A STUDY OF INTERCELLULAR RELATIONSHIPS AMONG VEGETABLE CELLS WITH SPECIAL REFERENCE TO "SLIDING GROWTH" AND TO CELL SHAPE

by

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(With the plates II—IV)

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STATEMENT OF THE PROBLEM.

> "It is pointed out that all instances where "sliding growth has been postulated between the "individual units of a meristem are under sus- "picion and deserve re-examination."
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> J. H. PRIESTLEY - NEW PHYTOL. 29 (1930), p. 138.

There exists much controversy in botanical literature about the true nature of the processes which are supposed to be involved in sliding growth of cells over the surface of adjacent cells of the same tissue. The term "sliding growth" (gleitendes Wachstum) was introduced by KRABBE in 1886 (**94**). KRABBE was convinced that sliding growth is a phenomenon of general occurrence and that it plays an important part in the development of meristematic cells to their mature condition. His conception found rather general acceptance and up to now it has been stated in several textbooks that cells slide over the surface of other cells during growth, e.g. in HABERLANDT (68B), EAMES and MCDANIELS (**40**) and KÜSTER (**97**).

Apart from these statements other investigations were published stating several instances in which the occurrence of sliding growth was contested, where, according to KRABBE's conception, sliding growth was to be expected. A precise analysis, however, of the processes occurring in the cell walls during sliding growth failed to appear.

In order to remove, if possible, the controversy existing in literature, which has been caused by the contradictory statements of different investigators — some of them confirming, others refuting KRABBE's conception — it seemed desirable to re-investigate this problem. It appeared to be necessary to submit all the instances, where mutual slipping of cells over each other's surfaces was said to be found, to a new experimental investigation. The less complicated cases were taken as a starting-point, the more complicated being subjected to an analysis later on.

Furthermore the cell shape in general and the structure of the cell wall were included in our investigations, although these two subjects do not immediately bear upon the subject of our present study. It became evident however, as this work was in progress, that several particulars relevant to the problem of sliding growth could not be satisfactorily explained without a closer examination of the

shape of cells (see especially Chapter II-C) and of the composition, structure and growth of cell walls (Chapter XI).

The meristematic tissues and their young derivatives, used to serve the main purpose of our investigations, formed excellent material for these minor examinations as well.

INTRODUCTION.

A. A CRITICAL SURVEY OF THE LITERATURE ON "SLIDING GROWTH".

1. *The development of the different opinions upon the subject.*

It has been mentioned before that the term "sliding growth" originates from KRABBE's monograph [1]). In older publications already the intrusion of cells in amongst their neighbouring cells, and consequently the phenomenon of their mutual slipping, had incidentally been recorded. The earliest statement of the kind was made by TRÉCUL (**165**) in an account of his investigations into the development of wood fibres: " . . . . elles (i.e. the wood fibres) s'introduisent et glissent entre les cellules qui sont placées au-dessus et au-dessous d'elles . . . .". Later HANSTEIN (**69**) remarked in his monograph on latex-ducts that "bast fibres" during growth slide along the walls of adjacent cells as they dovetail in amongst one another. Similar considerations are given by SANIO (**144**), HABERLANDT (**67**) and DE BARY (**36**).

KRABBE's monograph was in 1890 followed by a paper by the hand of MISCHKE (**122**), dealing with an investigation into the growth of *Pinus*-tracheids. The author thought, that by the result of his studies he had obtained additional proof of KRABBE's theory.

NORDHAUSEN (**127**), founding his opinion on his investigation into SANIO's "Initialentheorie" of the cambium, came to the conclusion that in the development of secondary xylem — especially in the formation of wood vessels — sliding growth does not play such an important part as KRABBE had suspected. NORDHAUSEN was of the opinion that a single layer of "initials" in SANIO's sense does not exist, but that different layers of cambial cells are able to divide, which, instead of sliding growth, may account for the increasing number of contacts between growing wood vessels (see p. 104). He

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1) See also D. H. S(COTT): Review of G. KRABBE, „Das gleitende Wachstum" etc. in Ann. Bot. 2: 127—136 (1888).

therefore attributed the changes in intercellular relationships, ascribed by KRABBE to sliding growth, chiefly to cell division.

In 1901 JOST (83) published an investigation into the "disappearance" of cambial initials during the burial of branch bases. He thought that the displacement of these initials, observed by him, could only be satisfactorily explained by assuming that these cells shift by sliding growth.

VON GUTTENBERG (66) and later KNOLL (90) found that certain idioblasts ontogenetically belong to the mesophyll but migrate to the surface layer, thus ultimately exposing a portion of the cell wall. These two authors concluded from their observations that the process in question could only be ascribed to sliding growth of the young idioblasts along the epidermal cells.

KLINKEN (89) investigated serial sections of the secondary phloem of *Taxus*. In this series of sections changes in the cell position appeared to take place in radial (centripetal) direction. From these changes KLINKEN now supposed to be able to reconstruct the intercellular readjustment brought about in the layer of cambial initials in course of time. He reported that the cambial cells occasionally show transverse divisions and start elongating again after each division. According to his opinion this elongation is brought about by sliding growth of the divided initials along other initials. His method was applied by NEEFF (125) to several species of Dicotyledonous trees and by BEIJER (24) to the secondary wood of a root with stratified cambium. These investigators both claimed to have gained by their work additional confirmation of KLINKEN's results. BAILEY (13), who most probably employed the same technique, also held this view.

GROSSENBACHER (65) came to the conclusion, on account of the occurrence of continuous rows of trabeculae extending through several annual rings, that sliding growth is likely to occur only at the ends of tracheids and wood fibres.

PRIESTLEY (136) took quite a different view of the matter. He contended KRABBE's conception in a critical paper, issued in 1930, which is not so much founded on new observations as on general considerations based upon the existing literature. He set up a theory of an alternative type of growth which does not involve sliding of cells and is indicated by the term „symplastic growth" (see p. 27) In a later paper (137) he stated to have found direct evidence for his conception that cells do not slide along other cells, basing his arguments on an investigation into the formation of a new wall at cell division.

MEEUSE (116) was able to show that, most probably, sliding

growth is not involved in the development of sclerenchyma fibres in certain Monocotyledons. PRIESTLEY and KUNDU came to the same conclusion after their investigation of jute (see BARKER, 22) and KUNDU after his examination of several other fibre plants (priv. comm.).

SINNOTT and BLOCH (155) found, by means of direct observation of living meristematic cells in young grass roots, that no changes in the relative position of the cells could be detected and that sliding growth in these meristems was, therefore, out of the question. For all those cases where a cell gains contacts with cells originally not adjacent the latter investigators assumed the occurrence of a localized apical growth instead of mutual slipping, introducing the term "intrusive growth" for this process (see p. 30).

For further particulars about these investigations we must refer to the later discussion of the various instances we have studied.

2. KRABBE's *conception of "sliding growth"*.

We must now devote some space to a more detailed discussion of KRABBE's monograph, since all later investigators based their researches on his statements and since no doubt about the correctness of his observations has ever been expressed. His conclusions, on the other hand, are not always right, nor are they up to date. We cannot be surprised at this, considering that in those times so little was known of the structure and properties of the cell wall.

KRABBE's starting-point was the change in intercellular relationships of mature tissues as compared with the meristem. We must well bear in mind that his investigations preceded BERTHOLD's monograph „Studien über Protoplasmamechanik" (25), in which monograph a conception of the intersection of cell walls was published,

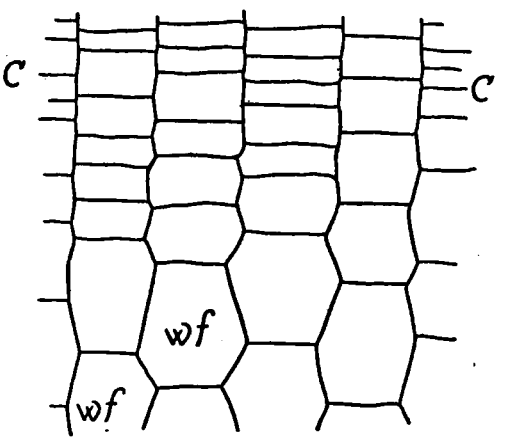

Fig. 1. Transverse section of the cambium (*cc*) and the adjacent young wood of a tree (*Salix alba*). Notice the alteration in the intersection of the cell wall when cambial cells differentiate into wood fibres (*wf*). Before the differentiation the cell walls meet at practically right angles, after the differentiation at approximately 120° angles.

at variance with SACHS's theory of the orthogonal intersection of cell walls (141). KRABBE described and figured various instances, which clearly illustrate that he did not take SACHS's theory for granted in all cases. He pointed out that cambial cells, as seen in cross section of the stem, are more or less rectangular, whereas the derivative elements of wood and phloem, also viewed in cross section of the stem, have become polygonal, mostly hexagonal, in outline. The original orthogonal intersection apparently has altered during the differentiation of these elements (fig. 1 and 2).

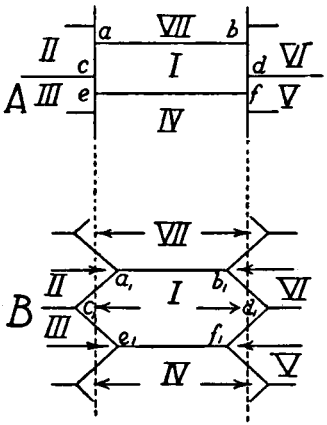

Fig. 2. Diagrammatic representation of the alteration in cell relationship brought about by the differentiation of cambial cells into elements of secondary xylem.

A. A cambial cell (I) and its surrounding cells (II-VII, only partially drawn), as seen in transverse section of the stem.

B. The same cells after having changed into wood fibres. The arrows indicate the direction of tangential growth. For further explanation see text.

The alteration brought about is involved in the dilatation of the cambial derivatives, as they pass into elements of wood and phloem. This dilatation occurs in radial direction and is perceptible in two zones, each consisting of several layers of differentiating cambial derivatives and situated on either side of the cambium. Since the older wood does not yield, the dilatation of the stem can take place in one direction only, namely centrifugally, and it is therefore accompanied with a slight displacement of the whole region of dilatation in centrifugal direction. This displacement increases the girth of the two dilating zones, so that each young element of xylem and phloem must necessarily show an increase in tangential diameter after the dilatation. In a trunk or branch that is not too thin a great number of cells is found in the circumference of the dilating zones. The increase in girth of the two zones is very small here and it is spread over a great many cells. Since one cell occupies only a small part of a zone of dilatation, a hardly noticeable expansion of a cell in tangential direction may be expected. Contrary to expectation, however, a conspicuous local increase in tangential diameter is to be observed (fig. 2). The tangential walls *ab* and *ef* in fig. 2A grow shorter in tangential direction, altering into a_1b_1 and e_1f_1 in fig. 2B, while the

radial walls show breaks (see the arrows in fig. 2B), the more or less rectangular transverse sections of cambial cells thus altering into polygons with more than four angles.

KRABBE did not observe a partial resorption of the shortening tangential walls, such as *ab* and *ef*, nor a compression of these walls, as they do not increase in thickness. Neither did he observe any folds or wrinkles. He therefore drew the conclusion that the growing cells slide along each other, namely in the direction of the arrows in fig. 2B. Accordingly cell II in this figure moves from left to right, cell VI from right to left, both dovetailing in between cells I and VII; cell I moves in two opposite directions simultaneously, from left to right, dovetailing in between cells II and III and from right to left, dovetailing in between cells V and VI. Consequently the walls of adjacent cells are supposed to show mutual slipping, thus wall *ac* of cell I sliding along wall *ac* of cell II, wall *ab* of cell I sliding along wall *ab* of cell VII, etc. (see fig. 2A). In this train of thought each cell is expected to possess a high degree of individuality. Hence KRABBE deduced that every cell must have a wall of its own, although the interjacent membranes in meristems appear to be quite homogeneous, except in the angular spaces where three or more cells adjoin.

KRABBE applied the same argument to various other cells differentiating from meristems in order to explain the changes in shape and in intercellular relationships of these cells. He had observed — as is the case during the transition of cambial cells into xylem and phloem — that the original orthogonal intersection of the cell walls passes into a pattern where, as seen in sections, the walls of dovetailing, polygonal cells meet at approximately 120° angles. The same process as described above, i.e. of mutual slipping of cells accompanied with breaks in certain walls, was therefore accounted by him to bring about the typical, more or less hexagonal, outline of parenchymal and other cells as seen in transverse section.

From measurements of the lengths of cambial cells and their derivatives (wood fibres, tracheids, secondary phloem fibres) it was already known that the derivative elements show a marked increase in length as compared with the original cambial mother cells (SANIO, 144, HABERLANDT 67). The above explanation would hold for these cases too, according to KRABBE, with the only difference that the cells, elongating at both ends and growing in amongst the cells situated immediately above and below, show mutual slipping in longitudinal direction instead of in transversal direction. It is possible that the tapering, elongating portions of the cells penetrate into the original radial rows of cambial derivatives, each row originating

from a single cambial initial by tangential division. The number of cells then multiplies in transverse section. This might account for the fact that the radial adjustment of wood fibres is often considerably upset by the intruding cell-tips of growing fibres, as is the case with *Quercus* and *Populus*. Also with the elongation of primary sclerenchyma fibres ("bast fibres"), tracheids of Monocotyledons with secondary growth and non-articulate latex-ducts this so-called "longitudinal sliding growth" was assumed to take place.

Another example of sliding growth dealt with by KRABBE is the development of the, sometimes, very wide wood vessels of some hard-wood trees, especially of the "ring porous" type (*Quercus, Ulmus, Fraxinus*). The fusiform initials of the cambium are all about the same size and they are bordered by about six other cambial cells, when viewed in transverse section (see figs. 1, 2, and Chapter II—A); a wide wood vessel, as seen in transverse section, is on the contrary bordered by many more than six cells (fig. 3). KRABBE explained that the young wood vessel, increasing in size, slides over the surface of adjacent cells in the same way as has been described for wood fibres or tracheids (see p. 24, fig. 2). His explanation implied that this sliding growth should continue until the vessel is finally placed in contact with many more cells than with the few originally surrounding the vessel initial, while some walls seem to disappear. (fig. 4). He ascribed the formation of wide sieve-vessels, for instance in *Cucurbita*, to the same process.

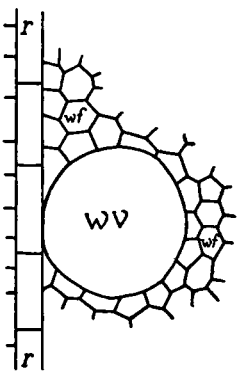

Fig. 3. Wood vessel and surrounding cells of *Populus* spec. in transverse section (semi-diagrammatic). The secondary walls are omitted. *wv* = wood vessel, *wf* = wood fibre, *rr* = ray.

The latter instances are distinguished by the term "transversal sliding growth" as opposed to the "longitudinal sliding growth" of fibres and tracheids (see p. 32). KRABBE observed that wood fibres and tracheids show longitudinal and transversal sliding growth operating at the same time. The distinction is a mere topographic one and is, to us, of no further significance.

We may conclude by summarizing KRABBE's work as follows:

The changes in relative cell-position and the alteration of the intersection of cell walls associated with it should be attributed to a sliding of cells — individually or mutually — over adjacent cells during their growth and differentiation. This so-called "sliding

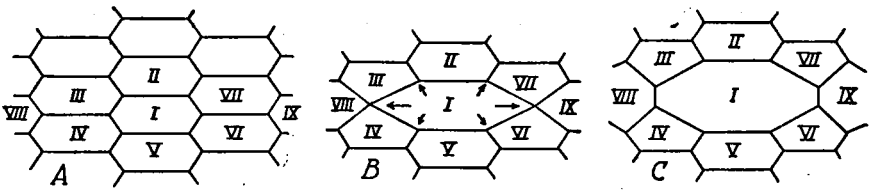

Fig. 4. Diagrammatic representation of the development of a vessel initial into a full-grown wood vessel. *A*, *B* and *C* represent three successive stages in transverse section.
In *A* all cells are the same size.
In *B* the vessel initial I has increased in size and by its enlargement causes adjacent cells to be pulled apart from each other. Sliding over the contiguous walls of cells III, IV, VI and VII, by this eliminating the wall between cells III and IV and between cells VI and VII until they are reduced to a point, the young vessel cell finally establishes contact with cells VIII and IX.
In *C* the points of contact of the wood vessel I with cells VIII and IX have developed into walls again.

growth" is the essential point of KRABBE's conception. Underlying his conception is the assumption that each cell should act as an individual unit, possessing a wall of its own, so that the wall of one cell slides along that of its neighbour as it grows and differentiates.

3. PRIESTLEY's *theory of "symplastic growth"*.

For many years KRABBE's conception of sliding growth was accepted as an ascertained fact. No possibility of another mode of growth seemed to suggest itself and later workers, little thinking of testing his results by serious reinvestigation, in the main supported his views. It was not until 1930, that PRIESTLEY published a critical paper in which he rejected KRABBE's conception and exposed a theory of an alternative method of growth, chiefly founded on conclusions drawn from the existing literature. Starting from the viewpoint that on account of their structure the walls of meristematic cells cannot possibly show mutual slip without being ruptured, he suggested that two adjacent cell walls with the intervening middle lamella ("three-ply membrane") behave as one single unit, so that all changes brought about in the structure of the tissue should be ascribed to a readjustment of all cell walls operating as one "common framework". Hence the term "symplastic growth".

PRIESTLEY further suggested that the cells, as seen in section, tend to assume their shape by their walls conforming to the rules of PLATEAU-ERRERA, i.e. the rules of the minimum surface area (see Chapter II C). Supposing that these rules are operative, a new division wall in an apical meristem cell will at first meet the parent walls at

right angles (see fig. 5 A, representing a very early stage). This position is, however, unstable. While the daughter cells grow, causing an expansion of the whole mass of cells, the common framework of cells will be readjusting itself. The lateral parent walls, perpendicular to the division wall, will break in the intersecting lines (compare fig. 5 B, in section, points *a* and *b*), which alters their original perpendicular position to the division wall. Their relative position will continue to change until the newly formed walls and those originally present finally meet again at angles approximating 120° and the cell sections will thus be restored to their original, hexagonal pattern without any mutual slip of cells having taken place. This method of cell-wall formation is supposed to repeat itself at every new cell division (indicated in fig. 5 B as broken lines).

Other phenomena, such as the development of the hexagonal (or polygonal) shape, as seen in section, of the elements of secondary wood and secondary bark from the almost rectangular shape of cambial cell sections, the "longitudinal sliding growth" in KRABBE's sense and the "intracambial sliding growth" of cambial initials as assumed by several investigators (**89**, **125**, **13**), were all interpreted by PRIESTLEY as to be brought about by the same process, namely by a readjustment of all cell walls as a whole. He made mention of one particular case, however, where his explanation would not hold. The full development of a growing wood-vessel, differentiating from a cambial initial and gaining contacts with additional cells, could not be accomplished by symplastic growth alone, but here the process

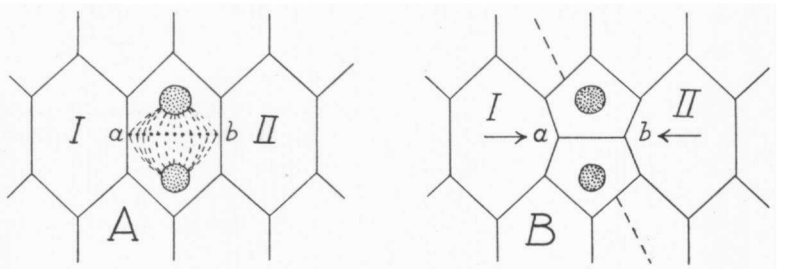

Fig. 5. Two different stages of cell division in a meristem, represented diagrammatically.
In *A* the cell-plate (*ab*) is coming into existence across the phragmoplast in the form of granules, in *B* it has grown into continuity, forming a new cell wall (*ab*). During this process the lateral walls show breaking in the points *a* and *b*, in the direction of the arrows.
Broken lines: walls likely to be formed at subsequent cell division in the meristem, changing the pentagonal sections of the new-grown daughter cells into hexagons again. See further text.

should be concomitant with the rupture of cells along their common middle lamella, while the expanding vessel slips with its walls along the walls of surrounding cells.

PRIESTLEY found further arguments to carry evidence for his theory, in the presence of corresponding pits and protoplasmic connections, and in the presence of continuous long radial series of trabeculae. Later in this paper the matter will be dealt with more fully.

4. *Some views regarding intercellular readjustments as correlated with cell wall structure.*

In our short survey of KRABBE's monograph we have already pointed out that his conception of sliding growth rests upon the assumption that a meristematic cell is enclosed by a wall of its own. Cells should then be able to move as independent units and retain their individuality as they shift their position in reference to one another during the actual process of sliding growth. KRABBE had not been able to observe these individual walls in all parts of the membranes which intervene the protoplasmic contents of adjacent cells in meristematic tissue and he had, therefore, no substantial evidence in support of his assumption. His own description of sliding growth is extremely vague and it is not quite clear how exactly he himself imagined the process of "sliding". It is known that he had observed the shortening of some walls and the elongation of others during so-called "sliding growth". He further suggested that a sliding cell, when moving over the surface of adjacent cell walls, might wedge into and so split two corresponding walls along their connection and he assumed that finally the sliding cell establishes contact with the separated walls.

It is remarkable that, in spite of KRABBE's vague description, most later investigators who occupied themselves with the same problem did not extend their observations to a closer examination of the changes that should occur in the cell wall during the process of sliding growth. They simply cite KRABBE or even ignore the matter entirely.

Conspicuous among those later investigations is the work of NEEFF (124), who thought that he had observed sliding growth of growing wood fibres in a direct way. From his observations he concluded that cells, during the process of elongation, digest the lamella substance between two adjacent cell walls with their expanding tips, causing a gradual splitting of those walls. While the cells elongate, their walls should move relatively to the adjacent cell walls. The protoplasmic connections would be broken by this movement

and the pit-pairs that originally corresponded in position across the middle lamella divided into two blind pits in the separated walls (see fig. 6).

A similar gradual splitting of adjacent cell-walls was suggested by SINNOTT and BLOCH (155). They supposed that in definite instances wall growth is restricted to a small region of a cell, usually to the ends, so that a cell sends out intrusions between neighbouring cells ("apical growth"). The elongating tip of the cell digests the cementing substance between the adjacent cell walls, gradually pushing the cells

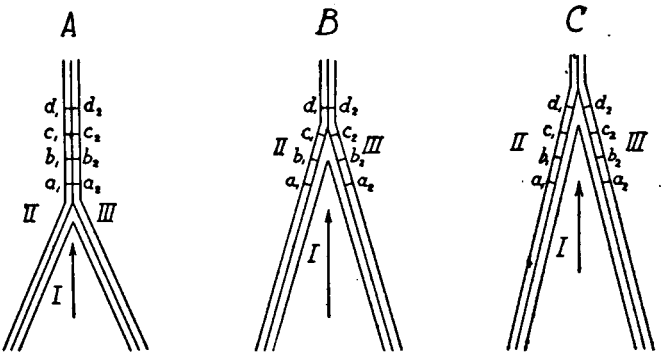

Fig. 6. Diagrams illustrating "intrusive growth" in three successive stages.
Fig. A represents a cell I with apical growth, at the point of growing in between cells II and III, that face one another across a common middle lamella.
In fig. *B* the apical growth of cell I is proceeding, causing a gradual splitting of the walls between cells II and III and separating successively the corresponding points of these walls (a_1—a_2, b_1—b_2, etc.).
Fig. *C* represents the final stage, when the newly developed portion of the wall of the intruding cell has established contact with the separated walls of cells II and III.
If the corresponding points a_1—a_2, b_1—b_2, etc. in fig. I should represent plasmodesmata, they are, one after another, starting with a_1—a_2, ruptured by the expanding cell tip and split into pairs of non-corresponding wholes (compare figs. *B* an *C*). Thus the connection of the protoplasts is destroyed.

apart. The protoplasmic connections are ruptured, the newly developed portion of the growing cell establishes contact with the separated walls and retains these new connections without any sliding growth taking place. Such a sharply localized apical growth does not affect the other parts of the walls of both intruding and separating cells, so that these other parts do not alter their relative positions. Also here slip of walls is unlikely to occur and the term "sliding growth" should no longer be applied. To distinguish this type of changing cell-relationship the authors proposed, therefore, to drop

the term "sliding growth" and replace it by "intrusive growth".

The conception of SINNOTT and BLOCH is not new, for a theory very similar to theirs had already been put forward by ZIMMERMANN in 1887 (182, p. 204), whose views were adopted by HABERLANDT in the second edition of his "Physiologische Pflanzenanatomie" (68A, p. 66) [1]).

PRIESTLEY, on the other hand, did not consider it very likely that cells are able to split in the way as described by KRABBE or NEEFF. He investigated meristematic cell walls by applying maceration techniques and various reagents and reached the conclusion that each meristematic cell is bordered by a complete limiting wall and is separated from the walls of neighbouring cells by a matrix, the middle lamella, which may be very tenuous and therefore even inconspicuous, at some places. The process of maceration appeared to be extremely difficult, since the cell walls are tightly knit together and, in PRIESTLEY's opinion, a splitting of cells could not take place, therefore, without a complete rupture of the tissue. PRIESTLEY was, moreover, of opinion that meristematic cell walls are plastic, inelastic and possibly even semi-liquid, so that presumably, even though they possess a certain degree of individuality, they are not sufficiently rigid to be split in the way as KRABBE had imagined. Deformation of these young cell walls should be brought about easily, it is true, but not by a movement of one cell past another as an entity in KRABBE's sense, neither by a gradual splitting of corresponding cell walls by the growing cell accompanied with simultaneous sliding, as suggested by NEEFF, but without the occurrence of any mutual sliding of cells over the surface of adjacent cell walls. PRIESTLEY, then, assumes that the intercellular readjustments and the deformation of the cell walls made necessary by growth and differentiation should be brought about by a gradual mutual adjustment of all cell walls "as a common framework", indicated by him as "symplastic growth".

B. ARGUMENTS IN FAVOUR OF "SLIDING GROWTH".

In recapitulating the foregoing chapters it appears that, on one hand, arguments may be found in favour of sliding growth, on the other hand, arguments that are plainly contrary to this idea.

If we first consider the points in favour of sliding growth, we may

1) N.B. In later editions HABERLANDT has altered his opinion on the ground of the investigations of VON GUTTENBERG (66) and KNOLL (90). He then speaks of "sliding growth" without further comment and simply cites KRABBE's monograph.

once more remember how KRABBE had already observed the shortening of cell walls and put this forward as an important argument in favour of his own theory.

More important is the argument that cells may gain additional cell contacts, as is the case for instance in developing wood-vessels (fig. 3), and in long wood fibres or tracheids originating from short cambial cells (*Robinia, Dracaena*) — amore detailed description of which follows below — or the argument that cells may obtain a secondary exposed surface by migration, as is the case in the idioblasts of *Citrus* (**66**) and *Dalechampia* (**90**).

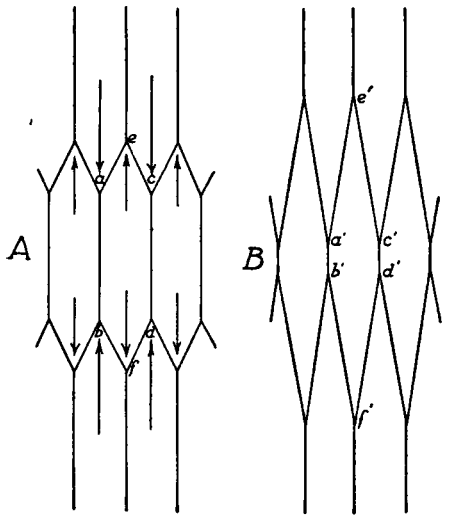

Fig. 7. Diagrammatic representation of "longitudinal sliding growth" in KRABBE's sense.
A. Some cambial cells as seen in longitudinal section.
B. The same cells after differentiation into wood fibres, attended with incidental elongation, the direction of which is indicated by arrows. The radial walls *ab* and *cd* (fig. *A*) shorten into *a'b'* and *c'd'* (fig. *B*), as the other walls *ae, ec, bf, fd* elongate.

With the development of wood fibres in young wood, the formation of secondary phloem fibres and the formation of the secondary vascular bundles in Monocotyledons with secondary growth it is revealed by direct measurements that the elements may show a considerable increase in length as compared with their cambial mother cells, whereas any part of the tissue as a whole does not increase in length. It is generally assumed that every cell elongation in the direction in which longitudinal growth has ceased, could be brought about only by sliding growth or intrusive growth. How the elongation of cells in such a direction might take place is illustrated in text-figure 7, which represents diagrams of a number of cambial cells (7A) developing into wood fibres (7B), as seen in longitudinal section. Certain walls are observed to decrease in length, compare *ab* and *cd* changing into *a'b'* and *c'd'*. In the end these walls decrease in length so much as to become reduced to veritable "points", so that they finally completely disappear from

the section, and the cells on the upper row come in contact with the cells on the lower row. That some walls are observed to grow less in length was mostly considered as an indication that, at a certain period of their development, sliding growth takes place. The fact that some walls completely disappear, which makes originally not adjacent cells come in direct contact with each other, seems to point still stronger to the occurrence of sliding growth.

A similar process is supposed to occur in the cambium itself. KLINKEN (89), NEEFF (125) and BAILEY (13) made out that in many cambia the fusiform initials continuously increase in length, after some time divide transversely, then start elongating again to divide anew and so forth. This manner of growth is sometimes distinguished as "intracambial sliding growth".

Cambial initials may also decrease in length, even to the extent of completely disappearing from the cambial zone, as was observed by JOST (83). The radial rows of xylem elements show an equivalent decrease in number in the latter case and JOST considered this strong evidence in favour of sliding growth in radial direction.

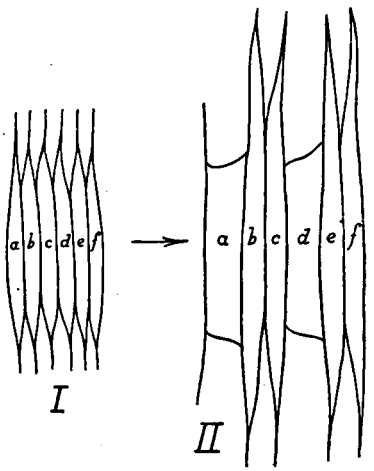

Fig. 8. Diagrams of uniform cambial cells (I: *a*—*f*) developing into longer and shorter elements of secondary xylem (II: *a*—*f*), as seen in longitudinal section.
Diagram II illustrates how the original cambial cells may differentiate into vessel elements that remain the same lengths as their cambial mother cells (*a* and *d*) and into wood fibres that by nature elongate to a considerable extent.

The elements of the secondary xylem are often of different lengths. In most Dicotyledonous woods short vessel elements are found next to much longer libriform fibres, though they have all been derived from cambial cells of practically uniform size (fig. 8). If sliding growth should be assumed to occur (from which, naturally, follows that each cell freely moves past neighbouring cells and elongates independently of all other cells) the presence of long and short xylem elements next to each other could be easily accounted for. The phenomenon might also be readily explained by intrusive growth, however.

In the majority of instances cited above cells dovetail, as a matter

of fact, in amongst their neighbours. Whether the changes in relative cell-position brought about by it should be associated with a mutual slip of cell walls or with a splitting along their common middle lamella, remains still a questionable point, as has already been stated by PRIESTLEY.

Also the occurrence of breaks in walls that were originally straight (compare fig. 2) is sometimes considered an indication that sliding growth should take place (KRABBE, **94**, BEYER, **22**). It will be recollected, that it was PRIESTLEY again who gave a different explanation of this phenomenon.

C. ARGUMENTS AGAINST "SLIDING GROWTH".

Summarizing the arguments against sliding growth we arrive at the following points:

Various difficulties arise when we consider the consequences involved in sliding growth. One of the most important problems presenting itself, which was already faced by KRABBE, is how far the plasmodesmata are affected by the process of sliding growth. The plasmodesmata run from protoplast to protoplast (**117**) and consequently consist of two corresponding parts in two corresponding cell walls. If sliding growth in KRABBE's sense should actually take place, the plasmodesmata will inevitably be destroyed during the process, or ruptured and split into two non-corresponding halves, as is represented in fig. 6. When the process of sliding growth has terminated, these plasmodesmata should either be rebuilt, which was assumed by KRABBE and several others (**94**, **83**, **109**, **124**), or the shifted halves of the plasmodesmata should be completed by newly-formed corresponding parts.

Opinion was divided on this matter. JOST (**83**) agreed with KRABBE, whereas STRASBURGER (**160**), on the strength of a more penetrating study of the plasmodesmata, took a different point of view. PRIESTLEY, being of STRASBURGER's opinion, maintained, also in consonance with his own theory, that the continuity of all protoplasts would be disturbed, if the connection of cells by plasmodesmata should be discontinued.

As regards the validity of this argument the following may be added:

a. the difficulty, that the presence of plasmodesmata should be inconsistent with the occurrence of sliding growth, might be avoided by assuming that the cells show local growth (intrusive growth), so that the greater part of the cell wall with its plasmodesmata remains unaffected and the continuity of the protoplasts main-

tained; in those places where the walls of the intruding cell and the separated walls have coalesced the plasmodesmata will then be missing or will have to regenerate.

b. JUNGERS (see **123**) claims to have made out that the "plasmodesmata" are no true protoplasmic connections, but belong to the "dead" cell wall constituents. If he should be right, the presence of plasmodesmata does not provide an argument against sliding growth. JUNGERS's assertion was, however, disposed of by MÜHLDORFF (**123**), who clearly proved that — with the exception of artefacts resembling plasmodesmata — all plasmodesmata are real protoplasmic structures. So finally the argument should retain its validity, since it has hitherto not been possible to demonstrate the regeneration of plasmodesmata. This point will be reconsidered in another chapter (see p. 54ff).

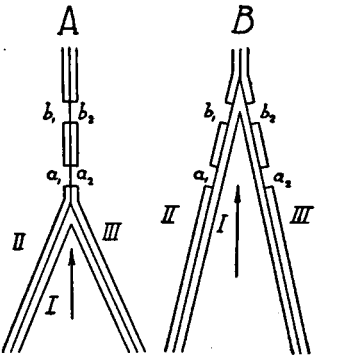

Fig. 9. Pitted walls as affected by sliding growth or intrusive growth. Diagrammatically after NEEFF (**124**).
A. Cell walls with pit-pairs a_1a_2, b_1b_2 before growth of cell I.
B. The pit-pairs a_1a_2, b_1b_2 are, after apical growth of cell I, split into pairs of non-corresponding blind pits a_1 and a_2, b_1 and b_2.
Compare also fig. 6.

Almost the same reasoning (whether or not the plasmodesmata appear in walls that show mutual slip) was applied by PRIESTLEY (**136**) to pit-pairs and used by him as another argument against sliding growth. The effect of sliding growth or intrusive growth on cell walls containing pit-pairs is represented in fig. 9. NEEFF (**124**) pretends to have actually observed in young growing wood fibres the splitting of pit-pairs into pairs of non-corresponding blind pits (see also p. 106), whereas in older wood only complete pit-pairs could be found. He, therefore, assumes that the existing blind pits are completed by new corresponding pits to form new pit-pairs. As will be shown later, the conclusions drawn by NEEFF are based either on inaccurate observations or on an erroneous interpretation of the facts observed.

We might, as PRIESTLEY did, use the presence of pit-pairs as a valid argument against sliding or intrusive growth, if only we should be able to prove that the pit-pairs present in the walls of young cells, or the structures resembling pit-pairs, are never split into separate halves during cell growth.

In a more recent paper PRIESTLEY (**137**) showed that in conse-

quence of the development of the intercellular spaces — already described by MARTENS (111, 112) — a group or file of cells often remains enclosed within the wall of the original parent cell from which the cells have been derived. The persistence of the parent wall around these groups or files is clear evidence that mutual slip cannot have occurred between the enclosed cells, which again provides an argument against sliding growth.

OWN INVESTIGATIONS.

CHAPTER I

MATERIAL AND METHODS.

The greater part of the material was taken from the Botanical Gardens at DELFT and LEYDEN and as a rule collected immediately before use. Part of this material was, if necessary, preserved in alcohol-glycerol.

The fixations for histological purposes were chiefly carried out with CARNOY's fixative, formalin-acetic acid-alcohol or sublimate-acetic acid-formalin after CHAMBERLAIN (30). The objects were imbedded and sectioned by the usual paraffin technique, except pieces of stems of *Dracaena* and *Cordyline*, which were desilified, and afterwards imbedded and cut in celloidin following CHEADLE's method (32).

The stains employed chiefly were FLEMMING's triple stain, haematoxylin HEIDENHAIN and DELAFIELD (counter-stained with erythrosin or orange-G), vesuvin, and tannic acid-ferric chloride (45).

Several maceration-techniques were employed; they were varied according to the object under treatment, for experience has taught that different objects require different methods to render the best results: boiling potassium hydroxide solution (1), 5 per cent. chromic acid solution, hydrogen peroxide solution (87), ammonium oxalate solution, alternating hot ammonia (5 per cent.) and hot hydrochloric acid solution (5 per cent.), Eau de Javelle and, finally, retting.

It is advantageous to use cells, isolated by maceration, for the study of the birefringence of the wall. PRESTON (133), however, has criticized the conclusions based on macerated and "swollen" material, and the products obtained by various maceration techniques were, therefore, compared "*inter se*" and, moreover, compared again with untreated material. It appeared from our investigation, that the

action of the reagents, if well-controlled and not too prolonged, did not change the structure of the birefringent constituents of the wall in such a degree that it considerably affected the direction of the major extinction position in the single wall.

The terms used in this paper have for the greater part been adopted from the Glossary of the "Committee on Nomenclature of the International Association of Wood Anatomists" (33), in so far as they do not occur there they have been brought in accordance with the nomenclature of EAMES and MCDANIELS (40).

CHAPTER II

APICAL MERISTEMS AND SOME DERIVATIVE TISSUES.

A. *Structure and growth of meristems and the shape of meristematic cells* [1]).

FOSTER (48) has reviewed the various theories of the structure of apical meristems. So far three different theories have been developed: the "apical cell theory", the "histogen theory" (HANSTEIN) and the "tunica-corpus theory" (BUDER-SCHMIDT).

The structure of apical meristems varies with the systematic rank of the object. Apical cells are found in the thallus of Thallophytes, in Bryophytes and in the stem and root of most Pteridophytes. A tunica and corpus are found in the apical meristems of the stem of Angiosperms. The shoot apices of Conifers (93), *Ginkgo* (47) and Cycads (49, 82) show a very peculiar structure, caused by the presence of a single layer of initials. The structure of the root tips of Angiosperms is usually in accordance with HANSTEIN's histogen theory, since here the meristem originates from a few superimposed initials, each of which furnishing a different portion of the root. Sometimes a single initial furnishes both epidermis and cortex (dermatoperiblem cell), whereas the central cylinder is a derivative of one or more other initials, for instance in *Saccharum*, *Hordeum* and *Secale* (graminaceous type), sometimes "calyptrogen" and "dermatogen" are formed by a common initial and the remaining tissues by other initials (for instance in many Dicotyledons), etc. A survey of the various types of root meristem is given by HABERLANDT 68, 6th Ed. p. 69—94).

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1) In these considerations it is supposed in anticipation, that in meristems sliding growth does not occur (compare Chapter II, B and Chapter VII).

For an analysis, the tunica meristem is the most suitable and therefore we start with this type.

SACHS (141) supposed to have found in apical meristems three orthogonally intersecting systems of cell walls, the periclinal, the anticlinal and the so-called "vertical" walls. These names are generally employed ever since, though SACHS's conception of the structure of the shoot apex is now obsolete, being too diagrammatic.

The tunica forms the peripheral part of the growing point and is built up of one or more self-perpetuating layers of cells which do not show periclinal divisions, except when a leaf primordium is formed. The periclinal walls separating the tunica layers consequently form a number of confocal paraboloids, which was already noticed by SACHS (141). The tunica grows chiefly in one direction, namely in the direction of the vertical walls, so that in the tunica these vertical walls correspond lengthwise with other vertical walls, thus forming long longitudinal planes which divide each tunica layer in a number of longitudinal cell columns. In adjacent columns the anticlinal walls do not correspond as a rule, but are placed at various levels.

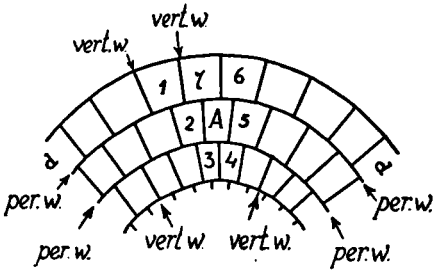

Fig. 10. Diagrammatic representation of a part of a transverse section of a growing point of an Angiosperm showing the dermatogen (*d-d*) and two underlying layers of the tunica. Intersection of the cell walls represented orthogonally. *vert.w.*: "vertical" walls, *per.w.*: periclinal walls.

In fig. 10 a part of a transverse section of a tunica is represented diagramatically, showing the periclinal planes separating the layers of the tunica (per w.) and the vertical walls, which are "shifted" in adjacent layers (vert. w.). The "shift" of the vertical walls is to be ascribed to the fact, that new vertical walls which occasionally form assume such a position as to avoid four-rayed intersections (see p. 60), so that they do not correspond in radial direction. Fig. 10 illustrates how every cell, as seen in cross section, is bounded by six other cells (except the peripheral ones), thus cell A e.g. is bounded by cells 2, 3, 4, 5, 6 and 7. If we further suppose, that the cells are of uniform length, a tunica layer in tangential view appears as is represented in fig. 11. A radial section of the tunica has the same appearance as a layer in tangential view (compare fig. 11, but then the vertical lines do not represent "vertical", but periclinal planes).

The cells of the tunica, as all meristematic cells, continuously divide, so that every longitudinal file of cells figured in fig. 11 is, properly speaking, the product of the elongation of a single cell which has been divided by a number of anticlinal walls into a number of derivative cells.

As was mentioned above, the anticlinal walls are placed at various levels, so that the periclinal and vertical walls, as seen in longitudinal section, face the walls of two neighbouring cells (fig. 11). Every longitudinal plane consisting of vertical cell walls is in contact with one adjacent column of the same layer of the tunica (compare fig. 10), so that a tunica cell faces two other cells with each of its "vertical" walls. The periclinal walls of a longitudinal cell column face the periclinal walls of two adjacent columns (see fig. 10), so that the periclinal walls of every cell both face the periclinal walls of four other cells. The anticlinal walls face the wall of a single cell, namely the anticlinal wall of the cell of the same column, placed above or below it.

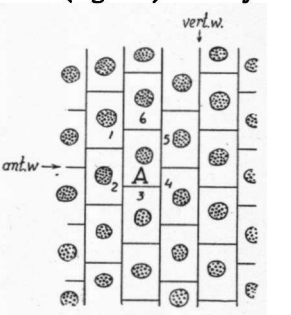

Fig. 11. Diagrammatic representation of a tunica layer seen in tangential view. The "vertical" walls (*vert. w.*) correspond lengthwise and form continuous planes (seen as lines), the anticlinal walls (*ant.w.*) do not correspond and are placed in adjacent columns at various levels. The periclinal walls are above and below the plane of section.

The arrangement of the cells and the number of contact faces are shown in fig. 12, in which a three-dimensional diagram of parts of three successive layers of tunica cells is represented. The total number of contacts of a single cell amounts to twice two (contacts of its "vertical" walls) plus twice four (contacts of its periclinal walls) plus twice one (contacts of its anticlinal walls), counting up to *fourteen*, as may be observed in fig. 12, cell *abcdefgh*, which cell is represented separately with all its contacts in fig. 13A and folded out in fig. 13B (compare also **102**).

The structure of the tunica is, as a matter of fact, less diagrammatic than represented in the figs. 10—13. The cells are usually not the same size. This is to be ascribed to the fact that the anticlinal cell divisions do not occur at the same time, but with irregular intervals, so that dividing and elongating cells are found together and the lengths of the cells vary in consequence of the alternation of division and elongation (see fig. 14). The shorter cells are, generally speaking, those which have just been formed by cell division; their vertical walls are mostly contiguous to one cell instead of to two (see fig. 14)

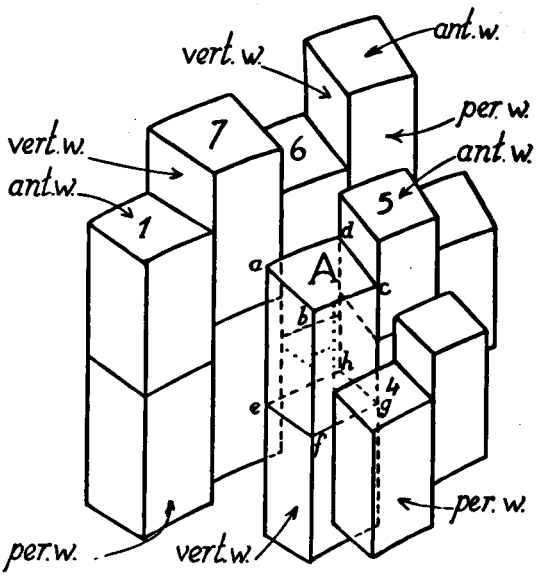

Fig. 12. A part of the tunica, diagrammatically represented in a block diagram to demonstrate cell arrangement.
A, 1, 4, 5, 6 and 7: cell columns identical with the cell columns seen in transverse section in fig. 10. Broken lines: edges of cells represented in the figure (not visible); dotted lines: edges of cells contiguous to cell *abcdefgh* not represented in the diagram. Compare figs. 10 and 11.

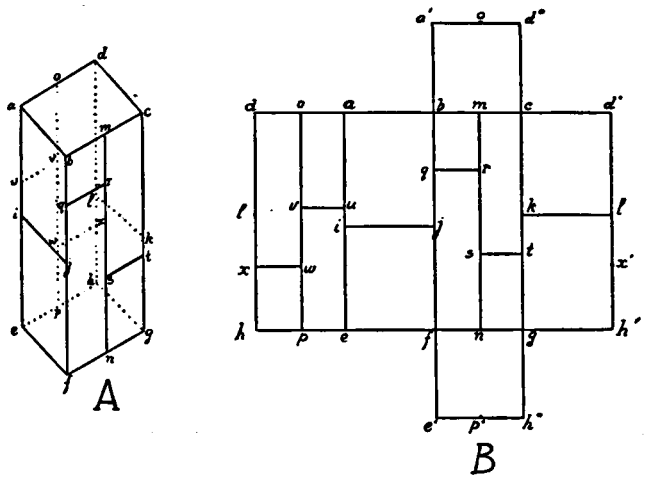

Fig. 13. *A*. Cell *abcdefgh* of fig. 12 represented separately. *B*. The same, its faces folded out in a single plane.

and their periclinal walls to two or three, instead of to four, cells (one may visualize this by dividing the cell *abcdefgh* of figs. 12 and 13 by an imaginary median anticlinal wall). The longer cells are, as a rule, those which are at the end of an elongating period and on the point of dividing; their vertical walls are usually contiguous to more than two (viz. three, exceptionally four) cells and their periclinal walls to more than four (five or six). It is not to be expected, therefore, that all cells of the tunica are in contact with fourteen other cells. This might be the case indeed, if all cells were the same size (see above), but this is only true in parts of the tunica, or in the tunica as a whole for a short period.

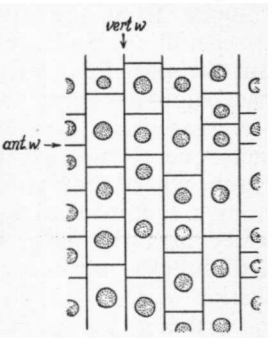

Fig. 14. As fig. 11, but less diagrammatic (the cells are not of uniform size).

In consequence of the varying lengths of the cells the number of contacts of the cells may be calculated in the same way as above: a vertical wall is in contact with one, two, or three cells, a periclinal wall with at least two and as a rule with no more than six cells and an anticlinal wall with a single cell. The total number of contacts, therefore, varies from eight to twenty, with an average of fourteen, which average is present in the cells of medium length and, accordingly, in the greater part of the cells. This number of contacts (14) was actually found by TUPPER-CAREY and PRIESTLEY (168) in macerated tissue of the radicle of *Vicia Faba*.

The calculation of the number of contacts of a tunica cell is only valid if the cell is completely surrounded by other cells, and consequently does not hold for the cells of the dermatogen [1]). Each dermatogen cell as a rule possesses (besides its exposed surface) two anticlinal and two "vertical" walls, but only one periclinal wall (see figs. 10 and 12). We may calculate the number of contacts in the way we did for other tunica cells and find, that dermatogen cells are surrounded by at least 6 and at most 14 cells, so by an average of 10, and that these cells have, the exposed surface included, from 7 to 15 (usually 11) faces (see also 101).

In the tunica there are still more complications. The intersection

1) The term "dermatogen" originated with HANSTEIN and is at present often used to indicate the peripheral layer of the tunica (and also the peripheral layer of cells in many root tips), as this layer usually forms nothing but dermatogen or epidermis and may, therefore, be considered a true "histogen".

of the cell walls, as seen in cross section of the tunica, is not orthogonal, except possibly in the youngest part. A cross section of a tunica shows the well-known "Schaumstruktur" of BERTHOLD (25) in which the cell walls tend to intersect at 120° angles. This is represented in fig. 15, which is more in accordance with the actual structure of the tunica and which may be considered to have developed from the arrangement shown in fig. 10 by breaks in the periclinal walls. The layers of the tunica are still recognizable; but the periclinal walls, though corresponding, do no longer form paraboloidal planes and show, when viewed in transverse section, a zig-zag line. The transverse sections of the cells of the tunica are consequently more or less hexagonal in shape, except in the dermatogen, where they are more or less pentagonal.

In a longitudinal section of the tunica, however, the anticlinal walls meet the other walls at approximately right angles (though little breaks may occur, which are less pronounced than in the cross section, see p. 57), so that the longitudinal planes formed by the vertical and the periclinal walls may clearly be recognized (they appear almost as is represented in fig. 11 and 12). From the transverse and longitudinal sections of the tunica cells it may be concluded, that these cells are shaped like a hexagonal prism as a rule (see fig. 25A). The average number of contacts is the same as in the case of tetragonal prismatic cells (fig. 12 and 13) and also amounts to fourteen.

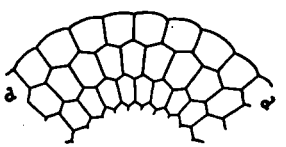

Fig. 15. A part of a transverse section of a growing point of an Angiosperm, as fig. 10, but less diagrammatic. See text.

The number of longitudinal cell columns of the tunica increases from apex to base, which accounts for the increase in girth of the tunica, as the cells do not show an appreciable growth in transverse surface area. The increase in number of columns is brought about by occasional vertical divisions.

The vertical divisions and subsequent readjustments of the cell pattern by breaks of walls change the outline of a divided cell into two different outlines of its daughter cells (see fig. 5) and consequently of the derivative columns of these daughter cells (see p. 45). Thus the hexagonal cell section of fig. 5A divides into a pair of pentagonal cell sections, whilst the two sections met by the new division wall become heptagonal in outline (fig. 5B, I and II).

Every increase in number of columns involves, therefore, a complex change, since a cell division does not only affect the shape of the cross section of the daughter cells and their derivative columns,

but also the outline of adjacent cells and their derivatives. Accordingly, not all columns of the tunica are hexagonal in transverse section (as supposed in fig. 15), but also pentagonal, heptagonal and even (though less frequently) tetragonal, octogonal etc. transverse sections occur.

LEWIS (**100, 101, 103**) has studied the effect of cell divisions and growth on the shape and size of cell sections in a two-dimensional cell pattern, considering that new walls are always placed in such a way as to avoid four-rayed intersections and that certain walls break, when a new partition wall is formed (compare fig. 5B, in the points *a* and *b*). As LEWIS's description is rather vague in some respects, we shall supplement his statements by some additional remarks. The breaks are caused by gradual symplastic readjustments (see p. 28), as every cell tends to assume a minimal surface area conforming to the Law of PLATEAU-ERRERA, so that the daughter cells of a divided cell grow relatively less than the adjoining cells which gain in surface area on account of the breaks (cf. fig. 5: the cells I and II grow relatively more in the direction of the arrows). The sections of the daughter cells have less sides than the section of the mother cell as a rule and originally about half its surface area. The smallest cell sections, viz. those of the cells just formed by a cell division, possess, therefore, the lowest number of sides. Cells which have been growing for a long time without dividing have increased in transverse surface area and usually the number of sides of their sections has also increased by breaks after division of adjacent cells, as every break adds a side to a section (fig. 5B). The largest sections consequently have the highest number of sides, so that cells immediately before a division, when they are at their largest, have many-sided sections, which change into a pair of less-sided sections when the cells divide (see above); the daughter sections enlarge again and so on. The cell sections of average surface area mostly possess a number of sides which does not, or but little, differ from the average number of sides per section.

LEWIS (**101**) has derived a simple device to analyse the form-size relationships in a pattern of dividing and growing cells: If every side is counted twice, that means if the wall of each cell is counted separately, it appears that a cell division adds *six sides* to the pattern of cell sections and *one section.*

We assume that in this pattern originally a sections with an average number of sides b were present. The total number of sides then amounted to ab. After a large number of cell divisions (n), $6n$ sides and n sections are added, so that the number of sides increases to $ab + 6n$ and the number of cells to $a + n$. The average number

of sides per section x has become $\frac{ab + 6n}{a + n}$. It is evident, that $x = 6$, if $b = 6$ and that x is approximately six, if n (the number of divisions) has been very high. This may be interpreted as follows:

(1): when the average number of sides per section in a two-dimensional cell pattern is six, the average number of sides does not change after a number of cell divisions and remains six, and

(2): when the average number of sides per section in a similar cell pattern differs from six, the average number of sides becomes approximately six after a great number of cell divisions.

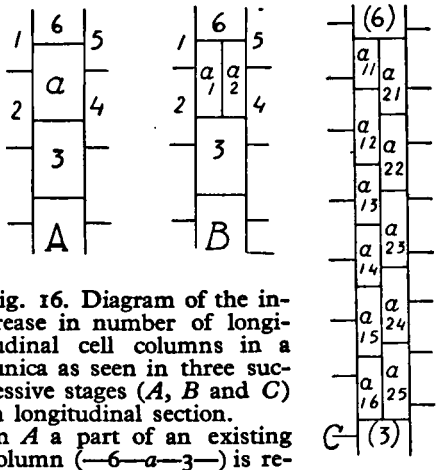

Fig. 16. Diagram of the increase in number of longitudinal cell columns in a tunica as seen in three successive stages (A, B and C) in longitudinal section. In A a part of an existing column (—6—a—3—) is represented, in B cell a has divided into the daughter cells a_1 and a_2 by a vertical wall and in C the cells a_1 and a_2 have both formed a new longitudinal column. a_{11}, a_{12}, a_{13} etc. are derivatives of cell a_1; a_{21}, a_{22}, a_{23} etc. are derivatives of cell a_1; (6) and (3) are derivatives of the cells 6 and 3 in figs. A and B.

These considerations have been confirmed by LEWIS by counting the actual number of sides of cell sections in a pattern of growing and dividing cells (**100**, **101**). The greater part of the cells, viz. the cells of medium size, possess hexagonal sections in consequence of the fact, that the cells with large transverse diameter divide first and that the smaller cells grow only (see above).

We may apply LEWIS's reasoning to sections of various tissues where as a rule only three-rayed intersections of walls are found, for instance to the tunica. In a tunica many vertical divisions occur, so that especially towards the base of the tunica the average number of sides per section is approximately six and the number of hexagonal transverse sections is high, which we know by experience and which we have anticipatively assumed in the preceding considerations on the structure of the tunica.

We return to the increase in number of the longitudinal cell columns. The effect of a vertical division and subsequent growth in a part of the tunica is represented in fig. 16. In fig. 16B a tunica cell a, belonging to a longitudinal file -6-a-3- (fig. 16A), divides into

the cells a_1 and a_2. As the anticlinal divisions prevail, the two daughter cells develop a new longitudinal cell colum, a_{11}, a_{12}, a_{13} etc. and a_{21}, a_{22}, a_{23} etc. respectively. In these new columns the new anticlinal walls are placed in such a way as to avoid four-rayed intersections, so that the anticlinal walls in adjacent files are placed at various levels and the new columns are placed in the same way as the existing columns with regard to adjacent columns. The cells of these new files consequently show the same particuliarities as mentioned on p. 41. Accordingly the number of contact faces of tunica cells is 14.

There is, however, a complication. The longitudinal wall dividing cell *a* in fig. 16B into a_1 and a_2 divides also the original anticlinal walls between the cells *6* and *a* and the cells *3* and *a* into two. The cell at the bottom of the file originated from cell *6*, and the uppermost cell of the file derived from cell *3*, the cells (*6*) and (*3*) in fig. 17C, face two cells with their anticlinal walls. This affects the shape of the cells (*6*) and (*3*) and the shape of the mature cells originating from these cells, as the average number of contacts has been increased by one and amounts to fifteen instead of fourteen.

The meristems which grow in the same way as the tunica, namely by elongating in one direction and by forming parallel new division walls perpendicular to the direction of the elongation, show the same structure as the tunica. The rib meristems and the cambia belong here.

The rib meristem ("Rippenmeristem") is the first type of "Halbmeristem" (i.e. a semi-meristematic tissue) in the sense of SCHÜEPP (151) and may be defined as a "Halbmeristem" growing chiefly in one direction. Rib meristems are found at the base of the apical meristems, where they form the transition to the parenchyma of cortex and pith, in the intercalary meristems of petioles and young stems and, finally, in the basal meristems of the leaves of many Monocotyledons.

Rib meristems and cambia are built up of files of meristematic cells which, as seen in a section perpendicular to the files, are as a rule in contact with six other cells, This is a consequence of the fact that these meristems originate from cells which were hexagonal in section and which have increased by divisions conforming to LEWIS's rules, so that the average number of six sides per section is maintained [1]). This is evident in case of the cortical rib meristem of the shoot apex, which is a derivative of the tunica, but it does also hold for other cases, as will be shown later (see pp. 47 and 48).

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1) In the cambium, the contacts with ray initials may change this average, however (see Chapter VII).

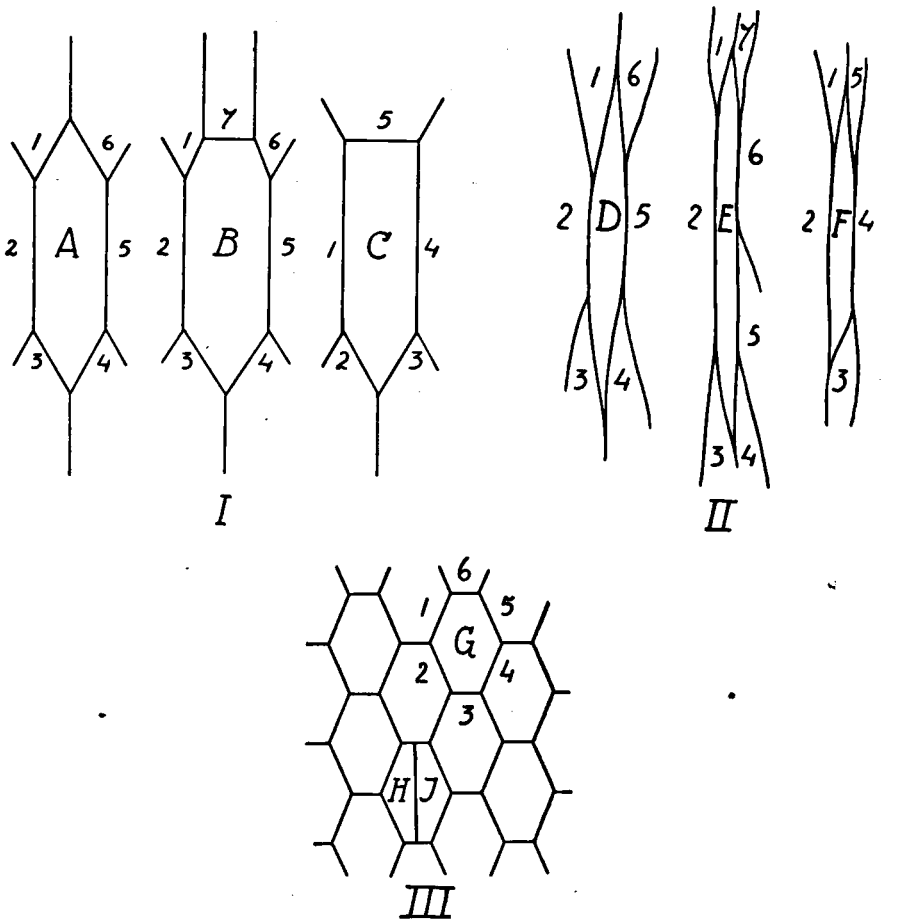


Fig. 17. I. Cambial cells of a stratified cambium in tangential view, diagrammatically after BEIJER (24). Cell A has 6, cell B 7 and cell C 5 lateral contacts with other fusiform initials. Ray initials omitted.

II. Cambial cells of a non-stratified cambium in tangential view D, E, F as A B C in fig. I. Ratio length-transverse diameter not to scale, the initials being greatly foreshortened. Ray initials omitted.

III. Cambium built up of short elements (*Cordyline*, semi-diagrammatic) in tangential view. The greater part of the initials with 6 lateral contacts (G). H and I formed by a recent division have 5 lateral contacts.

Rib meristems and cambia increase in transverse surface area by occasional divisions in the direction of the cell columns, so that the number of columns also increases. In the cortical rib meristem of the shoot apex these divisions occur in several directions, also periclinally, and therefore the original tunica-layers become indistinguishable. In the same way as has been done in the case of the longitudinal columns of the tunica it may be concluded that the average number of sides per section in rib meristems and cambia remains six (see above). In cambia, however, the intracambial elongation of the fusiform initials may implicate complications (see Chapter VII). A few examples of cambial cells are represented in fig. 17, in order to demonstrate that they are usually in contact with six other cells in tangential section, but sometimes also with four, five, seven, eight etc. cells.

The walls of rib meristems and cambia running in the direction of the cell columns may be compared with the corresponding walls of the tunica cell columns. Every wall is contiguous to the walls of one, two (this is usual) or three (only in exceptional cases four) cells of adjacent files, as is represented in fig. 1 for the radial walls of the cambium. The total number of contact faces of those cells which are hexagonal as seen in a section perpendicular to the cell columns is, therefore, usually fourteen, but there is as much variation in this number as is the case in the tunica. LEWIS (105) was able to show by reconstruction, that the cambial cells are indeed fundamentally tetrakaidekahedral, but that complications which may change this shape are likely to occur (see Chapter VII).

In the corpus of the growing point of the stem of Angiosperms the meristem is growing in all directions. In the peripheral parts of the corpus the directions of the divisions differ but little from the periclinal, anticlinal and vertical directions as a rule, but in the central part the division walls are placed in a more irregular fashion. The transverse surface area of the corpus increases considerably from the apex to the base by an increase in number of cells. We may, there fore, apply LEWIS's device to the cell divisions in the corpus for the same reasons as given for cell divisions in the tunica. Accordingly, in any one section of the basal part of the corpus the average number of sides per section approximates six, even if the average number of sides per section in the original initials of the corpus lying in its apex differs from six.

The greater part of the corpus gradually changes towards the base into the rib meristem forming the pith. This is brought about by a prevalence of the anticlinal divisions in the basal part of the

corpus, so that longitudinal files of cells are formed. In the transverse section of the basal part of the corpus the number of sides per section averages six and most sections have exactly six sides per section (see above), so that these files may completely be compared with the longitudinal columns of other rib meristems (see p. 39).

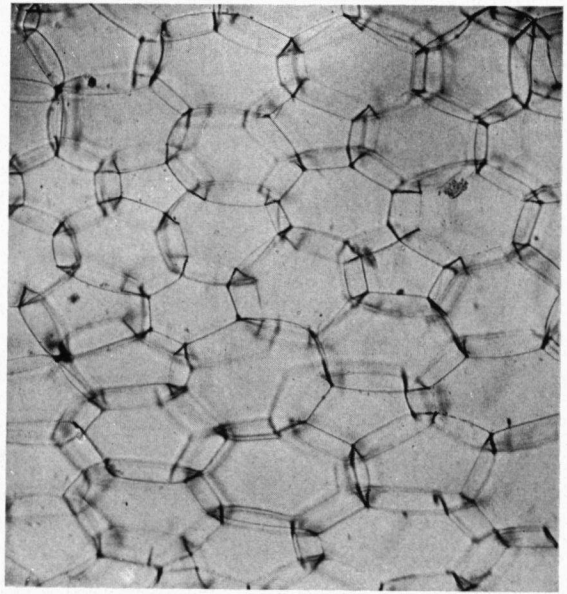
Apical meristems developing from an apical cell or from a few superimposed initials may in their structure be compared to the corpus of the Angiosperms, since the number of cells increases considerably, as seen in successive transverse sections, from the apex to the base. We may apply rule (2) of p. 44, so that the average number of sides per section approximates six and the greater part of the sections is hexagonal. At some distance from the apex of the meristem the anticlinal divisions prevail and longitudinal files of cells are formed passing into rib meristems of cortex and pith or central cylinder (**68**, **108**, **150**, **170**). The cells of these files have the same shapes and the same numbers of contact faces as the cells of other rib meristems mentioned above.

The meristems of the shoot apex of *Lycopodiaceae*, *Cycas* (**49**), *Zamia* (**82**), *Ginkgo* (**47**) and the *Conifers* (**93**) develop in a different way. A single peripheral layer of initials is present which develops laterally a number of cell layers by a few periclinal and many vertical and anticlinal divisions (which layers may be compared with the tunica layers of Angiosperms) and which centripetally develops a central mass of cells which may be compared to the corpus of Angiosperms, as the divisions take place in all directions. More extensive descriptions of the structure of these apical meristems are given by the authors referred to.

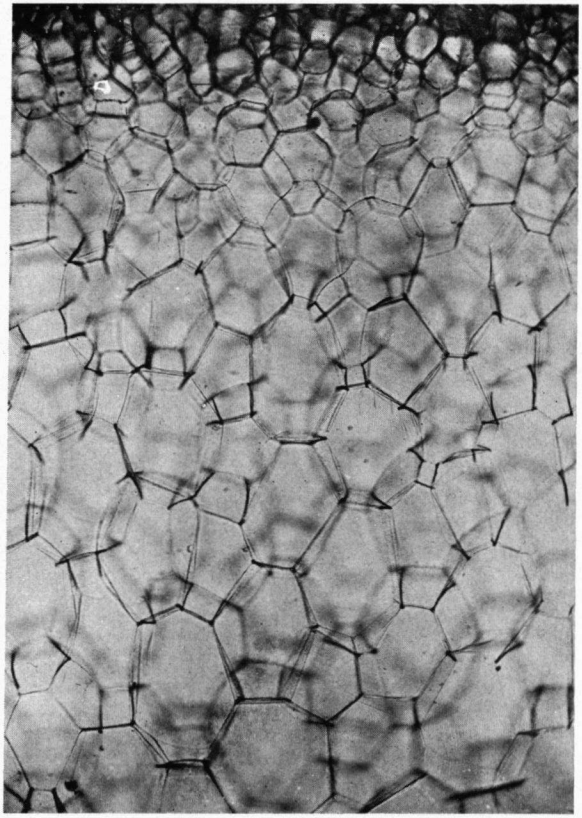
The peripheral layers pass into a rib meristem developing the epidermis and the cortical parenchyma; the central mass of cells passes into a rib meristem developing the greater part of the pith. These rib meristems may again be compared to various other rib meristems, as we may apply rule (2) of page 44, so that we may conclude that most cell files of the rib meristems are hexagonal and that the average number of sides per section in transverse section of the stem approximates six.

In all these meristems the number of contacts of an individual cell with its surrounding cells is varying. Firstly, this number varies on account of the fact that part of the cells is not hexagonal in transverse section, but tetragonal, pentagonal, heptagonal etc., and, secondly, on account of the alternation of division and growth of the cells (see p. 39 and fig. 14). A wall running in the direction of the files of cells (for instance a vertical wall in the tunica, a radial wall

A.



B.



Microphotograph A. Transverse section of a root tuber of *Asparagus Sprengeri*. The parenchyma cells possess hexagonal faces above. Magnif. 50.
Microphotograph B. Section of the same, made at an angle approximately 30°, so that many tetragonal faces are seen. Magnif. 50.

TAB. II

in the cambium) usually faces two cells, but also one cell or three (or exceptionally more) cells; a wall perpendicular to these files (for instance an anticlinal wall in the tunica or a tangential wall in the cambium) usually faces a single cell (see however fig. 16). There are consequently many possibilities. Cells which are hexagonal in section are prevalent and have as a rule fourteen contacts with surrounding cells. Cells which are pentagonal in section usually possess 5 times 2 plus 2, that is 12, contacts, with a minimum of 5 times 1 plus 2 that is 7, and as a rule no more than 5 times 3 plus 2, that is 17, contacts. For cells with heptagonal sections these numbers are 16, 9 and 23 respectively, in general: $P_n = 2n + 2$, $P_{min} = n + 2$, $P_{max} = 3n + 2$ in which P = number of cell contacts and n = number of sides of the transverse section.

A different type of meristem is found in the roots of many Monocotyledons. It was extensively described by VAN TIEGHEM (169) and later by BOEKE (27). In our investigation *Oryza sativa* and *Eichhornia crassipes* were chiefly used. At first the root develops in the ordinary way from a few apical initials as mentioned above (see p. 48), so that in the periphery a number of layers resembling tunica layers is formed, the dermatogen and the "periblem" the latter consisting of a few layers. The innermost layer of this periblem forms later (i.e. at a certain distance from the apex of the root) the endodermis and a number of layers which make up the greater part of the cortex when fully differentiated. These layers are formed by periclinal divisions which correspond in adjacent radial rows, so that they form continuous periclinal planes (see fig. 18). In the tangential longitudinal section of this meristem the cells retain the same rectangular shape as the tunica cells show in tangential section (see fig. 11) and are usually in contact with six other cell sections. The periclinal walls of these cells face a single adjacent cell (fig. 18) the vertical walls (radial walls in fig. 18) face two cells and the anticlinal walls face a single cell. The total number of contacts therefore amounts to eight. The cells are originally shaped like a hexagonal prism (longitudinal section: fig. 12, transverse section: fig. 18), but later, when passing into parenchyma, the tangential

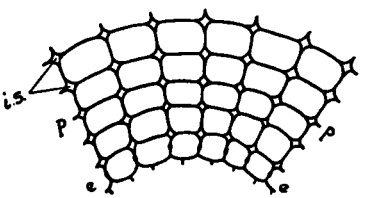


Fig. 18. A part of a transverse section of a young root of a Monocotyl showing the peculiar structure described by VAN TIEGHEM (*Oryza sativa*, semi-diagrammatic). *ee*: endodermis, *pp*: radially arranged cortical parenchyma, *i.s.*: intercellular spaces. Explanation see text.

section changes from tetragonal into hexagonal by breaks in the vertical walls, so that these tangential sections appear almost as in fig. 17 III, and the cell becomes shaped like a hexagonal prism.

SCHÜEPP's second type of "Halbmeristem", the "Flachenmeristem" (plate meristem), occurs in growing leaves (see FOSTER 46) and consists of several superimposed cell layers which increase in surface area by growth in a plane. Consequently every cell of a growing plate meristem after a number of divisions develops a layer of cells which is one cell in thickness. The meristematic cell may therefore be considered the mother cell of that layer. This has been represented in fig. 19. A cell has divided into four cells

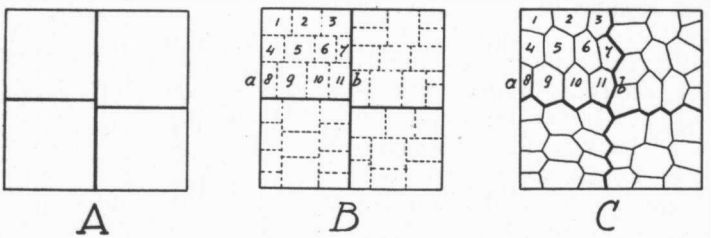


Fig. 19. Diagram of the development of a plate meristem.
A. A mother cell which has divided into four daughter cells.
B. Cells formed by subsequent divisions.
C. As *B*, but the cells tending to meet at 120° angles has implicated fractures in the walls, so that the sections become polygonal.
Heavy lines: walls separating the four original daughter cells and their derivative alls. *B* and *C* not to the same scale as *A*, because the growth of the cells in surface area is not accounted for. See text.

(fig. 19A) which again are the mother cells of four groups of cells (fig. 19B and fig. 19C, the four groups are separated by heavy lines). It appears that all cells of a plate meristem become polygonal as seen in surface view of the layers (fig. 19C) by gradual symplastic readjustments of the framework of cell walls. In these layers of the plate meristem one of the consequences of LEWIS's device, viz. (1) on p. 34, may be applied. The plate meristem initiates from a part of the tunica when the leaf primordium is formed, so that the original mother cells of the plate meristem are usually hexagonal as seen in surface view. After a number of cell divisions, therefore, the average number of sides per cell outline as seen in surface view of the plate meristem remains six and most of the cell outlines are hexagonal (fig. 19C).

The cells of superimposed layers of a plate meristem are dividing independantly, so that the new division walls forming the outlines of the cells, as seen in surface view of the meristem, do not correspond

in adjacent layers. Two layers of a plate meristem, when projected on each other, therefore appear as diagrammatically represented in fig. 20A, or, when we assume that the cells have become hexagonal, as in fig. 20B. We may replace the projection of a layer of a plate meristem by a pattern of identical regular hexagons to facilitate the analysis, since we have derived that the average number of sides is six and the cells do not vary very much in size. We may conclude from fig. 20, that every cell of a layer is contiguous to four cells of an adjacent layer, if all cells were identical regular hexagons (the contact faces of a single cell are numbered 1, 2, 3, 4). The actual structure of a plate meristem seen in projection is less regular, so that in a plate meristem a cell *usually* faces four cells of an adjacent layer.

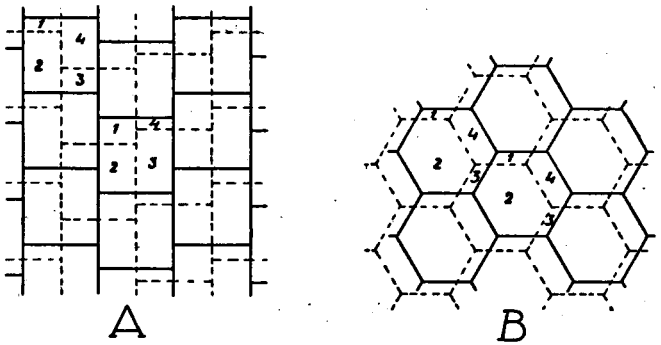


Fig. 20. Arrangement of cells in two adjacent layers of a plate meristem (diagram). A in the case of square cells (compare fig. 19*B*), B in the case of hexagonal cells (compare fig. 19*C*). Full lines: cells of one layer of the meristem, broken lines: bounding lines of cells of an adjacent layer. Each cell is contiguous to four cells of an adjacent layer (numbered 1, 2, 3, 4).

The number of contacts with cells of the same layer is usually six (see above); the total number of contact faces therefore amounts to twice four (contacts with cells of the two adjacent layers) plus six (lateral contacts with cells of the same layer), that is fourteen. Both peripheral layers of the plate meristem (dermatogens) usually have one time four plus six contacts, that is ten contacts and an exposed outer wall, that is eleven faces in all.

The layers of a plate meristem are separated by flat planes of cell walls, so that the shapes of these cells approach a hexagonal prism.

SCHÜEPP's third type of "Halbmeristem", the „massige Meristem" (mass meristem), increases by divisions and growth in all directions. It is found in sporangia, in antheridia, in the anthers of stamens and so on.

For an analysis of the shapes of the cells of a mass meristem another rule found by LEWIS (101) has to be employed. LEWIS concluded, that, on the same conditions as mentioned on p. 43, a cell division in a tissue consisting of tetrakaidekahedral cells adds *fourteen cell walls* to the tissue, if every wall is counted twice, and *one cell.* This number of fourteen walls is found as follows: every division wall in a tetrakaidekahedral cell meets six walls which break afterwards thus forming twelve *double* walls (the walls of the adjacent cells also break) that is 24 *single* walls. The division wall adds itself, that is two single walls, making up to 26 added walls; from this number the number of walls already present, that is the six double walls or the twelve single walls which break after the division, has to be abstracted, so that 26 minus 12, that is 14, walls are added.

We may change LEWIS's statement in this way:

(3): at a cell division in which the additional wall meets six other walls (i.e., is hexagonal), on the same conditions as mentioned on p. 43, 14 walls and one cell are added to the tissue.

We have seen before, that in a tissue after many divisions in a section made in any one direction the average number of sides per section is six or approximately six. A division wall is also a section of a cell, so that we may conclude, that, after many divisions and if four-rayed intersections are avoided, the average number of sides per new division wall also approximates six, and the average number of walls added after a division approximates fourteen. When in a mass meristem many divisions have taken place, that is when it has been growing for some time, therefore, on the average 14 walls and one cell are added per cell division. If originally in a mass meristem a cells with on the average b walls per cell were present, the number of walls amounted to ab. After a large number of divisions (n), $14n$ walls and n cells are added to the meristem, so that the number of cells increases to $a + n$ and the number of walls to $ab + 14n$. The average number of walls per cell x amounts to $\frac{ab+14n}{a+n}$, which means that $x = 14$, if $b = 14$ (this is often the case as mass meristems originate from cells with an average of 14 faces per cell) and that x is approximately 14 even if b has differed before from 14, if the number of divisions n is large, which is the case when the mass meristem has been growing for some time. In a mass meristem the number of contact faces, therefore, averages fourteen.

It may be stated in general as a result of the preceding considerations, that cells in meristems are usually in contact with fourteen surrounding cells, but that there is much variation in the number of these contacts.

B. *Does "sliding growth" appear during the growth of meristematic cells?*

In the preceding considerations we did not account for the possibility that mutual slip of cells may occur. If so, every meristematic cell must have a wall of its own, as was already assumed by KRABBE. It has indeed been shown that every meristematic cell is enclosed in a wall of its own.

We have seen before that two neighbour cells belonging to the same longitudinal cell column of the tunica have one common anticlinal face. It has never been observed that the cells of the same column show sliding on the anticlinal walls of their neighbours, as otherwise the files of cells would be broken up, which is not in agreement with the actual observations. This is made clear in fig. 21, in which *a* and *b* represent two cells of such a column, fig. 21A shows the actual arrangement. Fig. 21B the situation which would be brought about if a displacement of one cell relatively to the other by sliding growth would occur: the file to which cells *a* and *b* belong would be broken up.

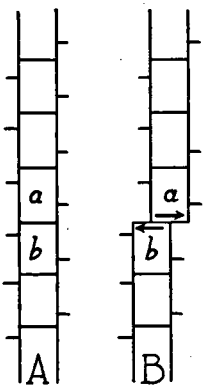


Fig. 21. The changes which might be expected in a cell column of a meristem, if sliding growth on anticlinal cell walls occurs. Explanation see text.

It may be concluded accordingly that in rib meristems and cambia the cells of the same file derived from a single cell do not show mutual slip. The cells of the radial rows in the roots of many Monocotyledons (see page 49) belong to two files of cells, viz. a radial and a periclinal row (see fig. 20). In this instance neither radial nor periclinal files of cells were ever seen to have broken, so that these cells cannot possibly show sliding growth in any direction.

The possibility still exists, however, that the cells of apical meristems slide over non-anticlinal walls, i.e. that adjacent cell files would show mutual slip.

Maceration of meristems is not an easy task and it is much more difficult than the maceration of mature tissues. We have already seen (see p. 31), that PRIESTLEY considered this an important argument against sliding growth. He is also of opinion that the walls of meristematic cells are "plastic" and not sufficiently rigid to slide on other walls, the more since a cementing substance (the middle lamella) is present. Walls containing cellulose are always more or less "elastic" (see 37), but it seems probable that meristematic cell

walls indeed possess more plastic properties than mature cell walls. Even in systems which are much more rigid, the friction between the walls is apparently too high to make slip of walls probable. This appeared for instance in our experiments with rubber balloons, which will be described in Chapter X, in which it was one of the main difficulties to make the balloons move past one another, for as a rule the balloons do not slip on other balloons without special precautions as greasing with vaseline or moistening with water, especially when they start flattening against one another. By the pressure the position of the balloons seems to be fixed. This applies probably also to tissues in which the cells are of almost uniform size (meristems, parenchyma).

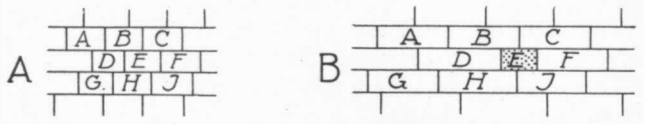


Fig. 22. Differential wall growth after SINNOTT and BLOCH (155). A. Younger, B. older stage. In *A* the cells are of uniform size, in *B* the cells have grown considerably, except cell *E*, so that the parts of the walls of cells *B, C, D, F, H* and I contiguous to *E* have not elongated, whereas the parts of the walls of these cells contiguous to the other cells have elongated to a considerable extent.

SINNOTT and BLOCH (155) presented other evidence against sliding growth in apical meristems. By studying living growing meristems of grass root tips they were able to follow the history of every cell of the outer layers of the root tip. They found that every cell in the meristem is only in contact with those cells with which it was in contact when it originated (i.e. after the cell division whereby the cell was formed). The changes in intercellular relationships among the cells are, according to these authors, brought about solely by unequal growth of various portions of the cell wall in the same cell (differential wall growth). These different growth rates depend on the growth of adjacent cells. This is evident in instances where a cell is in contact with two others of unequal growth rates (see fig. 22). The growth of the cells, therefore, takes place in mutual coherence by alterations in the common frame work of cell walls.

On p. 34ff. we have already mentioned a few particulars on the validity of conclusions based upon the occurrence of plasmodesmata in the cell wall. The main point is, if plasmodesmata may be regenerated after having been ruptured. We had therefore to investigate this point in meristems, before we were able to conclude, if the plasmodesmata in meristematic cell walls indeed present a valuable

criterion to decide whether these walls show mutual shift or not. We applied several methods for demonstrating the presence of plasmodesmata, especially MEYER's pyoktanin method and iodine-potassium iodide followed by sulphuric acid (cf. **123**). It appeared that practically all meristematic cell walls are interpenetrated by protoplasmic connections. Suitable objects are for instance the apical meristems of *Nerium* and *Viscum* and the cambia of various plants (see also **108, 74, 75**). It is, in the present state of our technique, only possible to demonstrate the presence of plasmodesmata when the wall has reached a certain thickness, as otherwise the wall does not swell sufficiently in the reagents which have to be applied to show their occurrence. Recently formed walls do not swell considerably and therefore in apical meristems the plasmodesmata often cannot be detected in anticlinal walls, whereas they clearly stain ou tin the other walls.

STRASBURGER has disposed of the old hypothesis that plasmodesmata were the remains of the spindle threads seen in the later stages of cytokinesis (**160** p. 498 ff.). For some reasons it seems probable, however, that in young cell walls plasmodesmata — even if we fail to demonstrate them — originate during or soon after a cell division (see **123**). If the plasmodesmata were formed only once, the number of plasmodesmata per unit of surface area would be very much reduced in walls showing considerable elongation, as compared with walls which have not, or not yet, been enlarging after their formation. In the tunica, in rib meristems and in cambia long cell wall planes are formed by elongation of existing surfaces. The other walls in these meristems, which are formed more recently and have originated directly from a cell plate, do not contain more plasmodesmata per unit of surface area than the walls which are a part of a cell wall plane formed by the elongation of existing walls. It has to be concluded therefore that the number of plasmodesmata in the latters in increasing. In which way this increase in number of plasmodesmata in growing walls comes about is not definitely known (see **136, 118**). Either new plasmodesmata are formed, or the existing plasmodesmata are split into a number of daughter plasmodesmata. If new plasmodesmata were formed, the presence of plasmodesmata does not seem to provide evidence against sliding growth at first glance, for it might be assumed that the plasmodesmata are all rebuilt after the cessation of the growth of the cell and the slipping of walls. But the plasmodesmata appear to be present in all stages of development of growing cells and a rupture or temporary absence of plasmodesmata was never observed by us, and consequently it may be concluded that protoplasmic connections al-

ready present persist, so that the argument retains it validity.

A treatment of macerated meristematic cells or young parenchyma cells with cellulose reagents (chloroiodide of zinc, iodine-potassium iodide and sulphuric acid) reveals, that often the cellulose is not equally distributed in the wall. If so, the wall shows a typical net-like structure of cellulose bands staining out sharp, which enclose fainter staining intervening places forming the meshes of the network. The intervening places may be covered by a meshwork of second order. Cellulose bands and intervening areas of third order may even occur, but these are usually only perceptible in young parenchyma cells and not yet in the meristem cells. These typical wall structure was already observed by BARANETZKI (**20**) as early as 1886 in the parenchyma cells of a number of objects, but was independantly rediscovered in meristematic cells of the radicle of *Vicia Faba* by TUPPER-CAREY and PRIESTLEY (**168**) and again in parenchyma cells by SCHAEDE (**146**). We found these structures for instance well developed in the apical meristems of *Nerium*, *Viscum*, *Asclepias* and *Calotropis*; for further particulars and for figures we refer to these authors.

These structures must not be confused with the structures which have been found by B. J. D. MEEUSE (**119**) in the walls of parenchymatous (and other) cells, which usually appear as striations and also become more clearly perceptible after application of chloroiodide of zinc. SCHAEDE, who also treated his objects with this reagent, most probably observed both structures (**120**).

The cellulose bars of the meshwork of first order are found in the places where three (or exceptionally four) walls meet in an edge, i.e. in the places where later the intercellular spaces will be formed and no pit-membranes will develop. The finer meshes of the network later on pass into the thin places in the walls of the parenchyma cells, thus appearing as pit-membranes. The finest meshes probably represents the places where plasmodesmata transverse the wall, or where they will form later. The reticulate structure of the wall thickenings in meristematic or semi-meristematic cells corresponds therefore in two walls facing one another across their common middle lamella, so that the cellulose bands and the thin places of first order are placed opposite one another, as well as the bars and meshes of second order, and so on. This may be concluded from the study of macerated shoot apices, in which the pits are seen to develop out of the meshes of the BARANETZKI-structure.

On account of the complexity of these wall structure the walls of meristematic cells cannot possibly show mutual slip, for every relative displacement of the walls would completely disturb the correspondence of bars and meshes in contiguous cells.

All the above arguments apply completely to other primary meristems and to the cambia (cf. Chapter VII).

In differentiating tissues often breaks of walls (KRABBE's „*Wandbrechungen*") occur. The original orthogonal intersection of the cell walls will then be changed (fig. 23), while some walls seem to grow less. In fig. 5A a cell dividing into a pair of daughter cells is represented. Old observations of TREUB, which were confirmed in recent time (see BECKER **23**), point out that two daughter protoplasts may behave independantly after nuclear division in the stage in which no wall has yet been formed and only a cell plate is present. This appears from their behaviour at plasmolysis: both daughter protoplasts contract individually and round off against one another. As will be shown later, the cells of plant tissues tend to assume a position in which the cell walls possess a minimal surface area. In the stage of fig. 5A the cells tend to form 120° angles in the points *a* and *b*, which results in a break of the walls in these points very soon after nuclear division and a decrease of the distance *ab*, which means that the cell plate must grow less in surface area. Since a cell plate is of protoplasmic nature (**23**) it will be subjected to surface forces and may therefore decrease in surface area. As soon as a wall *ab* has been formed, however, the position of the new wall is fixed and it is no longer subjected to surface forces, so that it does not grow less any longer. When a new wall has just been formed, the breaks of the walls formed by the action of surface forces form angles differing much from 120° angles (see fig. 5B), for the breaks only gradually become more prominent and are fixed in a stage where the action of surface forces has not been operative long enough to allow for the formation of 120° angles.

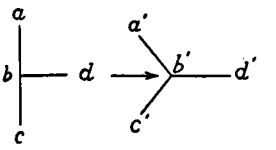


Fig. 23. Break of a cell wall ("*Wandbrechung*") when a meristem cell is differentiating into mature tissue (compare also fig. 1 and 2). The walls at first meet at right angles, but later they tend to meet at 120° angles.

The readjustments in the pattern of cell walls continue throughout the development of a tissue, but in the later stages these changes are brought about by a symplastic growth and an expansion of the whole mass of cells (see p. 27 and **136**).

The above explanation of the breaks of walls at cell division was already given by ERRERA (**41**, **42**) and is sometimes called "ERRERA's Law" (see e.g. **24**). According to this "Law" three cells meet in an edge and four-rayed intersections are avoided. If, therefore, after a nuclear division the phragmoplast assumes such a position as to

make four walls meet in an edge when the cell plate will have become a cell wall, surface forces tend to alter its position to avoid the four-rayed intersection. We must bear in mind, that there are probably more principles operative which determine the position of the new division walls, viz. R. HERTWIG's cytoplasmic-nuclear ratio theory (**70, 71**) and KNY's theory of the influence of pressure on the direction of new walls (**91, 92**), so that it may occasionally occur that more than three walls meet in an edge. This is an exception as a rule and we may therefore apply LEWIS's rules on the influence of cell division on the shape of cells and cell sections (see p. 43).

C. *The development and the shapes of parenchymatous, collenchymatous and epidermal cells* [1]).

Parenchymatous tissues are of different origin. Parenchyma may originate from a rib meristem at the base of the apical meristem (cortical parenchyma and pith), from various other rib meristems (parenchyma of intercalarily growing petioles, of leaves and of parts of the stem), from a plate meristem (leaf parenchyma), from a mass meristem (parenchyma of apple, pear and other fruits), from cambia (cork, parenchyma of the storage roots of *Beta vulgaris, Daucus Carota, Brassica* spec., *Cochlearia Armoracia, Phytolacca decandra*, etc. and the secondary stem parenchyma of Monocotyledons with secondary growth), or from other sources. Some of these types of parenchyma (ray parenchyma, xylem parenchyma) will be discussed later on (see Chapter VII).

In young living parenchyma cells plasmodesmata and often the peculiar structure described by BARANETZKI, or, if they originate from cambial cells, the so-called primary pit-fields, are present in all stages of development of the walls. The primary pit-fields will be dealt with more extensively later on (see Chapter VII); we report in anticipation, that the presence of primary pit-fields provides the same evidence against sliding growth as the occurrence of pits.

On the ground of the arguments described in the preceding paragraph (B), in connection with the occurrence of structural peculiarities of the wall, it is therefore unlikely, that sliding growth among the units of a parenchymatous tissue takes place. Additional evidence was supplied by PRIESTLEY and SCOTT (**137**), who drew the attention to the consequence of the formation of intercellular spaces as found by MARTENS (**111, 112**) being, according to expectation, that after cell division in young parenchyma (and also in young collenchyma and probably in some other tissues), the parent wall

1) Compare also G. VAN ITERSON Jr. and A. D. J. MEEUSE (**80**).

encloses the two daughter cells for some time before being ruptured. This wall may at last even enclose a file of cells, when the daughter cells have divided again. In macerated young parenchyma or collenchyma, therefore, often cohering rows of cells are found which appear to be enclosed in a common parent wall. This wall may be burst or partially torn, but still clearly perceptible. After some time in a growing tissue such walls are stretched beyond their elastic limit and consecutively torn to pieces by their growing derivative cells, so that the files continually form smaller groups of cells. This was already known long ago (GILTAY 1882), but it had been perfectly neglected for a long time. An analogous process of growth occurs in growing filamentous algae, where the daughter cells also remain enclosed within a parent wall and this wall is also ruptured only later on. This phenomenon likewise has been known for a long time (see **39**). It is evident that cells of a file enclosed within a common wall cannot possibly having been sliding on their neighbours.

The changes in intercellular relationship and in shape which differentiating parenchyma cells undergo are, therefore, brought about without mutual slip of cells by a process of "symplastic growth". This process is accomplished by gradual readjustments of the cell pattern as a common whole when the mass of cells expands. The almost rectangular longitudinal sections of the prismatic meristem cells alter into the polygonal longitudinal sections of the more "isodiametric" parenchyma cells, as the differentiating cells increase in size. This is associated with "breaks" in the walls (fig. 23) and with "differential wall growth", as is represented in fig. 24. The transverse sections of the cells in apical meristems are as a rule polygonal (usually hexagonal, cf. fig. 15) and their outlines, though enlarging, alter but little or not at all during the differentiation into parenchyma cells.

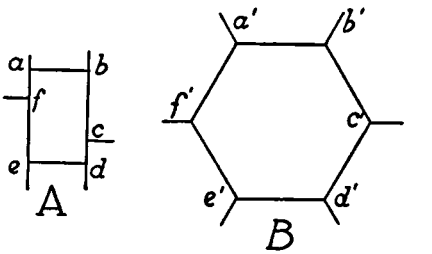


Fig. 24. Diagram of the differentiation of an apical meristem cell (*abcdef*) into a parenchymatous cell (*a'b'c'd'e'f'*) by "differential wall growth", as seen in longitudinal section. The parenchymatous cell is represented as a regular hexagon, though as a rule a parenchyma cell is not a regular hexagon as seen in a longitudinal section (see fig. 26*B*).

We shall now give an account of the various factore determining the shape of cells in tissues. These factors are:

a. the property of cell walls under tension to behave as liquid films

or stretched elastic membranes (ERRERA's principle of minimal surface area);

b. the unequal sizes of cells in a tissue and the varying number of cell contacts;

c. the pressure relationships between cells of a tissue;

d. external, unequal pressure or stretching, resulting in unequal dimensions of the cells in various directions; and

e. the formation of additional cell contacts between cells.

Factor a. PLATEAU's (**130**) physical laws concerning the rules of intersection in liquid film systems were applied to cell walls by ERRERA (**41**, **42**). ERRERA formulated his principle as follows: "A cellular membrane, at the moment of its formation, tends to assume the form which would be assumed, under the same conditions, by a liquid film destitute of weight" (see **162**). This principle may indeed be applied to cell walls at their formation, because a wall is initiated as a cell plate, the protoplasmic nature of which is beyond a doubt (see p. 57). It explains why a new cell wall usually forms perpendicular to the existing walls and does not meet the walls of the mother cells in an edge as a rule. A consequence of this mode of intersection of walls is, that in sections of a tissue rarely more than three cell sections meet in a point. As was already pointed out by ERRERA himself the above explanation of the position of cell walls may not be applied to older cell walls without restrictions, for older cell walls cannot change their position unhindered as liquid membranes do. Nevertheless older cell walls often assume a position conforming to the rule of minimal surface area and meet at angles approximating 120°. In this connection ERRERA (**42**) referred to experiments with elastic membranes under tension by which was found, that the stretched membranes assume the same position as would be assumed, under the same conditions, by soap films. A cubic metal skeleton frame coated with thin sheets of rubber for instance shows, when the internal is evacuated, the same figure which is obtained by dipping a cubic skeleton frame in soap water and subsequent emerging. The tension in the sheets apparently replaces the surface tension of the soap film, because the tension in the stretched sheets tends to reduce the surface area of the sheets.

We may therefore apply ERRERA's principle of minimal surface area to older cell walls with the restriction that these walls cannot change their position unhindered in the manner of liquid films. Hence it becomes clear why in sections of mature tissues usually three cells meet at angles approximating 120°.

One might ask, which shape is likely to be assumed by a number of cells of uniform size, if all cell walls would behave like liquid

membranes. This question can be replaced by the following one: how can space be filled without leaving interstices with congruent figures possessing a minimal surface area? W. THOMSON (later Lord KELVIN), extending PLATEAU's experiments with a cubic skeleton frame, mathematically derived a figure which fills up space in the most economic way (**164**, **85**). This figure, called the *orthic tetrakaidekahedron*, has six tetragonal facets which are flat planes and eight non-plane hexagonal facets, which all meet in curved edges. The edges enclosing the tetragonal facets are curved outward in the planes of the facets, the remaining twelve edges are curved inward toward the centre of the figure. When a number of these figures are stacked in a space-filling arrangement, always three faces meet in an edge at 120° angles and four edges meet in a vertex at 109° 28′ 26″ angles (these angles are the intersecting angles formed by soap films *in equilibrio*).

Lord KELVIN's figure is the most perfect realisation of PLATEAU's Laws and ERRERA's principle and is, therefore, often considered the cell shape of an "ideal" tissue and consequently the fundamental cell shape (cf. **162**, **98**, **104**, **114**). There are, however, circumstances which prevent most cells from assuming that shape.

In investigations of cell shape it does not matter as a rule, if we consider Lord KELVIN's figure, or a very similar figure with straight edges and plane facets, viz. a *hexoctahedron*, or a *cubo-octahedron, with edges of uniform length* [1]), the fundamental shape of cells. The latte ris simpler in structure and therefore easier to work with.

Factor b. The unequal sizes of cells and the varying numbers of cell contacts are due to the cell divisions and subsequent periods of cell elongation in meristems not being simultaneous, but occurring with irregular intervals (cf. Chapter IIA).

The position of a new wall is in most cases conforming to ERRERA's rule, but there are more influences determining this position (see p. 58). In cambia for instance a new tangential wall usually does not assume such a position that the surface area is a minimum. It may also occur that in meristems more than three walls meet in an edge. Besides, in meristems there are certain walls which have not formed after cytokinesis, but by an elongation of existing surfaces of cells. The positions of these walls are chiefly determined by the direction of growth. We have already seen that for these reasons many meristem cells possess more or less than fourteen contact faces. Since sliding growth does not occur, the number of cell

1) Prof. BAAS BECKING drew our attention to the fact, that probably the earliest representation of this figure was given by OZANAM (**128**) in 1735.

contacts remains unchanged as a rule (see however factor *e*) and the shape of mature cells will therefore also often differ from that of Lord KELVIN's orthic tetrakaidekahedron.

Factor c. The mutual compression of cells maintains the polyhedral shape of cells, for it keeps the cells flattened against one another. If every cell of a tissue might be able to expand unhindered it would become spherical. An illustration of this is given by the *Fucus* "eggs", which are polyhedral when still in the oogonia, where they are crowded together, but immediately become spherical when liberated. In the tissues of higher plants no loose packing of separate spherical cells is found, but stacked polyhedra in which usually only small interstices (the intercellular spaces) are present. This is a consequence of the cells not being able to expand in all directions, as the epidermis and other tissues resist to the expansion, and the cells being cemented together by the middle lamellae. It has to be born in mind, in this connection, that new walls are formed as planes in a polyhedral cell system, so that from the beginning the cells are polyhedral and do not originate from spherical elements by compression. Several investigators have attributed much importance to this factor *c*. It was assumed that the mutual compression of cells produces a general compression of every individual cell and it was attempted to visualize this assumption by compressing spheres piled in densest packing. D'Arcy THOMPSON (**162**) considered this "external" pressure of importance, because he thought that cell walls are not perfectly elastic and therefore cannot perfectly assume the shape of the orthic tetrakaidekahedron. He states that compression of plastic spheres stacked in the most economic space-filling arrangement yields rhombic dodekahedra at compression (which, like orthic tetrakaidekahedra and cubo-octahedra with edges of uniform length, also fill space without interstices). He concluded accordingly, that a cell may have the shape of a tetrakaidekahedron, but the shape of a rhombic dodekahedron as well.

PRIESTLEY (**135**) thought that cells of apical meristems have plastic, inelastic walls and that therefore external pressure determines the shape of these cells. He supposed, on account of incorrect conclusions based upon experiments carried out by GANE (**59**, compare also Chapter X), that compression of plastic spheres in densest packing yields tetrakaidekahedra, so that the external pressure accounts for the tetrakaidekahedral shape of meristematic cells.

It has conclusively been shown that compression of plastic spheres in densest arrangement always produces dodecahedra, as will fully be accounted for in Chapter X, so that PRIESTLEY's explanation of the shape of meristem cells is wrong. Dodecahedra produced by

compression of stacked spheres always have a number of tetrahedral angles. If the external pressure would determine the shape of cells, dodecahedral cells were to be expected, manifesting themselves by the frequent occurrence of tetrahedral angles. We have seen before, that in plant tissues tetrahedral angles are of rare occurrence, so that the shape of cells cannot possibly resemble the dodecahedra obtained by compression of spheres. For the explanation of the shape of cells, the external pressure is, therefore, of little importance.

Factor d. Unequal growth-rates in different directions causes the cells to be elongated or depressed when compared with the orthic tetrakaidekahedron. A considerable elongation of a shoot makes its constituting tissues grow more in the longitudinal than in other directions. When the elongation of the tissue by cell division does not keep pace with the growth of the shoot, the cells will become elongated in the direction of the axis of the shoot. In stems where a marked growth in width occurs and the thickening by cell divisions does not keep pace with the growth of the stem, the cells become elongated in the radial direction, or they become flattened, as is — with some more complications — the case in the pith of *Juncus* species (see **110**). It is evident that in such tissues for these reasons ERRERA's principle is not fully realized in all planes of section, so that in certain sections the angles of intersection may differ appreciably from 120° angles.

The shape of cells which are elongated or depressed in one direction or another, cannot directly be compared with the shape of Lord KELVIN's tetrakaidekahedron. In many instances the shape of these cells may be analyzed by comparing them with transformed orthic tetrakaidekahedra. A method to derive such transformed figures is the method of transformation as developed by D'Arcy THOMPSON (see **162**, Chapter XVII). Congruent transformed orthic tetrakaidekadedra (or cubo-octohedra) are stackable without leaving interstices, for the transformation may be imagined to occur in a space-filling piling of orthic tetrakaidekahedra (or cubo-octahedra). The shapes of cells which have been growing mainly in one direction (such as many collenchyma cells and fibres) may be compared with orthic tetrakaidekahedra which have been transformed by stretching. In meristems where growth in one direction is prevalent the shape of the continuous cell files derived from a single mother cell as a whole, therefore, approaches the shape of a tetrakaidekahedron which has been subjected to an infinite stretching, i.e. a hexagonal prism, which we had already concluded from direct observations (cf. p. 38ff.).

Transformation of orthic tetrakaidekahedra or cubo-octahedra

has already proved to be an excellent method for studying various types of cells (cf. **99, 104, 105**).

Factor e. The formation of additional cell contacts changes the shape of the cells, because every additional contact adds a face to the cell. These changes of cell shape will not be dealt with, for they occur only in special cases and the shape of the cells becomes less regular as a rule.

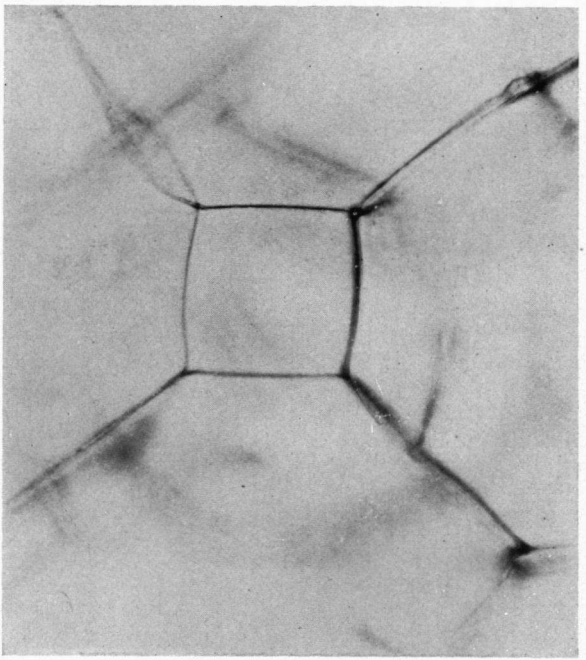
The ultimate shapes of cells actually come about in the following way:

1. in the meristematic condition the number of contact faces of the cell is fixed after the last cell division (and therefore the study of the structure of meristems is of great importance for the study of the shape of cells),
2. when maturing the cell expands and its walls tend to assume a minimal surface area, which results in the ideal case in a position in which they meet at 120° angles (factor *a*) and
3. when during the differentiation the cell has not been growing in all directions to the same extent, its shape is not isodiametric, but is elongated, depressed, or otherwise transformed if compared with isodiametric cells (factor *d*).

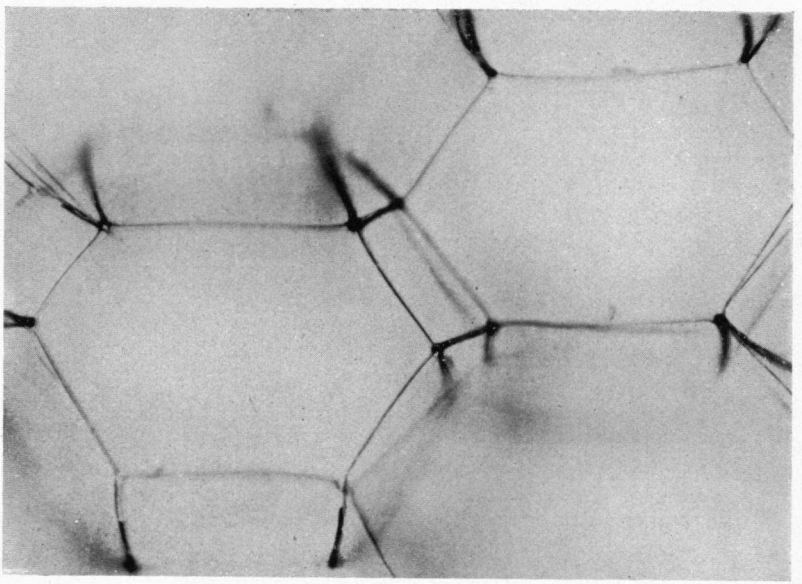
The last point may be neglected when the cells are able to expand in all directions, as in most parenchymatous tissues.

The question now may be put, whether it is possible, if from the hexagonal prismatic meristem cells mature cells having *exactly* the shape of Lord KELVIN's figure may develop. If so, at least part of the meristem cells must have such a shape as to make it possible to assume the shape of the orthic tetrakaidekahedron, when the cell walls of the maturing cells are readjusting themselves into a position conforming to ERRERA's principle of minimal surface area. In other words, the meristem cells must be so shaped as to yield an orthic tetrakaidekahedron after transformation from the hexagonal prismatic shape into the mature "isodiametric" shape. We may put the reversal: are there any meristem cells which are shaped like an orthic tetrakaidekahedron which has been transformed into a hexagonal prism? The required shape is represented in fig. 25A. The lateral facets of this figure are in contact with two cells in such an arrangement, that one part of a lateral facet is bounded by four other faces of the same figure (the faces marked by 4 in fig. 25A and B) and the other part by six (the faces marked by 6). Meristems shaped like this figure occur indeed, as may be concluded from the comparison of fig. 25 with fig. 14. The number of contact faces and the arrangement of the faces of the cells are

C.



D.

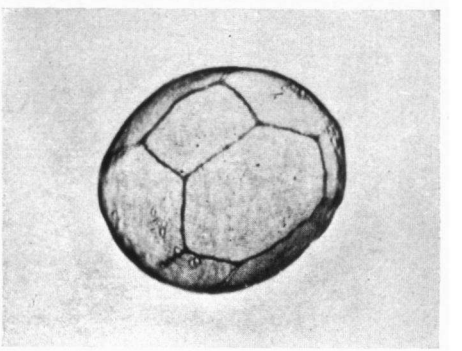


Microphotograph C. A tetragonal face of a parenchyma cell of *Asparagus Sprengeri*. Notice the resenblance with PLATEAU's "bourrelet": the edges are curved outward. Magnif. 200.

Microphotograph D. Two hexagonal facets of parenchyma cells of *Asparagus Sprengeri*. Notice that the edges are curved inward. Magnif. 200.

TAB. IV

E.



Microphotograph E. Cell of the tuber of *Asparagus Sprengeri*, macerated in hydrogen peroxide, swollen in alkali (cf. 37 p. 772) and stained in oxamin blue. The arrangement of faces is the perfect arrangement of the facets of an orthic tetrakaidekahedron (compare fig. 26C). Magnif. 80.

(Photographs: Laboratory for Technical Botany, *Delft*).

varying widely (cf. p. 49), so that many meristem cells do not conform to the requirements to be transformed into an orthic tetrakaidekahedron. Even the cells possessing fourteen contact faces

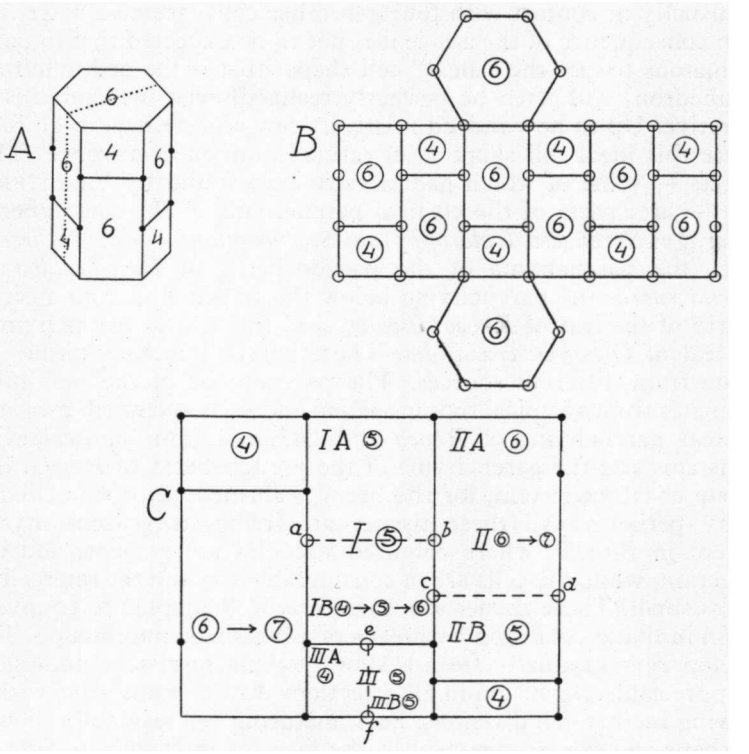


Fig. 25. A. Meristematic cell of the shoot apex showing the arrangement of faces which enables it to assume the shape of Lord KELVIN's tetrakaidekahedron after expansion in all directions.
B. The same, all faces folded out in the plane of drawing. **4** and **6** indicate facets bounded by four and six faces respectively and changing into the squares and hexagons of KELVIN's figure when expanding.
C. Part of the longitudinal facets of an arbitrary apical meristem cell, folded out in the plane of drawing as the cell in B. **4, 5, 6** etc.indicate facets bounded by 4, 5 or 6 facets of the same cell and changing into tetragons, pentagons, hexagons etc. in the mature condition. Explanation see text.

differ for the most part from the shape represented in fig. 25A, because their lateral walls do not consist only of faces bounded by six or by four other faces. In fig. 25C is represented that in a different arrangement of the faces also faces are present bounded by five other faces.

The required shape (fig. 25A) is, generally speaking, the most likely to be found in meristems (or parts of meristems) which are built up of cells of almost uniform size, because in this case they are usually in contact with fourteen other cells (see also p. 41).

In consequence of the above it is not to be expected that in parenchymatous tissues the "ideal" cell shape (that is the orthic tetrakaidekahedron) will often be perfectly realized, even if factor *d* is not operative. Up to now indeed relatively few objects have been found where this ideal cell shape is of rather common occurrence. These objects — some of which had already been found by VAN ITERSON (80) — are: parts of the cortical parenchyma of the root tubers of *Asparagus Sprengeri*, *Chlorophytum Sternbergianum* and *Anthericum* spec., the parenchyma of the pseudo-berry of *Basella alba* and *Basella rubra*, the parenchyma below the upper epidermis near the midrib of the leaf of *Rhoeo discolor*, and the central parenchyma of the leaf of *Othonna crassifolia*. These parenchymatous tissues originate from different sources. The parenchyma of the root tubers originates from an apical root meristem and subsequent rib meristem, the leaf parenchyma of *Rhoeo* and *Othonna* from intercalary rib meristems and the parenchyma of the pseudo-berry of *Basella* from a plate or rib meristem, for the berry is formed out of the enlarged fleshy perianth. All these tissues are living, turgescent, hyaline (except in *Basella*, where coloured vacuoles are present) and easy to section, while the cells are of considerable size and the intercellular spaces small. These tissues are, therefore, well adapted to an investigation in living condition by means of a binocular microscope. They develop very gradually from a slow-growing meristem undergoing an appreciable expansion in all directions during maturation without showing further cell divisions. Each maturing cell originally showing the shape and the arrangement of the faces of the figure in fig. 25A grows in all directions and the forces acting as surface tension forces can operate unhindered, so that the ultimate shape conforms to ERRERA's rule and approaches the shape of an orthic tetrakaidekahedron.

As appears from fig. 26, in which at left cells out of a root tuber of *Asparagus Sprengeri* and at right a cubo-octahedron are figured in three corresponding positions, and from our microphotographs (A, B and E), the ideal cell shape is sometimes indeed very closely approached. It is worth while to stipulate here, that, though in many papers on the subject of cell shape Lord KELVIN's orthic tetrakaidekahedron is considered the fundamental shape of cells, a perfect likeness has never been reported before, and that it has never been clearly demonstrated that cells actually approach the shape of a figure with curved edges as required by the rule of minimal surface area.

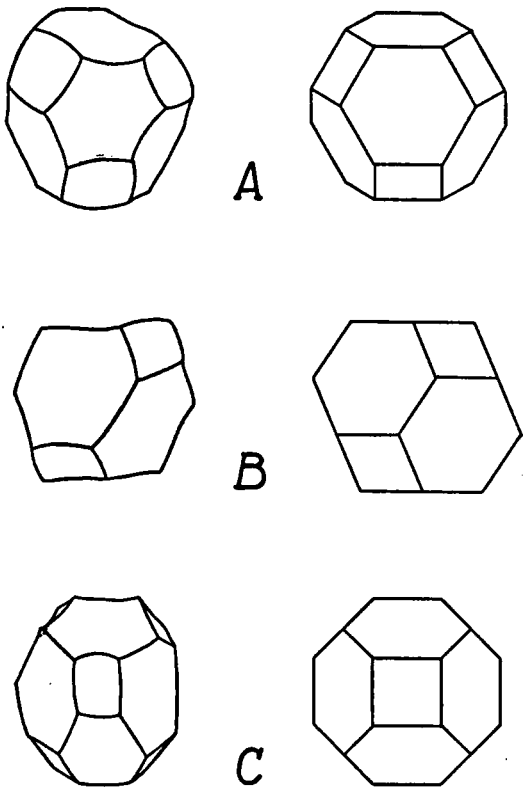


Fig. 26. Left: parenchyma cell of the tuber of *Asparagus Sprengeri*, macerated in H_2O_2 (87), swollen in alkali (see 37 p. 772) and stained in oxamine blue, represented in three different positions. Right: a cubo-octahedron with edges of uniform length in corresponding positions. Position A corresponds with a top view of the cell (seen in the direction of the root axis); B with a lateral view of the cell and C with an oblique view of the cell seen at an angle of about 30° with the long axis of the cell. It may be noticed that the cell and the cubo-octahedron show much resemblance, but that the edges of the cells are curved. (Compare our microphotographs A, B and E). Magnification of parenchyma cell 75.

We refer to our microphotographs, which show a section of the tuber of *Asparagus Sprengeri* in two different directions (A and B), a tetragonal plane with edges curved outward (C), hexagonal faces with edges curved inward (D) and finally an isolated cell (E). That no cells shaped like an orthic tetrakaidekahedron were found by older investigators is probably due to the fact that less suitable

objects, which were often dead or fixed and consequently shrunk moreover, were investigated (pith of *Sambucus* and *Eupatorium* etc. see 98 and 114).

When orthic tetrakaidekahedra (or corresponding cubo-octahedra) are stacked without interstices, all figures are oriented in the same fashion, i.e. they have all a face, an edge, or a vertex placed in a similar position. LEWIS has pointed out (104, 105), that in tissues a similar arrangement is found. Where horizontal divisions have prevailed (as in apical meristems, rib meristems and their derivative tissues) horizontal faces are found above and below. Accordingly, in stem parenchyma and in the parenchyma of *Asparagus* tubers the cells usually have horizontal hexagonal faces above and below (fig. 26A). Where vertical divisions have prevailed (as in cambia and plate meristems and their derivative tissues) the cells will have horizontal edges placed in the highest and lowest position. In leaf parenchyma originated from a rib or plate meristem the vertical divisions have prevailed (the lamina thought to be placed in horizontal position), so that when viewed from above the cells have an edge placed in the highest position above parallel to the leaf surface and appear as in fig. 26B.

Since ideal parenchymatous tissues do not exist in nature, we may expect several irregularities in the arrangement of the cells, which are the more important, the more the tissue differs from the ideal parenchyma. Not all apical meristem cells are hexagonal prisms, but also pentagonal, heptagonal etc. prisms occur (cf. p. 43), which never become orthic tetrakaidekahedra. Some apical meristem cells have *two* faces above or below instead of a single one (fig. 16), so that they will show an edge above or below when fully differentiated. The parenchyma cells resulting from these abnormally shaped meristem cells cannot assume the shape of the orthic tetrakaidekahedron, even though possessing fourteen contact faces, for the structure of the parenchyma requires *faces* and not *edges* above and below (cf. p. 66).

From the structure of the meristems still other deviations from the ideal tetrakaidekahedral shape may be explained. Many parenchyma cells have, besides tetragonal and hexagonal faces, also triangular, pentagonal, heptagonal, octogonal and nonagonal faces. This is due to the irregular arrangement of the cells in the meristem. In fig. 25C part of the walls of a meristem cell is represented folded out in one plane. Since in a meristem the cell divisions are steadily proceeding, existing lateral contact faces will be divided by edges formed by subsequent anticlinal divisions of the adjacent cells. Thus the newly-formed edge *ab* in fig. 25C, formed by a new anticlinal

division of the cell which had been facing face I, divides face I into IA and IB, and increases the number of cell contacts by one. Face I was originally bounded by five faces and its daughter faces are bounded by five (IA) and by four faces (IB) respectively. The point *b* becomes an additional future angle of face II, which is now bounded by seven faces instead of six. A new division of a neighbour cell intersecting face II along *cd* divides it into IIA with six and IIB with five future angles. By the presence of the point *c* the number of faces bounding IB is brought from four to five. The occasional longitudinal divisions increasing the number of columns also involves changes. *ef* is an intersecting line by which face III has been divided into IIIA with four and IIIB with five future angles by a vertical division of the cell facing III. The point *e* is an additional future angle to face IB. The cell divisions and consequently these changes proceed in young parenchyma as a rule. Meanwhile the lateral faces of the meristem cells, which are all tetragonal, change into pentagons, hexagons, heptagons etc. except the few remaining tetragonal. In this way the different outlines of the faces of the cells are brought about. The triangular faces, being of rare occurrence, are apparently formed in an advanced stage of development and not in the meristem proper, since in a meristem only tetragonal lateral cell faces bounded by four or more other faces are present. The formation of triangular faces probably occurs by an intersection of a polygonal face, for instance by the division of a pentagon into a triangle and a hexagon, or of a heptagon into a triangle and a nonagon, etc.

The largest lateral faces of a meristem cell or of a young parenchyma cell are usually bounded by many faces (7, 8 or 9). The formation of a new wall in these cells occurs near the middle of the cell (in the equator), so that the largest faces, reaching beyond the middle, are divided into two daughter faces with less future angles. The number of angles of these daughter faces is therefore reduced to 4, 5 or 6. This accounts for the faces of parenchyma having mostly four, five, or six sides, which was already established earlier in a direct way by cell reconstructions (cf. **98**, **99**, **114**).

All deviations from the ideal tetrakaidekahedral shape are more marked in less regularly built parenchymatous tissues than in the parenchyma of *Asparagus Sprengeri* root tubers and the other objects mentioned on p. 68.

As was communicated before, in a tissue which has not been growing in all directions to the same extent the cells may be elongated, depressed or otherwise transformed (p 63). As for parenchymatous cells, we find this condition e.g. in the storage regions of roots of *Beta vulgaris*, *Daucus Carota* etc. and in cork cells. Cells exactly

corresponding in shape with orthic tetrakaidekahedra are not to be expected here. Even if the meristem cells from which they have originated show the shape and the arrangement of contact faces of the figure represented in fig. 25A, the cells are prevented from assuming the ideal shape by the unequal growth rates in its various dimensions. The actual shapes of the mature cells approach to a greater or smaller extent the shape of figures derived from an orthic tetrakaidekahedron (or corresponding cubo-octahedron) by transformation. In order to find the fundamental cell shape of a tissue, this transformation has to be carried out in the same way and in the same direction as the actual elongation, foreshortening or any other change of the cells of the tissue if compared with the regular tetrakaidekahedral shape (cf. LEWIS **104**, **105** and Chapter IX).

Parenchyma cells of storage roots of *Beta*, *Daucus*, etc. and cork cells have been growing in radial direction to a considerable extent and but little in tangential direction (see also p. 24). The shapes of these cells are therefore more or less similar to the shape of a transformed tetrakaidekahedron which is intermediate between a hexagonal prism (fig. 25A) and an orthic tetrakaidekahedron (fig. 26B).

An exception, inasmuch cell shape is concerned, is made by the cortical parenchyma of certain Monocotyledonous roots, viz. by those which have originated from a meristem of the type described by VAN TIEGHEM (see p. 49). The meristem cells of these roots are in contact with some eight cells and so are the derivative mature parenchyma cells, so that their fundamental shape cannot be a fourteen-sided figure. The shape of these parenchyma cells does not change during differentiation and remains a hexagonal prism.

On account of the arguments mentioned above in the case of parenchyma, it may be concluded that also collenchymatous (cf. **137**) and epidermal cells assume their mature shape without showing sliding growth, so that the number of faces is determined after the cell divisions by which the cells originated.

Collenchyma cells, like parenchyma cells, are of almost uniform size as a rule and the number of faces per cell, therefore, averages fourteen. Collenchyma cells are mostly elongated in the direction of the stem they belong to and consequently their shapes resemble more or less the figure which can be derived from an orthic tetrakaidekahedron by a vertical stretching in a position with horizontal hexagonal faces above and below.

Collenchyma is usually adjacent to epidermis and parenchyma. The collenchyma cells have greater longitudinal extent than the cells of the adjacent tissues as a rule, so that a single collenchyma

cell placed at the boundary of collenchyma and a different tissue is contiguous to more cells of that tissue than it was contiguous to when still a meristem cell. This is to be ascribed to the fact that the cells of the tissues adjoining young collenchyma cells usually continue dividing, when the latter have already ceased to do so and elongate solely. The cells at the boundary of collenchyma and other tissues consequently have unequal numbers of lateral cell contacts and are irregularly shaped.

Epidermal cells originate from the outer layer of cells in apical meristems, known as the dermatogen. This dermatogen consists of cells which are almost the same size as the cells of underlying tiers and are in contact with some ten meristem cells. The exposed surface included they have some eleven faces in all (see p. 41). In mature organs the epidermal cells are sometimes still the same size as the cells of the adjacent tissue. If so, their number of contact faces still averages ten. When the underlying cells have been able to expand in all directions during maturation, these cells ultimately assume more or less the shape of an orthic tetrakaidekahedron. The shapes of the epidermal cells accord with the shapes of the adjacent cells and fit into the tetrakaidekahedra, having more or less the shape of the half of a bisected orthic tetrakaidekahedron. The bisecting plane meets two opposite hexagonal faces at right angles and bisects two opposite edges of this faces (cf. **101**). The additional face of the half of the bisected tetrakaidekahedron formed by the plane of intersection is represented by the exposed surface of the epidermal cell, which is convex instead of plane, however. This is in accordance with the principle of minimal surface area, for in consequence of the curvature the exposed walls and the walls perpendicular to the surface of the leaf meet at angles approximating 109° instead of at right angles.

Only those dermatogen cells may at maturation perfectly assume the shape of a bisected orthic tetrakaidekahedron which have ten cell contacts and besides possess the arrangement of faces shown in a figure which is obtained by bisecting the hexagonal prism of fig. 25A by a vertical plane (dotted line = intersecting line).

If the underlying cells are shaped like transformed tetrakaidekahedra, the epidermal cells are more or less shaped like the halves of bisected transformed tetrakaidekahedra.

If the cells of the epidermis and the cells of the adjacent tissue have different sizes, the above derivation of the shape of the epidermal cells cannot be applied. For an analysis of cell shape in this case other fundamental stereometric figures have to be derived, dependant on the mutual proportions of the dimensions of the epidermal

cells and those of the underlying cells, as was successfully achieved by LEWIS (**101**, **103**), to whom we refer for further details.

CHAPTER III

THE DEVELOPMENT OF THE CRYSTAL CELLS IN THE LEAF OF *CITRUS* AND THE STINGING HAIRS ON THE BRACTS OF *DALECHAMPIA*.

The development of the crystal cells in the leaf of *Citrus* was described for the first time by VON GUTTENBERG (**66**), to whom we refer for details not dealt with in our paper. In a young leaf, 2—3cm in length, certain cells of the subepidermal layer of the mesophyl become conspicuous by forming a small crystal (cf. fig. 27A). These are the future crystal cells. In a young leaf of that length cell divisions have already taken place for the most part and the further growth of the leaf is brought about chiefly by cell elongation and expansion.

The crystal increases in size as the cell matures. Most cells containing crystals appear to grow in between the epidermal cells (fig. 27B) and may even reach the surface of the leaf, thus obtaining an exposed face. In a transverse section of the leaf it seems as if a wall between two epidermal cells disappears during the development of the crystal cell. VON GUTTENBERG thought that this must be explained by sliding growth of the young crystal cell on the walls of the epidermal cells; SINNOTT and BLOCH (**155**) considered it a case of

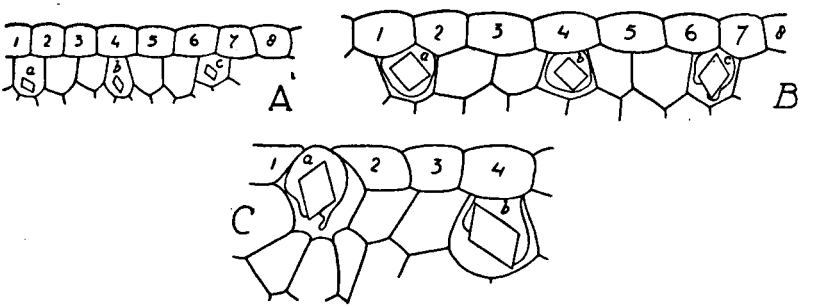


Fig. 27. Diagram of the development of the crystal cells in the *Citrus* leaf. A. Section of a young leaf, B. more advanced stage and C. mature condition. *a*, *b* and *c* are the crystal cells (in C only *a* and *b* are represented). Explanation see text.

intrusive growth. According to both conceptions the walls between the two contiguous epidermal cells must be split along their middle lamella.

An investigation of the cell walls in the leaf of *Citrus* reveals that in all walls — and consequently also in the walls which are supposed to split — plasmodesmata are present in all stages of development of the crystal cells. As was pointed out on p. 55, this is substantial evidence against sliding or intrusive growth. Accordingly, the difficulty is encountered how to explain, without assuming a splitting of walls connected by a middle lamella, that (as seen in a transverse section of the leaf) walls between epidermal cells situated above a young crystal cell may disappear during the maturation of the leaf. For this purpose we must examine the changes which occur in the cell wall *as a whole* and not only the changes seen in sections of the wall as represented in fig. 27. VON GUTTENBERG's conclusions were completely based on observations of such transverse sections only.

As appears from our observations, in *Citrus* three instances may be distinguished: a crystal cell may be in contact with one, with two, or with three (exceptionally four) epidermal cells. If a young crystal cell is contiguous to a single epidermal cell, it will — as was already noticed by VON GUTTENBERG — never reach the surface of the leaf during its development; this is represented in our diagram for cell *b* (fig. 27). Such cells do not obtain additional contacts; they do not show any indication of possible sliding growth and are therefore not of importance for the present problem. The two other instances are represented in the mature condition in surface view of the leaf in fig. 28A and B. Here also the crystal cells do not gain additional cell contacts (except the exposed surface) and a mature crystal cell contiguous to two epidermal cells also adjoined two young epidermal cells when still meristematic. The same applies to a crystal cell adjoining three (or four) epidermal cells.

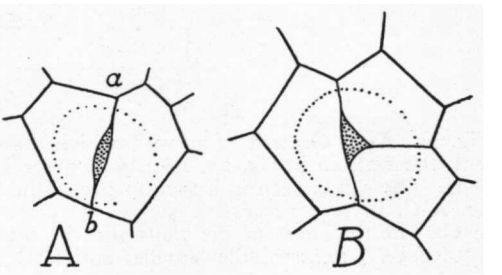


Fig. 28. A. A crystal cell of *Citrus* bounded by two epidermal cells, and B. a crystal cell bounded by three epidermal cells in top view. *ab*: the wall between the two epidermal cells; stippled: exposed outer wall; full lines: outlines of epidermal cells; dotted line: outline of crystal cell (below the plane of the epidermal cells).

We begin with the crystal cells adjoining two epidermal cells. The wall *ab*, which is seen in fig. 28 as a line, is represented in fig. 29A in a less advanced stage of development (corresponding to the stage of fig. 27A) as seen in front view in a transverse section of the leaf. This (double) wall *ab* locally grows less, viz. in the place

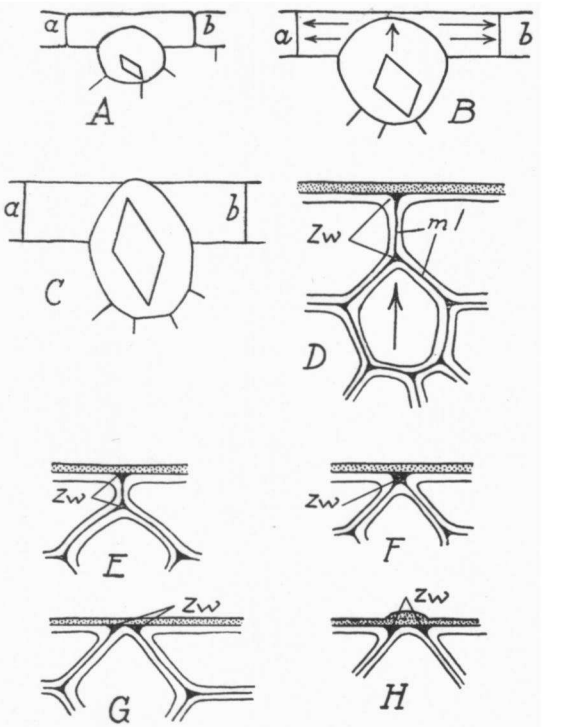


Fig. 29. A-C. Growth of a wall which corresponds in mature condition with the wall *ab* in fig. 28. Explanation see text.
D-H. The same, seen in a section perpendicular to the plane of section of fig. A-C, in five successive stages. D corresponds to A, F to B and H to C. The thickness of the walls and the middle lamellae exaggerated. *Zw*: "*Zwickel*", *m.l.*: middle lamella, cuticle stippled. Explanation see text.

where the underlying crystal cell grows upward, but it does not split, as may be concluded from the presence of plasmodesmata (see above). The local decrease in width of the cell wall is associated with a growth in surface area of the wall *ab* as a whole, because the epidermal cells increase in size, for the leaf is still growing, whereas most cell divisions have already taken place. If the growth of

such a wall is compared with the changes brought about in a sheet of rubber by stretching in one direction, a similarity is noticed. A sheet of rubber which is stretched in one direction increases in total surface area and grows less in width simultaneously (see fig. 30 and the experiments in Chapter X). The walls of epidermal cells are stretched by the turgor in all directions, but the expanding crystal cells produce a local counter-pressure, so that the action of the turgor stretching is chiefly perceptible in the direction *ab* of fig. 29A and B and not in a direction perpendicular to *ab*. This accounts for the wall *ab* growing less wide in the direction perpendicular to the surface of the leaf by simultaneous stretching in a direction parallel to the surface of the leaf.

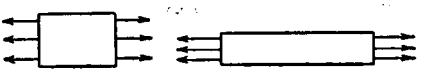


Fig. 30. The effect of stretching on a sheet of rubber. Left: before, right: after stretching. The sheet elongates and grows less in width simultaneously.

It is still unexplained hereby, however, how that a part of the wall may completely disappear, for a wall growing less in width cannot be reduced to nothing by stretching only. The explanation is most probably found in the presence of the angular thickenings of the middle lamellae in places where three or more cells meet. In fig. 29D and fig. 29E the transverse sections of the wall *ab* of fig. 29A and 29B are represented. In the angular spaces where three cells adjoin these typical, more or less triangular thickenings, known in the german literature as "*Zwickel*", are seen. They are also found in places where the middle lamellae of epidermal cells meet the cuticle. The *Zwickel* show exactly the same staining reactions as the middle lamella and disappear by the application of macerating reagents dissolving middle lamellae, so that they probably consist of pectic substances and do not contain cellulose.

In fig. 29F is represented the stage in which the wall *ab* has grown so less in width that the two *Zwickel* adjacent to this wall, which do not grow less, come in contact. When the pressure of the growing crystal cell continues, a rather sudden change occurs instead of the gradual decrease in width of the wall *ab* by stretching in opposite direction. The two separate cellulose lamellae constituting the double wall *ab*, which are now separated by the great mass of plastic *Zwickel* material (pectic substances), are pulled apart by deformation of the *Zwickel*, which first fuse (fig. 29F) and subsequently split up into two new *Zwickel* (fig. 29G). In consequence of these changes the crystal cell has reached the surface of the leaf through a small part of its wall. This portion of the wall may enlarge by symplastic

growth later on and become a wall of considerable extension, the crystal cell thus obtaining its exposed surface (fig. 29C and H, fig. 28A).

During the separation of parts of the walls as described above no protoplasmic connections are ruptured, because in the parts of the cell walls involved in the establishment of additional faces, i.e. the parts of the walls bounding the *Zwickel* (or their vestiges, the intercellular spaces) do not contain plasmodesmata (117).

The same explanation of the establishment of additional faces can be applied to the third instance, i.e. when a crystal cell is in contact with three (or four) epidermal cells. Here too first the changes come about by symplastic readjustments and the walls grow less wide by a simultaneous stretching in opposite direction. Then two *Zwickel* fuse and split up into new *Zwickel* afterwards. Three (or four) *Zwickel* are formed instead of two, because the new-formed outer wall is triangular (fig. 28B) or tetragonal in outline. The further development occurs in a symplastic way again.

The described mode of establishment of additional faces also takes place in other tissues, which will be dealt with later on, with the only difference that the growing cell instead of obtaining a new exposed surface establishes an additional contact with a cell originally not contiguous (see fig. 4).

The development of the so-called stinging hairs on the bracts of *Dalechampia Roezliana* was described by KNOLL (90) to whom we refer for further particulars. Up to a certain stage of differentiation the development is similar to the growth of the crystal cells of *Citrus* leaves: the cells of the subepidermal tier of the leaf ultimately becoming a hair cell obtain an exposed outer wall. After that a protrusion of the young hair cell is formed (fig. 31A). The protruding of the hair cell involves adjacent parts of the epidermal cells, so that they also form protrusions. The hair cell and the surrounding epidermal cells finally give rise to a columnar cell complex (fig. 31B).

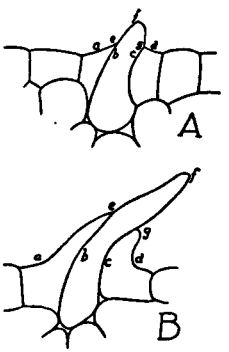


Fig. 31. Development of a hair cell of *Dalechampia* (after KNOLL). A. younger B. mature stage. See text.

KNOLL ascribed the formation of an exposed wall to sliding growth like VON GUTTENBERG in the case of *Citrus* crystal cells. In our opinion the same explanation as given above in the case of *Citrus* idioblasts applies to *Dalechampia* hairs as well. When the stage of fig. 29H has

been reached, the exposed part of the young hair cell and portions of the adjacent epidermal cells differentiate further in a symplastic way. This is a typical example of changes in intercellular relationships without sliding growth by means of differential wall growth: small portions of the wall of the young hair cell and small parts of the walls of the epidermal cells grow considerably, whereas the remaining parts of the walls grow relatively little. The points *a*, *b*, *c* and *d* in fig. 31 do not alter their relative positions, whereas the points *e*, *f* and *g* move outward by an appreciable growth of the portions *ae*, *be*, *cg*, *dg*, *ef* and *gf*.

CHAPTER IV

THE DEVELOPMENT AND GROWTH OF NON-ARTICULATE LATEX DUCTS CONSIDERED IN RELATION TO SLIDING GROWTH.

The latex ducts may be distinguished in two groups, viz. the articulate and the non-articulate latex ducts. In the literature only sliding growth of non-articulate latex ducts has been reported (KRABBE and others), the cells being compared with the hyphae of parasitic fungi pushing themselves through the tissues of the host plant.

Articulate latex ducts originate by cell fusion and therefore *a priori* but little or no sliding growth at all is to be expected. It is sufficient to state that the members of an articulate latex duct develop in the same way as parenchyma cells, but that they usually become longer than the surrounding parenchyma cells. This difference in length is brought about, because the young parenchyma cells go on dividing whereas the young latex vessel members elongate only, as is also the case with collenchyma cells adjacent to parenchyma cells (see p. 71).

The development and growth of the non-articulate latex ducts have been the subject of many investigations (HANSTEIN **69**, DIPPEL **38**, CHAUVEAUD **31**, ZANDER **176**, SCHAFFSTEIN **147** and others). It was not before recently that it appeared from the investigations of the last two authors, that two types of non-articulate latex ducts may be distinguished, viz. the *Euphorbia*-type, which has already been known for a long time, and the *Cannabis*-type. The *Euphorbia*-type occurs in nearly all Euphorbiaceae and Asclepiadaceae, in certain Apocynaceae, and in some other species belonging to different plant families;

the *Cannabis*-type thus far has been found in *Cannabis*, *Urtica*, *Humulus* and *Vinca minor*, and seems to be of less common occurrence. These two types differ in morphological and ontogenetical respect. The cells of the *Euphorbia*-type are branched and originate only once in the life of the plant, viz. in the embryo; those of the *Cannabis*-type are unbranched and originate repeatedly in the apical meristem of the stem, at every turn a single latex duct forming at the base of a leaf primordium.

In the course of our investigations, the following objects were studied:

Euphorbia-type: shoot apices of *Euphorbia Peplus*, *Euph. Lathyris* *Euph.* spec. div., *Asclepias syriaca*, *Ascl. curassavica*, *Calotropis*, *gigantea*, *Apocynum cannabinum* and *Nerium Oleander*, and embryoes of several *Euphorbia* species.

Cannabis-type: shoot apices of *Cannabis sativa*, *Humulus Lupulus*, *Urtica dioica* and *Vinca minor*. The best staining method proved to be FLEMMING's triple stain; the method recommended by SCHAFFSTEIN did not give satisfactory results. The *Cannabis*-type is the less complicated one and is therefore discussed first.

T h e *Cannabis*-t y p e.

It appeared from the investigations of ZANDER and SCHAFFSTEIN, that a latex duct of this type originates from a single meristem cell. According to these authors, this meristem cell at first does not distinguish itself from the other meristem cells, but already early in its development it becomes conspicuous by its greater size, by the possession of more nuclei and by the formation of granules in the cytoplasm which stain out intensely. The cell ceases dividing and elongates solely. The base of the cell gradually quits the growing zône by the meristem passing at its base into mature tissues. When in the tissue surrounding the latex ducts (the cortical parenchyma) all cell divisions have ceased and the parenchyma cells have reached their definite shape and size, the growth of the basal part of the latex ducts also comes to an end. The upper part of the ducts may however remain in meristematic condition and continue elongating for some time, until the internode and the leaf in which the apex of the cell ultimately arrives (in consequence of the differentiation of the leaf primordium into a leaf) have reached their definite length. ZANDER's and SCHAFFSTEIN's results were completely confirmed by our investigation and we therefore refer to their papers for further particulars and for figures.

As was already observed by SCHAFFSTEIN, no sliding growth occurs between the latex ducts and the surrounding cells. The

elongation of the latex ducts keeps pace with the elongation by growth and cell division of the surrounding parenchyma. This type of growth resembles the one occurring in the development of certain primary sclerenchyma fibres ("bast fibres") as described by ALDABA (1, see also Chapter V).

T h e *Euphorbia*-t y p e.

The situation is here entirely different, because the number of latex ducts remains constant. These cells originate in the nodal region of the young embryo, but later they are found throughout the embryo and still later throughout the plant. In the plant the tips of these cells remain continuously in the apical meristems of stem and root and keep growing with these meristems, sending out branches to all newly-forming organs. The older parts of the latex cells as a rule do not grow any longer.

One has, therefore, to deal with two instances, viz. *a*) the origin, development and growth of the latex ducts in the embryo, and *b*) the growth of the latex ducts in the meristems of older plants. The latex duct initials of the *Euphorbia*-type originate usually four or eight in number. At first they differ only by their size from the other cells of the embryo. Soon however they become more conspicuous by their form being elongated and later even branched, by their different cell contents and by their walls showing greater affinity to stains (compare the excellent figures in CHAUVEAUD's and SCHAFFSTEIN's publications). During their development the tips of the continually bifurcating, growing latex ducts arrive in all parts of the embryo, so that they finally extend from the apices of the cotyledons to the tip of the radicle. It is beyond a doubt, that additional cell contacts are formed by growth, for the latex ducts are originally separated from the apices of cotyledons and radicle by several layers of cells and must grow past these cells, thus meeting cells originally not contiguous. Is this growth accompanied by sliding growth of the latex ducts on the other cells of the embryo? In a growing embryo the metabolism is intensive as a rule. The growth of the embryo requires a quick translocation of food substances from one cell to another, so that a good communication between the cells is necessary. The growing latex cells especially have an intense metabolism, as they already soon start producing latex. The supply of food substances probably takes place through plasmodesmata and we have already seen, that walls cannot show mutual slip in consequence of sliding growth, because otherwise the connections between the protoplasts (the plasmodesmata) would be ruptured.

The latex cells therefore do not slide on the walls of their neighbour

cells. The relative displacement of the tips of the young latex cells in the embryo therefore probably comes about in the same way as in the case of crystal cells of *Citrus*, i.e. the cells alter their relative position chiefly by symplastic readjustment of the whole framework of cell walls, whereas occasionally additional cell contacts between the apex of the latex cell and other cells are formed by a process as described on p. 75 and 76 (compare fig. 28 and the experiments in Chapter X). In this process no plasmodesmata are ruptured.

It was shown that in all mature parts of a latex cell plasmodesmata may occur (**160**). From this it has to be concluded, that probably plasmodesmata also occur in parts of the wall originated from an additional cell contact formed in the embryo. These plasmodesmata must have been formed secondarily. This is, however, not contradictive to what is said on p. 55 about the presence of plasmodesmata: when they have been formed once, they are never ruptured later on.

The contents of the latex cells differentiate earlier than the contents of the other cells of the embryo and therefore the latex cells earlier possess vacuoles than the other ones. The ability of the latex ducts to deform the adjacent meristem cells plastically probably vests in the presence of vacuoles. In any case, it may be observed that sections of the latex ducts are rounded off and sometimes even may protrude a little into contiguous cells (fig. 32).

The walls of the meristem cells can grow less in width by the growth of the embryo in all directions, so that the cells may expand in all directions and are deformable.

When in a dividing meristem cell which is contiguous to a latex cell a new wall is formed which is about perpendicular to the longi-

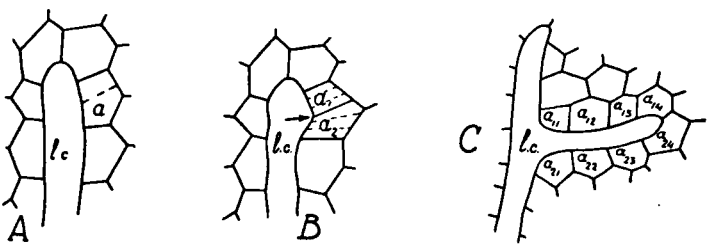


Fig. 32. Formation of a bifurcation of a latex cell of the *Euphorbia*-type A. A latex cell (*l.c.*) is surrounded by meristem cells, one of which (*a*) is dividing (broken line). B. the cell *a* has divided into the cells a_1 and a_2, so that breaks of walls occur and the latex cell forms a slight protrusion (in the direction of the arrow). C. The cells a_1 and a_2 have formed a group of daughter cells (a_{11}, a_{12}, a_{13}, a_{14} and a_{21}, a_{22}, a_{23}, a_{24} respectively) and the protrusion has become a side branch of the latex cell.

tudinal axis of the latex cell, the (double) wall between the meristem cell and the latex cell will show a slight break (see p. 57) and a slight protrusion of the latex cell is formed. In fig. 32 is represented how by a number of divisions in the daughter cells of the above-mentioned meristem cell (fig. 32A) a gradually increasing protrusion develops (fig. 32B). When a marked protrusion has been once formed, it develops into a branch of the latex duct by symplastic growth (fig. 32C).

In an embryo, which grows in all directions, the latex cells grow in their full length. During the development of the seedling the growth of the latex cells becomes gradually restrained to the apical meristems of the plant. In older plants the greater part of a latex cell does not grow any longer (e.g. in the mature cortex, the mature pith and the mature leaves). The cells potentially retain the ability to renew their growth, however. This occurs for instance in case of wounding as was found in *Euphorbia*-grafts by SCHAFFSTEIN. As appeared from our work, this phenomenon may also be observed in the would callus of cuttings. In rooting cuttings the latex ducts also occur in the tips of the new-formed roots (e.g. in cuttings of *Nerium Oleander* and *Synadenium Grantii*). In this case the growth is restricted to the growing zones of the graft or the cutting, i.e. restricted to the graft- or wound-callus and their eventual derivative meristems. The latex cells here grow only in places where they are surrounded by growing cells, and they do this only in a symplastic way.

Usually however a latex duct in an older plant elongates only at its extremities which lie in the apical meristems of stem and root, as was already mentioned above. It might be expected that in these meristems the growing parts of the latex cells would behave like the latex cells in the embryo. A relatively faster growth of latex duct tips resulting in the establishment of additional cell contacts cannot be detected as appears from the following points:

a) The distance between the apices of the growing latex ducts and the apex of an active meristem remains practically constant,

b) In a resting meristem (e.g. in the apical meristems of dormant lateral buds) the latex ducts do not grow, and

c) In the internodes of stems the latex ducts are not or but little branched, because the elongation is prevalent; in the nodes they are abundantly branched, because in these parts the growth in width is more important and the branching may occur towards all sides.

The latex ducts continue branching in the meristem. In connection with what has been mentioned above, it has to be assumed that the

latex ducts have the ability to deform the meristem cells. This deformation is only possible when the meristem cells may expand in alle directions. In young internodes and young roots the latex cells can grow practically in one direction only, because the surrounding tissue develops here in the manner of a rib meristem by growth in one direction. The cells surrounding the latex cells therefore cannot give way in lateral directions to the pressure of the latex cells, hence few bifurcations are formed. In the nodes and in the leaves growth in more than one direction occurs, so that the meristem cells may give way to the growing latex cells in more than one direction and the latex cells may bifurcate. For the same reason it is quite reasonable that in the nodes and in the growing leaves sometimes additional contacts may be formed.

The slight protrusions of the latex cells in a growing meristem which may eventually give rise to branches (fig. 32B) form towards all sides, i.e. in places turned to the apex of the stem or root as well as in places turned away from the apex. The branches develop only in lateral and apically oriented directions, however, and never in a direction turning away from the apex. This is connected with the elongation of stem and root in one direction and provides additional evidence against sliding growth of latex cells.

The elongation of a latex duct keeps pace with the growth of the adjoining meristem cells as a rule. This must be so, since the latex cells do not grow faster or slower than the surrounding meristem. If they should grow faster, the latex cells would overtake the meristem and reach at least the surface of the meristem, which is never the case; if they should grow slower, the latex cells would straggle and leave the meristem, which is never the case either.

We, therefore, reach the conclusion, that the growth of the non-articulate latex ducts comes about principally in a symplastic way. The growth of the latex ducts of the *Euphorbia*-type is interrupted now and then by the formation of additional cell contacts.

CHAPTER V

THE DEVELOPMENT AND SHAPE OF SCLERENCHYMA FIBRES IN PRIMARY TISSUES.

KRABBE (**94**) as well as HABERLANDT (**67**) was of the opinion that the so-called "bast fibres" show sliding growth when elongating during differentiation. This has not been substantiated by other investigators. TAMMES (**161**) found that the apical growth of elongating

flax fibres keeps pace with the growth of the surrounding meristem cells, whereas the older parts do not grow any longer and even form already secondary walls. TAMMES's observations were neglected for a long time, probably owing to the fact that they form only a minor part of the many investigations communicated in her monograph on the flax stem.

ALDABA (1) found additional proof of her observations and extended them studying *Linum* and *Boehmeria*. According to ALDABA, the elongating apex of a growing fibre remains thin-walled, while the older parts of the fibre do not elongate any longer and become gradually covered with successive telescoping secondary lamellae. This series of lamellae does not reach the apex before the elongation of the fibre has ceased and the fibre tip has arrived outside the meristematic zône of the stem. As was mentioned before (see p. 79) this mode of development resembles that of latex cells of the *Cannabis*-type.

In a previous study (116) we have already communicated that the sclerenchyma fibres of *Sanseviera*, *Musa* and *Agave* develop in a different way. In this instance every fibre grows *in its whole length*, until the cell has reached its definite size. The cell wall is of uniform thickness all over the place (except in the pits in the secondary walls), the secondary thickening initiates in every place of the cell wall simultaneously. During the development of these fibres the elongation of the unthickened fibres also keeps pace with the growth of the adjacent tissue. According to KUNDU the primary fibres of jute and hemp (cited after BARKER 22) and some other fibre plants (priv. comm.) develop in the same fashion.

A reinvestigation was carried out of a great number of objects, part of them having short and others long to very long elementary fibres. For the investigation of the earlier stages of development young, still growing parts of the various objects (shoot apices, growing leaf bases etc.) were embedded in paraffin and sectioned; the more advanced stages were studied by means of maceration techniques. For further technical particulars we refer to ALDABA (1) and our previous publication (116).

It appears, that two different methods of development of the fibres may be distinguished, viz. one occurring in plants having long, to very long, elementary fibres (one or more cm up to several dm long) and the other in plants having short fibres (a few mm long). The development of the long fibres comes about in the way described by TAMMES and ALDABA for *Linum*, the development of the shorter ones in the way described for *Sanseviera*. We shall therefore distinguish these two instances as "*Linum*-type" and "*Sanseviera*-type".

To the plants in which the *Linum*-type of fibre development is found belong *Linum usitatissimum, Boehmeria nivea, Cannabis sativa, Humulus Lupulus, Urtica dioica, Asclepias curassavica, A. syriaca, Calotropis gigantea, Vinca minor, V. rosea,* and *Nerium Oleander.* (The fibres concerned all belong to sclerenchyma in the primary tissues of the stem). It may be observed that we do not agree with KUNDU's conception (**96**) of the development of the fibres of *Cannabis.*

To the plants in which the development comes about according to the *Sanseviera*-type belong *Sanseviera guineensis, Agave americana, Cordyline australis, Pandanus stenophyllus* and several other *Pandanus* spec. (the fibres concerned belong to the sclerenchyma of the leaf), *Musa chinensis* (sclerenchyma of the pseudo-stem), *Salix alba, Vitis vinifera, Spartium junceum, Napaea dioica, Hibiscus cannabinus* [1]), *Hibiscus Sabdariffa* [1]), *Datura arborea, Campsis radicans, Calystegia Sepium, Cucurbita Pepo, Helianthus annuus, H. debilis* and *H. tuberosus* (primary sclerenchyma of stem and branches).

Not in a single case any indication of sliding growth between fibre and fibre, or between fibres and adjoining tissue, could be found. The absence of sliding growth is fully substantiated because of the presence of plasmodesmata between young fibres and between fibres and the contiguous parenchyma (*Cucurbita Pepo, Hibiscus cannabinus* and *Vitis vinifera,* cf. HILL 75).

The occurrence of forked sclerenchyma fibres (e.g. in *Cannabis*) is apparently contradictive to the absence of sliding growth. Yet the presence of forked tips need not necessarily be indicative of sliding growth, as we have already seen in the case of bifurcated latex ducts (see p. 81).

The forked fibre tips are very short as compared with the total fibre length. This is evidence that the bifurcations originate a short time before the cessation of the elongation of a fibre end. At that moment the meristem cells surrounding the end differentiate into parenchyma, the cells expanding considerably during this differentiation and their shapes altering from prismatic into about tetrakaidekahedral. In the last phase of elongation of the fibre bundle the peripheral fibres, or parts of the peripheral fibres, become deformed by the expanding young parenchyma cells to such an extent that the fibre wall may show the typical ridges and grooves which are so characteristic of the peripheral fibres of fibre bundles and were among others figured by KUNDU (cf. **22** and **96**). At the tips of the peripheral fibres in this way the "bayonet ends" may originate from

1) Communicated by A. G. L. ADELBERT Jr.

a compression of the wedge-shaped ends of the fibres (see below) by the parenchyma cells causing an outward buckling of a part of the tip. By a further compression and simultaneous elongation of the fibre a bayonet end may develop a bifurcation, more or less in the way figured in fig. 32C.

The forked tips may form in the peripheral layer of a fibre bundle at the moment that the base of a fibre leaves the meristematic zone, or at the moment that the apex of a fibre does so. The cells constituting the central parts of a fibre bundle cannot be deformed by the expanding parenchyma cells as described for the peripheral fibres — hence only relatively few forked tips are found.

It is often difficult to decide, if the fibres of a bundle originate from common apical meristem cells by elongation, or if at first a meristem cell divides longitudinally in a number of cells having the same length as the mother cell which elongate simultaneously. The first case is found in *Linum*, *Boehmeria* and *Urtica*, and is probably the rule with the fibres developing as in *Linum*, the latter case is conspicuously developed in *Sanseviera* and *Agave*, and is probably of common occurrence in the *Sanseviera*-type of fibre development.

The shape of the elements of a fibre bundle originated from the elongation of groups of ordinary meristem cells may directly be derived from the general shape of the meristem cells (i.e. from a hexagonal prism) by stretching it longitudinally. Accordingly, the fundamental shape of these elements is the shape of a considerably elongated hexagonal prism with hexagonal horizontal faces above and below. Since sliding growth does not occur during the development of the fibres, the central fibres of a fibre bundle, which are in contact with other fibres exclusively, have the same number of cell contacts as the meristem cells from which they have been derived, so that these fibres usually have fourteen contact faces. When a fibre bundle develops, the elongation of the fibres keeps pace with the growth and cell divisions in the neighbouring parenchyma cells. Consequently the peripheral fibres of a bundle ultimately adjoin a great number of parenchyma cells and possess many more cell contacts than the central fibres of the bundle. Their fundamental shape still resembles the shape of a hexagonal prism, however.

In the other instance bundles of fibre initials originate from meristem cells. These bundles develop in the same way as a plate meristem (see p. 50) by cell multiplications in a single plane, so that out of a single meristem cell a layer of cells of uniform height is formed (see fig. 33A, compare **116**). The number of contact faces therefore

averages fourteen (six lateral contacts with fibres of the same bundle and twice four with cells of the adjoining layers, see fig. 33B). At the development of new division walls slightly pronounced breaks of the horizontal walls may occur. During the elongation and expansion of the initials these breakings become more and more distinct, so that already soon the longitudinal sections of the cells appear as in fig. 33C, while the cross sections of the cells become polygonal

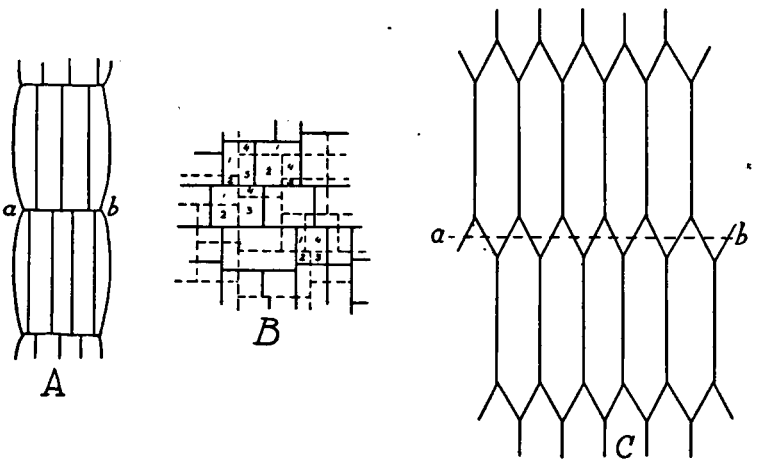


Fig. 33. A. The youngest part of a fibre bundle developing according to the *Sanseviera*-type. Two groups of initials formed by repeated longitudinal divisions of a single mother cell are represented.
B. The arrangement of the initials of two adjacent layers, as seen in the direction of the bundle; one layer projected on the other one (full lines and broken lines). Each cell is usually in contact with four other cells (groups of contacts of a single cell are numbered 1, 2, 3, 4). Compare also fig. 20A.
C. As A, but after the formation of breaks in the walls, so that the prosenchymatic shape begins becoming conspicuous.

(usually hexagonal) in outline. These changes are not brought about by sliding growth, but by differential wall growth.

The cells having fourteen contact faces, their fundamental shape is that of an orthic tetrakaidekahedron which has been stretched in a position with edges placed above and below. This is the tetrakaidekahedron "in prosenchymal orientation" (LEWIS **105**) and proves to be the fundamental shape of prosenchymatous cells (cf. **105**, Chapters VII, VIII, IX and fig. 38). This accounts for the fibres often possessing bevelled (chisel-shaped) ends.

The contacts made by a fibre initial at its upper and lower side with the adjoining initials of a higher or lower level, usually occurring

in fours, originally lie more or less in a plane, the breaks formed at the formation of walls being slight (fig. 33A). Later on these faces assume an oblique position and form the tapering tip of the young fibre (fig. 33C). The transverse sections of the tips of young fibres (e.g. at the level *ab* in fig. 33C) are *tetragonal*, whereas the initials when originating were in contact with *six* cells at any one level. This remarkable change is also accounted for solely by differential wall growth (the walls at the ends of the initials grow relatively more) and not by sliding growth.

Different parts of a cell, therefore, do not grow to the same extent. This is probably connected with the increasing tension in the expanding initials, which cannot act in all directions to the same extent (for the elongation prevails), so that usually the tapering ends elongate relatively more than the hexagonal middle parts of the cells (the "shafts"); this applies especially to the central fibres of a bundle.

The peripheral fibres grow symplastically with the adjoining young parenchyma cells and their elongation has to accomodate itself to the growth of the parenchyma cells. This is, besides of being the cause of the formation of ridges and grooves, and bayonet ends (see below), probably the main cause of the differences in lengths between the peripheral and the central fibres of a bundle. The differences in length between the peripheral and the central fibres of a bundle can be detected by separating after careful maceration the peripheral fibres first and the central fibres afterwards. In consequence of the growth of the adjoining tissue, an outer lateral wall of a peripheral fibre (such as *ab* in fig. 34) is as long as the total amount of the lengths of the contiguous lateral walls of the parenchyma

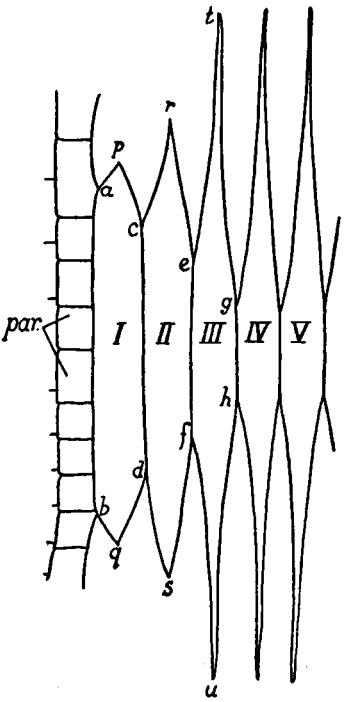


Fig. 34. Diagrammatic representation of a number of fibres (I-V) of a bundle which have originated from a common mother cell (compare fig. 33A and C) and the adjoining parenchyma cells (*par.*). The central fibres are longer than the peripheral ones. Explanation see text.

cells. Other lateral walls of the peripheral fibres, not facing walls of parenchyma (such as *cd* in fig. 34) are contiguous to fibres and, as we have already seen that the acute ends of the centrally placed fibres grow relatively more than their shafts, these lateral walls may become shorter than the outer lateral walls so that *cd* is shorter than *ab*. The central fibres of a bundle become longer and more acute than the peripheral cells of the same bundle. There is a gradual transition between the peripheral and the central fibres of a bundle — the wall *cd* is shorter than *ab*, the wall *ef* shorter than *cd*, etc., — but, a few layers deep in the bundle, the conditions are equal in all directions, so that the walls at both sides of a fibre are of equal length (the walls of cells IV and V etc.). From the preceding it is clear that ultimately longer and shorter fibres which have originated from initials of uniform length, such as cells I, II, III in fig. 34, are found in the same bundle next to one another without any sliding growth having taken place, for a gradual transition from shorter to longer elements is present, caused by the different growth rates of the lateral-longitudinal walls on either side of a fibre initial.

By this also another fact apparently indicative of sliding growth is explained without necessarily assuming sliding of cells, viz. the more or less paradoxal fact that fibres may become longer than the file of parenchyma cells adjoining a part of the fibre bundle which file has originated from a mother cell of practically the same length as the fibre initial (compare fig. 33 and 34: the parenchyma cells and the fibres originate from cells of almost the same length, i.e. the average length of the apical meristem cells, but later on, cells as cell III, IV or V of fig. 34 may become considerally longer than the file of parenchyma, as they elongate more than the peripheral fibre). The fact that fibres may be longer than a strip of parenchyma formed from a single initial was one of the points on which HABERLANDT based the opinion that fibres in primary tissues slide in between one another during their development.

CHAPTER VI

THE DEVELOPMENT OF ELEMENTS OF PRIMARY XYLEM AND PRIMARY PHLOEM.

The elements of primary xylem and primary phloem originate from procambial strands, which are formed in different organs of the plant (stems, leaves, roots) in the same way as the bundles of fibre initials by longitudinal divisions of meristem cells. The funda-

mental shape of the procambium cells is therefore the same as that of young sclerenchyma fibres, i.e. an elongated orthic tetrakaidekahedron in prosenchymal orientation (see fig. 38 and fig. 39). Some of the procambial cells differentiate into tracheids in the same way as fibre initials into fibres. The fundamental shape of the tracheids is consequently identical with the fundamental shape of mature sclerenchyma fibres (see Chapter V). These primary xylem tracheids may elongate more than adjacent cells, as is also the case with slerenchyma fibres (cf. p. 88 and fig. 34), and may finally even be longer than cells or groups of cells originated from mother cells having about the same length as the tracheid initial.

The remaining elements of the primary xylem and primary phloem do not elongate much more than the surrounding cells, but some of them grow considerably in width, so that appreciable differences in diameter of the cells — which have been of uniform width when still procambial cells — are brought about. This is connected with two processes, viz.

a. some cells grow in width without dividing, whereas the other ones continue dividing longitudinally, thus increasing the number of lateral contact faces and, by the implicated breaks in the walls, also the transverse surface area of the formers, and

b. the cells which grow in width may compress their neighbours, so that certain walls of these neighbour cells may grow less in width; this decrease in width is accounted for by the simultaneous longitudinal stretching of the walls due to the elongation of the elements concerned in the growing stem.

Both processes occur at the same time as a rule, as is shown in fig. 35. The decrease in width of walls may proceed so far as to

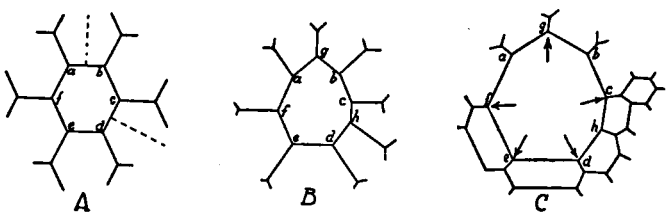


Fig. 35. Diagrammatic representation of the growth in width of an element of a primary vascular bundle.
A. A number of young initials of uniform size (only *abcdef* completely drawn).
B. Two additional angles are added to cell *abedef* by cell division in adjacent cells and the breaks of walls in these points *h* and *g* increase the surface area of the cell.
C. The cell *agbchdef* grows in width and compresses the adjacent cells in the direction of the arrows. See text.

make it possible that certain walls seem to disappear, as seen in transverse section, and additional cell contacts are formed (compare fig. 4). In all these growth processes sliding growth is not involved, as may also be concluded from the continuous presence of plasmodesmata in successive stages of development of the elements of a vascular bundle (e.g. in *Cucurbita Pepo*).

The shape of the sieve-tube elements and usually also the shape of the vessel elements differs from the shape of the tracheids, though they all have originated from procambium cells of uniform shape. During the differentiation of sieve-tube and vessel elements one of the terminal faces of a procambium cell — which mostly occur in fours — enlarges in a direction transverse to the long axis of the cell (i.e. transverse to the direction of the procambial strand), so that the longitudinal sections of the mature elements resemble parallelograms or trapezia. The enlarging end walls become sieve-plates and perforation plates respectively.

In primary vascular tissue tracheids are contiguous to shorter vessel elements. This is accounted for by a gradual transition from longer to shorter elements as described for sclerenchyma fibres (cf. fig. 34) and sometimes probably also by other means, which will be dealt with more fully in Chapter VIII (see p. 107, c).

CHAPTER VII

THE INCREASE IN GIRTH OF THE CAMBIUM AND THE SHAPE OF CAMBIAL CELLS.

A. *The increase in girth.*

KRABBE (94) himself did not mention sliding growth among cambial initials, though it had already been made very probable, that in certain cambia the average length of the initials continuously increases in an axis which has ceased elongating (SANIO 144, HABERLANDT 67). Later investigators (89, 125, 13, 24) were of the opinion that indeed sliding growth is involved in the changes occurring during the increase in girth of the cambium in an axis which has ceased elongating. KLINKEN (89) distinguished this supposed sliding growth of cambial initials as "intracambial sliding growth" from the so-called "extracambial sliding growth" which was supposed to occur during the elongation of differentiating cambial derivatives in the young secondary wood and young secondary bark outside the cambium.

As was already pointed out by BEIJER (24), several authors, after having studied a single or only a few cases of increase in girth, had

a turn for generalizing, so for instance NEEFF (125) and KLEINMANN (88). In order to avoid any confusion, it proves necessary to distinguish three different instances of cambial growth, viz.

a. The growth of the cambium in organs which are still elongating, so that the cambium elongates and grows in girth simultaneously. The cambia of young growing shoots, the cambia of storage roots (such as the roots of *Beta, Brassica, Phytolacca* etc.) and certain cork cambia, and, incidentally, most of KLEINMANN's objects belong here.

b. The growth of a non-stratified cambium in an axis which has ceased elongating. KLINKEN's, NEEFF's and some of BAILEY's objects show this type of cambial growth.

c. The growth of a stratified or storied cambium in an axis which has ceased elongating. BEIJER's principal object and some of BAILEY's objects show this type of growth.

Intermediate forms between the last two instances have been found and we shall, therefore, only deal with the extreme types. For further particulars on the intermediate forms we refer to BEIJER.

a. The origin of the cambium has been briefly discussed before (see p. 45). The cambium cells originate from procambium cells, from other meristem cells of the shoot apex (interfascicular cambium), or from parenchyma cells (phellogen, cambium of Monocotyledons with secondary growth). The growth in surface area of the cambial layer is brought about by an increase in number or in size of the cells, or by both. In a young cambium the cells elongate and grow in width as a rule, but the enlargement brought about hereby is by no means equivalent to the total increase in surface area of the cambium. Cell divisions account for the additional increase. It may be observed, that this manner of growth resembles the growth of a plate meristem, so that the cambial cells after a great deal of cell divisions enlarging the number of cells of the cambium layer, are still in contact with some six cells, as seen in tangential view. We refer here to the figures in KLEINMANN's paper. There is no indication, that the cells of these cambia show sliding growth. Breaks of walls frequently occur, but they are readily explained by symplastic readjustments, the cambium expanding in all directions in the tangential plane.

b. The growth of a typical non-stratified cambium was the subject of investigations carried out by KLINKEN (89), NEEFF (125), and BAILEY (13). SANIO (144) had already found that in successive annual rings of an old *Pinus* stem the average length of the tracheids continuously increases from the centre towards the periphery and finally becomes constant. The increase in length of the tracheids implies

that the average length of the fusiform initials has increased to the same extent. This was actually established by direct measurements of initials in cambia of different ages by BAILEY (11), who also found a growth in width of the initials. This elongation and growth in width of the initials is not the only way in which the cambium increases in girth. KLINKEN concluded from an investigation of successive sections of the mature phloem of *Taxus*, that the fusiform initials occasionnally divide transversely, after which the daughter cells elongate again and, after having reached the original length, divide anew, etc. According to KLINKEN, the new walls gradually alter their position during the elongation of the initials following their division, so that ultimately these walls have an almost vertical position. Meanwhile the daughter cells have been elongating, so that these cells, which were originally longitudinally successive are now placed side by side. These readjustments together with the increase in number and in surface area of the initials account for the increase in girth. KLINKEN noticed that not all fusiform initials elongate, but that a few of them grow less and may even completely quit the cambial zone, so that they cease being initials and their derivative radial rows of elements of wood and secondary bark end. As a result of the elongation of most initials and the disappearance of others, additional cell contacts may be formed.

The method employed by KLINKEN was described before (see p. 22). It has the difficulty, that the extracambial changes which may have had some influence on the shape of the mature cells are also registrated. This is the reason why PRIESTLEY (136) criticized results obtained by this method. As was pointed out by BEIJER, the tangential surfaces of the cambial cells are not changed appreciably, when differentiating into elements of xylem or bark without showing considerable extracambial elongation. By a proper choice of the objects and by studying secondary xylem instead of secondary phloem it may be avoided that these and other (secondary) changes, such as dislocations associated with the unequal tensions caused in the bark by the secondary growth, trouble the investigation. The method is, therefore, certainly very useful in certain cases for the study of the changes in intercellular relationships of cambial cells. From the changes observed in successive sections of a radial row of wood or phloem elements the alterations of the initials of that row can be reconstructed, for every cell in the secondary bark or secondary wood represents so to speak a "snapshot" of the form of its initial at the time when it formed that cell of the secondary bark or secondary wood. A cell which lies farther from the cambium corresponds with an earlier stage of the cambium cell than a cell which lies closer to the cambium.

When applying this method the conception of the term "initial" is not to be taken too strictly (i.e. in SANIO's sense), because no constant single initial can be discerned, for there are more cells of a radial row of cambial cells which are able to divide tangentially (RAATZ 138, SCHOUTE 149). According to SCHOUTE, one of these cells or one of its daughter cells usually remain in the cambial zone. Though no constant initial can be distinguished, it does not matter so far as KLINKEN's method is concerned, because all cambial cells of a radial row have practically identical tangential surfaces.

KLINKEN's technique was applied by NEEFF to the secondary xylem of Dicotyledons (e.g. *Tilia*) and by BEIJER (see *c*). BAILEY's investigations of the increase in girth of cambia were probably carried out in the same way. NEEFF and BAILEY confirmed and extended KLINKEN's observations. BAILEY demonstrated that the transverse wall by which a fusiform initial divides, which was supposed to have a horizontal position by KLINKEN, has already a slightly oblique position at its formation, which had, properly speaking, already been noticed by RAATZ (138).

The various investigators all came to the conclusion, that in the elongation of the initials sliding growth is involved. Certain facts contradict this conception however. The (double) radial walls of the cambium [1]) are not of uniform thickness, but show a series of thicker and thinner places. This peculiar structure, which is of general occurrence (cf. 95, 86) has been known for a long time and was already figured by DE BARY (36), STRASBURGER (158) and others (140, 145). The thickenings are caused by local thickenings of the middle lamella; they often disappear during fixation. The thin intervening places are the so-called primary pit-fields. They are comparable to some extent with pits. On the ground of what has been said of the changes which are to be expected in pitted walls if sliding or intrusive growth would occur, it may be concluded that walls containing primary pit-fields cannot be split by a process of sliding or intrusive growth, so that no sliding growth on the radial walls of cambial cells takes place, as otherwise the primary pit-fields would be separated into two non-corresponding halves, which has never been observed.

In the radial walls of cambial cells plasmodesmata are present (cf. 74, 75, 160), which are concentrated in the primary pit-fields as a rule (86). Their presence also indicates that no mutual slip of radial walls takes place.

The possibility still seems to exist, however, that the cambial cells

1) With "radial" walls is meant: all non-tangential walls. The term "radial wall" should not be understood too literally, the position of most walls not being exactly radial, but more or less oblique.

slide on the tangential walls, for in the tangential walls no primary pit-fields or plasmodesmata are found, so that we cannot use the above arguments against sliding growth. In the case of sliding growth on the tangential surfaces, a shift of radially successive cells might be expected, so that the radial files of cells in the cambium would be broken, which is never the case (see p. 45). Moreover, it is unlikely that growing cambial cells do not slide on their radial walls, but do so on their tangential walls, since the initials can only elongate by a growth of both radial and tangential walls. Lastly, radial rows of trabeculae may be present in the cambium, which again indicates that no relative shift of radially successive cambium cells can possibly occur.

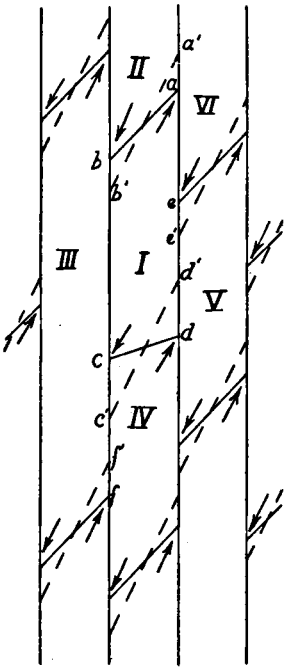


Fig. 36. Diagrammatic representation of the elongation of the fusiform initials of a non-stratified cambium as seen in tangential view. Full lines: younger stage, broken lines: after elongation of the initials (see the arrows). Explanation see text.

Intrusive growth is not likely to occur either, since also during intrusive growth a splitting of cell walls and its implications (though restricted to the ends of the cells) are to be expected.

All changes in intercellular relationships among the cells of the cambial zone must therefore be explained without assuming sliding or intrusive growth. These changes come about very gradually. KLINKEN showed, that the daughter cells of a transversely divided initial of *Taxus* in five years (i.e. after the formation of five annual rings) again reach the original length of the mother cell. This is also indicative of a gradual readjustment of the cell pattern by symplastic growth.

The elongation of cambial initials is represented diagrammatically in fig. 36. The cells are drawn as parallelograms, but the alterations are brought about in the same fashion, if the cambial cells are of a different shape (see this chapter, B). The cell *abcde* is supposed to have just been derived from a radial-transverse cell division (along *cd*) and elongates, as all fusiform initials usually do, in the direction of the arrows. The point *a* moves upward and arrives at *a'*, and so *d*

arrives at *d'* and *f* at *f'*; the points *b* and *c* move downward to *b'* and *c'*. The radial walls *ae*, *ab* and *cd* elongate. The radial walls *de* and *ef* grow less in vertical extent, however, which does not inevitably imply sliding growth, but is accounted for by the appreciable radial elongation of these walls due to the continuous growth of the cambial cells in radial direction (cf. p. 75). The growing less of cell walls in vertical direction by a simultaneous radial elongation may be observed in a direct way in the differentiating secondary wood ray of *Pinus*. The radial walls of ray initials passing into ray tracheids become elongated in radial direction and at the same time grow less in height, so that their mature height amounts to only 64 per cent. (in the early wood) to 80 per cent. (in the late wood) of the height of the corresponding ray initial (see **122**). A radial wall of a cambium initial may grow so less in height, that ultimately two *Zwickel* come in contact and additional contact faces are formed, whereas other cells become separated without sliding of cells or real splitting of cell walls (compare Chapter III). In this way all reported instances of intracambial sliding growth may be handsomely explained without sliding or intrusive growth. The occasional decrease in length and eventual disappearance of initials (JOST **83**, KLINKEN) is explained by a gradual decrease of all radial walls in vertical extent; the fusion or splitting of rays (**89**, **21**) is explained by the establishment of additional cell contacts by deformation of fused *Zwickel*; other phenomena, such as the alteration of the position of the long axis of the fusiform initials (NEEFF **126**, TUPPER-CAREY **166**) are all explained in the same manner.

c. The increase in girth of the so-called stratified cambia was studied by BAILEY (**13**) and later elaborately by BEIJER (**24**). The latter gave an excellent survey of the literature on the subject and made out definitely, that in the typical stratified cambium no intracambial elongation of the fusiform initials takes place when the axis has ceased elongating and that the divisions enlarging the number of initials in the tangential plane are placed almost vertically, thus accounting for the stratified character of the cambium. We, therefore, leave out the details and refer to BEIJER's paper, and shall solely consider the point, whether sliding growth is involved in the increase in girth, or not. The only reported instance of sliding growth in stratified cambia originates with BEIJER. On account of the arguments mentioned above (primary pit-fields, plasmodesmata, trabeculae) it is not likely that sliding growth plays a part in the changes in intercellular relationships. BEIJER thought that the breaks occurring in the walls in consequence of the formation of additional radial-longitudinal walls and the concomitant growing less of certain

radial walls are indicative of sliding growth. In fig. 37, which is copied from fig. 12 of BEIJER's paper, a radial-longitudinal cell division is represented in tangential view. The wall *ab* grows shorter. As was explained above, this decrease in height of the wall is accounted for by the growth of the cambium initials in radial direction; the breaks are merely a consequence of the forces in the stretched wall resembling surface forces, so that the walls, as seen in tangential section, conform to ERRERA's rule and tend to form 120° angles (in fig. 37 in the new angles *a* and *b*), as was already understood by BEIJER himself. The splitting and fusion of rays is explained in the same way as in non-stratified cambia (see *b*).

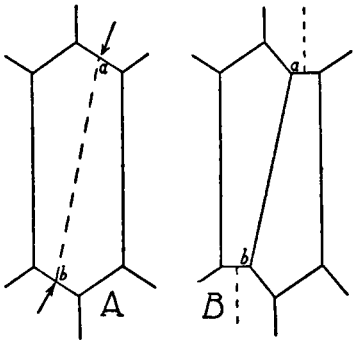


Fig. 37. Diagram of the formation of a new radial-longitudinal wall in a fusiform initial, of a stratified cambium as seen in tangential section (after BEIJER). In the points *a* and *b* breaks of walls occur, so that the distance *ab* grows less. Explanation see text.

Our final conclusion is, that sliding growth or intrusive growth is not involved in the increase in girth of any type of cambium.

B. *The shape of the initials.*

For the present in this paragraph only those cases will be dealt with, where fusiform initials are exclusively contiguous to other fusiform initials.

The shape of the initials is originally determined by the following points:

1. the shape of the original mother cells of a cambium (procambium, apical meristem and parenchyma cells);
2. the growth of the cells in radial direction and the formation of parallel tangential walls, resulting in the formation of radial cell columns;
3. the radial pressure to which cambial cells are subjected and which is probably responsible for their radially flattened form;
4. the elongation of the initials in the growing organ (*a* on p. 91).

These four account for the elongated hexagonal prismatic shape of the initials and an average number of fourteen contact faces, compare p. 47, p. 89 and p. 91. Meanwhile the number of cells in the cambial layer is increasing by

5. the cell divisions in the tangential plane.

The largest cells divide first and the smaller cells grow only, and, since in the tangential section usually three cells meet in a point, LEWIS' rule may be applied (see p. 44), so that the average number of sides per section remains six and the fundamental shape of the initials remains a hexagonal prism.

In the cambia additional cell contacts are formed and other cells are separated, so that

6. the number of sides in a tangential section is increased by two at every additional contact, but at the same time this number is reduced by two by the separation of two other cells, so that the number of sides per tangential surface still averages six.

The fundamental shape of the initials is therefore a hexagonal prism with on the average fourteen contact faces in all stages of development which was already gathered from direct observations of cambial cells (see p. 47). The tangential surfaces are elongated, often irregular, hexagons. In Conifers and in certain Dicotyledons with long fusiform initials (such as *Hamamelis*) the tangential faces are more or less linear-lanceolate (fig. 15D) — this is the form attributed to cambial cells by KLINKEN. The tangential faces of the shorter initials of most Dicotyledons are usually shaped like a parallelogram (fig. 35) — this is the form attributed to cambial cells by KRABBE (**94** p. 44). The shape of the fusiform initials of stratified cambia is represented in fig. 15A and fig. 39A. This form is to be considered the fundamental form of all fusiform cambium cell, because the other forms are modifications of this shape and because it shows the hexagonal prismatic shape best (KLEINMANN 88, PRIESTLEY **136**, LEWIS **105**).

Though cambial cells may originate from cells "in prosenchymal orientation" (procambial cells), as well as from cells "in parenchymal orientation" (apical meristem cells, parenchyma) — cf. LEWIS (**104**) —, the fusiform initials of the cambia producing xylem and bark usually have acute bevelled ends above and below (fig. 15A-F, fig. 36, fig. 39A). This is brought about by the position of the additional radial walls being almost vertically placed, either at the moment of their formation (in a stratified cambium) or after elongation of the initials (in a non-stratified cambium).

Now we shall take the presence of ray initials into consideration. The height of a ray in the cambium may be relatively small if compared with the length of the fusiform initials. In this instance the contacts of the fusiform initials with ray initials may be left out of regard, so that the shape of the fusiform initials may still be compared with the fundamental shape (*Taxus*, *Pinus*). Sometimes the ray

initials form an important part of the surface area of the cambium, so that their contacts with the fusiform initials are not negligible and the shape of the fusiform initials is irregular.

The average number of fourteen contact faces is not found in all cambia. The long fusiform initials of Conifers and certain Dicotyledons show a complication which causes a higher number of faces. KLINKEN established that in the yew the ends of the tracheids are bent inward toward the centre of the tree. The same condition was found in the white pine by LEWIS, who showed that this bending is already present in the cambium cells. The most probable explanation of this bending of the cells is the following: The cambial cells are originally bounded by parallel tangential walls and are therefore of uniform radial width, but their differentiating derivatives forming xylem expand more in their middle parts, which later form the central shafts of the tracheids, than at their extremities, which will form the wedge-shaped tapering ends of the tracheids. Since the dilation of the elements can only take place toward the periphery, the middle parts of differentiating cambial derivatives must buckle outward. These middle pieces will therefore be moved outward the difference between the dilation of the middle part and the terminal parts of the differentiating xylem elements so that the cells become bent. The effect of this bending of the tracheids, as seen in radial section, is, that the cambial cells also become bent. The overlapping ends of the cambial cells cross one another, so that the longitudinal edges bounding the radial walls are no longer parallel, but intersect one another, and more facets are formed. In a space-filling arrangement of elongated tetrakaidekahedra in prosenchymal orientation prolonged bending produces successively 18-hedra, 22-hedra, 26-hedra etc., the numbers of faces increasing in fours. In the actual less regular arrangement in cambium and wood the bending produces a continual increase of *some* four faces (**105**).

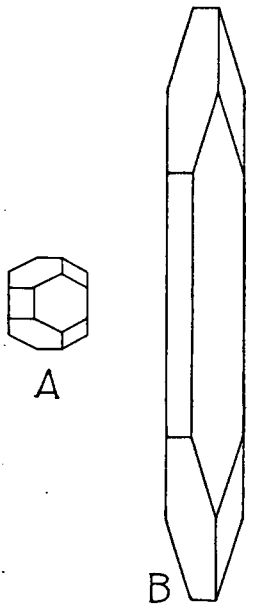


Fig. 38. Derivation of the fundamental shape of prosenchymal cells (B) by the elongation of an orthic tetrakaidekahedron with a horizontal edge above and below in the highest and lowest position (A). After LEWIS 1935.

The formation of the curved ends comes about little by little in

the development of the cambium by a gradual bending of the cells, resulting in a gradual crossing of the overlapping cell tips and the formation of additional faces when new tangential walls are formed. It has therefore nothing to do with sliding growth.

The modified shapes (18-hedra, 22-hedra, etc.) are only transformations of the fundamental 14-hedral shape and for the sake of convenience we shall, therefore, only consider the tetrakaidekahedral shape in the following chapter.

CHAPTER VIII

THE DEVELOPMENT OF THE ELEMENTS OF SECONDARY XYLEM AND SECONDARY BARK.

We shall start with a discussion of the less complicated instances, viz. the development of the elements in the stems of Gymnosperms without vessels (e.g. *Pinus*), whereas the objects showing a more differentiated type of wood and secondary bark will be subjected to an analysis later on.

It is generally assumed that the cambial cells differentiating into tracheids or libriform fibres show apical growth (**124**, **65**, **155**). This implies that, if traces of sliding or intrusive growth might be found, they are to be expected at the tapering ends of the cambial derivatives. In *Pinus* most bordered pits are found at the ends of the cells. These bordered pits originate in the primary pit-fields. The successive stages of their formation are found in the radially successive elements of the differentiating young xylem. The thickenings of the cambial walls separating the primary pit-fields may disappear, but part of them are persistent and their vestiges found as crassulae in the mature tracheids. These cell wall structures can all be made more clearly perceptible by a proper staining of the wals, for which we used *a.* chloriodide of zinc, *b.* iodinepotassium iodide and sulphuric acid and *c.* haematoxylin DELAFIELD after a previous short treatment with Eau de Javelle and subsequent thorough rinsing; the latter stain allows dehydration and preservation in glycerol for a permanent mount.

The development of bordered pits and crassulae was already described and figured long ago by SANIO (**145**), STRASBURGER (**159**) and RUSSOW (**140**), we, therefore, refer to these authors. As for our purpose, it is only of importance that the thicker and thinner places of the radial walls remain intact throughout the development of the tracheids.

The plasmodesmata, which mostly occur in the primary pit-fields (86), do not disappear until the living contents of the cell has died, that is only after the growth of the cell has ceased, and the thickenings of the cambial walls persist as crassulae, so that the (double) radial walls are not split and the cells do not slide on their radial walls when elongating. Now that sliding or intrusive growth on the radial walls is out of the question, a sliding on the tangential surfaces might still occur. The growth of the cells can only come about by a growth of both tangential and radial walls however. Since radial walls facing one another do not show any relative displacement, the tangential walls do not either. This is substantiated by the fact that rows of trabeculae, which are precisely radially placed, may be present (RAATZ 138, NORDHAUSEN 127), so that the cells of a radial row possessing trabeculae cannot possibly have been sliding on their tangential faces.

A local (apical) sliding growth or intrusive growth of wood elements, as suggested by NEEFF (124), GROSSENBACHER (65), and SINNOTT and BLOCH (155), is unlikely for the same reasons.

The ray cells also do not show sliding growth, either mutually or on adjacent tracheids, during development, for the ray cells are connected by plasmodesmata, and have pits which correspond with pits of contiguous ray cells or tracheids and which have originated from primary pit-fields.

Now the difficulty presents itself, that the development of the shape of the mature tracheids from the shape of the fusiform initials has to be explained without assuming sliding growth. We shall, therefore, at first establish, what changes a cambial cell differentiating into a tracheid undergoes and then give an interpretation of the facts which is in accordance with the theory of symplastic growth. These changes are (cf. fig. 1 and fig. 39):

1. the cell elongates,
2. the ends of the cells grow more acute, so that the typical, prosenchymal shape with two long tapering points is brought about, and
3. the original, almost rectangular, transverse section of the cell becomes more or less hexagonal by breaks of walls, except at the tips of the cells where additional breaks of the wall produce tetragonal transverse sections (see below).

The more or less hexagonal form of the cross section is brought about by the action of forces resembling surface tension forces, resulting in the formation of 120° angles of intersection (cf. p. 60). The originally radial walls grow considerably in width, whereas the tangential walls grow less (cf. figs. 1 and 2, and p. 24). This decrease in width of the tangential walls, which was considered substantial

evidence for sliding growth (transversal sliding growth) by KRABBE, is explained by the simultaneous longitudinal stretching of the tangential walls caused by the elongation of the cell.

The changes occurring in longitudinal direction are less easy to explain. In fig. 39, in which is assumed that no bending of the cell tips has taken place, a cambial cell and a derivative tracheid are represented in corresponding positions. The number of contact faces does not change during differentiation. Every face of the cambial initial can be found back in the mature tracheid and we shall now consider the changes of each wall separately.

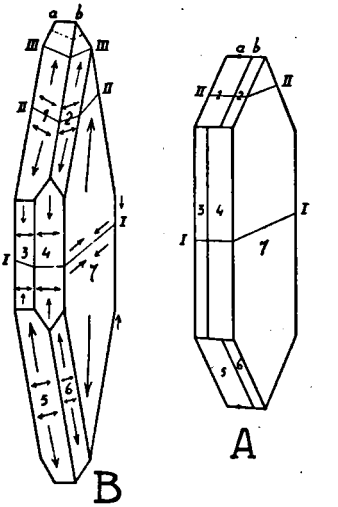


Fig. 39. A. Diagram of the fundamental shape of fusiform cambium initials. B. Diagram of the fundamental shape of tracheids and libriform fibres in corresponding position.
1, 2, 3, etc.: corresponding facets, I, II and III (thin lines): transverse sections corresponding with the sections represented in fig. 40. Arrows: directions of the growth of the faces.
Length foreshortened some 50 times.

During the elongation of the differentiating cambial derivatives the originally radially placed, oblique end walls (1, 2, 5, 6 and the corresponding facets on the opposite side: 8, 9, etc.) elongate as well, at the same time assuming a steeper position (cf. MISCHKE 122). Since sliding growth does not occur and these walls belong to two adjacent tracheids growing in opposite directions, the oblique walls grow at both ends and their middle parts do not show a relative displacement except for the steeper position. In consequence of the elongation of the oblique faces 1, 2, 5, 6, etc., the faces 3, 4, and the corresponding faces (10, 11) decrease in vertical extent. This is accounted for by the simultaneous growth in width of these walls in radial direction. The total extracambial elongation of the tracheids of *Pinus sylvestris* amounts to 20 per cent. of the length of the cambium initial. The elongation at the apical ends of the oblique walls (1, 2, 5, 6 etc.) amounts to half that amount, as seen in vertical projection, or 10 per cent. and, because these faces elongate at both ends, at their other ends also amounts to 10 per cent. In vertical projection the decrease in length of the vertical walls 3, 4, 10 and 11

therefore amounts to the total elongation of the cambial cell, that is much more than 20 per cent. of the length of the walls 3, 4, etc. The growth in width of the vertical walls is usually very considerable and may amount to several hundreds per cent., so that, if we assume, that the rectangular faces (see fig. 39A) remain rectangles, the total surface area of these faces does not grow less. In *Pinus Strobus* the extracambial elongation of the tracheids is less, viz. 5 per cent. (**105**) and consequently the decrease in length of the vertical walls is also well accounted for by the radial growth in width of these walls. We shall see later on, that in cases in which the extracambial elongation of wood elements is much more important than in Conifer wood more complications are involved and that the elongation of the oblique end walls is not only accounted for by the radial growth, but also by changes in position of certain edges.

The remaining walls, i.e. the tangential walls (7 and 14 in our diagram) elongate and grow less in width simultaneously (see p. 24) but since they are bounded by elongating faces (1, 2, 5, 6) as well as by faces growing shorter in vertical extent, a change in form takes place moreover. The vertical edges grow shorter and the oblique ones elongate. This remarkable change can be imitated in experiments (see Chapter X).

The breaks of walls occurring in the development of the tracheids transfer the straight horizontal edges (such as the edge through *ab* in fig. 39A) into broken lines. This accounts for the transverse sections of the apex becoming tetragonal, as may be seen from the comparison of fig. 39B with fig. 39A and fig. 40B with fig. 40A.

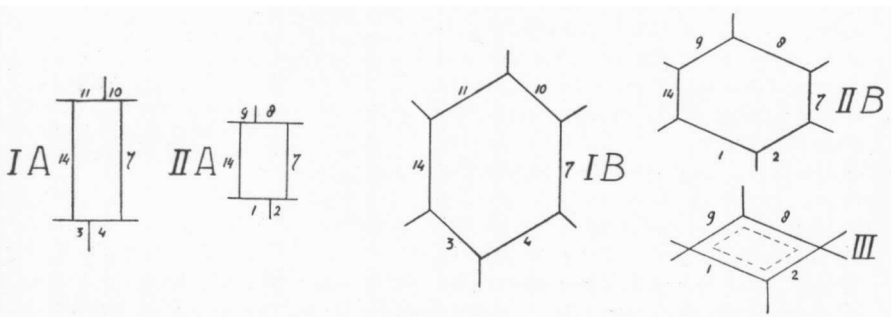


Fig. 40. A. Transverse sections of the fundamental shapes of fusiform cambial initials (left) and B of the fundamental shape of derivative elements (right), corresponding with sections made at the levels I, III and III in fig. 39. The broken line in fig. III corresponds with the section made at a level between III and *ab* in fig 39B (also represented by a broken line there). 1, 2, 3, 4 etc. are the facets corresponding with the faces in fig. 39.

This change is associated with elongation, so that during the differentiation of young wood these (usually tetragonal) tips seem to slide in between other cells. This is peculiar to differentiating wood and was one of the most important arguments for "longitudinal sliding growth" mentioned by KRABBE. As appears from the preceding, it may be satisfactorily explained without assuming sliding growth.

Actually, the tips of the tracheids of *Pinus* are bent and the cells less regularly shaped than represented in our diagram, but otherwise the explanation of the differentiation of a cambial initial into a tracheid by symplastic transformation is quite the same.

The differentiating sieve-tube elements of *Pinus* do not show an appreciable extracambial elongation. Accordingly, the width of their tangential faces is but little smaller than the width of the tangential walls of the cambium cells by lack of longitudinal stretching and the transverse sections of the sieve-tubes remain more or less rectangular.

After appropriate staining (see above) it may be noticed that the sieve-plates originate in places where primary pit-fields were present and that the protoplasmic strings connecting the contents of adjoining sieve-vessel members through the perforations of the sieve-plates originate from the plasmodesmata by an enlargement of the pores in which the plasmodesmata lie (HILL 74). This has been found in other objects as well (75, 123) and is probably of very common occurrence. Radial rows of trabecula have also been found in the phloem (138). Together with the above arguments this is clear evidence that no sliding growth of the sieve-tube elements takes place.

At both ends of a differentiating sieve-tube element one of the oblique end walls (one of the faces 1, 2, 5, 6 etc.), growing considerably in width, forms a large sieve-field, whereas the other oblique walls grow but little in width, the elements thus assuming the shape of an elongated parallelogram or an elongated trapezium. The enlargement of the sieve-field is accounted for by the radial dilatation of the differentiating phloem cells.

The above-mentioned arguments against sliding growth or intrusive growth in differentiating secondary wood and secondary bark of *Pinus* are also valid in the following objects.

Most probably the developments of the elements of secondary wood and secondary bark in other Conifers is much the same as in *Pinus*. At least no essential differences with *Pinus* could be noticed in the objects studied (*Picea*, *Taxus*). So it is in *Drimys Winteri*; though the structure of its secondary bark is more complicated, because fibres are present (see below).

The mode of development of the secondary xylem of *Ephedra* show the same particularities, but, vessels being present, there is a complication. The mature vessel members differ in length from the tracheids and, as seen in transverse section, are in contact with more cells than the cambial initials from which the have been derived, so that the number of cell contacts in a transverse section apparently has multiplied during vessel differentiation. This increase in cell contacts is more pronounced in the highly specialized secondary wood of many Dicotyledons (e.g. in *Populus*, *Quercus*, *Robinia*). A wood vessel member may ultimately be contiguous to a great deal of cells, e.g. in *Quercus* to up to 40 as seen in a transverse section, but even if the number is not as large as that, it is usually still larger than the total number of cell contacts of the vessel initial. Now it has to be made out, whether this increase in number of cell contacts must be explained by sliding growth or not (cf. p. 26).

As KRABBE already noticed, in certain instances (e.g. in *Salix* and *Populus*) tangential divisions occur far into the differentiating region of young wood. This was later used by NORDHAUSEN (127) to argue that sliding growth does not play an important part in the development of wood vessels. NORDHAUSEN's conception is, that a young vessel member grows in width, whereas the adjoining cells go on dividing tangentially, thus increasing the number of contacts of the vessel member. In certain cases tangential divisions do not occur in the young wood, however, but only in the cambium proper, as is the case in *Quercus*, so that NORDHAUSEN's argument is of no use.

More important is that in wood vessels trabeculae may occur (127, we found this condition for instance in *Ephedra*) and that in the walls between vessel initials and adjacent initials primary pit-fields (and consequently in the mature state pits) and plasmodesmata may be present.

In the structurally highly differentiated woods, such as *Quercus* and *Robinia*, a marked difference in length between vessel members and libriform fibres is found and sometimes the libriform fibres establish additional contacts with libriform fibres of a higher or lower level (see fig. 8). At first sight both facts seem indicative of sliding growth. Since sliding or intrusive growth does not occur, however, the following items have therefore to be explained without assuming that mutual slipping of cells or a splitting of cell walls along their common middle lamella takes place:

a. the formation of additional contacts between elongating libriform fibres,

b. the increase in number of cell contacts of a differentiating vessel member, and

c. the occurrence of long libriform fibres next to short vessel members. We shall discuss these points consecutively.

a. It appears that, generally speaking, the development of libriform fibres and congeneric elements (fibre tracheids and longer tracheids) in the secondary wood of Dicotyledons is much the same as that of *Pinus* tracheids. The only difference is that in certain cases in Dicoteledonous woods additional cell contacts may be established, either with elements of the same kind, or with a vessel (see *b*). If interpreted in our diagram of fig. 39, the formation of additional contacts comes about by a further elongation of the oblique end walls 1, 2, 5, 6, etc. (as compared with *Pinus*), until these walls come in contact. This implies that ultimately certain vertical faces (3, 4, etc). loose a vertical edge, because these faces themselves cannot disappear. The outline of these faces changes thereby. A rectangular face like 3 in fig. 39 is transformed into a triangular face, a hexagonal face like 4 into a pentagonal one, etc. It has been shown, that, when certain walls grow, certain bounding edges may grow shorter (in our diagram the vertical bounding edges of the tangential surfaces 7 and 14). It need only to be assumed, that this symplastic transformation continues till an edge had grown so short that two *Zwickel* come in contact (in the cambium and adjacent young tissues the *Zwickel* are well developed). After a fusion and subsequent deformation of these *Zwickel* (see p. 75) a new contact is established without a splitting of primary pit-fields in non-corresponding halves, a rupture of plasmodesmata or a derangement of the trabeculae having taken place. These new contacts may enlarge and form walls of considerable size. The new walls are formed at the tips of the cells and this perfectly agrees with the fact, that in the tips of long libriform fibres no pits occur; apparently because the pits of wood elements generally form in primary pit-fields, which are not formed in the additional walls.

So far as no additional contacts are formed, the fundamental shape of libriform fibres and congeneric elements is that of an orthic tetrakaidekahedron in prosenchymal orientation (fig. 38 and 39), usually with bent tips as in *Pinus* and with more than fourteen (some 18 or 22) faces. Formation of additional contacts makes the shape much more irregular, so that it cannot be derived from a transformed orthic tetrakaidekahedron. Another change which is often brought about by the elongation of differentiating cambial derivatives is, that the decrease in length and ultimate elimination of certain edges causes an alteration of the position of certain horizontal edges into an oblique position. The foreshortening of the vertical edge between faces 3 and 14 in fig. 39B, the other vertical

edge remaining of considerable length, would cause a slanting position of the horizontal edges of face 3 and consequently of the adjoining faces (1 and 5) of the figure, and, in a space-filling arrangement of these figures, also of the terminal horizontal edges of adjacent figures. One of the two terminal vertices at each end of the cell would move farther downward or upward than the other one, e.g. the vertex *b* in fig. 39B farther than the vertex *a*. The position of *ab* would become oblique and, after continued elongation, the wedge-shaped extremity would change into a tapering tip ending in a point instead of an edge and bounded by three faces instead of four, which is indeed the general form of the tips of long libriform fibres. By the formation of additional cell contacts new faces may be added to the ends of the cells, but the acute shape is not changed thereby.

In macerated wood regularly a few branched libriform fibres are found (143). The forked ends of cells are often considered clear evidence of sliding growth, but a different explanation is possible (136). By the mutual compression of the expanding young wood elements the chisel ends of young libriform fibres (which are shaped as in fig. 39B) may obtain a receding angle at their apex, so that two apices are formed, which may elongate symplastically and form a tapering tip. This of course requires considerable elongation and, accordingly, in woods where but little extracambial elongation of wood elements occurs (e.g. in Conifers) no forked tips are found.

NEEFF (124) thought he had actually observed that growing libriform fibres separate the cells placed above and below them along the middle lamella (see p. 35). He gave figures showing libriform fibre walls with single pits which were supposed to have been derived from pit-pairs by splitting (cf. fig. 26). These figures are undoubtedly founded on incorrect observations or false interpretations of the sections NEEFF had in study. The elongating elements of secondary wood do not yet possess secondary thickenings of their walls and, therefore, cannot possibly possess true pit-pairs. It might be imagined that NEEFF observed a splitting of primary pit-fields — being the only thickenings present — but as we have already communicated, such a splitting never occurs. More probably NEEFF drew his figures from sections of parts of the young wood already possessing secondary thickenings and pit-pairs, i.e. of elements which has completed their elongation. We have often observed similar figures in longitudinal sections of mature libriform fibres; it appears from careful observation, that the "splitting" of pit-pairs is never real and has to be ascribed to bad focussing or to obliqueness of the sections. NEEFF's so-called "direct observation of sliding growth" therefore proves to be wrong.

b. The increase in number of contacts of a vessel member comes about as follows: certain cells adjoining a vessel initial are deformed by the expansion of the young vessel element, so that certain walls of these cells, viz. those which are placed transverse to the walls of the vessel initial, grow shorter as seen in a transverse section (cf. fig. 4). This is accounted for by the simultaneous elongation of these walls, for the libriform fibres are still elongating in this stage of development. When the walls decrease in width to such an extent, that two *Zwickel* adjoin and subsequently fuse, an additional contact of vessel and other cells originally not adjacent is established (fig. 4C). It is clear, that, being the only elements showing considerable elongation, only libriform fibres, fibre tracheids and longer tracheids adjoining a wood vessel have walls which may grow less in width appreciably. Ray cells grow practically in radial direction only, so that the tangential walls of rays do not grow less in width as seen in transverse section. Rays are, therefore, never broken by the elimination of tangential walls by expanding vessels, but sometimes the pressure of the wood vessel is so high that the rays are curved near the vessel, or that disjunctive ray cells are formed.

At the formation of additional contacts by a growing wood vessel certain other cells become separated. Since tracheids mostly do not elongate so much as the libriform fibres, the separation may be incomplete and disjunctive tracheids formed.

As a rule, no pits occur in walls formed by enlargement of additional cell contacts between a vessel and other xylem elements (**136**). Hence pit-pairs often form in the walls between a vessel and an adjoining ray cell, but seldom in the walls between a vessel and adjoining libriform fibres.

c. The occurrence of long libriform fibres and shorter vessel elements in the wood is accounted for in several ways. Firstly, a gradual transition from a wood vessel member to longer elements may occur by means of cells (or cell strands derived from a single fusiform initial) of intermediate size (cf. fig. 34), viz. by means of vasicentric or paratracheal wood parenchyma strands, by means of short so-called vasicentric tracheids, which are often found next to vessels, e.g. in *Albizzia* (**159**, p. 170) and *Robinia*, or by means of shorter libriform fibres. In the same way, i.e. by means of cells of intermediate sizes, we must explain the transition of wood parenchyma strands or fusiform wood parenchyma cells (which show no appreciable extracambial elongation) to the longer libriform fibres (which show considerable elongation), the transition of early wood having longer to late wood having shorter elements (as is the case in *Pinus*), the transition of the last formed late wood elements to the

resting cambium (often the outer layer of the late wood is a ring of terminal parenchyma consisting of short strands) and, finally, the transition of the fusiform initials of an active cambium to the mature wood elements.

A second possibility is, that a fibre having only a single wall adjoining a vessel element does not grow at both sides to the same extent. The wall contiguous to the vessel may elongate but little, while some other walls facing fibres, may elongate appreciably. These differences in length of walls are, of course, much more important than the slight differences in length occurring in the case mentioned in *a*) and represented in fig. 34.

A third possibility has to be assumed in those cases in which libriform fibres are contiguous to two or to three superimposed vessel members and yet have elongated much more than a vessel element. It has been pointed but before (p. 102) and it has been represented in a diagram (see fig. 39), that in the differentiation of a libriform fibre elongation of certain (vertical) radial faces and decrease in vertical extent of other (oblique) radial faces is involved. The faces of vessel member initials adjoining the radial faces of libriform fibres also elongate and grow less respectively, so that the vertical radial walls of a vessel member initial grow less in vertical extent and the oblique radial walls elongate. As is the case in growing libriform fibres, some vertical edges grow less in length, which involves a multiplication of the number of cell contacts, as seen in transverse section, during vessel differentiation, for the elongating faces occupy a greater part of the length of the vessel element. Ultimately certain vertical edges may completely be eliminated, while libriform fibres gain contact with fibres of a higher or a lower level, causing a further increase in lateral contacts in a transverse section. A vessel member limits the elongation of the libriform fibres tangentially contiguous to it, because the elongation of the tangential faces of the vessel member is unimportant.

As a rule, a combination of these three possible methods of growth accounts for the differences in length brought about during the differentiation of the wood.

By the various changes the shape of a vessel member is so much transformed that the original shape of the cambial initial cannot be recognized in it any longer and that it cannot be derived from the basic tetrakaidekahedral shape. The two perforation plates enlarge considerably during the differentiation of the cell, assuming a horizontal or slightly oblique position, the originally radial walls of the cambial mother cell elongate and assume a steeper position, and the original vertical walls of the cambial mother cells remain vertical,

so that the shape of the vessel members ultimately becomes more or less cylindriform.

In the secondary bark of Dicotyledons, as in the secondary wood, a differentiation of the elements is present. Short sieve-tube elements and parenchyma strands having about the original length of the cambial cells are found next to much longer sclerenchyma fibres. Since sliding growth must be excluded on the same grounds as mentioned for elements of secondary wood (see p. 100), the explanation of the occurrence of long and short elements is the same as in the case of wood vessel members and libriform fibres (see p. 107).

The fundamental shape of parenchyma strands and fusiform parenchyma cells of secondary wood and bark, and of the sclerenchyma fibres in the secondary bark is the elongated tetrakaidekahedron in prosenchymal orientation (fig. 38B, 39B), except when additional contacts have been formed.

The cells of a uniseriate ray are adjacent to two radial rows of cells of the same ray — except the marginal cells which are contiguous to a single row — and to two rows of elements derived from fusiform initials (and consequently belonging to the so-called vertical cell system), such as libriform fibres, tracheids, vessels sieve-tubes and parenchyma strands. The shape of a cell of a uniseriate ray is, as seen in tangential section, rectangular or square, except that of a marginal cell which is more or less triangular. The cells are for the most part elongated in radial direction and appear in radial section as rectangles. Their shape is, therefore that of a tetragonal or trigonal rectangular prism placed with its axis in radial direction.

The radial dimensions of ray cells surpass those of the cells belonging to the vertical cell system. The number of cell contacts formed by a ray cell and the cells of an adjoining radial row of ray cells amounts to two as a rule, for the ray cells are formed by independant divisions of adjacent initials, whereas the number of contacts formed by that ray cell and the cells of an adjoining radial row of elements belonging to the vertical cell system is usually more than two, the ray cells having greater radial extent. The horizontal walls of a ray cell are, therefore mostly facing two cells each and the radial-longitudinal walls more than two each, so that their shapes are irregular and cannot be derived from an orthic tetrakaidekahedron by continuous transformation.

The cells of a multiseriate ray are either adjacent solely to other ray cells (the central cells of the ray), or to ray cells and cells belonging to the vertical cell system (the peripheral cells of the ray).

The central cells of a multiseriate ray show the same arrangement as other parenchymatous cells originating from cambia (see p. 70) and their fundamental shape is, therefore, the orthic tetrakaidekahedron. Having been expanding expanding in radial direction only, they are shaped like a hexagonal prism, however.

The contact faces of the peripheral cells with the cells of the vertical system show the same arrangement as in a uniseriate ray. Their shapes are there fore irregular and cannot be derived from the basic tetrakaidekahedral shape.

CHAPTER IX

THE DEVELOPMENT OF THE ELEMENTS OF SECONDARY VASCULAR BUNDLES IN MONOCOTYLEDONS WITH SECONDARY GROWTH.

In this chapter the development of the secondary tissues will be considered only in relation to sliding growth. For any further details we refer to SCOTT and BREBNER (153) and to CHEADLE (32). In our investigation we used *Dracaena* hybr., *Cordyline australis* and *Aloë arborescens.*

The cambium in Monocotyledons with secondary growth consists of small cells, which appear in tangential section as in fig. 16 III. These cells form parenchyma as a rule, but occasionally they form bundles of initials of secondary vascular elements by repeated longitudinal divisions of a single initial or a few radially successive initials. As to cell shape, the initials of the secondary vascular bundles are exactly like the initials of a bundle of sclerenchyma fibres (cf. fig. 33 and p. 85—86), so that their fundamental shapes are the same, viz. an elongated tetrakaidekahedron in prosenchymal orientation.

The initials possess a small diameter which increases considerably when the elements differentiate into vascular elements, which consist solely of long fibre tracheids representing the xylem and sieve-tubes representing the phloem. The sieve-tube elements do not elongate during their ageing, but the fibre tracheids elongate enormously. CHEADLE has found a maximum elongation up to about 40 times the original length, but usually it amounts to some twenty times that length. This is much more than is ever shown by elongating libriform fibres in the young secondary wood. Yet it is not likely, that the elongation is associated with a sliding of the cells in amongst one

another, for in the walls between the peripheral cells of a vascular bundle and the adjoining parenchyma cells pit-pairs are present which have originated from the primary pit-fields in the radial walls of their cambial mother cells. The differentiating elements of a vascular bundle are difficult to separate by maceration and apparently tightly knit together, which makes sliding still less probable.

The explanation of the process of elongation of the long fibre tracheids is, therefore, necessarily the same as that which was given in the case of libriform fibres, with the difference, that the fibre tracheids of Monocotyledons with secondary growth repeatedly establish contacts with other fibre tracheids in stead of only once at either tip as in the development of libriform fibres.

The transition between fibre tracheids and parenchyma or phloem elements is not brought about by a series of successive longer cells (p. 107*c*), for a sudden change from tracheid to parenchyma or phloemelement is found, but by the other possible methods (p. 108). The fibre tracheids are often bent at their tips, the tips of the outer ones are bent inward (toward the centre of the bundle), those of the inner ones outward (toward the periphery of the bundle). A fibre tracheids is often in contact with the parenchyma or the phloem in the middle only by a small portion of its wall, usually with no more than three cells of parenchyma or phloem. Fibre tracheids may also have only a small common contact face in the middle, whereas their tips are diverging. These contacts in the middle of the cells most probably represent some of the original lateral contact faces of the xylem initials with adjoining initials and have not been elongating appreciably, whereas the other faces of the cell have been growing considerably.

Forked fibre tracheids were occasionally found by SCOTT and BREBNER and by CHEADLE; we were able to confirm their observations. The explanation of the occurrence of forked ends is the same as that given for the formation of branched libriform fibres. The bifurcations are probably produced by the separation of a chisel end in two acute points. In accordance herewith at one end of a fibre tracheid but a single bifurcation is found. If sliding growth would account for the forked ends, not only single bifurcations, but also more complicated ramifications might be expected.

The shape of the fibre tracheids is so much changed by the formation of additional contact faces, that it cannot be derived from a known basic shape.

CHAPTER X

EXPERIMENTS FOR DEMONSTRATING MORPHOGENESIS AND CHANGES IN INTERCELLULAR RELATIONSHIPS OF PLANT CELLS.

In order to elucidate the actual morphogenesis of cells we attempted to demonstrate changes in cell shape by means of experiments. Similar attempts had been made earlier (**162, 59, 154, 113, 106**). One of the methods employed was the application of external pressure to stacked plastic spheres. A difficulty presented by the experiments with plastic bodies which are compressed, and by similar experiments in which peas are caused to swell in a glass vessel to eliminate the interspaces, is that the original arrangement consists of a piling of spheres leaving considerable interstices. As a matter of fact plant cells originally do not possess interstices; the intercellular spaces form later by the splitting or the digestion of middle lamellae in the corners where three or more cells adjoin. Besides, in these experiments, the elastic properties of the cell wall are not accounted for.

LEWIS (**98**) has shown, that different stacking arrangements of plastic spheres of uniform size and subsequent general compression yield figures of different shapes. If they are placed in such a manner that each sphere is in contact with six others, viz. with one perpendicularly above and below it and with four adjoining it laterally, according to LEWIS, general compression produces cubes. General compression of spheres in the most economic space-filling arrangement (i.e. when twelve balls are in contact with a central one) was supposed to produce rhombic dodekahedra, which has also repeatedly been reported by others (D'Arcy THOMPSON **162**, SEIFRIZ **154**, MARVIN **113**). LEWIS also showed how to stack spheres in order to produce tetrakaidekahedra (orthic tetrakaidekahedra with plane faces and straight edges) at compression.

As it is unlikely, that LEWIS actually carried out the experiments, we have done so employing GANE's method (**59**) in a slightly modified form. Plasticine balls covered with a talc layer were compressed in a mould with movable bottom and cover (i.e. they were bilaterally and not generally compressed), so that it had to be reckoned with that our method of compression foreshortens the figures produced in the direction of the pressure. In this way for instance in the first piling described by LEWIS (see above) not cubes, but rectangular prisms having a square upper and lower face and vertical edges about half the length of the horizontal edges are formed. Regular

figures may be obtained by starting from a piling of ellipsoids in which the long axes of the ellipsoids are placed in the direction of the pressure, instead of from a piling of spheres.

It appeared that indeed different figures are obtained by compression of spheres (or ellipsoids) in different stackings, e.g. cubes, rhombic dodekahedra and tetrakaidekahedra (cubo-octahedra). It may be noticed, that the *two* possible densest space-filling arrangements (in which twelve figures surround a central one) [1]) yield different dodekahedral figures after compression, viz. in one arrangement rhombic dodekahedra and in the other arrangement figures which shape can be derived from a rhombic dodekahedron by rotating one half of it 60° relatively to the other half around its axis. This had never been recognized by LEWIS or others studying cell shape.

At any rate it is impossible to produce tetrakaidekahedra by compression of spheres in closest arrangement (see p. 62), as was erroneously assumed by GANE (59), on which assumption PRIESTLEY (135, 136) based the theory that meristem cells become tetrakaidekahedral by the action of external compression causing plastic deformation (see also MARVIN 113).

Piling arrangements different from the above-mentioned yield figures with various irregular shapes. This is probably the reason why MARVIN (113) produced figures with widely varying shapes by the compression of lead shot poured at random into a mould. The pouring out at random causes namely various kinds of stacking and forms irregular interspaces. We therefore should not attribute much significance to the average number of faces of the compressed shot found in this experiment, nor to the average number of faces found in a similar experiment carried out by LEWIS (106) in which peas poured out at random into a vessel were caused to swell.

The experiments in which plasticine balls are compressed can be imitated by stacking peas in regular arrangements in vessels and causing them to swell. This method implicates some technical difficulties however. The swelling is difficult to control, so that the vessel may burst too early, peas are not of uniform size and mostly not perfectly spherical, and the small dimensions of the peas make the counting of faces and edges often difficult. So far as we are able to decide, both methods yield identical results.

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1) Compare the text-books on crystal structure and on X-ray analysis of crystals, e.g. W. L. BRAGG, The crystalline state, London 1933, and F. HALLA and H. MARK, Leitfäden für die Röntgenographische Untersuchung von Krystallen, Leipzig 1937.

Though compression of stacked plastic spheres and swelling of peas may produce tetrakaidekahedra, the occurrence of cells having the shape of Lord KELVIN's figure is still unexplained hereby. Especially the two objections raised above invalidate these experiments as a simulation of the actual morphogenesis of cells. GIESENHAGEN's experiments (**60**) do account for the elastic properties of the cell wall and are actually a demonstration of some factors governing intercellular relationships in plant tissues, such as the forces caused by the tension in the wall resembling surface tension which account for the cells tending to assume a minimal surface area. Against his experiments one objection may still be raised however, viz. that GIESENHAGEN started from arrangements leaving considerable interstices.

In connection with GIESENHAGEN's experiments we repeated the experiments carried out with swelling peas (see above) by stacking spherical rubber balloons of uniform size in a vessel in various piling arrangements followed by evacuation of the air from the vessel. The interstices grow smaller and smaller during the evacuation and the balloons flatten themselves against one another. It is possible to fix the shapes obtained by heating the vessel and its contents to 60° C and, whilst still evacuated, pouring molten WOOD's metal into the vessel, which fills up the interspaces. After a cooling a cast of the interspaces, corresponding with the "edges" of the figures, is obtained. Depending on the fashion of stacking, the balloons in the evacuated container assume the shape of a cube, a dodecahedron, a tetrakaidekahedron, or other shapes.

In order to compose an experiment which is of more importance for demonstrating the morphogenesis of plant cells, we considered the following points:

1. we should start from a space-filling arrangement of cell models, which had to be transformed into another space-filling arrangement;
2. the original shape of the cell models had to be identical with the initial shape of meristem cells;
3. the figures must be able to expand in all directions;
4. the walls must be elastic;
5. the figures must be connected by some cementing substance, so as cells in tissues are connected by middle lamellae; and
6. if possible, the transformation should be permanent in order to simplify later investigation.

This lead us to the following experiment:

Hexagonal prismatic leaden frames were coated with a rubber membrane (not absolutly air-tight) and a spherical balloon was

enclosed in each of them. These figures had the shape of meristematic cells (see fig. 25), the wall was elastic, the enclosed balloon produced the internal pressure which caused the expansion of the figure when the vessel containing the prisma was evacuated and simulated the turgescent vacuole and tonoplast. The leaden frame could be permanently transformed. The figures were glued together in the arrangement shown in fig. 14 for meristem cells, so that a central prism was surrounded by fourteen other figures. The above points 1, 2, 4, 5 and 6 were consequently well accounted for. Point 3 was not, for the cell models were not able to expand in the longitudinal direction, since the leaden frames could not be stretched longitudinally and could only buckle outward laterally. This difficulty was met by making the prisms about three times as high as the length of the edges of its hexagonal faces, so that its height grew relatively smaller and its width relatively more, and finally its dimensions became almost equal in various directions. Thus the same final condition is created as in a mature parenchymatous tissue, but the development of the "isodiametric shape" in plant tissues is different, as here both length and width are increasing. The stacked and glued figures were put in a vessel from which the air could be evacuated. Care was taken that the figures might be able to expand laterally, but, as some counter-pressure proved desirable, an elastic substance was put around them. Wooden blocks were placed against the free hexagonal faces to replace the counter-pressure which properly had to be produced by adjacent prisms, so that they could not buckle out there. By evacuation of the air a transformation of the figures was caused, which was shared by the leaden frame. In the above piling arrangement the shape of the innermost cell model approaches the shape of an orthic tetrakaidekahedron. Other shapes were obtained by

a. taking prisms of different heights, so that the number of contact faces varies;

b. taking not only hexagonal, but also pentagonal, heptagonal, etc. prisms; and

c. placing the basal face or upper face of one prism opposite to the upper or lower faces of two different prisms (cf. fig. 16),

thus accounting for the various irregularities actually found in meristems (cf. Chapter II, A).

These experiments indeed handsomely exemplified the morphogenesis of parenchyma cells.

Other experiments dealt with the changes in intercellular relationships, especially with those, in which certain cell walls grow less in width and certain edges grow shorter.

The mode of growth of a wall between two epidermal cells of *Citrus* and *Dalechampia* situated above a growing young idioblast was demonstrated as follows: Two cylindrical balloons were glued together with their long side and, after having been blown out, placed on a glass plate. A third balloon C slightly blown out was placed along side above the connection of A and B (see fig. 41).

Fig. 41. Experiment for demonstrating the growth of a crystal cell in a *Citrus* leaf. Explanation see text.

The balloons were kept in their place by glass plates at the long sides and above. The balloons A and B represented the two epidermal cells, the balloon C the growing idioblast. Then the balloon C was further inflated, but the balloons were prevented from lateral expansion by the glass plates, so that the balloons A and B were only able to expand longitudinally. The balloon C compressed A and B, which both elongated, while their jointure (*ab*) grew less in vertical extent. The action of balloon C may be replaced by a pressure with a glass rod.

A rubber sheet of the form represented in fig. 42A was stretched in the direction of *ab*. The result is seen in fig. 42B. The narrowest place in the sheet decreases in width. This illustrates the changes occurring in a wall growing less in one direction by a simultaneous elongation in another direction (cf. fig. 29 and p. 75).

Three sheets of rubber of the form represented in fig. 42 were

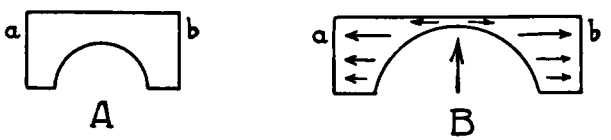

Fig. 42. Demonstration of the decrease in width of cell walls by simultaneous elongation. Explanation see text. Compare also fig. 29A-C and fig. 30.

joint in a fashion represented in fig. 43 in top view and in lateral view. A stretching in the direction of the sheets caused them to grow less in the narrowest place. This is a demonstration of the local elimination of walls placed in threes above a growing crystal cell of *Citrus*, cf. fig. 28B, cells at the apex of a growing latex cell (see p. 80) etc.

In another experiment an elongated hexagon *abcdef* was drawn in

ink on an inflated cylindrical balloon (fig. 44). When the balloon was laterally compressed, the hexagonal figure *abcdef* elongated in the direction the arrows pointing to *c* and to *f*, so that the figure changes into *a'b'c'd'e'f'*. If care was taken that the points *a,b,d* and *e* are kept in their original position, e.g. by keeping them in their places by the fingers, the hexagon is transformed in a different way (for *ab* and *de* remain constant, whereas *cf* elongates), viz. into *abc'def'*. If the balloon was sufficiently blown out, it proved to be possible to reduce the distances *ab* and *de* by counter-pressure with the finger or by pulling at strips of rubber glued on the balloon in the points *a, b, d,* and *e*. A combination of elongation of *cd* and reducing of the distances *ab* and *de* is also possible. Then the figure changes into *a"b" c'd"e"f'*. The balloon was for that purpose considerably elongated by pulling at its ends, while in the points *a, b, d* and *e* a stretching in opposite direction was applied by pulling at strips of rubber attached to these points. A more elegant form of this experiment was carried out by gluing four conical balloons on a cylindrical one as represented in fig. 46. After blowing out the balloons, the pressure in the conical balloons was increased and the cylindrical balloon was stretched by pulling at

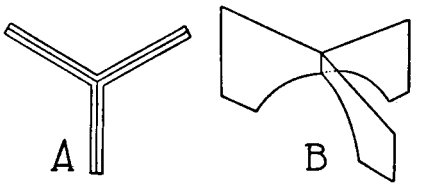

Fig. 43. As fig. 42, but in a three-dimensional arrangement of the sheets. Explanation see text.

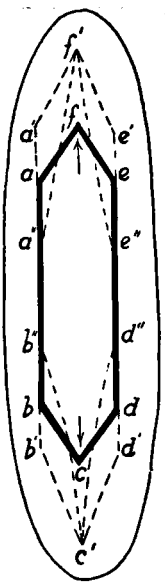

Fig. 44. Demonstration of the change occurring in the tangential walls of differentiating cambial derivatives. Explanation see text.

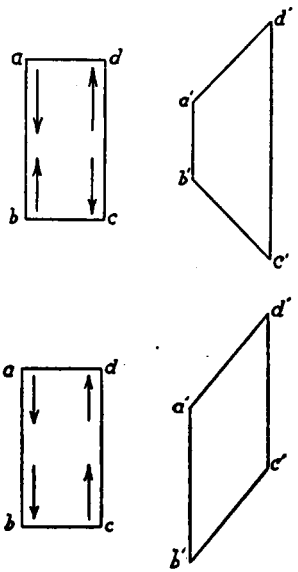

Fig. 45. Demonstration of changes in shape of the walls of differentiating cambial derivatives. Explanation see text. Compare also fig. 44 and p. 88.

its ends. The conical balloons elongated in the direction of the arrows. The transformation of the face (partially) bounded by the four conical balloons (*abcdef*) is the same as the transformation of *abcdef* into *a"b"c'd"e"f'* in fig. 44.

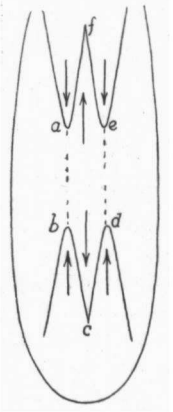

Fig. 46. As fig. 44, but slightly modified. See text.

These experiments simulate the changes occurring in the tangential faces of growing tracheids and libriform fibres, which elongate, whereas certain edges grow less (fig. 39). The conical balloons represent the acute tips of four growing libriform fibres partially bounding the tangential wall *abcdef* of a fifth (i.e. the cylindrical balloon). The acute tips elongate and so does the fifth "libriform fibre" represented by the balloon, so that the length of certain edges decreases.

The last experiments were modified by using other arrangements of the stretching and counterpressure so as to transform rectangular faces into parallelograms and trapezia (cf. fig. 45 and p. 105).

The above demonstrations are clear evidence that an explanation of certain processes implicated in changes in intercellular relationships is possible without assuming a splitting of cell walls along the middle lamella.

APPENDIX

OBSERVATIONS ON THE CHEMICAL COMPOSITION AND FINE STRUCTURE OF CELL WALLS.

1. *Meristem cells.*

The separate cell walls of individual meristem cells are connected by middle lamellae, which — except in the angular thickenings where three or more cells adjoin — are extremely tenuous. As to the nature of these middle lamellae it may be stated that

a. In suitable objects (e.g. the cambia, cf. **86**) without previous treatment, in other instances after previous swelling the middle lamellae appear truly isotropic under polarized light. This proves that most probably the middle lamellae of meristem cells do not contain cellulose,

b. in all meristems where the primary wall and the middle lamella are seen as separate layers the middle lamella never shows the cellulose reactions in contradistinction to the primary wall,

c. the middle lamellae do not dissolve in cuprammoniumhydroxide,
d. in several objects at the formation of a new wall in a dividing cell first an isotropic lamella is formed, on either side of which later an anisotropic lamella is deposited (23) and
e. the middle lamellae show the usual reactions on pectic substances (intense staining with ruthenium red and haematoxylin DELAFIELD, a violet coloration with methylene blue, a reddish-brown colouration with neutral violet and a pale orange-yellow coloration with safranin).

From this it seems evident that the middle lamellae in meristems consist mainly of pectic substances. In meristematic tissues maceration with pectin-dissolving reagents often fails, however. This is probably due to the persistence of parent walls around files of derivative cells and does not necessarily indicate the presence of other substances besides pectic substances as suggested by TUPPER-CAREY and PRIESTLEY (167) who suppose the middle lamella of meristematic tissues to be a pectin-protein complex. Protein cannot be demonstrated in older cell walls in any appreciable quantity, as was found by CORRENS (35) and later by WOOD (174). Analyses carried out by WOOD showed only traces of protein, which might well be accounted for by remnants of protoplasts or plasmodesmata. The results of the analyses of meristematic cell walls made by TUPPER-CAREY and PRIESTLEY are therefore to be regarded with some doubt and deserve to be verified.

KERR and BAILEY (86) reported that the middle lamellae in cambia consist completely of pectic substances and do not mention any further constituents.

Other possible constituents are lipoids or phosphatids, which have been found in several meristematic tissues (167, 28) but which may be confined to the primary wall and lacking in the middle lamellae.

The true wall of the meristematic cell, which is the primary wall in the sense of KERR and BAILEY (86), on the other hand always contains cellulose. ZIMMERMANN (182) and others reported positive reactions with various cellulose reagents without any previous treatment, but in most cases the cellulose reactions fail to appear, however, but for applying special methods (167), BARANETZKI (20) for instance succeeded in obtaining positive reactions after macerating apical meristems. Our experience is that the reaction with iodine-potassium iodide and sulphuric acid, if not occurring instantly, is positive after prolonged treatment. The reactions prove to be positive after a previous treatment with Eau de Javelle (cf. 167). The presence of cellulose may further be established by the double refraction of the

walls, by the positive dichroism after staining with iodine reagents or congo red, and by its solubility in cuprammonium hydroxide.

Almost without exception in meristems positive reactions with ZIEGENSPECK's "amyloid" and "collose" reagents were obtained. ZIEGENSPECK (177) and some others are of the opinion that these reactions are specific for certain cell wall substances, but more than once this has been doubted in good reason. At any rate these reactions are not specific for the so-called "*Primärsubstanz*" of HESS and coworkers (72) which proves to be identical with certain waxy substances (SISSON 156, WÜHRMANN-MEYER 175). The amyloid and collose reactions are still positive after the extraction of the waxy substances by means of alkali.

To support the presumption which was already stated elsewhere (116), viz. that the amyloid and collose reactions, which mostly occur in young growing tissues, are merely indicative of a low quantity of cellulose in the walls, the following arguments may be adduced:

a. the collose and cellulose reactions are always positive when the amyloid reaction is positive; the amyloid reaction is never positive when the other ones fail to appear,

b. a positive collose reaction never occurs when no positive cellulose reaction is obtained;

c. all three reactions may cause a positive dichroism in the stained walls (the amyloid and collose reactions from steel blue to almost colourless, the cellulose reaction from blue to grey) which is indicative of the formation of a "*Mischkörper*" in WIENER's sense and consequently of a micellar structure of the walls. Most probably the blue colour obtained by applying iodine reagents sets in when the so-called intermicellary spaces are above a certain width (52), so that the amyloid reaction is indicative of wide intermicellary spaces, the collose reaction of less wide intermicellary spaces, which need to be enlarged by a slight swelling of the wall, and the reaction with chloroiodide of zinc of comparatively small intermicellary spaces, which need an intense swelling of the wall. In some algae, even this reagent does not cause the wall to swell enough and a swelling with cuprammonium hydroxide is needed (57). This assumption explains why in older cell walls, which are relatively richer in cellulose and consequently have smaller intercellular spaces, the amyloid and collose reactions usually fail to appear.

d. After a prolonged treatment with cuprammoniumhydroxide all three reactions stay out.

e. It has been observed at the formation of secondary cell walls that the cellulose is formed from the protoplasm without intermediate

stages between glucose and cellulose (see **158**, **39**, **1**, **4** and especially **77**). In growing cells the protoplasm is tightly adherent to the growing primary wall. At plasmolysis in both instances the protoplasts do not retract from the walls, but contracts at best together with the walls, as may e.g. be observed in the apices of growing fibres developing according to the *Linum*-type (**1**) and of growing hyphae of fungi, and in transverse sections of fibres forming secondary lamellae (**4**). This is also indicative of a close relation of cellulose and protoplasm. It has also been emphasized from a biochemical point of view, that in biological synthesis complex organic compounds, including cellulose, are formed at once by the protoplasm from elementary units, viz. glucose molecules (**81**). This is not in accordance with ZIEGENSPECK's conception of the formation of cellulose, in which a very gradual synthesis by means of many intermediate steps is assumed (glucose → cellobiose → molecules built up by a few cellobiose groups → . . . → "amyloid" → "collose" → cellulose).

Birefringence of meristematic cell walls was already established by ZIMMERMANN (**182**) as early as 1887 in the cambium of *Cytisus*, but later DIPPEL (**39**) denied that meristematic cells have refringent walls. It has often been shown since, that DIPPEL was wrong in this respect (cf. **86**, **175**).

Besides cellulose, the young primary walls contain appreciable quantities of pectic substances, the presence of which may be demonstrated by several reactions (see above), and waxy substances probably identical with HESS's *Primärsubstanz*. The presence of pentosans and phosphatids is to be expected (**28**), the occurrence of proteins seems doubtful, however (**35**, **174**).

2. *Cells of mature tissues.*

The middle lamellae of mature cells — if not lignified — change but little if compared with the middle lamellae of meristem cells. They are thicker and more easily recognizable as a rule. Maceraration of the tissue with pectin-dissolving reagents is easier than in the meristems, presumably on account of the fact that no longer groups of cells enclosed in a common parent wall are present, the parent walls having been ruptured by the elongation of the cells during maturation, and probably not because of radical chemical changes in the middle lamella. In certain tissues middle lamella and primary walls ultimately lignify.

In parenchymatous and collenchymatous cells of primary tissues the thickening layers of the walls are not clearly distinguishable from

the primary layer. No good criterion can be found to define the various layers, because by their growth the cells cause the outer lamellae to rupture successively (see **137** and p. 58 and 59), so that KERR's and BAILEY's definition (viz.: "The primary wall is the meristematic wall and its homologues in other tissues") is useless. A different definition might be: "The primary wall is that part of the wall which grows or has been growing in surface area, the secondary wall is laid down or has been laid down after the completion of the growth of the primary wall", a definition which always holds good in the case of primary sclerenchyma fibres (**1**, **116**) and elements of secondary wood or secondary bark (**86**), but fails in the case of parenchyma and collenchyma cells, for these cells keep growing even after the formation of thickening lamellae.

The cell wall constituents in these tissues are mostly the same as those of meristematic cell walls (cellulose, pectic substances, etc.), sometimes later secondary changes occur (lignification, suberization or cutinization). The cell wall substances are equally distributed in the wall as a rule, but in a few cases a marked stratification was observed, caused by unequal distribution of certain of these substances, e.g. by an alternation of layers consisting of pure pectic substances and layers of cellulose mixed with pectic substances (**3**), of cellulose, pectic substances and cutin in various quantities (**5**) or layers of cellulose of different submicroscopic structure (**18**, **19**).

Generally speaking the epidermal cells show the same peculiarities, though the secondary changes, especially those in the outer wall, are more pronounced in connection with the functions of the epidermis.

In the elements of primary sclerenchyma, the elements of secondary wood and bark and some other cells (cotton hairs and other hair cells) primary wall and secondary layers are clearly distinguishable. The primary wall originates from the meristematic wall, the secondary layers form later after the completion of the primary wall. Fibres developing according to the *Linum*-type by apical growth have growing tips with solely a primary wall, while the remaining parts, which have ceased growing, already show secondary thickenings (**1**). In the mature tissues the primary wall is mostly lignified.

The secondary walls show various structures. They may appear optically quite homogeneous, but usually two to many layers may be discerned, the innermost of which is sometimes distinguished as "tertiary layer". Some cases of lamellation (e.g. those in the secondary walls of cotton hairs) were studied by ANDERSON and MOORE (**8**). It appeared that certain walls show a lamellation when they have

been growing under varying external conditions, whereas they are quite homogeneous when they have grown under constant climatological conditions. Other walls are always lamellated, no matter under which conditions they had been growing.

The conspicuous lamellation of the secondary wall of tracheids, fibre tracheids and libriform fibres of the secondary wood is of special interest. It is present without exception (15). Three layers may be distinguished as a rule: a thin outer layer, a subsequent broad layer (which usually shows finer lamellation) and a thin inner layer, which is identical with the tertiary lamella of the older authors (Cf. VAN WISSELINGH 172). This innermost layer may be lacking. According to FREY (51) and BAILEY and KERR (15) the main extinction positions (m.e.p.'s) of the primary wall and the layers of the secondary wall are different. Their conclusions are especially based upon investigations under polarized light. Other arguments, such as the direction of the long axes of slit-like pit apertures and the directions of striations in the different layers of the wall, were derived from older investigations (181, 39, 157). Later BAILEY and VESTAL (17) found additional confirmation by producing iodine crystals in the walls which appeared to be placed in the direction of the cellulose chains.

PRESTON (131, 132) on the ground of X-ray analysis of cell walls thought that this conception of the structure of the walls of wood elements is wrong and suggested a different structure in which he assumed the existence of a single, continuous, spiral complex of cellulose chains in the wall.

BESEMER (26) lately investigated the main object used in PRESTON's studies, viz. tracheids of *Pinus sylvestris*. By studying the successive stages of development of the wall in surface view of single walls he confirmed the older conception. The cambial wall, which we will designate as P, is followed by a layer in which a transverse m.e.p. is found, the first (outer) layer of the secondary wall (sensu KERR and BAILEY), or S I. On S I the thick second layer of the secondary wall, which will be designated as S II, is deposited. The m.e.p. in S II forms an angle smaller than 45 with the long axis of the cell. A third layer (S III) is lacking in *Pinus*, but it is of frequent occurrence in the wood cells of other Conifers (e.g. *Seqoia*). Its m.e.p. is placed transeversely. We were able to confirm BESEMER's results in *Pinus* and refer to his publication for further details. Additional confirmation was found by using a peculiarity of many fibres, namely, that they show swelling phenomena after a treatment with certain swelling agents (the so-called "*Kugelquellung*", see 107, or "ballooning"). GRIFFIOEN (62) and FREY-WYSSLING (54) showed

that this ballooning occurs only if the long axis of the swelling ellipsoid in the outer layer(s) of the wall is placed more or less transversely and in the inner layers more or less longitudinally, which had already been surmised by several others (34, 15, 78). The position of the long axis of the swelling ellipsoid is perpendicular to the m.e.p. (180). This explanation of the *Kugelquellung* presumes almost perpendicular m.e.p.'s in the outer and inner layers of the wall and does not tally with PRESTON's conception of a single spiral complex. Accordingly, PRESTON critisized all conclusions based upon phenomena caused by swelling of cell walls (e.g. the work of BAILEY and VESTAL) and proposed a different explanation of the *Kugelquellung*. He thinks that the swelling of the outer layers of the wall precedes the inner layers of the wall, so that the position of the cellulose chains in the outer layers of the spiral complex is altered into a transverse position, thus preventing the inner layers from further lateral swelling in certain places by forming the constricting bands. The formation of transeversely placed iodine crystals in the walls was also explained by a change in the position of the cellulose chains caused by the swelling of the wall.

Actually, the regions of a swollen fibre in which the constrictions are found at ballooning are about the original width of the unswollen fibre and therefore have not swollen appreciably. In these places the direction of the cellulose chains consequently cannot have been changed as much as PRESTON's explanation demands and yet — according to PRESTON as well — in the constricting bands a transverse chain direction is present. The transverse chain direction is original, therefore, and PRESTON's conception of a single spiral complex does not hold true.

We used this ballooning as an indication of layers with different m.e.p.'s. In young tracheids of *Pinus* no ballooning occurs before the formation of S II. In S II therefore a more or less longitudinal m.e.p. is found, accounting for the lateral swelling, and in S I a transverse m.e.p. accounting for the constricting bands.

The development of the walls of the libriform fibres in *Populus* and *Quercus* is much the same as the development of the walls of *Pinus* tracheids, but an additional layer (S III) is formed. The m.e.p.'s in S I and S II are also much the same as in *Pinus*, which besides from direct investigation under polarized light appeared from the balloon swelling (see above).

On the ground of the structure of the mature wood elements (see also 15) it seems very likely that in almost every Conifer and Dicotyledon the same structure of the secondary walls of tracheids, fibre tracheids and libriform fibres is present. Additional evidence

could be obtained by producing iodine crystals in S I and S II (17, 26) and by causing balloon swelling.

The walls of the initials of the secondary vascular bundles of *Cordyline* and *Dracaena* are slightly birefringent without showing a distinct m.e.p. During the enormous elongation of the elements differentiating into fibre tracheids, the micelles become transversely oriented by that elongation. This is in accordance with the general rule, that in cells which have been showing considerable elongation a so-called "*Röhrenstruktur*" is present, i.e. the m.e.p. is transversely placed (FREY-WYSSLING 53, 54). This rule is in accordance with the direction of the tensions in the walls (VAN ITERSON, CASTLE 29) and has been confirmed in a great deal of cases (e.g. 37, 58, 110, 173, 178, 179). Especially in free cells such as hair cells and the cells of filamentous algae the *Röhrenstruktur* is well developed. In elongating cells of tissues, as in young *Cordyline* fibre tracheids, and in differentiating cambial derivatives of Dicotyledons this structure is less pronounced, but often sufficiently developed to be perceptible.

The primary wall of the fibre tracheids in Monocotyledons with secondary growth may be identified with P. After the completion of the elongation the first layer of the secondary wall, identical in structure with S I of *Pinus* tracheids, is deposited. In this layer the places where the bordered pits will be formed remain unthickened and are clearly perceptible under polarized light or after treatment with chloroiodide of zinc. Exactly like in *Pinus*, this indicates that S I belongs to the secondary wall, for pits have been formed. The m.e.p. in S I is slightly slanting and follows a left spiral forming an angle between 85° and 65° with the long axis of the cell. As seen in a transverse section of the cell, S I is stronger birefringent than P. After S I a thick layer is deposited comparable with the layer S II of libriform fibres. The cellulose chains in this strongly birefringent layer follow a right spiral forming a 0°—25° angle with the long axis of the cell. Finally, a third layer comparable with S III of libriform fibres is deposited. The separate layers were also found in the mature lignified fibre tracheid by pulling them apart with needles and investigating them separately under polarized light.

The directions of the cellulose chains near the bordered pits are the same as near the bordered pits of *Pinus* (17), i.e. in S I the chains are placed concentricly round the pits, in S II this arrangement alters into an arrangement in which the chains are placed in the general direction of the m.e.p. in this layer.

Sclerenchyma fibres differentiating according to the *Sanseviera-*

type possess a primary wall which has been derived from the wall of the original meristematic fibre initial and grows till the cell has reached its definite shape and size. As a result of considerable elongation the primary wall possesses a "*Röhrenstruktur*", so that its m.e.p. lies transversely. The elongation of the fibre nearing completion, the primary wall often increases in thickness without showing any lamellation. This is probably due to the fact that the wall is no longer thinned by stretching, while the amount of cell wall material deposited per unit of time remains constant for some time. (An analogous phenomenon was observed in parenchyma cells of decapitated *Helianthus* seedlings by RUGE (139). These walls thicken, because the elongation is inhibited, whereas the deposition of cell wall substances continues).

On the unlamellated primary wall the thick secondary wall consisting of one or more layers is deposited. Usually the m.e.p. is placed more or less longitudinally in this wall, but there are transitions of sclerenchyma fibres to shorter elements which otherwise closely resemble sclerenchyma fibres (sclereids) and in which a transverse m.e.p. is found. This was extensively described elsewhere (116).

The fibres differentiating according to the *Linum* type have growing tips covered solely by a primary wall and older parts which have ceased growing and form secondary walls. This mode of growth was described in detail by ALDABA (1). The primary wall possesses a *Röhrenstruktur*, the secondary wall shows a m.e.p. which is usually placed almost in the direction of the long axis of the cell ("Faserstruktur", FREY-WYSSLING 53), except in the "tertiary wall", which is of frequent occurrence and has the same structure as the layer S III in libriform fibres.

An exception to this general type of wall structure in prosenchymatous cells is made by the ductile libriform fibres and the ductile sclerenchyma fibres, which show a transverse m.e.p. in the whole of the secondary wall. SONNTAG (157) made an elaborate study of these ductile elements.

The structural variations of the walls of primary sclerenchyma fibres were investigated in the same way as in the secondary wood (see p. 123 ff.) by studying successive stages of development of the wall under polarized light and its dichroism after staining or after metal impregnation (50), by producing iodine crystals in the walls (17, 26), by balloon swelling and by separating the various layers in mature condition and investigating them separately. The ballooning of the cells only takes place after a secondary layer has been deposited. Interesting in this connection is that sclereids and

short sclerenchyma fibres having a transverse m.e.p. in its secondary walls (see above) do not show ballooning at all, because no antagonistic swelling indices are present in the outer and inner layers of the wall.

The structure of cellulosic walls is always the same in one respect: they are built up by homogeneous lamellae which cannot be split into thinner lamellae. The number of lamellae varies from a single one to many. When the wall is deposited it may often be noticed that a lamella is formed as a concrete layer; this is for instance clearly perceptible in the formation of secondary lamellae in fibres of *Linum* (1, 4) and *Boehmeria*. A formation of the lamellae from small microscopic units could not be observed. By applying special maceration methods it is possible to obtain cell walls which consist of practically pure cellulose (see also 28, 116, 7), but are still concrete and do not disintegrate into smaller units. Cell walls may break into small fragments which are of different sizes and shapes and are known by various names: fibrils, dermatosomes, ellipsoidal particles (43), chemical sections (84), "*Querelemente*" (107), "*Baueinheiten*" (171), etc. A single concrete lamella may also show an inhomogeneous structure perceptible as striations, lines or cracks in the walls or as slip-planes. There is reason to believe that the formation of these irregularities is strongly influenced by mechanical action (119). After the formation of these irregularities the cellulose is usually irregularly distributed in the wall. By the action of concentrated solutions of sulphuric acid, hydrochloric acid, alkalis or cuprammonium hydroxyde, which, as is known, break up the cellulose chains, or by strong mechanical bruising, the coherent framework of a single lamella can be ruptured. Strong action ultimately causes fragmentation. The action of the reagents commences in the places where the cellulose is less compact, so that the shape of the fragments depends — besides on the technique employed — largely on the structure of the walls. Out of walls showing a fine longitudinal parallel striation (such as libriform fibres, especially the layer S II, sclerenchyma fibres) a number of parallel fibrils are formed. In our opinion in many cases the structures of a cell wall lamella is changed after its formation (cf. 119, 120), so that weaker places are formed which are the future lines of separation of the fragments. This has e.g. to be concluded from the evident connection between parallel longitudinal striations and fibrils. Fibrils are only formed if the cell wall consists of parallel cellulose chains, as is the case in the secondary walls of wood fibres and sclerenchyma fibres. This regular parallel orientation is recognizable by the sharp extinction under polarized light, by the marked dichroism and exactly parallel arrangement of

iodine crystals formed in these walls (17) and finally by the sharp fibre diagram. The above arguments lead to the conclusion that a cell wall lamella is the fundamental unit which is formed at once from the protoplasm and which does not consist of smaller concrete microscopic entities, but of a coherent cellulose meshwork (cf. 56, 14, 37). All investigators who pretend to have found such building stones either saw fragments produced by desintegration (see 43, 84, 62) or mistook other parts of the cells for units, such as plastids (43, see 7).

Studying the development of tissues we had an excellent opportunity of testing GRIFFIOEN's (63) theory of the origin of lignin by means of microchemical methods. Sections of a tissue in various stages of development were treated with reagents on pectin (see p. 119e) with reagents on lignin (phloroglucinol-hydrochloric acid, the MÄULE reaction) and with metachromatic stains as oxamine blue and neutral violet. Inasmuch as reliable conclusions may be drawn from this staining reactions, our results obtained in Angiosperms are perfectly in agreement with the theory, but in Conifers however, the reactions indicated that the lignin is not, or at least only partially, formed from pectic substances. In other respects the lignin of Coniferous woods also differs from the lignin of Angiosperm woods; a striking difference is for instance that the MÄULE reaction does not stain Coniferous wood. (Other probable sources of lignin are the pentosans, which may account for the bulk of the lignin in Conifers (64). Another suggestion was made by FREY-WYSLING (55), who considers proteins the universal fundamental material of many cyclic organic compounds including lignin. If this holds true the proteins have to migrate from the protoplast into the walls and the middle lamellae during the process of lignification, but as appears from old experiments (see 35), dissolved proteins do not penetrate into cell walls and it is therefore most unlikely that proteins are able to migrate to the cell walls and middle lamellae. Besides, no appreciable amount of protein can be demonstrated in mature cell walls, so that FREY-WYSSLING's idea does not seem to be very attractive).

The staining reactions used in our investigation enabled us to estimate roughly the amounts of pectic substances and lignin by the difference in colour intensity, especially when ruthenium red, phloroglucinol and hydrochloric acid, or chloroiodide of zinc were used. Our observations clearly demonstrated the transfer of pectic substances into lignin, for

a. when in the young cell wall the pectic substances are abundant, the completely lignified mature wall is rich in lignin;

b. when a small quantity of pectic substances or none is found, the maximum lignification is slight or no lignification occurs at all

(secondary walls of many sclerenchyma fibres: *Boehmeria, Urtica, Vinca, Nerium, Asclepias*, etc.); sometimes the middle lamella and primary wall are rich in pectin and later heavily lignified, whereas the secondary wall is almost free of pectic substances in young condition and later not or but slightly lignified;

c. in sclerenchyma fibres of *Linum* the middle lamella and primary wall, though fairly rich in pectic substances, as well as the secondary wall, which contains little pectic substances, do not lignify as a rule and the mature fibre still shows all reactions on pectic substances, but in special cases (in the so-called hypocotyl fibres) the walls lignify and the pectic substances disappear;

d. during the lignification process the pectic substances gradually disappear; the lignification reaches its maximum and ceases as soon as the pectic substances are completely used up; and

e. in sections in which successive stages of lignification are seen simultaneously, as in transverse sections of differentiating wood, the intensity of the pectin reactions decreases as the intensity of the lignin reactions increases.

SUMMARY

1. A study was made of the growth of vegetable cells during their differentiation from the meristematic to the mature condition, and of problems connected with it such as the shape of cells and the presence of certain cell wall structures. As the objects studied proved to be excellent material, certain particularities of the submicroscopic structure and the chemical composition of the cell walls were included in the investigation.
2. A discussion was given of various theories of changes in intercellular relationships, of which KRABBE's theory of "sliding growth" and PRIESTLEY's theory of "symplastic growth" are the most important.
3. It appeared that KRABBE's conception does not hold true and that it is possible to explain all changes in intercellular relationships which were ascribed to sliding growth in literature satisfactorily without assuming any sliding of cells.
4. It was shown that changes in intercellular relationships are principally brought about by symplastic readjustments of the cells as a common whole associated with an expansion of the cells. In those cases only in which cells form additional contact with other cells another process occurs in which certain walls

grow less in width and ultimately are separated by the fusion and subsequent deformation of the angular thickenings of the middle lamellae, but which does not implicate sliding of cells either.

5. A discussion of the various factors determining cell shape was given. It was concluded accordingly that the most probable cell shape in a tissue consisting of cells of uniform size which have been able to expand in all directions is the shape of the figure which was described by Lord KELVIN as the shape formed by liquid films dividing space homogeneously and called the *orthic tetrakaidekahedron.*
6. It was shown that in meristems the total number of contact faces per cell averages fourteen and the number of sides per cell section averages six. When no additional cell contacts are formed during differentiation, in mature tissues the same average number of contacts per cell and the same number of sides per cell section are found.
7. It was demonstrated that the shape and the arrangement of faces of certain meristem cells are so as to yield mature derivative cells approaching the orthic tetrakaidekahedron much in shape by a general expansion during differentiation. For several reasons many meristem cells do not possess the required shape or the required arrangement of faces, and their mature derivatives therefore do not assume the shape of an orthic tetrakaidekahedron, but more or less different shapes.
8. It was explained that in tissues in which the cells have not been expanding in all directions to the same extent, none of the cells possesses the shape of an orthic tetrakaidekahedron. The cells which might have assumed that form by uniform expansion assume a shape which may be derived from the orthic tetrakaidekahedron by transformation; the remaining cells assume more or less different shapes.
9. Changes in shape and in intercellular relationships occurring during the growth and differentiation of cells were demonstrated by means of experiments.
10. It was shown that ZIEGENSPECK's amyloid and collose reactions are not to be considered indicative of certain special cell wall substances, but are probably only indicative of a less compact structure of the cellulose framework of the wall.
11. It was proved that PRESTON's conception of the cell well as a single spiral complex of cellulose chain molecules does not hold true in many cases and that the direction of the cellulose chains in various lamellae of the wall may be entirely different. Ac-

cordingly, PRESTON's explanation of the "ballooning" of swollen fibres also has to be rejected.

12. By means of michrochemical reactions GRIFFIOEN's theory of the origin of lignin from pectic substances was completely confirmed inasmuch cell walls of Angiosperms were concerned.

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LIST OF THE NAMES OF PLANTS USED IN THIS INVESTIGATION.

1. Agave americana L. var. albomarginata Hort.
2. Alcë arborescens Mill.
3. Anthericum spec.
4. Apocynum cannabinum L.
5. Asclepias curassavica L.
6. Asclepias syriaca L.
7. Asparagus Sprengeri Regl.
8. Basella alba L.
9. Basella rubra L.

10. Beta vulgaris L.
11. Boehmeria nivea (L.) Gaudich.
12. Brassica oleracea L. var.
13. Calotropis gigantea (Willd.) Ait.
14. Calystegia sepium (L.) R.Br.
15. Campsis radicans (L.) Seem. =Tecoma radicans(L.) Juss.
16. Cannabis sativa L.
17. Chlorophytum Sternbergianum Steud.
18. Citrus Aurantium L.
19. Citrus medica L.
20. Citrus nobilis Lour.
21. Cochlearia Armoracia L.
22. Cordyline australis Hook. f.
23. Cucurbita Pepo L.
24. Dalechampia Roezliana Muell. Arg.
25. Datura arborea L.
26. Daucus Carota L.
27. Dracaena hybr.
28. Drimys Winteri Forst.
29. Eichhornia crassipes (Mart.) Solms.
30. Ephedra distachya L.
31. Ephedra major Host.
32. Euphorbia Lathyris L.
33. Euphorbia Peplus L.
34. Helianthus annuus L.
35. Helianthus debilis Nutt.
36. Helianthus tuberosus L.
37. Hibiscus cannabinus L.
38. Hibiscus Sabdariffa L.
39. Humulus Lupulus L.
40. Linum usitatissimum L.
41. Lochnera rosea (L.) Reichb. = Vinca rosea L.
42. Musa chinensis Sweet.
43. Napaea dioica L.
44. Nerium Oleander L.
45. Oryza sativa L.
46. Othonna crassifolia Harv.
47. Pandanus amaryllidifolius Roxb.
48. Pandanus Lais Kurz.
49. Pandanus stenophyllus Kurz.
50. Pandanus utilis Bory.
51. Phytolacca decandra L.
52. Picea Abies (L.) Karst.
53. Pinus silvestris L.
54. Populus spec. prob. P. tremula L.
55. Quercus Robur L.
56. Raphanus sativus L.
57. Rhoeo discolor Hance.
58. Robinia Pseudo-acacia L.
59. Salix alba L.
60. Sanseviera guineensis Willd.
61. Spartium junceum L.
62. Synadenium Grantii Hook.f.
63. Taxus baccata L.
64. Tecoma radicans (L.) Juss. = Campsis radicans (L.) Seem.
65. Urtica dioica L.
66. Vinca minor L.
67. Vinca rosea L. = Lochnera rosea (L.) Reichb.
68. Viscum album L.
69. Vitis vinifera L.

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