NOTICE OF BOOK.

DAS GLEITENDE WACHSTHUM BEI DER GEWEBEBILDUNG DER GEFASSPFLANZEN, Von Dr. G. KRABBE. Berlin, 1886.

The existing investigations on the development of the tissues of plants have dealt rather with the course of the cell-divisions to which the different tissue-systems owe their origin, than with the peculiarities of growth by means of which the elements assume their permanent form. Of late years there has been a tendency, chiefly owing to the influence of Hofmeister and Sachs, to minimise the importance of the single cell, and to regard its growth as subordinate to, and dependent on, that of the whole organ to which it belongs. This view has undoubtedly received support from the recent researches on the continuity of protoplasm through the walls of cells. The brilliant results obtained in this direction by Gardiner, Russow, and others, seem to afford direct anatomical evidence of the mutual dependence of the constituent cells of a tissue1. A work, therefore, which is entirely devoted to the investigation of those changes in the tissues of plants which are due to the independent growth of their individual cells, claims quite exceptional interest. Such a work is the treatise by Dr. G. Krabbe on sliding growth in the tissue formation of vascular plants.

The object of the present paper is to give a critical account of the more important results of Dr. Krabbe’s work on this subject, and to call attention to the conclusions which seem to follow from the facts that he has brought forward.

By the term ‘sliding growth’ those processes of growth are meant which are accompanied by mutual displacements of certain cells or groups of cells. The fact that changes of this kind occur during the

1 See especially the introductory passage in Gardiner, Continuity of Protoplasm, in Phil. Trans. Royal Soc., Part iii, 1883, p. 817.
development of the tissues of plants has long been known. For example, the so-called 'false tissues' of most Fungi and some Algae consist of felted masses of interwoven branched filaments arising from a small number of originally distinct hyphae. It is evident that during the growth of such tissues the constituent hyphae must constantly have to force their way between their neighbours, and that thus complicated processes of sliding growth are involved.

A similar case is found in the development of laticiferous cells. These cells, as is well known, attain an enormous length, and send out branches into every part of the plant, so that the whole complex laticiferous system consists of the innumerable ramifications of a small number of undivided cells. The penetration of these branches into the various tissues of the plant necessitates the continual sliding growth of the laticiferous cells on the adjacent cells. As has often been pointed out, these organs behave quite like the hyphae of a parasitic fungus when making their way through the tissues of the host.

Nor has the occurrence of sliding growth in the formation of other kinds of tissue been wholly overlooked. The definition of 'prosenchyma,' for example, even in the older text-books, contains the statement that the end of the cells 'are insinuated into the spaces between those lying above and below them.' This implies a change in the relative position of the elements in question.

In De Bary's work on the Comparative Anatomy of the Phanerogams and Ferns the occurrence of mutual displacements of cells during their development is explicitly mentioned in various cases. Thus, at p. 462 (English edition) the possibility of such displacements during the formation of irregular groups of sieve-tubes is recognised; and at p. 470 it is stated that the fibrous elements of the wood 'show a great elongation on transition from the cambial condition to that of mature tissue, in the course of which they insert their tapering ends, which are the principal seat of growth, between each other.' Displacements in the transverse direction, due to the growth of large vessels, are also referred to, p. 470.

It would be easy to cite many other passages from the various works on the anatomy of plants, showing that some of the changes comprehended under the term 'sliding growth' have long been known.

to botanists. But, though the existence of phenomena of this kind has been recognised, it will be admitted that Dr. Krabbe is justified in saying that they have never yet been made the subject of accurate study. It is proposed to deal seriatim with the principal points of Dr. Krabbe's work, leaving to the end the more general conclusions suggested by it.

Having defined 'sliding growth,' the author goes on to speak of the cases in which it is well known to occur, pointing out that the most obvious examples, such as those above described in the growth of fungal hyphae and laticiferous cells, are connected with the ramification of cells. He then calls attention to the fact that sliding growth, so far from being limited to cases of this kind, takes place wherever single cells of a tissue grow in such a manner that their original arrangement cannot be maintained. In all such instances there must be independent growth of the several elements of the tissue, resulting in certain definite displacements and changes in their form. These changes are not only remarkable in themselves, but are of interest in relation to the superficial growth of the cell-wall, and also from their influence on the characteristic structure of the various tissues.

The author illustrates the importance of his subject by pointing out that cell-divisions by themselves only play a limited part in the differentiation of the tissues of the vascular plants. The most characteristic constituents of the vascular bundle, namely vessels and sieve-tubes as well as tracheides, and bast and libriform fibres, all owe their mature form to processes of sliding growth. It is further maintained that the differences in the structure of successive annual rings and of spring and autumn wood depend on differences in the individual growth of their cells.

The striking statement is made that whole tissues may be formed by sliding growth, without any cell-divisions taking place; the author here refers, not to the familiar case of laticiferous cells, but to the development of the xylem in the secondary bundles of Dracaena and its allies. To this important point we shall have to return. Dr. Krabbe further shows that with the proof of the general occurrence of 'sliding growth' in the higher plants, the distinction between the so-called 'true' and 'false' tissues is obliterated.

The above general considerations serve to define the position of the author, and to introduce his detailed work.
The first part of the subject examined is the sliding growth in the transverse direction, which occurs during the formation of the vessels of the xylem. Attention is chiefly directed to the vessels of the secondary wood of Dicotyledons, as here the regularity of the radial arrangement of the cambial cells and their immediate derivatives renders it comparatively easy to follow the subsequent displacements. In the first instance the growth of the developing vessel in the tangential direction is considered. The author proves that the tangential extension of the cambial zone as a whole, during the development of any one vessel, is so insignificant that it may be left out of consideration.

The exact description of the tangential growth of the young vessels would not be intelligible in all its details without reference to the author’s figures. It is shown, however, that the extension which these elements undergo cannot be accounted for in any other way than by the hypothesis of sliding growth between the vessel and the cells of the neighbouring radial rows. Three other possibilities are here discussed; of these only one is sufficiently probable to need mention here, namely, that the vessel in its growth simply compresses and obliterates certain of the adjacent cells. According to Dr. Krabbe’s observations such obliteration takes place very rarely, a statement with which those who are familiar with transverse sections of wood will probably agree.

The facts to be accounted for are: that the vessel increases in diameter; that it is in contact with more numerous cells when mature than it was at its first origin, and that the radial rows of cells adjoining the vessel on either side become interrupted by its tangential extension. This penetration of the growing vessel between the adjacent cells is shown by careful measurements to involve sliding growth between the growing portion of the wall of the vessel, on the one hand, and the walls of the cells, between which it penetrates, on the other. In cases where larger vessels are formed this tangential growth may extend through several radial rows. In describing these phenomena the author points out that they cannot be explained without supposing that each cell has a distinct membrane of its own,—a point which does not admit of direct microscopic demonstration at so early a stage.

It is shown that the tangential growth of the vessel is only possible so long as the tissue to which it belongs is undergoing extension in
the radial direction, as is actually the case during the development of the young wood from the cambium. Owing to this radial extension of the tissue the growth of the vessel is able to take place without involving the obliteration or even any serious reduction in the dimensions of the neighbouring cells. In this case it is only the tangential extension of the vessel which is due to sliding growth, the increase in its radial diameter being accounted for by the growth of the tissue as a whole. This, however, only applies to vessels of moderate size; the very large vessels, such as are found in the spring wood of the oak, require, as we shall see, sliding growth in the radial direction also for their development.

In connection with this part of the subject the author discusses the interesting question, whether the extension of the vessel is due to growth all round or to localised growth at the points where it penetrates between the neighbouring cells. He decides in favour of the latter alternative. There is nothing improbable in this view, as localised growth often occurs in other cases; at the same time this conclusion cannot be said to rest on any decisive observations.

In the formation of the larger vessels, as already mentioned, sliding growth must take place in the radial, as well as in the tangential direction, for here the radial extension of the vessel is in excess of that of the young wood generally. It is obvious that in this case the growth of the vessels inwards, that is, towards the already formed wood, can only go on so long as the cells in this region are still capable of extension. Towards the cambium the radial growth will be able to go on for a longer time.

Dr. Krabbe next proves that the growth of the vessel may induce sliding between cells not immediately in contact with it. This will be the case wherever the radial growth of the vessel is greater than the average radial growth of the young wood, for here the growth of the cells in the same radial row with the vessel will be less than the average, as the cambium is not displaced. Hence sliding must take place between the slowly growing cells of this radial row (which are passively pushed out by the growth of the vessel) and the cells of the neighbouring rows, which grow at the average rate.

Another case of induced sliding growth occurs wherever the vessel, in its tangential extension, exerts pressure on a medullary ray. The medullary rays are never interrupted by the growth of the vessel, a point of some physiological interest; but they are often, as it were,
bulged out by it. It is shown by the author that the curvature thus induced in the ray causes the cells of the ray to slide on those elements which adjoin it on its convex side.

It is unnecessary to follow Dr. Krabbe in his consideration of the sliding growth of sieve-tubes; the facts are here quite similar to those observed in the development of the xylem vessels.

The cases next dealt with differ essentially from those just described, in so far as the sliding takes place in the longitudinal, instead of in the transverse direction. This occurs in the development of the tracheides, and of the bast and libriform fibres. It is here that the process is most obvious. Where, for example, a fibre of the secondary wood or bast grows to many times the length of the cambial cell from which it is derived, and that at a time when the elongation of the organ as a whole has long ceased, it is clear that mutual displacements must go on between the growing cells. This fact has been insisted on by many observers. The author shows in detail that these displacements necessitate sliding between the growing ends of the cells undergoing elongation. He further points out, that the process can only take place in a tissue which is still growing in the transverse direction. The tracheides or fibres insert their ends between cells, which are at first in contact with one another, and thus additional room is required, which can only be afforded by general transverse growth of the tissue. Dr. Krabbe shows that the small cell-lumina, which are found in transverse sections between the larger elements, represent the cut ends of intruding protenchymatous cells. All elements, which thus force their way between those lying above and below them, must necessarily undergo changes of form in this process.

It would have added to the interest of this part of the work if the author had been able to add figures of the fibrous elements at intermediate stages of their development from the comparatively short cells of the cambium. This would have given a much clearer idea of the phenomena actually involved than can be attained by the aid of reasoning alone.

Although the occurrence of sliding growth is most evident in the case of the secondary tracheides and fibres, which are developed in regions no longer undergoing general elongation, there is no reason to doubt, that the same process goes on during the formation of the primary tissues. The author points out, that the disturbances actually
observed in the arrangement of the cells afford evidence for this. Careful comparative measurements, both of the growth of the whole organ and of the individual fibrous elements, are clearly necessary in all such cases.

Dr. Krabbe then proceeds to discuss the development of the xylem in the secondary bundles of those Monocotyledons which are capable of indefinite growth in thickness. These bundles are formed from the cambium in parts of the stem in which longitudinal growth has ceased. *Dracaena Draco* is the first example considered. In most cases all the elements of a bundle seen in any transverse section arise from a single cell of the cambium. The bundles are here concentric, the small phloëm being surrounded on all sides by the xylem. The latter contains some woody parenchyma, but is chiefly composed of very long tracheides. The formation of a new bundle begins with the appearance of longitudinal divisions in a cell of the cambial zone. The cells thus formed only differ from the cambial cells in their smaller diameter and in their transverse walls becoming slightly inclined instead of horizontal. These young elements of the vascular bundle may be termed, for the sake of clearness, the sub-cambial cells. Now the length of these cells, which is very constant, is found by Dr. Krabbe to average 0.1 mm. The average length of the mature tracheide is 3.8 mm. Thus, as each sub-cambial cell, which becomes a tracheide, grows to thirty-eight times its original length, while there is no elongation of the organ as a whole, it follows that in any given transverse section the mature tracheides cut through will appear on the average thirty-eight times as numerous as they would have appeared before their elongation. Or, in other words, each mature tracheide will make its appearance in successive transverse sections thirty-eight times as often as the sub-cambial cell from which it is derived. The author has repeatedly counted the tracheides seen in a transverse section of a fully formed bundle. He finds that their number varies from thirty-two to forty-four, the mean thus being thirty-eight. On the author’s assumptions it is possible to calculate from these data the number of sub-cambial cells at any one level, which give rise to the tracheides. It may be convenient to give a general expression for his calculation, as it is applicable to all cases of longitu-

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1 This is not the terminology used by the author, but the terms adopted here will probably be more intelligible to English readers.
dinal sliding growth, if branching of the cells be left out of consideration. If the total number of mature tracheides seen in a transverse section be called \( x \), the number of sub-cambial cells from which they are derived will be \( \frac{x}{m} \), where \( m \) is the ratio of the length of the mature tracheide to that of the sub-cambial cell. In *Dracaena Draco* the average value of \( x \) is thirty-eight, and that of \( m \) is also thirty-eight. Hence the number of sub-cambial cells at one level, which become tracheides, will be one, i.e. the whole system of tracheides in each bundle arises from a single vertical row of sub-cambial cells. Here then, according to Dr. Krabbe, we have a most striking case of the formation of a system of tissue from a simple row of cells, without the aid of any further cell-division. The tracheides form by far the most important constituent of the bundle, and the author estimates that fourteen-fifteenths of the whole sectional area of the bundle are occupied by tissues developed by sliding growth. Thus, on this hypothesis the central phloëm must gradually become enveloped by the growing tracheides, as by a web of hyphae. It is unnecessary to enter into a more detailed consideration of this case or of the similar phenomenon alleged to occur in *Aloe* and *Yucca*. It will be well known to many readers, that a totally different explanation of the development of the so-called tracheides of these plants has been given by Professor Kny, in a work published almost simultaneously with that of Dr. Krabbe. Professor Kny finds that the elements in question are not tracheides at all, but short vessels, arising from the fusions of a series of sub-cambial cells. If this be the case, their formation does not necessarily involve sliding growth, though Professor Kny allows that this may occur to a small extent at the ends of the elements.

So direct a contradiction in the results obtained by two competent observers is certainly remarkable, and further investigation is urgently required. The writer of this article has himself made some observations on this subject, but they are not yet sufficiently complete for publication. The very pointed ends and occasional branching of the tracheides indicate that a certain amount of sliding growth must take place, but this by no means excludes the possible occurrence of cell-fusions.

The remainder of Dr. Krabbe's work, though touching on many points of great interest, will not require detailed consideration.

Some of the points here discussed, as, for example, the causes of annual rings and the relation of turgidity to growth, have only an indirect connection with the immediate subject of the paper.

In my opinion it must be granted that Dr. Krabbe has succeeded, not only in demonstrating the occurrence of sliding growth, but in showing that it is probably universal among vascular plants, and that thus the difference between their tissues and the false tissues of the Fungi and Algae is only a difference of degree. Special cases, like that of Dracaena and its allies, will clearly require much further investigation, and in all cases of longitudinal sliding growth there is room for additional evidence from direct observations of the elements at various stages of development.

In the light of the author's researches it is clear, that greater importance must be attached to the independent growth of the individual cell than has been usual in recent years. The structure of the most important tissues depends to a great extent on the special mode of growth of certain of the constituent cells.

The fact that sliding growth takes place between very young cells is also of interest as proving that the wall between them must be a double one, even at this early stage. This conclusion agrees with the observations of Wiesner.

The localised growth of certain portions of the cell-wall is no new discovery, but Dr. Krabbe's observations supply additional instances of its occurrence. It is probable that the careful study of cases of this kind will confirm the author's conclusion, that the turgidity of the cell is by itself quite insufficient to account for the phenomena of growth.

Dr. Krabbe is of opinion that continuity of the protoplasm through the cell-wall cannot exist in the case of any cells between which sliding growth takes place. In this I am unable to follow him. It is well known that the perforation of the sieve-plates is a secondary process, the plate at its first origin being a continuous cellulose wall. It appears quite possible that the same may be true of the more delicate perforations through which the protoplasm is continuous.

from cell to cell, and if this be so there is no reason why the pores should not be formed after the sliding growth is completed. It is certain that vessels and other elements with sliding growth have corresponding pits. These pits must be developed when the mutual displacements are at an end, and it is quite likely that the perforation of their closing membranes may take place at the same time. We must wait for further researches on the development of the protoplasmic strands in the cell-wall before this point can be determined. It is of interest to note that, according to the researches of Fischer, the sieve-tubes are connected by fine protoplasmic strands, not only with one another, but also with their companion cells; but that neither of them are connected with the cambiform cells. The latter, however, are in communication among themselves. It would be important to ascertain whether these differences have any relation to the sliding growth of the various elements on one another.

It may be hoped that Dr. Krabbe's work will lead to much important investigation along the lines which he has indicated.

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