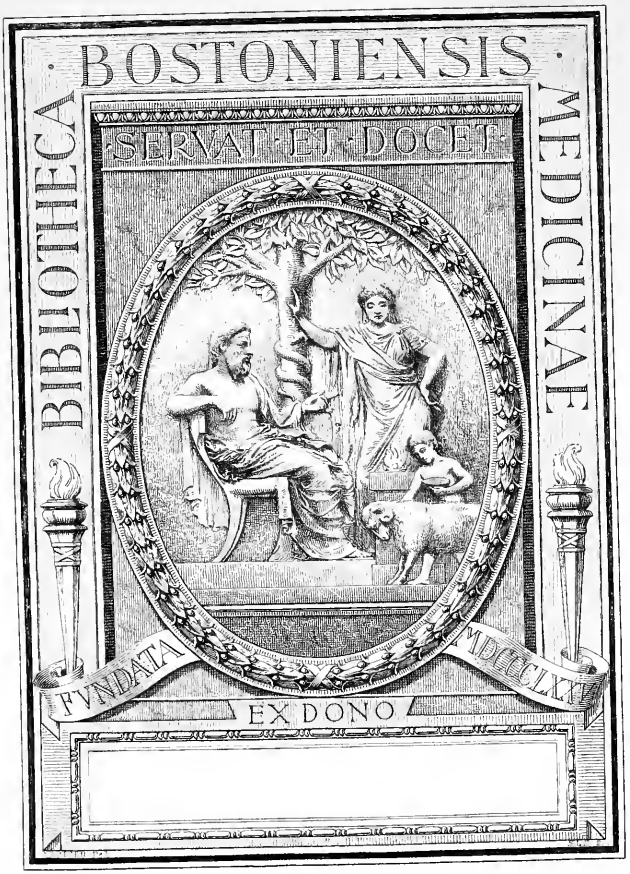
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Intracellular Pangenesis

INCLUDING A PAPER ON

FERTILIZATION AND HYBRIDIZATION

BY

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FOREWORD

The *Intracellulare Pangenesis,* of Hugo de Vries, was such a source of stimulation to me at the time of its appearance that I feel greatly indebted to its author. By creative imagination Hugo de Vries predicted much in his book that gained a material basis only through the histological research of the following decades. That is what makes the study of his book to-day as interesting as it is instructive.

In his paper, entitled *Befruchtung und Bastardirung,* a translation of which is included in this volume, de Vries has shown the same faculty of utilizing our present knowledge from every point of view, and of looking prophetically into the future. For in this paper also, on the ground of theoretical considerations, he predicted phenomena which were to furnish the basis for our conceptions of fertilization and heredity, but which have become actually known to us only through later works on the most intimate processes of nuclear division.

Therefore I gladly comply with the wish of the translator to introduce his translation with a few words. I say expressly "to introduce," for works of Hugo de Vries do not need a recommendation.

Bonn,
June, 1908.

E. Strasburger.

" . . . . . my well-abused hypothesis of pangenesis"

Charles Darwin, *Autobiography.*

TRANSLATOR'S PREFACE

Every student of heredity is brought face to face with the problem of some mechanism of inheritance. Pangenesis was Darwin's solution of this problem. But it was not in the form in which Darwin left it that pangenesis became directly fruitful of results; and no one felt the insufficiency of his hypothesis more keenly than Darwin himself. Writing to Asa Gray in 1867 he said: "The chapter on what I call Pangenesis will be called a mad dream . . . . . but at the bottom of my own mind I think it contains a great truth."[1] And to J. D. Hooker, in 1868, he wrote: "I feel *sure* if Pangenesis is now still born it will, thank God, at some future time reappear, begotten by some other father, and christened by some other name."[2]

Many men discerned the weak features of the hypothesis, but to Hugo de Vries belongs the credit of having detected the "great truth" it contained. He became its "other father," and rechristened it with another name —a name more nearly like the original, no doubt, than Darwin could have imagined.

The pangenesis of Darwin was hardly susceptible of experimental verification, except to the extent that a more intimate acquaintance with the facts showed that the assumption of a transportation of "gemmules" was super-

[1]Darwin, C. Life and Letters. **2**: 256. New York, 1901.
[2]*Loc. cit.* p. 261.

fluous. But it contained the germ of de Vries's intracellular pangenesis, the direct progenitor of the mutation-theory. It was primarily because of this genetic relationship, together with the masterful way in which the hypothesis is developed, and the accompanying wealth of illustration, that the little German volume, here done into English, was deemed worthy of translation at the present time.

As those who have followed the more recent literature of theoretical biology well know, Delage has argued against accepting any of the micromeric theories of the structure of protoplasm. His argument is based upon the idea that, by the law of probabilities, no one can ever, by pure imagination, correctly conceive of the ultimate structure of protoplasm in detail. Kellogg[3] cites this criticism of Delage as "a sufficient reason against accepting any one of these highly developed theories of the structural and functional capacity of invisible life units." Possibly this is correct, but that depends upon what the given hypothesis is to be accepted for. Of course no unverified hypothesis should be accepted for truth. As soon as the hypothesis can be so accepted it ceases to be a hypothesis, or even a theory, and passes into the rank of ascertained fact.

But that the argument of Delage can be advanced as a reason for rejecting any hypothesis, not inherently improbable or absurd, as a working hypothesis, a point of departure for further experiments, serving to orient a whole body of investigators, seems to me entirely to miss the point of the purpose of a hypothesis. Hypotheses are not statements of truth, but instruments to be used in the ascertainment of truth. Their value does not de-

[3]Kellogg, V. L., Darwinism To-day. p. 223. New York, 1907.

pend upon ultimate verification, but is to be measured by their effect upon scientific research. All this is now a truism.

What does it argue that no one, as Delage insists, ever anticipated by imagination the striation of muscle fibers, the existence of chromosomes and centrosomes, or any other fact of minute structure revealed by the microscope. May it not be asked in reply how long we should have had to wait for the discovery of the inert gases of the atmosphere, the accessory chromosome, and the ion, had they not first been conceived in imagination and formally embodied in working hypotheses? It is not pleasant to contemplate what the effect on the development of chemical science would have been had Dalton's (micromeric) hypothesis of indivisible units been rejected on the *a priori* grounds that the ultimate structure of matter is beyond the power of the human intellect to imagine in detail.

The hypothesis of intracellular pangenesis can never be absolutely demonstrated as true—can never advance beyond the rank of a theory—because the hypothetical pangens are conceived to be invisible, ultra-microscopic units, whose existence can never be more than inferred; but the formulation of the hypothesis marks the beginning of the greatest and most important forward step in the study of the origin of species since 1859. The notion of pangens became the parent-idea of unit-characters, offered a simple mechanism for the disjunction of characters in hybrids, and for continuous and discontinuous variation, and thus lead up directly to the conception of mutation as one method of the origin of species.[4] And, most important and significant of all, it resulted in per-

[4]Cf. footnote, p. 74 *infra*.

manently removing the entire question of organic evolution from the realm of ineffective speculation, and establishing it upon the firm basis of experimentation.

The term pangen is employed in its original sense by Strasburger in his paper on "Typische und allotypische Kertheilung."[5]

Recognizing the existence of some material entities as the ultimate units of heredity, conceiving of them as invisible, and accepting for them the name pangen, he interprets the chromatin granules (chromomeres), which can be directly seen, as larger or smaller pangen-complexes, and suggests that we designate them "pangenosomes." The pangenosomes, owing to a "certain elective affinity," he considers as combining into ids, (from the idioplasm, of Nägeli), and the ids, in turn, into chromosomes.[6]

Referring to de Vries's supposition, that the pangens influence the cytoplasm by wandering out into it from the nucleus and thus changing from an inactive to an active state, Strasburger[7] records his failure to detect any visible evidence that the bodies which he calls pangens thus wander out from the nucleus into the cytoplasm, but refers to the period in cell-division when the nuclear membrane disappears and the spindle forms, as serving to bring the chromosomes into direct contact with the cytoplasm, and thus establishing a condition favorable for the "formative influencing" of the cytoplasts by the nucleoplasts. A similar influence might also result from extranuclear nucleoli distributed in the cytoplasm. In the fertilization

[5]Jahrb. Wiss. Bot. **42**: 1-71. 1905.

[6]Mottier's use of the word pangen to designate the visible chromomeres (Ann. Bot. **21**; 307-347. 1907.), employs the term in a sense entirely at variance with that for which it was originally proposed (*cf.* p. 49.)

[7]*loc. cit.* p. 74.

of the egg he postulates a fusion of maternal with paternal pangens.[8] Thus, in the gametophytic generation, the pangens must be considered as univalent (*haploid*), in the sporophytic as bivalent (*diploid*). This would lead us to look for larger nuclei in the cells of the sporophyte than in those of the gametophyte. This hypothesis was verified in a number of plants, widely separated systematically. In *Taxus baccata,* for example, the nuclei of the prothallus were noticeably smaller than those of the sporophyte: and in nuclei with equally marked granulation, Strasburger counted fifty granules in an optical section of the nuclei of the nucellus, and only one-half that number in the nuclei of the adjacent prothallus.

But I cite this paper of Strasburger's chiefly to show how the hypothesis of intracellular pangenesis, in other hands that its author's, may assist in forming some comprehensible picture of the mechanism of matter in the living state. The idea and the term pangen are also adopted by Pfeffer in his Physiology of Plants.[9]

At the suggestion of Professor de Vries, a translation of his Haarlem *Vortrag* on *"Befruchtung und Bastardierung"* is included in this volume, for the purpose of showing the bearing of more recent research on the hypothesis of intracellular pangenesis, and of thus bringing the problem more nearly down to date. The translation of this *Vortrag* also appeared in "The Monist," for November, 1909.

It is a pleasure to record my profound gratitude to Professor de Vries for his careful reading and annotation of the manuscript of the translation, and for his interest and encouragement throughout the undertaking.

[8] *loc. cit.* p. 61.

[9] Pfeffer W. The Physiology of Plants. Eng. Trans. by Alfred J. Ewart. **1**: 49. Oxford, 1900.

I am deeply indebted to Professor Strasburger for his kindness in preparing an introductory note, and wish, also to express my sincere thanks to Miss Marie Onuf, whose invaluable assistance rendered the completion of the work possible.

C. S. G.

University of Missouri,
Department of Botany.
Nov. 13, 1909.

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AUTHOR'S INTRODUCTION

AUTHOR'S INTRODUCTION

In the year 1868, in the second volume of his celebrated work, *"The variation of animals and plants under domestication,"* Darwin formulated the provisional hypothesis of pangenesis. The discussion of this hypothesis is preceded by a masterly survey of the phenomena to be explained. Owing to this, as well as to his clear conception of the whole problem, this part of his book has attracted universal attention. We find it mentioned in almost all works which deal with general biological questions. While, however, the general part of the chapter has until now remained the basis for all scientific considerations of the nature of heredity, the hypothesis itself has not enjoyed such general appreciation.

Darwin assumes (Variation 2: 369) that the cells, as is generally accepted, multiply by division, and that in so doing they preserve essentially the same nature. He considers that this rule forms the basis of heredity. By it, however, not all of the groups of phenomena brought together by Darwin may be explained. Especially does it not explain the effects of use and disuse, the direct action of the male element on the female, and the nature of graft-hybrids. In order to take into account these phenomena, Darwin assumes that there exists, in addition to cell division, yet another means of transfer of hereditary qualities. Each unit of the body, according to his theory,

throws off minute granules[1] which accumulate in the germ cells and buds. These granules are the bearers of the characters of the cells from which they are derived, and thus transmit those characters to the germ cells and to the buds.

Thus all the hereditary characters of the organism are represented in the egg-cells, pollen-grains, sperm-cells, and buds by minute particles. These they have received, partly by descent from former germ cells, i. e., directly, but partly by later addition from the cells and organs of the body. These minute granules are not the chemical molecules; they are much larger than these and are more correctly to be compared with the smallest known organisms. Darwin calls them gemmules (small germs).

The hypothesis of these gemmules threw an unexpected light on a series of facts which had hitherto been in absolute darkness. And if one reads attentively Darwin's discussion, he sees more and more clearly that the transmission of gemmules by cell-division, from the mother-cell to the daughter-cell, suffices to explain large groups of phenomena. Only isolated groups of facts demand in addition the hypothesis of transportation. The doctrine of latent qualities and of atavism particularly are drawn from their former darkness by Darwin's hypothesis, and his discussion of this subject (p. 357) clearly shows what great significance he imputes to this circumstance. It demands, however, only the transmission of the gemmules in cell-division, not their transportation from the growing and full-grown organs to the germ-cells.

[1]This is the term Darwin first uses. The Variation of Animals and Plants. **2**: 358. New York, 1900. *Tr.*

It has always seemed to me that most authors have not sufficiently distinguished these two aspects of the hypothesis, and that their objections against accepting the theory of transportation have misled them into overlooking the paramount significance of the doctrine of gemmules.

To my mind Darwin's provisional hypothesis of pangenesis consists of the following two propositions:

1. In every germ-cell (egg-cell, pollen-grain, bud, etc.) the individual hereditary qualities of the whole organism are represented by definite material particles. These multiply by division and are transmitted during cell-division from the mother-cell to the daughter-cells.

2. In addition, all the cells of the body, at different stages of their development, throw off such particles; these flow into the germ-cells, and transmit to them the qualities of the organism, which they are possibly lacking. (Transportation-hypothesis).

The second assumption possessed, for Darwin himself, only limited importance, in the case of plants and corals, as he considered a transportation of gemmules from one branch to another impossible. It does not apply to the workers of ants and bees, nor to the double stocks (gilliflower) mentioned several times by Darwin. These do not possess any stamens and pistils themselves, and their characteristics must therefore be transmitted from one generation to the other through the fertile single specimens of the race. The facts, for the explanation of which the theory in question was brought forth, have gained neither in number nor in trustworthiness during the twenty years since the publication of Darwin's book.

Doubts of its necessity, therefore, are quite permissible, and it is the chief service of Weismann to have

repeatedly emphasized these doubts, and to have shattered the rather generally accepted doctrine of the heredity of acquired characters.[2]

But even if, with this investigator, one rejects the second proposition, that is no reason for likewise doubting the other part of the hypothesis of pangenesis. On the contrary, it seems to me that by doing so its great significance only becomes clearer. Besides, there have been no convincing arguments brought forward against this first dogma, and no other hypothesis concerning the nature of heredity takes account of the facts in so simple and clear a manner.

Yet most authors have considered that, by refuting the transportation hypothesis, they have also refuted that of the bearers of individual hereditary characters, and they have hardly devoted any special discussion to it. In consequence of this Darwin's view has unfortunately not borne such fruit for the development of our knowledge as its originator had a full right to expect.

My problem in the following pages will be to work out the fundamental thought of pangenesis independently of the transportation hypothesis, and to connect with it the new facts which the doctrine of fertilization and the anatomy of the cell have brought to light.

I shall be guided by the thought that the physiology of heredity, and especially the facts of variation and of atavism indicate the phenomena which are to be explained, while microscopic investigation of cell-division and fertilization will teach us the morphological substratum of those processes. We shall not try to explain the mor-

[2]The designation "acquired" is not exactly well chosen. The question is: Can characters which have originated in somatic cells be communicated to the germ-cells. This possibility is rejected by Weismann. Compare Part II, § 5. (p. 93).

phological details of those processes; our knowledge is yet too limited for that. But, following the method of Darwin, to find in the special cases the material substratum of the physiological processes, that is our problem.

As the most important result of cell-investigation of the preceding decades, I consider the theory that all the hereditary predispositions *(Anlagen)* of the organism must be represented in the nucleus of the cell. I shall try to show that this theory leads us to assume a transportation of material particles which are bearers of the individual hereditary characters. This does not mean, however, a transportation through the whole organism, nor even from one cell to another, but one restricted to the limits of the individual cells. From the nucleus the material bearers of the hereditary characters are transported to the other organs of the protoplast. In the nucleus they are generally inactive, in the other organs of the protoplast they may become active. In the nucleus all characters are represented, in the protoplast of every cell only a limited number.

The hypothesis, therefore, becomes one of *intracellular pangenesis.* To the smallest particles, of which each represents one hereditary characteristic, I shall give a new name and call them *pangens,* because with the designation "gemmule" *(Keimchen)* is associated the idea of a transportation through the whole organism.

PART I

PANGENESIS

A. The Nature of Hereditary Characters

Chapter I

THE MUTUAL INDEPENDENCE OF HEREDITARY CHARACTERS

§ 1. *The Combination of Specific Characters Out of Hereditary Characters*

Among the many advantages which have lent such a prominent significance to the theory of descent in the investigation of living nature, the shattering of the old conception of species occupies an important place. Formerly every species was regarded as a unit and the totality of its specific attributes as an indivisible concept. Even the latest theories on heredity accept this concept as one that does not require any further analysis.

But if the specific characters are regarded in the light of the theory of descent it soon becomes evident that they are composed of single factors more or less independent of each other. One finds almost every one of these factors in numerous species, and their varying groupings and combinations with less common factors causes the extraordinary diversity in the organic world.

Even the most cursory comparison of the various organisms leads, in this light, to the conviction of the composite nature of specific characters. The power to produce chlorophyll and, by means of this, in light, to decompose carbon dioxide, is evidently to be regarded as a property which, in great measure lends to the botanical world its peculiar stamp. This power, however, is lacking in many groups throughout the system, and therefore

is by no means inseparably connected with the other factors of plant nature.

Other factors are the predispositions *(Anlagen)* which enable many species to produce definite chemical compounds. First of all, the red and blue coloring matter of flowers, then the different tannic acids, the alkaloids, etherial oils, and numerous other products. Only a few of these are limited to a single species, many recur in two or more species, which are often systematically far apart. There is no reason for supposing that, in every individual case there is a different mode of origin for the same compound; rather it is obvious that essentially the same chemical mechanism underlies the same process, wherever we find it.

In a similar manner we must also accept as possible the analysis of the morphological characteristics of the species. It is true that morphology is not by any means so far advanced that such an analysis could be carried out in every individual case. But the same leaf-form, the same leaf-edge, coarsely or delicately notched, recur in numerous species, and even the customary terminology teaches us that the configurations of all the various leaf-forms are composed of a comparatively small number of simple characters.

It would be superfluous to accumulate instances which are easily accessible to every one, and it is only a question of thoroughly familiarizing one's self with these ideas, so that the synthesis of the whole out of its component parts is clearly recognized. It will then be seen that the character of each individual species is composed of numerous hereditary qualities, of which by far the most recur in almost innumerable other species. And even if, in the building up of any single species, such a large number of these

factors is necessary that we almost shrink from the consequences of an analysis, it is clear, on the other hand, that, for the building up of the sum total of all organisms, there is required a rather small number of individual hereditary characters in proportion to the number of species. Regarded in this way, each species appears to us as a very complex picture, whereas the whole organic world is the result of innumerable different combinations and permutations of relatively few factors.

These factors are the units which the science of heredity has to investigate. Just as physics and chemistry go back to molecules and atoms, the biological sciences have to penetrate to these units in order to explain, by means of their combinations, the phenomena of the living world.

Phylogenetic considerations lead to the same conclusions. Species have gradually been evolved from simpler forms, and this has taken place by the addition of more and more new characteristics to those already existing. The factors which compose the character of a single species are, therefore, in this sense, of unequal age; the characteristics of the larger groups being in general, older than those of the smaller systematic divisions. But the very consideration that the characteristics have been acquired singly or in small groups, shows us again from another side their mutual independence.

It is a striking, yet by far insufficiently appreciated fact that frequently, in distant parts of the genealogical tree, the same character has been developed by wholly different species. Such "parallel adaptations" are extremely numerous, and almost every comparative treatment of a biological peculiarity shows us examples thereof. The insect-eating plants belong to the most varied natural families, yet they all possess the power of

producing from their leaves the necessary mixture of an enzyme, and of an acid which is needed for dissolving protein bodies.[1] The agreement, emphasized by Darwin, of this mixture with the gastric juice of the higher animals justifies even the supposition that those plants and the animal kingdom have some hereditary qualities in common.

The indigenous creeping and climbing plants, the tropical lianas, the tuberous and bulbous plants, the fleshy, leafless stems of the Cactaceæ and Euphorbiaceæ, the pollinia of the Orchidaceæ and Asclepiadaceæ, and numberless other instances show us parallel adaptations. Very beautiful pictures are furnished on the one hand by the desert plants, which all have to protect themselves in some way against the disadvantages of evaporation, and whose anatomical relations have been so thoroughly described by Volkens.[2] On the other hand are the ant-plants, into the adaptations of which to harmful and useful species of ants Schimper has given us an insight.[3]

Everywhere we see how one and the same hereditary character, or definite small groups of the latter, can combine with other most diverse hereditary characters, and how, through these exceedingly varied combinations, the individual specific characters are produced.

[1]This statement is now known to hold true only in the case of *Nepenthes* (Vines, *Ann. Bot.* **11:** 563. 1897. **12:** 545. 1898) and of *Drosera* (see Fr. Darwin's articles). Schimper found no proteolytic enzyme secreted by Sarracenias. (*Bot. Zeit.* **40:** 225. 1882). His results were confirmed by Miss Robinson, but she demonstrated the secretion, by *Sarracenia purpurea,* of a starch-digesting enzyme. (*Torreya* **8:** 1908). *Tr.*

[2]Volkens, G. *Die Flora der Aegyptisch-Arabischen Wüste.*

[3]Schimper, A.F.W. Die Wechselbeziehungen zwischen Pflanzen und Ameisen im tropischen Amerika. *Bot. Mittheil. aus den Tropen.* Band I, Heft 1, 1888.

§ 2. *The Similarity of the Differences Between Species and Between Organs*

The comparison of species with the organs of a single individual leads us to quite similar conclusions as does the comparison of species with each other, for the differences between the organs can be traced back, in the same way, to various combinations of individual hereditary qualities.

Even the simplest observation teaches us this. Just as chlorophyll is lacking in some species it is also lacking in single organs and tissues of higher plants. The red coloring matter of flowers is limited to certain plant species, and in these again to definite organs. Tannic acid, etherial oils, and like substances, where present, show a local distribution. Calcium oxalate is lacking in most ferns and grasses, and on the other hand in the roots of many species rich in calcium. The same is true, apparently, of morphological attributes. I need not cite examples, for it will certainly be granted that a very close agreement exists between the manner in which the organs of a single plant differ from each other and the distinction between different species. Both depend upon varying combinations and a varying selection from a great range of given factors.

A series of phenomena, which we may summarize under the name *dichogeny,* leads to similar conclusions. I mean all those cases where the nature of an organ is not yet decided during the early stages of its development, but may yet be determined by external influences. Thus, under normal conditions, the runners of the potato-plant form at their tips the tubers, but on being exposed to light, or when the main stem has been cut off, they de-

velop into green shoots. By severing the stems, the rhizomes of *Mentha, Circaea,* and many other plants, can be made into ascending stems, and the transformations which the thick almost resting rhizomes of *Yucca* undergo after such treatment are remarkable. In a similar manner Goebel has succeeded in causing the rudiments of bracts to develop into green leaves,[4] and Beyerinck[5] observed even the transformation of young buds of *Rumex Acetosella* into roots.

In such cases it is clear that the possibility of developing in either of two different directions is dormant in the young primordia. For this very reason I should like to apply the name *dichogeny* to this phenomenon. And it evidently depends upon external influences what direction is taken. Therefore a selection must take place from among the available hereditary characters of the species, and this selection may be influenced by artificial interference. For the theory of hereditary characters such experiments are therefore of the highest interest.

Here are naturally included the phenomena of bud-variation. Many of these are cases of atavism. Let us select an example. In plants with variegated leaves one frequently observes single green branches. Since the variegated plant is descended from green ancestors, this case is regarded as a reversion. The variegated individual evidently still possessed the characteristics of the green ancestor, though in a latent condition. During the bud-formation it split its entire character, but in such a way

[4]Goebel, K. Beiträge zur Morphologie und Physiologie des Blattes. *Bot. Zeit.* **40**: 353. 1882.

[5]Beyerinck, M. W. Beobachtungen und Betrachtungen über Wurzelknospen und Nebenwurzeln. *Veröffentl. Akad. Wiss.* Amsterdam, pp. 41-41. 1886. Cf. also Tafel I, Fg. 9.

that in one branch the variegated combination predominated, in the other one the green color.

As a further illustration of bud-variation, I may mention the nectarines. These are hairless peaches, which originated in several varieties, and in some of them repeatedly through bud-variation. This fact can be explained only by saying that the possibility of producing hairy fruit can become lost in single branches, easily and independently from all other characters, or at least become latent.

The characteristics which originate through bud-variation are usually preserved by propagation by means of grafts, cuttings, et cetera, and, in isolated cases, are even constant from seed. New varieties may therefore be produced in this manner. And, since we regard varieties as incipient species, this consideration is further evidence of an accordance in the differences between species and between organs.

Naturally included with bud-variations is the consideration of monoecious plants, for the latter agree with the former in the fact that different branches allow different qualities to develop. In the young plant the sexes are not yet separated, and frequently for a long time the possibility of producing both is retained. If this process, however, is started, it is accomplished by a kind of separation: one bud develops into a staminate, the other into a pistillate flower. Or staminate and pistillate inflorescences are produced, or whole branches are predominantly pistillate and others staminate. The specific character was therefore present in the young plant as a whole, but in a latent state, and, in order to manifest itself, it had to split into its two chief parts.

The formation of organs, bud-variation, and the pro-

duction of staminate and pistillate branches in monoecious plants are therefore due to a kind of splitting. The potentialities, united in the young plant, separate from each other in order to be able to unfold. And the grouping of the hereditary characters in the separate branches and organs shows a very great agreement with the combination of such characters to form the various specific marks of related organisms.

§ 3. *The Similarity Between Secondary Sexual Characters and Specific Attributes*

Continuing in a similar manner as in the previous paragraph we will now take into consideration the secondary sexual characters, for they lead to exactly the same conception of a specific character.

This is most clearly seen in those cases where the two sexes of one species, upon being first discovered have been described as different species.[6] But otherwise, too, the secondary differences between the individuals of both sexes are of the same order as the differences between the various species in the same and in allied genera.

It is the same with those plants which bear flowers on various individuals, the sex-organs of which exhibit constant differences, the so-called cases of heterostyly. In the Primulaceæ we distinguish one form with long and another with short style; in some species of flax there occur three different forms of flowers in different individuals.

Although here the individuals belonging to two or three different groups of the same species are different

[6] *Catasetum tridentatum* has three different forms of flowers, which were formerly considered to belong to three different genera: *Catasetum, Monachanthus* and *Myanthus.* de V., 1909.

neither according to sex nor to generation, nevertheless they are distinguished by attributes which are as constant and of the same order as the specific attributes taken from the same organs in allied genera.

In the way of a supplement I will consider, in this connection, the alternation of generations, because here also the differences between the physiologically non-equivalent individuals, belonging to different generations, are of the same order as the specific characters. This we are taught by the Uridineæ and the Cynipideæ, and all those cases where the presence of an alternation of generations was discovered only after the single forms had been described as species, and had been classified with different genera and families of the system. And even to-day it is impossible to prove morphologically that two forms belong together; experimental cultures alone can decide this question. The successive alternating generations cannot be reduced to the same primary form, for each of them compounds its characters by means of a different selection from the available hereditary endowments of the species.

In summing up the result of this paragraph and the two preceding ones, we find that every thorough consideration of a specific character, and every comparison of this with other characters, leads us to regard the former as a mosaic, the component parts of which can be put together in various ways.

§ 4. *The Variation of the Individual Hereditary Characters Independently of One Another*

A comparative consideration of the organic world convinced us that the hereditary characters of a species, even if connected with each other in various ways, are

yet essentially independent entities, from the union of which the specific characters originate. Now let us see whether or not this conclusion is supported by experiment.

For this purpose let us turn to experiments on the formation of varieties, especially to those which have been made on a large scale by plant breeders. They teach us that almost every character may vary independently from the others. Numerous varieties differ from their ancestral form, in only one attribute, as, for example, the white sports of red-flowered species. The red color changes in the corolla through all gradations, into white; it may be lacking or it may be present not only in the blossoms, but also in the stems and leaves, and can be developed to every conceivable degree, without any other hereditary quality being necessarily involved in the variation. In the same way the hairiness, the arming with thorns and spines, the green color of the leaves, may each vary by itself, and even disappear completely while all other hereditary characters remain quite unchanged. Frequently some characters that belong together vary in groups without exercising any influence on the other groups. Thus an increase in the number of petals is not rarely accompanied by a petal-like development of the calyx or the bract-leaves, while otherwise the plant remains normal. I have cultivated a *Dipsacus sylvestris,* which offers all conceivable diversities in the arrangement of the leaves, and which is otherwise constant in thousands of specimens. The *Papaver somniferum polycephalum* deviates only in the transformation of numerous stamens into carpels. It is the same for the cultivated *Sempervirum tectorum.* Such instances are so numerous, in the plant kingdom as well as in the animal kingdom, that the independent varying of single

characteristics forms the rule, while the combined variation of several of them is the exception. It is true that in most cases it cannot be decided whether the given attribute is determined by a single hereditary character or by a small group of them.

On the other hand an accumulation of several variations in one race can easily be accomplished, and it occurs quite commonly in cultures as well as in nature. But the cases which were sufficiently well controlled and described, usually show that the single variations have not evolved simultaneously, but one after another, and this is sufficient to prove their independence.

Such an hereditary character, isolated from the rest, can now become the object of experimental treatment. Through suitable selection it may be gradually strengthened or weakened, and at the will of the breeder it may be brought into a certain relation to the other unchanged characters. The red color of the copper-beech has been so much intensified that even the cell-sap in the living cells of the wood became intensely red. The doubling of flowers frequently leads to a complete disappearance of the sexual organs. And in numerous instances only those organs change which are subjected to selection while the others remain unaffected by it. The adaptation of the cultivated plants of agriculture to the needs of man, and of the horticultural ones to his æsthetic sense, demonstrates this to us in the clearest manner.

Experimental treatment further leads to the study of the influence of external circumstances on the unfolding of hereditary characters. Here again these prove themselves to be factors of which each may vary independently from the others. Young varieties especially are objects for study, and all those which have not as yet

been sufficiently fixed, and in which, therefore, external influences will still play a prominent part in answering the question as to whether a given seed will produce a true or an atavistic individual. Rimpau and others have taught that with a given kind of seed disturbances and interruptions of growth exercise a powerful influence on the number of specimens that bear seed in the first year.[7] And in horticultural and teratological literature one finds scattered numerous data from which the importance of external influences generally is clearly evident. To the experimental investigator there is here opened a large and almost untrodden field. Theoretically the chief task will consist in isolating as much as possible the variations of the hereditary characters in order to obtain, in this way, a knowledge of the individual factors of the respective character.

The variations which we observe in nature frequently appear to us as if they had suddenly sprung into existence, and the same is true of cultures on a small scale, or when the single indivduals are not completely under control.

However, experience with cultivated plants, during the first years after the beginning of their cultivation, teaches us that the deviations often develop but slowly, and that the modifying influences, as a rule, have to operate through several generations before they can accumulate their effect in such a manner that it becomes evident.[8] The facts with reference to this, collected by Darwin, give the impression that the new characters at first arise only in a latent state, and in this condition grad-

[7]Rimpau, A. W. Das Aufschiessen der Runkelrûben *Landwirtschaft. Jahrbücher.* **9**: 191. 1880.

[8]On this point compare Darwin, *The Variation of Animals and Plants under Domestication.* Ed. 2. **2**: 39. 1875.

ually gain in strength, until they finally reach the stage necessary to make them visible. Here again it must therefore be assumed that every hereditary character is miscible to any extent with the others.

The independence of the hereditary characters is most beautifully shown in atavism. A character may remain latent through a number of generations while all the others unfold normally. From time to time it appears again, mostly without exercising any kind of influence on the other characters. We do not know what external circumstances condition this reappearance; in all probability they do not act simply on the atavistic individuals, but we must conceive that the given potentiality is always latent in the others, only it is very fluctuating in its strength. To us only the crests of the highest waves are visible.

To all appearance such qualities can be transmitted through a long series of generations, from one generation to another. Their existence can be reckoned by millenniums in those cases where they are at least as old as the species itself. I mean the cases of reversion to the ancestors of the species, of which the zebra-like stripes of the horse form such a well-known instance.[9] We have a similar illustration in the *Primula acaulis* var. *caulescens,* which occurs from time to time in the field as a quite isolated specimen among thousands of non-umbellate plants, and then forms an inflorescence quite similar to that of the most nearly allied umbellate species. Cultivation has taken possession of this more richly flowering variety, and has put it on the market in many nuances of color.

I should not close this section without having pointed

[9]Darwin, *loc. cit.* **1**: 59.

out one phenomenon which greatly complicates the study of hereditary characters. I refer to the circumstance, already repeatedly alluded to, of their being commonly united in smaller and larger groups which behave like units, the single members of the groups usually appearing together. We see this in the staminate and pistillate flowers and inflorescences of monoecious plants, in the described cases of bud-variation and dichogeny. The sexual characters of various individuals and the difference between the alternating generations of the same species teach us the same thing.

This combination of the individual characters into groups is therefore quite general, although it occurs in all degrees, and although some hereditary characters, as for instance the power of assuming a red color, do not unite, as a rule, into a group with certain others. It is recognized most clearly in those cases of the formation of groups of green bracts instead of flowers, caused by aphids, phytopters, and other parasites, where the stimulus calls forth a whole series of characters that ordinarily develop in other parts of the plant.

Every theory of heredity has to take into account this combination of the hereditary characters into larger and smaller groups, and different authors, like Darwin and Nägeli have strongly emphasized this point. But right here lies a great difficulty which interferes with a working out of the theory in detail, for in many cases it will obviously be extremely difficult to decide whether one is dealing with a single hereditary character or with a small group of them. There is here a large field for morphological analysis which awaits working up.

§ 5. *The Combination of Hereditary Characters*

Hereditary characters can be combined to any extent

and in any proportion. This is shown in variegated leaves and striped flowers, where the result of this combination, after corresponding splitting, is almost directly demonstrated to us. Almost endless is the diversity of pattern of variegated leaves, frequently on the same plant, or at least on the different individuals of one and the same crop. Striped flowers, according to Vilmorin, arise through partial atavism from old white-flowering varieties of red or blue species.[10] Young varieties usually revert by leaps to the ancestral form, while the older ones do so by steps, through the appearance of isolated stripes of the original color on the white back-ground. It is as if the color potentialities were already too much weakened to tint the whole corolla in one effort. The descendents of the first striped flowers, however, soon form broader stripes, and finally return, after a few generations, [at least in some specimens,[11]] to the uniform color of the ancestral form.

Extremely peculiar are those cases where hereditary potentialities, which in the active state necessarily exclude each other, occur together in a latent state. Instead of giving a long enumeration of many cases, I prefer to describe a well-known case of variability, and select for the purpose the arrangement of leaves in whorls.

Two-ranked whorls, the leaves of which stand crosswise over each other on the successive nodes, belong to the best and most constant characteristics of entire natural families. Less frequent are the cases of three- and more-ranked whorls. Quite frequently, however, one

[10]Vilmorin, L. Lévêque de. *Notices sur l' améliorations des plantes par le semis.* pp. 39-41. 1886. (According to modern views the stripes are due to a separate character. de V. 1909.)

[11]Matter in the body of the text in brackets has been introduced anew into the translation by the author of the original. *Tr.*

species will change from its normal type into another form of whorl, and in numerous plants with decussate leaves, single branches with three- and more-ranked whorls have been observed. The Fuchsias and the Weigelias of our gardens, are common examples. The transitions from one number in the whorls to the other usually take place by leaps, in such a way that the whole shoot springing from one bud is alike in this respect; however, branches with another number in their whorls will frequently develop from its terminal bud or its lateral buds. More rarely a shoot will change, during its development, from one number to another, as is the rule, for example, in *Lysimachia vulgaris*. Intermediate forms between two- or three- and four-ranked whorls are exceedingly rare, although from our present knowledge, they may develop quite readily, and have actually been observed from time to time in most plants with whorled leaves.[12] I mean those whorls in which one leaf is more or less deeply split at its apex, while the mid-vein forks. This splitting occurs in all conceivable degrees and leads to a complete doubling in those leaves which bear two blades on one cleft petiole. Consideration of numerous examples gives the impression that the single whorl-forms are antagonistic to each other, and that each tries to exclude the other. It is rare that they do not succeed in this effort, and then we get the above mentioned leaves with the forked mid-vein, the complete series of transition of which, from one leaf to two leaves has been figured and described by Delpino.[13]

Therefore, even such qualities, which in the developed plant exclude each other, are miscible, apparently

[12]Cf. Delpino, F. Teoria generale della Fillotassi. *Atti R. Univ. Genova* **4**: 197. 1883.

[13]*Loc. cit.* p. 206, Taf. LX, Fig. 60.

without difficulty, in the latent state. In truth, the principle illustrated by this example holds good also in the phenomena of monoecism and dioecism, of the di- and trimorphism of flowers, and indeed, throughout the entire range of organ-formation. Everywhere we find characteristics which cannot exist simultaneously in the same organ, and yet must be associated in a latent state during its youth.

In summarizing briefly what has been said, we see that experiments and observations on the origin and fixing of variations teach us to recognize hereditary characters as units with which we can experiment. They teach us further that these units are miscible in almost every proportion, most experiments really amounting merely to a change in this proportion.

The above considerations are verified in a striking manner by experiments in hybridization and crossing. In no other connection does the concept of a species as a unit made up of independent factors stand forth so clearly. Everyone knows that the hereditary characters of two parents may be mixed in a hybrid. And the excellent experiments of many investigators have taught us how, in the descendents of hybrids, an almost endless variation can usually be observed, which is essentially due to a mixing of the characteristics of the parents in a most varied manner.

The hybrids of the first generation have quite definite characteristics for each pair of species. If one produces a hybrid of two species, which previous investigators have already succeeded in crossing, he can, as a rule, rely on the description given of it tallying exactly with the newly produced intermediate form. If the hybrid is fertile without the help of its parents, and if its progeny are

grown through a few generations in thousands of specimens, one can almost always observe that hardly any two are alike. Some revert to the form of the pollen-parent, others to that of the pistil-parent; a third group occupies a central position. Between these are placed the others in the most motley variety of staminate and pistillate characteristics and in almost every gradation of mutual inter-mixture.

Many and prominent authors have pointed out the significance of hybrids for establishing the nature of fertilization. With the same right we may use them in trying to penetrate into the mystery of specific character. And then they clearly prove to us that this character is fundamentally not an indivisible entity. The characteristics of a hybrid (of the first generation) are as sharply defined and as constant, and on the whole of the same order as those of the pure species, and the frequent specific name, *hybridus*,[14] might go to prove that even the best systematists felt this agreement.

Kölreuter, Gärtner, and others have combined in one hybrid two, three, and more species, and there is no reason why any other than a purely practical limit should be put to this number, and that, in fact, there should not be combined in one hybrid characteristics which have been taken from an unlimited series of allied species. But this is of small importance, the chief point being the proposition that the character of a pure species like that of hybrids, is of a compound nature.

Crossings of varieties of the same species belong, especially in horticultural practice, to the most common operations. Ordinarily the object pursued is simply that of producing intermediate forms. Not infrequently,

[14] E. g. *Papaver hybridum* L., *Trifolium hybridum* L.

however, one desires to impart single definite qualities to one variety and he derives these from another variety, sometimes even from another species. Hardening against winter-frost has frequently been transmitted in this manner from one form to another. Carriére[15] cites instances of Begonias which, through crossing with a variety of another species with variegated leaves, have been made varigated without having their other qualities changed. The conviction is really quite general in horticultural practice that, by crossings, one may combine the characters of varieties at will, and thus improve his races according to his needs in many as well as in individual desirable points.

§ 6. *Cross- and Self-fertilization*

In addition to the arguments dealt with in the preceding paragraph, which gives us the results of experiments in crossing and hybridization, we will now consider normal fertilization and see to what extent, in this domain, the facts support our conception of the mutual independence and miscibility of hereditary characters.

To fathom the meaning of fertilization is one of the most difficult problems of biology. The numerous adaptations of this process to the most varied conditions of life, and the powerful influence which it has exercised on the differentiation of species, especially through the development of the secondary sexual characters, threaten always to mislead us, and to make us mistake its essential nature through its later acquired significance. Here, as in so many cases, the conditions in the plant kingdom are clearer

[15]Carriére, E. A. *Production et fixation des variétés,* p. 22. 1865. Other examples are given by Verlot, *Sur la production et la fixation des variétés.* pp. 46 and 65. 1865. Cf. also Darwin, *loc. cit.* **2**: 73.

and simpler than in the animal kingdom, in which especially the exclusive limitation of propagation of the higher animals to the sexual method makes us only too easily over-estimate the significance of this process. To this must be added the fact that, for the vegetable kingdom, quite an unexpected light has been thrown on the nature of this process through the exhaustive comparative study of the significance of cross- and self-fertilization, for which we are indebted to Darwin.

Darwin's experiments have taught us that the essence of fertilization consists in the mixing of the hereditary characters of two different individuals.[16] Self-fertilization, which takes place so readily in the vegetable kingdom, and is so easily accomplished experimentally, has not by any means the same significance. From seeds obtained in the last named manner the individuals produced were always weaker in Darwin's experiments than those obtained in a crop from crossed flowers. The first ones were smaller, with less profuse branching, flowering less abundantly and less constantly, and accordingly they bore less seed. Crossing two flowers of the same plant was more deterimental than the pollination of the flowers with their own pollen.

Even the crossing of different individuals was not sufficient to keep the species normal when it was cultivated year after year in the same bed, and protected from being fertilized by specimens of a different origin. The whole colony deteriorated steadily and distinctly in the course of a few years; not only did the plants become smaller and weaker, but their individual differences decreased so much that they resembled each other almost completely. A

[16]Darwin, *Origin of Species.* 6 Ed., pp. 76-79, and *Cross and Self Fertilization in the Vegetable Kingdom.* 1876.

single cross, however, of such a colony with individuals of another origin restored the original vigor.

The process of fertilization, in its essence, does not consist, therefore, in the union of two sexes, but in the mixing of the hereditary characters of two individuals of different origin, or at least of such as have been subjected to different external conditions. Therefore, a difference in hereditary characters is obviously a condition for attaining the full advantage of fertilization; this difference, however, must have been acquired in the last instance through a life under different influences.

Let us regard the individual hereditary factors as independent units, which can be combined with each other in different proportions into the individual character of a plant. Let us further assume that their relative increase or decrease depends on external influences. Evidently there is then a great probability that, under similar external conditions, the same factors will deteriorate in different individuals, while under different conditions this fate will befall other factors in every individual. Thus, on crossing the plants of the same bed only, the individual deviations of the same kind are strengthened; the weakened factors are therefore made still weaker. But if we cross individuals of the most different culture possible, the differences in the individual factors are clearly balanced, at least in part; and this the more so, the more numerous the specimens which deviate from each other, and which are used for the crossing.

It is well known to plant breeders that luxurious conditions which are varied as much as possible lead to an accumulation and increase of individual differences, while simple and uniform circumstances make them disappear gradually, and thus further the uniformity of all speci-

mens. The first method is applied in improving races, the latter in fixing newly acquired varieties.

To maintain a species with the required proportion of all its hereditary factors, only an occasional crossing is necessary. It need not precede every generation. Where sexual generations alternate with asexual ones, as in the gall-fly, and even where the latter occur in the majority, as in many aphids, this is clearly seen.

With bees the fertilized eggs become females, the unfertilized ones males. But since every male descends necessarily from a female that originated through fertilization, it evidently profits sufficiently by the advantages of an occasional crossing. The aphids, in which the male as well as the female originate parthenogenetically, teach us that here we have to do not with fundamental relations, but with special adaptations.

The never-opening, so-called cleistogamous flowers, the numerous devices for insuring self-fertilization in flowers in case they are not visited by insects, and the almost unlimited use of vegetative multiplication in plants, all serve to teach us that an occasional fertilization is all that is necessary for the normal preservation of the species. That in higher animals every individual originates in the sexual way, is therefore obviously only a special adaptation.

In summarizing the result of these considerations, we may say that the true essence of fertilization consists in mixing the hereditary characters of the different individuals of a species. Hybrids have taught us how we are to conceive this co-mingling. There is no doubt that the process of mixing is, in principle, the same in both cases. And just as Wichura[17] succeeded in producing hybrids

[17]Wichura, Max. *Bastardbefruchtung im Pflanzenreich erläutert an den Bastarden der Weiden.* Breslau, 1865.

from six different kinds of willows, so should it be possible to combine, by crossing, the hereditary qualities of several individuals into one.

In the preceding paragraphs we have seen how the single hereditary characters occur as independent units in the experiments of hybridization and crossing, and how they can be attained in almost every degree. In the same way, evidently, must we think of those units as independent in the ordinary process of fertilization as well.

§ 7. *Conclusion*

Seemingly elementary, the specific character is actually an exceedingly complex whole. It is built of numerous individual factors, the hereditary characters. The more highly differentiated the species, the higher is the number of the component units. By far the most of these units recur in numerous, many of them in numberless organisms, and in allied species the common part of the character is built up of the same units.

On trying to analyze species into these individual factors, we are confused by their number, which, in the higher plants and animals reaches probably into the thousands. If, however, we regard the entire world of organisms as the subject of our analysis, then the total number of hereditary characters which is needed for the building up of all living beings, is indeed large in itself, but, in relation to the number of species it is small. In that limited sphere our method of investigation leads apparently only to complications, but, on the whole, it evidently leads the way towards a very considerable simplification of the problems of heredity.

The hereditary factors, of which the hereditary characters are the visible signs, are independent units which may

have originated separately as to time, and can also be lost independently from one another. They can be combined with each other in almost every proportion, every individual character from complete absence through all gradations being capable of attaining the highest development. Frequently the conditions are so unfavorable for some of them that they cannot manifest themselves at all, and so remain latent. In this condition, they may either persist for thousands of generations, or they may appear in every generation during the development of the individual from the fertilized egg, in which they are nearly all latent.

The hereditary factors compose the entire specific character; there is no separate basis to which they are attached.

Although independent to the degree that each, of itself, can become weaker and even disappear completely, they are yet, as a rule, united into smaller and larger groups. And the condition is such that, when external influences, such as a stimulus to gall-formation, bring a definite character into dominance, the entire group to which it belongs is usually set into increased activity.

Independence and miscibility are therefore the most essential attributes of the hereditary factors of all organisms.

To find a hypothesis which will make these characteristics more comprehensible to us, is, according to my opinion, the chief problem of every theory of heredity.

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 in-

dividual 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 phenom-

ena 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 hered-

itary 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 cur-

rent 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.

PART II

INTRACELLULAR PANGENESIS

A. Cellular Pedigrees

Chapter I

THE RESOLVING OF INDIVIDUALS INTO THE PEDIGREES OF THEIR CELLS

§ 1. *Purpose and Method*

Since the founding of the cell-theory by Schleiden and Schwann, cells have come more and more to the foreground of anatomical and physiological consideration. The theory of heredity, also, which about two decades ago was hardly at all in touch with the cell-theory, has given up this isolated position, and sees in the more recent investigations on cell-division and the process of fertilization an important furtherance of its problems.

Omnis cellula e cellula. Not only does this saying dominate microscopic science, but it is steadily rising into supreme command over all Biology. That every cell has originated from a material part of its mother-cell, and that it owes its specific characters to this origin, is now accepted in the theory of heredity as the basis of all thorough considerations. Whether or not this source is sufficient for the explanation of all phenomena was the question which induced Darwin to formulate his pangenesis. And this question remains the first to be answered with reference to every new group of facts appearing within the domain of heredity.

The phenomena known at present, at least in so far as they have been sufficiently thoroughly investigated, demand an affirmative answer to that question. This was conclusively demonstrated by Weismann, as has been

already mentioned in the first Part. We need therefore not deal with that question in this Section.

Not the organisms, but the cells, are therefore the units of the theory of heredity. One has to go back to these for a clear understanding. In the practical pedigrees of the animal- and plant-breeders of course only the individuals figure, but for a scientific insight, these are not sufficient, as is well known to the greatest authorities among breeders.

Here the germ-cells (egg- and sperm-cells) come into the foreground for consideration. They are the material parts of the parents from which the children issue, and hence form the material bond between the successive generations. For every germ-cell we may trace a series of ancestral cells back to the last preceding generations. In this way we may proceed further, and follow up the pedigree of the germ-cells through a series of generations. The great scientific significance of these sequences of cells has been strongly emphasized by Weismann; they form, without doubt, the basis for the theory of cell-pedigrees.

But this kind of treatment leads to a one-sided conception of the problem. We ought rather to trace the ancestral line of all the cells of the entire body back to the first cell from which the organism started. It is true that thereby the task becomes much more extensive and complicated, and it is a question whether a sufficient anatomical and ontogenetic basis is at hand for its solution. Nevertheless it is only in this way that we can approach a uniform treatment of the subject, and group the available facts in such a way that they do not deceive us, nor lead us to an overestimation of the significance of isolated cell-sequences selected by us arbitrarily.

We should, therefore, trace out the pedigree of the

individual cells for the whole organism. Or, in other words, we should resolve the individual into its cells and and their lineage. To this end the history of development must furnish us the requisite facts which, however, must include all forms of reproduction.

The cellular pedigrees that are to be traced are of a purely empirical nature. As Sachs has already emphasized, we have but to record the facts in as simple a grouping as possible,[1] and see what conclusions can be drawn from them without resorting to any hypothesis. The harvest will, to my mind, be much richer than would be imagined at first glance.

That the chief results of the consideration of cellular pedigrees in both the plant and animal kingdoms will lead to the same general conclusions, probably no one doubts at present. But the conditions are quite different in the plant world from those in the animal kingdom. The various kinds of reproduction in the latter are not nearly as numerous as in the former. A study of animals is therefore much more exposed to the danger of one-sided treatment than that of plants. Moreover, with the botanist, the conviction that the anatomical and ontogenetic investigation should always penetrate at least to the individual cells has, under the influence of Mohl and Nägeli, for almost half a century, taken much deeper root. Accordingly the ancestral sequence of by far the greatest number of cells is, in innumerable cases, if not without gaps, demonstrable with sufficient certainty at least in its main lines.

Therefore I shall be able to limit myself in this section, without danger, to the cellular pedigrees of plants. And this the more so, as the most important lines of

[1]Sachs, J. von. *Vorlesungen über Pflanzenphysiologie.* 1882.

those pedigrees have lately been frequently emphasized for the animal kingdom by Weismann and others, and a comparison of both kingdoms with reference to this point does not, therefore, offer any considerable difficulties.

§ 2. *The Cellular Pedigrees of the Homoplastids*

In unicellular species the pedigrees of the individuals coincide with the cellular pedigrees. But such is also the case with those organisms of few cells, the cells of which are as yet quite alike and not organized for various functions. The Oscillariae are many-celled threads, but all the cells are alike, every one of them is equally able to propagate the species. Gőtte has named such organisms homoplastids, as compared with the heteroplastids, the cells of which are adapted for various functions.

It is clear that the ancestral trees of cellular descent of the homoplastids are entirely composed of like branches. It depends only upon external circumstances, and the struggle for existence, which of the cells will become new individuals, and which branches of the family tree, therefore, will continue the descent through the series of generations.

In the higher plants and animals, on the contrary, only definite branches of the cellular pedigree lead, in the normal course of development, to the cells that begin the next generation, the other branches being already excluded, by their nature, from taking part in the normal propagation of the species. The branches of the tree are here, therefore, not only morphologically different, but also intrinsically unlike in their relation to the pedigree of the species.

The differentiation of the cellular pedigrees started

with the development of the heteroplastids from the homoplastids. The undifferentiated cellular pedigrees of the latter do not afford us any clue for judging the phenomena of heredity. Hence we leave them aside, and turn our attention entirely to the heteroplastids.

§ 3. *The Cellular Pedigree of Equisetum*

Before we begin describing, at least in their main lines, the extremely complex cellular pedigrees of the higher plants, we will elucidate the whole method with a rather simple example. I choose for the purpose the genus of the horsetails (*Equisetum*). Their cellular pedigree belongs, in spite of their alternation of generations, to the simplest that are to be found among the leaf-forming plants, or Cormophytes. There are two ways of arriving at a conception of the main lines of the picture. One of them is the progressive, the other the retrogressive. The first one follows up the track of ontogeny, the second one descends in the opposite direction. If one is interested in deciphering the combination for all the cells of one plant, then the first method is obviously the simplest and the safest. But, in choosing it, the relative value of the two new twigs, into which the stem divides, can only be judged when the ends of both twigs are constantly and simultaneously kept in view. But, in tracing only the main lines of the picture, it is, in most cases, much more convenient to choose the opposite direction. For, in the retrogressive direction, all paths evidently lead back to the egg-cell, so that in this direction no erring is ever to be feared.

I assume that through a combination of both methods the picture of the cellular pedigree of an *Equisetum*-species, e. g. of *E. palustre* has been developed and lies

before us.[2] The fertilized egg-cell in the archegonium begins its growth by divisions, the first of which stands nearly at right angles to the axis of the archegonium; this is followed by two walls at right angles to this and to themselves. From the lower octants develop the root and the foot of the young sporophyte, the latter by the formation of a small-celled tissue body due to continued divisions. These branches of the pedigrees are thus ended. From one of the upper octants of the embryo the apical cell of the first shoot originates, the other octants participate in the formation of the annular thickening which represents the first leaf-whorl, and thus soon end their growth, after continued divisions.

The growth of the first, as well as of all successive shoots is dominated by the apical cell. The latter occupies the apex of the shoot, its upper cell-wall is spherically arched, while downward it is limited by three almost plane walls. It has, therefore, the shape of an inverted three-sided pyramid. It divides only by walls which run parallel to the three sides of the pyramid; every detached piece is called a segment. By numerous divisions, the three successive segments, parallel to the three sides of the pyramid, always form an internode with a leaf-whorl at its upper end. The whole shoot, therefore, consists of sections each of which owes its origin to a segment whorl of the apical cell.

The apical cell, therefore, evidently represents the main stem of our pedigree; every segment corresponds to a branch. During the development of the shoot, and consequently, during the first year of vegetation of the

[2]Illustrations of the required stages of development are found in Goebel, K. *Grundzüge der Systematik und Speziellen Pflanzenmorphologie* pp. 286-304. 1882.

individual, the main stem remains simple, and, since the first shoot never bears a sporophore without modification of its activity, it ends with the death of the shoot at the end of the first summer.

Each segment that separates from the apical cell divides first into an upper and a lower half; these, through further walls, into a body of tissue, from which now all the cells of the respective part of the internode and the leaf-whorl arise. The sequence of division has been explained by Cramer and Rees and can be found in the *Lehrbuch der Botanik,* of Sachs and Goebel. Furthermore, there should be emphasized, first of all, the fact that, in the outer cell-layer of the body of tissue, and alternating with the teeth of the leaf-blade, favored cells are formed, each of which can grow into a lateral shoot. The green shoots of older plants as a rule actually bear, in every leaf-whorl, a circle of as many branches as the whorl has members. But, in the first shoot, they usually do not reach development. Every lateral bud, when developing into a shoot, possesses an apical cell, which starts the development of the branch in the same manner as the terminal cell of the main shoot.

Thus in every branch the apical cell again forms the main line of the pedigree. It is true that this line does not join the main stem in a simple manner but it can be clearly traced back, through the first divisions of the segment, to the stem. Now every segment, and within it, during their first cleavages, those cells from the later divisions of which the apical cells of the lateral branches arise, we shall regard as the main stem of our pedigree. All other cell-sequences will be considered as lateral branches, for only in this manner can we get a clear picture.

Let us return now to the shoot during its first year of vegetation. At the end of the summer it perishes. A lateral bud in one of the basal leaf-whorls, however, continues to live, and develops during the next year into a new shoot, which grows stronger and larger than the first one, but does not yet bear any organs of fructification. This course continues for several years, until the plant has become quite vigorous. Sometimes the third or one of the following shoots grows downward into the ground, to form the rhizome, which, from now on, forms the main-shoot of the plant, branching beneath the ground and sending up into the air the leaf-bearing and spore-bearing shoots. These are distinct in *Equisetum arvense* and some other species. In the spring the pale, fertile unbranching shoots arise, in the summer the extensively spreading, green but sterile branches.

The cellular pedigree of the whole large plant would very soon present an inextricable picture. To avoid this danger, we must mark especially the main lines, perhaps by indicating them by heavier marks. We must also draw the lines as straight as possible. Supposing all of this executed, we get a pedigree of the apical cells which in the picture stands out clearly as a connected system, and to which all the rest is laterally added. We shall call the lines of the pedigree of the apical cells the branches, the other ramifications the twigs. In order to avoid misunderstandings, it must be remembered, that the pedigree of apical cells does not consist exclusively of apical cells, since these do not originate directly from each other.

According to this definition the development of the twigs of the pedigree is always limited, only in the branches resides the ability of new ramifications, and

thence of a continuation of the main-lines. But this is not the case to the same extent for all branches as we shall soon see.

In our picture two important parts are still lacking, one of them being the roots, the other the organs of reproduction. The roots need only briefly be mentioned. They grow by means of apical cells, the same as the shoots, and are present in the lateral buds before the latter arise from the leaf whorls. As a rule, every bud at first forms only one root, which develops from an inner cell, situated on its under side. This cell becomes the apical cell of the young root. Therefore, in the genealogical tree every root, as well as every shoot, is represented by a branch with its numerous twigs. But since the roots never bear leaf-buds, as in many ferns and phanerogams, and therefore never produce any organs of reproduction, they are always only sterile branches of the pedigree.

In the case of *Equisetum arvense* this is the fate of by far the greater portion of the branches of the cellular pedigree. Because here only the pale, yellow shoots of the later years, without chlorophyll, are selected for reproduction. Thus, here too, we distinguish sterile and fertile branches.

At the apex of the fertile shoots stand the sporangia in crowded spikes of four- to six-sided shields, which have their stems in the center. Every one of these corresponds in its origination to a tooth of a leaf-whorl. Hence, the cell-pedigrees of the individual shields can be derived in a similar manner from the apical cell of the shoot, as in the vegetative part; and in the same way the origin of each single spore can be traced back to it. These lines again we call branches, while all the lines leading to the

other cells of the sporangial tissues must be regarded as twigs. For here, too, the branches possess the power of continuing the pedigree, but the twigs do not.

On germination the spores produce the male and the female prothallia. The former bear only the male sexual organs or antheridia, the latter only the female organs or archegonia. In the cell-pedigrees we again imagine heavy straight lines for those cell-sequences which lead to the egg-cells and to the spermatozoids. These represent for us the branches, all the others the twigs.

We have arrived at the completion of our sketch,[3] since we have been through the much ramified path from the fertilized egg-cell to the new germ-cells, and have taken in its numerous side-paths. Let us glance once more over the whole, and we shall see that, by emphasizing the branches instead of the twigs we have, in spite of the great complication a simple and clear picture. For the branches again, we have to make a distinction between the fertile and the sterile. Only the former lead finally to egg-cells, or to spermatozoids, i. e., to new individuals; the sterile branches do not do this. Fundamentally, then, they behave towards the fertile ones like the twigs; they take no part in the pedigree of the species.

§ 4. *The Main Lines in the Cell-Pedigrees*

For those cell-sequences, which in the cell-pedigree lead from the fertilized egg-cell through the individual to the next generation, I may, as a continuation of Weis-

[3]In order not to complicate the illustration I have not discussed here the vegetative multiplication. I shall come back to it in the next Section.

mann's clear statements employ the name *germ-track.* This conception would then correspond exactly to the fertile branches of the cell-pedigree in the illustration selected above. We shall, in the future, keep this shorter designation for it, and in contradistinction we shall call all other sequences of generations of cells, the sterile branches as well as the twigs of our illustration, the *somatic tracks.*

A germ-track then, always leads in our cell-pedigree from the fertilized egg-cell to the new egg- or sperm-cell; we imagine it drawn very straight and clear in our diagram. Somatic tracks begin at all points of the germ-tracks and lead, constantly branching, to all the vegetative cells of the body. The cells which are situated on the germ-tracks, can be called germ-track-cells or, according to Jäger, phylogenetic, or perhaps still more distinctively, phyletic cells. They are thus sufficiently distinguished from the ontogenetic or somatic cells.

It is a matter of course that the distinctions introduced here, and therefore also the names and their definitions, are of a purely descriptive nature. There can be no question as to their correctness since they are quite arbitrary. The question is only, are they practical, i. e., can they lead us to a clear insight.

We must not wish to substitute a theoretical meaning for the conception of the germ-tracks. Otherwise the definition would not be sufficiently clear. Therefore Weismann's germ-cells correspond only in their main features, and not everywhere, with our germ-track cells. This is especially shown by the circumstance that, according to his theory, sexual cells are frequently produced by somatic cells, and that he devotes a detailed discussion to the fact that the splitting off occurs a little sooner in

some groups of the animal kingdom and a little later in others.[4]

In my picture, however, sexual cells are never produced by somatic ones, but the main lines are always drawn through the ancestral rows of the germ-cells. Accordingly these produce all the somatic rows of cells. We see that it is merely a matter of choosing the main lines for the picture, and not of a comprehension of the facts. But with my choice the picture becomes simple and clear, and essentially the same for plants as for animals. To my mind the germ-cells of the hydroids and of the phanerogams are not, as Weismann assumes,[5] secreted by the Metazoon itself, but are formed, as in the case of all other sexually differentiated heteroplastids, on the germ-tracks, only the number of cell-divisions which precede their origin on this track is here very great.

According to my definition, a germ-track never originates from a somatic track. A continuity of the germ-cells does not occur as a very rare case,[6] but everywhere, and without exception, although sometimes at a great distance, along the germ-track. The whole question of whether somatic plasm can change into germplasm[7] is, on the basis of my conception, deprived of any foundation in fact. But it certainly is not always easy to decide whether a track is to be regarded as a somatic one or as a germ-track, as will be seen from the next chapter.

For a clear comprehension of the phenomena of heredity the conception of the germ-tracks, as it has been

[4]Weismann, A. Zur Frage nach der Unsterblichkeit der Einzelligen. *Biolog. Centr.* **4**: 683.

[5]*Loc. cit.* p. 685.

[6]Weismann, A. *Die Kontinuität des Keimplasmas.* p. 11.

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

modified above, seems to me to be of prime importance. While natural selection appears to act upon the qualities of the finished organism, in reality it acts upon the bearers of these characters hidden in the germ-cells.[8] This important law has been raised above all doubt by the experiences of animal and plant-breeders. Vilmorin, in his breeding experiments, distinguished the individuals which possessed in a higher degree the power of transmitting their visible qualities to their descendants from those that possessed it to a lesser degree.[9] The former he called *bons étalons,* and those he selected for breeding. But whether a plant belonged to this privileged group the plant itself did not show. This had to be decided by the descendants and by these was the great breeder guided in the selection of his breeding plants.

The body of the individual, therefore, gives only a one-sided and very incomplete indication of the qualities represented in its germ-tracks. But when one grows from its seeds hundreds and thousands of specimens, these furnish such a many-sided picture that the average may be regarded as a criterion of those latent attributes.

By far the most of the hereditary character-units attain their development only in the somatic paths; it is only here that the corresponding characters of the organism become visible to us. But the transmission of a character and its development are, as Darwin says,[10] distinct powers which need not necessarily run parallel. The transmission is accomplished invisibly, in the germ-tracks,

[8]Weismann, A. *Ueber die Vererbung.* p. 56.

[9]Vilmorin, L. L. de. *Notices sur l' amélioration des plantes par le semis.* Nouvelle Edition. p. 44. 1886.

[10]Darwin, C. *The Variation of Animals and Plants.* **2**: 38. New York, 1900.

the development mostly on the somatic tracks. It is only with caution that we may utilize the latter in judging the former.

In the following chapter I will discuss more in detail the germ-tracks and the somatic tracks in the cell-pedigree of the higher plants. In doing so I shall divide the former into primary and secondary germ-tracks. Both lead from the fertilized egg-cell to the new egg- or sperm-cell. The former ones, however, do so by the shortest route, that is usually within one individual, and, in the case of alternation of generations, through the usually small number of individuals involved. The latter, on the contrary, reach their end indirectly, by means of vegetative multiplication, e. g., through adventitious buds. They may frequently pass through an apparently unlimited number of individuals before returning to an egg-cell.

Chapter II

SPECIAL CONSIDERATION OF THE INDIVIDUAL TRACKS

§ 5. *The Primary Germ-Tracks*

I designate as primary germ-tracks those sequences of generations of cells which, in the normal course of development of the organism, lead from the fertilized egg-cell to the new germ-cells (egg-cells, spermatozoa, pollen-grains). They will form the subject of the first paragraphs. The secondary germ-tracks, leading through adventitious buds, will be considered in the subsequent paragraphs.

The primary germ-tracks, then, form the common, or at least the shortest of the common, paths from one to the next following generation of egg-cells. They are never completely unbranched, because the normal multiplication of the species is incumbent on their ramification. They probably always give off somatic twigs along their entire length. But the manner and means of their ramification, the number, position, and relative significance of the individual somatic tracks, is subject to much modification.

Among extreme cases may be counted one one side the well known instance of the Diptera, on the other hand the Vertebrates, and, contrasted with both, the higher plants and the corals. In the Diptera some of the first cells that usually form from the egg develop into the sexual glands of the body. Thus the initial cells for practically the entire body are directly separated from the

germ-track at the first divisions, and this forms thereafter, only the somatic tracks lying in the sexual glands. To the Diptera must be added the Daphnoidae and *Sagitta,* for the whole body of which, with the exception of the organs of reproduction, the initial cells are also split off very early from the germ-track, and by means of a relatively small number of cell-divisions. In the vertebrates the germ-track probably goes through hundreds of successive cell-divisions, for the purpose of body-formation, before it begins the development of the sexual organs.

Leaving the sexual organs out of our consideration, we find that the somatic tracks composing the body arise from the germ-track, in the Diptera as a single twig, in the Daphnoidae and *Sagitta* as a small number of them, in the vertebrates, however, as very numerous twigs. But all the tracks for the body are always formed before the germ-track begins to split into equivalent branches in the region of the sexual organs.

Here lies the difference between the higher animals and the plants. For in the latter the germ-track splits at a very early period, and the majority of the somatic tracks do not originate in the main-stem of the germ-track, but chiefly in its branches. The picture of the pedigree of the germ-cells coincides here with the picture of the much ramified organism itself; it does not require a detailed description. The colony-forming polyps present a similar case.

The difference becomes clearest on introducing into the picture only the germ-tracks, and leaving out the somatic tracks. The cell-pedigree of a higher animal stands, then, as a straight tree, ramifying only a little at its top, while that of the higher plants is so richly and repeatedly branching from its very origin that the branches fre-

quently overtop the main-stem which thus, not infrequently, is in the back-ground of the picture. Or, more correctly speaking, there is no real main-stem, or at least hardly any.

§ 6. *The Secondary Germ-Tracks*

In the higher animals the secondary germ-tracks are lacking, in the vegetable world they are widely distributed. It is especially this circumstance which makes the study of cell-pedigrees in the vegetable kingdom so much more profitable than in the animal world, and the objections raised by Sachs, Strasburger, and other botanists against Weismann's conception regard essentially the circumstance that the latter did not give due attention to the secondary germ-tracks.

The secondary germ-tracks can by no means be regarded as exceptions. In no tree, in no shrub are they lacking. Among perennial plants they are, if not of general occurrence, at least very widely distributed, and only the annual and biennial species are without this kind of propagation. On the other hand the adventitious formations exhibit so many forms, such high differentiations, and such beautiful adaptations, that they also are not placed in the background, in this respect, as compared with the primary germ-tracks.

For our purpose three cases are to be kept separate:

1. Nearly all cells of the body can develop into new individuals.

2. Adventitious buds arise only from definite cell-groups or cell-tracks preformed to this end, namely:

   a. from meristematic tissues,

   b. from mature cells.

The phenomena of regeneration of the Thallophyta

and the Muscineae have in recent years repeatedly been the subject of investigation, and the conviction has become rooted in regard to them that, at least in some cases of mutilation, every, or almost every cell that remains unhurt can grow into a new individual. Pringsheim examined the mosses, Vöchting the liverworts, Brefeld the fungi.[11] On continuing, under favorable conditions, the cultivation of pieces cut off from these plants, one can grow a new plant from every part that is not too small. The stipe and the pileus of the fungi grow new pileuses from the cut surfaces, the mosses form buds from any given cell of the roots, leaves and shoot, even from the sporangium and its stalk. At first the cells grow into the thread-like protonema, on which the leaf-buds can then develop in the usual manner. The Marchantiaceae, according to Vöchting, can be chopped up fine, and every particle which has a sufficient number of uninjured cells to keep it alive, will form a new plant. In the case of *Marchantia polymorpha* I can confirm this observation from my own experience.

In these cases, therefore, all, or nearly all the ramifications of the cell-pedigree form either primary, or at least secondary germ-tracks. Somatic, that is, necessarily sterile twigs are possibly present, although it has not yet been proven. This case, which for Weismann forms an exception, and demands a special assumption for its explanation,[12] is for us only an extreme one in the rich abundance of examples.

[11]Pringsheim, N. Ueber Sprossung der Moosfrüchte. *Jahrb.* Wiss. Bot. **11**: 1. 1878.

Brefeld, O. *Botanische Untersuchungen über Schimmelpilze,* Vol. I. Vöchting, H. Ueber die Regeneration der Marchantiaceen. *Jahrb. Wiss. Bot.* **16**: 367. 1885.

[12]Weismann, A. *Die Kontinuität des Keimplasmas.* p. 68.

The second group of secondary germ-tracks, the adventitious buds from meristematic tissues, is by far the most widely distributed in the vegetative world. Adventitious buds arise in part directly from the normal meristematic tissues, in part throught the medium of the callus-tissue which leads to the closing up of wounds. Those that originate from stems or branches, usually become new twigs of the individual bearing them, the leaf-born ones and the root-buds, however, develop for the most part into new plantlets.

Bud-formation from callus is chiefly found in woody plants, and almost every part of a branch or a root, if cut for a slip or otherwise injured, can develop from the youthful cells of the cambial zone, situated between the wood and the bark, that undifferentiated tissue, oozing out like drops of a semi-fluid substance, in which later cork, bark, and wood, as well as the rudiments of numerous buds develop. According to circumstances the buds become roots or leafy twigs, and usually replace the lost members of the individuals.

Since, as far as we know, every cell of the cambium may contribute to the callus, and can produce therein the mother-cell of a bud, we must designate the entire cambium as a secondary germ-track which is as profusely ramified as the cell-pedigree of the respective cambium itself, and which bears the normal products of its activity, wood and bark, as countless somatic twigs. It is to be remembered, however, that many cells of the wood and bark retain, for a longer or shorter time, the power of contributing to the formation of the callus, and even of producing mother-cells of callus-buds.[13] The line of demarcation between the secondary germ-tracks and the

[13]This point indeed still requires thorough investigation.

somatic tracks is therefore to a great extent, obliterated here, and perhaps even quite undemonstrable.

Callus-buds are also to be found in many herbaceous plants. On leaves, too, they are not rare, but in such cases they usually form new rooted plantlets.

Adventitious buds on leaves are very frequent phenomena among the ferns. In the phanerogams they arise at the base of detached leaves, especially in bulbous plants and Crassulaceæ. Very well known instances are further furnished by *Bryophyllum calycinum, Cardamine pratensis,* and *Nasturtium officinale.*[14] There can be no doubt that in all of these cases there is present in every leaf a germ-track, which is very frequently much ramified.

Root-buds are probably the most common and certainly the most completely and most thoroughly investigated adventitious buds.[15] And since many leaves, like slips from stems and roots, can form roots after having been detached from the plant and, by means of these roots, give life to new plantlets, the importance of the root-buds can hardly be exaggerated. Many plants, such as *Monotropa,* multiply, except by seed, only in this manner, others, like *Rumex Acetosella* and the thistles become the most tenacious weeds by means of root-buds. Of all species that possess this power, we can therefore say that their root-system represents, in the cell-pedigree, a much ramified germ-track with its somatic twigs.

[14]From the abundant literature on this subject I cite: Regel, Vermehrung der Begonien aus ihren Blättern. *Jenaische Zeits. Naturw. p.* 478. 1876. Beyerinck, Over het ontstaan van knoppen en wortels uit bladeren. *Ned. Kruidk. Archief.* **3**: 1. 1882. Wakker, J. H. *Onderzockingen over adventieve knoppen.* Amsterdam, 1885.

[15]This subject has been most exhaustively treated by Dr. M. W. Beyerinck in his "Beobachtungen und Betrachtungen über Wurzelknospen und Nebenwurzeln." *Verhandl. Kon. Akad. Wetenschappen.* Amsterdam, 1886.

I should like to go further into this rich and tempting field. But the reader who is familiar with the literature will not need my guidance in forming a picture of the secondary germ-tracks in the cell-pedigree, and in arriving at the conclusion that almost every larger branch of this tree is to be regarded as a germ-track.

We still have to deal with the third case, that of the adventitious buds from mature cells. Here the secondary tracks run through formed cells, which frequently begin only in an advanced age to rejuvenate, and to grow into buds. This is illustrated by the begonias, which Darwin has already used in his pangenesis for the explanation of the almost universal distribution of the hereditary characters throughout all the parts of the plant-body,[16] and which Sachs and Strasburger considered as opposing Weismann's theory of the germ-plasm. This phenomenon has been thoroughly studied by Regel, Beyerinck, and Wakker,[17] and it seems sufficiently important to me to be sketched here in its main lines.

The epidermal cells of the leaves and petioles, and also, in some forms (e. g., *Begonia phyllomaniaca,)* those of the stem and its branches, possess the power of becoming buds. This power is not limited to individual, privileged cells, at least not in the leaves, but is inherent to the same extent in all cells of the epidermis, especially in those of the veins. If part of a leaf is laid on the ground in moist air, after the veins have been previously cut through in several places, there may be found, after some time, near each wound, one or several new plantlets. The first primordium of these is a true rejuvenation. The epidermal

[16]Darwin, C. *The Variation of Animals and Plants.* **2**: 362. New York. 1900.

[17]See citations above (p. 98).

cell, poor in contents, divides, without at first gaining in size, into a small-celled body of tissue, in which rich protoplasmic contents can now be observed. Gradually this new formation grows and differentiates, by means of numerous further cell-divisions into a bud.

Since these germ-tracks, which lead through a mature but rejuvenating cell to a new generation, possess a high theoretical value, and will be frequently mentioned in the following pages, I shall give them a new name, and call them *pseudosomatic.*

§ 7. *The Somatic Tracks*

As Nussbaum has so strikingly put it, the germ tracks are "the continuous foundation stock of the species, from which the single individuals, after a short existence, fall like withered leaves from a tree." With the difference that every leaf is attached to the tree at some point, whereas most individuals consist of the products of numerous somatic tracks, which have originated successively from the germ-track, and therefore cannot fall off without a piece of the foundation stock.

The somatic tracks composing the individual usually differ greatly from each other. Not only morphologically, in regard to the kind of cells, tissues, and organs to which they lead, but also in their size and the extent of their ramification. The whole aerial plant of *Equisetum,* in the first year of its existence, represents a somatic ramification. The leafy twigs of *Taxodium,* which fall off in the autumn, and the leaves of all those plants which are not capable of reproducing their species by means of those organs, are further illustrations. There is an uninterrupted line of intermediate steps from these to the one-

celled somatic tracks which do not ramify any further, as for example, the wood-fibres of some trees which are produced by the cambium.

The somatic tracks are, in general, the cell-pedigrees of the single cells of the grown individual, with the exception of the germ-cells. In the case of every cell and every cell-complex one can trace them back to the germ-track from which they have evolved. In plants all the profusely branching primary and secondary germ-tracks are probably closely set, along their entire length, with such bushy lateral twigs. These give its characteristic appearance to our picture. In the Diptera they originate chiefly from one point of the germ-track, and thereby the picture is entirely changed. In the higher animals, however, they gradually branch off from the unramified part of the germ-track, and very greatly surpass it in the richness of their further ramifications.

The cells of the somatic tracks are usually composed of the same protoplasmic organs as those of the germ-tracks. Only here these organs are frequently adapted to other functions, and therefore they bear other names. Thus, in some somatic elements, the amyloplasts of the germ-track cells become chlorophyll-grains. Usually this change is not only a more special adaptation, but also a further differentiation. Especially do we meet again, almost without exception, in all somatic cells, such individual parts of the germ-track cells as nucleus, trophoplast, vacuoles, nucleo-plasm, and lining layer.

Against this general rule some individual exceptions must be mentioned. I do not take into account the numerous cells, such as the many wood-fibres, and the stone-cells and cork-cells, which die soon after their development and lose their entire protoplast. They render their ser-

vices to the organism in this lifeless condition, and form the extreme instance of a reduction on the somatic tracks.

But there are also cases of a lesser reduction. Frequently, in the Algae, as Schmitz describes, "In the interior of the cells, the chromatophores, of which there is no longer any need, and which, in the economy of the whole plant, were equipped and adapted exclusively for a definite single function, disappear."[18] Especially is this often the case in complexly organized and highly differentiated algae. Sometimes, as it would seem, in the inmost tissue-cells, but most commonly in the hairs and rhizoids.

A further instructive instance is given by the spore-sacs of the Ascomycetæ. In these flask-like cells there originate, through the division of the nucleus, the nuclei for the individual spores, while the mother-cell, according to the available data, does not retain any nucleus. When the spores are formed the mother-cell has, therefore, become a non-nucleated protoplast, although it has by no means completed its life-task, since it has still to take a very active part in the extruding of the spores, for which purpose it must retain, in the interior of its numerous vacuoles, the necessary osmotic pressure.

In our cell-pedigrees the ripe ascus forms the last somatic twig of the germ-track which culminates in its spores. This twig is simple, i. e., it does not necessarily branch further. What lends importance to this illustration, however, is the present conception of the significance of the nucleus. For, if it is the seat of the latent hereditary characters, we may assume that these are lacking in the ripe ascus. And evidently the latter does not need

[18]Schmitz, *Die Chromatophoren der Algen.* p. 137. 1882.

them for the fulfillment of the functions still devolving upon it.

Therefore, we have here an instance of a somatic path without latent hereditary qualities. At least, this is as certain as observation can make it in the present state of our knowledge. And it is evident that this instance compels the assumption that on many other somatic tracks, as well, a reduction of the hereditary characters, although less extensive, may take place. But since our task is to group facts, and not to make assumptions, we shall not discuss this point any further.

§ 8. *The Difference Between Somatic Tracks and Germ-Tracks*

We see now before us the rough lines of the picture of the cell-pedigrees for the higher plants. And whoever followed my description attentively, will have seen that the picture is a purely empirical one, in which the prominent lines are indeed arbitrarily chosen, but have been drawn without any hypothesis. Especially is the difference between the somatic and the germ-tracks purely a matter of fact, and in harmony with our present knowledge. It claims nothing except to serve as an indication as to whether any cell can, through its descendents, contribute to the propagation of the species.

But, as a basis for theoretical considerations, the cell-pedigrees will attain their full value only when we have realized the significance of the difference between somatic and germ-tracks. This is by no means a difference in kind, but one of degree.[19] This becomes clearest to us when we try to define the limit exactly. We shall find,

[19]Weismann, A. Zur Annahme einer Kontinuität des Keimplasmas. *Ber. Naturf. Ges.* Freiburg. **1**: 7. 1886.

then, that an apparently uninterrupted line of transitional forms leads from the germ-tracks to the somatic tracks.

In the cell-pedigrees of one-celled organisms and of homoplastids all the twigs are primary germ-tracks. In the next higher plants primary and secondary germ-tracks are to be distinguished and, the more highly the organism is differentiated, the more are the latter pushed into the background. They are lacking in the higher animals. But in such highly developed Thallophytes as the fungi, and even in the mosses and liverworts, it is apparent that all twigs in our picture have still the value of germ-tracks. At least sterile side-twigs, that is, somatic tracks, have not yet been demonstrated there. But, in the case of the vascular plants, most of the tissue-cells, at least when fully developed, can without doubt no longer reproduce the species. Therefore the somatic tracks form here an important part of the picture.

But let us now compare the somatic tracks of the vascular plants with the secondary germ-tracks of the Muscineæ. Were not the significance of the latter known to us through the investigations of Pringsheim and Vöchting, we would designate at least some of them as somatic tracks, for the question can be decided only by the presence or absence of the power of reproduction. On the other hand, it may possibly be shown, at some future time, that some somatic cells of the vascular plants have this power after all, and what we now call somatic tracks, we will then have to regard as secondary germ-tracks.

The somatic tracks have obviously developed phylogenetically from the secondary germ-tracks. Not suddenly, however, and at a leap, but quite gradually. The loss of the power of reproduction makes them such. By this means, however, only an adaptation, and no intrinsic dif-

ference is conferred. It is true that, through further adaptions, the differences may have become greater and greater; the use of the power of reproduction, at first limited to less and less frequent cases, may finally have become quite impossible by the loss, not only of the adaptive, but also of the inner conditions thereto. Doubtless all transitions to the non-nucleated spore-sacs will have been made.

But, in the plant world, by far the greatest number of the somatic tracks are evidently still so much like the secondary germ-tracks that we cannot assume an essential difference between them. This is most clearly demonstrated in those cases where homologous organs among allied species consist, in one of them, of somatic tracks only, while the other possesses secondary germ-tracks in addition.

The most instructive illustration is given in the pseudo-somatic germ-tracks of the begonias.[20] Phylogenetically these have obviously originated from tracks that we should call somatic. But the very circumstance that, in the process of the formation of species, this power of reproduction can make its appearance in cells in which it is lacking in almost all the other phanerogams, teaches us that this absence is only adaptive, I might almost say only apparent. We are therefore compelled to attribute to the epidermal cells of the leaves of the phanerogams in general a latent power of reproduction. Yet they remain recorded as somatic tracks in our empirical picture. Nevertheless it seems perfectly clear to me that the difference is not qualitative.

Furthermore, the correctness of this conception is corroborated by the not at all infrequent instances where

[20]Cf. p. 100.

parts of plants, which normally cannot form buds, produce such in accidental variations or in varieties. Flower-bearing twigs have been observed on a petal of a *Clarkia* and of a *Begonia,* on the stem of the compound leaf of *Lycopersicum,* and on the leaves of *Levisticum, Siegesbeckia, Rheum, Urtica,* and *Chelidonium.* Caspary saw more than a hundred of them on a petiole of *Cucumis.* Everyone is doubtless familiar with the flowers on the glumes of the variety of barley cultivated as *Hordeum trifurcatum.*

Some leaves can take root when cut off and stuck into moist ground. I saw those of *Aucuba* and of *Hoya carnosa* keep alive, in this way, for two years, without forming buds; some are said to have existed for seven years in this condition.[21] Whether buds are ever developed from the roots of such leaves, either normally or after wounding, seems to be unknown. But this is not at all impossible, and in general the whole case deserves to be more thoroughly investigated. Other leaves fail to take root under like conditions, and simply perish. But those of the Crassulaceæ, and of bulbous plants, grow buds from their base. Here, too, the line of demarcation between somatic tracks and secondary germ-tracks is evidently not a sharp one, at any rate not qualitative.

Finally, we have still to emphasize the fact that very frequently the power of reproduction is restricted to youth. This is most clearly shown by the callus-formation of woody plants, where the still living older cells of the bark and the wood usually do not take any part in it. In the petioles of plants that are rich in juice, as *Peper-*

[21] I have since succeeded in keeping a rooted leaf of *Hoya carnosa* alive for more than six years. It did not produce any bud. de V. 1909.

omia, grown cells also take part in the callus-formation, but, as it seems, only in a subordinate way. Perhaps by far the greatest part of the somatic cells of plants have this power in their youth, and the line of demarcation between secondary germ-tracks and somatic tracks would lose still more of its distinctness through this possibility.

§ 9. *Phyletic, Somatarchic, and Somatic Cell-Divisions*

We will now look a little more closely into the cells themselves, which are distributed along the individual tracks. In the homoplastids all the cells and all the cell-divisions have the same importance. The two daughter-cells evolved from one mother-cell are of the same value. But in the higher plants such processes are relatively rare. They happen chiefly only where a germ-track divides into two equivalent branches, or where a uniform tissue is deposited on a somatic track. By far the greatest number of divisions, however, furnish unlike products, and to this fact is due the entire differentiation.

It seems more important to me to distinguish between phyletic, somatarchic, and somatic cell-divisions. Those divisions in which a germ-track-cell splits into two daughter-cells, both of which, although in different ways, continue the germ-track, are obviously phyletic. All the somatic cell-divisions are divisions on the somatic tracks. Where a track is laid down of such a nature that through the division of a cell of the germ-track, there develops, on the one hand, a cell which continues the germ-track, and on the other hand, a somatic cell, the division is somatarchic.

There can be no doubt that, in the phyletic divisions, the hereditary factors are transmitted to the two daughter-

cells. Such is the case, also, in the somatarchic divisions, with reference to the daughter cells that continue the germ-track. But as to whether or not this also holds true of the other sister-cell, which forms the beginning of a somatic track, opinions differ. As to whether or not, in the somatic cell-divisions, a corresponding reduction of the latent factors goes hand in hand with the advancing adaptation and specialization of the cells will be discussed in the next chapter.

I have still to emphasize that the successive generations of cells from the germ-tracks, which evolve from somatarchic cell-divisions, are not all alike. They have been designated at times either as germ-cells or as embryonic cells. But there is no necessary reason for this in the plant kingdom. It is true that they are all alike in being the bearers of all the hereditary characters of the species, but they bear them only in a latent condition. They may be intrinsically very different in respect to their active hereditary characters. And, even if the whole germ-track does not pass through such a rich variety of forms and adaptations as are furnished to us by the somatic cells, yet, compared with a single somatic path, however profusely the latter may branch, it may, by no means, be second to the latter in regard to differentiation. On the contrary, the very power of producing, one after another, the most varied somatic tracks, indicates a continuous alteration in its activity.

The cells of the germ-tracks are by no means always such as remain in a juvenile condition during the whole duration of their existence, or which, between quickly succeeding cell-divisions, have only a short individual life. The prothallia of ferns and horse-tails consist of green, vigorously assimilating cells, through the divisions of

which there is, at first, an increase in number, until, at last, from some of them the sexual organs develop. Therefore the cells on the main germ-tracks are here not distinguished by any visible characteristic from the purely vegetative cells. The same is true of the already repeatedly mentioned pseudo-somatic germ-tracks of the begonia.

Everywhere we are confronted with the statement of Darwin, quoted above, that the transmission and the development of hereditary characters are different powers. In the cell-pedigree they run almost nowhere parallel.

Chapter III

WEISMANN'S THEORY OF THE GERM-PLASM

§ 10. *The Significance of the Cell-Pedigree for the Doctrine of the Germ-Plasm*

In the first two chapters of this section I have comprehensively described the cell-pedigrees for the plant world, and, in order to draw a clear picture, I have been compelled to introduce a number of new names. The fact that all the cells of the whole plant-body are produced by division, is now universally recognized, and herewith the possibility of the establishment of cell-pedigrees is admitted as a matter of course. Furthermore, the scientific value of such consideration has been pointed out by different investigators in botany as well as in zoology.

The elaboration of the picture, however, as I mentioned in the beginning of this division of Part II, seemed indispensable to me, because, up to the present time, the higher animals have been put to the front in these considerations, and for the further reason that this fact leads only too readily to a one-sided conception. For here the distinction between the germ-cells and the body-elements is so great that it only too easily gives the impression of a qualitative difference.

This contrast has been strongly emphasized by Weismann in his interesting speculations on the "mortal" somatic cells and the "immortal" germ-cells,[22] and forms, to a large extent, the basis for his theory of the germ-plasm.

[22]Weismann, A. *Ueber die Dauer des Lebens.* 1882. *Ueber Leben und Tod.* 1884.

This doctrine, and the hypothesis of the ancestral plasms which is based on it, have already been critically reviewed in the first Part. I have there (p. 56) also pointed out the fact that, in the face of a detailed consideration of cell-pedigrees, it cannot be maintained. Now that we have become more familiar with these latter, it must be our task to endeavor to establish this claim.

The true significance of the difference between the germ-tracks and the somatic cells can be correctly judged only when glancing over the whole richness of the ramifications of a highly differentiated cell-pedigree. And it is only in plants that this differentiation reaches its highest degree. Numerous intermediate forms lead here, with almost imperceptible transitions, from the main germ-track to the somatic tracks.

For this very reason I have laid particular stress on the discussion of the secondary germ-tracks. They are wanting in the higher animals. In the plant kingdom they are present in all gradations. I have not attempted to draw a sharp line of demarcation between them and the main germ-tracks; such an attempt would be thwarted by the same difficulties which make impossible the exact limitation of the concept "individual." We must be satisfied here with an arbitrary limit, and choose the one that seems most convenient.

The difficulties that confront us on the border-line between secondary germ-tracks and somatic tracks are of a different nature. Here they are due to the incompleteness of our knowledge. I call those tracks that do not lead to a propagation of the species somatic. But many cells, many a tissue-complex which, on this ground, we now call somatic, will prove itself, on further experimentation, to be provided with the power of reproduction.

The group of the pseudo-somatic tracks may be chosen as an illustration,[23] and I shall come back to further instances in the last paragraph of this Section.

Therefore germ-cells and somatic cells do not present any qualitative contrast in the plant kingdom. They are the extremes of a long line of quantitative differences. This law I regard as one of the most important results of the consideration of vegetative cell-pedigrees. Sachs, Strasburger, and others, have pointed out the importance of this law, and it seems to me that the foregoing comprehensive descriptions ought to contribute in causing the conviction of its correctness to become general.

On the distinction between germ-cells and somatic cells Weismann founded his theory of the germ-plasm. The latter must, therefore, be present in all the germ-cells. But according to Weismann, it is only in these that it needs to be retained, while it must be lacking in the somatic cells, because they cannot reproduce the species. They are limited to the unfolding of a limited number of hereditary units, and thus need only that portion of the germplasm requisite thereto. These considerations induced Weismann to regard the germ-plasm as a special substance, which, in contrast to the remaining or somatic plasm, is the vehicle of heredity.

In the first part we have seen how the theory of a germplasm fails us in the explanation of the differentiation of organs. There the assumption of one substance is not sufficient; special material bearers of the individual hereditary characters, the so-called pangens, were necessary for the explanation. Their assumption, however, rendered the assumption of the germ-plasm with its consequences, superfluous.

[23]Cf. Section 6. p. 100.

Now we have demonstrated that the empirical basis for the assumption of the germ-plasm, which was to lie in the qualitative difference between germ and somatic cells, was only an apparent one and disappears when we consider cell-pedigrees in detail, and from every point of view.

Nor from this point of view can we recognize as justified the assumption of the germ-plasm. Because if we were to attribute germ-plasm to all the cells of the entire organism, the hypothesis would thereby become superfluous, and the term practically synonymous with nucleo-plasm.

I propose to follow out these general discussions more in detail in the two following subdivisions of this chapter.

§ 11. *The Views of Botanists*

That all the cells of the germ-tracks must contain the hereditary characters of their species, in either the active or the latent state, can hardly be doubted. How the somatic cells behave in this respect, cannot on the whole be determined by experiment. Especially not negatively, because the absence of latent hereditary characters can never be experimentally proven. The quite isolated, non-nucleated cells of nucleated organisms form possibly an exception. But positive experimental results would lead us to recognize the investigated cells, which, up to that time had been called somatic, as elements of secondary germ-tracks. Therefore they only shift the limit without deciding the question.

And yet, as we have seen in the preceding paragraph, the question is one of high theoretical value. And as long as this point has at all been an object for reflection, botanists have been of the opinion that all, or at least by

far the most, of the cells of the plant-body have been equally endowed in regard to latent characters. Turpin and Schwann, later Müller and Hanstein, but in recent years, especially Vöchting, have taken up the pen in the support and development of this view.

This prevailing and so well substantiated doctrine was opposed by Weismann in the year 1885. He advanced his well known theory of the continuity of the germ-plasm, and thus sought to create a basis for a theory of heredity.

The material bearer of the hereditary characters in their totality, and including therefore the latent ones, Weismann calls germ-plasm; the bearers of the active qualities in any given cell, somatic plasm. The somatic plasm is, therefore, lacking in no cell, because they are all active to a certain degree, even if only to the extent of being capable of further division. The germ-plasm, however, is, according to him, restricted to those cells which are charged with the transmission of the hereditary characters to the following generations. In the true somatic cells this power is said to be lacking.

Intimately connected with this conception, according to Weismann, is the law that the character of every cell is determined by its nucleus.[24] The specific nature of a cell, according to him, is dependent on the molecular structure of its nucleus; every histologically differentiated kind of cell possesses therefore its specific nucleo-plasm.[25] Identical nucleo-plasm, *ceteris paribus,* means also identical cell-body; in every somatarchic cell-division, as well as in most of the somatic divisions, the nucleo-plasm must therefore split into two unequal parts, only that part of the hereditary characters being given to each daughter-cell, which

[24]E. g. *Die Kontinuität des Keimplasmas.* p. 30.

[25]*Loc. cit.* p. 70.

is necessary for the functions of its descendents.[26] If the progeny be unlimited, as in the germ-tracks, then the nucleus receives the entire germ-plasm; but since the progeny of a somatarchic cell is limited, and since it is restricted in its morphological and physiological range of development, it gets only the corresponding part of the hereditary characters. Therefore they have no true germ-plasm, but only somatic plasm.

On the hypothesis of the germ-plasm, Weismann builds that of the ancestral plasm, which is directly opposed to pangenesis, and has been critically considered in the last division of Part I. But the empirical justification for the basis of that assumption, may here be considered from every possible point of view.

That Weismann has not succeeded in convincing botanists is shown by the various objections to him, made especially by Sachs and Strasburger. The essence of these objections is that Weismann has not sufficiently considered the secondary germ-tracks, and has thus been induced to assume a sharp contrast between germ-plasm and somatic plasm. Now, not only the oft mentioned example of the begonias, but the entire and very rich doctrine of adventitious buds, teach that there is nowhere a sharp line of demarcation between the secondary germ-tracks and the somatic tracks of the plant. The latter have developed only quite gradually out of the former. And even though they have in fact often lost the power of reproduction, everything speaks in favor of the fact that they still very frequently possess it potentially. In other words, the loss of germ-plasm need not necessarily go hand in hand with the loss of the power of reproduction.

In his book, *Ueber Organbildung im Pflanzenreich,*

[26] Cf. also Part I, Chapter III, § 6, p. 53.

published about ten years ago,[27] Vöchting brought together the facts known at that time and the results of his own rich experiments. At the end of the first volume he discusses the pending question in detail. The experiments teach directly (p. 251), that "in every fragment, be it ever so small, of the organs of the plant-body, rest the elements from which, by isolating the fragment, under proper external conditions, the whole body can be built up." Of course, this is true only if the fragment contains a number of meristematic cells. On this basis the question is discussed, "Whether there is a sufficient support for extending our proposition over any given complex of living vegetative cells." This discussion again leads to the assumption that every morphological form of tissue is potentially in a condition to produce meristematic cells, and therefore to reproduce the entire organism. But since experiments involving the isolation of very small portions of tissues encounter unsurmountable difficulties, and since, on the other hand, the power of reproduction as an adaptation may very likely have been lost in many tissues, there is, as a matter of course, no "strict proof attempted, and it is simply claimed that this very plausible assumption is probably correct."[28]

This assumption, however, in the now current language, has no other meaning than that *all, or at least the greatest number of the cells of the plant-body contain all the hereditary characters of the species in a latent condition.* And this same assumption I have sought to establish, as far as possible, empirically, through a detailed description of cell-pedigrees available through the most recent investigations on the phenomena of regeneration.

[27]Vol. I, Bonn, 1878; Vol. II, Bonn, 1884.

[28]*Loc. cit.* pp. 251-253.

It is, indeed, not to be denied that Weismann's view finds strong theoretical support in the usual economy of nature. Why endow numberless cells and long generations of cells with characters which they will never need? But it must not be forgotten that such parsimony would perhaps necessitate special adaptations, and that therefore it might, in the end, be simpler not to make any differences at all between the individual cells in regard to their latent characters.

However, I should not like to go quite so far as to attribute to every somatic cell all the latent qualities. First of all, as was pointed out at the beginning of this Part, it would be impossible to support such a view experimentally, and therefore it would remain permanently sterile. Then I have pointed out the non-nucleated asci, which doubtless represent somatic tracks without latent hereditary units, and therefore permit the assumption of a reduction of these qualities in other tracks. Here, too, a very slowly advancing differentiation and specialization is, on the whole, much more probable, according to our present conception of living nature, than the sharp contrast between the chosen bearers of heredity and the somatic cells equipped only with the hereditary particles required for their functions, as assumed by Weismann.

Weismann also expresses himself, on the ground of botanical facts, to the effect "that he can see no theoretical obstacle to the germ-plasm, under certain conditions, being admixed with cells of a pronounced histological differentiation, or, indeed, even with all the cells of the entire plant." For the liverwort, serving as an illustration, he admits this conclusion to be correct.[29] And the more

[29]Zur Annahme einer Kontinuität des Keimplasmas. *Ber. Naturforsch. Ges.* Freiburg. **1:** 10. 1886.

we study the cell-pedigrees of the plant kingdam, the more we become convinced that there is no qualitative distinction in nature between the cells of the germ-track and the somatic cells.

§ 12. *A Decision Reached Through the Study of Galls*

In the foregoing paragraphs we have repeatedly emphasized how, on the whole, it is impossible to decide the pending question experimentally. The phenomena of reproduction by excised parts of plants make manifest the existence of secondary germ-tracks hitherto unknown; but they do not teach us anything about the nature of the remaining somatic tracks.

An experiment which we cannot carry through is made by the gall-forming parasites in such a great variety of ways that a glance at their products may be made at this point. The thorough and detailed examinations by Beyerinck have so far enriched our knowledge in this field, that the whole history of development, as well as the anatomical structure in the grown condition, is clearly laid before us in the case of all the more important forms of galls.[30] Two laws, especially important for our purpose, have resulted from these studies. First of all, the galls, even at their highest differentiation, are built up of only such anatomical elements as are otherwise found in the plant bearing them. Only the peculiar layer of stone cells of some Cynipid-galls, which later change into a thin-walled nutritive tissue, forms a hitherto unexplained, but

[30]Beyerinck, M. W. Beobachtungen über die ersten Entwickelungsphasen einiger Cynipidengallen. *Veröffentlicht Kais. Akad. Wiss.* Amsterdam. 1882. The same, Die Galle von Cecidomia Poae. *Bot. Zeit.* **43**: 305, 321. 1885, and Ueber das Cecidium von Nematus capreæ. *Bot. Zeit.* **46**: 1. 1888.

probably only apparent, exception from this rule. In the second place plants have no special adaptations for the purpose of gall-formation; the adaptations lie completely with the parasite which works only with the characters that belong to its host.

But the galls are not at all restricted to the anatomical elements of the organs on which they originate. Cells which the plant otherwise forms in the bark of its stem only, can frequently be found in the galls of leaf-inhabiting Cynipids and Diptera. The same holds true for the galls of the stem and the root. We may conclude from this that the power of producing these elements belongs not only to those organs which develop them normally, but probably also to all the other parts of the plant.

Worthy of special notice here are the roots which, for the purpose of covering the galls of *Cecidomia Poae,* develop in a place, where, in the normal course of development, neither the plant bearing them, *Poa nemoralis,* nor any other kind of grass, is able to produce roots.[31] Thus the larvæ here make use of a potentiality, the existence of which we could never have conjectured, still less proven. In Beyerinck's experiments, these gall-roots grew into normal, profusely ramifying roots; the cells of the internode, stimulated to activity, must therefore have possessed, in a latent condition, the qualities necessary thereto.

Through the experiments of this investigator, even a direct transformation of apparently somatic tracks into germ-tracks has been, if not entirely accomplished, at least brought quite near completion.[32] The galls which the leaf-wasp *Nematus viminalis,* produces on the leaves of *Salix purpurea,* possess an exceeding vitality. At the be-

[31] *Bot. Zeit.* 1888. l. c.

[32] *Bot. Zeit.* **46**: 1, 17. 1888.

ginning of autumn, when left by their inhabitants, they are still quite turgescent. If they are now buried in humus, they will keep through the winter, and can even enter upon a new life in the following summer. They will then form new chlorophyll, by means of which they are nourished, and the best among them will gradually begin to put forth adventitious roots. These originate either on the outer or on the inner surface of the wall surrounding the cavity, and are always located on the vascular bundles of the gall. Judging from their microscopic structure, these rootlets, reaching a length of a few centimeters, are identical with the normal young roots of the respective species of willow. The required hereditary characters must therefore be present in a latent state in the gall, in which probably nobody would otherwise have looked for a germ-track.

These important experiments will become still more instructive for our purpose, when we shall succeed in making the gall-roots develop so far that they are enabled to form adventitious buds. But, since the roots of all woody plants have this power, we may predict even now that this experiment will succeed. Perhaps it will require special measures, as for example, a graft on the roots of a willow. But without doubt we may conclude from the complete agreement in the anatomical structure, as proven by Beyerinck, that the physiological properties also, of the normal and of the gall-roots are the same.

And if anyone is ever successful in growing in this way an entire willow from a gall, it will be clear, that, in the latter, all the hereditary characters of the willow are present in a latent state.

This would obviously be much more useless than their presence on any given normal somatic track. The con-

clusion, however, *that germ-plasm is by no means limited to those cells which need it for their own development, nor to their progeny,* we may even now regard as perfectly certain.

And this is probably the most important inference which we may deduce from this entire section. With it we have established one of those laws which can be applied as bases for our hypothesis. But we shall revert to this in the last Section.

B. Panmeristic Cell-Division

Chapter I

THE ORGANIZATION OF PROTOPLASTS

§ 1. *The Visible Organization*

Protoplasm is the vehicle of the phenomena of life, and therefore also of hereditary characters. Hence, any theory of heredity must start from a definite view in regard to the structure of this important substance. But anatomical investigation, in spite of its astonishing progress during the last decade, has in this very field not yet achieved a clear and generally accepted conception of this structure.

This is essentially due to the circumstance that the newer methods for the study of the nucleus and its division have disclosed a field so important, and so rich in surprising results, that attention has been directed chiefly, and frequently exclusively, to this organ. Often one even meets with views which put the protoplasm (cytoplasm) into the background with reference to the nucleus.

But the study of the nucleus is so much advanced at present that one may hesitate at this one-sided treatment. The researches of Flemming, Strasburger, and so many other investigators, have disclosed the structure of the nucleus and the changes of this structure during division, and have, in the main, brought our knowledge to a definite conclusion. Now, especially in botany, the investigation of cell-division itself comes again to the front. And it is not only a question of establishing the relation of the nucleus to the cytoplasm; it is just as essential a problem to

find out the attitude of the individual organs of the latter and especially of the vacuoles, the granular plasm, and the plasmatic membrane. For the knowledge of cell-division will be complete only when all the organs of the protoplast have been equally considered.

The described course of investigation makes it clear why even a practical and simple designation of the living cell-contents has not yet gained general recognition. Such a designation was suggested by Hanstein, in his well-known lectures, by the word "protoplast."[1] The word "protoplasm" was coined by Mohl for the semi-liquid nitrogenous substance "which furnishes the material for the formation of the nucleus and the primordial utricle," and from which originate the first solid structures of the future cell.[2] The formed body, built up from this substance, has frequently been called protoplasmic body, plasm-body, sometimes even protoplasmic globule or drop, expressions which are obviously inadequate to create a clear conception in the minds of readers and hearers.

Compared with these designations, Hanstein's word clearly and distinctly describes the individuality of the living cell-contents. This individuality has long been recognized by the best investigators. As early as 1862 Brücke said that protoplasm was an organic body; not a drop of fluid, but an elementary organism.[3] But the lack of an appropriate name obscured the clearness of the conception, and it was Hanstein who supplied this want. Klebs and others have accepted his designation and

[1]Hanstein, J. von. *Das Protoplasma als Träger der pflanzlichen und thierischen Lebensverrichtungen.* 1 Theil. 1880.

[2]Mohl, H. von. *Bot. Zeit.* **4**: 75. 1846.

[3]Brücke, E. Die Elementaroganismen. *Sitzungsber. Kais. Akad. Wiss. Wien.* **44**[2]: 381. 1861.

through their influence it will doubtless be more generally adopted.*

Protoplasts are elementary organisms in the true sense of the word. They consist distinctly of individual organs, which are more or less sharply distinguished from each other and which possess a high degree of mutual independence. In the greatest number of plants this structure is clearly evident, but in the lowest organisms this differentiation is entirely wanting, or at least it is limited to a great extent. Sometimes one meets with the expression "unorganised plasm," even for organisms which by no means lack differentiation. But doubtless this expression must be understood to mean that the methods so far employed have not yet revealed any insight into the organization, and not that the want of any kind of organs has been thoroughly studied and definitely proven.

*As is well known, the term is now in common use. *Tr.*

Chapter II

HISTORICAL AND CRITICAL CONSIDERATIONS

§ 2. *The Neogenetic and the Panmeristic Conceptions of Cell-Division*

Only a few decades back it was generally believed that individual organs, such as the nucleus and the chlorophyll grains, could always, or at least very frequently originate from the undifferentiated protoplasm through differentiation. However, in recent years, investigations have not confirmed this neogenesis in a single instance. Wherever the origin of an organ has been thoroughly and comprehensively studied, with the present means of investigation, the organ has been shown to originate by a division of differentiated members already present.

The organization of the protoplasts is not periodical, nor evident only in grown cells. It is permanent, inherent in all cells, and in all stages of their development. The assumption of formation *de novo* gives place everywhere to the recognition of divisions; the neogenetic conception gives way to the panmeristic.[4]

It is of interest to glance over the course of development of our knowledge. In his "Lehre von der Pflanzenzelle," Hofmeister describes the nuclei according to the knowledge of that time. They appear in the protoplasm as drops or masses of a transparent homogenous substance, either in cells with few nuclei, of a definite

[4]The view that all the organs of protoplasts, as a rule, multiply only by division I call *panmeristic*. This assumption was maintained for plant-cells for the first time in my plasmolytic studies. Cf. Vries, H. de. *Jahrb. Wiss. Bot.* **16:** 489. 1885.

size from the beginning, or in cells with many nuclei, first as small formations which increase through growth. Sometimes they contain granules as soon as they become visible, but frequently they occur at first without any internal solid structure, and attain this only later. Every cell-division is usually preceded by a disappearance of the nucleus, which is then followed by the appearance of two or more new nuclei.[5]

The comprehensive investigations of Strasburger and Schmitz have proven this assumption to be erroneous, at first for isolated and then for an increasing number of cases, and wherever a disappearance and subsequent reappearance of nuclei was assumed, the origination of the new nuclei through division of the original ones could be proven. Exceptions to this rule are no longer known.

The history is exactly the same for chlorophyll grains. Even in the last edition of his text-book[6] Sachs said: "The chlorophyll bodies originate in young cells through the separation of the protoplasm into clearly distinct colorless portions that are becoming green. The process can be conceived to mean that, in the originally homogenous protoplasm, most minute particles of a somewhat different nature are distributed or originate for the first time and then accumulate at various points, appearing as differentiated bodies." That the green bodies which had formed in this way could multiply through division, and that the chlorophyll bodies of many algae are usually cut through at every cell-division by the forming wall, can easily be observed and was not unknown at that time.

But it was Schmitz who first showed that, in the algae,

[5]Hofmeister, *Die Lehre von der Pflanzenzelle*. p. 79. 1887.

[6]*Lehrbuch der Botanik*. 4. Auflage, p. 46. 1874.

division is the only way in which the chromatophores are newly formed.[7] Following up this idea with the phanerogams, Schimper discovered the colorless organs of the youthful cells, which in these cells are exclusively charged with the formation of starch and through whose assumption of green color the real chlorophyll grains are formed. In all cases that have been observed those amyloplasts multiply only through division, and Schimper, as well as Arthur Meyer, has accumulated such a number of observations on this manner of development that the former view has been abandoned by all botanists. Some special cases, it is true, still await explanation, but as long as they have not been thoroughly investigated, there is no reason for regarding the old conception more plausible than the new one.

It is similar with reference to the vacuoles. Until about four years ago they were generally regarded as a new formation in the protoplasm, caused by the secretion of superfluous water of imbibition. In my *"Plasmolytische Studien über die Wand der Vacuolen,"* I have established the claim that, for them as well, the mode of origin of nucleus and trophoplast[8] must be the only real one.[9] I supported this claim by showing that all vacuoles are surrounded by a living wall, which, according to the method suggested by me, can always be easily and convincingly demonstrated, and which I believe may be regarded as an organ of the protoplast, with as much right as the nuclei and the chromatophores.

This conclusion, drawn from my panmeristic conception of cell-division, has been completely confirmed by

[7]Schmitz, F. *Die Chromatophoren der Algen.* Bonn, 1882.

[8]By this name Arthur Meyer designates the amyloplasts and their derivatives (chlorophyll grains, chromoplasts, etc.)

[9]*Jahrb. Wiss. Bot.* **16**: 489-505. 1885.

Went's investigations.[10] Thereby, to my mind is proven the correctness of this conception as opposed to that of neogenesis. Now the situation is reversed. While up to the present time the condition with reference to the nucleus and the chromatophores could be regarded as peculiar, there is now great probability that the different members of a protoplast have the same mode of origin, and therefore that they can claim the rank of independent organs only in so far as they follow this rule.

Now that the mode of origin for nucleus, trophoplasts and vacuoles has, in the main, been established, and that the works of Wakker[11] have taught us to recognize the crystals, most of the crystalloids, and the aleurone grains as contents of the vacuoles, the problem is chiefly concerned with the plasmatic membrane and the granular plasm.[12] In regard to their behavior during cell-formation our knowledge is essentially the same as at the time of Mohl and Hofmeister. Our insight into the process of cell-division has indeed become deeper, chiefly through Strasburger's work; but the very point in question, the beginning of the dividing wall, which for some time, seemed to be decided neogenetically, has again become extremely uncertain through the discovery (to be discussed later) of the cell-ring by Went[13] as well as through the objections of other investigators.

[10]Went, F. A. F. C. *De jongste toestanden der vacuolen.* Amsterdam, 1886. Les premiers états des vacuoles. *Arch. Neerl.* 1887, and Die Vermehrung der normalen Vacuolen durch Theilung. *Jahrb. Wiss. Bot.* **19:** 295. 1888.

[11]Wakker, J. H., Studien über die Inhaltskörper der Pflanzenzellen. *Jahrb. Wiss. Bot.* **19:** 423. 1888. Preliminary contributions are found in *Maandblad v. Natuurwetensch.* 1886, Nr. 7. 1887, Nr. 5 and 6, and in *Bot. Cent.* **33:** 360, 361. 1888.

[12]Cf. § 6 below. p. 150.

[13]Cf. § 7 and 8, pp. 157 and 160.

For these reasons I believe that a critical review of our knowledge in this field will be of substantial usefulness. It will then be shown how, in almost all cases, the attitude of the plasmatic membrane and of the granular plasm, during cell-formation, is in fact unknown. At least in all the cases which seem to contradict the panmeristic conception.

It is not a question of whether this latter conception is correct or not. This seems to me to have been proven above any doubt by the researches of the investigators that have been quoted. The question is whether, with this conception, we are to regard the granular plasm and the limiting membrane as two intrinsically different organs, which pass over into one another as little as the nuclueus and the chromatophores, or whether they stand in a similar relation to each other as the amyloplasts and the chlorophyll-grains. As long as it was thought that the granular plasm had the power of producing the other members by a process of differentiation, it was natural to assume a like mode of origin for the plasmatic membrance. It is therefore not astonishing that, even at present, this view is still regarded as the one that actually obtains. The instance described by Mohl as a type of cell-division, and which involved the historically noteworthy discussions of the question as to whether the protoplasmic body played a passive or an active rôle during this process is well known to all. Like Mohl's type of the filamentous algae, *Cladophora, Spirogyra* is in more recent times preferred for this study. At the future plane of division the limiting membrane and granular plasm fold into a ring which, growing inwards, apparently simply cuts in two the remaining part of the cell-contents. For the daughter-cells the two new parts of the limiting membrane

originate as a continuation of the old membrane. According to Klebs's[14] descriptions the Euglenidae also offer a beautiful example of panmeristic cell-division.

It is very unlikely that in the case of such a fundamental process, the higher plants should behave differently from the lower ones. That there are differences in minor points is self evident, and everybody knows that there are important distinctions, especially in the relative duration of the individual steps in the process. And the same holds for the manner in which it is provided that every daughter-cell gets its own nucleus. But, that the completion of the plasmatic membrane should take place through the insertion of a quite newly formed piece is so much at variance with the rest of our knowledge, that one cannot by any means accept it on the basis of the older investigations. At any rate it must be held in doubt until supported by direct observation.

Such, however, is not the case at present, as I shall try to show in the last Chapter of this Section. On the contrary many facts already speak in favor of the complete autonomy of the membrane, although not with sufficient certainty to serve as conclusive proof.

However that may be, whether the limiting membrane can develop from the granular plasm, or whether both are mutually autonomous, it is certain, at any rate, that on the one hand these two, and on the other the nucleus, the trophoplasts, and the vacuoles are independent organs, which, in the normal course of things, multiply only by division.

Hence, the organization of the protoplasts is hereditary, and this not in the sense that the organization of the higher organisms is reproduced in each individual through

[14]Klebs, G. *Arbeiten Bot. Institut.* Tübingen. **1:** 282.

the development of invisible hereditary units, but through the direct passage, from the mother-cell to the daughter-cells, of all the organs which compose the organism.

The significance of this law for our hypothesis of intracellular pangenesis will be discussed in the last division of this Part. Here we will familiarize ourselves more thoroughly with the actual basis on which it is founded.

§ 3. *Cell-Division According to Mohl's Type*

The *"Grundzüge der Anatomie und Physiologie der Vegetabilischen Zelle,"* by Hugo von Mohl,[15] was for a long time the chief source from which beginning botanists got their knowledge. It is only Hofmeister's *Pflanzenzelle* (1867) and Sachs's *Lehrbuch* (1868) which put an end to its reign, but many illustrations and statements from the *"Grundzüge"* are still vividly remembered by older botanists.

The multiplication of cells through division is described in the following manner in this book of Mohl's.[16] It "is introduced by changes which the primordial utricle of the dividing cell undergoes, in consequence of which the dividing walls develop, growing gradually inward from the periphery of the cell, and separating the cell-cavity into two or more cavities." We have to distinguish those cases where the cell-division is preceded by a doubling of the nucleus, from those in which this is not the case (our present poly-nucleate cells). This latter, less frequent, but simpler case occurs in *Conferva glomerata,* and therefore Mohl begins his description with this alga. But even where the formation of two new nuclei precedes the formation of the dividing wall,

[15] Published in Wagner's *Handwörterbuch der Physiologie,* 1851.
[16] *Loc. cit.* p. 211.

this latter process takes place in the same manner as in the *Conferva* above mentioned. And this as well among the algae as in the higher plants. According to Mohl, then, the plasmatic membrane is always produced by new parts growing out of old ones.

As to the historical aspect, it needs only to be emphasized that this law for the algae, which Mohl put into the foreground, has been confirmed by all later investigators.[17] Here its correctness is beyond any doubt, and can be easily controlled by anybody. Who, therefore, on theoretical grounds, is inclined, to assume that, in cell-division, the same principles are valid for the entire plant-world, must with Mohl, still regard the case in question as a type.

In the uni-nucleate cells there are usually present very peculiar structures, the function of which is to make the new dividing wall pass exactly between the two new nuclei. From our present conception of the significance of the nucleus this cannot be wondered at, for what would a cell be without its hereditary characters. In the higher plants these structures are not cleared up in every respect, though with the spirogyras this is, to a large extent, the case, especially through the repeated publications of Strasburger. We shall therefore describe the process in this plant, making use of the last description of this investigator as far as this serves for our purpose.

At the time[18] when the nucleus approaches the end of the prophase, the protoplasm collects around it and

[17]Cell-division through constrictions is widely distributed among the lower algae. Cf., e. g., Klebs, *Arbeiten Bot. Inst.* Tübingen. **1**: 336-343.

[18]The following is taken from Strasburger, *Ueber Kern- und Zelltheilung im Pflanzenreich.* pp. 9-23. Jena, 1888.

assumes, in the region of the poles of the nucleus, a structure of parallel fibres. It soon becomes clear that we have to do with the first signs of the spindle-fibres. These develop quickly and continue through the interior of the nuclear cavity, until they come into contact with each other. There is no valid reason for the eventual assumption that the spindle-fibres developing in the interior of this cavity are of a different origin from the external ones. On the aequator of the spindle the chromatic substance accumulates, touching the individual fibres at their circumference.

Next occurs the formation and longitudinal splitting of the nuclear skein, followed by the separation and moving apart of the two halves of the segments. During this period one sees clearly that not all the spindle-fibres have succeeded in uniting with the opposite ones. Only those that were successful in this are retained as connecting fibres between the two young nuclei which move apart. The space forming between them is surrounded by a protoplasmic mantle toward the outside, and apparently there collects in it a substance with osmotic action which enlarges this space and drives the young nuclei apart. In the meantime the number of the connecting fibres on the mantle of this space is lessened more and more, the mantle itself is made to bulge more and more in a transverse direction, and becomes correspondingly thinner. Yet it remains sharply and plainly visible. The space has assumed now the well-known barrel-shape, its wall is called the connecting cylinder, and remains for some time as an extended vesicle, closed in on all sides. Finally, by being strongly distended in an aequatorial direction, this vesicle reaches the protoplasmic accumulation at the margin of the protruding dividing wall. It

unites with the latter, and is now gradually flattened by it, and finally constricted.

According to the principles of the theory of the vacuoles ascertained by Went and myself, it is probable that the space containing osmotic substance and surrounded by the connecting cylinder is a vacuole, which, contrary to Strasburger's conception,[19] must have penetrated from the outside between the two younger nuclei. It is just as evident that this vacuole must be surrounded by a wall of its own, and that this also forms the inner layer of the connecting cylinder. The latter is also separated from the other vacuoles of the cell-space, by a wall, and between the two walls there lies, at least in the beginning, granular plasm. The changes of that vacuole which forms the interior of the barrel during the whole process require, of course, special investigation, made on living material.[20]

But there can be no doubt about the correctness of Strasburger's conception, where he places the whole process of cell-division, with the one exception of the division of the nucleus, in the protoplasm itself. The daughter-nuclei are passive in this, the cytoplasm alone is the active element.

The chlorophyll-bands, the vacuole, and the granular plasm are simply constricted by the plasmatic membrane growing into the interior. The membrane itself finally separates in the same manner, after having entirely closed up the space remaining in the middle of the ring.

In those poly-nucleate algae, the nuclei of which are evenly distributed over the entire lining layer of proto-

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

[20] Zacharias, in his discussion of Strasburger's work *(Bot. Zeit.* **46:** 449. 1888), emphasizes also "that, on the living object, things may exist which can be better recognized and interpreted there than by fixing and staining."

plasm, no particular devices have been observed for assuring the possession of one or more nuclei at the cell-divisions of each daughter-cell. Moreover they do not seem necessary, owing to the great number and regular distribution of the nuclei. Nuclear spindle and nuclear barrel have therefore lost their significance in this case, and accordingly they are probably not present, at least not as a rule. Cell-division is essentially performed by the plasmatic membrane and the granular plasm only.

For the correct understanding of the processes of normal cell-division, one law, which has been ascertained by experiments on artificial division of living protoplasts in former and more recent times, is of extreme importance. I do not mean the adaptive processes of regeneration after wounding (these will be discussed in the next paragraph), but the constriction of the uninjured cell-contents in entire cells, and the division of the protoplasts into two or more pieces during plasmolysis. The respective cases I have put together in my *"Plasmolytische Studien über die Wand der Vacuolen."*[21] They teach that, in artificial constrictions of a protoplast, the limiting membrane, the wall of the vacuole, and the granular plasm close their edges, apparently without any difficulty, and round off to form a new unit. In plasmolytic experiments this is easily verified. Here one sees also, how upon the restoration of turgor, the parts flow together again, their members uniting with the corresponding organs of the other parts of the same protoplast.

This power of combining with homologous parts seems to be universally inherent in the three mentioned organs of the plant-protoplast. The walls of the vacuoles show it wherever the numerous vesicles of cell-sap

[21] *Jahrb. Wiss. Bot.* **16**: 501-505. 1885.

in young tissue-cells combine into one large vacuole during the rapid growth in the transition to the adult condition. When two or more like protoplasts unite to form a so-called symplast, something similar takes place in their walls, at least in some cases, as in the plasmatic membrane and the granular plasm. The ontogeny of the latex-vessels teaches this more clearly than anything else. A fusion of like parts in the "feet" of many rhizopods has also been repeatedly observed and described.

As far as we know, only simple contact is needed for this fusion, besides the required degree of homogenity. We may, therefore, regard it as a mechanical process and use it as an element in the explanation of normal cell-division. In *Spirogyra* it evidently accomplishes the fusion of the spindle with the inward growing ring, and later determines the final closing up of the opening that was left in the ring.

§ 4. *The Regeneration of Protoplasts after Wounding*

Even though, in the normal course of development, the individual organs of a cell multiply by division, this does not necessarily imply that this rule must be without exception, and that there cannot be cases where nature tries to achieve its ends in another way. Especially where, through outward interference, such as wounding and mutilations, individual members of a protoplast are completely lost, it might be expected that a regeneration in another way might be possible.

To be sure observations now available do not warrant the assumption that such cases actually occur. But this does not, by any means, exclude their possibility. And on this possibility I want to lay great stress in this connection, for the hypothesis of intracellular pangenesis

allows us to regard as possible an occasional neogenesis of such organs out of pangens proceeding from the nucleus.

Judging from the facts published up to the present time, however, the phenomena of regeneration after wounding are closely connected with the normal processes. Nobody, at least recently, has maintained that in such a case there is a new formation of nucleus and chromatophores. There have been only few investigations in regard to a possible occurrence of new vacuoles. These were made by Went for the very purpose of testing the point in question, and teach at least one thing with certainty, that so far, wherever it had been thought necessary to assume a formation *de novo* of normal vacuoles, such does not really take place. For the vacuoles which have been observed originate partly through constriction from the large sap-vesicle of the cell, and partly through the swelling of the smaller ones which are suspended in the granular plasm. Especially in the case of the *Vaucheria*, which was studied first by Hanstein, and later by so many investigators, there surely can no longer be a well founded doubt on this point.[22]

Since the time when, in my *"Plasmolytische Studien,"* I expressed the opinion and sought to establish the fact that the plasmatic membrane is a separate organ of the protoplast[23] no decisive facts on this subject have been published. Klebs is opposed to my assumption on the ground of an observation made on *Vaucheria*.[24] For the study of these processes this investigator introduced a new method, which makes it possible to demonstrate, easily and with certainty, the beginnings of the formation

[22]Went, F. A. F. C. *Jahrb. Wiss. Bot.* **19:** 330-341. 1888.
[23]*Jahrb. Wiss. Bot.* **16:** 493. 1885.
[24]*Arbeiten Bot. Inst.*, Tübingen. **2:** 510.

of a cell-membrane around exuded masses of protoplasm. He stains the water or the diluted solution in which the threads are cut through, with Congo-red, which is stored up with great avidity by these young cell-membranes.

Nevertheless this method does not yet decide the question raised by me, because, as Klebs also says, there is no means of deciding the presence or absence of a plasmatic membrane on a portion of the mutilated protoplast that forms a cell-membrane. "Among the free swimming balls of protoplasm there are always a number of such that are quite large and rich in contents which live several days but without forming a cell-membrane." In the case of most of them, however, the beginnings of the formation of a cell-membrane are very soon evident.[25] Wherein the difference in the behavior of these two kinds of fractional parts consists, was not further investigated by Klebs. My assumption that the former lacked the limiting membrane, while the latter got a part of this organ when cut off, has not been at all disproved.

Nor does the great extensibility of the plasmatic membranes during the enormous swelling of the vesicles which later form the cell-membrane seem to me by any means improbable or even surprising. Plasmolytic experiments teach us at every step that the extensibility, not only of the plasmatic membrane, but also of the wall of the vacuoles and perhaps even of the granular plasm is very considerable. And Went has comprehensively demonstrated that the swollen spheres of *Vaucheria* contain only such vacuoles as have originated by the enlargement, and mostly also by division of the sap-vesicles present in the uninjured plant. The assumption of an extensibility of the plasmatic membrane which need not be much greater than the proven elasticity of the wall of the vacuoles can-

[25] *Loc. cit.* p. 507.

not seem very surprising. The phenomena of regeneration of *Vaucheria* demand renewed investigation in this respect also. As long therefore, as there is no actual proof of a neogenesis of this organ, independently of the old one, we cannot recognize such great significance in this instance as some authorities attribute to it.

Here also the observations by Haberlandt[26] on the same phenomenon are important. This investigator directed his attention chiefly to the nuclei, and familiarized himself with their behavior during regeneration. The nuclei accumulate near the wound in the plasma deprived of chlorophyll bodies, and are evidently more important than the latter for the growth of the new cell-membrane. In the exuded globules of protoplasm which remained alive, Haberlandt succeeded almost always in demonstrating the presence of one or more nuclei, but never the absence of any. In spite of this, not all of them formed a new cell-wall. "At times there occur cell-forms devoid of a membrane and rich in plasm. If the sap-cavity is lacking, the chlorophyll-bodies aggregate in the center, and the nuclei lie in the peripheral, colorless plasma. In case a cavity for cell-sap is present, the chlorophyll-grains lie in the innermost layer of the plasma-body the nuclei more toward the outside."[27] The possession of nuclei is therefore, in itself, not sufficient for the formation of a cell-membrane. It would be important to find out whether the parts of plasma referred to are perhaps the very ones that did not get part of the old limiting membrane.

It seems to me to be of great interest to regard the whole pending question from another point of view, and one which has already been considered by Haberlandt.

[26]Haberlandt, G. Ueber die Beziehungen zwischen Funktion und Lage des Zellkernes. pp. 83-97. Jena, 1887.

[27]*Loc. cit.* p. 92.

Regeneration is obviously an adaptation to guard against the results of injuries which occur frequently in nature. In such cases the higher plants usually give up the affected cells; the large-celled algae and fungi, especially those that have been designated by Sachs as non-cellular, evidently cannot do that. Therefore one generally finds in them the power of closing up wounds. That it would, however, be of particular importance to keep escaped globules of protoplasm alive is the less probable, as it is only possible to do so in solutions which are quite a little more concentrated than those in which the respective plants naturally live. Therefore, the closing up of the wound is primary, the processes in the escaped plasma secondary. From the adaptive characters available for the first, it ought to be possible to explain the latter. And as long as the first can be explained without the hypothesis of an independent neogenesis of the plasmatic membrane, this assumption must be regarded as at least improbable for the latter.

This consideration leads us to include in the field of these studies even the closing up of wounds in latex-tubes. The investigations of Schmidt on the latex-vessels, and of Schwendener on the latex-cells may serve as important points of departure in this.[28] For they teach that in parts of latex-tubes which adjoin the wound of the cut, a closing up of the tube can be accomplished in the same way as in some Siphoneae (e. g., *Bryopsis, Codium, Derbesia)* and in many pollen-tubes the injured part of the cell-cavity is separated from the uninjured one.[29]

[28]Schmidt, E. Ueber den Plasmakörper der Geliederten Milchröhren. *Bot. Zeit.* **40**: 462. 1882. Schwendener, S. Einige Beobachtungen an Milchsaftgefässen. *Sitzungsb. Kais. Akad. Wiss.* Berlin. **20**: 323. 1885.

[29]Schmidt, E. *loc. cit.* p. 462.

Chapter III

THE AUTONOMY OF THE INDIVIDUAL ORGANS OF THE PROTOPLASTS

§ 5. *Nucleus and Trophoplast*

A review of our knowledge concerning the anatomy of the nucleus can be regarded as superfluous in this connection. This knowledge is to be looked upon at present as an established achievement of science, the significance of which for the theory of heredity can hardly be doubted any longer. Flemming in the zoological, Strasburger and Schmitz in the botanical field have broken the way, and their observations have been verified and extended in the main by numerous other investigators.

It does not seem to be quite fully decided whether the amitotic nuclei, which have originated through constriction and scission, are of significance in questions of heredity, or whether they occur in somatic cells only, and not on the germ-tracks. In *Chara* the nuclei in the apical cells divide, according to Johow's investigations, according to the usual scheme of indirect nuclear division; the smaller cells of the grown plant, for example in the nodes, remain forever uni-nucleate, while the larger ones become multi-nucleate through constriction. This kind of nuclear formation, however, is never followed by cell-division.[30] According to Zimmermann direct nuclear division in the plant-world "is limited to only those cases in which the nuclear division is not accompanied by cell-division."[31]

[30]Johow, F. Die Zellkerne von *Chara foetida*. *Bot. Zeit.* **31**: 729. 1881.

[31]Zimmermann A. *Morphologie und Physiologie der Pflanzenzelle*. p. 34.

In the multi-nucleat cells of *Valonia* Schmitz[32] has frequently observed division, and always observed it to take place by constriction. It does not seem to be established with certainty, for all cases, how the nuclei of the swarmspores originate here and in the case of the other Siphonocladiaceae, whether through direct or indirect division.

In this connection it should be mentioned that, according to Van Beneden and Julin, direct and karyokinetic nuclear divisions alternate in the spermatogenesis of *Ascaris megalocephala.*[33] Thus we see that this subject is not yet ripe for theoretical use.

The amyloplasts, with all their derivatives, among which the chlorophyll bodies are the most important, Arthur Meyer calls trophoplasts. In the lowest plants they are not yet differentiated, and, as far as these belong to the Phycochromaceæ, the whole non-nucleated protoplasm of the cell, according to Schmitz, is stained.[34] But later Hansgirg demonstrated nuclei and chromatophores in some algae of this group.[35] From the Chlorophyceæ upward they are universal in the green plants. In the higher plants, where they were discovered by Schimper,[36] they are usually colorless in young cells. As a rule they remain so in the underground parts, which are normally not exposed to light.

Phylogenetically, therefore, plants with undifferentiated colored protoplasm are probably older than those

[32]Schmitz, F. *Die vielkernigen Zellen der Siphonocladiaceen.* p. 27. 1879.

[33]Van Beneden et Julin, *La spermatogénèse chez l'Ascaride mégalocéphale,* Bruxelles, 1884.

[34]Schmitz, F. *Die Chromatophoren der Algen.* p. 9. 1882.

[35]Hansgirg, A. *Ber. Deut. Bot. Ges.* **3:** 14. 1885.

[36]Schimper, A. F. W. Ueber die Entwickelung der Chlorophyllkörner und Farbkörper. *Bot. Zeit.* **41:** 105, 121, 137, 153. 1883.

which possess special chromatophores. Hence we must imagine them to have originated from the others through differentiation. A further step in the differentiation is then the development of colorless conditions of these chromatophores. These are still lacking in the lower Algæ, occur first in the highest groups of this class, and attain their full significance only in the higher plants. In other words, we must regard the amyloplasts, although they are generally the young condition from which chlorophyll bodies develop, as the consequences of a higher differentiation and assume that they have developed phylogenetically from the latter. This discussion is important for the reason that it brings nearer to our understanding the not infrequent changes of form of the trophoplasts on the germ-tracks. On the whole, the cells of the germ-tracks of the higher plants are, as many authors emphasize, of an embryonic nature, and such cells probably always possess colorless trophoplasts. But according to our definition of the germ-tracks, there are many exceptions to this rule. Thus, to name only one instance, the prothallia of ferns, in their youthful state, consist of green, dividing cells, with well-formed chlorophyll-grains, from which later the amyloplasts of the egg-cells will originate. Also in the callus-formation of cut petioles of *Begonia, Peperomia,* and other species, a reversion of green trophoplasts into colorless ones may take place, especially in the case of the production of adventitious buds. And, since generally the amyloplasts occur in young cells and their derivates in grown protoplasts, these and similar cases would be illustrative of a pronounced rejuvenation.

On the germ-tracks the amyloplasts usually take on a simple roundish form, on the somatic tracks they change

their shape considerably, and with it the structure and size of the starch-grains produced by them.

Among the most peculiar characters of the chromatophores in connection with the organization of the protoplasts, belong their autonomous movements. Since the researches of Sachs on this subject, we know that the chlorophyll grains of some plants are moved about by streams of the granular plasm in such a way that, under the influence of light, they take up positions which are favorable for the assimilation of carbon dioxide. But in this process they are passive. The beautiful researches of Stahl, however, have disclosed independent movements of these structures under the influence of the same stimulation. They consist chiefly in changes of shape, through which the organs in question either approach a more or less globular shape, or that of a flat, circular disc. Thus it is brought about that, in direct sunlight, they present a smaller, in diffuse daylight, a larger surface for receiving the rays. And to us they afford an insight into the high degree of their inner differentiation such as we could never have attained by the simpler study of their chemical activity.

According to Weiss, the yellow and orange chromoplasts at times also make autonomous movements, which, according to the descriptions of this author, resemble the changes of form of the amœba and the white blood-corpuscles.[37] These structures, therefore, may also be more highly organized, and play a more important rôle, than that of the simple task of giving their color to the respective plants.

I wish to lay quite particular stress here on these

[37]Weiss, A. Ueber spontane Bewegungen und Formänderungen von Farbstoffkörpern. *Sitzungsb. Kais. Akad. Wiss. Wien.* **90**: 1884.

phenomena, for up to the present time they have probably not been utilized for the theory of heredity. But the more plainly we see the independence of the individual organs of the protoplasts, and the more clearly our conviction grows that they require a high inner differentiation for exercising their functions, the more will we be inclined to give them their due place in our theory, and especially will we try to investigate the more thoroughly their relation to the hereditary factors accumulated in the nucleus.

Wherever, hitherto, we have succeeded in demonstrating with complete certainty the origination of trophoplasts, we have found that they arise through a division of those already present. That the chlorophyll grains, in the higher plants as well as in the algæ, can multiply through constriction and scission has long been known. But it was Schmitz who showed that this process is the only form of their multiplication in the algæ.[38] In the Characeæ he discovered, in the apical cells, the colorless bodies from which the green organs of these plants are derived in the same way. These investigations are now so generally known that it would be superfluous to describe them here in detail. I shall only emphasize, as especially important, the fact that the swarm-spores also possess only such chromatophores as they have received from their mother-cell, a fact that was especially mentioned in the case of *Cladophora* and *Halosphaera*.[39]

The investigations by Schimper and others, who discovered this same law for the phanerogams, have already been discussed in one of the preceding Chapters.

Special consideration is still due to the rarer forms derived from the more general chromatophores. In the

[38] Schmitz, *Die Chromatophoren der Algen.* 1882.

[39] *Loc. cit.* pp. 135, 136.

first place we must mention the eye-spot[40] observed in many swarm-pores, and which, according to the opinion of those investigators who have examined it more carefully, is probably a metamorphosed chromatophore, the same as the chromatic bodies of the higher plants studied by Arthur Meyer.[41] In the Euglenæ its origin has been more carefully studied by Klebs. Here it always originates by division, the organs being always preserved in the resting cells.[42] It is not yet definitely decided whether or not the pyrenoids in the chorophyll bodies of *Spirogyra* and other algæ are to be regarded as specially differentiated parts of these organs. But it seems certain that, at least in isolated cases, they multiply through division.[43]

On the origination of oil in plant-cells little is known with certainty. Pfeffer has demonstrated that the oil does not form in the vacuoles, but lies imbedded in the granular plasm. Special organs which accumulate it within themselves have lately been described by Wakker for *Vanilla planifolia,* and have been called elaioplasts. Although it has not been possible to find out their mode of origin, the most natural assumption is that they are metamorphosed chromatophores.[44] In some cases, as for example in the diatomes, the oil-drops of the Algæ evi-

[40]Cf. Zimmerman, *Die Morphologie und Physiologie der Pflanzenzelle.* p. 71. 1887.

[41]Meyer, Arthur, *Das Clorophyllkorn.* 1883.

[42]Klebs, Ueber die Organisation einiger Flagellatengruppen. *Unters. Bot. Inst.* Tübingen. **1:** 233.

[43]Schmitz, F. *Die Chromotophoren der Algen.* pp. 42 and 65. 1882. Schmitz, F. Beiträge zur Kentniss der Chromatophoren. *Jahrb. Wiss. Bot.* **15:** 142. 1884. Strasburger, E. *Ueber Kern- und Zelltheilung.* p. 26. 1888.

[44]Wakker, J. H. De Elaioplast. *Maandbl. v. Natuurwetensch.* No. 8. 1887.

dently do not lie in the chromatophores, and this, according to Schmitz, is a general rule.[45] But in the higher plants this seems at times to be the case.[46]

Last to be mentioned here are the microsomes. In most cases it seems to be unknown what they are. Small oil-droplets, starch-grains, inactive vacuoles, amyloplasts, protein bodies formed by fixation[47] through the coagulation of the protein dissolved in the protoplasm, and perhaps many other formations are frequently all classed under this name. Very justly has Strasburger claimed "that not the microsome but the hyaloplasm is to be considered the active substance."[48] At any rate it ought never to be forgotten that the word microsome stands only for a question mark, and that we can talk of an insight into the significance of these structures only after the question concerning their nature in the cases concerned shall have been answered.

§ 6. *The Vacuoles*

Vacuoles were formerly regarded as empty spaces in the interior of the protoplasm. This accounts for their name, and explains the small interest shown in them, until recently, in the study of the anatomy of the cell. It is only since Sachs discovered that the turgidity of growing cells is not due to an imbibition of water in their walls, as was previously assumed, but to an osmotic tension between the wall and the cell sap, that attention was directed to the significance of the vacuoles.[49]

[45] Schmitz. *Loc. cit.* p. 164.

[46] Cf. Meyer, Arthur. *Das Chlorophyllkorn,* pp. 14 and 31. 1883.

[47] i. e. artifacts caused by the "fixing" fluid. *Tr.*

[48] Strasburger, E. *Neue Untersuchungen.* p. 107. 1884.

[49] Sachs, J. von. *Lehrbuch der Botanik,* 3 Aufl. 1872; 4. Aufl. 1874, p. 757.

This was still more the case through the demonstration furnished by the same author, that the tension to which growing cell-membranes are subjected by the cell-sap is one of the most essential mechanical causes of the surface growth of these membranes. For with this demonstration Sachs laid the foundation still valid, for the whole mechanical theory of growth in length.

Building on this foundation, many investigators have enlarged our knowledge of the mechanical causes of growth in various directions. Some have especially measured and analyzed the degree of extensibility of the cell-membranes and the amount of force supplied by the cell-sap. Others have studied the causes governing the variations of extensibility of the wall in one and the same cell, and which occur in different spots and in different directions, and have explained them, as due, with great probability, to local differentiations in the protoplast itself, which might regulate this elasticity through the secretion of certain enzymes. Others again have attacked the doctrine of intussusception, which was the prevailing one at the time of the discoveries mentioned, have proven it to be incorrect, and have tried to ressuscitate in its place, in a new form, the old "apposition theory."

Although subject to misunderstandings from some sides,[50] Sach's theory has acquired a prominent position in plant-physiology, and, since the two decades of its establishment, it has become, in ever increasing measure,

[50]In my "Untersuchungen über die Mechanischen Ursachen der Zellstreckung" (p. 3, 1877.), I have distinctly emphasized the fact that there are also phenomena of growth independent of turgor, and that therefore this turgor is neither the only, nor even the first reason for growth. Krabbe and Klebs arrived later at the same conclusion. Cf. *Arbeiten Bot. Inst.* Tübingen. **2**: 530. 1888.

the starting point of new investigations. It has been, without doubt, one of the most fruitful thoughts for the development of our science.

The further study of the cell-sap and the vacuoles, suggested by this theory, has led in regard to the morphological aspect, which alone interests us here, to the proof that the wall of the vacuoles is an essential, never wanting part of the plant-protoplast.[51] The method which made it possible always to demonstrate the presence of this wall consisted in the treatment of the living cells with a 10% solution of potassium nitrate, which has been stained with eosin. Directly, or after a shorter or longer period, the outer protoplasm dies in the reagent, while the wall of the vacuoles remains living for a while. It is then visible as a distended bubble, more or less completely separated from the dead parts, and entirely preventing the penetration of the eosin. In colorless cells, therefore, the bubble carries contents as clear as water, while the remaining protoplasm is stained red or brown by the eosin. Frequently the original vacuole separates into several smaller ones; and not infrequently one can follow this process directly under the microscope.

The wall of the vacuoles is to be regarded as a special organ of the protoplast, which regulates the secretion and accumulation of the substances which are present in the cell-sap in solution, and because of this function, it has been given the name *tonoplast*. But frequently the sap-spaces together with their walls are now designated as vacuoles.

In living cells the tonoplasts are, as a rule, not visible, because they consist of translucent vesicles of an extreme

[51]Vries, H. de. Plasmolytische Studien über die Wand der Vacuolen. *Jahrb. Wiss. Bot.* **16**: 465. 1885.

thinness. But they are clearly and distinctly visible in the tentacle-cells of some insectivorous plants, especially of the *Drosera rotundifolia* and *D. intermedia.* The process of aggregation, discovered by Darwin,[52] taking place here during the digestion of the prey, belongs to the most interesting phenomena that the life of a cell presents for our admiration. In the resting tentacle-cells there lies usually a large vacuole containing red cell-sap. Under the influence of stimulation it separates into several, and soon into numerous smaller ones. These contract, while secreting part of their contents, and are now carried through the cells by the currents of the granular plasm, with great rapidity, and in the most various directions. Thus they lie as red vesicles in unstained substance, and can therefore be seen very distinctly. During these movements they undergo striking changes of form; sometimes they are drawn out into long tubes, and thereupon split into numerous small globules, sometimes two or more unite to form larger vesicles. Toward the end of the phenomenon this last process has the precedence, and finally all the sap-bubbles have again united into one, of the original volume.[53]

The above mentioned phenomena of aggregation, and the division of the vacuoles, as it is so frequently observed in plasmolysis placed the ability of these organs to multiply by this process beyond any doubt. From the analogy of these structures with the chromatophores I then deduced the assumption, that "like the amyloplasts, they can be produced in no other way than by division."[54]

[52]Darwin, C. *Insectivorous Plants.* Chap. III. 1875.

[53]Vries, H. de. Ueber die Aggregation im Protoplasma von *Drosera rotundifolia. Bot. Zeit.* **44**: 1, 17, 33, 57. 1886.

[54]Vries, H. de. Plasmolytische Studien über die Wand der Vacuolen. *Jahrb. Wiss. Bot.* **16**: 505. 1885.

This supposition has since been completely confirmed by Went.[55] He showed first, that, contrary to the prevailing opinion, vacuoles are present even in the youngest cells of the meristem. These multiply continuously through division, and observation teaches that during cell-division one-half of the vacuoles present goes to one daughter-cell and the other half to the other. Sometimes it was possible to observe the constriction and afterwards the transmission of the two sap-vesicles, formed in this way, to the daughter-cells. From the vacuoles of the meristem all the vacuoles of the entire plant can thus be derived. Divisions of these structures are to be found everywhere; formations *de novo* nowhere. In the same way, in the cryptogams that grow with an apical cell, all the vacuoles originate from the original vesicles present in these cells.

According to these investigations the vacuoles behave exactly in the same way as the chromatophores, and are just as independent cell-structures as the latter. And through the demonstration of this independence, the panmeristic conception of cell-division has been definitely proven as correct, in opposition to the former neogenetic one.

According to later communication by the same author, he succeeded also in observing the formation of vacuoles in some special cases which had not been studied before. Here should be emphasized the formation of these organs in the swarm-spores which, according to a communication by letter from Went, comes about by a division of the sap-vesicle in the mother-cell in such a way that every

[55]Went, F. A. F. C. Die Vermehrung der normalen Vacuolen durch Theilung. *Jahrb. Wiss. Bot.* **19**: 295. 1888.

swarmer receives into its body a portion divided off from this bubble.

In the literature, an origination of sap-cavities in nuclei, chromatophores, or even in the granular plasm, outside the vacuoles already present, has repeatedly been described. But, on investigating these cases, it was found that here one had to deal, not with normal vacuoles, but with pathological formations, which occur with the ageing or dying of the cell. Frequently they are also due to the influence of the water in which the preparations are examined.[56]

From the theory that the vacuoles originate only through division, it may be concluded that the sap-vesicles of germinating seeds are derived from those present in the ripening ovules, and that, therefore, in the ripe condition, the vacuoles must indeed be dried out, but cannot be entirely lacking. Following up this thought Wakker arrived at the noteworthy discovery that the aleuron-grains are the dry states of the vacuoles in the seed.[57] During the process of ripening, the amount of protein matter dissolved in the cell-sap gradually increases until the fluid becomes of a thick, slimy consistency. In drying, some of the protein bodies crystallize and form the well known crystalloids, while the remaining protein hardens into an amorphous mass around them. When soaking the seed, these masses soften gradually and are later utilized as nourishment. By using a solution of one part nitric acid in four parts

[56]Went, F. A. F. C. *De jongste toestanden der vacuolen,* pp. 45-65.

[57]Wakker, J. H. Aleuronkorrels zyn vacuolen. *Maandbl. v. Naturw.,* Nr. 5. 1887. Over kristalloiden en andere lichamen die in de cellen van zeuvieren voorkomes. *Bot. Cent.* **33:** 138. 1888, and *Jahrb. Wiss. Bot.* **19:** 423. 1888. Since that time this result has been confirmed by Werminski, *Ber. Deut. Bot. Ges.* **6:** 199. 1888.

of water, one can bring about at will this hardening in the still liquid cell-sap, and in this way artificially produce the formation of aleuron-grains under his very eyes.

It is important that, in some seeds more, in others less, the vacuoles divide during the process of ripening into several smaller, frequently into very numerous extremely minute vesicles, which gradually fuse again into one large vacuole at the beginning of germination.

The processes in the seed, therefore, fit beautifully into the conception that the vacuoles originate only by division.[58]

Just as the chromatophores can differentiate into the most various organs, so also can the vacuoles, although to a lesser extent. Went observed how, in different cells, there lie vacuoles which remain separated throughout their existence, and are distinguished by their different contents.[59] Frequently some of them are stained, others are colorless, or some contain tannin, which is lacking in others. In such cases the latter are called by that author adventitious vacuoles.

The contractile or pulsating vacuoles form a special system. In the swarm-spores of the algæ they probably originate from the other vacuoles[60] through further differentiation, but in the Euglenæ, according to the investi-

[58]In Müller's bodies of the ant-plant, *Cecropia adenopus,* Schimper illustrates formations in the cell-contents which, at first glance, look like vacuoles, and which, on account of their semi-fluid contents, he compares with the aleuron-grains. Their origination from vacuoles can hardly be doubted. Schimper, A. F. W. *Die Wechselbeziehungen zwischen Pflanzen und Ameisen.* 1888. Cf. especially Taf. II, Fig. 11. Also Wakker, *Jahrb. Wiss. Bot.* **19**: 467. 1888.

[59]Went. *loc. cit.* pp. 65-91.

[60]Or have the turgor-vacuoles possibly originated phylogenetically from the pulsating ones?

gations of Klebs, they multiply by division.[61] They possess here a wall of their own which resembles the walls of ordinary vacuoles in its great power of resistance. Klebs observed how the pulsation may continue for a long time after the rest of the protoplast has been killed by some mechanical interference. The view that, in systole, the contents of these vacuoles are expelled into the surrounding tissues, while, in diastole, fluid is taken from the protoplast, is probably generally accepted for rhizopods and flagellates. My own observation convinced me of its correctness in *Actinophrys Sol.* The same opinion may also apply to the pulsating vacuoles in the plant-world.[62]

§ 7. *The Relation Between the Plasmatic Membranes and the Granular Plasm*

While the investigations of the last two decades have thrown a clear light on the organs of the protoplasts just discussed, the relation between plasmatic membrane and granular plasm is still completely in the dark. In our knowledge of the mode of origin of the nuclei, trophoplasts, and vacuoles, the theory of heredity, as I have tried to explain in this Section, finds its indispensable basis. On the mutual relation of the two other mentioned parts of the protoplast, no facts have yet been found, which might be utilized for the theory.

As already mentioned, what the nature of that relation is, is certainly not of essential importance for the hypothesis of intracellular pangenesis. Yet it remains an important question whether granular plasm and plasmatic membrane are mutually as independent as the granular

[61]Klebs, G. *Arbeiten Bot. Inst.* Tübingen, Bd. I. p. 250. ff.
[62]Pfeffer, *Pflanzenphysiologie,* pp. 399-401.

plasm and the wall of the vacuole, or whether they stand in the same genetic relation as amyloplasts and chlorophyll-grains. As long as this question remains undecided, the application of my hypothesis to the plasmatic membrane and therewith to the surface growth of the cell-membrane and all the formative processes of the cells, is rendered very difficult. For this reason may I be allowed to subject the respective phenomena to a critical revision in order to encourage further research. I think it will then be seen that the prevailing opinion that the plasmatic membrane originates in every case from the granular plasm is, for the present, not supported by certain and closely observed facts, but is adhered to only from habit. This, however, it seems to me, ought not to be allowed in view of the newer knowledge in regard to the origin of the wall of the vacuole. For, as long as no special wall was assumed for the vacuoles, it was natural not to regard the plasmatic membrane as a special organ. Since the independence of the former has been established, such is obviously most probably the case for the latter also.[63]

Besides the incompleteness of the observations, which is to be demonstrated in the next paragraph, the whole course of the development of our knowledge in the field of cell-anatomy on the one hand, and the already repeatedly described differentiations of the plasmatic membrane and the granular plasm on the other hand, controvert the prevailing opinion. The latter does not form at all, as

[63]A method by which the plasmatic membrane could be artificially separated everywhere from the granular plasm, just as strong plasmolytic reagents separate the wall of the vacuole, is particularly desirable. Such a method could also render great service in judging the hypothesis mentioned on page 160, Note 2, on the growth in thickness of the cell-membranes.

the old conception would have it, a ground-substance of protoplasm, mixing constantly by its movements, and therefore not organized in the ordinary sense. This is most clearly seen in the Characeae. Here it consists, first of all, of a moving portion and of a resting part that contains the chlorophyll grains. When, sometimes the green plastids are torn from their position, and carried away by the current, one sees that they did not adhere separately to the plasmatic membrane, for they are not carried off singly, but in bands and groups, while within these the grains retain their mutual position and distance. Neither does the moving part form a whole, for the rapidity of the current is not at all everywhere the same on a cross-section. It is greater near the chlorophyll-grains than next to the wall of the vacuole, and furthermore it increases from the two indifferent zones toward the center of the green areas which are separated by them. With declining vital energy the more torpid currents are the first to suspend movement, while the more rapid ones continue to move, and with decreasing rapidity the width of the current diminishes at the same time.

Quite generally speaking, the granular plasm seems to consist, in the plant-world, of moving and of resting parts, the limits of which can be shifted by more or less favorable life-conditions, or can also shift spontaneously in the course of development, adapting themselves to changing needs.

The latter condition is illustrated by the beautiful investigations by Dippel, Crüger, and Strasburger on the relations between the plasma-currents and the internal sculpture of the cell-wall.[64] For along those places where

[64]Dippel. *Abhandl. Naturf. Ges., Halle.* **10:** 55. 1864. Crüger, H. Westindische Fragmente. *Bot. Zeit.* **13:** 623. 1855. Strasburger, E. *Jenaische Zeitschr. Naturwiss.* **10:** 417. 1876.

ledges, jutting into the interior, are in the process of formation there generally run strong currents which evidently bring and distribute the requisite food. But this differentiation in the granular plasm is, to all appearances, controlled by a corresponding differentiation in the plasmatic membrane. For, according to Dippel, the bands which form the layers of cellulose, consist of an outer hyaline band, which is thicker than the rest of the plasmatic membrane, and, like the latter, cannot be stained with iodine, together with an inner, moving layer of the granule-bearing plasm, which takes a deep yellow tint when treated with iodine.[65] The hyaline band is evidently a differentiated part of the plasmatic membrane which, on its inside is covered and nourished by the current, and on its outside forms the ledges of the cell-membrane.[66]

In naked protoplasts the cilia also bespeak an inner organization of the plasmatic membrane. These are described by Strasburger[67] for the swarm-spores of *Vaucheria*. Here all the cilia adhere to a denser part of this layer; they appear to be embedded in it by a thick root.

§ 8. *The Question of the Autonomy of the Limiting Membrane*

While in cell-division, according to the type described by Mohl, the multiplication of the limiting membrane by

[65] *Loc. cit.* pp. 57, 58.

[66] Strasburger's hypothesis that the growth of the cell-wall is accompanied by a transformation layer by layer of the outermost strata of the limiting membrane into cell-wall can, without difficulty be combined with the assumption of the autonomy of this organ with reference to the granular plasm, and therefore need not be discussed in detail here.

[67] Strasburger, *Studien über das protoplasma*, p. 400. 1876.

division and growth is generally recognized, the insertion of a new layer and its connection with the old membrane is usually assumed for cell-formation in the higher plants. In addition to this, there are some cases of cell-formation which seem to argue quite directly in favor of a formation of the limiting membrane *de novo* from the granular plasm.

All these cases seem urgently to demand renewed investigation. It is only with the intention of encouraging it that I shall briefly discuss them here.

In regard to the ordinary mode of cell-division the situation has greatly changed during the past year through a discovery by Went[68] which has been confirmed by Strasburger.[69] This discovery concerns the nature of the so-called cell-plate, which, when nuclear division is completed, forms at the equator of the now barrel-shaped figure. As the name indicates, the cell-plate is regarded as a layer which, cutting across the figure, later divides into two layers, and between these secretes the new cellulose lamella. These two halves of the layer are the two complementary pieces of the plasmatic membrane; as the barrel becomes flattened and extends laterally toward the cell-walls, they increase until they reach the old limiting membrane of the mother-cell and blend with it.

Went succeeded in loosening this whole division figure from the cells after they had been fixed and stained, and allowed it to float around in the fluid of the preparation. In this way it became possible, by turning the cell-plate, to study a polar view of it, while hitherto only the side-view had been studied and figured. As long as

[68]Went, F. A. F. C. Beobachtungen über Kern-und Zelltheilung. *Ber. Deut. Bot. Ges.* **5**: 247. 1887.

[69]Strasburger, *Ueber Kern-und Zelltheilung*. 1888.

the cell-plate is smaller than the daughter-nuclei, this view, of course, does not teach anything, because it has not been possible to remove the nuclei. But as soon as the cell-plate protrudes sideways from betwen the nuclei, it can be seen that it is not, by any means, a continuous plate, but only a rather thin ring. This ring lies in the connecting tube that separates the interior of the figure from its surroundings and has probably the same significance as in *Spirogyra*.[70] This "cell-ring," as we must now call the cell-plate, enlarges until it unites, first on one, then gradually on all sides, with the peripheral protoplasm of the mother-cell.

That the plane of the cell-ring is the place where the dividing wall forms, is certain, and agrees essentially with the previous conception of the cell-plate. But it has not yet been possible to discover whether or not the secretion of cellulose in the cell-ring begins before the latter has joined the wall of the mother-cell at least on one side. As soon as its presence can be proven by reagents, the new membrane is already joining the wall of the mother-cell, at least on one side.[71] Likewise it has not been decided, whether, in the plane of the ring there is extended a membrane which crosses the vacuole situated there and separates it into two separate sap-vesicles. But this is not probable.

It is clear that, with the discovery of the cell-ring, the old conception of cell-division that contradicts the autonomy of the plasmatic membrane, is weakened. For its final refutation, however, further researches are necessary, especially such as will include the wall of the vacuoles in the figures of division.

[70]Cf. pp. 132-134.

[72]Strasburger, E. *Bot. Praktikum,* p. 597. 1884, and *Ueber Kern- und Zelltheilung.* p. 171 ff. 1888.

I agree here with Zacharias[72] who, from observation on *Chara,* is of the opinion that the cell-plate elements originate from the cytoplasm surrounding the nuclear figure. I wish also to recall here an opinion of Flemming's, according to which, cell-division in plants and animals generally begins with a constriction of the protoplast. This constriction has not been observed in many preparations for the only reason that it is frequently unilateral, and therefore requires a special position of the cell under the microscope in order to be seen.[73]

Platner's view that the spindle fibers are currents of the granular plasm requires further investigation. For this purpose direct observation on the living object is necessary. Obviously the plasma-currents have, until now, been sadly neglected in the study of cell-division.

There are still left for us to consider the instances of so-called free cell-formation, which probably represent the most striking exceptions to the rule of the autonomous origination of the plasmatic membrane. By free cell-formation is meant those cases in which not all of the protoplast of the mother-cell is used in the formation of the daughter-cells.[74] The new cells were thought to have originated in the interior of the mother-cell, and therefore without any contact with the limiting membrane.

[72]Zacharias, E. Ueber Strasburger's Schrift Kern-und Zelltheilung im Pflanzenreiche. Jena. 1888. *Bot. Zeit.* **46:** 456. 1888.

[73]Flemming. *Zellsubstanz, Kern-und Zelltheilung.* p. 243. 1882.

[74]In the most recent interview of the pertinent literature, Zimmermann suggests that the name free cell-formation be not used for these phenomena, but for the formation of free cells, i. e., of such that lose their connection with the mother-cell. If it should be discovered that a free cell-formation in the old sense, does not exist in the plant-world, this suggestion would certainly be acceptable. Cf. *Die Morphologie und Physiologie der Pflanzenzelle,* p. 160. 1887.

Hence it was clear that their limiting membrane must have been derived from the granular plasm.[75]

In the formation of the endosperm a new plasmatic membrane seems to be formed only in contact with that of the mother-cell. In small embryo-sacs, where each nuclear division is followed by a cell-division, the conditions are, evidently, not essentially different from those in vegetative cell-division. And, for those embryo-sacs which continue to grow after fructification, I am not able to find, in the literature in question, any proof against the correctness of this assumption.[76]

In a number of algæ *(e. g., Acetabularia, Hydrodictyon, Ulothrix)* the swarm-spores arise from only a part of the protoplasm of the mother-cell. In such a case this part is always the peripheral layer, and every swarm-spore receives, as far as the present literature allows us to judge, not only a nucleus, chromatophores, and vacuoles,[77] but also a part of the limiting membrane of the mother-cell. Similar conditions seem to exist among the fungi, e. g., in *Protomyces macrosporus.*[78] In the case of *Hydrodictyon,* Pringsheim states that the colorless, ciliated, anterior end of the swarm-spores represents the maternal membrane.[79] In the Saprolegniaceæ also, the

[75]At this point in the original occurs a discussion of the processes of cell-division within the embryo-sac in their relation to the question of the autonomy of the limiting membrane. Since the points there considered are now definitely settled and agreed upon, the two paragraphs are here omitted with the author's approval. *Tr.*

[76]See especially Hegelmaier, Zur Entwickelungsgeschichte endospermatischer Gewebekörper. *Bot. Zeit.* **44**: 529, 545, 561, 585. 1886.

[77]According to the communication by Went mentioned on p. 154.

[78]Cf. de Bary. *Vergleichende Morphologie und Biologie der Pilze, Mycetozoen und Bacterien,* p. 86. 1884.

[79]*Monatsbericht Kais. Akad. Berlin,* p. 246. 1871.

oöspores are formed in such a way that each takes up in itself a part of the maternal membrane.[80]

We meet with a greater difficulty in the ascospores. But their origin has not been carefully studied in late years. Thus, though we know that divisions of the mother-nucleus always precede their formation, the question as to how they acquire their other organs has not yet been studied. It is clear that every spore must get one or more vacuoles through the division of the maternal sap-vesticles, but how this comes about, nobody has yet investigated. The consideration of the other question also as to whence the spores obtain their plasmatic membrane, must be most urgently recommended.

In the same way the origination of the egg-cell in the oogonium of the Peronosporales awaits study by means of modern methods. In this case, too, nothing definite can be said for the present in regard to the origination of the plasmatic membrane. Concerning the membrane of the spermatozoids, consult the following Section (pp. 174-176).

As a final result of this review, we may therefore say that, in all cases in which the arising of a new plasmatic membrane is supposed to take place without contact with the old one, this assumption is chiefly due to investigation by the older and imperfect methods. Exceptions to the rule are not at all known with certainty, although, according to the hypothesis of intracellular pangenesis, they must not be considered, *a priori,* as impossible.

[80]De Bary. *Abh. Senckenb. Naturf. Ges.* **12**: 261. 1881.

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 germplant. 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 grand-father. 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 posi-

tion. 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 pro-

tein, 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 de-

scendents. 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 multiplica-

tion 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!

FERTILIZATION AND HYBRIDIZATION

A Paper

read at the 151st annual meeting to the Dutch Society of Science in Haarlem, May 16, 1903

The essay on "Fertilization and Hybridization" was read in Haarlem in the Dutch language, and appears here in an enlarged form. My conception of the life-processes in the nuclei is chiefly based on the renowned investigations of van Beneden and of Boveri, as well as the most recent researches by Conklin (*Contr. Zool. Lab. Pennsylvania,* XII, 192), Sutton (*Biol. Bull.* IV, Dec., 1902), Eisen, (*Jour. Morphol.* XVII, 1), Errera (*Revue Scientif.* Feb., 1903), and of many others. For the literature I refer to E. B. Wilson, *The Cell in Development and Inheritance,* and V. Häcker, *Praxis und Theoric der Zellen-und Befruchtungslehre.*

My presentation of the processes of fertilization and hybridization is an outcome of the experiments which I have described in the second volume of my *Mutationstheorie* (Leipsic, Veit & Co., 1901-1903. English translation by Open Court Publishing Co., 1909-1910.)

H de V.

FERTILIZATION AND HYBRIDIZATION

"Vom Vater hab' ich die Statur,
Des Lebens ernstes Führen,
Vom Mütterchen die Frohnatur
Und Lust zu fabuliren."[1]

In these lines lies the whole problem of heredity and fertilization. What everybody can see, Goethe has voiced clearly and concisely in beautiful, simple words. We have one part from the father, the other from the mother. Or, as it is now usually put, the hereditary characters of the two parents are combined in the offspring.

It became the problem of scientific investigation to seek out the cause of this phenomenon. It could not be limited to man. The law mentioned by Goethe[1] must be general, it must be true of the entire plant and animal world, wherever two beings unite for the production of progeny. Furthermore it cannot concern ordinary fertilizations only, but also those abnormal cases in which unlike individuals, belonging to different varieties or species, fertilize each other. The products of such crosses we call hybrids, and for science they possess the great importance that; in them, the manner in which the characteristics of the parents are combined can be studied more easily and clearly than in the children of a normal union. For the more the parents differ from each other, with the greater certainty must it be possible to determine the share of each in the characteristics of the offspring.

[1]Goethe, "Sprüche in Reimen," *Gesammelte Werke,* III, 83, 1871.

Everywhere this law is confirmed, that the child inherits one part of its nature from the father, the other from the mother. The child is, therefore, on the whole, a double being, with twofold qualities, more or less distinctly separated, that may still be traced back to their origin. This *principle of duality,* as we might call it, dominates the entire theory of heredity; it forms the thread that binds together apparently separated cases; it serves as a guidance for the whole investigation.

This investigation occupies two different fields. On the one hand we have experimental research, on the other hand microscopical. Physiology ascertains the relations of the offspring to their parents; it analyzes their characteristics into their individual units, and tries to demonstrate their origin. The history of development discloses to us the corresponding microscopic processes; it looks for the smallest visible bearers of heredity in the cell, and investigates how they are maintained during life, and how, during fertilization, they pass on from father and mother to the offspring.

Few investigators master both provinces; their extent is much too great for that. And especially has the study of hybrids so greatly advanced in recent years, that even here a division of labor will soon be necessary. Both lines of work have therefore developed more or less independently of each other. In both, the main features of the problem begin gradually to arise out of the abundance of individual phenomena. And thereby there is disclosed, one might almost say, beyond all expectation, an agreement in the results of both lines of investigation, which is so great, that almost everywhere the physiological processes are reflected in the microscopically visible changes.

It is true that the final analysis lies yet beyond the

limits of our present microscopical vision. Compared with the enormous complexity of the herditary characters of the organisms the anatomical structure of the cells and their nuclei, as it is known to us, is much too simple. The individual traits of father and mother can not yet be found in the cells of the offspring, but the investigations of most recent times indicate clearly that here also the limits of knowledge are being constantly extended.

The double nature of all beings that have sprung into existence through fertilization, is seen in their external appearance, as well as in the finest structure of their nuclei. The principle of duality obtains everywhere, even if, in individual cases, the demonstration of it is yet in its beginnings. But as far as the visible marks can be analyzed and the individual component parts of the nuclei can be traced, so far can the validity of the principle be proven even at present.

Let us consider first the external part, then the internal.

Goethe derived his stature from his father, and not from his mother, and it was not a stature between the two. The sum total of his qualities he had partly from his father, partly from his mother. The illustration explains the rule in a clear manner. In the offspring the characters of the parents are combined. Not always does the child get an even half from each; on the contrary, as everybody knows, it resembles the mother more in some respects, and the father more in others.

It is exactly the same with hybrids. With them a single character is generally derived either from the father or from the mother. The hybrids of white and blue flowers usually bloom blue, those of a hairy or a thorny parent crossed by one without hairs or thorns are usually

hairy or thorny. The crossing of a common evening-primrose with a large-flowered species results in a flower of the size of the former. But, if there are two or more points of difference they may be transmitted to the children partly by the one parent and partly by the other, and it is thereby possible in practice to combine the good characters of two varieties into a single race. Thus has Rimpau created a series of hybrid-races of wheat, and Lemoine has produced his large-blooming sword-lilies, able to withstand the winter, and thus have originated, in agriculture and horticulture, the countless hybrids, in which the favorable characteristics of various varieties are combined with more or less diversity. Combined, or as we usually say, mixed; though this is an expression which makes us only too easily lose sight of the independence of the individual factors in the mixture.

This independence is frequently difficult to demonstrate in the mixtures, that is, in the characteristics of the hybrids. Our means of differentiation only too frequently prove insufficient. In the clear cases, however, it appears very distinctly, and the greater the number of hybrids that are studied accurately and thoroughly, the more generally is the validity of the principle established.

If, for example, we find combined in a wheat-hybrid, the loose ear of the mother-plant, with the lack of awns in the father, the share of each appears simple and clear. In the mixture of the characteristics these two are so far apart, that they are always easily recognized. How are such characters united in the hybrid? Are they fused into one whole, or do they simply lie loosely side by side?

The splittings, which occur regularly in many hybrids, when propagated by seed, and also, in the case of a few, in vegetative propagation, give us an answer to this question.

Of the last kind the *Cytisus Adami* serves as the most beautiful and striking instance. It is a hybrid between *C. Laburnum and C. purpureus.* Unfortunately its great significance for the main features of the whole problem has been underrated for a long time owing to the fable of its having originated as a graft. As a matter of fact, no hybrids are obtained by grafting, no matter how great the mutual influence of the wild stock and the crown graft. As far as historical evidence goes, the *Cytisus Adami* has always been propagated by grafts since its first appearance, but it did not originally spring into existence in this way.[2]

This tree teaches us how the qualities of the two parents are combined. Ordinarily they occur mixed, the leaves as well as the flowers having some features of the *Laburnum* and others of the *purpureus.* The totality of the characters lies, therefore midway between the two parents. But splittings do occur, and not at all rarely, or rather so commonly, that indeed every specimen of the hybrid, if not too small, will show them. In these splittings the types of father and mother separate sharply and completely. Some twigs will grow that are purely *Laburnum,* while others are only *purpureus.* The former are vigorous and long-lived, the latter remain weak and often die after a few years, which is the reason for their being seen less frequently. But even in this point they resemble exactly the respective parents.

Within the hybrid, the bearers of the parental characters are therefore arranged in such a manner that, so to speak, they can be completely separated, at any moment,

[2]Strasburger (Jahrb. Wiss. Bot. **42**: 69-70. 1905.) finds entire absence of any cytological evidence that *C. Adami* originated as a graft-hybrid. *Tr.*

by a simple cut. And, if not by a simple cut, then at least by a physiological splitting, which passes exactly between the two parental groups and does not leave in one of them any trace of the other.

In this manner we have to picture to ourselves, in a general way, the internal, invisible structure of the hybrids. The bearers of the characters of both parents are intimately connected, and together dominate the visible characteristics. But they are not, by any means, fused into a new indivisible entity. They form twins, but remain separable for life.

In all nature there is probably not another such beautiful instance of splitting as the above-mentioned *Cytisus*. But with lesser differences between the parents, splittings of the parental types occur frequently in the vegetative life of hybrids. Many horticultural plants, and especially the bulbous plants, furnish instances thereof; peas, corn, wood-sorrel, anagallis, oranges, and several others are known instances. The fruits that are half lemon and half orange, belong doubtless to this group. Among the hybrids of the common and the thornless thornapple (*Datura Stramonium*), individuals have been found, although very rarely, that showed a similar splitting, and which even bore on the same fruit armed, as well as thornless cells. In my garden, I cultivated, for many years, a *Veronica longifolia* which was a hybrid from the blue species and the white variety, and correspondingly had blue flowers. But from time to time splittings occurred; either one single spike bloomed white, or a few isolated white flowers appeared on an otherwise blue spike.

During the entire life, up to the time of the formation of the reproductive cells this internal dualism manifests itself in this way. Sometimes proofs of it are even found

in the anatomical structure of the tissues, and of the individual cells, where the parental characters are set free and a mosaic-like structure results.

MacFarlane, who has made the most thorough study of the anatomical structure of hybrids, recognizes everywhere the principle of duality, and goes so far as to regard every individual vegetative cell of a hybrid as a hermaphrodite formation. And the renowned French investigator of hybrids, Naudin, also expressed himself about forty years ago in a similar manner. *"L'hybride est une mosaique vivante,"* said he; we do not recognize the individual parts as long as they remain intimately blended, but occasionally they separate and then we are able to distinguish them.

We therefore regard it as established that, in the children, the inheritances from the fathers and mothers are indeed combined, but not fused into a new entity. Acting always conjointly under ordinary circumstances, they yet do not lose the power of separating occasionally.

But now arises the question as to what is anatomically visible of this union. Can the dualistic formation be observed within the cell? Do the parental inheritances, here too, lie side by side as twins?

The hereditary characters are contained in the nuclei, as was first declared by Haeckel, and later demonstrated by O. Hertwig, and, for plants, by Strasburger. This important law forms, for the present, the basis of the whole anatomical theory of heredity, and is recognized as such by all investigators. We may, therefore, expect to find in the nuclei, as well, the dualism of the parental qualities.

Every cell, as a rule, possesses a nucleus. This nucleus dominates the life-activity, and although the current functions can run their course without it, no new ones can be

introduced. In certain filamentous algæ (*Spirogyra*) Gerassimow succeeded in producing cells without nuclei; they retained life for several weeks, feeding vigorously, but nevertheless they always perished without any reproduction. In some tissue-cells the nucleus is constantly in motion, and according to Haberlandt's investigations, it stops longest where the work of the cell is most pronounced for the time being, as for instance in unilateral growth, the formation of hair, local accumulation of chlorophyll, etc.

This concentration of hereditary characters is most distinctly seen in the sexual cells. Here the other functions are reduced to a minimum. The nucleus dominates completely. In the male sperms the activity of the protoplasm is limited to moving around and to seeking the female cells. The body is made up almost entirely of the nucleus. In the higher plants the spermatozoids lack even the organs of free motion; they are carried to the egg-cell passively, in the pollen-tubes. The egg-cells are usually immovable and heavy in comparison with the male elements, since they contain the food substance necessary for the incipient growth of the germ, and for the first cell-divisions.

Now fertilization consists in the union of two cells, the male spermatozoid and the female egg-cell. This union is the means of combining the inheritance of the two parents, and therefore the nuclei play the main rôles. The nucleus of the egg-cell lies usually in its center; the male nucleus reaches it by passing straight through the surrounding plasm. Sometimes one sees quite distinctly that it no longer needs its own protoplasm since it strips it off and leaves it at the border of the egg-cell. In the Cycadaceae, in which the spermatozoa are just large

enough to be discernible with the naked eye, the cytoplasm with all its cilia remains in the outer layers of the egg-cell, while only the nucleus penetrates more deeply. The beautiful investigations of Webber and Ikeno have brought this process to light.

Finally the two nuclei come into contact and unite into a single body. This is the most important moment of fertilization, the whole physiological process is concluded by this union.

Let us ask now what has been achieved by it. Apparently very little, for the two parental nuclei are only closely appressed to each other. A penetration or fusion of their substance does not take place. They remain separate in spite of the union. With fertilization the life of the new germ begins, and in most cases immediately. Originally a single cell, the germ soon divides into two and then into more cells. But this beginning of the vegetative life takes place everywhere before the two parental nuclei have entered into closer union. Only after the first division does the limit become unrecognizable, the contact of the constituent parts of the male and female halves being now so intimate that there is at least the appearance of a fusion.

It was the Belgian investigator, van Beneden, who discovered this all-controlling fact. He first observed the independence of the paternal and the maternal nuclei in the intestinal worm, *Ascaris,* then elsewhere in the animal kingdom, and immediately recognized its significance. Since life could begin without fusion of the two nuclei, he considered that such a thing was not necessary, and assumed that all through life the two nuclei preserve their independence more or less completely.

According to this view the nuclei are double beings,

and we thus find, in the material bearers of the hereditary characters, the duality of which Goethe sang in his "Sprüche in Reimen," and which the splittings of hybrids put so clearly before our eyes. Van Beneden chose the name *pronuclei* for the male and the female nuclei that are thus united, and speaks of a *pronucleus mâle* and a *pronucleus femelle*. This designation has been retained since that time, and recommends itself especially for the reason that the union of the two nuclei is usually simply called the nucleus of the cell; and this latter designation will probably not be changed, although the double nature of the nucleus is recognized. Therefore the pronuclei are the entities that concern us; the nuclei are really double nuclei.

If the border line between the two pronuclei remained as distinct through life as before the first cleavage and at the time of it, van Beneden's view would hardly meet with any difficulty. But this is not so. Gradually the line of demarcation becomes blurred, and in most cases nothing more is to be seen of it in later life. But the richness of forms in nature is fortunately so great that the general phenomena in different organisms appear to us with an extremely varied distinctness. And thus it is also here. In one species the border line of the pronunclei is lost sooner, in others later. It is only a case of finding the best illustrations, that is, of selecting a species in which the paternal and the maternal inheritances remain longest visibly separate.

The discovery of such instances is the great merit of Rückert and Häcker. In the one-eyed water-flea of our fresh waters, the well-known *Cyclops vulgaris,* and its nearest allies, they found a group of animals in which the pronuclei remained distinctly separate for a long time. Sometimes during several consecutive cell-divisions, some-

times for a longer period, and, in the best cases, during almost the entire vegetative life, the double nature of the nuclei can here be directly seen. What van Beneden concluded from the incipient stages was here irrefutably proven.

The double nature of the nuclei was also demonstrated more or less distinctly, and during a shorter or longer series of cell-divisions, in other cases, by other investigators. It was observed in *Toxopneustes* by Fol, in *Siredon* by Kölliker, in *Artemia* by Brauer, in *Myzostoma* by Wheeler, in the *Axolotl* by Bellonci. These and numerous other observations now place the law quite beyond doubt. The independence or autonomy of the pronuclei corresponds everywhere with the mode of union of the visible parental characters in the offspring.

In the snail-genus *Crepidula,* Conklin recently discovered a case in which the double nature of the nuclei can be demonstrated perhaps even more clearly and easily than in the Cyclops. If the nuclei remain side by side all through life, the question arises as to how they dominate together the development of the child, the unfolding of its characteristics. Here, too, the results of physiology and of anatomy work beautifully together, and here, too, Goethe's lines serve as a guide. Certain peculiarities are inherited from the father, others from the mother. One individual inherits them in this, another in that mixture. The inheritance therefore consists of separate qualities, which may be united in various combinations in the offspring. We are taught the very same thing by hybrids, especially in their progeny, and the rich floral splendor of our horticultural plants shows us what an endless number of combination-types have already been achieved with comparatively few characteristics.

But we shall not yet leave the subject of the nuclei. The independence of all the hidden potentialities, which in the physiological field is most sharply defined in the theory of pangenesis, we can of course not hope to see reflected in the nuclei. We must, at least for the present, be satisfied to find here any independent parts in the nuclei.

It was well known to the older investigators, and, among botanists, especially to Hofmeister, that the nuclei are not structureless formations, but that they exhibit more or less distinctly certain internal organs. But only about a quarter of a century ago by means of better methods of investigation did Flemming in the zoological field, and Strasburger in the botanical, succeed in getting a deeper insight into this structure, and soon afterwards Roux showed how these achievements are entirely in harmony with the requirements of the theory of heredity. Since then, numerous investigations have confirmed and extended these results, and especially has Boveri brought out the main features in the wide range of phenomena. To him we owe the principle of the independence of the individual visible component parts of the nuclei, a principle, which, in spite of much opposition, is more and more strongly supported, and which has found in the most recent studies of Sutton a brilliant confirmation.

What Boveri's theory offers us is, in the main points, as follows: All the bearers of hereditary characters lie in the protoplasm of the nucleus, in the nuclear sap, as it is usually called, as definite particles, which can be brought out by various methods as distinctly recognizable parts, and which are combined into threads. It is true that one cannot see the individual bearers, because there are too many of them and they are too small. Even a counting of

the smallest visible granules succeeds only rarely. In the nuclei of an American salamander, *Batrachoseps,* the members of the nuclear threads are most distinct; at least Gustav Eisen succeeded in making an approximate count of the smallest visible granules. In every pronucleus they form 12 chief parts, the so-called chromosomes. Every chromosome showed as a rule a subdivision into six sections or chromomeres, and every chromomere, in turn, appears again to be built up of six smallest granules, the chromioles. All in all there are here then about 400 distinguishable particles in the individual pronucleus. The number of hereditary characters must certainly be much higher than 400 for such an organism; it would more likely have to be estimated at ten times that value. We must therefore be satisfied, for the present, with the observation of groups of units in the nuclei.[3]

In the end there will surely be found a way of seeing the individual units also. But the resolving power of our microscope will finally reach its limit, and we shall probably never be able to see much smaller granulations than the smallest elements that are visible now. So far, even the causes of many contagious diseases, in plants as well as in animals, are still quite invisible. But the calculations which Errera has lately made on the limits of the smallness of organisms still allow us full play. In *Micrococcus* he finds a structure composed of about 30,000 protein molecules, but many nuclei are much larger. It cannot yet be estimated of how many molecules a whole nuclear thread is composed, but it may be assumed with certainty that not every one of its granules has such a complicated structure that it could hold the factors for all peculiarities of the

[3]Cf. Translator's Preface, p. viii.

whole organism. Their smallness would rather lead us to suppose that every one of them could, at the most, represent only a small group of such units.

To prove this, on the one hand microscopically, on the other hand experimentally, is the task that Boveri set for himself.

The filamentous framework in most nuclei, recognizable by certain staining methods, is now admitted by all investigators as the idioplasm, the bearer of the hereditary qualities. This thread is very delicate, and seems to form a skein. But when the nucleus prepares to divide, the thread contracts, and thereby is seen, what had hitherto been invisible, that it is composed of several separate threads. In the nucleus there are several threads and not one single one. When the contraction of the thread is advanced so far that the individual parts have become quite short and thick, they are called chromosomes. In the nuclei of the body-cells these always occur in an even number, one-half belonging to the paternal, the other to the maternal pronucleus.

In a series of classical investigations Boveri succeeded in showing that the individual chromosomes, on elongating again, when the division is accomplished, retain their independence. They remain the same during their whole life, elongating and shortening alternately throughout their entire development. The purpose of the shortening is to make possible an even division of all parts during cell-division; the threads then split lengthwise, in such a way that every single bearer of heredity first doubles, and then sends the two halves into the daughter-nuclei. This, of course, could hardly be accomplished in a skein. On the other hand elongation has for its object the freeing of the bearers of heredity from that crowded accumulation,

their task being to control and to direct the life functions of the cell, and to that end they must be able to enter into as free a contact as possible with the granular plasm. An arrangement in rows, at least of those bearers that are to become active, is the necessary condition thereto, and it is evidently reached by means of the elongation of the threads and the formation of the skein.

In order to make possible an orderly retreat of the individual threads out of the tangle of the skein, every thread is firmly attached by one end to the nuclear wall. It retreats to this point, which is at the same time the point at which its two halves, during cell-division, are pulled apart after the splitting. The whole regularity of the process would be hard to explain without this firm implantation of the individual nuclear threads, as demonstrated by Boveri. Where the nuclei are sinuate and the nuclear threads are attached in the individual curves, the conditions are specially clear.

In the species of locust, *Brachystola magna,* Sutton found the same implantations of the nuclear threads on the curves of the nucleus. But here every thread, of which there are eleven in every pronucleus, forms a skein after the cell-division. These skeins of one and the same nucleus remain separated from each other for a long time, and the independence of the chromosomes can hence be directly demonstrated, even at the stage of the skein. This locust has also proven very instructive in another point of Sutton's studies.

In general, one finds the individual chromosomes to be of unequal length in the most various nuclei. But, in the species of locust mentioned, this length occurs in such a characteristic manner that the chromosomes can be easily recognized in the successive cell-divisions. The pictures

taken at the successive stages allow one to follow up, without difficulty, the identity of the short and thick nuclear threads. In doing so one sees that, in the double nuclei, the nuclear threads lie in pairs, that is, that there are two nuclear threads of each individual length. Evidently these belong together in such a manner, that in every pair one thread belongs to the paternal and one to the maternal pronucleus. A border line between them is nowhere to be seen, and yet their independence is very evident. And this harmonizes with the conception, as detailed above, that, according to the species examined, this limit can be observed for a longer or shorter time.

Microscopic examinations teach us, then, to recognize the independence of the two pronuclei, as well as the autonomy of the individual nuclear threads or chromosomes during the development of the entire body. The agreement of this observation with the phenomena of heredity may be considered as fully established.

But it is another question whether the individual chromosomes correspond also to special groups of hereditary characters, or, in other words, whether the bearers of the latter are strictly localized in the nuclear threads. Obviously, this question can be answered only physiologically. It amounts to a decision as to whether, if definite chromosomes, or definite parts in them, as for example, single chromomeres and chromioles, were wanting, definite external characters of the organism would also be lacking. If it were possible to kill a nuclear granule without otherwise injuring the germ, what would be the consequences?

Engelmann has taught us, in his revolutionizing investigation on the activity of the individual chlorophyll grains, how the focal point of a lens can be moved over

the field of a microscopic preparation, thereby lighting up quite small portions of a cell, and how these portions can thereby also be heated, and in that way killed. If a part of a nuclear thread could be killed in this way, the externally visible consequences would certainly allow us to draw conclusions on the relations of this part to the hereditary characters. Perhaps an analaysis of heredity can some day be made by this method, but the technique is not yet sufficiently advanced for this purpose.

However, there is another means of removing individual chromosomes, and this again we owe to the classical investigations of Boveri. He found it in abnormal processes of fertilization as they occur at times in eggs of sea-urchins and star-fish, and it can be quite easily produced artificially. It would lead too far from the main question to go into details here. The important point for our purpose is that, by certain interferences, a fertilization of one egg with two spermatozoa can be achieved. This process of dispermia leads in the nucleus of the germ, not to a double, but to a triple number of chromosomes. In the successive divisions the conditions become correspondingly intricate, and almost any imaginable abnormal number of chromosomes occurs. Nevertheless, the germs develop in some cases, and then show deviations from the normal type which allow a recognition of their normal relations to the structure of their nuclei. Without doubt the germs can, in every case, develop only those qualities the representatives of which happened to be preserved in their nuclei.

We shall leave the nuclear threads, at present, and return to the two pronuclei. We saw them intimately combined during the entire development of the body. Now the question arises as to how long this union persists.

And since the double nuclei of the body originated during fertilization, it is evident that the conjugating cells must have single nuclei, and therefore that the separation of the pronuclei must take place at the origination of these cells.

This fact is now so generally established, for animals as well as plants, that it may be regarded as one of the strongest foundations of the whole theory of fertilization. Wherever it is possible to count the chromosomes, we find in the somatic cells twice as many as in the sexual cells. The former contain double nuclei, the latter single nuclei, or pronuclei.

The sexual cells in animals originate directly from the somatic cells, but in plants there is more or less preparation. Correspondingly, the two pronuclei separate in animals at the formation of the egg- and sperm-cells, but in the case of plants before that. In the seed-bearing plants it is the period of the origination of the mother-cells of the pollen and of the embryo-sacs. Therefore all cell-generations which appear after this moment, and up to the final production of the egg-cells in the embryo-sac, and of the sperm-cells in the pollen-grains and their tubes, possess only pronuclei. Such cells are called sexual, and the period of their formation the sexual generation. In ferns the entire life-period of the prothallium lies between the origination of the sexual cells and the appearance of the egg- and sperm-cells. This small plantlet, though built up of hundreds of cells possesses, therefore, as Strasburger has demonstrated, only pronuclei. The alternation of the sexual prothallia and the asexual fern-plant is called the alternation of generations; the two generations are hence distinguished from each other fundamentally by their nuclei, which in the leafy plants are always double nuclei, and in the prothallia always pronuclei. This difference

is so constant that one feels almost inclined to call the pronuclei prothallial nuclei.

At the moment when the two prounclei separate, single nuclei appear in place of the double nuclei, and the double number of nuclear threads is thereby reduced to a single one. This process is usually called the numerical reduction of the chromosomes; but this imposing name means nothing but the separation of two nuclei which had so far worked together for a period. It is like the parting of two persons who have walked along together for a while, and will be looking for other companionship presently. And this they achieve by fertilization.

This parting has been minutely studied by numerous investigators. It has the appearance of a nuclear division of a very special nature, and is frequently called the reduction-division, or heterotypic nuclear division. It is necessarily accompanied by a cell-division, since the two separated pronuclei can only part in separate cells, but this cell-division does not always follow immediately, but only after a second essentially normal division of the nuclei. There result, in that case, four sister-cells instead of the usual two.

Shortly before their separation, the chromosomes lie together in pairs, always one in the paternal pronucleus united with the corresponding thread of the maternal pronucleus. They are placed lengthwise side by side. Hence the separation evidently occurs by a longitudinal line, and, in by far the greatest number of cases, this so-called longitudinal splitting of the chromosome-pairs has been observed in the origination of the prouclei. It is true that this does not always succeed at a first glance, and it is right here that the differences of opinion between different investigators have blurred the picture for a long

time. But gradually it was discovered that there are a number of secondary details which may obscure the main features, and we owe it chiefly to Strasburger that the latter stand out clearly in the plant-kingdom. In the animal kingdom, however, there is still a series of cases which do not follow this rule, and where the chromosomes of the pronuclei are not placed lengthwise side by side at the moment of separation, but are connected at one end. Hence the separation here takes the form of a transverse division. Some insects and fresh-water crabs, some molluscs and worms offer the best known instances, but according to the most recent studies of de Sinéty, Cannon, and others, the assumption gains ground that here too the microscopic pictures, on closer observation, disclose a better fitting into the otherwise general scheme. It is also possible that, after the longitudinal splitting, the nuclear threads still remain connected for a while by their ends, before they finally separate.

The male and the female sexual cells usually originate in separate organs, frequently on special individuals. This goes to show that, at their origination from the body-cells, the paternal pronuclei do not become sperms and the maternal ones egg-cells. On the contrary, the two pronuclei of a mother-cell in the ovary can become egg-cells, and the two pronuclei of a pollen mother-cell can both give rise, by further splitting, to the formation of spermatozoids. Accordingly, one-half of the forming sperms gets paternal or now grand-paternal pronuclei, and the other half grand-maternal. The same is true of the egg-cells, and this holds good in spite of the circumstance that, in consequence of the crowded condition of the ovaries, the larger part of the female cells has regu-

larly to be sacrificed every time.[2] Therefore fertilization may result in offspring with pronuclei from the grandfather or grandmother only, or from both. This circumstance may not be without significance in considering the resemblance between grandparents and grandchildren among men.

But it is not by any means decisive; daily experience teaches that not only in a part of the progeny, but doubtless in all the offspring, there may be an admixture of the characters of the grand-parents also. This indicates that the separation of the pronuclei is not of as simple a nature as the microscopic pictures might lead one to believe. Another process, which, until now, has defied detection, must take place, probably in the smallest, but to us invisible granules of the nuclear threads. That this is the case we learn especially from the processes in hybrids and their propagation. Here, splittings and new combinations of the characteristics of the grand-parents occur in apparently incalculable numbers, and here it is distinctly seen that the pronuclei do not separate without a lasting reciprocal influence.

We shall first try to get a conception of this influence, for the facts concerning hybridization are rather involved; they can be most clearly explained by means of such a hypothetical conception. We shall accordingly assume a mutual influence as an established fact, and inquire how this can take place.

First of all it is clear that it must be finished before the separation of the pronuclei. Once they are apart all intimate relation between them ceases. They go their separate ways, each living for itself. Only in the double

[2]The reference is to the resorption of the sister-cells (when such occur) of the embryo-sac mother-cell. *Tr.*

nuclei do the paternal and the maternal pronuclei lie so close together that their individual parts can exercise an influence on each other.

We have further seen that, during the life of a double nucleus, throughout the successive cell-divisions, from the origination of the germ to the complete formation of the offspring, the contact of the pronuclei becomes gradually more intimate. Before the first cell division they are, as a rule, still visibly separated; soon afterwards the border-line begins to look more indistinct, and, shortly before the formation of the sexual cells, the double nature is disclosed with certainty only in the rarest cases by special structural relations. It is, therefore, clear that their opportunity for mutual influence gradually increases during somatic life. Perhaps it first occurs only at the end, possibly even, only at the moment immediately preceding their separation. A decision on this point has not yet been reached.[4] But the above-mentioned vegetative splittings of hybrids indicate that the process is deferred as long as possible. It also seems simpler to assume that it occurs only in those cells which actually lead to the formation of sexual cells, because in the leaves, bark, and other vegetative parts of the body, it would evidently be without significance.

We therefore imagine the mutual influence to be exercised towards the end, or even at the very last moment before the separation of the pronuclei. In the first case

[4]More recent investigations indicate that the fusion of the male and female chromatin elements is completed during the stage known as *"synapsis,"* which immediately precedes the reduction-division, or heterotypic nuclear division, referred to above. During synapsis the chromatin is aggregated into a compact mass within the nuclear cavity. *Tr.*

it could extend over a long time; in the latter it must take place suddenly. In the first case the individual parts of the nuclear threads could be mated one by one; in the latter this would have to take place everywhere simultaneously.

How this process comes about is self-evident when we assume special units, special granules in the nuclear threads, for the visible characters of the organisms. There must be as many units in the nucleus, as a plant or animal possesses individual characters. And this, of course, is the rule for both pronuclei. In the condition of the short and thick chromosomes these units lie crowded together. This is a definite stage in cell-division; the units, at least those of the interior of the group, remain in a condition of enforced rest. But as soon as cell-division is completed, the nuclear threads stretch; they become quite long and thin, and indeed so long that a large part, perhaps most of them, possibly all of them, come to the surface. At least stretched out in a row in this way, the granules must then be arranged one after another, perhaps in the threads themselves, perhaps in their finest ramifications. Now they become active, and if, at this time, nuclear threads of the paternal and the maternal pronuclei lie together in pairs, every granule can enter into communion with its corresponding unit in the other pronucleus.

There is no reason to assume that the exceedingly fine structure of the nuclei, which is so strikingly to the purpose and yet so simple, should be limited to what is visible to us at present. On the contrary everything points to the probability that, in the internal structure also of the nuclear threads this same serviceable rule must prevail. The whole complicated process of nuclear division has for its object the division of the two pronuclei in such a

way, that their daughter-nuclei will share alike in the hereditary characters that are present. The lengthening of the nuclear threads at the close of division, their so frequent ramification, and the seemingly irregular intertwining of their parts, evidently indicates the possibility of a domination of the cell-life by the bearers of the inheritable qualities. These must impress their character on the surrounding protoplasm either dynamically or, as I have assumed in my *Intracellulare Pangenesis,* through a giving out of material particles to the surrounding protoplasm, and thus promote growth and development, in the prescribed direction, into the specific form of the species to which the organism belongs.

This secretion of material chromatin particles from the nuclei was recently demonstrated by Conklin in *Crepidula.*[5] In this way considerable quantities of chromatin, and therefore probably of pangens also, are transferred into the somatic protoplasm.

Thus we consider that the structure of the nuclear threads is such that it not only makes possible, but regulates and dominates the relations of the two pronuclei. In an ordinary animal, or in a plant which is not a hybrid, both pronuclei possess the same units, only with a somewhat unlike degree of development. We assume, therefore, that the cooperation comes about in such a way that the individual units in the stretched threads lie in the same numerical order. Then, when the threads are closely appressed lengthwise, in pairs, we can imagine that all the like units of the two pronuclei lie opposite each other. And this is obviously the simplest assumption for a mutual influence.

[5]Strasburger failed to find any direct evidence of such a transfer of particles in plants. Cf. the Translator's Preface, p. viii. *Tr.*

If every unit, that is, every inner character or every material bearer of an external peculiarity, forms an entity in each pronucleus, and if the two like units lie opposite each other at any given moment, we may assume a simple exchange of them. Not of all (for that would only make the paternal pronucleus into a maternal one), but of a larger, or even only a smaller part. How many and which, may then simply be left to chance. In this way all kinds of new combinations of paternal and maternal units may occur in the two pronuclei, and when these separate at the formation of the sexual cells, each of them will harbor in part paternal, in part maternal units. These combinations must be governed by the laws of probability, and from these, calculations may be derived, which may lead to the explanation of the relations of affinity between the children and their parents, the grandchildren and their grand-parents. On the other hand a comparison of the results of this calculation and of direct observation will form the best, and for the time being, the only possible means for a decision as to the correctness of our supposition.

The mutual influence of the two pronuclei shortly before their separation is therefore brought about, according to our view, by an exchange of units. Every unit can be exchanged only for a like one, which means for one which, in the other pronucleus, represents the same hereditary character. This rule appears to me to be unavoidable and really self-evident. For the children must inherit all specific characters from their parents, and they must also transmit all of them to their own progeny. This exchange must hence be accomplished in such a way that every pronucleus retains the entire series of units of all the specific characters, and this result can evidently

be obtained only when the interchange is limited to like units.

We distinguish here specific characteristics from individual features. The units in the hereditary substance of the nuclear thread compose the former. Every species has an often exceedingly large and yet definite and invariable number of them. The sum total of these units forms that which distinguishes any given species from all others, even from its nearest allies. A complete diagnosis of a species would have to embrace all of these characteristics, and therewith all the material bearers underlying them.

The individual features, that is, the differences between the individuals within the species, and not only of the systematic but of the so-called elementary species, are of quite another nature. It is true that they are, in a way, hereditary, but with that they are subject to constant changes. The average stature of man remains the same in the course of centuries, for the same race (elementary species), but the individual stature changes constantly from one individual to another. In the somatic cells of man the bearers of the stature of the father lie opposite those of the mother. At the moment of exchange these are mutually transferred, and the sexual cells receive partly one, partly the other stature, but this in the most various combinations with the other characters. Thus one might continue. Every visible quality, every trait of character is to be found in all individuals, only in some they are strongly developed and prominent, in others weak and recessive. Ordinary observation takes more interest in differences than in similarities, and for this reason the former are designated by contrasting expressions, as large and small, strong and weak, forward and

modest. But these are, in each instance, only degrees of the same hereditary characteristic, or the same trait of character. And such more or less differing stages of development of the same inner units we represent to ourselves as the entities which are exchanged by the nuclear threads.

Individual differences are thus not included in the type of the species. They form deviations from this type, and are conditioned by causes which were formerly generally described as conditions of nutrition, but now more frequently as environment. Under these influences every character can develop more or less strongly than the average type. And the environment, provided it remains constant during the entire period of development, must affect all the unfolding characters in the same way. If it is favorable it furthers all parts of the body and all mental gifts, if it is unfavorable it has the opposite effect on all of them. Not, by any means, to the same degree upon all of them: that does not depend upon the environment but upon the units themselves; this, however, can not lead to essential differences between separate individuals. But our supposition of such a uniform environment would probably be met with only in the rarest of cases. And, as soon as it changed, it would influence one individual differently from the others. Moreover the characters do not unfold simultaneously, but successively, the higher ones for the most part later than the lower ones, mental characters later than those of the body, the reason later than the memory. And all those wheels work into each other so that small deviations will rather tend to become greater than to be equalized. Though children of the same parents but of different age might, during their entire youth, live under the same circum-

stances, they will yet react differently to them. This also holds true for plants where, in the same bed, a delay of only one day in germinating will, according to the weather, lead either to equal or to quite surprising differences in size and qualities.

If favorable and unfavorable conditions of life alternate during the individual development, and if they strike a group of individuals sprung from like seeds at different periods of their growth, quite a considerable degree of individual differences must thereby result.

These differences play in nature the same rôle as in human society. One is adapted for this kind of task, the other for that. With men it is the duty of every one to develop his own talents to the best of his ability, and to render as favorable as possible the circumstances for the most perfect development of his children. The highest efficiency of society in general demands of each the strongest effort in the direction of his most favorable talents. To ascertain this direction ought to be one of the chief aims of education and instruction. In animals and plants this highest efficiency can obviously not be achieved in the same way. And especially are the conditions different for plants, which are tied for life to the place where they germinated. Here, as is well known, nature is assisted by the astonishingly great number of seeds; she sows so many in every individual spot that only the best, that is, the individuals best adapted for the given locality, need retain life. But, by sacrificing countless seeds, she also accomplishes here that adaptation of the individual specimens which is the condition for the complete unfolding of their abilities and advantages.

Very great weight is therefore given to individual differences in the life of the entire species. The greater

they are, the greater the power of adaptation, the greater the chance of victory.

And in this I see the significance of sexual reproduction. It mixes the potentialities that have developed in the single individuals in the most complete manner imaginable; it achieves, at one stroke, all possible combinations. It cancels, as Johannsen expresses it, the previous correlations. Asexual propagation confers a certain degree of variability, and this may be quite sufficient in many cases, especially in the case of a low organization or of quite special adaptation, as in many parasitic and saprophytic organisms. Under such conditions the variability remains, in a certain sense limited, more or less one-sided, because every individual is the result of the varying, but, on the whole, one-sided environment in which his progenitors existed. Only an exchange of qualities can help to overcome this one-sidedness; only this can cause all the combinations to arise which are demanded by the varying environments. If we assume that the bearers of the individual characters are, as a rule, independent of each other during their exchange, and also that the latter is ruled by chance, two pairs of characteristics would directly result in four, three in eight, four in sixteen combinations. The sum total of the points of difference of two parents must therefore give rise to such an incredible number of possibilities that no struggle for existence, no annual rejection of hundreds and thousands of germs could demand a richer material.

Hence sexual reproduction brings individual variability to its highest point. It produces a material that corresponds to almost any environment. It is the principal condition for the greatest efficiency of cooperation, be it by a selection as free as possible of the line of develop-

ment for the single individuals, or by a sacrifice of all the individuals that do not quite meet all the requirements.

This service of sexual reproduction is evidently not limited to a single generation. It exercises its influence throughout successive generations, and it is probably indifferent whether the effect follows directly, or whether it manifests itself in the course of time. Even without that, the complete utilization of all given possibilities requires, as a rule, more individual beings than are born in a single generation. And with this, the otherwise strange fact is explained, that the exchange of the units does not immediately follow fertilization, but only takes place a short time before the succeeding period of fertilization. But obviously an exchange, ruled by laws of chance, could not benefit a given isolated individual or, more correctly speaking, it would most likely, just as frequently be harmful as useful. It can only be of use in connection with an increase in the number of individuals, for it is its task to bring about as great a variety as possible, and with that, the highest possible prospect for the required quantity of superior specimens. At the moment when the production of the sexual cells begins, in such enormous numbers, it also finds the best opportunity for fulfilling its task.

Thus, sexual reproduction has only a subordinate significance for the children, while for the grandchildren it is of the utmost importance, because only for them does the urn mix up all its lots.

The same laws that govern normal fertilization, are, of course, valid for hybrids also. There cannot be special biological laws for them, because they are only derived phenomena, deviations from the normal. Now the question is, to which results, departing from the rule, will the common laws lead in these special cases. And with this

it is clear that the phenomena must keep nearer to the normal the less the deviation is from the type.

This type is conditioned by the fact that the two organisms that fertilize each other belong to the same small or elementary species. They have then, on the whole, the same characters, even if these are, according to their environment in various degrees of development. There are no differences among them independent of this, at least if we consider the cumulative effect of uniform influences in the course of several generations.

As soon as such independent differences occur, and as soon therefore as there are present constant contrasts, which are retained in the sequence of generations and cannot be blended by environment, we call the sexual union of two individuals a crossing or a hybridization. If the contrasts are slight, we call the two races varieties, if they are greater, they assume the rank of species. The crossing of varieties keeps quite near to normal fertilization; that of the species deviates the more the slighter the relationship between them. The crossing of varieties forms a type complete in itself, that of the species forms a series which descends from almost normal processes, by gradual progress, to a complete reciprocal sterility. The variety-hybrids are fertile like their parents, but in the species-hybrids the diminished fertility indicates abnormal phenomena either in fertilization or in the exchange of the units.

We must therefore discuss these two groups separately, and we shall begin with the varieties.

In daily life and in horticulture, any thing that deviates from the normal is called a variety. Even the new forms obtained by crossing are quite commonly counted among the varities. In science, therefore, the word would really

be useless. Nevertheless it has been retained and its meaning has been gradually limited. Especially in describing horticultural plants the conception is sufficiently restricted by excluding on the one hand the hybrids, on the other hand the improved races obtained by selection, and finally the so-called elementary species that, taken together, form our ordinary species.

Upon reviewing the cases that are left, two types can be plainly distinguished, the constant and the inconstant varieties. The former are not inferior to true species in point of constancy. Their characters vary, in the single individuals, around a mean, but in the main not more so than the corresponding characteristic of the species. From this they are separated by a decided chasm. In pure fertilization they never bridge this chasm, or at least, extremely rarely, but in crossing they revert very easily to the species. It is this very reversion that stamps them varieties, and when the crossing is not artificial but natural, brought about by insects, it escapes observation, and only the fact of the reversion strikes the gardener.

These constant varieties are, as a rule, distinguished from the species to which they belong, by lacking some striking quality that adorns the latter. Most frequently it is the coloring of the flower or, in the case of flowers with combined colors, as in the yellow and red tulips, one of the individual colors, that is wanting. Often they lack hairs or thorns, very frequently the development of the blade is arrested, and split leaves originate. In all of these cases there is no ground for the opinion that the failure of the visible character means also the loss of the respective unit. Rather does everything point to the fact that the unit has simply become inactive, that it is in a state of rest, or as it is usually expressed, that it has be-

come latent. Especially the reversions, which in individual specimens of such varieties are, at times, quite common phenomena, betray this latent presence.

Inconstant varieties are distinguished by a strikingly high variability, by an exceedingly great range of departure from the norm. But here we encounter the double meaning of the designation inconstancy. On the one hand the word means a certain relatively great richness of individual forms, on the other hand it relates to differences between the parents and the progeny. In choosing from an inconstant variety a single individual, and sowing its seed, after pure fertilization, the whole play of forms of the variety can be found again in the children,—hence a palpable proof of the inconstancy. But, on choosing several individuals, and on sowing their seeds separately, each of them will produce almost the same series of forms. The whole group is transmitted from year to year, and does not change. The variety has a definite circle of forms in which the descendants of every specimen choose freely their place, but they do not go outside the circle. The limits are constant, and remain so in the course of generations; within the limits, however, a motley variety prevails.

Such is the concept of plants with variegated leaves, of double and striped flowers, and many other most highly variable garden-plants. The new character is not based here on the loss or the latency of some characteristic of the species. Indeed, on the contrary, it is usually a peculiarity which is already present in the species itself, or at least in one of its races, in a latent state. Especially do variegated leaves occur, not so very infrequently, on otherwise green plants, and the same is true of stamens with petal-like broadenings. The relation of the incon-

stant varieties to the species from which they are derived, is therefore quite different from that of the constant varieties.

Nevertheless, the two crossings behave in the same manner in regard to their mother-species. From the latter they are distinguished, for the most part, only in one point, though sometimes in several. But we have always to deal with the distinction between active as contrasted with latent, be it that the given character is active in the variety and latent in the mother-species, or latent in the former and active in the species itself.

If to this we apply the conception of the arrangement of the units in rows on the nuclear threads, as explained above, it is quite evident that everything will follow exactly the same course as in normal fertilization. Every unit in the paternal pronucleus corresponds to the representative of the same peculiarity in the maternal one. The nuclear threads fit as nicely into each other as in a pure species, and all the units which do not directly bring about the point of difference behave quite normally. Cooperation in vegetative life, and exchange during the formation of the sexual cells need not be disturbed. We may confine our whole consideration to the point of difference, and we shall select, for the purpose, as simple an illustration as possible, one in which there is only one difference between the species and the variety, for example, the color of the flower.

The material bearer of the color-characteristic is situated in the mother-species so that it can display its full activity while in the variety it is unable to do so. If the paternal and maternal nuclear threads of the hybrid come into contact for the purpose of exchange, and with the same sequence of units in both, the active unit of coloring

matter naturally gets the equivalent inactive unit as an antagonist. With this it must therefore be exchanged. We assume that in this the latent condition is without significance, that hence the exchange comes about in the same manner as in normal fertilization.

Over this, however, the crossings of varieties have the great advantage that there the origin of the characteristic in question can always be clearly and positively recognized. Both units of a pair of antagonists are otherwise distinguished only by a more or less of development, here by a sharp contrast. And for this reason it is experimentally much easier to discover the laws with varieties than with purely individual differences.

In doing this, two points have to be distinguished; the consequences of fertilization and the consequences of the exchange of the units. The former we see in the hybrid itself, the latter in its descendants.[6] And since fertilization and exchange are two such fundamentally different things, we must not wonder that there exist such decided differences between a hybrid and its descendants. These differences show themselves essentially by the fact that the hybrids of a mother-species with a variety of the same are alike, even if they are obtained in great numbers, while their descendants always display a certain variety.

Let us first consider the first generation of variety-hybrids. How do the two pronuclei, notwithstanding

[6]In the fertilized egg, resulting from the crossing, the chromatin from the male and female parents is not completely fused. As pointed out in a preceding footnote (p. 240), this fusion, called synapsis, occurs as almost the last step preceding the nuclear and cell-divisions that give rise to the reproductive cells. The characters of the first hybrid generation are a result of fertilization. Following synapsis, the pure bred offspring of this generation differ from their parents and also among themselves. *Tr.*

their inequality, cooperate in order to regulate the evolution? This question amounts to the same as asking, what is the sum of the influence of an active and a latent unit? At first glance one would expect that this influence would correspond to half the value of a pair composed of two active units. Previously this opinion was rather generally accepted, and there was an inclination to regard plants with intermediate characters as hybrids. Especially many plants with pale red or pale blue flowers were regarded as such. But the experience of later years has decided differently.

Variety-hybrids generally bear the characteristic of the species, sometimes fully developed, sometimes more or less weakened, but this for the most part only so little that superficial observation sees no difference. An active and a latent unit are not essentially different in their cooperation from two active ones; a fact which may probably be best explained by the assumption that two cannot accomplish more than one already does. This conception finds a very strong support in the results of the most recent investigations by Boveri on dispermia, which we have already partly discussed. By fertilizing one egg with two spermatozoa the composition of the structure of the nuclear threads can be altered in different ways, for instance, in such a manner that in one nucleus there lie not two, but three pieces of any one of its chromosomes. It might then be expected that the given characters would be very strongly developed, to about one and one-half of their intensity. But, as far as can be judged from Boveri's experiments, this is not the case, and the influence of the three equivalent units is not noticeably greater than that of two.

We come now to the progeny of hybrids, and we, of

course, presuppose self-fertilization. At the formation of the sexual cells the two pronuclei separate; this happens at the origination of the egg-cells as well as of the sperms. Through exchange, the active units of our differing pair combine partly with new units of the other pairs, and thereby new combinations originate as in ordinary fertilization. But if we consider only the differing pair, exactly one-half of the egg-cells must obviously have the paternal, and the other half the maternal character. Or, in other words, in one-half of the egg-cells the given character occurs in the active, in the other in the latent state. Exactly the same is true of the male sexual cells, the sperms, in animals as well as in plants, and independently from the circumstance that in the higher plants the sperm-cells are conducted to the egg-cells in the pollen-tube.

The male sexual products of a hybrid are therefore unlike each other, and the same holds true of the female. In the simplest case selected both groups consist of two types, in the more complicated cases this number will obviously become greater. The paternal and maternal factors of the hybrid become, in its progeny, grandpaternal and grandmaternal. Hence, in regard to the point of difference, one-half of its egg-cells and one-half of its sperm-cells have grandpaternal factors, while the other halves possess grandmaternal ones.

By means of this principle the composition of the progeny in the simple as well as in the complex cases, and for constant as well as for inconstant varieties can be calculated. Thus we obtain the formulæ which are now universally known as Mendel's law.

They indicate, for any given number of points of difference between two parents, how many children correspond to every individual combination of the respective

character. And, on the whole, experience has so far proven the reliabilty of these formulæ for animals as well as for plants.

It would be too great a digression to consider here the formulæ themselves. We shall therefore leave the field of the variety-hybrids, and turn to the hybrids between different species, especially between allied elementary species.

In order to understand these we must get a clear idea of the nature of the points of difference in this case, or in other words, what is meant by relationship. Species originate from each other in a progressive way. The number of the units in lower organisms is evidently only small, and must gradually increase with progressing organization. Every newly arising species contains at least one more than the form from which it has arisen. Only in this way can one imagine the progress of the entire plant and animal world.[7]

It is indeed questionable whether the acquisition of a single new unit, the increasing by one unit of the entire stock, amounting to hundreds and thousands, would be sufficient to make the impression of progress on us. The

[7]A quite different hypothesis is thinkable, as, for example, that suggested by G. H. Shull, "The Significance of Latent Characters," *Science* N. S., **25**: 792. 1907.

"All the visible variations of the present plant and animal world were once involved in some generalized form or forms, and the process of differentiation pictures itself to us as a true process of evolution brought about by the change of individual character-determining units from a dominant to a recessive state. This conception results in an interesting paradox, namely the production of a new character by the loss of an old unit."

This hypothesis, however, as de Vries has pointed out, seems too much like a revival of the old evolution theory as opposed to epigenesis. *Tr.*

difference will in most cases be too slight. Only when two or three or more units have been added successively to those already present, will we recognize an increase in the degree of organization.

The progress of every individual species can apparently take different directions. In some genera there are species so typical that they may be regarded as the common origin of the others. Where these are lacking it is manifest that the systematic relations are still too incompletely known to us, or that the given forms have died out. Every species can therefore be compared with its own ancestors or with other descendants of the same ancestors.

This consideration leads us to the recognition of two different types of relationship, and therewith also of two groups of crossings between allied species, which have to be kept absolutely apart. One of them we shall call the avunculary, the other the collateral. In the first case we cross a form with an "avunculus" or ancestor in the direct line, in the latter case with one of its lateral relatives. Obviously the first relation is very simple while the latter is more complicated.

Every character and every unit corresponding to it, which in a crossing is present in one species and lacking in the older one, forms a special point of difference. Hence the simplest case is the one in which there is only one such difference between the two parents of a cross. But generally several of them exist.

Now in such a cross, the differing factors evidently do not find any antagonists in the sexual cells of the other parent. When, during fertilization, the pronuclei unite into a double nucleus, all the other units are present in pairs. Not so the differing ones; they lie unpaired in the hybrid.

If we apply this reasoning to our conception of the arrangement of the units in rows on the nuclear threads, the immediate result would be that their cooperation must be disturbed. The threads no longer fit, neither during fertilization and in vegetative life, nor later when the units are exchanged before the formation of the sexual cells.

If we imagine two corresponding chromosomes of the two pronuclei placed exactly side by side, and in such a way that every unit of the one has the corresponding unit of the other for a neighbor, this will occur in a species-cross only as far as the point of difference. Here one nuclear thread has one unit more than the other. The latter has, so to say, a gap.

The greater the number of points of difference, the more numerous are these gaps, and the more will the cooperation of the two nuclei be interferred with. And this must diminish the vitality of the germ or at least the normal development of all characters.

If the differences between the two parents are too numerous, a crossing, as is well known, remains quite without effect. Crossings between species belonging to different genera succeed in very rare cases only, indeed within by far the most genera even the ordinary systematic species are not fertile when united. Genera such as *Nicotiana, Dianthus, Salix,* and others, which are rich in hybrids, are, as a rule the very ones in which the species are exceedingly closely related to each other.

Even if the agreement of two species is great enough for mutual fertilization, the life of the hybrid is by no means assured thereby. Some of them die as seeds within the unripe fruit, as has been specially described by Strasburger for the hybrid seeds of *Orchis Morio* after fertilization with *O. fusca.*

Others become young plantlets, but are too weak to develop any further, and perish during the first weeks after germination, as I have frequently seen, for example after crossings of *Oenothera Lamarckiana* and *O. muricata.* Or only the most vigorous individuals continue to grow, while the weaker ones perish, and this, in diocious plants, sometimes results in the male seedlings perishing while some of the more vigorous female ones develop flowers, as Wichura observed in several willows. Finally there might originate hybrids that grow vigorously, but do not flower at all or only incompletely, or begin too late to do so. There is a whole series of cases between the unsuccessful crossings and the development of hybrids into adult plants. And on the whole this series runs parallel with the increasing systematic relationship.

If the hybrid has succeeded in reaching the period of flowering, that is, the period of the formation of the sexual cells, a new difficulty arises at the moment of the exchange of the units. Whereas, up to that time, the cooperation of the two pronuclei was more or less disturbed, now the gaps become very important. Hence the quite common phenomenon that the production of egg- and sperm-cells fails more or less completely, that the hybrids either produce no ovules that are capable of being fertilized, or no good pollen, or neither. They are more or less or even completely sterile. They either form no seed at all, or only an insufficient quantity. Only where the differences between the parents are quite small, does one succeed in harvesting any seed, and even here frequently only a little.

How the unpaired characters behave during the exchange, when they are not numerous enough to make a failure of the entire process, is at present unknown. Ex-

perience teaches, however, that in these cases the descendants of the hybrids do not display that multifariousness of type, nor those splittings that are characteristic of variety-hybrids. They usually all resemble each other and their parents, the original hybrids, and this constancy persists through the course of generations. Accordingly there originate races of hybrids which, apart from their possibly diminished fertility, can hardly be distinguished from true species. Sometimes they are found wild, as for example a hybrid race between two Alpine roses and other races of the kind in the genera *Anemone, Salvia, Nymphaea,* etc. Sometimes they have been obtained artificially or have accidentally originated in the gardens. The genus *Oenothera* is exceptionally rich in such hybrid races, especially in the sub-genus of the common evening-primroses, *Onagra.* Very frequently such hybrids are simply described as species, on the one hand because they can be reproduced, without deviation, from seeds, and on the other hand because systematic works frequently do not sufficiently consider the elementary species. The distinguishing of the latter from hybrid races is frequently by no means easy.

The purpose of my explanations compels me to restrict myself to simple and clear cases. In nature these occur relatively rarely, and the individual elements of the phenomena are usually commingled in most motley variety. By far the greater number of crossings take place between parents whose mutual relations do not wholly fit either the one or the other concept, but where the characteristics of the different types of hybrids are intermingled. I cannot consider these cases here; they are of too complicated a nature for an address.

Only one point I wish to touch upon. In the preceding

pages I have always taken for granted that the species and varieties are in their ordinary and unchanging state. But this is by no means always the case. The origination of new species and varieties demands that their immutability should not be absolute, or at least should be suspended from time to time. Experience confirms this by showing that there are periods in the life of species, during which they are, so to speak, especially inclined to produce new types. At that time they produce the new varieties and species, not only once but repeatedly, and not only a single one, but frequently a considerable number. Genera rich in species, such as the pansies and the rock-roses,[7] are the remains of such periods of variability, and everywhere in nature we meet with similar ones. In garden-plants we see, from time to time, periods during which certain varieties occur by preference, as the double dahlia of about the middle of the last century, the forms of tomatoes in recent decades, and numerous other instances teach us. On its first appearance the gardeners call the new form a conquest, the later appearances are only repetitions, and are therefore of only very secondary practical value.

The power of reproducing one or more new species indicates a condition of unstable equilibrium of the given internal units. In the nuclei the new characteristic is already invisibly present, but inactive. Certain causes, unknown to us, can transform this into a permanent condition. This state of unstable equilibrium may be maintained in the great majority of individuals, through a series of generations, as is the case with my *Oenotheras*. But from time to time, sometimes in individual cases every year, there is a shock, and the equilibrium becomes

[7] *Sonnenröschen (Helianthemum). Tr.*

stable. The given individuals overstep their bounds, abandon the earlier type, and form a new species.

It is evident that in crossings such unstable units will behave differently from normal, stable ones. Their chance of becoming stable is evidently considerable, owing to the phenomena of fertilization and the exchange of units. In this way constant races originate, at least in the genus *Oenothera,* and this, on the one hand, with the respective characteristic in an unstable condition, or in other words, in a state of mutability; and on the other hand with stable equilibrium corresponding to a new species. But researches in this field are only in their beginning, and do not yet permit of a detailed analysis. Besides they represent, for the present, a case in themselves.

* * *

In conclusion, on reviewing the course of our deductions, we see that hybrids follow normal fertilization quite closely, the more completely the less numerous and the less pronounced the points of difference between the parents of the crossing. If these are of such a kind that the number of units in one parent is different from that in the other, disturbances take place which, if of lesser influence, diminish the fertility of the hybrids, and if of greater significance, affect their own power of development, or even make the crossing a failure. If these units are present in equal numbers on both sides, and if the differences are limited to latency in one parent and activity in the other, the normal process is not at all disturbed, but striking phenomena occur, which find their explanation in the peculiar manner in which the parental inheritances co-operate in the hybrid and in the formation of its sexual cells.

This co-operation is reflected in the life of the nuclei.

In fertilization the nuclei of father and mother simply touch each other. In the course of development the contact becomes gradually closer, bringing their equivalent elements as near to each other as possible, in such a way that the latter finally all lie side by side in pairs. But the pronuclei by no means lose their independence thereby, and for the purpose of every nuclear division they separate their component parts more or less distinctly. Shortly before their separation, their leave-taking, they are still the same as before. But now they exchange their individual units, and thus cause the creation of those countless combinations of characters, of which nature is in need in order to make species as plastic as possible, and to empower them to adapt themselves in the highest degree to their ever changing environment.

This increase of variability and of the power of individual adaptation is the essential purpose of sexual reproduction. It can be attained only by a mutual combination in all conceivable forms of the peculiarities developed in different individuals in different directions and degrees. To this end the pronuclei mutually exchange their units from time to time, and by assuming, on the ground of experiments with hybrids, that this takes place, on the whole, according to the laws of chance, that is, according to the theory of probability, we have gained a basis which allows us to probe to its very bottom this most significant and mysterious process.

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