CHAPTER VI

THE FORMATION OF GERM-CELLS

1. The Continuity of the Germ-plasm

If heredity depends on the presence of a substance, the germ-plasm, which causes the production of the new individual by directing the process of division in ontogeny, in the course of which it becomes changed in a regular manner, the question arises as to how unaltered germ-plasm can nevertheless reappear in the germ-cells of the new individual. The transmission of characters from parent to child can only depend on the germ-cell from which the offspring arises containing ids of germ-plasm precisely similar to those of the germ-cell from which the parent was developed. The germ-plasm, however, undergoes an enormous number of changes during the development of the ovum into the parent: how is it possible therefore that this substance can reappear in the germ-cells of this parent?

There are obviously two possible solutions of this problem. The changes which the germ-plasm undergoes during the construction of the body must either be of such a kind that they can take place in the reverse order when the idioplasm of all, or at least of a portion of, the somatic cells is re-transformed into the germ-plasm from which it was, in fact, *indirectly* derived; or, if such a reversal is impossible, the germ-plasm of the germ-cells must be handed on *directly* from parent to offspring. This latter hypothesis was suggested by me some years ago under the name of the *continuity of the germ-plasm*.* A third solution of the problem is impossible, for it is quite out of the question that the germ-plasm can be entirely formed anew.

The hypothesis of the continuity of the germ-plasm depends on the assumption of a contrast between the *somatic* and the *reproductive* cells, such as can be observed, in fact, in all multicellular plants and animals, from the most highly differentiated forms to the lowest heteroplastids amongst the colonial Algæ.

* 'Die Continuität des Keimplasma's als Grundlage einer Theorie der Vererbung,' Jena, 1885 (English translation, 2nd ed., p. 163).

I assume that germ-cells can only be formed in those parts of the body in which germ-plasm is present, and that the latter is derived directly, without undergoing any change, from that which existed in the parental germ-cell. Hence, according to my view, a portion of the germ-plasm contained in the nucleus of the egg-cell must remain unchanged during each ontogeny, and be supplied, as such, to certain series of cells in the developing body. This germ-plasm is in an *inactive* condition, so that it does not prevent the active idioplasm of each cell from impressing a specific character on the latter in a greater or less degree. It must, moreover, differ from ordinary idioplasm, inasmuch as the determinants it contains are kept closely together, and are not distributed in groups among the daughter-cells. This accessory germ-plasm is thus passed on in an unalterable condition through longer or shorter series of cells, until it ceases to be inactive in a certain group of cells, more or less remote from the egg-cell, and then impresses upon the particular cell the character of a germ-cell. The transmission of the germ-plasm from the ovum to the place of origin of the reproductive cells ('Keimstätte') takes place in a regular manner, through perfectly definite series of cells which I call *germ-tracks*. These are not actually recognisable, but if the pedigree of the cells in the embryogeny is known, they may be traced from their termination in the germ-cells backwards to the ovum.

This assumption is supported by the fact that a direct, or at any rate a very close, connection can be proved to exist, although only in rare instances, between the germ-cells of two consecutive generations. In the *Diptera* the first division of the egg-cell separates the nuclear material of the subsequent germ-cells of the embryo from that of the somatic-cells, so that in this case a direct continuity can be traced between the germ-plasm in the germ-cells of the parent and offspring.

The process in this case must certainly, however, be looked upon, not as a primary one which has been passed on unchanged from very ancient times, but as a special arrangement peculiar to this order of insects. It nevertheless proves the possibility of each generation of germ-cells being derived directly from the preceding one, and also that the germ-plasm which has been prevented from taking part in the construction of the somatic portion of the embryo is not required in this process.

We may next take the case of the embryogeny of the

Daphnidæ. In these animals the primary germ-cells become separated from the somatic cells in the first stages of the segmentation of the egg; and in *Sagitta* again, this separation takes place at the gastrula-stage. In Vertebrates this process occurs much later, although it always takes place within the first half of embryogeny; while in Hydroids — both in colonial and solitary forms — the germ-cells do not appear in the 'person' which is developed from the ovum at all, and only arise in a much later generation, which is produced from the first by continued budding. The same is true as regards the higher plants, in which the first shoot arising from the seed never contains germ-cells, or even cells which subsequently become differentiated into germ-cells. In all these last-mentioned cases the germ-cells are not present in the first person arising by embryogeny as special cells, but are only formed in much later cell-generations from the offspring of certain cells of which this first person was composed. These ancestors of the germ-cells cannot be recognised as such: they are somatic cells, — that is to say, they, like the numerous other somatic cells, take part in the construction of the body, and may be histologically differentiated in various degrees.

A series of organic species might therefore be formed in which the formation of the germ-cells begins at very different degrees of remoteness from the egg-cell. This would admit of the interpretation that the fertilised egg-cell of the earliest Metazoa first divided into two cells, one serving for the formation of the body (soma), and the other for that of the germ-cells; and that a shifting had occurred subsequently, owing to a separation of the material for both parts in the germ-plasm, so that the portion of the germ-plasm which remained unchanged was supplied in an inactive condition, in the form of accessory idioplasm, to one of the somatic halves of the egg-cell, and was transmitted by the latter to a somatic cell of the second, third, or fourth generation. The shifting of the process of separation into germ-cells and somatic cells finally reached its extreme limit, as in the case of the Hydroids, and the unchanged germ-plasm of the fertilised ovum then only led to the formation of germ-cells after passing through a long series of somatic cells.

These facts do not, however, as yet constitute an actual proof of the correctness of this interpretation: they might be taken as indicating that the series has been developed in the reverse direction, the late differentiation of the germ-cells being the primary condition and the earlier separation of the two parts then having arisen gradually in individual cases. There can hardly be any doubt, indeed, that the early differentiation of the germ-cells of the Diptera and Daphnidæ is of a secondary nature; and it will presently be shown that in the case of Hydroids such a shifting of the formative areas ('Bildungsstätte') of the germ-cells — *i.e.*, the fact of their earlier differentiation — can be actually proved. But the facts which have been stated still support the interpretation of them given above, in so far as they show that the germ-cells are by no means formed at the time and in the place where they are actually wanted, and that the time of their formation, in fact, varies very much, and must have been changed in the course of phylogeny. The direction in which this shifting originally took place — that is to say, whether it proceeded from the egg to the close of ontogeny or in the reverse direction — must be decided when our knowledge of the facts is more complete.

We might here lay stress on the fact that the destruction of the sexual glands in an animal, however low in the scale, is not followed by the formation of sexual cells in any other part of the body. Castration might be expected to have this effect if germ-cells could be formed from any young cells of the body. But just as in the case of any other highly specialised organs, such as the liver, kidneys, and central portions of the nervous system in Vertebrates, such a replacement never occurs. This fact is to be explained according to our present view by supposing that the formation of these latter organs anew is impossible, because the determinants necessary for such a development are not present in any other cells of the body. The same conclusion will, it seems to me, be inevitable in the case of the germ-cells; *the idioplasm necessary for the formation of germ-cells — i.e., germ-plasm — must be absent in these cases, and germ-plasm at any rate cannot be formed from somatic idioplasm.*

The case of the Hydroids * is probably still more convincing, for here a natural shifting of the place of origin of the germ-cells has actually taken place. As has already been mentioned, the germ-cells of Hydroids first arise very late in the life-cycle,

* Weismann, 'Die Enstehung der Sexualzellen bei den Hydromedusen,' Jena, 1883.

and hundreds or even thousands of cell-generations are passed through from the fertilised egg-cell onwards before they appear. In species which exhibit a complete alternation of generations, they are first formed in particular parts of the medusæ which have arisen from the polype-stock by budding — usually in the ectoderm of the manubrium. No trace of them is to be seen in

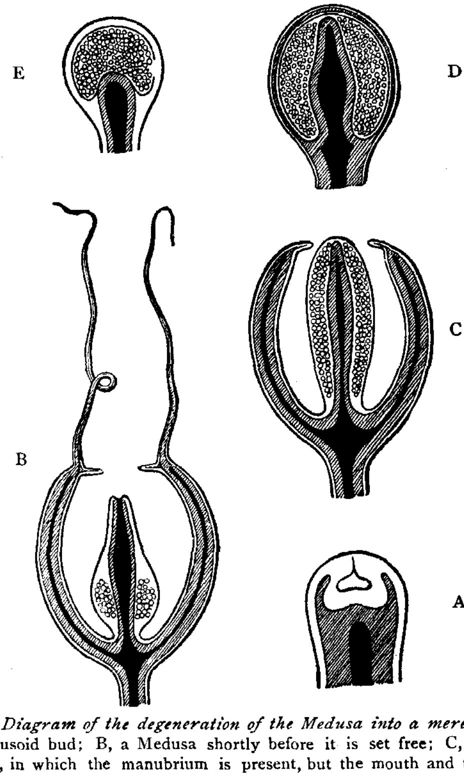

FIG. 12. — *Diagram of the degeneration of the Medusa into a mere gonophore.* A, Medusoid bud; B, a Medusa shortly before it is set free; C, degenerated Medusa, in which the manubrium is present, but the mouth and tentacles are wanting; D and E, further stages in degeneration. (From Hatschek's 'Lehrbuch der Zoologie.')

the young bud, and in many cases they only become differentiated from the other ectoderm-cells after the medusa has become detached from the stock, and has developed into an independent, free-swimming animal. Some of the ectoderm cells of the part in question then become transformed into egg- or sperm-cells.

In the case of certain species of polypes, free sexual medusæ were produced in the earlier period of the development of the species, but at the present day these do not become detached, but always remain attached to the stock: they thus no longer serve for the dispersal and ripening of the sexual products but only for their production and ripening. These species illustrate the different stages in the process of degeneration of the medusæ to mere gonophores, or sexual sacs. In some species the form of the medusa is completely retained in the sexual persons of the stock, only the eyes and marginal tentacles being absent; in others, the bell has become degenerated into a closed sac, the walls of which still retain the circular and radial canals; and in other species again, these canals have also disappeared, only the three characteristic layers of the medusa remaining, and even these have become so thin that their presence can only be detected in microscopic sections. Finally, these three layers also undergo degeneration, the wall then consisting of a single layer, so that the derivation of the sac from the bell of the medusa can only be proved indirectly. Throughout all these stages of degeneration, however, the ova or spermatozoa always ripen in the gonophores.

The behaviour of the germ-cells is the chief point of interest to us in the course of this process of degeneration. For the entire degeneration of the medusa proceeds from its germ-cells, and is due to the fact that *the development of the latter has gradually to be thrown back to earlier stages, so that the sexual elements are ripened more quickly*.

It will not be necessary to enter into the reasons for this hastening of the sexual maturity; it is sufficient to know that in some species in which the medusæ become detached, *e.g.*, *Podocoryne cornea*, the egg-cells are developed earlier than the medusæ in which they subsequently ripen, and in proportion as the degeneration of the medusa advances the place of origin of the germ-cells recedes more and more into the older and earlier formed parts of the stock. The advantage of this is, that the germ-cells develop earlier, and afterwards enter the germ-sacs in a riper stage: they thus reach maturity much more quickly.

The remarkable thing about this process is the fact that active migrations of the germ-cells take part in it. Originating in the ectoderm, these cells wander into the endoderm, and subsequently back again into the ectoderm; and this remarkable process occurs in a definitely prescribed and regular manner. In spite of the relegation of their place of origin to earlier persons of the stock, the germ-cells always originate from *the same layer of cells* as that from which they arose in the ancestors of the species. It may thus be said that they are developed ontogenetically from the ancestors of those cells from which they would have arisen if the polype stock still produced free medusæ; or, in other words, *they arise lower down on the germ-track at present than they did formerly*. Thus in *Hydractinia echinata*, for instance, the youngest egg-cells first become visible in the endoderm of certain polypes in the same regions from which gonophores (degenerate medusæ) subsequently bud out. The egg-cells then migrate into the latter, and enter the ectoderm of the manubrium as soon as it is formed; and in this way *they return to the old place of ripening, which in earlier times was also the place in which they were formed*. At the present day, however, the egg-cells only apparently originate in the endoderm of the polype: it can indeed be proved that they are derived from the ectoderm, but migrate into the endoderm while still in a very young condition, before they exhibit the definite character of egg-cells. They therefore originate in the same region in which at an earlier phyletic period the ectodermal layer of the manubrium of the medusa was developed; or, in other words, *the same ontogenetic series of cells which produce the egg-cell at the present day did so in former times*. This fact probably only admits of one interpretation, and this is, that *only certain series of cells contain the primary constituents of the germ-cells*, and wherever it became useful in the course of phylogeny for the germ-cells to be situated in another position and in another layer of the body-wall, this change of position could only be effected by the cells of the germ-track becoming transformed into germ-cells at an *earlier stage*, and at the same time migrating into the other layer of the body-wall. If any — I will not say all — of the cells could give rise to germ-cells, this complicated mode of procedure would be quite inexplicable, for Nature always takes the shortest possible course.

If this reasoning is correct, the hypothesis of the *germ-tracks*, as I have formerly stated it, is inevitable; and the fact that the cells lying in these tracks are alone capable of giving rise to germ-cells, can hardly be explained otherwise than by assuming that these cells alone contain germ-plasm along with their special idioplasm. If germ-plasm could be produced from the idioplasm of ordinary somatic cells, it would be impossible to see why germ-cells should not be formed in Hydroids in case of need by the transformation of young ectoderm cells: but this never happens. And even if we wished to assume that the endoderm cells, as such, possessed an idioplasm which could not be transformed into germ-plasm, while the nature of the ectoderm cells rendered such a transformation possible, this assumption would be contradicted by other facts; for, as far as we know, the germ-cells arise exclusively from the endoderm cells in the higher medusæ, and in the polypes nearly related to them. In this case therefore the germ-tracks are situated in the endoderm, — that is to say, the germ-plasm is only passed into certain series of cells in the endoderm, and the reserve material of unalterable germ-plasm, which will serve for the formation of the germ-cells, is passed into the primary endoderm cell only in the process of segmentation of the ovum, and is handed on by it. In the Vertebrata the germ-cells become differentiated from certain groups of mesoderm cells, and they are never found in any other part of the body. In this case the germ-track passes from the fertilised egg-cell into those segmentation cells from which the primary cells of the whole mesoderm are formed, in which latter it follows a closely confined course.

All these facts support the assumption that somatic idioplasm is never transformed into germ-plasm, and this conclusion forms the basis of the theory of the composition of the germ-plasm as propounded here. It is obvious that its composition out of determinants which gradually split up into smaller and smaller groups in the course of ontogeny, cannot be brought into agreement with the conception of the re-transformation of somatic idioplasm into germ-plasm. If, as we have assumed, each cell in the body only contains *one* determinant, the germ-plasm — which is composed of hundreds of thousands of determinants — could only be produced from somatic idioplasm if cells containing all the different kinds of determinants which are present in the body were to become fused together into *one* cell, their contained idioplasm likewise combining to form *one* nucleus. And, strictly speaking, even this assumption would be by no means sufficient, for it does not account for the architecture of the germ-plasm: the material only would be provided. Such a complex structure can obviously only arise historically.

The fact that somatic idioplasm cannot again give rise to *germ-plasm serves as an additional support for the theory of the* germ-plasm as here developed. Invisible, or at any rate unrecognisable, masses of unalterable germ-plasm must have been contained in the body-cells in all cases in which such a transformation has apparently occurred.

These masses need not necessarily be invisible, for they cannot be smaller than ids; and if it should subsequently be proved that the microsomes of the nuclear rods do actually correspond to ids, we may hope to ascertain the exact number of these ids in the individual species. An extensive field would then be opened out for further investigation, for it would be possible to decide by direct investigation whether the cell-series of the germ-tracks carry along with them a larger or a smaller number of ids than is contained in the fertilised egg-cell, and also the *relative proportion of the number of ids in the somatic cells in* the germ-track. We may thus hope that facts will come to light which can be utilised in connection with this theory.

Observations of this kind have already been made which indicate an actual continuity of the germ-plasm. Boveri * observed that the differentiation of the somatic cells from the primary sexual cell in the segmenting egg of *Ascaris megalocephala* is accompanied by a peculiar diversity in the nuclear structure. The nuclei of the somatic cells throw off a large part of their chromatin, in which process each idant loses a similar amount of substance. Further facts and illustrations of the process are still wanting, but even did we possess them it would be necessary to postpone the detailed theoretical explanation of such observations until we were able to judge as to the universal occurrence of the process. Observations which my assistant, Dr. V. Häcker,† has made on the segmenting ovum of a crus-

* Theodor Boveri, 'Anatom. Anzeiger II. Jahrgang,' No. 22, 1887; and 'Zellen-Studien,' Heft 3, Jena, 1890, p. 70.

† Valentin Häcker, Zool. Jahrbücher, Abth. f. Anat. und Ontog., Bd. v., 1892; and Archiv. f. mik. Anat., Bd. 40, 1892.

tacean (*Cyclops*), have indeed also proved that the behaviour of the somatic segmentation cells is different from that of the primary sexual cell, but the process differs essentially from that which occurs in *Ascaris*. When we are in possession of similar observations on various types of animals, we shall be able to recognise the essential parts of the process, and shall then be in a position to offer an explanation of them.

From a theoretical point of view, we must expect that the ids of germ-plasm become doubled in the nucleus of the fertilised egg-cell or even previously, one half of such a double id being in the active condition in which it can undergo disintegration, and the other being in the inactive and unalterable condition. The former direct ontogeny, and the latter are passed on in a passive condition to the primary sexual cells. As these, however, behave at first like somatic cells, — that is to say, they multiply in a regular manner, and are distributed amongst definite series of cells to definite parts of the body, — they must possess active idioplasm in addition to unalterable germ-plasm. They must therefore contain *more* ids in their nuclear matter than do the somatic cells. The above-mentioned observations on *Ascaris* can thus be explained in accordance with our theory up to this point, but more than this cannot be stated at present.

2. The Germ-tracks

Taking sexual reproduction only into consideration for the present, the course of the germ-tracks in existing Metazoa apparently varies both as regards its length and the direction it takes. The germ-track is shortest in the *Diptera*, in which the primary germ-cell becomes separated off in the first division of the ovum, so that in this case we might speak of a division of the ovum into a primary germ-cell and a primary somatic-cell. In the *Daphnidæ* the germ-track is longer; for, counting from the ovum, five successive divisions occur before the primary germ-cell is formed. In the free-swimming marine worm *Sagitta* it is longer still, two primary germ-cells only appearing after ten or more successive divisions have occurred, and the mass of embryonic cells has already given rise to a gastrula-larva. In other worms, such as the Nematodes, the primary germ-cells become separated from the somatic cells in a still later generation of cells, which has so far not been actually determined; and in most of the higher Metazoa this only occurs after the formation of hundreds or thousands of cell-generations.

The position of the germ-track may also vary. In the *Diptera* it is quite distinct from the somatic cell-tracks, and the genealogical trees of these two kinds of cells separate at the root. In the *Daphnidæ* the germ-track passes through each of the first four segmentation-cells, and then branches off from the somatic

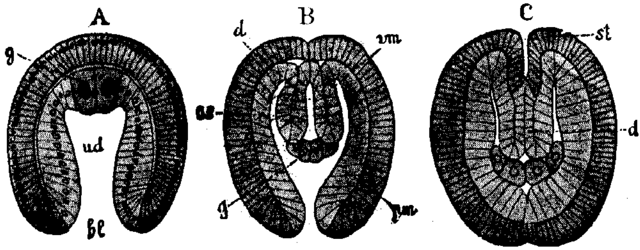

FIG. 13. — *Three early stages in the development of Sagitta.* — (After O. Hertwig.) In *A* the differentiation of two primitive germ-cells (g) from the endoderm, and in *B* and *C* the multiplication and separation of these cells is shown. (From Lang's 'Lehrbuch der vergleichenden Anatomie.')

tracks. In *Sagitta* it passes through the primary endoderm cell, and the primary germ-cells separate from the primary endoderm before the definitive endoderm of the alimentary canal has been formed from the latter. In *Rhabditis nigrovenosa* the germ-track extends through three generations of endoderm cells, passes into the primary mesoderm, and after several generations branches off from two of the mesoderm cells. In most of the Metazoa, however, the formation of the primary germ-cells is postponed to a still later period, so that the separation of the germ-branch from the somatic branch takes place at a much higher level on the genealogical tree of the cells, and often first occurs in the younger and smaller lateral branches. The primary germ-cells do not always branch off from the track of the endoderm, but may just as often diverge from that of the ectoderm. In the lower Medusæ, for instance, in which the development is a direct one, the germ-cells become differentiated at a very late stage from the ectoderm cells of the body, which is already fully formed and often independent and self-supporting; while in the higher Medusæ and Ctenophora the primary germ-cells are derived from the endoderm. We thus see that the germ-tracks or series of cells which lead from the egg-cell to the primary germ-cells frequently take very different courses: they are in some cases very short, and in others longer — sometimes so long that they pass through very different embryonic cells; in some instances they branch off from the primary endoderm-cells, and in others from those of the mesoderm, and they may even arise from later generations of the mesoderm, ectoderm, or endoderm-cells.

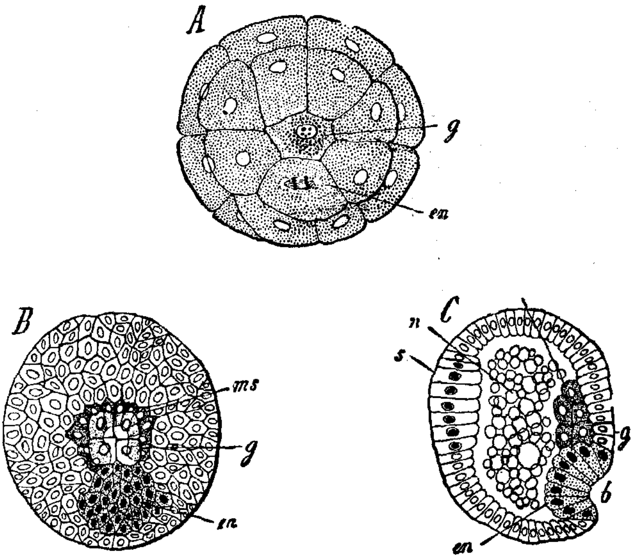

FIG. 14. — *Three Stages in the development of the summer eggs of Moina.* — (After Grobben.) *A*, Stage of segmentation viewed from the vegetative pole, in which thirty-two cells are present; *B*, Blastula stage, from the vegetative pole; *C*, Gastrula stage, in longitudinal section; *g*, the primitive germ-cells. (From Korshelt and Heider's 'Lehrbuch der vergleichenden Entwickelungsgeschichte.')

The same germ-track is always strictly followed in each of these cases respectively, no deviation ever taking place: thus the primary germ-cells never arise from endoderm-cells in a group in which the normal germ-track lies in the ectoderm, and *vice versâ*. We consequently cannot help arriving at the conclusion *that the cells in the germ-track must have some advantage over the rest of the cell-tracks in ontogeny, for they* *alone are capable of giving rise to the primary germs-cells.* Moreover, if we remember that in the case of the Hydroid polypes the period of the separation of the primary germ-cells can be relegated to earlier or later stages, it will be clear that not only the cells at the terminations of the germ-track in which this separation actually occurs in individual cases, but also the entire preceding series of cells, possess qualities which are absent in the other cells of the organism, and which, sooner or later, render the cells of the germ-track capable of giving rise to primary germ-cells.

The cells of the germ-track do not themselves correspond to primary germ-cells, the character of which latter is not as yet apparent; they are cells of a mixed character, — that is to say, they contain different primary constituents, which are *gradually separated off until eventually only two of them remain,* and these then separate from one another by means of a final cell-division.

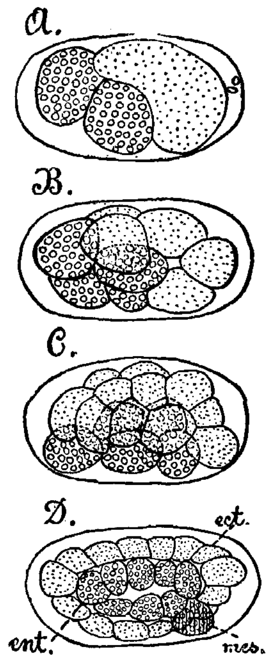

FIG. 15. — *Stages in the segmentation of the ovum and formation of the germinal layers in Rhabditis nigrovenosa.* —(After Götte.) *ect*, Ectoderm; *ent*, Endoderm; *mes*, Mesoderm.

The embryogeny of a parasitic worm (*Rhabditis nigrovenosa*) from the frog's lung may serve to illustrate this point. In fig. 15, A to D represent the first four stages in segmentation up to the differentiation of the primary mesoderm-cell (*mes*). This and the following stages are represented diagrammatically *in fig. 16, which shows the genealogical tree* of the cells and the germ-track. The ovum (*Eiz*) must of course be considered as containing the whole of the primary constituents of the organism before its first division into a primary ectoderm (*urEkt*) and a primary endoderm cell (*urEnt*). The latter retains all the primary constituents of the mesoderm and primary germ-cells, in addition to those of the endoderm, and is therefore not *merely* a primary endoderm cell. This then divides again and forms two cells, of which the one marked 3 on the left side of the figure only contains primary constituents of the endoderm, and is therefore an endoderm cell proper; while that marked 3′ represents the first rudiment of the mesoderm and of certain portions of the endoderm, and *contains in addition the primary constituents of the primary germ-cells*. This cell (3′) divides into two (4′ and 4″), thus separating the above-named rudiments into those for the right and the left sides of the body; and finally, the

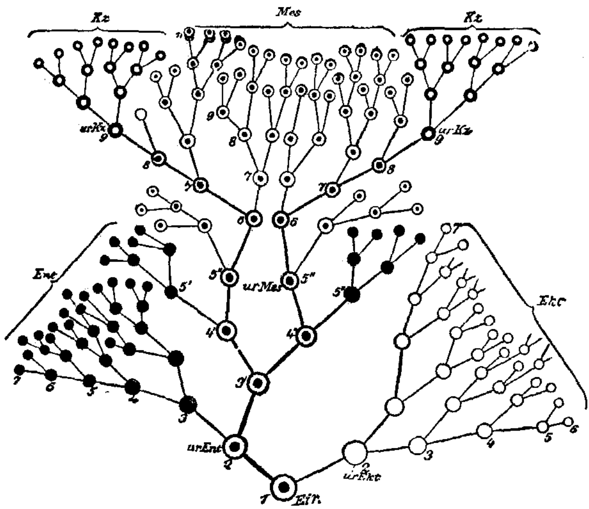

FIG. 16. — *Diagram of the germ-track of Rhabditis nigrovenosa.* — The various generations of cells are indicated by Arabic numbers, the cells of the germ-track are connected by thick lines, and the chief kinds of cells are distinguished by various markings: — the cells of the germ-track by black nuclei, those of the mesoblast (*Mes*) by a dot in each, those of the ectoderm (*Ekt*) are white, those of the endoderm (*Ent*) black; in the primitive germ-cells (*ur Kz*) the nuclei are white. The cells are only indicated up to the twelfth generation.

complete separation of the rudiments of the mesoderm and endoderm occurs, and results in one daughter-cell (5″), containing the primary constituents of the mesoderm and primary germ-cells, while the other gives rise to a cell of the endoderm proper. The primary constituents of the primary germ-cells remain connected with certain of those of the mesoderm during several generations of cells, and in each subsequent division certain of the latter pass out *alone* into one of the daughter-cells, the other retaining the primary constituents of the primary germ-cells in addition to those of the mesoderm. Finally, in the ninth series of cells in the diagram — in which the processes are represented as greatly abbreviated — the separation of these two sets of primary constituents occurs, and the first primary germ-cell (*ur Kz*) is formed.

So much is certain, and does not depend on any hypothesis. Opinions may differ as to whether the cells situated in the germ-track are to be described as real somatic cells. I have called them so, because in many cases the germ-tracks extend far beyond the period of embryogeny into the fully-developed functional tissues, and because it can be proved that *even cells which are histologically differentiated may produce germ-cells under certain circumstances.* This occurs amongst plants — in the prothallus of ferns, for instance — and also in the cells of certain Polyzoa from which gemmation may take place, and which must therefore contain inactive germ-plasm. In these cases it is certain that real somatic cells are situated along the germ-tracks; in all cases the cells of the germ-track *are not germ-cells from the first*, and they always take part in the construction of the body. And if we further consider that a large number of somatic cells must contain accessory idioplasm of some kind, — either that which will serve for simple regeneration, or for the regeneration of more complex parts, or again, for the formation of buds, — we can hardly assume that the character of a somatic cell is thereby abolished: I can see no advantage *in objecting to describe a cell of the germ-track as a somatic cell.*

The change which the idioplasm of the cells constituting the germ-track undergoes, can obviously only consist in its *active* portion gradually becoming separated off in the course of the ontogenetic cell-divisions, so that ultimately the cell contains germ-plasm only, which then stamps it as a germ-cell. Even then the germ-plasm remains unalterable as long as this first or primary germ-cell continues to produce others similar to itself. The cells only become differentiated into spermatozoa and ova when this multiplication ceases, and this presupposes the splitting off of special spermatogenetic or ontogenetic determinants. The disintegration of the germ-plasm which results in a new embryogeny — provided that the necessary conditions have been fulfilled — can only begin when this has occurred.

3. Historical Account of the Theory of the Continuity of the Germ-plasm

When my essay on the 'Continuity of the Germ-plasm' appeared seven years ago,* I was under the impression that I was the first to give utterance to this conception. Since then, however, I have found that similar ideas had arisen, in a more or less distinct form, in other brains; and I gradually discovered that a number of authors had independently recognised more or less clearly the distinction between the body-cells and germ-cells and the direct connection between the germ-cells of different generations: some had merely made the assertion, and others had attempted to support it by facts. I shall here give an account of those theories which preceded mine, taking them in chronological order.

As early as 1849, Sir Richard Owen had indicated that differences may arise in the developing germ-cells between those which become greatly changed and form the body, and those which only undergo a slight change and form the reproductive organs.†

Francis Galton was the first to express certain ideas which bore some resemblance to the conception of the continuity of the germ-plasm. In a paper which appeared as early as 1872, the individual is conceived 'as consisting of two parts, one of which is latent, and only known to us by its effects on his posterity, while the other is patent, and constitutes the person manifest to our senses. The adjacent and, in a broad sense, separate lines of growth in which the patent and latent elements are situated, diverge from a common group, and converge to a common contribution, because they were both evolved out of elements contained in a structureless ovum, and they jointly contribute the elements which form the structureless ova of their offspring.' ‡

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* 'Der Continuität des Keimplasma's,' Jena, 1855 (Essay iv., p. 163, in the second English edition).

† I quote this statement from Geddes and Thomson's 'Evolution of Sex' (London, 1889), p. 93, in which the original authority is not given.

‡ Proc. Roy. Soc., No. 136, p. 394.

A few years later, Galton changed his opinion and adopted Darwin's theory of pangenesis, which he modified considerably, and only used 'as a supplementary and subordinate part of a complete theory of heredity.' This theory has already been discussed in the Historical Introduction to this book. The 'gemmules' which are contained in the fertilised ovum together constitute the 'stirp' or stock, which by means of the egg-cell gives rise to a new individual. Each 'sort of gemmule' is represented by a number of gemmules which differ somewhat from and compete with one another; and since the successful ones in the competition for taking part in the construction of the body form the various parts of the body and are therefore contained in them, the rest remain unused, thus constituting the 'residual germs.' These, then, are 'the parents of the sexual elements and buds.' The 'dominant' gemmules may also take a part, though only a slight one, in the formation of the germ-cells, 'as they are the least fertile in the production of gemmules.' The germ-cells are therefore mostly formed from gemmules which have remained latent, and this accounts for the fact that the offspring usually do not exhibit the most marked peculiarities of the parent. As this hypothesis only accounts for the dissimilarity between parent and child, so far as it exists, and not for the far commoner resemblance between them, Galton assumes that the parts of the body can also give off gemmules which become distributed and extend beyond the boundaries of the cells in which they arose, and so may even penetrate into the sexual elements. He thus substitutes the idea of a locally restricted distribution of the gemmules for Darwin's view of their 'free circulation.' If we attempt to make this somewhat vague and unrealistic idea rather more comprehensible, by considering the 'residue of the stirp' as equivalent to the 'unalterable' reserve germ-plasm, Galton's hypothesis will be found to bear some resemblance to the theory of the continuity of the germ-plasm. But there is still a fundamental difference between them, for Galton's idea is only conceivable on the presupposition of the occurrence of sexual reproduction, while the theory of the continuity of the germ-plasm is entirely independent of any assumption as to whether each primary constituent is present in the germ *singly* or in numbers. According to my idea, the active and the reserve germ-plasm contain precisely similar primary constituents, gemmules, or determinants; and on this the resemblance of a child to its parent depends. The theory of the continuity of the germ-plasm, as I understand it, is not based on the fact that each 'gemmule' necessary for the construction of the soma is present many times over, so that a residue remains from which the germ-cells of the next generation may be formed: it is founded on the view of the existence of a special adaptation, which is inevitable in the case of multicellular organisms, and which consists in the germ-plasm of the fertilised egg-cell becoming doubled primarily, one of the resulting portions being reserved for the formation of germ-cells.

Gustav Jäger * was the first to express the idea that in the higher organisms the body consists of two kinds of cells, which he calls respectively 'ontogentic' and 'phylogentic;' and that the latter, or reproductive cells, are not a product of the former, or body-cells, but are derived directly from the germ-cell of the parent.† He took it for granted that the 'formation of reproductive substances occurs in an animal during the early embryonic stages,' and imagined that he had thus proved the existence of a connection between the germ-cells of the parent and those of the child. Although these opinions were not founded on fact or followed out in detail, they ought to have led to further ideas on the subject. They, however, together with the book in which they were contained, remained unnoticed.

A few casual remarks made by Rauber,‡ in a paper on 'Formbildung und Formstörung in der Entwicklung von Wirbelthieren,'

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* Gustav Jäger, 'Lehrbuch der allgemeinen *Zoologie*,' Leipzig, *1878*, II. Abtheilung.

† The praiseworthy attempt to do justice to my predecessors in this particular subject has perhaps been carried too far. In Geddes and Thomson's 'Evolution of Sex' (p. 93), for instance, a quotation is given from Jäger which seems to prove that he anticipated me with regard to the theory under consideration. The quotation in which this idea is expressed is, however, not taken from the book published in 1878, but from an essay written ten years later, and it concludes with the following words: —'This reservation of the phylogenetic material I described as *the continuity of the germ-plasm*.' But no mention is made by Jäger of the continuity of the germ-plasm in his book which appeared in 1878, in which a connection between the germ-*cells* of different generations is supposed to exist: — and this is not the case. The entirely new statement of his ideas has been influenced by those contained in my essays which had appeared in the meanwhile.

‡ 'Morphol. Jahrbuch,' Bd. 6, 1880.

suffered the same fate. This author states that 'as regards the effect of fertilisation, it can only convert a *portion* of the egg, viz., the personal part, into the form of a person; the other portion does not experience this effect, for it has a stronger power of persistence.'

Finally, Nussbaum * was likewise led to the idea of the continuity of the germ-*cells*. He, too, assumed that 'the segmented ovum divides into the cell-material of the individual and the cells for the preservation of the species,' and he supports this statement by quoting the cases already mentioned of the very early differentiation of the sexual cells.

I will conclude this section with the words which appeared in the preface to a short paper intended as a defence against the accusation of plagiarism which had been made against me. 'A fertile scientific idea has rarely appeared without having been contested on the one hand, and set down as already known on the other. The former is certainly a perfectly justifiable and even necessary course of proceeding, for a clear and definite knowledge of the truth can only result from the contest of opinions; and even the latter is to some extent justifiable, for an idea of this kind probably very rarely arises without having been preceded by similar attempts directed towards the same object; and it is only natural that those who first made such attempts should overlook the difference between these struggles towards the desired object and its attainment.'

Others may decide the reason why no attention had been drawn to the suggestions mentioned above as having been made previously to my theory of the continuity of the germ-plasm, and why these did not exert any influence on scientific thought. This is certainly the case: and it practically follows from the fact, that all the objections which have been made have been directed against *me*. Some of these objections will be discussed in the following chapter. That I am far from desirous of detracting from the merit of others, has, I trust, been shown by the fact that as soon as I became aware of previous views on the subject I brought them forward. Jäger's ideas, for instance, might have long remained unnoticed, had not I brought them to light. But an historical account of the various previous views

* M. Nussbaum, 'Die Differenzirung des Geschlechts im Thierreich,' Archiv. f. mikr. Anatomie, Bd. xviii., 1880.

on this subject * cannot be considered to be an impartial one, if *no mention is at the same time made of the fact that all these suggestions remained unnoticed, and had no effect on the progress of scientific thought.* That this is the case there can be no doubt. And although it may be a satisfaction to every one to have expressed a correct idea, no such idea can be considered as fertile, and as having an important influence on the progress of scientific thought, unless its meaning is so obvious that it results in further progress. Such a result, however, only followed after my essays had appeared.

4. Objections to the Theory of the Germ-plasm

Important objections to this theory have been raised by several botanists; and at first sight the facts on which these are based may easily give rise to the impression that the theory cannot be carried out in the case of plants. If this were so, however, its correctness would be altogether doubtful, for the hereditary mechanism cannot be totally different in plants and animals. We must therefore make a closer examination into the facts as they concern plants, and I hope to be able to show that the fundamental ideas which I have assumed are applicable to plants as well as to animals, although they did not originate from the botanical point of view.

Certain misconceptions and inaccurate representations must first be put on one side. Many botanists deny the *existence* of the germ-plasm entirely.

Vines † considers the assumption of a special 'reproductive substance' unnecessary, as the capacity for reproduction is a fundamental property of protoplasm. A cutting gives rise to a complete plant, just as a broken crystal becomes complete when immersed in the mother-liquor, for it produces the missing parts, viz., roots. It is not necessary to assume the existence of a special 'reproductive substance' in either case.

I need not especially emphasise the fact that this stimulus which results in the completion of a part is not by any means a universal phenomenon, and that, for instance, some parts of plants cannot be reproduced from cuttings. I shall simply

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* *Cf.* the account given in Geddes and Thomson's 'Evolution of Sex,' pp. 93 and 94.

† *Cf.* 'Nature,' Oct. 24, 1889; and 'Lectures on the Physiology of Plants,' Cambridge, 1886.

confine myself to calling attention to the fact that even if a universal reproductive power existed in protoplasm, it certainly would not explain matters. *For this power is just what has to be explained.*

If we know, for instance, that Infusoria are able to replace great losses of substance, — so that when the oral region is cut off, it, together with *all the cilia and other minute structures*, can be formed anew, — a proof is thereby obtained that these unicellular organisms actually possess the universal reproductive power which Vines wishes to ascribe to vegetable protoplasm. But does this help us in the slightest degree to understand the fact, or to explain why the ultimate particles of the cell-body become rearranged and transformed after a loss of substance has occurred, just as is necessary for the reappearance of the species? Do we thereby gain the faintest idea as to how and why the residual particles of the cell-body are compelled to give up their previous form and connection, and to reconstruct exactly that part which is required in order to render the whole complete? The assumption of a 'reproductive power' simply amounts to the statement of the fact that regeneration occurs; and this, it seems to me, is equivalent to saying that the reproductive power is a fundamental property of vegetable protoplasm.

In the case of the unicellular Infusorian we can, however, hardly venture at present to attempt an explanation of this problem, as we know very little of the vital units of which the cell-body is composed, and of the forces situated within them. But the case is different with regard to those organisms which consist of many physiologically differentiated cells: in these we are at any rate acquainted with the form and function of one *arrangement of the vital units of which the whole aggregate is* composed, and so we can attempt to deduce the functions of the whole body from those of the units, and conversely to refer the latter processes to a distribution of the forces amongst the units composing the whole. We need not therefore confine ourselves to the mere statement of the fact that a process occurs by means of which the whole is completed, but we may further inquire as to when this occurs, from what elements it proceeds, how the whole body arises at all, and how so complex a structure can be formed from the apparently simple substance of the germ.

In order to give a satisfactory answer to these questions, I have assumed the existence of a germ-plasm, but have not primarily regarded this as a 'special reproductive substance' which is very different from all other substances in the body; I have looked upon it, on the contrary, as *the substance which gives rise to all the other formative substances of the entire individual.* Every part of the body contains a *portion* of this substance, and the whole organism can only be formed anew when all the portions of this controlling substance (the idioplasm) are combined; that is to say, when germ-plasm is present. The assumption of germ-idioplasm or germ-plasm is, I consider, quite unavoidable, for we must at the present day take it as proved that the hereditary tendencies are connected with a substance. In my opinion, it is also an irrefutable fact that this germ-plasm undergoes regular changes from the ovum onwards: it must, indeed, undergo change from cell to cell, for we know that the individual cell is the seat of the forces which give rise collectively to the functions of the whole. The forces which are virtually contained in the germ-plasm can therefore only become apparent when its substance undergoes disintegration, and its component parts, the determinants, become rearranged. The difference in function seen in the various groups of cells in the body compels us to suppose that these contain a substance which acts in various ways. *The cells are therefore centres of force of different worth, and the substance (idioplasm) which controls them must be just as dissimilar as are the forces developed by them.*

The apparent similarity of many young plant-cells may account for the vagueness with which Vines, following Sachs's example, speaks of an '*embryonic substance*' from which reproduction is supposed to proceed in all cases, and which is assumed to be present in all 'young' cells. In my opinion the hereditary value of a cell can be estimated as little by its age as by its appearance. The mass of cells resulting from the segmentation of an animal egg certainly possess the character of youth, and in a certain stage of development these cells are all of the same age and all look alike. They have, however, entirely different hereditary values; and if we are accurately acquainted with the ontogeny of the animal in question, we can tell what hereditary tendencies lie hidden in each cell. The primary constituents of the entire endoderm, for instance, may be contained in one cell, and that of the ectoderm or mesoderm in another; or, again, in a later stage, only a rudiment of a particular part, organ, or portion of an organ belonging to the germinal layer in question, may be present in an individual cell. But if we inquire whether the entire body could arise from each of these cells, known facts give a very decided answer in the negative. Only one, or a few perfectly definite cells amongst them, which we speak of as germ-cells, can reproduce the whole animal under favourable circumstances. This is true of all the higher Metazoa: *the cells of the segmenting ovum are completely dissimilar as regards their hereditary value, although they are all 'young' and 'embryonic,' and are not infrequently quite similar in appearance.* It therefore seems to me to follow from this, as a logical necessity, that the hereditary substance of the egg-cell, which contains all the hereditary tendencies of the species, does not transmit them *in toto* to the segmentation-cells, but separates them into various combinations, and transmits these in groups to the cells. I have taken account of these facts in considering the regular distribution of the determinants of the germ-plasm and the conversion of the latter into the idioplasm of the cells in the different stages of ontogeny. All these cells contain 'embryonic substance,' but the determinants contained in one set differ from those in another, and therefore contain different hereditary tendencies. Hence it is comparatively meaningless to speak merely of an 'embryonic substance.'

De Vries regards some of my views in a very different way, and from an entirely different aspect. In an extremely able manner he brings forward a number of facts concerning heredity in plants, and finds that they usually do not fit in with my views. I have followed his deductions with great interest, and have gratefully made use of the facts which he has brought forward; but I nevertheless believe that the chasm which separates his views from mine can be bridged over.

In the first place, de Vries accuses me of having taken a one-sided view of the question by considering the processes as they occur in animals only: in these it may be possible, as I have assumed, to draw a sharp line of distinction between somatic- and germ-cells, but this cannot be done in the case of plants. In the latter, those series of cells which I have called germ-tracks may give rise to many other cells besides germ-cells, although this as a general rule is only exceptionally the case:

that is to say, it occurs in response to definite external influences. It would not, however, only take place in those parts of the plant which might be assumed to be specially adapted for this capacity, but might also occur in those in which adaptation is out of the question. We are therefore compelled to assume that *most*, if not all, of the *cells contain all the primary constituents of the species in a latent condition.*

I will first discuss the manner in which de Vries applies my hypothesis of the germ-tracks to the case of plants, and the conclusions at which he has arrived and has illustrated by describing a number of genealogical trees representing the various series of cells in plants.

De Vries draws a distinction between 'primary' and 'accessory' germ-tracks. The former correspond to the germ-tracks I have already assumed: that is to say, to those cell-series which normally lead from the fertilised egg-cell to the new germ-cells (ova, spermatozoa, pollen-grains). By 'accessory germ-tracks' are meant those cell-series which lead to germ-cells 'through adventitious buds.' These accessory germ-tracks are, according to de Vries, absent in the higher animals, but are of common occurrence amongst plants, and I am accused of not having taken them sufficiently into account. The 'accessory germ-tracks,' if I understand the term aright, are regular germ-tracks, which do not, however, always come into use. In many of the lower plants, such as mosses and fungi, 'almost all of the cells may develop into new individuals;' and in the higher plants, buds, from which entire plants possessing germ-cells may arise, can, under certain circumstances, be formed at any rate from certain kinds of tissue, which may consist of young (meristematic) cells or indeed even of full-grown cells.

Let us first consider the 'primary germ-tracks.' De Vries thinks that their behaviour is essentially different in the higher animals and in plants: in the former, the genealogical tree of the cells of the germ-track 'is straight, and only slightly branched at the apex,' while in the higher plants 'the branches are so numerous and subdivided from the base upwards that they frequently overtop the main stem; or, more accurately, the main stem is hardly recognisable.' No objection can certainly be raised to this statement, which we may illustrate by a blossoming apple tree, in which the blossoms which crown the top may be taken as corresponding to the germ-cells. But how is this difference to be proved, and on what does it depend? It is not based on the animal or vegetable nature of the organisms, for as de Vries himself incidentally acknowledges, we find a similar kind of branching of the primary germ-tracks in the Hydroid-polypes. It simply depends on the fact that a *higher individuality of the stock* exists in these animals, just as in the case of the higher plants. In both cases we have to deal not with a single person and the formation of its germ-cells, but with a number of persons which arose from the primary one by budding, each of which has a body of its own, and gives rise to its own germ-cells. The germ-track is concealed within the first person of the stock produced from an egg, and gives off a lateral branch as soon as this first polype develops a bud. Shortly afterwards, *the polype gives rise to a second bud, into which a lateral germ-track* likewise extends; and when these two buds have developed into complete polypes, they again give rise to buds, into which germ-tracks are once more given off, and so on. The copious branching of the germ-track is thus accounted for, and it is quite immaterial whether the separate persons of the stock are more or less independent and perfect, and to what extent they may be regarded as 'individuals.' In those cases in which a periodic segmentation of the body into serially homologous segments or metameres takes place, — each of which has almost a similar origin and is able to produce germ-cells, — the type of the genealogical tree of the germ-track, as described above, results.

If, however, we inquire as to the conclusions which can be drawn from the course taken by the germ-tracks in animals and plants, we receive a reply from de Vries which is very significant of the way in which this problem is at present regarded by many botanists: — *the whole question which I have raised with regard to the continuity of the germ-plasm is an idle one.* In his opinion, 'the whole question as to whether somatoplasm can become transformed into germ-plasm has no basis in fact.' 'A germ-track,' says de Vries, 'never arises from a somatic-track,' and 'a continuity of the germ-cells exists, not merely in the very rarest cases, but universally and without exception, although it often takes place through a long series by means of the germ-tracks.'

With the exception of the last one, these sentences merely repeat my own views, and the apparent contradiction of the latter is simply due to the fact that de Vries adopts expressions which

I have used in another sense. In stating that germ-cells arise from somatic cells in innumerable cases, I referred to the somatic cells which are situated along the germ-track, the existence of the latter being assumed for this special purpose. De Vries, however, disputes the somatic character of these cells, because he considers that they also contain 'germ-substance.' I should attach slight importance to a mere name, if a very definite idea did not depend on this name, the abandonment of which would lead to confusion. It appears to me to be dangerous to introduce a third category of cells — viz., those of the germ-track — between the somatic and the germ-cells. In the first place, it is unpractical to do so, for the appearance of a cell does not reveal to us whether it is situated in the germ-track or not; and secondly, *it would lead to a total confusion of the ideas of* somatic and germ-cells; for, as has been shown in the previous chapters, there are a number of cells in plant- and animal-stocks which are undeniably somatic, and which must *therefore* contain germ-plasm. Since we regard the 'blastogenic' idioplasm of plants and Hydroids as a modification of germ-plasm, we must also look upon a very considerable number of the cells which constitute these organisms as *cells of the germ-track*, and we should therefore arrive at the absurd conclusion that a soma (body) is not present at all in these cases. The soma nevertheless *is* present, and a contrast also exists between it and the germ-cells in plants as much as in animals.

De Vries contradicts himself when he states that a universal 'continuity of the germ-*cells*' exists through the germ-track; for in other passages he emphasises the fact that germ-cells do not as a rule arise directly from one another (p. 84), and that a distinction must be made between germ-cells and cells of the germ-track. The somatic character of the cells of a fern-prothallus, for instance, cannot be denied, for they function as somatic cells, and at first are all similar in appearance, so far as we are able to observe. But nevertheless some of them are situated on the germ-track, and give rise to male and female germ-cells.

If de Vries puts aside the whole question of the *continuity of* the germ-plasm because he is able to prove that germ-cells always arise from cells of the germ-track, it is evident that he must be labouring under a similar delusion to that which induced Sachs to claim precedence as regards the theory of the continuity of the germ-plasm. Both these observers consider it self-evident that each apical cell contains the germ-substance of the ovum, because in plants all growth takes place from the growing point and originates in the apical cells, which are derived directly from the egg-cell.

This, however, is at any rate only self-evident in the case of the first apical cell of the main shoot, and is certainly not so in that of the lateral shoots, which are, indeed, only derived indirectly from the former. All the cells of a plant are undoubtedly descended in a direct line from the ovum; but this fact does not imply that they must all give rise to apical cells or must all contain germ-plasm, nor does it in any way explain the fact that only relatively few of them can become germ-cells and the rest cannot. These were the very facts which the hypothesis of the continuity of the germ-plasm was intended to make comprehensible, to some slight extent at any rate. The origin of a cell from the ovum gives no clue to its nature; and, as de Vries himself says, the entire description in detail of the cell-series leading from the ovum to the first apical cell, although very interesting in itself, gives us no information as to the origin of the germ-substance present in certain parts of the plant-body. I do not understand therefore how de Vries can look upon the fact of the existence of these cell-series as constituting in itself an important explanation of the problem, without attempting to explain it further. It seems to me that the cell-series can only be of any explanatory value when they are regarded as germ-tracks in the sense in which I use the term, — that is to say, as those series through which the germ-substance is transmitted from the egg-cell to the remotest parts of the plant.

I must say that it seemed to me to be a somewhat crude idea to suppose that the same kind of idioplasm is contained in all the cells of the germ-track, including the apical cell, and that it is equivalent to 'germ-substance.' Why do not the apical cells in the sterile shoots of the horse-tail give rise to germ-cells, while those of the fertile shoots do so? This must be due to a difference in the idioplasm of the apical cells of these shoots. And although structures bearing germ-cells may become developed from the apical cell of a fertile shoot of the plant, all the cells of the latter do not nevertheless give rise to germ-cells: only *certain* cell-series lead from the apical cell to the new germ-cell, and these are the cells of the germ-track which contain germ-plasm! The process of the formation of a shoot from an apical cell is analogous to that of the production of a single polype by budding from a polype-stock. But both these processes are essentially the same as that of the development from the ovum in a higher animal. In all three cases the formation of the new animal originates in one cell. The latter must therefore possess an idioplasm which contains all the primary constituents of the organism; and, moreover, if the organism is to be 'fertile,'—in the sense in which this term is used by botanists,—the original cell from which it is derived must contain the primary constituents of *all* the structures characteristic of the species in its idioplasm: that is to say, it must contain germ-plasm. If we trace the development of such a shoot or organism, we shall find that it follows a precisely similar course to that which we have already described in the case of embryogeny; and that at each cell-division the primary constituents break up into smaller and smaller groups, until at last each cell only contains *one* such element. And yet all these very different kinds of cells are descended in a direct line from the original cells. How, then, can we account for the fact that one or several of them contain all the primary constituents of the species in a latent condition, in addition to one specific primary constituent of a particular kind of somatic cell, as must be the case in those which give rise to germ-cells? It would, indeed, be a very simple matter if a continuous series of cells which contain 'germ-substance' *only*, led from the original cell to the new germ-cells. But as simple a case as this only occurs in the Diptera: in all other instances *the intermediate cells which constitute the germ-track can be proved to contain perfectly definite somatic elements in addition to the germ-plasm; and this is the case in plants as well as in animals.*

To make this clear, it is only necessary to glance at the genealogical tree representing the ontogeny of *Rhabditis nigrovenosa* (fig. 16). How does it come to pass, for example, after the division of the primary endoderm cell into the first endoderm and first mesoderm cell, that the latter is nevertheless capable of producing cells subsequently which contain 'germ-substance,' *i.e.*, germ-cells? At its origin this cell gave up the primary constituents of the endoderm to the sister-cell; by what means do these primary constituents—even those of the ectoderm which were previously given up—reach the germ-cells which eventually arise from this cell? My answer to these questions has already been given, and is as follows: — in addition to their active mesoderm-idioplasm, the cells which will give rise to germ-cells carry along with them a certain amount of germ-plasm in an unalterable condition. De Vries, and those botanists who agree with him, consider my answer superfluous. Every one, of course, is at liberty to reject the solution of a problem, but in that case he must not claim to have explained it.

I now come to the consideration of de Vries's 'accessory germ-tracks.' As has already been stated, this term is used to describe those series of cells which give rise to germ-cells through the agency of 'adventitious buds.' According to Sachs,* adventitious buds correspond to those growing points which are not derived from those already present, or 'from embryonic tissue already present,' but which 'originate at places where the tissue has already passed over into the permanent condition, — in fully-developed roots, in the interfoliar parts of shoot-axes, and more particularly in foliage leaves, the tissues of which are already completely differentiated and developed.'

In my former essays I have endeavoured to account for these 'adventitious' buds, — such as are formed, for instance, in a Begonia leaf when it is placed on damp soil, — by supposing them to be adaptations of particular species of plants to this peculiar method of reproduction: I assumed that certain series of cells which in these species take part in forming the leaves contain unalterable and inactive germ-plasm in addition to their own active idioplasm.

In opposition to this interpretation much may be, and in fact has already been, said, and the principal objections must now be considered.

It has, in the first instance, been urged that the capacity possessed by leaves, roots, and so on, for producing adventitious buds, cannot be regarded as an adaptation, because so many cases are known in which this process only occurs exceptionally, and is of no advantage to the plant. There can be no doubt, however, that the power possessed by *Begonia*, *Bryophyllum*, *Cardamine pratensis*, and *Nasturtium officinale*, of giving rise to buds in those parts in which they are not formed in most plants, is due to an arrangement peculiar to these plants. Neither in *Begonia* nor in *Bryophyllum* can the buds and young plants arise from

* 'Lectures on the Physiology of Plants,' p. 477.

all parts of the leaf; they are only formed in *perfectly definite regions*, *e.g.*, on the margins of the leaves in *Bryophyllum* and in the angles between the points of origin of the large veins in *Begonia*. All the cells of the leaf do not, therefore, as de Vries supposes, possess this capacity, which is limited to perfectly definite though numerous cells. These therefore correspond to somatic cells, quite as much as do those which produce the several cells in the prothallus of a fern, which contain unalterable germ-plasm in addition to the active somatic idioplasm, the former only becoming active by the influence of particular external influences.

These conditions may be fulfilled in thousands of other leaves without resulting in the production of young plants. There are indeed a whole series of observations which apparently prove that 'every small fragment of the members of a plant contains the elements from which the whole complex body can be built up, when this fragment is isolated under suitable external conditions.' Phenomena of this kind are exhibited by cuttings and adventitious buds which arise on a twig the apex of which has been cut off. In the higher plants, the development of roots on a cutting, or the formation of adventitious buds, does not take place in all parts of the plant, but only in those which contain 'a number of cambium cells.' These cells alone therefore contain accessory idioplasm, which, according to the nature of the stimulus acting on them, renders them capable of growing in a manner which is very different from the normal. There can be very little doubt that the whole of the cambium layer of these plants is endowed with the capacity for reproduction. The only question is, whether this is a result of special adaptation, or only the outcome of the normal constitution of each plant-cell.

I should still, however, be inclined to consider it as a special adaptation, and will endeavour to state my reasons for this view; not being a specialist in botany, however, I am unable to deal with the various groups of the vegetable kingdom in such detail as I could wish.

The question to be decided is, whether each cell was provided with all the specific primary constituents in a latent condition at the time when the multicellular plant arose from the unicellular form; or whether, owing to the diversity of the differentiation of the idioplasm, a sharp distinction first arose between the somatic cells and the germ-cells, and the idioplasm of the somatic cells was only subsequently provided with germ-plasm in a latent condition in those cases in which this arrangement was a useful one. I hold the latter view, and de Vries the former one. It is important for the theory of the germ-plasm to decide between these two opinions; for it would be incompatible with this theory for germ-substance to be present as the idioplasm of the somatic cells at the phyletic origin of the soma. According to my conception of the germ-plasm, the phyletic origin of the somatic cells depends on the determinants contained in the germ-plasm being separated into groups. It would entirely contradict this assumption if those somatic cells which were phyletically the first to be formed, had contained all the other characters of the species in a latent condition in addition to their manifest specific characters. De Vries thinks that the marked distinction which actually exists between the somatic and germ-cells of the higher animals has led me to assume the universal existence of this contrast, which is not nearly of such a decided nature in the case of plants in which gradual transitions from somatic-cells to germ-cells can be proved to exist.

This, however, I believe is not the case: transitions between somatic and germ-cells never occur, and de Vries's opinion simply rests on the fact that he confuses germ-cells with the cells of the germ-track. That the latter must be regarded as somatic cells has already been shown.

In my opinion, germ-cells were sharply distinguished from somatic cells on their first appearance in phylogeny, and this distinction has since persisted. In no species, whether animal or vegetable, can there be any doubt as to the cells which are to be looked upon as germ-cells; and as regards the somatic cells, such a doubt can only arise when cells in the germ-track are regarded as germ-cells.

I know of no more convincing proof of my view than that which is furnished by the *Volvocinæ*. These organisms consist of communities of cells which may or may not exhibit a division of labour, and in which a contrast between the somatic and germ-cells may or may not exist. In *Pandorina* all the cells of the colony are similar to one another, and each performs all the vital functions. In *Volvox* the cells are differentiated: some of them have the function of maintaining the individual, and others that of preserving the species: that is to say, they are differentiated into somatic cells and germ-cells. The heteroplastid genus *Volvox* must have arisen phyletically from a homoplastid form; but we can hardly imagine that there can be

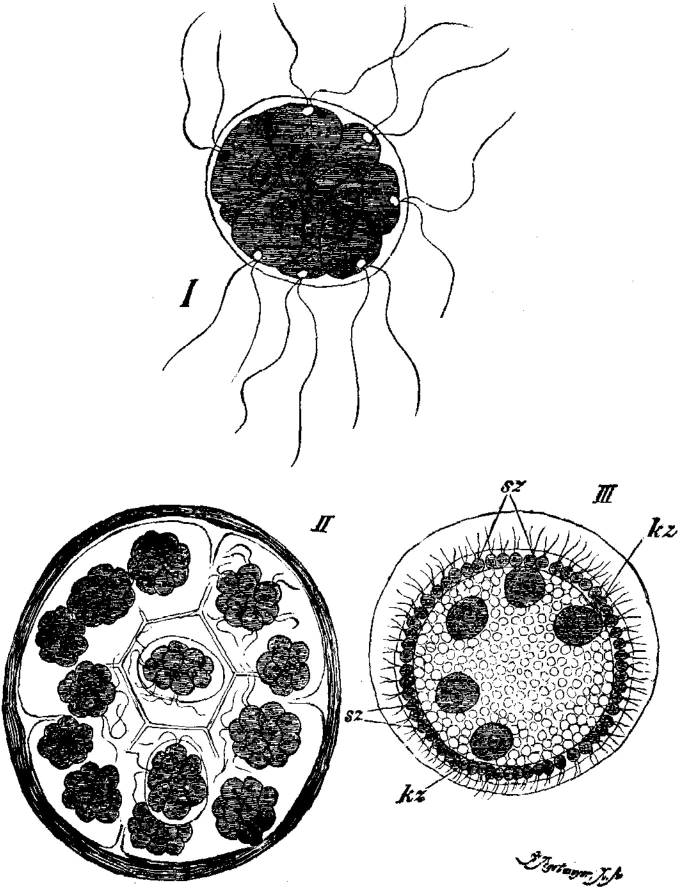

FIG. 17.—I. *Pandorina morum.*—A colony of swarming cells. II. A colony which has given rise to daughter-colonies:—all the cells are similar to one another. (After Pringsheim.) III. A young individual of *Volvox minor*, still enclosed within the parent (after Stein): the cells are differentiated into somatic- and germ-cells.

many intermediate stages between these two, for at the present day the two kinds of cells in *Volvox* hardly differ as much as do the somatic- and germ-cells in the case of the higher organisms. The somatic cells have nevertheless entirely lost the capacity of reproducing the entire organism.

Transitions between these two kinds of cells could naturally only arise by the germ-cells first becoming only slightly differentiated from the somatic cells, and could not have been produced, as de Vries thinks, owing to all the cells containing germ-substance in a more or less latent condition from the first. There is no germ-substance in the somatic cells of *Volvox*, which, figuratively speaking, have only just become differentiated from the germ-cells. If the latter are artificially removed from a colony, the somatic cells continue to exist for a long time, but they do not give rise either to new germ-cells or to a new colony.

And why should they do so? Of what advantage would this be to the species, since millions of individuals, each of which again produces daughter-individuals, exist in the same pond? The ordinary process of multiplication is so vigorous that special means for ensuring the existence of the species are unnecessary.

Such means have, however, been adopted in very many, if not by far the greater number, of the more highly organised plants.

The power possessed by fungi and mosses of reproducing a new individual from any bit of the plant under favourable conditions, has been supposed to contradict my view. But I do not see what prevents us from regarding this power as an adaptation for ensuring the existence of a species surrounded by dangers of all kinds. When the top of a toadstool is knocked off, a new one is formed (Brefeld); and this arrangement is obviously of great use in the preservation of the species. An entire liverwort can be regrown from the smallest fragments of the plant (Vöchting). Why therefore should the assumption be improbable that this power has been acquired in order to insure the persistence of a species the existence of which is threatened by every sudden drought? My knowledge of plant life is not sufficient for me to be able to support this statement in detail, but other facts will, I think, to some extent confirm my opinion from the opposite point of view.

Why is this power of regeneration not possessed by adult ferns and horse-tails? If a frond of a fern is cut off, it is not reproduced from the stalk, and even the individual pinnæ cannot be formed anew. In answer to this it might be urged that the somatic cells of ferns have become too highly differentiated: but this is contradicted by the fact that many, although by no means all, ferns can produce bulbils on their fronds. I must leave botanists to decide why this occurs; but were I asked whether the power of producing entire plants from somatic cells would not have been of advantage to the other ferns, and would therefore be expected to be possessed by them, I should be inclined to reply that all ferns are able to replace lost fronds by forming new ones, — not by the regeneration of the injured leaf, but by budding from the stem. This suffices to restore the plant when it has been injured.

We must now consider the Phanerogams in this connection. In these plants, again, 'accessory germ-tracks' are usually absent in the leaves: that is to say, the cells of the leaves are not capable of producing buds or even of restoring a piece which has been cut out. The axes of the shoots, on the other hand, possess this power in a high degree, and it depends on the presence of cambium cells, all of which are apparently capable of giving rise to new growing points, which produce new shoots with leaves and blossoms, and consequently also germ-cells. *The power of regenerating the leaves is, as a rule, useless; for the formation of new persons of the plant stock can take place to an unlimited extent by means of the cambial layer*; and this mode of compensation for losses sustained is more effectual than the restoration of defects in the leaves would be. The power of growing adventitious buds is probably unnecessary in the case of most leaves, on account of the enormous number and certain dispersion of the seeds produced by the plant. Amongst animals the same is true as regards polype-stocks. Cells are distributed throughout the stock which have the appearance and functions of ordinary somatic cells, but which can give rise to new persons under certain circumstances, such as, for instance, when the stock has become injured. In a living stock of *Tubularia mesembryanthemum*, which I once brought from Marseilles to Freiburg, the crowns of the polype died one after the other within a week, probably on account of want of nourishment; but within a few days afterwards all the stalks had given rise to new crowns; and though these were very small, they would undoubtedly have grown to the full size had it been possible to supply them with food. The capacity for regeneration is apparently provided for in this case; it is at any rate stated by Loeb * in a recent paper that a shedding and new formation of the crowns occurs periodically. The same writer also showed by experiment that, under favourable circumstances, crowns may bud out at any point of the stem, either at the distal end or at the base. On the other hand, he never succeeded in getting the root-like organs of attachment to be produced at the apical end.

No one will be surprised that such a growth did not occur who agrees with me in looking upon all these processes of regeneration and budding as resulting from adaptation. Under natural conditions the apex of a stem could hardly be situated in such a position as to render the formation of roots necessary, for it never comes to lie upside down in the earth, and consequently none of the cells in the apex contain 'rhizogenic idioplasm' ('Wurzel-Idioplasma'). On the other hand, however, it is easy to understand why the power of budding exists in such a marked degree in polypes, if one considers how liable the soft body is to be attacked by crabs, worms, gasteropods, Pycnogonids, and other small enemies. If these polype-stocks did not possess the power of continually producing new crowns, —*i.e.* new individuals, —when the old ones have been bitten off, the whole colony would soon perish owing to the absence of 'nutritive persons.' The fact that regeneration is possible to such an enormous extent results, at any rate *in part*, from the aggregation of persons to form the higher stage of individuality of the stock. For such a combination of individuals procures the advantage of permanent nutrition as long as *all* the individuals of the stock have not fallen victims to their enemies, and thus it is favourable to the production of new buds.

Amongst the *Polyzoa* the case is very similar. In many of these animals the normal form of gemmation takes place with great regularity, and the region at which the next bud will arise can be predicted beforehand: on this fact depends, as in the case of the Hydroid polypes, the characteristic form of the stock in the different species, which is sometimes branched like a foliage tree, and sometimes like a fir-tree or a feather. In these animals, therefore, definite cells must be provided with 'blastogenic' idioplasm in advance, and merely the stimulus due to ordi-

* Jacques Loeb, 'Untersuchungen zur physiolog schen Morphologie der Thiere,' I. Uber Hetermorphose,' Würzburg, 1891.

nary nutrition is required in order to incite them to form buds. The series of cells which lead directly to the cells of these buds must be looked upon as the main germ-tracks, using the term in de Vries's sense. According to Seeliger's researches, however, budding takes place from other regions as well as the ordinary ones in certain Polyzoa, *e.g.*, *Pedicellina*. If the crown is lost in this animal, so that only a stump of the stalk remains, new crowns are produced on the end of the stalk; and in this case, therefore, *budding originates in the flat epithelial cells characteristic of the ectoderm*, which did not previously appear to be capable of proliferating at all. This is another instance of the presence of accessory germ-tracks. The cells of the epidermis are provided with blastogenic germ-plasm, although they do not as a rule take part in the formation of buds, but only give rise to them in response to unusual stimuli. These cells are just as much exposed to destruction as are those of the Hydroid polypes, and we need therefore not be surprised that arrangements for budding should have been made in the stalk, even were we not aware of the fact that in *Pedicellina*, under normal conditions, the crowns drop off periodically from the stalk, and are replaced by others which bud out afresh. This process certainly occurs at the upper end of the stalk, but it is quite comprehensible that it would be advantageous for the lower end of the stalk also to be provided with blastogenic idioplasm.

The arrangement which exists universally in the higher plants for the production of adventitious buds is, in my opinion, to be explained in a similar manner. In this group of organisms the cambium layer in particular is provided with the means of replacing lost leaves and entire shoots. This obviously affords an important protection against numerous enemies — such as insects more especially — the number of which is often incalculable. It is therefore not surprising that such an arrangement — viz., the addition of unalterable germ-plasm to the cambium cells — is here met with.

5. Galls

De Vries has also brought forward the question of the formation of galls as furnishing an additional argument against my views. In his opinion the production of galls proves that a vegetable cell, even when it exhibits a specific histological differentiation, contains the primary constituents of every other kind of cell in a latent condition, and these are ready to become active as soon as a suitable stimulus is brought to bear upon them. This proof he considers to be incompatible with the assumption of the existence and continuity of a germ-plasm.

The development of galls is undoubtedly a highly interesting problem, which, in my opinion, has not yet been fully explained, in spite of the numerous and excellent researches on the subject which have been made within the last ten years. Amongst these, the contributions of Adler * and Beyerinck † in particular have materially helped to throw light on the problem.

The most important point in the consideration of this question is the fact that galls are not by any means exclusively composed of those kinds of cells which occur in the organs of the plants upon which they arise, but may also contain cells of other kinds. 'Cells which are usually only developed in the bark of a plant may also frequently be found in the galls produced by those *Cynipidæ* and *Diptera* which infest leaves.' It is therefore certain that the power of producing forms of cells which do not usually occur in the leaf, for instance, 'is not confined to those organs in which they are developed normally,' but is present also in certain cells of the leaf, and even indeed, de Vries thinks, 'in all other parts of the plant.'

This is not surprising if we look upon the formation of the gall as due to an adaptation of the plant to its parasites, such as we may assume to have occurred with regard to the peculiar arrangements exhibited by certain tropical plants for the protection of ants, which in their turn again protect the plant. Reciprocal adaptation has taken place in this case; the animal has become adapted to the plant, and the plant to the animal, because a joint existence is advantageous to both of them. In the case of the galls of the *Cynipidæ* and *Tenthredinidæ*, the advantage which might result to the plant from the presence of the parasite is not apparent, and we may therefore be inclined

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* Adler, 'Beiträge zur Naturgeschichte der Cynipiden,' Deutsche entomolog. Zeitschr. xxi., 1877, p. 209; and 'Uber den Generationswechsel der Eichengallenwespen,' Zeitschr. f. wiss. Zool., Bd. xxxv., 1880, p. 151.

† M. N. Beyerinck, 'Beobachtungen über die ersten Entwicklungsphasen einiger Cyidipidengallen,' Akademie d. Wiss. zu Amsterdam, 1882; 'Die Galle von Cecidomyia poæ,' Bot. Zeitung, 1885; 'Uber das Cecidium von Nematus capreæ,' Bot. Zeitung, 1888, No. 1.

to explain their formation as due to a reaction of the plant in response to the stimulus exerted by the animal. If, as was formerly supposed, the gall resulted from the action of a poison which is inserted into the tissues of the plant by the female during oviposition, this explanation would be totally inadequate; for it is not conceivable that the infusion of a poison, which happens only *once*, could with such regularity produce a gall which grows slowly, and only gradually attains its definitive and often complex structure. Moreover, several kinds of galls, differing very much from one another, may be produced from the *same* substratum, such as an oak-leaf, for instance. We know, however, from the researches of Adler and Beyerinck, that the formation of the gall is not due to the sting of the parent animal, but to the activity of the larva after it has been hatched. We must therefore suppose that this peculiar specific proliferation of the tissues of the plant is due, in the first instance, to the stimulus produced by the bodies of the larvæ when they begin to move about and to feed, the specific secretion of their salivary glands then also having an effect. The diversity of the galls arising from the same substratum must therefore be due to differences in these factors; and the conspicuous adaptations of the galls, which serve to protect, support, and nourish the parasite, must depend on adaptations of the latter as regards its mode of feeding and movement, and the chemical composition of its salivary secretion. We cannot help accepting this interpretation of the facts since no other is forthcoming; and we must therefore suppose that natural selection has operated so long on these factors, and has gradually effected such an improvement, that the kind of gall which provided the best protection and nourishment for the species was ultimately produced by the larva.

Beyerinck has, in fact, proved that cells and tissues often occur in galls which very closely resemble those in different parts of the plant, but which do not exist in the substratum (*e.g.* a leaf) on which the gall is produced. De Vries infers from this fact that the primary constituents of such tissues must have been contained in the cells of the leaf, although they could not previously be recognised as such. This inference does not seem to me to follow of necessity, for the stimulus produced by the parasite might conceivably have modified the idioplasm of the cells of the leaf so as to result in the formation of cells differing from those ordinarily present in the leaf. It will be shown in the chapter on Variation that changes of this kind do occur, and that somatic idioplasm *may* at times, owing to known or unknown causes, become so modified as to produce a deviation from the inherited form of the cells of the series. The sudden appearance of such peculiarities as those exhibited by the moss-rose may be taken as an instance. It is very possible, therefore, that owing to the specific stimulus produced by the larva, and more especially by its secretion, the idioplasm of certain layers of cells in the gall becomes modified and causes the cells to assume another character, such as that of woody fibres.

This view receives decided support from the circumstance that *the gall is by no means only composed of those kinds of cells which occur in other parts of the plant.* A similar statement to this is, indeed, made by de Vries, who, however, makes an exception in the case of 'the peculiar layer of sclerenchyma in some Cynipid galls, which afterwards becomes modified into thin-walled, nutritive tissue.' I cannot look upon this as being 'only an apparent exception' to the rule, for it seems to me to be a very valuable proof that no such rule exists, and that the above instance is to be explained as an apparent reversion to inherited forms of cells, such as were already contained in a latent condition in the cells of the leaf. I should rather be inclined to regard these 'exceptions' as a proof that *definite new formations occur in galls, and that these are due to modifications of the cells from which they arise* in response to the stimulus produced by the larva. It can hardly be a matter of surprise that a marked resemblance exists between these cells and those occurring in other parts of the plant, for the changes produced by the larva take place in an idioplasm consisting of determinants of the species in question; these changes would not therefore at first result in combinations of biophors (determinants) very different from those which ordinarily occur in the plant. *The new combination of the biophors in different ways results, I believe, from the action of the larva, and thus modifications of the determinants are produced.*

The galls of *Cecidomyia poæ*, which de Vries mentions when contesting my views, are probably to be accounted for in the same manner. In response to the stimulus produced by the larva, these stalk-galls become covered with a thick felt of rootlike outgrowths, which doubtless serve as a protection: these, when they gain access to the soil, become branched like ordinary roots. The assumption that under certain circumstances the idioplasm of certain somatic cells becomes modified in response to the stimulus produced by the parasite, so as to give rise to a structure similar to that of another tissue or even organ of the same plant, seems to me by no means to prove that the primary constituent of this tissue must previously have been contained in these cells. In animal tissues transformations of this kind are certainly not known to occur. Pathological anatomists are now of the opinion that only those kinds of cells occur in tumours which actually belong to the sort of tissue from which the tumour arises. This is not surprising, for tissues of animals are far more highly differentiated than those of plants, and corresponding elements in the idioplasm must also differ in a corresponding degree; and consequently, in spite of the displacements and re-arrangements which may be produced by stimuli, they can never form precisely the same combinations as those which occur in the various other tissues of the body.

I shall not discuss the case of the gall of *Nematus*, as Beyerinck's observations with regard to it are not yet complete. If it should be shown that a complete willow can be produced from the leaf-gall of the plant, as de Vries considers probable, it will then certainly have been proved that the cells in the leaf contain germ-plasm, just as in the case of the leaves of *Begonia*. At present, however, it is only known that the gall can give rise to roots, and although normal roots are always capable of forming adventitious buds, it cannot be said at present whether these abnormal roots are able to do so. In the willow, in any case, the primary constituents of roots are distributed throughout the stem in the form of invisible determinants, contained within visible cells, and this accounts for the fact that the production of new individuals by means of cuttings takes place exceptionally easily in this plant. This may perhaps be accounted for by a wider distribution than usual of the merely 'unalterable' group of determinants for roots taking place in the plant, in connection with the wide distribution of the corresponding primary constituents. But I do not by any means imagine that in all these cases in which the cells of a plant possess inactive germ-plasm, its presence is actually useful *at the present day*. If the distribution of unalterable germ-plasm once took place in an organism to such a considerable extent as has occurred in most plants, it would be a matter of slight importance in the economy of the plant whether the cells of those organs which at the present day are no longer in a condition to make use of this substance were provided with a minimum of germ-plasm or not. Such a provision might have been of advantage to the ancestors of the species; and if this were not the case, we know so little of the processes by means of which the various qualities of the idioplasm become separated mechanically in nuclear division, that we cannot altogether reject the assumption of an occasional chance admixture of germ-plasm to somatic idioplasm, especially in the case of the higher cormophytes, which must in any case possess a number of cells containing germ-plasm throughout the entire plant. Time will show whether we require this assumption.

The difference between my view and that of de Vries does not consist in the fact that I am compelled to deny the admixture of germ-plasm in the case of a large number of cells in the body on principle, but in my assumption that each somatic cell contains a definite somatic idioplasm consisting of a limited number of definite determinants, to which any other 'unalterable' accessory idioplasm may be added if required. De Vries, on the other hand, considers that the whole of the primary constituents of the species are contained in the idioplasm of every, or nearly every, cell of the organism. But he does not explain how it is that each cell nevertheless possesses a specific histological character. A new assumption, which would not be easy to formulate, would therefore be required to explain why only a certain very small portion of the total amount of idioplasm — which is similar in all parts of the plant — becomes active in each cell. This theory explains the differentiation of the body as being due to the disintegration of the determinants accumulated in the germ-plasm, and requires a special assumption, — viz., that of the addition of accessory idioplasm when necessary, — in order to account for the formation of germ-cells, and the processes of gemmation and regeneration. The reconstruction of entire plants or of parts from any point can be easily accounted for by de Vries's hypothesis, just as it can by Darwin's theory of pangenesis, for the pangenes or gemmules are present wherever they are wanted. But de Vries is unable, on the basis of his hypothesis, to offer even an attempt at an explanation of the *diversity* of the cells in kind and of the *differentiation* of the body.

These two assumptions appear to me to be of equal value in explaining the fact that in many of the lower plants each cell, under certain circumstances, can apparently reproduce an entire individual. The differences between the somatic cells are here only slight ones, and are so few in number, that we might be inclined to consider them as due to reactions of the same idioplasm to different kinds of influences exerted by the environment. Such is the case, for instance, in liverworts. But this assumption ceases to be tenable as soon as the soma can become variously differentiated, and any explanation must in the first place account for this differentiation: that is to say, the diversity which always exists amongst these cells and groups of cells arising from the ovum must be referred to some definite principle. De Vries's principle is of no use at all in this case, for it only accounts for the fact that entire plants may, under certain circumstances, arise from individual cells, and does not even touch the main point. In fact, no one could even look upon it as giving a partial solution of the problem, if differentiation is supposed to be due to that part alone of the germ-plasm always becoming active, which is required for the production of the cell or organ under consideration. But the higher we ascend in the organic world, the more limited does the power of producing the whole from separate cells become, and the more do the numerous and varied differentiations of the soma claim our attention and require an explanation in the first instance.

The presence of idioplasm in all parts containing *all* the primary constituents does not help us in this respect; and even in attempting to explain the formation of germ-cells, it is of very little use to assume that they arise from cells which, like the rest, contain all the primary constituents of the species. How is it that these cells, and these alone, in the entire soma of the animal, give rise to germ-cells? In the lower plants the fact of the differentiation of the soma is liable to be overlooked or underrated, but this cannot possibly be the case as regards the higher animals.