

CONTRIBUTIONS TO PHYTOGENESIS,

TRANSLATED FROM THE GERMAN

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THE general fundamental law of human reason, its undeviating tendency to unity in its acquisition of knowledge, has always been evinced in the department which treats of organized bodies as fully as in all other branches of science; and manifold have been the endeavours to establish the analogies between the two great divisions of the animal and vegetable kingdoms. But eminent as the men have been who have devoted their attention to this subject, it cannot be denied that all attempts which have been hitherto made with this view must be regarded as entirely unsuccessful. If, indeed, the fact has of late been pretty generally admitted, still the reason of the circumstance has not always been quite correctly apprehended and put forth in its full precision and clearness. The cause of this, however, is, that the idea of individual, in the sense in which it occurs in animal nature, cannot in any way be applied to the vegetable world. It is only in the very lowest orders of plants, in some *Algæ* and *Fungi* for instance, which consist only of a single cell, that we can speak of an individual in this sense. But every plant developed in any higher degree, is an aggregate of fully individualized, independent, separate beings, even the cells themselves.

Each cell leads a double life: an independent one, pertaining to its own development alone; and another incidental, in

¹ [These first appeared in Müller's *Archiv für Anatomie und Physiologie*, Part II, 1838. But as they have been republished with some additional notes in a collected edition of Schleiden's papers, entitled 'Beiträge zur Botanik,' I have made use of the latter work as my text; with the exception of the notes, I believe it corresponds precisely with the paper in Müller's *Archiv*; which, it is also right I should state, has been already most faithfully translated by Mr. Francis, in Taylor's 'Scientific Memoirs,' vol. ii, Part VI.—TRANSLATOR.]

so far as it has become an integral part of a plant. It is, however, easy to perceive that the vital process of the individual cells must form the very first, absolutely indispensable fundamental basis, both as regards vegetable physiology and comparative physiology in general; and, therefore, in the very first instance, this question especially presents itself: *how does this peculiar little organism, the cell, originate?*

The great importance of the subject is the only excuse I can adduce for venturing at the present moment to publish the following remarks, feeling as I do only too well convinced that more extended researches can alone impart to them their proper scientific value. Perhaps, however, I may succeed by these remarks in drawing attention to this very important subject.

Since no real advance in science results from the attempt to explain natural phenomena hypothetically, and least of all, where all the conditions for the erection of a tenable hypothesis, namely, guiding facts, are wanting, I may omit all historical introduction; for, so far as I am acquainted, no direct observations exist at present upon the development of the cells of plants. Sprengel's pretended primitive cells have long since been shown to be solid granules of amyllum. To enter upon Raspail's work appears to me incompatible with the dignity of science. Whoever feels any desire to do so, may refer to the work itself.

The only work connected with this subject, the highly distinguished one by Mirbel, I shall have occasion to refer to subsequently, since even he does not make any allusion to the process of cell-formation. It is to be regretted that Meyen, who perhaps has studied vegetable anatomy more comprehensively than any one up to the present time, should have confined himself almost exclusively to the investigation of developed forms, and not yet have brought the formative process itself in any degree within the sphere of his enquiries. I still have many doubts, the solution of which I had hoped to have found in his Physiology, but hoped in vain.

It was Robert Brown who, with his comprehensive natural genius, first realized the importance of a phenomenon, which, although observed previously by others, had yet remained totally neglected. He found, in the first instance, in a great

many of the cells in the epidermis of the *Orchideæ*, an opaque spot, named by him *areola*, or *nucleus of the cell*. He subsequently pursued this phenomenon in the earlier stages of the pollen-cells, in the young ovulum, in the tissue of the stigma, not only in the *Orchideæ*, but also in many other *Monocotyledons*, and even in some *Dicotyledons*.

As the constant presence of this *areola* in the cells of very young embryos and in the newly-formed albumen could not fail to strike me in my extensive investigations into the development of the embryo, it was very natural that the consideration of the various modes of its occurrence should lead to the thought, that this nucleus of the cell must hold some close relation to the development of the cell itself. I consequently directed my attention particularly to this point, and was fortunate enough to see my endeavours crowned with success.

Before, however, I proceed to the communication of these observations, I must first give a somewhat more detailed description of the nucleus. As I have to treat of a peculiar and, I think, universal elementary organ of vegetables, I do not consider it necessary to apologise for applying a definite name to this body, and therefore call it *Cytoblast* ($\kappa\upsilon\tau\omicron\varsigma$, $\beta\lambda\alpha\sigma\tau\omicron\varsigma$) in reference to its function, which will be described hereafter.

This formation varies in its outline from oval to circular, according as the solid which it forms passes from the lenticular into the perfectly spheroidal figure. I have found the oval and flat cytoblasts more frequently in *Monocotyledons*, in the albumen and pollen; the globular chiefly in the *Dicotyledons*, and in the leaf, stem, articulated hairs, and similar structures; no exclusive rule, however, can be laid down on this point.

The colour of the cytoblast is in general yellowish, but it sometimes passes into an almost silvery white. I remarked it as being most transparent in the albumen of some water plants, in the unripe pollen, in some *Orchideæ*, and also in the rudiments of the leaf of *Crassula portulaca*. Its excessive transparency renders it scarcely perceptible in the spores of some *Helvelloids*. It is coloured by iodine, according to its various modifications, from a pale yellow to the darkest brown.

It varies considerably in size. It is in general largest in *Monocotyledons*, and in the albumen; and smallest in *Dico-*

tyledons, in the leaf, stem, and their metamorphosed parts. The largest which I have seen measured 0·0022 Paris inch in diameter (in *Fritillaria pyrenaica*); the smallest, in the embryonal extremity of the pollen-tube of *Linum pallescens*, from 0·00009 to 0·0001 Paris inch. In the albumen of *Abies excelsa* I found the average of several admeasurements of examples, which appeared of equal size, to be 0·00034-0·00059-0·00079. In the young leaves of *Crassula portulaca*, 0·0003; and in the albumen of *Pimelea drupacea*, 0·00095-0·001055. Little importance, however, can, on the whole, be attached to these admeasurements, since they increase and diminish, and we cannot determine in what period of its existence the cytoblast may be at the time.

Its internal structure is in general granulous, without, however, the granules, of which it consists, being very clearly distinct from each other. Its consistence is very variable, from such a degree of softness as that it almost dissolves in water, to a firmness which bears a considerable pressure of the compressorium without alteration of form. The more recent its formation, the softer it is; and this also applies to cases in which its existence is merely transitory. It is denser and more sharply defined when it endures throughout the whole vital process of the plant as a permanent tissue, as in the *Orchideæ*.

These peculiarities have been more or less fully described by R. Brown (*Organs and Mode of Fecundation in Orchideæ and Asclepiadæ*; Linn. Trans. 1833, p. 710), and recently by Meyen (*Physiologie, &c.*, Bd. I, p. 207). A phenomenon, however, has escaped both of these most acute observers, which I am notwithstanding disposed to regard as one of the most essential. In very large and beautifully developed cytoblasts, for example, in the recently formed albumen of *Phormium tenax* and *Chamædorea schiedeana* (pl. I, fig. 5), there is observed (whether sunk in the interior or on its surface, is not yet clear to me) a small, sharply defined body, which, judging from the shadow that it casts, appears to represent a thick ring, or a thick-walled hollow globule. In examples which are not so well developed, only the external sharply defined circle of this ring can be observed, and in its centre a dark point; for example, in the stipes of the embryo of *Limnanthes Douglasii*, *Orchis latifolia* (pl. I, fig. 21), *Pimelea drupacea* (figs. 14, 15).

In still smaller cytoblasts it appears only as a sharply circumscribed spot; this is most frequently the case, as in the pollen of *Richardia aethiopica*, in the young embryo of *Linum pallescens*, and in almost all *Orchideæ* (fig. 16); or, lastly, only a remarkable small dark point is observed. I have not, as yet, succeeded in discovering it in the very smallest and most transitory cytoblasts (in the leaves of *Dicotyledons* for instance). I have also found two in some very rare cases, but they occurred as exceptions to the general rule, and always where the majority exhibited the simple nucleus; for example, in *Chamædorea schiedeana* (figs. 6, 7), *Secale cereale*, *Pimelea drupacea* (fig. 14); in the two latter I have sometimes found even three (fig. 15). The observations I have made upon all plants in which it was possible to trace the entire process of formation completely, lead to the conclusion, that these small bodies are formed earlier than the cytoblast (pl. I, figs. 1, 2); and I am almost inclined to conjecture that they are not altogether unallied to the nuclei which Fritsche has shown to exist in starch, and may probably indeed be identical with them.¹ The size of this corpuscle also varies considerably, from the extent of half the diameter of the cytoblast to the most minute point, whose size could not be measured in consequence of the thread in the diaphragm of the microscope exceeding it so much in thickness. In the albumen of *Abies excelsa* I found it to average from 0.000045-0.000095 Paris inch; in *Pimelea drupacea*, from 0.00029-0.0003. Sometimes it appears darker, at others brighter, than the remaining mass of the cytoblasts. In general it has more consistency than the rest of the cytoblast, and continues sharply defined after that has been changed by pressure into an amorphous mass, as in *Pimelea drupacea* for example.

There is a second point, on which I must say a few words, in order to be enabled to express myself more briefly hereafter without being unintelligible, which relates to the different inorganic substances that occur during the vital process of plants, and pertain to the series of starch and woody fibre. I make no pretensions whatever to a complete enumeration of all

¹ More accurate investigation of the structure of the starch granules has shown this supposition to be quite untenable.

the substances which differ in a chemical sense; and just as little do I require that chemists should approve all my terms and characteristics (independent of this, perfection at the present time would be an impracticable task); I shall merely notice in a few words the most important modifications, their consequence and signification in the course of the development of vegetable organization, in order to avoid repetitions in future.

In the plant starch appears almost to take the place of animal fat. It is superfluous nutritive material, which is deposited for future use; and we therefore usually find it in places where a new formative process is to commence after a short repose, or where a too luxuriant life has generated a superabundance of nutritive material. It has of late been the subject of such deep research that it is unnecessary for me to enter upon it more fully; I will merely refer the reader to the most recent and practical summary of the results in Meyen's *Physiologie*, Bd. I, p. 190, &c.

The starch is sometimes supplanted by a semi-granulous substance; for instance, in pollen, the albumen of some plants, and frequently in the cells of the leaf, as matrix of the chlorophylle. It is chiefly distinguished by its occurrence in irregular, granulous forms, which have no internal structure, and from its being coloured a brownish-yellow or brown by tincture of iodine. This substance, which I shall call mucus, is probably identical with that of which the cytoblasts are composed, and with the small granules in gum, which I shall presently mention. Meyen has already remarked the probability of the first supposition (*Physiologie*, Bd. I, p. 208).

But when the starch is to be employed in new formations, it becomes dissolved, in a manner as yet quite unknown in chemistry, into sugar or gum, the latter sometimes appearing to pass into the former, or *vice versá*. The sugar appears in the form of a perfectly transparent fluid, which is almost as clear as water, is not rendered turbid by alcohol, and receives from tincture of iodine only so much colour as corresponds to the strength or weakness of the solution of the reagent.

The gum appears as a somewhat yellowish, more consistent, and less transparent fluid, which is coagulated into granules by tincture of iodine, assuming a pale yellow permanent colour.

In the further progress of organization (in which process the gum is always the last, immediately preceding fluid), a quantity of exceedingly minute granules appear in it, most of which, on account of their minuteness, look like mere black points. Iodine then seems to colour the fluid a somewhat darker yellow. The granules, however, when their size is sufficiently large to render their colour perceptible, become of a dark brownish-yellow under its influence.

It is in this mass that organization always takes place, and the youngest structures are composed of another distinct, perfectly transparent substance, which presents an homogeneous colourless mass when subjected to pressure; when dried it imbibes water and swells; it is not at all affected by tincture of iodine, nor does it ever imbibe it; after pressure it appears as colourless as before, and is so completely transparent as to be altogether invisible when not surrounded by coloured or opaque bodies. This substance frequently occurs in plants (for example, in great quantity, together with a little starch, in peculiar large cells in the tubers of *Orchis*); for brevity's sake I shall call it vegetable gelatine; and am inclined to class under this head, as mere slight modifications, pectine, the basis of gum tragacanth, and many of those substances which are usually enumerated under the term vegetable mucus.

It is this gelatine which is ultimately converted by new chemical changes into the actual cellular membrane, or structures which consist of it in a thickened state, and into the material of vegetable fibre.

I now pass on to our subject itself. There are two situations in the plant in which the formation of new organization may be observed most easily and clearly, in consequence of there being cavities closed by a simple membrane, viz. in the large cell, which subsequently contains the albumen of the seed, the embryonal sac, and in the extremity of the pollen-tube, from which the embryo itself is developed. The embryonal sac never contains starch originally, but probably, in most instances, the saccharine solution (which gives the sweet taste to unripe pod-fruits and the *Cerealia*), or gum.

The pollen, on the contrary, always contains starch, or the above-mentioned granulous mucus representing it, as an essential constituent part. The so-called vegetable spermatozoa

will, probably, on more accurate investigation, be mostly reduced to one of these substances. These substances, however, soon become dissolved, and converted either into sugar or gum; both changes take place at times, even before the pollen-grain has commenced to send forth tubes upon the stigma, frequently during the gradual descent of the pollen-tube through the style to the ovule; so that in some cases unaltered starch may still be found even in the embryonal extremity.

At both these situations the before-mentioned minute mucus-granules are very soon developed in the gum, upon which the solution of gum, hitherto homogeneous, becomes clouded, or when a larger quantity of granules is present, more opaque. Single, larger, more sharply defined granules next become apparent in the mass (fig. 2, the upper part); and very soon afterwards the cytoblasts appear (fig. 2, the lower part), looking like granulous coagulations around the granules. The cytoblasts, however, grow considerably in this free state; and I have observed, in *Fritillaria pyrenaica* for instance, a gradual expansion from 0.00084 to 0.001 Paris inch.

So soon as the cytoblasts have attained their full size, a delicate transparent vesicle rises upon their surface. This is the young cell, which at first represents a very flat segment of a sphere, the plane side of which is formed by the cytoblast, and the convex side by the young cell, which is placed upon it somewhat like a watch-glass upon a watch. In its natural medium it is distinguished almost by this circumstance alone, that the space between its convexity and the cytoblast is perfectly clear and transparent, and probably filled with a watery fluid, and is bounded by the surrounding mucus-granules which have been aggregated together at its first formation, and are pressed back by its expansion, as I have endeavoured to represent it in plate XV, figs. 4, 5, 6. But if these young cells be isolated, the mucus-granules may be almost entirely removed by shaking the stage. They cannot, however, be observed for any length of time, for in a few minutes they become completely dissolved in distilled water, leaving only the cytoblasts behind. The vesicle gradually expands and becomes more consistent (fig. 1, *b*), and, with the exception of the cytoblast, which always forms a portion of it, the wall now consists of gelatine. The entire cell then increases beyond the

margin of the cytoblast, and quickly becomes so large that the latter at last merely appears as a small body enclosed in one of the side walls. At the same time the young cell frequently exhibits highly irregular protrusions (fig. 1, *c*), a proof that the expansion by no means proceeds uniformly from one point. During the progressive growth of the cell, and evidently arising from the pressure of the neighbouring objects, the form becomes more regular, and then also frequently passes into that of the rhomboidal dodecahedron, so beautifully defined *à priori* by Kieser. (Compare fig. 1, from *b* to *e*, with fig. 8.) The cytoblast is still always found enclosed in the cell-wall, in which situation it passes through the entire vital process of the cell which it has formed, if it be not, as is the case in cells which are destined to higher development, absorbed either in its original place, or after having been cast off as a useless member, and dissolved in the cavity of the cell. So far as I could observe, it is only after its absorption that the formation of secondary deposits commences upon the inner surface of the cell-wall (fig. 9).

As a general rule, it is rarely that the cytoblast accompanies the cell which it formed through its entire vital process; nevertheless, it is,

1. Characteristic of the families of the *Orchideæ* and *Cactea*, that in them a portion of their cellular tissue remains in a lower stage of development during the entire period of life.

2. In various plants it occurs that cellular tissue, which has merely a transitory signification, is not perfectly developed, but retains the cytoblast, and is absorbed together with it at a subsequent period. Yet I have also remarked that the latter in the middle period of its existence lost much of its distinctness and sharpness of outline, which, however, reappeared when absorption commenced; for example, in the nucleus of the ovule of *Abies excelsa*, *Tulipa sylvestris*, and *Daphne alpina*. It is most extraordinary that some physiologists should have felt prepared to deny the fact, that absorption takes place in plants, since even very considerable portions of cellular tissue of the nucleus of the ovule, for instance, become completely fluid again, and are received into the common mass of the sap. It is true this only takes place so long as the cell still consists of the simple original membrane, and is not so far advanced

in its individual development that its wall is thickened by secondary deposits.

3. The cytoblasts also remain persistent in the pollen-granules in some rare instances; such is the case in some, perhaps in all the *Abietinæ*. The lenticular cytoblast has already been observed by Fritsche in *Larix europæa*, but the true nature of it was not recognised.

4. Lastly, many hairs, particularly such as exhibit motions of the sap within their cells, retain the cytoblasts (*c, f*, fig. 25). It is at the same time remarkable, and a proof of the close relation which the cytoblast bears to the whole vital activity of the cell, that the little currents which frequently cover the entire wall like a network, always proceed from and return to it, and that when *in statu integro* it is never situated without the currents (fig. 25).

I have observed the above-described development of the cells throughout its entire course in the albumen of *Chamadorea schiedeana*, *Phormium tenax*, *Fritillaria pyrenaica*, *Tulipa sylvestris*, *Elymus arenarius*, *Secale cereale*, *Leucoji spec.*, *Abies excelsa*, *Larix europæa*, *Euphorbia pallida*, *Ricinus leucocarpa*, *Momordica elaterium*, and in the embryonal extremity of the pollen-tube of *Linum pallescens*, *Oenothera crassipes*, and many other plants. It was in the summer of 1837, after this treatise had been written, that I first began to examine the *Leguminosæ*, and found to my surprise that these plants, so constantly investigated and everywhere employed as illustrations for the history of vegetable development, afforded the most beautiful and ready opportunities for the study of this process, which had been overlooked by all observers. No one, however, had considered the saccharine fluid contained in the embryonal sac as worthy of examination.

Without exactly tracing the entire course of the formation of the cells through all its details, I found the cell-nuclei, previous to the appearance of the cells, floating loose in the fluid in very many plants. Finally, I have not met with a single example of newly-developed cellular tissue, the cambium excepted, in which the cytoblasts were wanting. I therefore consider that I am justified in assuming the process above described to be the universal law for the formation of the vegetable cellular tissue in the *Phanerogamia*.

My observations are much more limited with respect to the *Cryptogamia*; nevertheless, I found the cytoblasts in the sporidia of the *Helvelloids*, where, however, in consequence of their great transparency, they are only perceptible with a very strong magnifying power, and after the field has been much darkened. I have seen them in the large yellowish cells in the interior of the so-called anthers in *Chara vulgaris*. I also observed their development into cells in the sporules of *Marchantia polymorpha*, one of which, pushing the original wall of the sporule before it, forms the long capillary root (pl. I, figs. 18-20).

It is evident from the foregoing, that the cytoblast can never lie free in the interior of the cell, but is always enclosed in the cell-wall, and (so far as we can learn from the observation of those cytoblasts which are sufficiently large to allow of this very difficult investigation) in such a manner that the wall of the cell splits into two laminae, one of which passes exterior, and the other interior to the cytoblasts. That upon the inner side is generally the more delicate, and in most instances only gelatinous, and is also absorbed simultaneously with the cytoblast (figs. 8, 16, 21). In making a section, they are sometimes detached and scattered over the object, which might lead to the supposition that they lay free. It is probable also that subsequently, when absorption commences, they do become disengaged from their connexion with the cell-wall, and a slight touch may then be sufficient to move them from this position. The cell-wall is often considerably thickened in their neighbourhood, especially when they are somewhat globular; for instance, in the pollen-tube, which has become cellular in certain *Orchideæ* (figs. 16, 20).

Meyen, who should always be consulted with reference to anatomical questions, has endeavoured, in his *Physiologic*, vol. i, p. 45, &c., to establish the opinion, that the cell is formed of spiral fibres which lie closely one upon another, founding his view in a most ingenious manner upon his own beautiful observations on the relations of structure in fully-developed cells. My direct observation, which may easily be repeated by every one, shows, it is true, quite a different mode of formation; I must, however, bring the facts related by Meyen into unison with my discovery, in order not to permit an apparent contradiction to remain unresolved.

Meyen himself correctly observes, when treating of those spiral tubes whose very narrow fibres lie close upon one another, that an enveloping membrane could not indeed be observed, but that this by no means justified our concluding on its absence. For if the thickenings of the cell-walls which are formed in most, perhaps in all, cases in spiral lines, in those instances in which they make their appearance early, whilst the original cell-wall itself is yet *in statu nascentie* and soft, become firmly connected with the latter; and if at the same time the separate coils of the spiral fibre lie perfectly close one upon another, so that with our present microscopes no space remains perceptible between them,—it naturally follows that on tearing the entire membrane (the so-called unrolling of the spiral vessels), the fracture in the direction of the coils of the fibre must be so sharp that our instruments could not possibly show the inequalities. At the same time it should be remembered that the original cell-membrane, especially in long hair-cells, frequently undergoes so great an expansion that it must at last become infinitely delicate, so that even the thinnest and apparently most simple cell-wall does not exclude the possibility of its being composed of the original membrane and the secondary deposit. If, then, we proceed from those spiral cells and vessels whose coils are so far distant from one another as to admit of no doubt with respect to the existence of an external enveloping membrane, and if we trace the presence of this membrane through all the forms of the constantly approximating coils of the fibre, until only the feebleness of our optical instrument renders further direct observation impossible, the laws of sound analogy require that we should, in such instances, also admit the presence of a similar membrane. There is yet a more direct mode of proof, namely, the investigation of the history of the development.

It is an altogether absolute law, that every cell (setting aside the cambium for the present) must make its first appearance in the form of a very minute vesicle, and gradually expand to the size which it presents in the fully-developed condition; an extended investigation of this formative process also invariably shows that a cell never exhibits a trace of spiral formation, discoverable either from its aspect, or on tearing it, previous to its complete development, i.e. before

it has absorbed the cytoblast. In all spiral cells, particularly such as exhibit detached fibres, we find the walls of the fully-developed cells to be perfectly simple at the commencement. For instance, I remarked this in the outer parchment-like layer of all aerial roots.¹ Meyen discovered the spiral fibres in *Oncidium altissimum*, *Acropera Loddigesii*, *Brassavola cordata*, *Cyrtopodium speciosum*, *Aërides odorata*, *Epidendron elongatum*, *Cattleya Forbesii*, *Colax Harrisonii*, and *Pothos crassinervia*. This is still more evident in the true cortical layer of those aerial roots, where I discovered in *Colax*, *Cyrtopodium*, and *Acropera* the far more beautifully developed and much broader spiral fibres. There is no trace of them to be found in quite young aerial roots, and their formation pertains decidedly to a process of lignification.

We find further evidence that the spiral fibres do not occur until a subsequent period in the pericarp of the *Casuarinæ*, the cells of which, previous to or shortly after impregnation, do not evince a trace of spiral formation. Meyen, in his *Physiologie*, has taken too little notice of these fibre-cells in the envelopes of many seeds, which is the more to be regretted, as these interesting and sometimes extremely pretty formations promise some explanation respecting the physiology of the cell-life, especially if the opportunity should occur of investigating the individual development of several of them accurately. I may be permitted to communicate a few observations on this subject.

Their occurrence is more extensive than is generally supposed. They are found in the hairs of the pericarp in some *Compositæ*, where they were found by Lessing in *Perdicium taraxaci* and *Senecio flaccidus*, and by myself in *Trichocline humilis* and *heterophylla*.

¹ Meyen, in his *Phytotomie*, p. 163, called this an outer cortical layer, which was situated on the true epidermis of the aerial roots. Some doubts have recently been raised as to the correctness of this view. It may, however, be almost incontestably proved, since the cellular layer, which Meyen calls epidermis, possesses actual stomata, which, in consequence of their being covered, usually indeed occur only in a rudimental form, frequently exhibit a more complicated structure, although deviating only in appearance, as in *Aërides odorata*, but often likewise appear of quite the ordinary form, as in *Pothos crassinervia*. Moreover it was not Dutrochet, as would seem from Meyen's *Physiologie*, p. 48, but Link, who first drew attention to this layer.

They occur in the epidermis of the pericarp in many *Labiatae*, as in *Ziziphora*, *Ocymum*; in most *Salviae*, for instance, *limbata*, *hispanica*, *Spielmanni*, &c.; and lastly, in *Horminum pyrenaicum*. My uncle Horkel was familiar with them in all these many years ago; Baxter noticed and published their occurrence in *Salvia verbenacea* only. I can add to these *Dracocephalum moldavica*.

R. Brown discovered them in the parenchyma of the pericarp in the *Casuarinae*, and I in the spongy inflated cellular tissue in *Picridium vulgare*, where they mostly occur in a reticular form, and present an extremely beautiful appearance.

Horkel also discovered them in the epidermis of the seed itself in the *Polemoniaceae* long before Lindley made known their presence in *Collomia linearis*. They occur in *Collomia*, *Gilia*, *Ipomopsis*, *Polemonium*, *Cantua*, *Caldasia*, and perhaps in the entire family, with the exception of *Phlox*, with which genus *Leptosiphon*, in which are the first indications of them, is closely allied. Horkel had also studied them in the seeds of *Hydrocharis*, where they occur in the highest degree of development, long before Nees von Esenbeck published the fact. Robert Brown mentions them in the *Orchideae*, which statement I find confirmed as to most of our native species of *Orchis*. I have also discovered very beautiful spiral fibre-cells in the epidermis of the seed of *Momordica elaterium*, and a very delicate reticular formation of fibres in *Linaria vulgaris*, *Datura stramonium*, in *Salviae*, and in several other *Labiatae*; probably it is common to the whole family.

Lastly, they occur, according to Horkel's discovery, in the parenchyma of the integuments of the seed in *Cassya* and *Punica*.

Whether these formations be studied in their individual development in a single species, or in their progressive stages in a series of allied plants, some highly interesting general results will be obtained in either case. The universal and altogether absolute fact at which we first arrive is, that the fibres are never formed free, but are developed in the interior of cells; and that the walls of these cells in the young state are simple, and generally very delicate. Corda's statement respecting spiral cells without an enveloping membrane (*Ueber*

Spiral faserzellen, &c., pp. 7, 8) is based upon inaccurate observation.

These cells are at first generally filled with starch; rarely with mucus or gum. The starch always passes into the latter substance in the progress of development; and this is converted into jelly, the change, as it would seem, taking place from without inwards. This jelly finally is converted at its outer surface into vegetable fibre, following the direction of a spiral line, the coils of which are sometimes narrower, sometimes wider. When these forms are observed in their different stages of development and in their various conditions, the idea involuntarily forces itself upon the mind that the spiral formation is the result of a spiral movement of a fluid on the walls of cells between them and the central jelly. Horkel once actually observed the motion of small globules between the coils of the fibre in progress of formation in *Hydrocharis*.

The great variety in the appearance of the fibres seems to depend upon the period of their origin, and on modification in the chemical changes of the formative material. It probably depends solely upon the former circumstance whether the spiral fibre lies free in the cell, when it is formed very late, or whether it is blended with the membrane of the cell, if its development commence at a period when the cell-membrane itself is yet very soft and gelatinous, and may consequently become agglutinated to the fibre, which is likewise still in a gelatinous state.¹ This is the case in *Casuarina*, *Cassyltha*, *Hydrocharis*, *Trichocline*, *Orchis*, &c.; in most cases, however, the cell-wall is too far developed to unite with the fibre, and the latter then lies loose in the interior of the cell. In rarer instances the material is almost entirely applied to the formation of the fibre (always indeed when the fibre coalesces with the wall), for example, in *Salvia Spielmanni*, *Momordica elaterium*. I have reason to suppose that this complete consumption almost always takes place in spiral vessels, and is the cause of their subsequently conveying only air. More frequently, however, one or more fibres are formed; but then a great portion of the jelly has still remained uncon-

¹ Subsequent researches have produced important modifications in this opinion. Consult my essay on the Spiral Formations in Vegetable Cells. *Flora*, 1839, Nos 21, 22, Pl. V.

sumed, which, when the cell is moistened with water, comes forth in form of an intestine (wie ein Darm hervortritt), and in swelling expands itself over the fibres, thus appearing to surround them; this is the case in most *Salviæ* and *Polemoniaceæ*, in *Senecio flaccidus*, *Ocimum polystachyum* and *polycladum* (*Lumnitzera*, Jacq.) There is an intermediate form between this and the former, when the jelly itself forms a broad spirally-wound band, which appear upon its surface to be composed of innumerable delicate fibres; their occurrence in this state is very beautifully shown in *Perdicium Taraxaci* and *Ziziphora*. A still less advanced stage of development exhibits merely a cylinder or cone of gelatine in the interior of the cell, the surface of which, however, is marked with delicate spiral lines. This is seen in some *Salviæ*, in *S. verticillata* for example, and in *Leptosiphon androsaceum*. Finally, the lowest stage of development is where the gelatinous cylinder, which is furnished with spiral striæ, has a cavity in its interior containing starch, which has not as yet undergone decomposition; this instructive phenomenon is found in *Dracocephalum moldavica*, *Ocimum basilicum*, and some allied species. In illustration of the above, consult plate 2, figs. 1-10, with their explanations.

Before quitting the subject of spiral fibre, I will merely add, what indeed has been of late admitted by every good observer, that the only difference between spiral cell and spiral vessel consists in the dimensions, although constant transitions may be observed between them just as well as between the cells of the liber and the parenchyma; and consequently, as regards this doctrine at least, there is no longer any place for natural-philosophical phantasies about the arrestment of ideal forms of higher types, and such like empty words. That which forms a liber-cell out of a round cell, the preponderating expansion of an organ lengthwise, is also that which transforms the spiral cells (the vermiform bodies) into spiral vessels. The function of the spiral fibre, however, is, as every candid vegetable physiologist will certainly admit, entirely unknown to us at the present time. It is certain that spiral vessels and spiral cells occur in the living plant quite as frequently filled with sap (in the younger vegetating portions) as with air (in the older organs which have attained their full size); and it is this which has

given rise to the conflicting views of authors. But the same also occurs in all cells under certain circumstances, and the influence of the spiral fibre remains meanwhile altogether obscure and unexplained. Perhaps the foregoing may render it probable that the spiral is everywhere only a secondary variation of form in the product of the vital power (the fibrin) produced by a different tendency of the vital activity of the cell, so soon as this is compelled, as a certain stage of its development, to give up its independent individuality, and enter as an integral portion into the complex of the entire plant.

I also think that we may venture, in conclusion, to deduce from the data above enumerated, that this indication of a spiral formation is the surest sign that we have no longer anything to do with the simple cell-membrane.

I now return, after this somewhat lengthy digression, to my subject. The process of cell-formation, which I have just endeavoured to describe in detail, is that which I have observed in most of the plants which I have investigated. There are, however, some modifications of this process which make the observation of many parts very difficult, and sometimes indeed render it impossible, although, notwithstanding this, the law remains undisturbed and universally valid, because analogy requires it, and we can fully explain the causes of the impossibility of direct observation.

The difficulties which I now notice depend especially upon the physical and chemical properties of the substance which precedes the formation of cells. The materials enumerated above are to be regarded as scarcely anything more than separate facts, which, for the purpose of giving a general view and rendering the classification more easy, I have intentionally selected from the organic chemical processes of vegetable life, which are constantly in operation, and with which we are as yet totally unacquainted. Almost all these materials constantly exist together in the living plant, and it is merely their preponderance in a greater or lesser degree which enables us to say that the cell contains amyllum or gum, and so forth. Only towards the termination of the individual life of the cells do we find them filled with a less number of different substances; the cells which contain ethereal oil are probably the only instances in which we find but a single one.

If we now assume a cell to be completely filled with a transparent solution of sugar in which there is rapidly generated just so much gum, as may form, by an equally quick conversion into jelly, a delicate cell-membrane, the existence of which we cannot possibly recognise with the microscope, in consequence of the similar refracting power of the wall, the contents, and the surrounding medium; it then becomes exceedingly probable that a number of such formative processes may go on which escape our observation, and become known to us only in their results, when, after the absorption of the parent-cell, we suddenly find two new ones in its place. If, on the other hand, our attention has been previously directed to this process, we have, in the application of reagents, especially iodine, which is quite indispensable to the physiological botanist, several means of rendering it visible in instances where it is suspected to be going forward. Gradual transition to the completely invisible processes are readily found by more extended investigation; I will just mention one of the most difficult instances which I have met with, by way of example. It occurs in the germination of the sporules of *Marchantia polymorpha*. Only a few, generally only from two to four of the cell-nuclei which appear in the sporules, serve for the formation of cells; the others become quickly enveloped with chlorophyll, and are thus withdrawn from the vital process. The transparent fluid, however, in which these cytoblasts float, passes through the remaining stages of the metamorphosis into cell-membrane only just at the boundary of the latter, and with such rapidity that the exceedingly delicate young cells cannot be distinguished by anything else than a minute, generally more or less uninterrupted circle of infinitely small, black granules, and by a scarcely perceptible greater transparency of the contents of the newly-formed cells in comparison with that of the parent-cell, and finally, under the most favorable circumstances, by the spot at which the newly-developed cells come into contact, the point of juncture being still covered by the membrane of the parent-cell. (Pl. I, figs. 18-20.) This may perhaps be general in the *Cryptogamia*, and especially in water plants, and probably Mohl's division of the cells of *Confervæ* may be thus explained.

If we consider, however, that there are undoubtedly many plants, among which the *Fungi* and infusorial *Alge* should pro-

bably be classed more especially, in which we are, as yet at least, totally unacquainted with the cytoblasts, in consequence of their absolute minuteness and transparency; if we further bear in mind that the nucleolus in the cell-germ, even in the larger cytoblasts, frequently appears immeasurably small, or even entirely escapes the eye with the highest magnifying power; and, lastly, if we deduce from what has been previously stated, that nevertheless this granule, which can no longer be rendered perceptible, probably furnishes in the suitable medium a sufficing cause for the formation of a cytoblast which serves as an introduction to the whole formative process of the cells; then, indeed, we are forced to confess that the imagination obtains ample latitude for the explanation in every case of the generation of infusorial vegetable structure, even without the aid of a *deus ex machina* (the *generatio spontanea*). But my present object is to communicate only facts and their immediate consequences, and not to dream; I will therefore rather add a few more observations on the growth of the plant.

What is meant by to grow? is a question to which every child quickly replies, "when I am getting as big as father." There is truth in this answer, but not sufficient to satisfy science. Words have no value in themselves, but are like coin, merely tokens of a value not exhibited in specie, in order to facilitate commerce. And to carry the simile further, insecurity in this intellectual property, and frequently bankruptcy results, if this coinage has not its unchangeable, accurately-determined standard; in a word, the utility of a scientific expression depends upon the accurate definition of the idea on which it is based. Unfortunately the perplexity of our social relations has caused us to forget entirely the original meaning of money, the sign has become to us the thing itself; may some good genius protect us from similar mistakes in our intellectual life. We must here be on our guard against two dangerous rocks: first, when we transfer words from one science to another, without first accurately testing whether they fit their new situation as respects all their accompanying significations also; and, secondly, when we voluntarily lose sight of the signification of a word consecrated by the spirit of the language and its historical development, and employ it without further cere-

mony in compound words, where perhaps, at the most, only some unessential part of its signification suits.

Thus E. Meyer, for example (Linnæa, vol. vii, p. 454), after repeating the well-known experiments of Duhamel, lays down this position: "the law of the longitudinal growth of the internodes is to grow in a direction from above downwards." He requires this position for his theory, and must consequently defend it in every way, although he himself confesses that this reversed growth must appear paradoxical to every one of his readers. He would never have arrived at this position if he had more accurately analysed the word "grow" (with which animal physiology had rendered him familiar), with reference to its applicability to the plant; he would soon have discovered that the generation of new cells, and so far the actual growth of the plant, constantly takes place in its outermost portions in an upward direction, and that his very simile of the building up a voltaic pile is exceedingly well adapted to refute himself. The experiments of Duhamel and Meyer would have no further result than to show that the inferior, that is, the earliest generated, older cells of the internode possess a greater capability to extend in the longitudinal direction, and retain this power longer than the younger cells.

We have an excellent illustration of the second point in the proposition so frequently expressed of late, that the stem of the plant is composed of the *coalesced* petioles. The word "coalesce" (*verwachsen*, to grow together) has possessed, however, from time immemorial, both in ordinary life and in science, the signification that two or more originally and naturally separate parts have become by the process of growth either abnormally or, under certain circumstances, normally united. If therefore the word "coalesce" be applied to the stem of the plant, an organ, which, in every period of its existence, under all forms of its appearance, is a simple and undivided one, and at the origin of the plant even constantly appears earlier than the leaves with their petioles, it certainly involves a mischievous abuse of language, by which science itself can gain nothing, and will even lose in the estimation of the intelligent non-professional man, who sees through such a play upon words. What would the zoologist say were we to regard the trunk as a coalescence of the extremities.

I return then to my question: what is the meaning of to grow? In hackneyed phrase we are told, "To grow signifies increase of the mass of an individual, and takes place in the inorganic world by juxtaposition, in the organic by intussusception." Have we gained anything for vegetable physiology by this reply? I think not. If the plant is to grow by intussusception, then I say it consists of an aggregate of single, independent, organic molecules, the cells; it increases its mass by new cells being deposited upon those already existing; consequently by juxtaposition. But the single cell in the progress of its expansion, which frequently reaches an enormous bulk in comparison with its original size (I will merely remind the reader of the pollen-tubes), also increases in substance in the interior of its membrane, and by this means also the mass of the entire plant is increased; it consequently grows by intussusception also. Finally, after a certain period the cell deposits new organic material in layers upon its primitive membrane; thus another form of juxtaposition, which still, however, belongs to the cycle of vegetable vitality. It hence becomes readily apparent that, in respect to scientific botany, the idea "grow" still requires a new foundation in order to be capable of being applied with certainty.

Of the three instances just cited, the second and third belong more to the individual life of the cells, and are of secondary importance only, as respects the idea of the whole plant, regarded as an organism composed of a certain number of cells. The plant considered in its totality increases its mass, that is, the number of the cells composing it, in the first way only.

We must therefore here discriminate three processes essentially distinct from each other in a physiological sense, which, when strictly regarded, scarcely find an analogy in the other kingdoms of nature.

1. The plant grows, that is, it produces the number of cells allotted to it.

2. The plant unfolds itself by the expansion and development of the cells already formed. It is this phenomenon especially, one altogether peculiar to plants, which, because it depends upon the fact of their being composed of cells, can never occur in any, not even the most remote form in crystals or animals.

3. The walls of the fully-developed cells become thickened by the deposition of new matter in layers, a process which, in accordance with the old rule, *a potiori fit denominatio*, may be most aptly termed the lignification of the plant.

If, in respect to the growth of the plant, we now hold to the literal sense conveyed under No. 1, then this question must arise,—Where are the new cells formed? Here three instances comprise all possible replies. Namely, the new cells are either formed outside on the surface of the entire previous mass, or in its interior; and in that case again either in the intercellular spaces or in the cells themselves; *quartum non datur*.

Mirbel, in two extremely ingenious and profound memoirs on the *Marchantia polymorpha*, which he presented to the French Academy in 1831 and 1832 (p. 32), has expressed the opinion, that all the three cases just now mentioned as possible do actually occur in plants. Without intending here to anticipate what follows, I must remark that only one case (the formation of new cells within the old ones) appears to be proved by his direct observations. The second case is merely a conclusion drawn, and the germination of the sporules of the *Marchantia*, which was to elucidate the third case, has been observed by me to be quite different, as I have already represented above.

Finally, however, we have yet to examine whether the difference of the organs may not establish such a physiological difference of growth as may merit our attention. We may distinguish here four instances. We observe: 1. The development of the plants in the upward direction (*in puncto vegetationis*, C. Fr. Wolff). 2. The elongation downwards. We thus comprise the formation of the necessary organs of the plant, the stem, the leaves (with their metamorphoses), and the root. 3. We have to keep in view the production of accidental organs, for example, bulbs, &c. And, 4. We find an annual thickening of the axile formations, the development of the woody stem.

Let us now see which of the three possible modes of formation of new cells is actually realised in each of the cases just enumerated. I have already explained how the new cells are developed in the embryonal sac; in other words, within a large

cell. A similar process occurs in the embryonal end of the pollen-tube, consequently in a highly elongated cell; I shall now proceed to describe the further development of the embryo. After the first cells, generally few in number, are formed, they rapidly expand to such an extent that they fill the pollen-tube, which soon ceases to be perceptible as the original enveloping membrane; but at the same time several cytoblasts originate in the interior of each of these cells, and generate new cells, on the rapid expansion of which the parent-cells also cease to be visible and become absorbed. The same process is repeated indefinitely. But since the newly-generated cells have continually less room to expand, and therefore constantly become smaller, the previous transparency is soon lost in consequence of the continual production of new cytoblasts in the interior, and the tissue becoming more and more compressed; and from this stage to the perfect completion of the embryo we are conducted by the clearly logical inference that the process thus introduced continues the same, since no new force comes into operation which could induce us to assume a sudden variation of the vital action, more especially as we soon meet with the same manifestation of the vegetative power again.

Meanwhile the seed germinates, and the embryo becomes a plant; and then indeed the question may arise,—Does the process of life continue the same thenceforward in the internodes and foliaceous organs? Now we are here very quickly convinced of the negative, that is, that a formation of new cells on the surface of the existing organs does not take place. The surface is always smooth, and generally covered in a very early state with a kind of epidermis, the outer layer being more transparent and almost as clear as water; and we never find even an indication of a newly-formed cell upon the surface.

But if the embryo be the type of the entire plant, and the latter do not present anything which is not a repetition of its organs, if we have found the growth of the embryo to consist only in the formation of cells within cells, we may then expect to find the same result also in the process of the growth of the whole plant. It is especially a foliaceous organ, the anther, which has hitherto been studied and followed in its development by many celebrated men (particularly well by Mirbel); and here it is quite decided that the increase of cells takes

place within the old ones. It is also certain that in this case the formative process accords with that above described. R. Brown and Meyen have enumerated many instances where they observed the cytoblast in very young pollen-cells. In *Pinus*, *Abies*, *Podostemon*, *Lupinus* and others, I have traced the development of the pollen after Mirbel perfectly; I have distinctly observed the cell-nuclei and their development into new cells within one another in *Abies*, never having missed the cytoblast in young cells.

Now if the pollen-grains be nothing more than converted leaf-parenchyma, if the anther be merely a metamorphosis of the leaf, we may certainly infer inversely that the process which we have observed in it, and which characterized the formation of the embryo and cotyledons (as prototypes of the leaf) will be again found in all foliaceous organs. For the same reason which was stated with respect to the later stages of the development of the embryo, actual observation is infinitely difficult in this case. I have nevertheless examined a great many buds in reference to this point, and have most decidedly convinced myself of the identity of the process both in the constantly elongating apex of the axis, and in the leaves which always originate somewhat beneath it. Succulent plants, the *Aloineæ* and *Crassulaceæ*, are best adapted for this purpose. *Crassula Portulaca* seemed to me most advantageous, for in it I first succeeded in separating some cells from their connexion, in whose interior young cells were already developed, without, however, entirely filling the parent-cell. But having once become familiar with the subject, I was afterwards able to detect these individualities from amongst the apparently semi-organised chaos in all other plants. Another circumstance indeed presents itself here, which renders the subject much more difficult than in the case of the embryo. For, independently of the minuteness of the cells, their walls, in those parts of the plant which are just newly formed, still consist merely of jelly, and are so delicate that it is exceedingly difficult to separate the parts intended for examination without completely destroying the organization. (Compare plate I, figs. 22-4.)

This process is more easily perceptible in articulated hairs, and in such as have a head consisting of several cells, where the same appearances which I have so frequently observed in

the young embryo, and such as Mirbel has so beautifully described in the development of the gemmæ in the cups of *Marchantia*, may be readily and beautifully seen; for example, in the common potato. Meyen has also made similar observations, although he still expresses himself with some doubt on the subject. (Wiegmann's Archiv, 1837, vol. ii, p. 22.)

It is not until after as many cells are formed as the organ requires for its completion that the cell-walls become firmer, and then commences the unfolding of the organ by the mere expansion of the cells already formed.

But I must here enter somewhat more into detail, in order to explain the probable origin of the vascular bundles and epidermis. At a somewhat early period a stripe of more transparent cells is defined in the axis of the leaf which is in the act of formation, within which no more new ones are developed, and these cells soon considerably exceed in size those of the remaining mass, which are constantly becoming smaller by continual division. These cells are the basis of the future vascular bundle which forms the midrib of the leaf; for whilst the parenchymatous cells subsequently expand in every direction, these are developed in their longitudinal dimension only, and are thus enabled, although fewer in number, to follow the expansion of the other cells in the longitudinal direction of the leaf. It is not till a later period that these cells, in consequence of a difference in the depositions in their interior, become distinguished into spiral vessels and cells of the liber. The spiral vessels are always first perceptible in the newly-formed parts, and in the entire bud also, in the immediate neighbourhood of the old, previously-formed spiral vessels; and they proceed in this manner downwards from the stem into the new parts. I do not understand therefore what is intended when the fibres of the stem are regarded as descending from the buds; one might just as well conceive the river to run from the ocean to its source.

A similar process occurs in the development of the side nerves of leaves. The formation of new cells generally ceases at an early period in the outermost layers of cells. The cells there are soon filled with a limpid fluid, and, by the expansion of the subjacent parenchyma, naturally become superficial, flat, and expanded.

The cells of the vascular bundle and of the epidermis appear in this way to be less potentialized,—are as it were cells of lower dignity than those of the parenchyma; and perhaps this physiological peculiarity is connected with the fact, that they more rarely secrete peculiar chemical substances, but for the most part become thickened only by depositions within their walls of new vegetable fibrous (or more correctly membranous) substance. I cannot forbear venturing some suggestions in this place, which are perhaps less closely connected with the subject of this memoir, but which may possibly at some future time be of importance for the understanding of the entire plant. Let us recapitulate the process of growth of the plant just now represented. A simple cell, the pollen-tube, is its first foundation. Within this, cells are generated; in them new cells are developed, and so forth, throughout the entire life. But here the above-mentioned mode of the origin of the vascular bundles and of the epidermis in relation to the parenchyma would indicate, that the lower the dignity of the cell, the greater power does it possess, in the first place, of expanding and extending in length, and the less capacity does it possess, in the second place, of forming peculiar finer substances in its interior. If now the potentialization (potenzirung) of the cells proceed throughout the entire growth of the plant, there thence results a constantly advancing approximation of organs otherwise kept asunder, and continually rising ennoblement of the substances developed in the cells. Consequently, the lower parts of the internodes will appear to be more elongated than the upper; the leaves and young shoots (*summitates herbarum*, Pharmacol.) to contain nobler saps than the stem; the members become shortened as they approach nearer to the upper terminal point of the plant, the leaves come closer together, and the result of the continually increasing potentialization of the cell, of the constantly diminishing expansion in length, of the constantly advancing approximation of the lateral organs, of the constantly rising ennoblement of the substances developed, is, finally, the flower in its individualised distinctness, with its splendour of colour, its perfume, and its mysterious capacity of determining, by means of its juices, a single cell to be developed afresh into an independent plant, and to pass anew though the same cycle.

I return, after this digression, to my subject. So far I believe I have demonstrated tolerably conclusively, and in accordance with nature, that the entire growth of the plant¹ consists only of a formation of cells within cells. Let us now pass on to the root. I can contribute but very little to the explanation of this part of the subject; for I have not as yet succeeded in arriving at any satisfactory result, from the somewhat limited researches which I have instituted; for instance, I have been altogether unsuccessful in deciding *the* question as to whether a fluid is secreted at the extremity of the radicle, in which new cells are developed. On the other hand, it is certain that there exists in the extremity of the root a concavo-convex mass (a *meniscus*) of cellular tissue, in which the process of cell-formation takes place in the same manner as in the parts of the plants which grow in the ascending direction. A chief cause of the elongation of the root consequently consists in this,—that new cells are continually formed in the interior of the existing cells, on the convex side of that mass of cells, while on the concave side, the cells already formed expand simultaneously, and chiefly indeed in the longitudinal direction, and in this way constantly push the extremity of the root before them.

The third case, the formation of the accidental organs of the plant, I must entirely pass over, as I am altogether unprovided with any personal observations upon the subject. Probably, however, the process here is the same as in the previous cases, for Meyen (*Physiologie*, vol. i, p. 209) observed the cell-nuclei in germinating tubers of *Orchideæ*. Analogy also leads to a similar conclusion, since all these parts are nothing more than morphological modifications of organs which have been already treated of in this memoir. The fourth point, however, still remains for discussion, namely, the increase in thickness of plants which form woody stems (Dicotyledons). The origin and signification of cambium is the nut on which so many young phytologists have already broken their milk-teeth, the Gordian knot which so many botanical Alexanders have cut instead of untying, and the enigma, for the solution of which almost all the Coryphæi of our science have laboured with more or less

¹ I beg to observe, that generally throughout the entire memoir phænogamous plants only are referred to.

success. My researches also with respect to this newly-arising formative layer between bark and wood are by no means concluded.

Before, however, I proceed to communicate my observations on this subject, it is necessary once more to take up the question of the individuality of plants. I have already remarked above that, in the strictest sense of the word, only the separate cell deserves to be called an individual. If we go a step further, we might define each axis with its lateral organs to be individual beings. If, however, we disregard this circumstance of the plant being composed of cells and similar axes, and conceive the term individual, as applied to the organic world, to signify a body which cannot be divided into two or more similar ones without the abolition of its idea of totality, and whose vital process has a fixed point of commencement and termination in definite periodicity, it thence follows that the herbaceous (*planta annua*) and the true biennial plants, which flower in the second year, and then die off *entirely*, are the only ones which can be regarded as individuals in the vegetable kingdom. The idea of individual life also necessarily requires as a characteristic that individual death should be a condition of the organization itself. But where such a death does not take place as a final termination from internal necessity, as an internal preconditioned cessation of the organizing force, there also must individuality be out of the question. This is the case, however, only in the above-mentioned plants, and from them solely, therefore, as from the *prototype*, must we set out, in all researches into the nature and life of the vegetable organism.

In order to facilitate the transition to what is to follow, I will now proceed to the exposition of the two different modes of propagation. It either takes place by a process which has hitherto been called impregnation in plants, and to which a sexual difference has been ascribed (Wiegmann's Archiv, 1837, vol. i, p. 290, &c.), or by division; the plant, for instance, developing on itself a perfectly similar individual, and then at an appointed time dismissing it. This latter, the formation of so-called bulbilli, &c. occurs, together with the former, in only a small number of plants. We must, however, make ourselves somewhat more intimately acquainted with it. This formation,

for instance, does not always take place in such a manner that the parent plant separates itself entirely from them, and scatters them about singly, but it most frequently forms, previous to its own individual death, a peculiar organ, which places the offspring in a peculiar vital connexion with one another, and at the same time serves as a reservoir for a certain quantity of nutritive material, by which the first development of these young individuals is facilitated. But in most cases this organ is merely a metamorphosis of some other one with which we are already familiar, for example, the stem or the root, or, as in the potato, the axillary buds; and no scientific person has therefore ever hesitated to speak of these things as mere *portions of a plant*, which continue to live as connecting members between the younger *individuals* after the death of that one which has generated them. On the other hand, a different course has been taken, where stem and root simultaneously, and therefore almost the entire totality of the plant, take part in the formation; and although the result in this case may perhaps be that there can be no question at all of an heteromorphy of a known portion of a plant, still the physiological identity in the signification of this and the former part has not been maintained with precision, and the view has thus been obscured.

Most manuals are silent upon this subject, as though it were quite self-evident that the tree was to be regarded as the perfect plant; and I believe it not difficult to prove that, where vegetable physiology still lies very deep in error, this particular misconception is solely in fault. Two entirely distinct ideas have here been confounded, namely, the highest stage of development to which vegetable life can raise itself, and the type upon which the idea of the individual must be based. If, then, the first of these ideas may be maintained with regard to the tree, still the application of the second to it fails completely in every respect, as has been very correctly asserted before by E. Meyer (*Linnæa*, vii, p. 424). It necessarily pertains to the notion of a plant, that it produces foliaceous organs on its stem, yet there is no tree which has leaves. Paradoxical as this may sound, it is still not the less true. It is a fact, of which certainly no botanist is ignorant, that no lignified part of a plant, even though it be only in its second year, is capable

of producing a leaf; but the direct consequence is by no means so generally acknowledged, that for that very reason the woody stem cannot come under the idea of plant. Much confusion has arisen in our physiology from the error of regarding the tree as a *single* plant, the ideal definition of root, stem, bud, &c. have become very vague, and bitter controversies have been carried on with respect to the functions of these parts, which could have no result, because the one party spoke of this, the other of that, this one of the stalk, the other of the stem, this of root-fibrils, that of ligneous root-substance.

The so-called lignified root is, however, just as little a root, as the lignified stem is still a stalk, but both together form an inseparable, and, moreover, altogether purely accidental organ for the plant, which has secreted the annual individual upon its surface, in order to bring into connexion, by means of a single organized membrane, the whole sum of the newly formed young individuals. The tree corresponds precisely to the polypidom, and it appears to me to be as unsound to set out from it as the type in plants, as it would be for the zoologist to take a *Gorgonia* as the ideal of animal individuality. This analogy, however, is in no way weakened by the circumstance, that we meet with this woody stem most frequently in precisely the highest developed plants; but, on the contrary, it is natural that, if the animal kingdom in a certain measure receive the vegetative part of its character from the vegetable kingdom, this should connect itself by the lowest stage of animals to the highest plants, whilst even this vegetative half of the vital phenomena in the higher animals is in like manner purified and ennobled by its individuality constantly gaining in independence.

With this explanation of the woody stem (the root included), it will henceforward appear by no means remarkable that this organ (as if it were a mere organized soil) can generate upon every part of its surface young vegetable individuals; that is, buds, so soon as it is in a condition to convey nutritive material to those buds from any part, whether it correspond apparently to the former root or to the stem; while this refined idea of the plant conducts to the law, that in the regular course of vegetation, neither root nor internode, but only the axilla of the leaf, is capable of generating a bud, i. e., a new axis with lateral organs.

But the following remarks, which in nature (who never, like a bad artist without a plan, fluctuates between the most opposite methods) would be, in the usual mode of treating it, an inexplicable contradiction and an absolute miracle, will serve for the decisive establishment of this view.

So soon as the secretion of this organized mass, the wood, takes place, for instance, we suddenly miss the influence of the law of formation, which, until then, had without exception directed the growth of the entire plant in all its parts. Here, so far as we are at present acquainted with the subject, there is no formation of cells within cells, here no expansion on all sides of the originally minute vesicle occurs, there is here no cyto-blast upon which the young might be developed; but beneath the outermost layer of cells, which are comprised in the term bark, an organisable fluid is poured out, as it were, into a single, large, intercellular space, which fluid, as it seems, consolidates quite suddenly throughout its entire extent into a new, altogether peculiarly-formed tissue of cells, which are deposited one upon another, the so-called prosenchyma. Here, moreover, there is decidedly no formation of vascular bundles from cells of lower dignity, for all of them originate simultaneously and of their full size; and what has been called (spiral) vessels of the wood, is something which differs immensely from the spiral vessels of herbaceous plants, both in respect of their origin, and probably of their physiological signification also.¹ In like manner, no result has been obtained from the controversies which have been sometimes carried on with great warmth respecting the function of spiral vessels, nor could any be gained, because each party meant the spiral vessels of herbaceous plants, or of the wood, *ad libitum*, completely losing sight of the possibility that the two might be very different things. If, for instance, we examine the cambium in the earliest period at which it begins to acquire organisation,

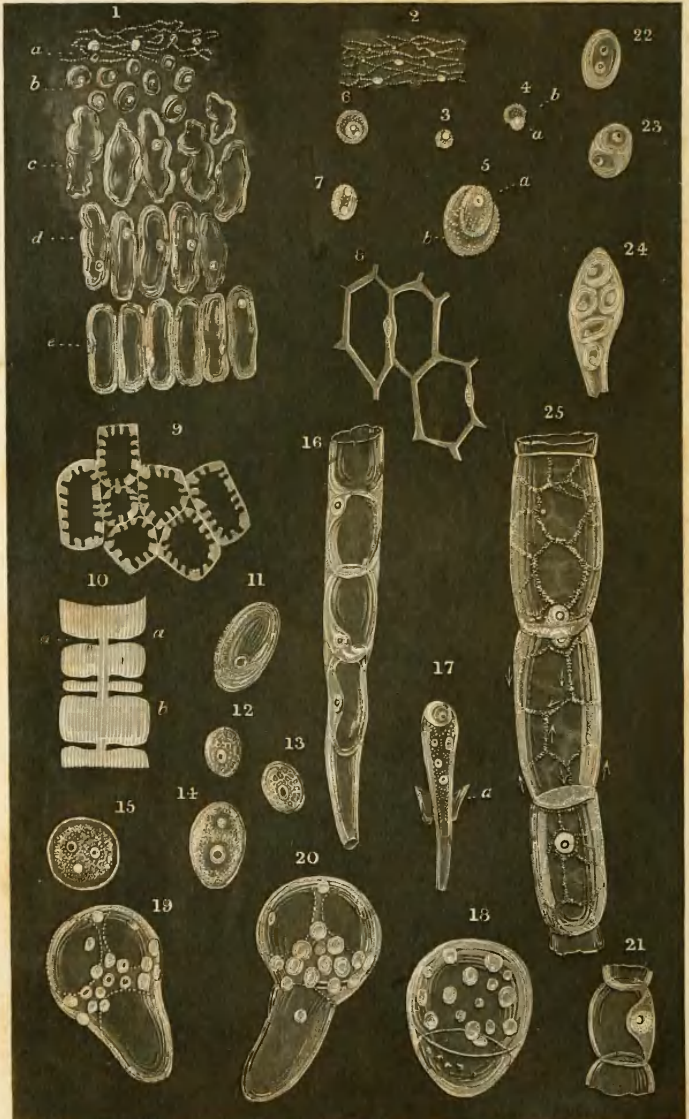
¹ This position has undergone essential modifications, in consequence of subsequent researches which I have made with respect to the cambium, and which proved that a cambium, in the sense in which it had been previously used in physiology, namely, as denoting an amorphous formative fluid between the wood and bark, had no existence at all; that the wood and the bark, on the contrary, form one uninterrupted continuity, and their margin is merely denoted by a layer of delicately-walled, gelatinous cellular tissue.

we find that it consists throughout of gelatinous prosenchymatous cells which perfectly resemble one another. Shortly afterwards, some separate longitudinal rows of these cells appear to have increased somewhat in breadth, which is the only circumstance that distinguishes them from the adjacent mass. As development advances, we observe that some dark spots appear upon the walls of some of these expanded cells, which we soon recognise to be small, flat air-bubbles, that have been formed between their walls and those of the neighbouring cell. Gradually all the expanded cells which are so disposed one upon the other are changed in this way: the air-bubble gradually appears more sharply defined, assuming the circular or oval figure; and there appears in its centre a smaller circle which constantly becomes more distinct, and which originates in the following manner: when the deposition of new masses takes place upon the inner wall of the cell, the parts corresponding to the outer air-bubble remain free from the deposit, thus forming a small canal which traverses the newly-deposited mass. We now recognise the fully-developed porous vessel, the partition walls between each two superincumbent cells appearing at the same time to be more or less absorbed. This history of the formation of the porous vessels, which may readily be observed in limes and willows, greatly contradicts the general notion that the porous canals serve to facilitate the communication of the sap. As the air-bubble is first formed on the outside of the wall, it renders the passage of the sap at that spot impossible, and for this reason the origin of the porous canal might be most readily and naturally explained as a local atrophy of the cell-wall. At the same time the above shows that the distinction between fir-wood and that of trees which bear leaves, in respect to anatomical structure, cannot be of such vast physiological importance; since, with similar elements and development, the distinction is really based on the larger or smaller number of cells that are converted into porous vessels.

There are still, however, a great many gaps to fill up. In particular the origin of the medullary rays, and their relation to the wood; the formation of the new bark; and, lastly, the origin of the buds in the body of the wood, are so many questions for extended researches, to the execution of which, however, we

may look forward at no distant time, when we consider the ardent and gratifying zeal which has been awakened and cherished, especially amongst our contemporaries, in favour of the sound and scientific study of the anatomy and physiology of plants.

I have attempted in this Memoir, so far as lay in my power, to solve many interesting questions in Vegetable Physiology, or, by more accurate definitions of the subject, to advance nearer to a future solution. May these observations meet with a friendly reception at the hands of the vegetable physiologists of Germany, and be speedily improved upon and extended.



EXPLANATION OF THE PLATES.

SCHLEIDEN'S TREATISE.

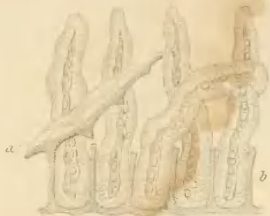
PLATE I.

- Fig. 1. Cellular tissue from the embryo-sac of *Chamadorea Schiedeana* in the act of formation. *a.* The innermost mass, consisting of gum with intermingled mucous granules and cytoblasts. *b.* Newly formed cells, still soluble in distilled water. *c-e.* Further development of the cells, which, with the exception of the cytoblasts, may still coalesce, under slight pressure, into an amorphous mass.
2. The formative substance from fig. 1, *a.*, more highly magnified, gum, mucous granules, nuclei of the cytoblasts, and cytoblasts.
 3. A single and as yet free cytoblast, still more highly magnified.
 4. A cytoblast with the cell forming upon it.
 5. The same, more highly magnified.
 6. The same. The cytoblast here exhibits two nuclei, and is delineated in
 - 7, isolated after the destruction of the cell by pressure.
 8. The same cellular tissue in a higher degree of development than that represented by fig. 1, *e.* The contiguous cell-walls have already united. By making a transverse section, it may be distinctly perceived that the cytoblast is enclosed in the cell-wall.
 9. Cells from a delicate transverse section of the almost matured albumen.

- Fig. 10. Common partition-wall between two cells from fig. 9, under a higher magnifying power. The stratiform depositions may be observed at *b*, and the porous canals produced by their local failure at *a*. I could distinctly enumerate from nine to twelve layers which had been deposited within fourteen days.
11. A sporule from *Rhizina levigata* Fries, with the cytoblast.
- 12, 13, 14. Different cytoblasts from the embryo-sac of *Pimelea drupacea* before the appearance of cells.
15. A young cell with its cytoblast, from the same. The latter in this instance presents the unusual number of three nucleoli.
16. A portion of the embryonal end of the pollen-tube projecting from the ovulum in *Orchis Morio*, within which, towards the upper part, cells have been already developed. At the lower part, the original pollen-tube may still be distinguished. The almost globular cytoblasts are, in this instance, distinctly enclosed in the cell-wall.
17. Embryonal end of the pollen-tube from *Linum pallescens*, together with an appended lobule of the embryo-sac (*a*). The process of the formation of cells is commencing. Above, a young cell with its cytoblast is already perceptible, beneath this several cell-nuclei are seen floating free.
- 18, 19, 20. Commencing germination in the sporules of *Marchantia polymorpha*. Compare the text, p. 248.
21. Portions of the pollen-tube which have become cellular, from *Orchis latifolia*, in the highest stage of development; the investment of the pollen-tube is no longer perceptible. The cytoblast is enclosed in the cell-wall, just as in fig. 16.
- 22 and 23. Two isolated cells from the terminal shoot (*punctum vegetationis*, Wolff) of *Gasteria racemosa*; 22 exhibits two free cytoblasts; 23, two newly-formed cells within the original cell.



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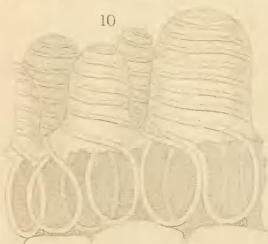
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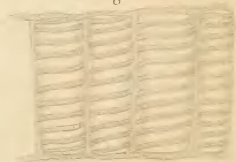


Fig. 24. A very young leaf of *Crassula portulaca*, the five cells which solely compose it being still surrounded by a parent-cell.

25. Three cells from an articulated hair of potato, with a retiform current of mucus upon their walls. In the central cell the direction of the currents is partially indicated by arrows.

In all the instances in which I have observed the movements in the cells of phænogamous plants, I have constantly found the moving matter to consist of a yellowish mucous fluid, perfectly insoluble in distilled water, and mixed with minute black granules, but differing entirely from the other aqueous sap of the cells; and even when the currents were so small as to appear merely as excessively minute delicate lines of black points, I succeeded with higher magnifying powers in distinguishing the yellowish mucous fluid, especially when aided by the favorable circumstance (which not unfrequently occurs) of the current becoming arrested by some impediment, which causes a somewhat larger quantity of the moving material to accumulate, and is generally followed either by a change in the direction, or a division of the current.

PLATE II.

Fig. 1. Cells from the epidermis of the pericarp of *Ocymum basilicum*, moistened with water, so that the mucous globule has expanded, and torn the outer cell-wall (*a*) from the side walls (*b*).

2. Cells from the pericarp of the epidermis of *Ziziphora dasyantha*.

3. Cells from the pericarp of the epidermis of *Salvia verticillata*.

4. Cells from the pericarp of the epidermis of *Salvia Horminum*.

5. Cells from the pericarp of the epidermis of *Salvia Spielmanni*.

2, 3, 4 and 5, *a*, exhibit the remains of the side-walls of the ruptured cells.

6. A portion of the epidermis (*a*) and of the integument (*b*) of the ovule of *Collomia coccinea*. The epidermis-cells contain merely granules of starch.

- Fig. 7. The epidermis-cells of the half-ripe seed of the same plant, for the most part containing gum; at *a*, some still undecomposed starch.
8. The same cells from the same seed nearly ripe. Beautiful spiral fibres have been formed from the contents, which are entirely consumed.
9. Cells of the epidermis of the seed of *Leptosiphon androsaceum*, moistened with water, so that the cone of jelly has come forth. *a*. The remains of the cell-walls.
10. Cells from the epidermis of the seed of *Hydrocharis Morsus ranae*. In the lower part of the cells, where they are connected together, the spiral coils take a direction different from that in the upper and free part.

For the figures in Plate II consult the text, pp. 243-6.

THE END.

