I.—On the Circulation of the Sap in the Interior of Cells.

By Hugo Von Mohl*.

In a series of observations which I made in the course of last summer on the development of the vegetable cell, the results of which it is my intention to communicate on a subsequent occasion when they have been rendered more complete by further investigation, my attention was directed to the phenomena presented by the nitrogenous constituents of the contents of the cell. I had for years endeavoured to obtain a clear insight into the succession of the metamorphoses these substances, which are constantly changing their form, undergo during the development of the cells; but I could not succeed in making out a fixed rule in this respect, not knowing how to separate sufficiently the individual and accidental phenomena from those of constant occurrence. Now although the more recent investigations I have made have not presented me with any appearances which I had not frequently seen before, yet I think I have obtained a definite result, in so far as these observations prove that the successive changes of the nitrogenous substances take place in the great majority of vegetable cells in a perfectly analogous manner.

If we consider the place at which, in the interior of a cell, new

cells are on the point of being formed, and at which the nuclei have already made their appearance, as the centres of the future cells, we find that the future mother-cell never contains a transparent aqueous sap, but that a viscous colourless mass, mixed with minute granules, is diffused in greater or less quantity through the cellular space, and is especially concentrated in the vicinity of the cell-nucleus, so that very frequently the outlines of the nuclei appear through this mass but very indistinctly, and cannot be seen accurately without the use of iodine. That this mucous mass which is found in the cavity of the cell previous to the occurrence of the nuclei is the material for the formation of the cellular nuclei (they are coloured yellow by iodine precisely in the same way as the fluid mass) can scarcely be doubted: but whether the nucleus, as Schleiden supposes, is formed simply by the union of the globules floating in the mucous fluid, or whether, which is my own opinion, it is not rather an organic formation increasing by intus-susception which is sharply bounded externally by the mucous fluid, has not yet been determined sufficiently by microscopical observations, and we are unacquainted with any chemical data capable of affording assistance in this examination, both the chemical constitution of the globule and that of the nucleus itself not being satisfactorily explained. It certainly however deserves to be remarked, that according to the investigations of Mulder and Harting, neither the nucleus nor the primordial utricle can be regarded as proteine compounds, as they are frequently imbued with proteine, but are also met with perfectly free from it, and consist of a substance which it is true cannot yet be well characterized chemically, but which is distinct from the other solid structures of the cell. Precisely in the same way as a separation occurs interiorly between the viscous mass mixed with granules and the solid substance of the nucleus, does the formation of the primordial utricle likewise appear at the periphery to proceed from this mucous fluid; but as it is not my object to enter at present upon an examination of the primordial utricle, and the question whether it should be considered as an independent membrane, or as a layer of the above fluid merely coating the walls of the cell, having treated of those questions on a former occasion, I shall reserve some further observations on this subject for a future paper, and shall confine myself for the present to the consideration of the phenomena which are observed in the semifluid nitrogenous substance diffused in the cavity of the cell.

Since, as we have already observed, this viscous mass everywhere precedes the first solid formations indicative of future cells where cells are to be formed; since we must moreover admit
that it furnishes the material both for the formation of the nucleus and of the primordial utricle, which stand not only in the nearest relation as to space, but react towards iodine in an analogous manner, consequently that their organization is the process which induces the formation of the new cell, I trust it will be considered justifiable if I propose to designate this substance by the word protoplasma, a term which recalls to mind its physiological function.*

With respect to the relative position of the protoplasma to the nucleus, the form of the latter, and its position with reference to the wall of the cell, I cannot quite agree with my friend Schleiden. According to his statement (Grundz. d. wiss. bot. 2nd edit. i. p. 198), the nucleus represents a plano-convex, generally lenticular body, which is applied to the inner wall of the cell, frequently adhering firmly to it, and in many cases being even enclosed by a doubling of the cell-wall. I must, from my investigations, take a different view of the relation of the nucleus to the cell-wall. In my paper on the structure of the vegetable cell I have already mentioned that the nucleus is not immediately applied to the cell-wall, but is situated within the primordial utricle, either resting against one of its side-walls or being suspended by filaments in its centre. My recent researches have shown me that the apposition of the nucleus to the side of the cell is a secondary state under all circumstances, and that in the earliest stage of the cell the nucleus is always situated in its centre, surrounded by a layer of protoplasma. I have on a former occasion† described the remarkable changes in position of the nucleus in the mother-cells and spores of Anthoceros laevis, and I have found that this relation is very general. That the position of the nucleus is originally central may most readily be observed by the examination of young hairs; for here, when they are turned round their axis, not the least doubt can exist as to the central position of the nucleus; for instance, in the hairs of the filaments of Tradescantia virginica, T. Sellowiana; in the hairs on the young leaves of Saxifraga decipiens, &c.; and likewise in cells which lie together in masses, for instance, in the cells of the albumen of Paeonia, of Leguminosae, in the young vascular utricles of monocotyledonous roots; in short, I arrived at the same result wherever I examined young cells. The space between the nucleus and the cell-wall is, in most cases, somewhat narrow in the young cell, the nucleus occupying at first a very

* The author objects to the term mucilage, employed by Schleiden to designate this substance, as the term vegetable mucilage, in the sense in which it is ordinarily used in chemical works, conveys a totally different meaning.
† On the development of the spores of Anthoceros laevis, Linnean, 1839.
considerable space in proportion to the cell; so that, for instance, when a whole series of cell-nuclei overlying one another lengthwise is formed in hairs, the intermediate space between the individual nuclei is very narrow; and when subsequently the horizontal walls have formed, each nucleus almost joins the upper and lower horizontal walls of its cell.

This relation generally disappears very soon, the cell either expanding alone, or when the nucleus, which frequently happens, grows even after the formation of the permanent cell-membrane, the cell increases far more considerably in its relative size.

The space between nucleus and cell-wall is at the commencement, almost in all cases, entirely filled with the granular mucous protoplasm. On treating such a cell with dilute tincture of iodine, the protoplasm shrinks together, coagulating with the assumption of a yellow colour; and when the cell is already somewhat advanced in its development, it does not solidify uniformly to form a dense globular mass, but in such a manner that some smaller and larger roundish cavities are formed in its interior, which mostly run into one another at some points. The appearance of the cell is essentially modified by this. In its centre is situated the nucleus surrounded by a thick layer of protoplasm, its walls are in a similar manner coated with a layer of this substance, and between the two layers are some thicker or thinner diagonal walls or columnar connecting pieces which maintain the nucleus in its position and which traverse the cell diagonally.

Analogous changes in the distribution of the protoplasm to those which may be produced artificially by tincture of iodine in the young cells, occur naturally in those cells whose development is more advanced. Irregularly scattered cavities form in the protoplasm, which become filled with aqueous sap. At first these cavities are generally small and separated from one another by thick layers of protoplasm; but in other cases, likewise at an early period, some larger cavities occur, while the remaining space of the cell is still uniformly filled with granular protoplasm. The older the cell and the more it expands, the more numerous and large do these cavities become; at first they are separated from one another, and it has then frequently the deceptive appearance as if thin-walled cells filled with an aqueous fluid were contained in the granular protoplasm. Two circumstances however prove the assumption that these bright spaces are surrounded by membranes to be erroneous, however deceptively they may frequently possess the appearance of cells. In the first place, the protoplasm, when it flows out of an injured cell, appears as a viscous fluid which does not mix with the aqueous sap of the cell, and whose cell-like spaces filled with the cell-sap may be made to unite by moving backwards and forwards the
entire mass between two glasses, without the least trace of a surrounding membrane being detectable. On the other hand, an internal movement begins sometimes to be perceptible in the protoplasm even at this period, which does not, it is true, as yet possess the form of a distinct current, but produces a slow change in the form and position of the cavities above-mentioned; thus likewise indicating that they are not cell-spaces inclosed by a membrane, but vesicular cavities in a viscous fluid.

The older the cell becomes, the more do the spaces filled with this aqueous sap increase in size in proportion to the mass of protoplasm. In consequence of this the cavities run into one, and the viscous fluid now forms, instead of perfect septa, only more or less thick filaments, which radiate from the mass surrounding the nucleus like an atmosphere towards the cell-wall, where they turn back, and unite to form retrogressive filaments, and in this manner form a more or less ramified anastomosing network. When the cells lie one above another in longitudinal series, as in the simple articulated hairs for instance in Tradescantia, the chief mass of these filaments, united into a thick cord, mostly proceeds in the axis of the cell from the centre of the one diagonal wall of the cell to the centre of the opposite diagonal wall, and inclose the nucleus in the middle of the cell on all sides. Where, on the contrary, the cells lie together in masses, the filaments generally radiate from the central nucleus towards all sides uniformly. There is however no general rule in this respect; thus for instance, in Zygmena, notwithstanding the bead-like apposition of the cells, the nucleus is suspended to filaments which radiate on all sides without any particularly thick and numerous filaments proceeding through the axis of the cell.

It may perhaps not be superfluous to draw attention to a phenomenon which I am not yet able to explain. At the period when the previously isolated cavities begin to flow together the cell acquires a very peculiar appearance, resulting from the different refracting powers of the substances contained in it. The spaces, for instance, situated in the protoplasm frequently appear, not as if they were cavities filled with a thin aqueous liquid, but as if they consisted of masses of a semi-fluid substance, refracting the light more strongly than the surrounding protoplasm. Except in the absence of colour, they look very much like the red masses which are contained in the cells of Bangia atropurpurea. This appearance subsequently changes, and frequently under the eyes of the observer, when the cells are placed in water, and these places are then readily perceived to be cavities which are filled with an aqueous liquid. Now whether at the time when they resemble solid masses a substance is dis-
solved in the liquid filling these cavities possessing a great refractive power, and which subsequently again disappears, or whether the phenomenon is due to other causes, I have not been able to ascertain.

When the protoplasm has assumed the form of filaments, a current may almost always be observed in them. This may of course be easily detected when readily perceptible globules are contained in the currents, as in the filamentary hairs of *Tradescantia*, in the stinging hairs of *Urtica*, in the hairs of the melon, &c.; but where, on the contrary, this is not the case, and the filaments consist of a very homogeneous transparent mass, as for instance in the hairs of *Alsine media*, the existence of the current can only be inferred from the change of position in the filaments. With respect to this alteration in the position of the currents, the cessation of some and the origin of others at fresh places where none previously existed, this phenomenon had been already described by others, especially by Meyen and Schleiden, so accurately, that it would appear quite unnecessary to mention it here were it not for the sad reality, that in opposition to all the earlier and very accurate observations, the correctness of these observations have not merely been denied with the most positive certainty by two parties quite recently, but that perfectly untenable theories have been advanced of the perforation of the cell-walls by the milk sap-vessels in which the currents described are said to occur, or of secondary cells contained in the cell-cavity in whose intercellular spaces the granular fluid is said to be contained. The assumption of solid tubular or membranous formations in or between which the moving fluid is said to be contained, must be entirely rejected by every one who has had an opportunity of convincing himself of the variability of these currents, and any observation made with tolerable care will soon yield this conviction most satisfactorily. It has frequently happened to me, that even in the short time which I required for drawing the currents contained in a cell, for instance of *Tradescantia*, their position and number were essentially altered; but not merely the delicate currents which run free through the cell-cavity or along its walls alter their position, but in many cases even the position of the nucleus, when it is situated in the axis of the cell in the midst of the mass of currents which run from the centre of one horizontal wall to the centre of the opposite one, is subjected to a slow but still very decided change. I have observed this motion taking place in the direction of the axis, alternately ascending and descending, and repeated in a very decided manner, on the filamentary hairs of *Tradescantia Sellowiana*, some of which I took from buds which were not more than half deve-
loped, and others from flowers which had just opened*. This movement took place so slowly that the nucleus required from a quarter to half an hour to pass through one-third or half the longitudinal axis of the cell, progressing not more than about \( \frac{1}{4300} \) th of a Paris line in a second. A somewhat slower motion, the velocity of which however I forgot to measure, in which the nucleus glided along the cell-wall, was observed in the linear primordial leaves of *Sagittaria sagittifolia*; the same may be very readily observed in the leaves of *Vallisneria spiralis*, the nucleus here following the current of sap with the same velocity as the granules of chlorophyll. The following phenomena, which I observed on the stinging hairs of *Urtica baccifera*, yield, together with this change of position of the sap current and nucleus, a further proof against the existence of a vascular system or inner cells. I left a leaf of this plant lying for a couple of days on the table, so that with the exception of the large ribs and the stinging hairs situated on it, it was perfectly dry. Now in these faded hairs the currents appeared to be very much altered; some still existed in the natural state and were in motion, but in the greater portion the granules had separated and were distributed with tolerable uniformity over the surface of the cellular membrane, and exhibited a molecular motion. When some of the hairs which had been cut off had lain in water for half an hour and were again full of sap, the granules arranged themselves more and more into filaments, between which were some free spaces and in which the circulating motion was completely restored. In this case, therefore, every possibility of the currents being inclosed between membranes is excluded; indeed the form of the currents of sap, as exhibited in the stinging hairs of this plant, is opposed to that view.

The movement of the current is mostly very irregular; if we leave *Chara* out of the question, it is most regular in *Vallisneria*, but even here it is far from being uniform. The sap flows quicker in one cell than in another, in one current quicker than in the adjacent; frequently stoppages occur at some spots, so that the sap becomes increased for a time, and some granules are overtaken by those behind them, &c. This inequality of the motion renders the determination of the velocity of the current

* It may perhaps be of interest to those persons who may wish to observe the circulation of the sap in the hairs of *Tradescantia* if I describe a manipulation by means of which the layer of air which adheres tenaciously to the surface of the hairs when they are placed in water may be removed, as it diminishes the transparency of the hair and renders the observation more difficult. For this purpose it is only necessary to dip the filament with its hairs for a moment in alcohol, and to wash this off again immediately with water, when the disturbance is got rid of without the circulation of the sap being modified.
somewhat uncertain, or rather it compels us to make a larger
series of admeasurements and to draw the mean from them.

Since, as far as I am aware, no observations have been pub-
lished on the velocity of this motion excepting in Chara, the
following statements may not be considered out of place. I have
only to observe, that all these admeasurements were made at a
temperature of 66° to 68° Fahr., and that the influence which
different temperatures exert on the phenomenon has not yet
been investigated. In filamentary hairs of Tradescantia virginica
the velocity of the current varied from $\frac{1}{3}00$ to $\frac{1}{9}00$ Par. lin. in a
second; the mean was $\frac{1}{5}00$. In the leaves of Vallisneria spiralis
the quickest motion was $\frac{1}{2}3^3$, the slowest $\frac{1}{5}00$, and the mean
$\frac{1}{1}83$ line. In the stinging hairs of Urtica baccifera the quickest
motion was $\frac{1}{6}27$, the slowest $\frac{1}{6}37$, the mean $\frac{1}{7}30$ line. In the
cellular tissue of a stolon of Sagittaria sagittifolia the velocity
varied between $\frac{1}{7}20$ and $\frac{1}{10}50$, and amounted on the average to
$\frac{1}{8}37$; in the leaf of the same plant it varied between $\frac{1}{1}170$ and
$\frac{1}{1}390$, the average being $\frac{1}{1}33$ line. In the hairs of Cucurbita
Pepo the quickest movement amounted to $\frac{1}{7}0$, the slowest to
$\frac{1}{2}60$, the average being $\frac{1}{1}83$ line. The smallness of these
numbers will probably surprise many, especially when they are
compared with the apparently considerable velocity which the
circulation of the sap, in Vallisneria for instance, exhibits under
the microscope. But it must not be forgotten, that in these ob-
servations the motion is seen quickened several hundred times.
The above admeasurements were made in the following manner:
while I observed the passage of the image of the globule across
the field of a glass micrometer fixed in the ocular, I counted
the strokes of a second-pendulum. What the nature of the gra-
nules floating in the protoplasma may be, cannot in most cases
be ascertained on account of their minute size; but it appears
that they are in all cases coloured yellow by iodine, and are
therefore most probably nitrogenous. When granules of chlo-
rophylle occur in the cells, they are situated either, as for instance
is the case in the hairs of the melon, isolated and close to the
walls of the cells without having any definite relation to the cur-
rent, and only a few move on with the current, or they are all
connected with the current and move with it, as in Stratiotes
aloides and Sagittaria sagittifolia. This form mediates the
transition to Vallisneria, in whose cells it is not the cellular sap
itself which is in rotation, as appears at first sight, but a mucil-
aginous fluid with which the chlorophyll granules and the nu-
cleus are connected, and which flows in an uninterrupted current
along the cell-walls, but on account of its great transparency and
slight thickness is not very easily seen. Likewise in Chara it is
not, as is generally supposed, the cell-sap itself which moves, but
a denser fluid present in large quantity and occupying the outer parts of the cell-cavity, as has been already shown by other observers*.

I dare not venture to express the slightest suspicion as to the cause of this motion. It might be thought that the nucleus acts an important part in it, forming as it does in most cases the centre of the current, which might lead us to suspect that the force producing it may have its principal seat in the nucleus, as in Chara it cannot be denied that the chlorophyll granules situated adjacent to the cell-wall have an influence on the circulation of the sap. It appears to me however not probable that the nucleus possesses any such influence. In the first place, it is in many cases in the act of being dissolved precisely at the time when the current is most rapid, at least it is smaller than previously, for instance in the filamentary hairs of Tradescantia; on the other hand, the nucleus does not form the centre of the current in Vallisneria in those cells in which the circulation is very regular and rapid, but, like the isolated granules of chlorophyll, follows the current without any quickening of the movement being perceptible in its neighbourhood, or any other circumstance tending to show that it had any special function. It is true, I do not recollect having seen such currents in cells in which the nucleus is already perfectly re-absorbed; but this co-existence of the nucleus and current may be accidental, and may be explained from the protoplasm which forms the current being re-absorbed earlier than the nucleus after the development of the cell-walls.

It is remarkable that the nucleus, considering its central position, can be kept in its position in the cavity of the cell, not by solid fibres, but by currents of a fluid, even though tenacious. The observations above described respecting the changes in the position of the nucleus destroy all idea of these currents, and with them the nucleus, possessing a support in fibrous or membranous tissues. We must therefore admit that the protoplasm, notwithstanding its motion, still has sufficient viscosity to retain floating in the aqueous sap of the cell so small a body as the nucleus. The older the cell becomes the more does the substance of the current appear to harden, so that in some cases at least it loses all its liquid and the currents become solid filaments. I noticed this appearance most strikingly in the flesh of the fruit of Rhamnus frangula, in which there are some cells which are far larger than the surrounding, and in which is situated a nucleus fixed to filaments. These filaments

* Schleiden, Grundzuge, 2nd edit., p. 292, and Hassall, British Freshwater Algae, i. p. 85.
possess such firmness that they can be cut through horizontally with a sharp knife and nevertheless remain in their position. The larger of them are frequently flattened, but I could not find a trace of membranes by which they might be retained so firmly in their position. Similar solid filaments are met with in the larger cells of the fruit-parenchyma of *Ribes nigrum*; in this case also the upper and lower side of the cell may be cut away without the filaments running through their centre being moved out of their position.

II.—List of the Birds observed to winter in Macedonia; from Notes made by Capt. H. M. Drummond, 42nd R. H., during a two months' Shooting Excursion in the Interior during the winter of 1845-46.

I am not aware if Macedonia has ever been fully explored by any naturalist with a view to its ornithology, but from the general appearance of the country, its rich and varied landscape, abounding in high mountains as well as extensive plains, in some parts richly cultivated, in others clothed with vast extents of forest intersected by numerous lakes, rivers and marshes, as also from its geographical position, being so directly in the line of migration of all those species which pass up the Archipelago, it becomes one of the most interesting fields to the ornithologist, and I have no doubt, were it visited also during the spring and summer months, it would be found to possess many rare and beautiful species, and some even new to the European fauna.

*Vultur cinereus.* A few of these rare and magnificent birds were seen in the large wooded plains, generally perched on the naked limb of some dead tree, where they sit for hours, seeming to prefer perfect solitude, never mixing with the other vultures; they were never observed on the mountains, but probably regulate their movements according to the herds of cattle which at this season are all brought down to the low grounds.

*V. fulvus.* Most numerous on the plains as well as the moun-
tains.

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\begin{align*}
\text{Cathartes percnopterus.} & \quad \text{A few seen on the mountains.} \\
\text{Gypaëtus barbatus.} & \quad \text{Common.} \\
\text{Falco peregrinus.} & \quad \text{F. subbuteo.} \\
\text{F. æsalon.} & \quad \text{F. tinnunculus.} \\
\text{F. imperialis.} & \quad \text{Rare.} \\
\text{F. fulvus.} & \quad \text{F. albicilla.} \\
\text{Most numerous on the large wooded plains, fifteen} & \quad \text{or twenty being often observed in the air at once,} \\
\text{and their nests may be seen in every direction, the largest} & \quad \text{trees being}
\end{align*}
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