

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,<sup>1</sup> 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

<sup>1</sup>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 Oscillariæ are many-celled threads, but all the cells are alike, every one of them is equally able to propagate the species. Götte 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.<sup>2</sup> 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

<sup>2</sup>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,<sup>3</sup> 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-

<sup>3</sup>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.<sup>4</sup>

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,<sup>5</sup> 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,<sup>6</sup> 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<sup>7</sup> 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

<sup>4</sup>Weismann, A. Zur Frage nach der Unsterblichkeit der Einzellig-en. *Biolog. Centr.* 4: 683.

<sup>5</sup>*Loc. cit.* p. 685.

<sup>6</sup>Weismann, A. *Die Kontinuität des Keimplasmas.* p. 11.

<sup>7</sup>*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.<sup>8</sup> 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.<sup>9</sup> 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,<sup>10</sup> distinct powers which need not necessarily run parallel. The transmission is accomplished invisibly, in the germ-tracks,

<sup>8</sup>Weismann, A. *Ueber die Vererbung*. p. 56.

<sup>9</sup>Vilmorin, L. L. de. *Notices sur l'amélioration des plantes par le semis*. Nouvelle Edition. p. 44. 1886.

<sup>10</sup>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 on 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 polyyps 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.<sup>11</sup> 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,<sup>12</sup> is for us only an extreme one in the rich abundance of examples.

<sup>11</sup>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.

<sup>12</sup>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 through 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.<sup>13</sup> The line of demarcation between the secondary germ-tracks and the

<sup>13</sup>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*.<sup>14</sup> 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.<sup>15</sup> 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.

<sup>14</sup>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. *Onderzoekingen over adventieve knoppen.* Amsterdam, 1885.

<sup>15</sup>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,<sup>16</sup> 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,<sup>17</sup> 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

<sup>16</sup>Darwin, C. *The Variation of Animals and Plants*. 2: 362. New York. 1900.

<sup>17</sup>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."<sup>18</sup> 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

<sup>18</sup>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.<sup>19</sup> This becomes clearest to us when we try to define the limit exactly. We shall find,

<sup>19</sup>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 adaptations, 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.<sup>20</sup> 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

<sup>20</sup>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 carnososa* keep alive, in this way, for two years, without forming buds; some are said to have existed for seven years in this condition.<sup>21</sup> 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-*

<sup>21</sup>I have since succeeded in keeping a rooted leaf of *Hoya carnososa* 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,<sup>22</sup> and forms, to a large extent, the basis for his theory of the germ-plasm.

<sup>22</sup>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,<sup>23</sup> 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 germ-plasm 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 germ-plasm 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.

<sup>23</sup>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 nucleoplasm.

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

#### § II. *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.<sup>24</sup> 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.<sup>25</sup> 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

<sup>24</sup>E. g. *Die Kontinuität des Keimplasmas*. p. 30.

<sup>25</sup>*Loc. cit.* p. 70.

is necessary for the functions of its descendents.<sup>26</sup> 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 pangensis, 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*,

<sup>26</sup>Cf. also Part I, Chapter III, § 6, p. 53.

published about ten years ago,<sup>27</sup> 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."<sup>28</sup>

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.

<sup>27</sup>Vol. I, Bonn, 1878; Vol. II, Bonn, 1884.

<sup>28</sup>*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.<sup>29</sup> And the more

<sup>29</sup>Zur Annahme einer Kontinuität des Keimplasmas. *Ber. Naturforsch. Ges. Freiburg*. 1: 10. 1886.

we study the cell-pedigrees of the plant kingdom, 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.<sup>80</sup> 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

<sup>80</sup>Beyerinck, M. W. Beobachtungen über die ersten Entwicklungsphasen einiger Cynipidengallen. *Veröffentlicht Kais. Akad. Wiss. Amsterdam*. 1882. The same, Die Galle von *Cecidomyia Poae*. *Bot. Zeit.* 43: 305, 321. 1885, and Ueber das *Cecidium* von *Nematus capreae*. *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.<sup>31</sup> 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.<sup>32</sup> The galls which the leaf-wasp *Nematus viminalis*, produces on the leaves of *Salix purpurea*, possess an exceeding vitality. At the be-

<sup>31</sup>*Bot. Zeit.* 1888. 1. c.

<sup>32</sup>*Bot. Zeit.* 46: 1, 17. 1888.

ginning of autumn, when left by their inhabitants, they are still quite turgescient. 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.

