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XVI.—*On the Growth of Cell-Membrane.* By HUGO v. MOHL*.
 SINCE my doctrine, that cell-membrane increases in thickness by the deposition of successive layers of membrane deposited internally, has recently been contradicted on various sides, and, in opposition to it, the theory has been propounded, that the innermost cell-layer is the oldest and the most external the youngest, it is only natural that I should accept the challenge and enter the lists in defence of my views.

The first attack proceeded from Prof. Hartig of Brunswick: I endeavoured to set aside his objections to my view two years ago in the '*Botanische Zeitung*'†, without success so far as that author was concerned, as since that time a second treatise of his has appeared (*Das Leben der Pflanzenzelle*, 1844), which contains an answer to my objections and a more extended exposition of his theory. In reference to this second treatise however I must stand aloof, since my own observations agree so little with the researches there brought forward, that they afford me no point on which I can bring forward either opposition or confirmation; in the following pages therefore I can take no notice of it. Otherwise it is connected with the observations on which the Utrecht professors, Harting‡, and Mulder§ rest their objections to my theory. As to the matters of fact in these researches I agree in many respects with my honourable adversaries, and there are I believe but few points which they have not taken into consideration, these however I must bring forward against the conclusions they have drawn.

According to my views, the primary membrane of the young cell is not perforated with orifices, and certainly no definite structure is visible in it||. On the other hand, Harting and

* From the '*Botanische Zeitung*,' May 15th—22nd, 1846. Translated by Arthur Henfrey, F.L.S. &c.

† *Jahrg.* ii. 273. *Scientific Memoirs*, vol. iv. p. 91.

‡ *Mikrochemische onderzoekingen*, &c., vide *Bot. Zeit.* *Jahrg.* iv. p. 64.

§ *Versuch einer physiologischen Chemie.*

|| Vide my essay on the Structure of Vegetable Cell-Membrane in my *Vermischte Schriften*, p. 314.

Ann. & Mag. N. Hist. Vol. xviii.

Mulder now assert that, almost universally, the yet unthickened membrane of young cells, when coloured blue by iodine and sulphuric acid, is perforated like a sieve by a great number of small pores, through which the light appears bright and uncoloured; the cells of the pith of *Asclepias syriaca*, *Hoya carnosæ*, *Ricinus communis*, of the bark of *Euphorbia caput medusæ*, of the wood of *Asclepias syriaca*, and *Clematis Vitalba*, are especially named in relation to this. Harting states that in the old medulla-cells with thickened walls of a great many dicotyledonous trees, *e.g.* *Æsculus Hippocastanum*, *Syringa vulgaris*, *Rosa canina*, *Sophora japonica*, there are, among the canals of the dots closed by a membrane, others which are quite open; and from his investigations he was led to the conclusion that these open pores are not the result of the absorption of the membrane closing the canal, but that they are the remains of the pores occurring in the young cell, which have not, like the others, become closed at a subsequent period.

I confess that to me this statement was unexpected. I had already, in cells I had coloured blue by iodine, often seen very bright dots, which appeared like real orifices, but I always believed that I saw a closing membrane; as I might have been deceived in my earlier observations, I submitted this point to a new investigation. In the first place, however, I must remark that I do not wholly approve of the mode of examination with iodine and sulphuric acid, chosen by Harting and Mulder; a deep blue colouring of the young cell-membrane is indeed obtained by this means, but in fact this deep colour is not advantageous, as will hereafter appear; moreover, when too strong an acid is employed a considerable expansion of the cell-membrane is readily caused, by which the dots may be closed; this indeed cannot give rise to a delusion in reference to the presence or absence of a closing membrane, but renders the making of a new preparation necessary. Both evils are avoided when no sulphuric acid is used, but the cell-wall coloured blue by the application of very concentrated tincture of iodine and subsequent moistening with water. In this way we are not exposed to the risk of producing a mechanical alteration of the cell-membrane, and there is the further advantage, that the preparation coloured by iodine may be allowed to dry again, by which means, as is known, the detection of very thin and transparent membrane is especially facilitated.

I treated in this way the medulla-cells of the young developing bud of *Sambucus nigra*, *Asclepias syriaca*, and of the apex of the stem of *Euphorbia caput medusæ*. The result of the microscopical examination of these does not at all agree with that offered by Harting and Mulder. It is certainly quite true that the

dots are so transparent, and appear so bright in the coloured cell-membranes, especially when they have acquired a deep indigo tint, that by an illusion they look like true openings. But to make the fact certain, we must ascertain accurately the performance of our microscope, and carefully select the suitable objective and covering glass of the proper thickness, regulate the proper illumination, in short, we must neglect no circumstance which may influence an important microscopical examination. Since the question, whether in these young cells actual openings are present or not, is one of the principal hinges on which the doctrine of the development of cell-membrane turns, I may be permitted to enter somewhat minutely into the qualifications of the microscope employed by me in these investigations. I am indeed, generally speaking, of opinion that the accuracy of a microscopical observation does not depend upon the fact of the microscope being a little better or worse, since experience in observation frequently counterbalances the inferiority of the instrument; but I consider that the present case is one of those in which an instrument of the most superior quality is necessary, and in which we cannot come at the truth without a microscope of great penetrating power. I commonly make use, in important investigations, of the three strongest of Plössl's objectives (N. 5-7), with an Amici's achromatic ocular, since this combination gives an image of surpassing sharpness and clearness with a magnifying power of about 300. Notwithstanding the superior performance* of this combination, I was not in a condition ever to detect any trace of a membrane closing the dot in the young medulla-cells of *Sambucus*, since the light shone through perfectly bright and clear, and apparently quite uncoloured as through a true opening. But when I used the strongest of Amici's objectives, which can only be employed with profit in few cases and to very delicate and transparent objects, and which with the same ocular gives a magnifying power of 500 diameters, every doubt was dissipated as to whether a membrane was stretched over the dot or not, since such a membrane was now distinctly to be perceived: it was indeed very transparent, but small granules, &c. were distinctly to be seen adhering to it. If this was not to be mistaken in the preparation which was lying in water, the result of the examination of dried preparations was yet more decisive, since no doubt was longer possible as to the presence of a closing membrane, and of the bright violet colouring of the same.

* For instance, the transverse stripes on the scales of the upper side of the wing of *Hipparchia Janira* are quite clearly seen with it; these scales afford an object which cannot be sufficiently recommended for testing the microscope.

One is less readily exposed to the risk of an illusion in examining the medulla-cells of full-grown yearling shoots of *Syringa*, *Æsculus*, or *Sophora japonica*, than in the young cells previously mentioned; but here also, and especially in *Sambucus* and *Sophora*, when the cell-membrane has acquired a deep blue tinge, we must be cautious, since the contrast between the dark blue of the thick portion of the membrane and the brighter colour of the thin allows the membrane closing the dot to be easily overlooked. If, on the contrary, we expose the specimen from twenty-four to forty-eight hours to the air, till part of the iodine has again evaporated and the cell-membrane has acquired a bright violet colour, we can readily make out the thin and also violet-coloured membrane. When, as not unfrequently happens in the full-grown medulla-cells of *Syringa*, &c., the outer cell-membrane is coloured yellow, and the inner, in which canals of the dots lie, blue, the membrane stretched over the dot appears yellow, in which case also a delusion as to its presence is not easily possible.

The presence of dots on medulla-cells of buds of *Sambucus* shows that we have here no longer to do with a simple membrane; in other cases, *e. g.* in the buds of *Asclepias syriaca*, on the contrary, I found the membrane quite homogeneous and without any trace of dots.

I believe these observations to be decisive, and consider myself entitled to persevere in the view, that the primary cell-membrane is closed.

Another question is, whether the outermost cell-layer, as I believe, or the innermost, as Harting and Mulder assume, is the oldest.

Before I enter upon the action which chemical agents exercise upon the different layers of cell-membrane and the consequences deduced from the appearances observed under such circumstances, I may be permitted briefly to state the reasons which, on anatomical grounds, induce me to declare the most external membrane to be the oldest.

It is a universal phenomenon, that the membrane of young cells and vessels is smooth and thin; that, on the other hand, when the membrane has become thickened in the course of time, two principal layers may be distinguished in it; one exterior, thin, and imperforate, and an interior, of greater or less thickness, pierced with slits and holes. If the holes are small, the inner layer appears as a continuous membrane, pierced like a sieve with holes; if they are large, or elongated into slits and approximated together, it appears as a deposit of fibres, which are sometimes combined in a reticulated manner, sometimes running spirally, sometimes annular, &c. In many cases, *e. g.* in

the cells of the endothecium of anthers, the inner layer forms a continuous layer on one side of the cell, while on the other it is split into fibres which run out like rays from the membranous portion,—a distinct proof that fibres and membrane are merely different varieties of form of one and the same element of the cell. Lastly, it may happen that the inner membrane is only deposited along the angles of the cells, and not on the surface, and forms semicircular borders projecting more or less into the cavity of the cell.

If now it be proved, and I believe that I have furnished the proof in the foregoing, that the membrane of young cells possesses no openings, and if by following the development of cells we see in an indubitable manner that their membrane becomes gradually thicker, and that in these thickened cells, under all circumstances*, an imperforate membrane is present on the exterior, while in the layers lying on the inner side of this membrane, and becoming continually thicker, there are holes which in proportion as these layers become thicker assume the form of canals, which are closed externally and open to the cell-cavity; when we further see that this inner membrane is not homogeneous, but consists of many, superposed, delicate lamellæ,—in these mechanical relations, in the earlier presence of an imperforate membrane and in the subsequent production of the inner, continually thickening mass perforated with holes, lies a necessity for the assumption that this latter layer is of later origin, and has been deposited upon the inner side of the imperforate membrane. In these relations there is throughout no ground for the further assumption that the lamellæ, which constitute the inner secondary layer, have also become deposited in a series from without inwards; but mechanical relations occur in peculiar cases which would make any other assumption appear very improbable. In evidence of this we have the fact, that in very thick-walled cells many of the canals of the dots converging toward the interior of the cell become blended; especially however that in cells which merely deposit a secondary layer in the angles, these possess a form convex toward the cavity of the cell, and consist of many superposed layers convex to the interior; and that in these cases we find in the young cells only few and narrow layers of this kind, while in the full-grown cells a number of broader layers lie upon the inner side of this narrow one†.

These are briefly the anatomical grounds which decided me in

* Those rare cases in which an absorption of the free membrane in the canals of the dots takes place subsequently, from only an apparent exception.

† Vide Bot. Zeit. ii. 323. tab. 2. figs. 2, 3. Scientific Memoirs, vol. iv. p. 106. plate 1. figs. 2, 3.

proposing my theory, and which up to this time have their full value to me, since I know of no anatomical facts which are in contradiction to this theory, or would render any other explanation half so probable. Prof. Harting mentions two circumstances, the first of which he considers makes it unlikely that the secondary layer is deposited upon the inner side of the primary membrane, while the second affords him a positive proof of the deposition of the secondary layers upon the outer side. The first circumstance is the direct correspondence* of the dot in contiguous cells, which it is very difficult to comprehend when we adopt my theory. I confess distinctly that I do not at all comprehend it; I know only that it is so. We do not generally understand the reason of a special organization, because we know nothing of the nature of the power producing organization; thus we do not comprehend, for instance, how it happens that in the putamen of the cocoa-nut the embryo inclosed in albumen is situated opposite an eye. We see the object of this arrangement, but do not understand how it is that it becomes developed at this point of the pericarp rather than in any other situation.

The second circumstance, which Harting brings forward as a proof of the deposition of secondary layers taking place upon the outer side of the primary cell-wall, is somewhat complicated. From a large number of micrometrical measurements (worthy of all praise) which he made on yearling stems of dicotyledons in the course of development†, Harting draws the conclusion that in the internode of a dicotyledonous plant no multiplication of cells takes place in a radial direction after it has passed beyond the condition of bud, but that in the course of the first year the resulting thickening of the internode is to be ascribed to the expansion of the cells already existing in the bud.

In reference to this he distinguishes two periods; in the first, which precedes the thickening of the walls of the ligneous cells, this expansion proceeds in a similar proportion in all the layers

* At the same time it must not be forgotten that this apposition is peculiarly circumstanced. It is true that roundish dots correspond accurately in position and generally in form; elongated and obliquely placed dots, on the contrary, come into apposition only at their middles, and no longer correspond in their form, since they cross; finally, slits (much-elongated dots) which run between spiral or annular fibres, &c. are usually without any relation of position to each other, in contiguous cells. The connexion therefore is not so simple as Harting appears to have conceived, when he assumes that openings from one cell into another occur in the primary membrane which directly correspond; of these however it would be as difficult to explain why they form of exactly the same size and in corresponding situations in the two cells, as it is easy to explain the origin of the dot when my view of the structure of cell-membrane is admitted.

† Tijdschrift voor natuurlijke Geschiedenis, 1844.

of the stem ; in the second period, on the contrary, in which the wood-cells become thickened, they expand in a greater proportion than the remainder of the cells, and, indeed, in such a manner that the expansion of their cell-cavities is in proportion to the expansion of the cells which do not become thickened, and that besides this, the radial diameter of the ligneous cells becomes increased by the thickening of their wall. From the circumstance that by the occurrence of a deposition of secondary layers in the cavity, this latter must necessarily be contracted,—that however such a contraction is not indicated by the micrometrical measurement of this cell, the cavity of the cell enlarging to the same size as where no thickening of the wall takes place,—Harting draws the conclusion that the deposition of layers of increment takes place upon the outside of the cell.

Let us examine these assertions as to the ligneous cells somewhat more closely. First, it is stated that in the wood of dicotyledons no multiplication, but only an expansion of cells takes place. Here Harting rests, not so much on the direct counting of the cells lying in the said direction in the woody bundle, as on the estimate depending on the measurement of the cavities and the thickness of the walls of certain of these cells. I wholly disregard the question, whether, from the different magnitude of the ligneous cells, of which those lying in the outer part of the wood are mostly much smaller, while the larger are situated toward the interior, this method of investigation is adapted to furnish an accurate result, and whether Harting has proceeded with the necessary regard to all circumstances in carrying it into effect, since distinct facts exist which demonstrate the view that the ligneous cells do not multiply in a radial direction to be completely erroneous. There is, to go no further, evidence of this in the direct calculation of the ligneous cells which lie in the radial direction in different internodes of the same yearling shoot.

The following calculations were instituted on transverse sections, always from the middle of the internodes, of twigs which were cut off in January, in which therefore all the woody cells of the first year's ring were fully developed. The internodes are indicated from below upward by the numbers 1, 2, 3 ; that marked 1, however, not being always the lowest internode of the twig. The number of cells refers to the perfect wood-cells lying in the direction of a radius between the pith and the cambium layer. They were counted in those places where no vessels, or as few as possible, lay in the direction of the radius ; when however, as is unavoidable in the thicker internodes, one or more vessels were situated in the row of cells, the calculation of the

extent occupied by these vessels was obtained from the cells lying next them*.

a. Twig of *Tilia parvifolia*; 1st internode 149 cells, 5th intern. 110, 8th intern. 79, 13th intern. 29 cells.

b. Twig of *Robinia pseudo-acacia*; 1st intern. 141, 5th 96, 10th 74, 15th 42, 20th 18, 23rd 9 cells.

c. Twig of *Gingko biloba*; 1st intern. 42, 4th 36, 9th 17 cells.

d. Twig of *Morus alba*. Here the interior portion of the vascular bundle, which consists almost wholly of vessels, and in which six or eight vessels lie immediately behind one another in the radial direction, is excluded from the enumeration, and only the number of the wood-cells is determined, which in every internode lie outside this very conspicuous group of vessels: 1st intern. 228, 10th 134, 20th 58, 30th 2—3 cells.

We arrive at similar results if we examine twigs which are actually in a condition of rapid growth; for instance, this was shown by a twig of *Hoya carnosa* about 2 feet long, the leaves of which were yet all in the form of small scales; the 1st internode 20 cells, 2nd 19, 3rd 17, 4th 12, 5th 7, 6th 4. In this case the smaller number of ligneous cells in the upper internodes could not at all be attributed to the circumstance that a larger proportion of the cells were in the condition of cambium cells, since in every internode only three to five cambium cells were situated behind each other in the radial direction.

Calculations instituted on other twigs and in other plants may furnish other numbers; but the great difference in the above numbers renders it incontestable, that at the conclusion of the first period of vegetation the upper and younger internodes contain a much smaller quantity of ligneous cells in the radial direction than the lower and old internodes of the same shoot; also, that during the greater proportionate length of the time of vegetation in the lower internodes than in the upper, a very evident multiplication of cells has taken place.

As it may be objected to the result of the above enumerations (though very falsely, since anatomical examination of young twigs bears evidence to the contrary) that a greater number of wood-cells already existed in a nascent state while the internode was yet in the condition of bud, and that the greater number

* I was originally undecided whether the vessels and cells should be counted together or separately. Neither method however appears to me to furnish so certain a result as that which I have followed, on account of the irregular distribution of the vessels. At the same time, the very immaterial relative differences which arise from these various methods of enumeration are not worth consideration in reference to the general result.

which we meet with in the fully developed condition of the internode is not to be ascribed to the occurrence of a new formation of cells during the summer, it may not be superfluous to direct our attention to a second relation, which decides the fact in the most indubitable manner. In the examination of young shoots of dicotyledonous trees, *e. g.* of oaks, poplars, robinias, &c., we find, without exception, that their vascular bundles run downward from the base of the leaf through several internodes in a parallel direction without entering into any lateral connexion with each other*. The medullary ray lying between two vascular bundles has also a length equal at least to an internode. The same relations are met with also, unchanged, in full-grown twigs in the inner part of the wood, in the so-called *corona*, which corresponds to the young vascular bundles; the larger and more externally situated portion of the wood, on the contrary, exhibits an essentially different mechanical arrangement of its constituent elements. There are, in particular, no longer any separate vascular bundles to be distinguished, but the whole woody mass forms a continuous cylinder, the fibrous bundles of which exhibit not a straight but a serpentine course, and have grown together at certain distances, so as to form a network of narrow and not very long meshes, which are filled up by the medullary rays. In the very young internode there is not the slightest trace of all this reticulated layer, which at the end of the year forms the greater proportion of the body of the wood; in the course of the summer therefore a new part is produced upon the outside of the typical vascular bundle which existed in the bud, and the cells of this part are developed at a later period.

By what we learn both from the increased number of the wood-cells of older internodes as well as from the dissimilar structure of the outer and more considerable portion of their woody bundles, the commonly received opinion, according to which the formation of new wood-cells takes place in the cambium layer during the summer, is fully confirmed, and the theory of Harting, which ascribes the extension of the wood in thickness solely to the expansion of its cells and the deposition of secondary membrane on the outside of their primary wall, is wholly set aside.

In reference now to this latter point, the deposition of the secondary layers outside the primary membrane, it would be naturally very easy to decide the correctness or falsity of this view

* It is not here meant that lateral connexion between the vascular bundles of the medullary sheath is absent in all dicotyledons; on the contrary, I know well that in many dicotyledons the course of the vascular bundles is quite different from what is stated above, but such connexions are found only at the nodes, and are altogether wanting in most trees.

by micrometrical measurement, if it were possible to examine one and the same cell at different periods of its development. Since this is not possible, we are obliged to compare the older and younger cells of the same internode with each other; here however the unequal size which different wood-cells attain brings us into a difficulty which is almost insurmountable, since not only would a vast number of measurements, robbing us of much time, be involved in order to obtain a value moderately approximating the truth if all the cells of the woody mass were developed in a tolerably similar manner, but the detection of alterations which the size of the wood-cells undergoes in the course of time is rendered particularly difficult, by the fact that cells lying in different layers of the ring of wood annually produced attain a different size. However, before I give certain measurements which I made in relation to this, there is a point to be considered which Harting appears to have totally overlooked. The cambium-cells evidently become thickened on all sides in their transition into wood-cells; the cells, which form the innermost layer of the cambium, before becoming thickened, have already pushed forward their walls so as to be in immediate contact with each other laterally, and thus form a circle which straitly incloses the outermost circle of thickened perfect wood-cells. Let us assume with Harting, that during the transition of cambium-cells into wood-cells their cavity is not lessened in size, but that the increment of their walls is referable to the application of new layers upon the outer side of their walls. In this case it would necessarily follow, from mechanical reasons, that the cavity of the cambium-cell inclosed by the primary walls, under these relations, as the side walls would be thickened by each new deposit, would be compressed laterally and the cell must become extended in the direction of the radius, since otherwise the ring formed from the cambium layer must, in consequence of the production of deposits between the side walls of each cell, become expanded to a much more considerable size than they previously possessed, and be torn away from the outer circle of the wood-cells. Since the latter evidently does not happen, we must assume that if the surface of the transverse section of the cell-cavity does not become enlarged in the conversion of the cambium-cells into wood-cells, yet in any case an alteration of form and an expansion of the cell-cavity in the radial direction must take place. Now to prove whether this is really the case or not, I selected a twig of *Hoya carnosa*, which plant appears to me to be especially suited for these investigations, because its wood-cells are of tolerably equal size, and because during the development of its cylinder of wood, the limit between the wood and the cambium shows itself very distinctly. That I might not be exposed

to the risk of selecting arbitrarily for measurement such rows of cells as would best correspond in the form and size of their outermost wood-cells and innermost cambium-cells to a preconceived theory, I measured, with the screw micrometer, in ten rows of cells lying together in a radial direction, the radial diameter of the two inmost cambium-cells and the two outermost wood-cells, as well as the radial diameter of the cavities of the latter. To extend the measurement to a greater number in the radial direction did not appear to me to be at all to the purpose, as the size of the cambium-cells diminishes very rapidly toward the bark; on which account those cells lying further out are much less suitable for comparison with the wood-cells than those cambium-cells at the border of the wood which are closely approaching their conversion into wood-cells.

The average results of these measurements, expressed in fractions of a millimetre, are as follows:—radial diameter of the outer cambium-cell $\frac{1}{102}$, the inner cambium-cell bordering the wood $\frac{1}{98}$, the outer wood-cell $\frac{1}{77}$, the inner wood-cell $\frac{1}{71}$, the cavity of the outer wood-cell $\frac{1}{114}$, and the cavity of the inner wood-cell $\frac{1}{109}$.

[To be continued.]

XVII.—On *Zoophytes*. By J. D. DANA*.

THE singular features of the growing coral field, the resemblance to vegetation in its productions, as well as their beauty and variety, have long excited the attention even of those little curious in the forms of living nature. Trees, shrubs, and other plants of various kinds are represented with wonderful exactness, as if they had been the types of this branch of the animal kingdom; and they grow mingled together often in rich profusion like the plants of the land. The similarity, moreover, is not confined to general form: corals have their blossoms; for polyps are flowers both in figure and beauty of colouring. Like the pink or Aster, they have a star-like disc above; and while some are minute, others are half an inch or even two inches in diameter. Every part of a Madreporæ when alive is covered with these blossoms:

* From Silliman's American Journal for July 1846.

In the series of articles on *Zoophytes*, which it is proposed to prepare for publication, the writer presents the facts and principles that have been published in his Report on *Zoophytes*, one of the volumes of the late Exploring Expedition under Capt. Charles Wilkes. The subject is however condensed, and the style and arrangement altered to adapt it to these pages, and give it a somewhat more popular character. It is the writer's endeavour to present a succinct account of this department, about which there is little generally known, without confining himself to original observations.