. I need not assume a penetration of the extruded pangens or their descendents into other nuclei. And this hypothesis would be inevitable if one were to connect Darwin's transportation of gemmules with the results of more recent cell-study. In this case one would have to resort to a new ancillary hypothesis in order to explain facts, which, according to the discussions mentioned above, do not at all require such an explanation.

Let us summarize the difference between the two transmission hypotheses. The pangens of the intracellular pangenesis, having once left the nucleus, need never re-enter it. For the gemmules of Darwin's transportation hypothesis, however, this power is the essential condition, because without it, the hereditary properties of which they are the bearers, can never develop into visible characters in the descendants of the respective germ-cells.

§ 6. *The Multiplication of Pangens*

The hypothesis, that the entire living substance of a cell is built up of pangens, naturally implies that in every protoplast every kind of pangen must be represented in great numbers. In addition, the relative number of the bearers of the individual hereditary characters is of very great importance. In the cytoplasm it determines the function of the individual organs, in the nucleus the power of inheritance. If a new character in the nucleus is represented by only a few like pangens, the likelihood of this character becoming visible, is evidently very small. But the greater the number of those pangens, in comparison with the others, the more prominent will the character appear. From seeds of a twisted specimen of *Dipsacus sylvestris* I have grown over 1,600 plants, of which only two showed torsion of the stem. The pangens which caused this torsion must, therefore, have been in such relatively small numbers that their chance of becoming active amounted to 1 per 1,000 at the most. In other young varieties this proportion is more favorable, and, by making the right selection, that chance increases quite considerably in the course of a few generations. The simplest explanation for this is obviously, that by breeding those specimens in which the characteristic is represented by the greatest number of like pangens, the relative number of these is gradually increased.

I have repeatedly emphasized the fact that, according to my hypothesis, the pangens can multiply in the nucleus as well as in the cytoplasm. This multiplication is of the same order as that of the cells and of the organisms themselves. When a large tree bears, every year, thousands of seeds, the pangens of the egg-cell from which the tree has grown, must have multiplied in an incredible manner. And the same thing is taught by the enormous number of eggs that a single tape-worm can produce. In the face of such phenomena the multiplication of the pangens in the cytoplasm of an individual cell is only minimal.

The giving off of the pangens by the nucleus must, as a matter of course, always be done in such a way that all kinds of pangens remain represented in the nucleus. Always only a relatively small number of like pangens must leave the nucleus. The division of the nuclei, however, must take place in such a way that all the different kinds of pangens are evenly distributed over the two daughter-cells. Only in certain somatarchic cell-divisions[18] is there a deviation from this regularity.

The two kinds of variability which Darwin distinguishes on the ground of pangenesis, are naturally also to be deduced from the description here given.[19] Fluctuating variability is simply based on the varying numerical relation of the individual kinds of pangens, which relation can indeed be changed by their multiplication and under the influence of external circumstances, but most quickly by breeding selection. The "species-forming" variability,[20] that process by which the differentiation of living forms has come about, in its main lines, must essentially be reduced to the fact that the pangens, in their division, produce, as a rule, two new pangens that are like the original one, but that exceptionally these two new pangens may be dissimilar. Both forms will then multiply, and the new one will tend to exercise its influence on the visible characters of the organism.

In harmony with this is the idea that we must imagine the higher organisms to be composed of a greater number of unlike pangens than the lower ones.

[18]Cf. pp. 102 and 107.
[19]Cf. p. 74.
[20]Now commonly called mutability (de V. 1909).

Chapter II

SUMMARY

§ 7. *Summary of the Hypothesis of Intracellular Pangenesis*

The view of Darwin (apart from the hypothesis of the transportation of gemmules through the entire body), that the individual hereditary qualities are dependent on individual material bearers in the living substance of cells, I call pangenesis. These bearers I call pangens. Every hereditary character, no matter in how many species it may be found, has its special kind of pangen. In every organism many such kinds of pangens are assembled, and, the higher the differentiation that has been reached, the more there are.

The hypothesis that all living protoplasm is built up of pangens, I call intracellular pangenesis. In the nucleus every kind of pangen of the given individual is represented; the remaining protoplasm in every cell contains chiefly only those that are to become active in it. This hypothesis leads to the following conclusions. With the exception of those kinds of pangens that become directly active in the nucleus, as for example those that dominate nuclear division, all the others have to leave the nucleus in order to become active. But most of the pangens of every sort remain in the nuclei, where they multiply, partly for the purpose of nuclear division, partly in order to pass on to the protoplasm. This delivery always involves only the kinds of pangens that have to begin to function. During this passage they can be transported by the currents of the protoplasm and carried into the various organs of the protoplasts. Here they unite with the pangens that are already present, multiply, and begin their activity. All protoplasm consists of such pangens, derived at different times from the nucleus, together with their descendants. There is in it no other living basis.

The elaboration of this hypothesis, given in the preceeding chapters, is only an outline, the purpose of which was to make the main idea comprehensible. It is, for the present, the simplest form in which pangenesis can accommodate itself to our present knowledge of the structure of the cell. In details I am well aware of not having been able always to find the right explanation. But the only object I had in mind was to demonstrate how easily the greatly misjudged pangenesis covers all the facts discovered since its establishment!