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Anticlinal divisions, intrusive growth, and loss of fusiform initials in nonstoried cambium*

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The laying down of wood increases the distance of the cambium from the pith and, thus, the girth of the cambium must also increase. In the case of nonstoried cambium the decisive part in this process is played by intrusive growth of fusiform cambial cells, which consists in that these cells grow at the tips forcing their way inbetween the radial walls of the neighbouring cells and push them apart (Klinken 1914, Bailey 1923, Whalley 1950, Bannan 1956). Owing to anticlinal divisions the increase of the cambium girth is accompanied by an increase in the number of fusiform initials: an initial divides into two shorter ones lying one above the other (Bailey 1923). According to Klinken these divisions are transverse and take place midway along the length of an initial: the oblique position of the cell-wall is caused, in the opinion of that author, by secondary intrusive growth of the newly formed tips of these cells. Contrary to this opinion Bailey believes that the division wall assumes from the start an oblique position. Whalley (1950) and Bannan (1957) share the opinion that the divisions are of the pseudotransverse and not the transverse type reported by Klinken.

The anticlinal divisions increase the number of fusiform initials in the nonstoried cambium and at the same time they constitute the mechanism counteracting the average-length growth of these cells caused by instrusive growth. They also directly influence the rate of intrusive growth. According to Bannan (1956) and Whalley (1950) the most rapid intrusive growth takes place immediately after an anticlinal division.

Klinken (1914), Whalley (1950), Bannan (1951, 1953), Barghorn (1940, 1941), and Evert (1960) report that the nonstoried cambium is permanently losing some of the fusiform initials in the course of its development. According to Klinken this happens because in the cambium zone the cambial cells with a greater turgor force themselves sidewards inbetween the tangential walls of cells in the radial

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row, where the loss of the initial is to take place, causing breaks in this row.

W h a l l e y (1950) as well as B a n n a n and B a y l y (1956) state that just before an initial cell loses its initial function it is shortened and its tangential width decreases. Simultaneously the cell often goes through several anticlinal divisions and in the course of this process all or some of the segments may be eliminated. The remaining segments give rise to new rays (B a n n a n 1956). The elimination rate of cells in the cambium of older stems with a very sligth thickness growth is sufficiently high to prevent the number of these cells from increasing, in spite of the constantly proceeding anticlinal divisions of fusiform initials. E.g., among eleven fusiform initials in the cambium of *Thuia* twelve anticlinal divisions occurred during a certain period, but only ten initials remained, though, if they all were to survive there would have been at the end of that period 23 of them (B a n n a n 1960).

B a n n a n and B a y l y (1956) have demonstrated that there is a tendency to eliminate mainly the shorter initials. They have also found a relationship between the number of contacts of a fusiform initial with rays and the probability of its survival.

It is worth noting, moreover, that the elimination of one initial cell stimulates the specially strong intrusive growth of the neighbouring cells (B a n n a n 1956).

All these data on the changes occurring in nonstoried cambium have been obtained from investigations on the xylem or the phloem but not from direct examinations of the cambium itself. It seems plausible to suppose, therefore, that the picture of the development of the cambium obtained in this way is not complete. More detailed information about the changes taking place in the cambium in the course of its development can be assembled only by direct anatomical examinations. The preliminary results from such an investigation on the cambium of *Larix europea* are reported in this paper.

MATERIAL AND METHODS

The different kinds of cambium of *Larix europea* collected for examination in the first half of July were as follows:

1) cambium from a root with six annual growth rings,

2) cambium from the stem of a tree six years old taken off the surface of the 4-th ring at the height of 1.5 m.,

3) cambium from a tree 40 years old taken at the height of 1.2 m., and

4) cambium from a tree 80 years old taken at the height of 1.5 m.

The Preparation of Slides

Pieces of the surface tissue reaching into the wood having been cut out from the stems or the root the surface tissue was removed from them down to the young phloem layer. The pieces were then divided into strips about 0.8 cm. wide and the strips were cut obliquely at the lower end to mark the basal direction. Next the surface layers about 0.8 mm. thick containing the cambium inbetween the young phloem and the xylem layers were cut off the strips with a sharp razor. In this way rectangular trapeziums about 2 cm. long containing the cambium were obtained. These were immediately fixed with Cr-A-F solution (0.4—3—10) and then embedded in paraffin after dehydration in an alcohol-benzene series. Transverse sections 16 μ thick of cambium from stems and 20 μ thick of cambium from roots were cut on a rotating microtom taking care to obtain continuous series extending over at least one centimetre of the cambium length. The cutting was started from the top end. The sections were arranged on slides, about 60 sections in three rows on every slide. First safranin (2% solution in 50% alcohol during 5 hours) and then anilin blue (1% solution in 96% alcohol during 1 min.) was used for staining. The sections in every series were numbered marking every tenth section with an ink dot and writing the number of the first section in every row. Several series suitable for examination were obtained from every kind of cambium.

Negative photographs were obtained using a microscope fitted with a strong source of light and a projection equipment for projecting the image of the suitable part of a section onto photographic paper. Every second or fourth section was photographed and the series of negative photographs thus obtained were glued on a paper tape, which greatly facitated the anatomical analysis. Every series consisted of about 400 photographs.

From the series of the negative photographs of transverse sections it was possible to reconstruct the spatial arrangement of cells. In particular it was possible to reconstruct the tangential sections through the cambium and to plot diagrams of these sections. The drawings thus obtained were the starting point for the analyses of the changes occurring during the cambium growth.

RESULTS

Anticlinal divisions

Fusiform initials dividing anticlinally just at the moment of fixation are seldom found in the cambium. On the other hand, there are many such fusiform initials in which anticlinal divisions occurred in the

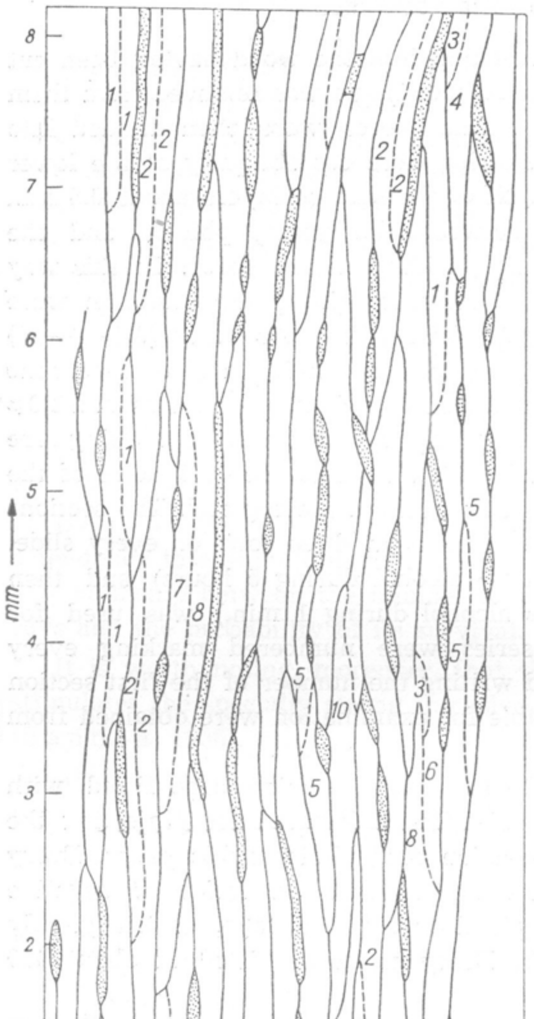


Fig. 1. Reconstructed tangential section through the root cambium as seen from the side of the phloem. The long lines correspond to the long walls of the fusiform initials and the broken lines to walls derived from anticlinal divisions in fusiform initials. The dotted areas mark the groups of the initial cells of rays. The numbers marking the anticlinal walls indicate the number of periclinal divisions, which occurred after the anticlinal divisions till the time of fixation + 1 (i.e. the number of cells produced by the new initial). The basal border of the cambium at the bottom of the figure

course of only a few periclinal divisions preceding fixation. In the cambium of the young root such cells made up about 50 per cent of all the fusiform initials, whereas the corresponding proportions in the cambium of stems were about 25 per cent for the four-year old tree and a few per cent for trees 40 and 80 years old. (These figures do not include the divisions at the ends of the fusiform initials associated with the formation of rays, since these divisions were not considered in the course of this research).

Figures 1, 2, and 3 show the reconstructed tangential sections of the various kinds of cambium. In the diagrams the broken lines mark the

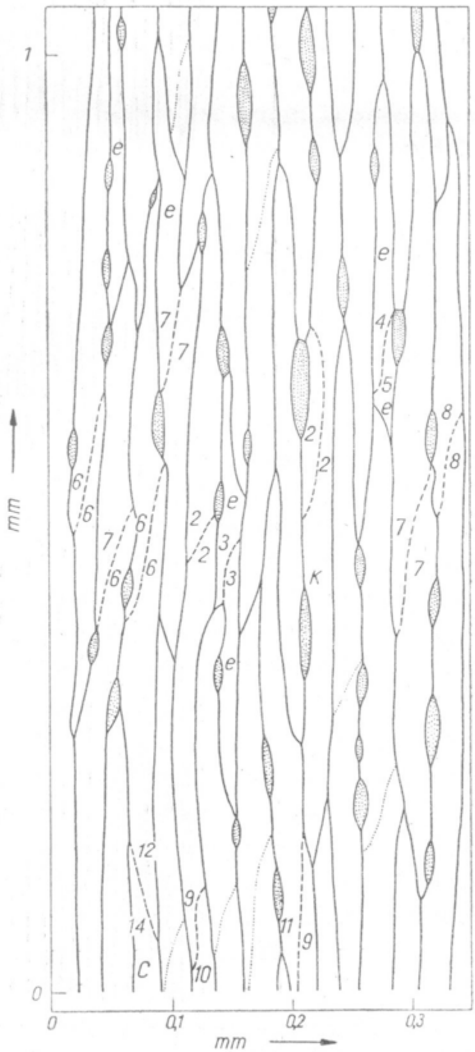


Fig. 2. The same as in fig. 1, but for the cambium of a four-year old stem. The dotted lines mark the projections of the walls from anticlinal divisions in the phloem mother cells. The initials in the course of elimination are marked with the letter "*e*". The one-directional character of the anticlinal divisions is well visible

walls from anticlinal divisions the number of the subsequent periclinal divisions being recorded in each case.

Let us consider first the anticlinal divisions in the cambium of the root. As is to be seen in fig. 1 the walls derived from anticlinal divisions in the fusiform initials have an appreciable length and are more or less

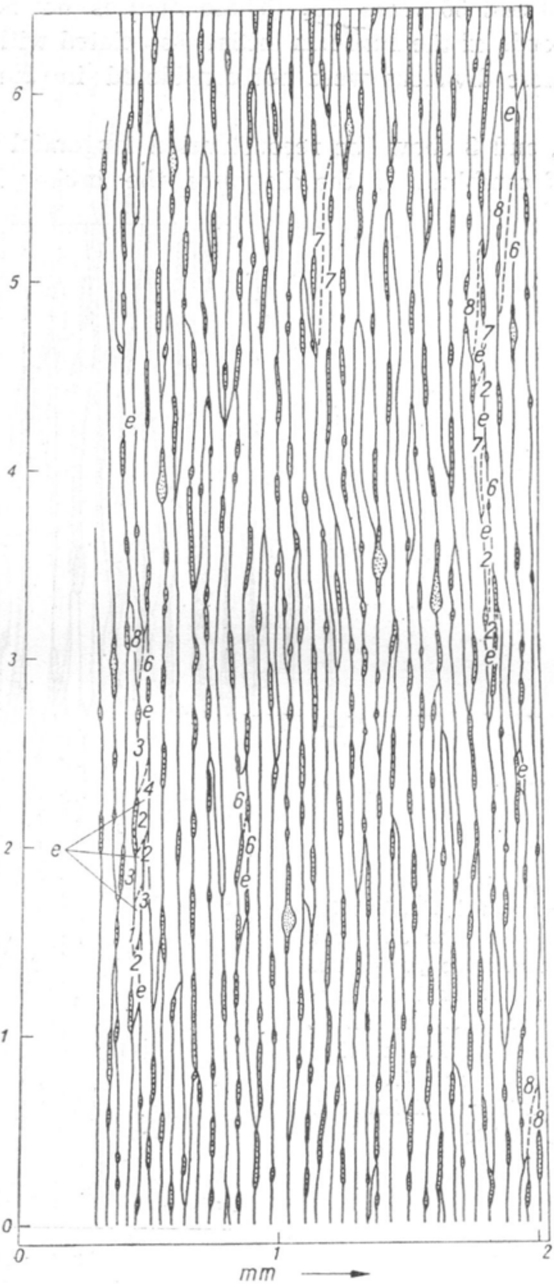


Fig. 3. The same as in fig. 1 and 2, but for the cambium of an 80-year old stem. Two kinds of anticlinal divisions are visible: 1) long divisions taking place singly in the fusiform initials, and 2) shorter ones taking place in groups in the fusiform initials undergoing elimination

symmetrically distributed with regard to the ends of the mother cells. The walls are of two kinds: either they are oblique, and then they run from one wall to the opposite wall of the mother cell, or they begin and end at the same wall of the mother cell. In the former case they result from anticlinal divisions shortening the cells, i.e. from pseudotransverse anticlinal divisions, and in the latter they result from divisions causing the separation of the long side segment.

The question now arises whether the sharply oblique position of the anticlinal walls separating the sister fusiform initials is of primary origin, i.e. produced by an oblique division, or whether its origin is secondary. In the latter instance the division would be transverse and would be followed immediately by strong intrusive growth causing the oblique arrangement of the wall separating the sister cells.

A detailed analysis of the cells derived from anticlinal divisions shows that it is possible to distinguish between the segments od walls formed in the course of cell divisions and the walls formed by intrusive growth. The part of a cell formed as the result of intrusive growth is forced inbetween neighbouring cells and owing to this it has a different appearance than the part along the plane of anticlinal division.

The series of photographs "*A*" in Plate 1 show fragments of root cambium containing cells from an anticlinal division: in row "*a*" an anticlinal division, which occurred in a fusiform initial and was followed by one periclinal division, is distinctly visible beginning with the level of 200 μ. At the levels from 20 μ to 160 μ the upper end of a cell derived from an anticlinal division and undoubtedly formed as the result of intrusive growth already after the anticlinal division is to be seen forced inbetween the rows of neighbouring cells (in circle).

The part forced inbetween the neighbouring cells is short as compared to the part limited by the wall derived from the anticlinal divison. On the photographs of the same series in row "*b*" there are two sister fusiform initials produced in the course of a pseudotransverse division which had not yet time to divide periclinally. (In the same row there is among the mother cells of the phloem another earlier anticlinal division which should not be mistaken for the one just mentioned). The lower end of the left initial in row "*b*" is visible on the last photograph of the series. There is no evidence to indicate intrusive growth in this initial derived from an anticlinal division. All this leads to the conclusion that the anticlinal divisions are not followed by intrusive growth of special intensity and, therefore, the oblique arrangement of cell-walls derived from an anticlinal division in the root cambium is of primary origin.

Mention has been made earlier that the anticlinal divisions in the root cambium can be of two kinds, i.e. there can be pseudotransverse and side divisions. Divisions of both kinds may lead to the formation either of the fusiform initials or of cells which in the course of transverse divisions develop into ray initials.

This investigation was mainly concerned with the direction of the walls derived from pseudotransverse divisions. In the cambium of the root this direction may vary being either right-or left-handed.

In the cambium of stems there are, similarly as in the root cambium, pseudotransverse divisions, but the essential difference between the two kinds of cambium is that the pseudotransverse divisions in the cambium of stems almost exclusively follow the left-hand rotation i.e. the direction of these divisions is conformable with the direction of a left-hand spiral (it was proved that the methods of drawing the figures does not invert the direction). Among the 36 identified pseudotransverse divisions in the four-year old cambium there were only 3 with a right-hand rotation. Fig. 9 shows nine anticlinal divisions in fusiform initials of which seven have the left-hand rotation. There is one right-hand division in cell "*c*" and one side division in cell "*k*". In the four-year old cambium there are rather frequent anticlinal divisions in the phloem mother cells: the projections of the walls from these divisions onto the surface of the cambium are shown in fig. 2 by dotted lines. These divisions have also the left-hand rotation.

In the cambium of the two older stems the left-hand rotation of the pseudotransverse divisions is even more distinct. Out of the 56 examined divisions, some of which are shown in fig. 3, as many as 54 have the left-hand rotation and only two have the right-hand rotation.

Side anticlinal divisions in the fusiform initials of the cambium of stems are rare. They have been found occasionally in the four-year old cambium and none have been found in the cambium of the older stems.

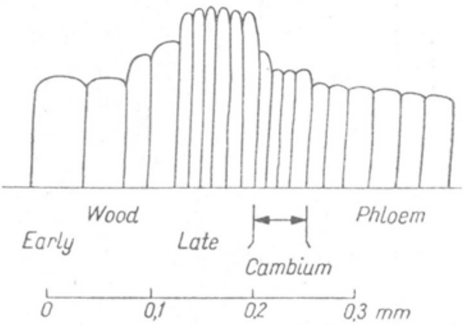
Later in this work we shall deal more fully with the process in the cambium of stems leading to the elimination of fusiform initials. This process has a great influence on anticlinal divisions, which in the stems always occur at the points of the elimination of initials. Besides the strongly oblique pseudotransverse divisions in the long fusiform initials there are also relatively short divisions occuring in groups in the eliminated initials. The various kinds of pseudotransverse divisions in the cambium of older stems are shown in fig. 3.

Intrusive growth

Intrusive growth in the fusiform initials can be recognized by comparing the length of these cells with the length of the phloem cells produced previously in the same row, since presumably the phloem cells do not increase in length during differentiation. The fusiform initials are usually longer than the young phloem cells in the same row and a negative difference of length may occur only in the case of cells just in the course of elimination. The difference between the length of fusiform initials and the length of the young phloem cells in the same row can be, therefore, regarded as an indicator of the magnitude of the intrusive growth which took place in these initials in the time between the formation of the phloem cells concerned and the fixing of the cambium.

Fig. 4 shows the levels of the ends of cells forming a radial row of common origin. The figure illustrates the average conditions in rows not directly neighbouring upon the initials which are eliminated in the cambium of the 80-year old tree. As is to be seen the cambium cells are somewhat longer than the young phloem cells, but somewhat shorter than the

Fig. 4. The ends of cells of common origin forming one radial row in the cambium of an 80-year old tree. The diagram illustrates the average conditions prevailing in rows not neighbouring upon the initials undergoing elimination. The intrusive growth of the fusiform initials is so weak that it is not marked on the diagrams in fig. 5—7. The vertical and the horizontal scales are the same



tracheids of late wood. In the rows neighbouring directly upon the initials undergoing elimination the differences in the length of the phloem cells and of the cambium cells are much greater. The differences in the levels of the ends of the fusiform initials and of the corresponding young phloem cells in the three investigated cambium kinds are shown in figs. 5, 6, and 7. For the particular fusiform initials this difference is represented by an arrow beginning at the level at which the phloem cells end (in the zone of the first ring of albuminous cells) and ending at the level of the tip of the fusiform initial.

As is to be seen there is a considerable variability in the intensity of intrusive growth of the particular fusiform initials in the same cambium. The intrusive growth is specially strong in the initials neighbouring upon the cells undergoing elimination and marked „*e*" in the diagrams (the places where the elimination of an initial or its part ended shortly before fixation are marked with broken lines). The three series of photographs in Plates 1, 2, and 3 show the points in the cambium where fusiform initials are being or were eliminated and where the intrusive growth of the neigh-

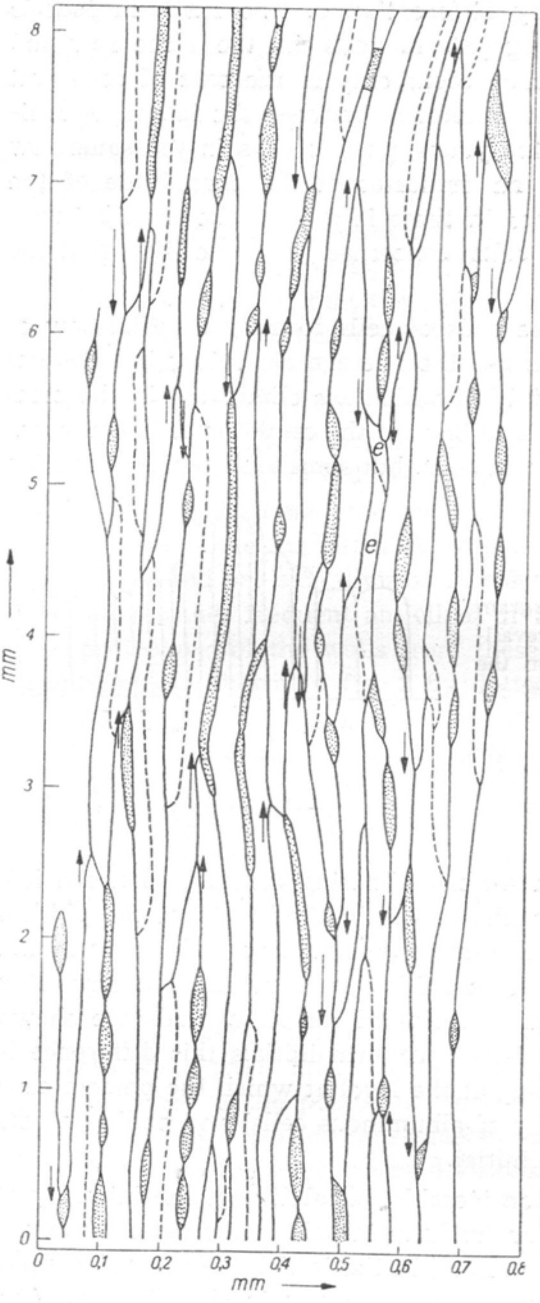


Fig. 5. Reconstructed tangential section through the root cambium. The arrows show the distances between levels of the endings of the fusiform initials and of the corresponding young phloem cells. The arrows beginning at the level of the phloem cell ends extend to the ends of the fusiform initials. In this way the length of the arrows is a relative measure of the intensity of intrusive growth in the fusiform initials. Differences of lengths smaller than 40 μ (see fig. 4) are disregarded and the cells showing only such differences are not marked with arrows. The fusiform initials undergoing elimination are marked with the letter "*e*". The other denotations are the same as fig. 1

bouring cells is very strong. In order to bring out more clearly what is taking place in these places the plates are supplemented with diagrams (figs. 9, 10, and 11) showing the reconstructed tangential sections of the corresponding parts of the cambium in the plane of the fusiform initials and in the plane of the young phloem cells. In each of these figures the diagrams *B* show the state of the fusiform initials at the time when they were fixed and the diagrams *A* the conditions which prevailed in the cambium somewhat earlier at the time of the formation of the phloem layer with the albuminous cells.

The analysis of all these illustrations as well as of photographs of the other parts of the cambium not reproduced in this report leads to the conclusion that the places round the eliminated cells are the centres of especially strong intrusive growth.

The intrusively growing ends of cells force their way inbetween the anticlinal walls of the neighbouring cells. The new walls derived from anticlinal divisions are accessible to this intrusive growth during a short time after their formation. Cell ends have been observed between the walls from anticlinal divisions with only a few periclinal divisions following the anticlinal division.

At this point the question arises what is the direction of overlapping when the ends of two cells growing in opposite directions meet? It seems that in the places where there is no elimination of cells and where the intrusive growth is week the fusiform initials may overlap either to the right or to the left. However, in the places where an intial is eliminated, and where the intrusive growth is strong, the left-hand shift of the ends is always observed. This state of things is illustrated e.g. by the series of photographs in Plate II (the upper end of the initial „*d*" in fig. 11). At the point where an initial is eliminated the direction of intrusive growth of the ends of neighbouring cells is probably determinated by the direction of the anticlinal divisions in the eliminated cell.

The intrusive growth is strongest in the cells from the middle of the cambium zone, i.e. in the fusiform initials (see photographs in fig. 8, the level of about 800 μ in series *C* on Plate I, and the level of about 4440 μ on Plate III).

Mention has been made earlier of intrusive growth derived from a pseudotransverse division. Generally speaking this growth is not noticeable till some time after the anticlinal division, already in the course of the periclinal divisions.

In the root cambium where the elimination of initials is very limited intrusive growth after an anticlinal division is not specially strong. The situation is different in the cambium of stems, where after an anticlinal

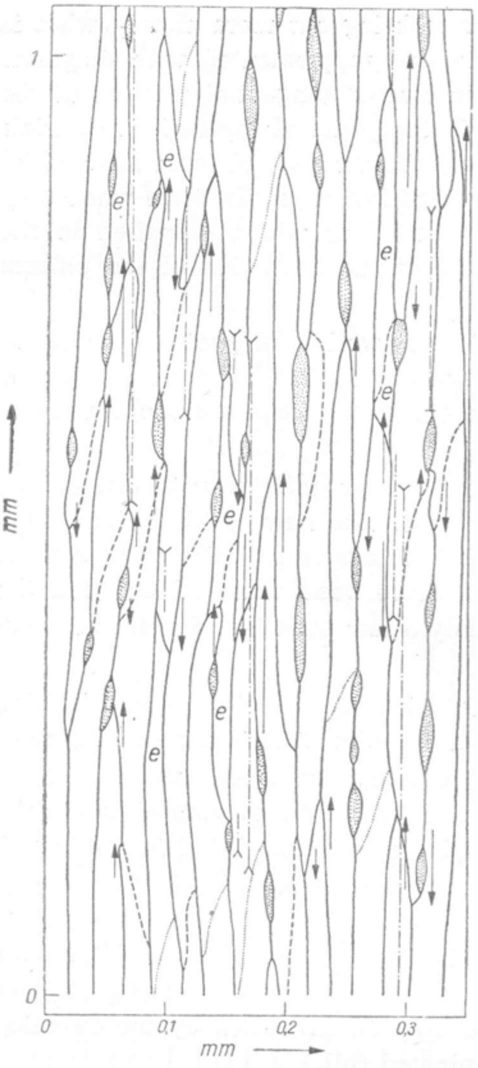


Fig. 6. The same as in fig. 5, but for the cambium from a four year old stem. The dot-dash line marks the place where a fusiform initial or its part was not long ago eliminated from the cambium, i.e. the place where the radial row is interrupted in the cambium zone. The level corresponding to the ends of phloem cells in the interrupted row is marked with the sign v: thus the dot--dash line without the sign v corresponds to the level at which a fusiform initial still not eliminated from the cambium begins and this initial is marked with the letter "*e*"

division the growth of the newly formed initials often is very strong (series *C*, Plate I). However, this intense growth is always associated with the elimination of some neighbouring cells, even if it is a sister cell from the anticlinal division. Owing to this circumstance it is difficult to distinguish the intrusive growth following on an anticlinal division from the intrusive growth associated with the elimination of a neighbouring cell.

There is no intrusive growth in the fusiform initials which are in the course of elimination.

No noticeable difference in the intensity of growth of the lower and the upper ends of the fusiform initials has been observed. In some particular initial usually the growth of one end only is intense (if there is any

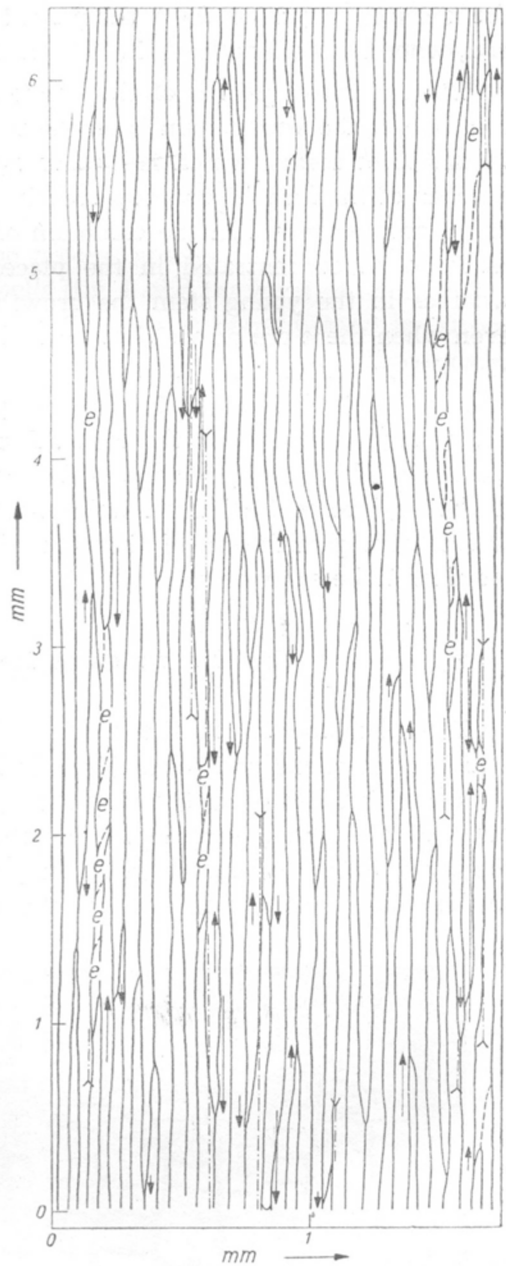


Fig. 7. The same as in fig. 6 but for the cambium from an 80-year old stem

intense growth in the cell at all). The strongly growing end is the one which neighbours with the eliminated cell.

Similarly, no differences have been observed between the ability for intrusive growth of the upper and the lower ends of the xylem mother cells. In the stem of the 80-year old tree intrusive growth associated with the differentiation of the tracheids of late wood is about 80 μ at each end, whereas the length of the cells is 4.5 mm.

The intrusive growth of the fusiform initials in the cambium of the root and of the young stem is on the whole stronger than in the cambium of the older stems, which is clearly apparent when the lengths and the number of the long arrows representing the intrusive growth in figs. 5, 6, and 7 are compared. In the cambium of the older stems intrusive growth tends to be concentrated in the places where initials were eliminated, whereas in the young stem the growth of most initials is rather strong even when there are no visible traces of elimination in the neighbourhood. This difference seems to be associated with the difference in the relative rate of the girth increase in the young stem and the root on one hand and of the older stem on the other. The increase of the girth of the older trees is so slow that probably, if there was no elimination of initials and if the replacement of the eliminated cells was not necessary, the rate of intrusive growth and of the other changes in the cambium would be too slow to be apperceivable.

The elimination of the fusiform initials

The phenomenon of the elimination of initials is common in the cambium of stems and takes place both in the young as well as in the old cambium. However, the elimination is the most distinct in the cambium of old stems, because in the old stems the changes occurring in the cambium are concentrated at the points of the elimination of initials. In the stem of the 80-year old tree there are on the average about 20 cells

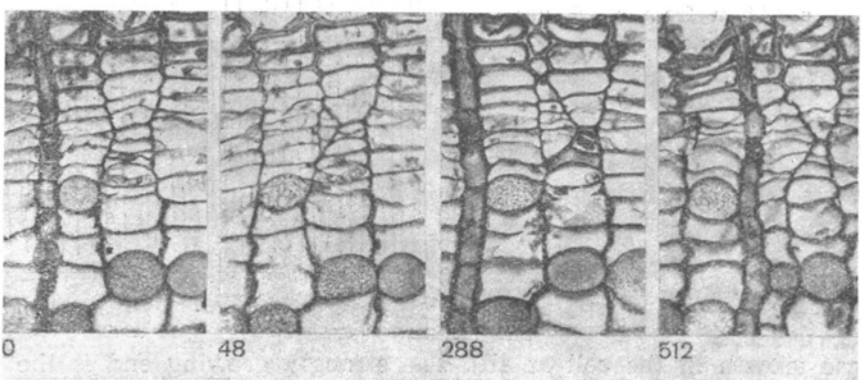


Fig. 8. A series of photographs of the cambium from an 80-year old stem showing a fusiform initial in the course of elimination and the intrusive growth of the neighbouring initial. The figures indicate the distance in μ of the level of each photograph from the level of the first one

in the course of elimination to one centimetre of the circumference of the cambium containing about 200 fusiform initials. In the cambium of the root used for the investigation the elimination ot the fusiform initials is very rare.

The phenomenon of the elimination of fusiform initials consists in the breaking of continuity of the radial row of the cambium cells so that the cell which so far was an initial cell, is moved either to the phloem or to the wood (Plates I, II, and III). The process always begins by the narrowing down of the row of cambium cells (fig. 8 and the level of about 3000 μ on Plate III). The narrowing down of a row is accompanied by strong intrusive growth of the ends of the neighbouring cells (i.e. the ends of the cells directly neighbouring upon the cells undergoing elimination); the intrusion proceeding on the whole along the radial walls of the contracting row is caused by the cells responsible for the elimination forcing their way sidewards inbetween the cells which are to be separated. Even the initial cells of the ray may take part in the sideward pushing apart of the other cells (see e.g. level 2400 μ in series B on Plate I) though is possible that ray cells play only a passive part under the pressure of the neighbouring fusiform initials.

The elimination may affect one of the cells derived from a pseudotransverse division of a long fusiform initial (then the other cell grows strongly at the newly formed end and takes part in the elimination of its sister cell), or it may affect a whole initial which does not begin to divide anticlinally into several segments till after it is submitted to sideward pressures. The final break of the continuity in a riadial row of cambium cells (divided anticlinally into segments) takes place in stages in such a way that the pushing apart affects one segment. Cells of each segment are forced apart over the whole of their length simultaneously. The sequence of the anticlinal divisions in the fusiform initials in process of their elimination is such that the initial is first divided into long but not necessarily equal segments and then each part is again divided into smaller segments. This is illustrated by the group of anticlinal divisions in row „*e*“ of series B on Plate I.

DISCUSSION

The results of this investigation may help in the understanding of the processes taking place in the nonstoried cambium, though on the whole these processes are known. The problems considered are not new, but the method applied in this work of directly observing the cambium itself was new. Owing to this many details of the investigated phenomena have appeared more clearly than in the earlier researches. Among the new details there is an important one: the divisions taking place in the cambium of larch all have one direction. We may as well start the discussion with this trait.

The earlier investigations carried out by B a n n a n and his school (B a n n a n, W h a l l e y, B a y l y) have brought no decisive information as to the direction of the anticlinal divisions. It is impossible to say whether in the species studied by that school (larch was not one of them) the anticlinal divisions were one-directional or not (it is noteworthy that in the root cambium of larch the anticlinal divisions are not one-directional). This trait might have occurred in those species, but it was not noticed when the history of the development of cambium was reconstructed from the tangential sections of the xylem or the phloem. Although, on the few drawings illustrating the reports of B a n n a n's school walls from anticlinal divisions can be seen running from right to left or in the opposite direction, it is impossible to decide how far these diagrams are comparable because, apart from other reasons their orientation is unknown (for a given direction of the rotation it is not the turn in the plane of the cambium that is important but the side from which this plane is observed).

The question thus arises, what may be the significance of the fact that the divisions in fusiform initials are one-directional?

As is well known, the secondary wood elements are often arranged in a spiral. This is clearly visible in the trunk from which a long splinter was cut out by lightning. The spiral arrangement of fibres is a well known defect of timber when the spiral is so compact that it makes difficult the working of the wood. The causes of the spiral arrangement of fibres in timber are unkown (B r o w n et al. 1949). According to C h a m p i o n (1925) compact spiral may be a hereditary trait. It seems probable that in general the spiral arrangement is a characteristic trait of an individual or of a species, but the normal spirals are too loosely wound to be easily noticeable.

Examinations of the trunks of the European larch, including also the trees of this investigation, show that the cracks in the rhytidome usually run along a spiral.

The spiral arrangement of cells in the xylem and in the phloem is evidently caused by the spiral arrangement of the fusiform initials in the cambium. Thus, to explain the reason for the presence of spirals in wood it is necessary to explain the circumstances in which spirals are formed in cambium. In this last case the reason for the formation of spirals may easily be the fact that anticlinal divisions are one-directional.

The significance of one-directional anticlinal divisions in the formation of the spiral arrangement is obvious. Their effect can be either direct, by determining the direction of the walls formed in the course of anticlinal divisions, or indirect, by determining the direction of intrusive growth which is another source of anticlinal walls. It, therefore, seems plausible to suppose that the greater the number of anticlinal divisions with the same direction of rotation and the stronger the intrusive growth accompanying these divisions, the greater will be the probability for the formation of a spiral arrangement.

If the frequency of the anticlinal divisions and the intensity of intrusive growth were only just sufficient to increase the girth of the cambium, then the development of a spiral arrangement would be less probable. However, the elimination of the fusiform initials may be considered to be the mechanism accelerating the rate of the changes in the cambium. Owing to the elimination of these cells both intrusive growth and anticlinal divisions may take place more rapidly than what is indicated by the rate at which the distance of the cambium from the centre of the trunk increases.

According to B a n n a n the elimination of the fusiform initials reflects the competitive conditions prevailing among the initials and acts as a mechanism of selection. In his opinion the most successful initials in the competition are the longest ones and the ones having the greatest number of contacts with the rays. In his later reports B a n n a n considered this selection to be a part of the mechanism resposible for the well known regular changes in the length of the xylem elements.

However, it seems that selection is not the only motive for elimination of fusiform initials. The results of the present investigation indicate that the elimination effect plays a part in accelerating the rate of intrusive growth and of the anticlinal divisions in cambium allowing the rearrangement of the fusiform initials and thus of wood. This role of the elimination would then have a special significance in the formation of the spiral arrangement, which for mechanical and also physiological reasons can be sometimes more effective than the parallel one.

There is still another question worth considering here. On the ground of statistical analyses B a n n a n concluded that the growth of the fusiform initials newly formed in the course of an anticlinal division followed a familiar growth patter in which the early rapid extension gave way to a gradually decreasing rate of growth as lengthening proceeded. But the results of this investigation indicate that the rapid growth takes place only in the neighbourhood of an eliminated initial. Since such eliminations often take place in the neighbourhood of the fusiform initial which divides anticlinally or one of the daughter cells is eliminated, it is obvious that the maximum of the intrusive growth rate must statistically occur in the initial stage of the development of a cell formed in an anticlinal division.

It is impossible to say at present how far this is caused by some inner rhythm in the cell development and how far it is the result of the influence derived from the cell undergoing elimination, but the latter factor should not be disregarded. There is, of course, the possibility of reversing the whole problem by saying that it is the capacity of a cell for rapid growth after an anticlinal division which causes the elimination of a neighbouring cell. However, it is necessary to keep in mind that the anticlinal division of a cell not necessarily must imply the rejuvenescence of a cell. As has been demonstrated, it may have a contrary effect if the division occurs in the course of the elimination of a cell.

CONCLUSION

This paper reports on an investigation carried out on a series of sections through the cambium of *Larix europea* from the root and from the stems of different age. All the changes taking place in the cambium described by Bannan and his school from examinations of the phloem and the xylem have been confirmed, i.e. intrusive growth, anticlinal divisions, and the loss of fusiform initials. The newly discovered element in these processes is the one-directional character of the pseudotransverse divisions. In the cambium from the stems of larch these divisions are left-hand directed but in the root cambium the directions of the divisions are different.

The results of this investigation lead to the conclusion that the elimination of the fusiform initials constitutes the mechanism accelerating the rate of the changes taking place in the cambium. Owing to the elimination of some fusiform initials the intrusive growth and the anticlinal divisions in the remaining initials can proceed more rapidly than it is indicated by the rate at which the circumference of the cambium increases.

The following hypotheses have been advanced: 1) the one-directional character of pseudotransverse divisions is an important factor of the mechanism controlling the formation of the spiral arrangement of cambium cells and thus also of the spiral grain in wood; and 2) the rate of the structural transformations of the cambium, e.g. the rate at which the spiral arrangement of the cells is formed, is controlled by the intensity of the processes in which the fusiform initials are eliminated.

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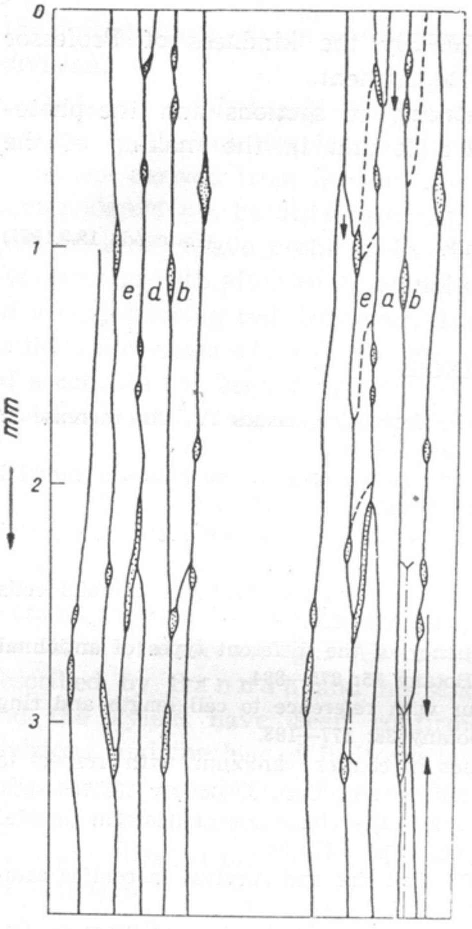

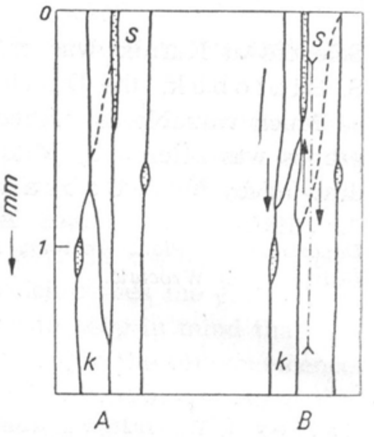

Fig. 10. The same as in fig. 9, but for the series *C* on Plate I. The diagrams illustrate the intense intrusive growth after an anticlinal division in the neighbourhood of a cell undergoing elimination

Fig. 9. Reconstructed tangential sections for the fragment of the cambium from which the photographs in series *B* on Plate I were made. *A* — reconstructed section in the plane of young phloem, *B* — reconstructed section in the plane of the fusiform initials. The broken lines represent the walls from anticlinal divisions. The arrows show the intensity of the intrusive growth of the fusiform initials (from the time at which the young phloem was formed to the time of fixation). The dot-dash lines show the places where the elimination of the fusiform initial or of its part has already ended.

Plate I

Three series of photographs of the cambium from *Larix europea*

Series *A* — root cambium: note the fusiform initials after pseudotransverse division. Series *B* — cambium from an 80-year old stem: the various anticlinal divisions are visible. The reconstructions of the corresponding tangential sections are shown in fig. 9. Series *C* — cambium from an 80-year old trunk: the photographs show intense intrusive growth in a fusiform initial neighbouring upon an initial undergoing elimination. The reconstructions of the corresponding tangential sections are shown in fig. 10.

The numbers in the left bottom corner of each photograph give the distance in μ of the level of the photograph from the level of the first photograph in the series. The distance was measured from the top downwards.

Plate I

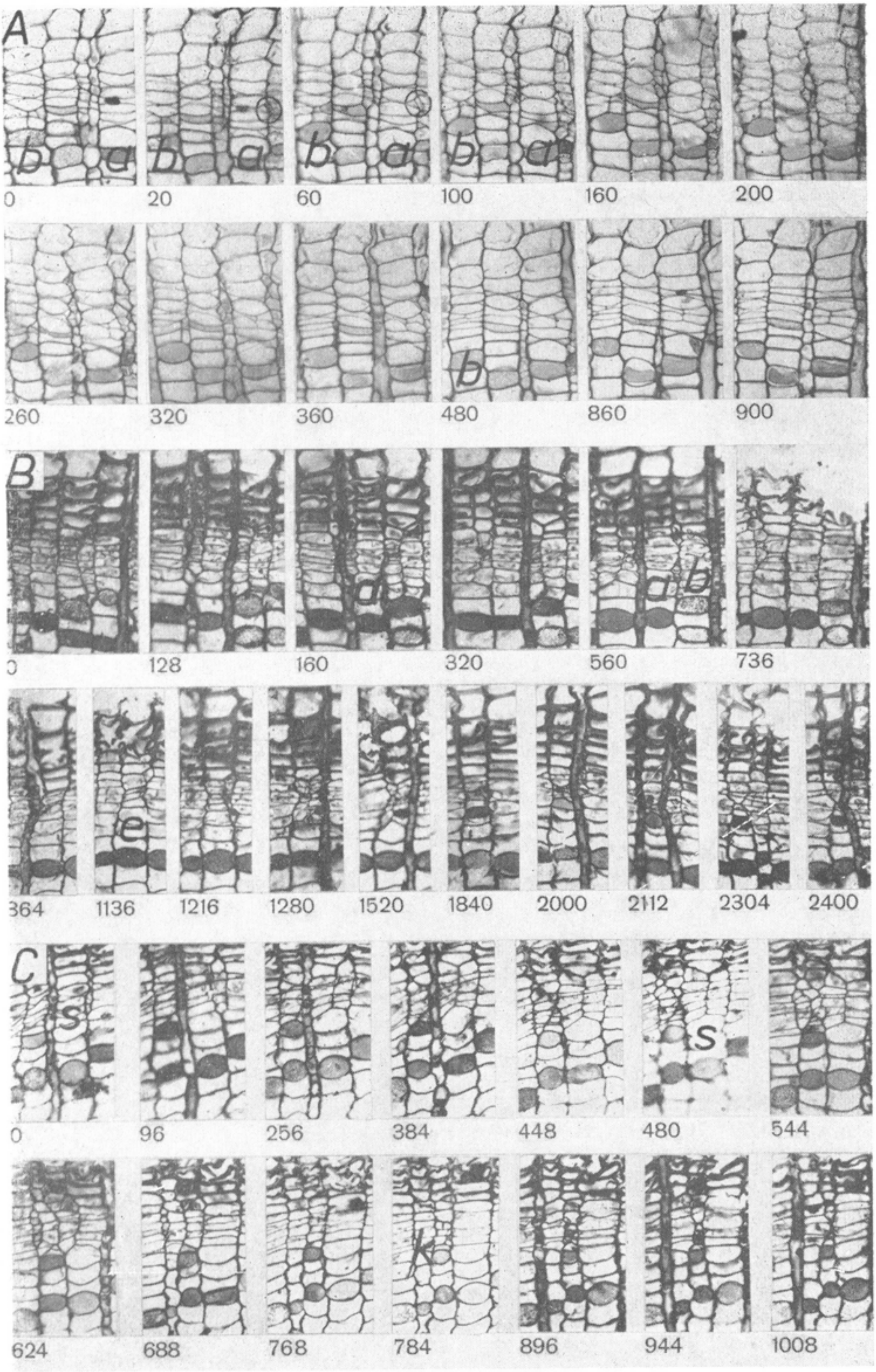
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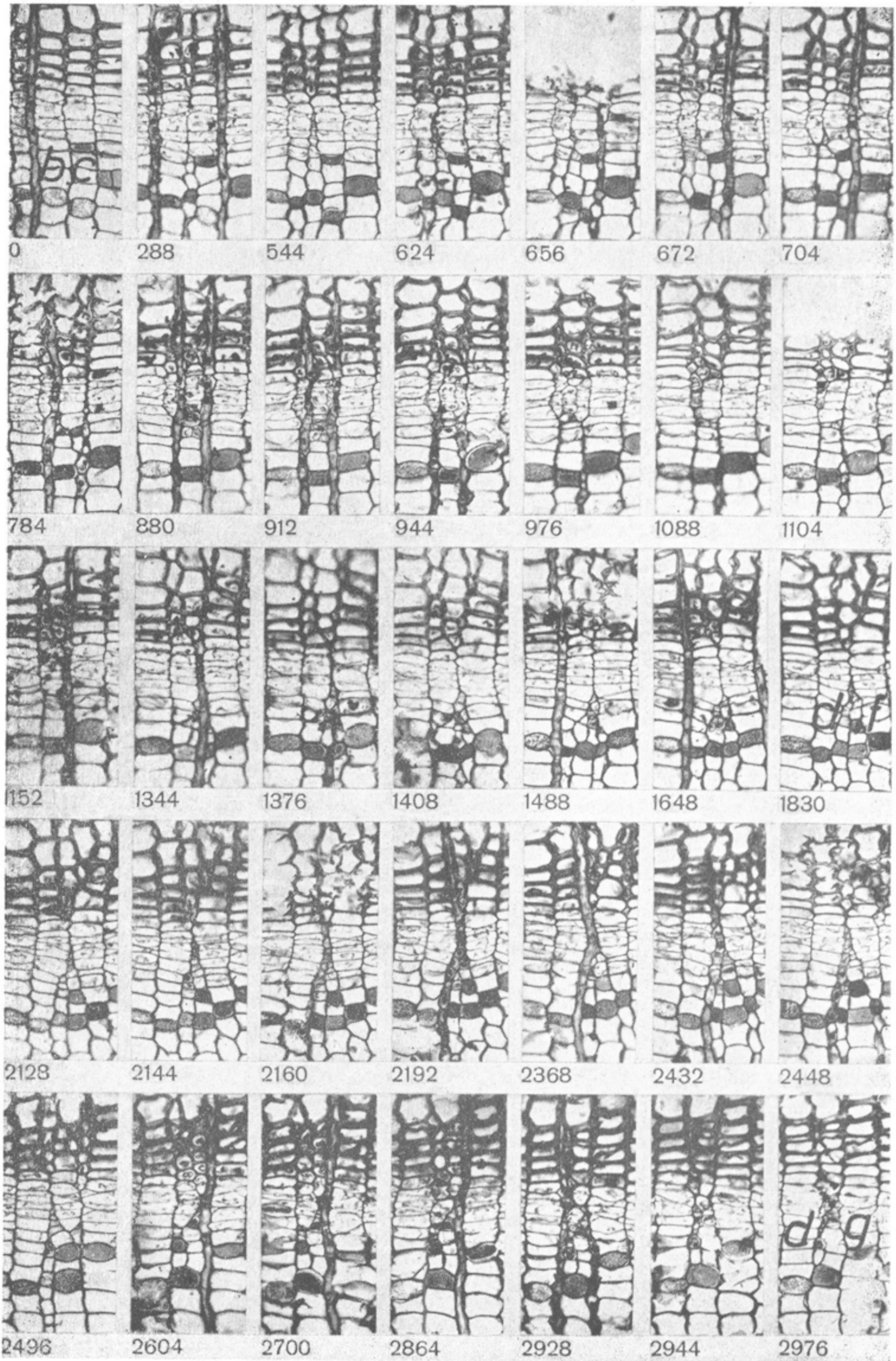
Plate II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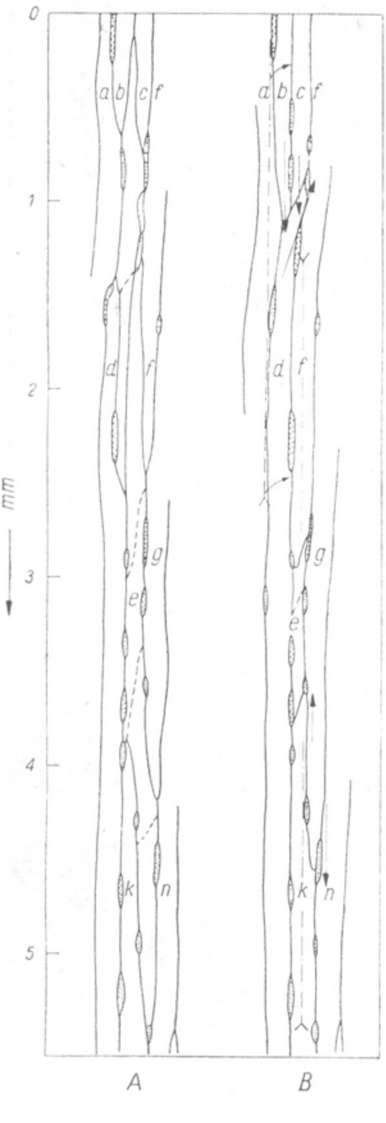
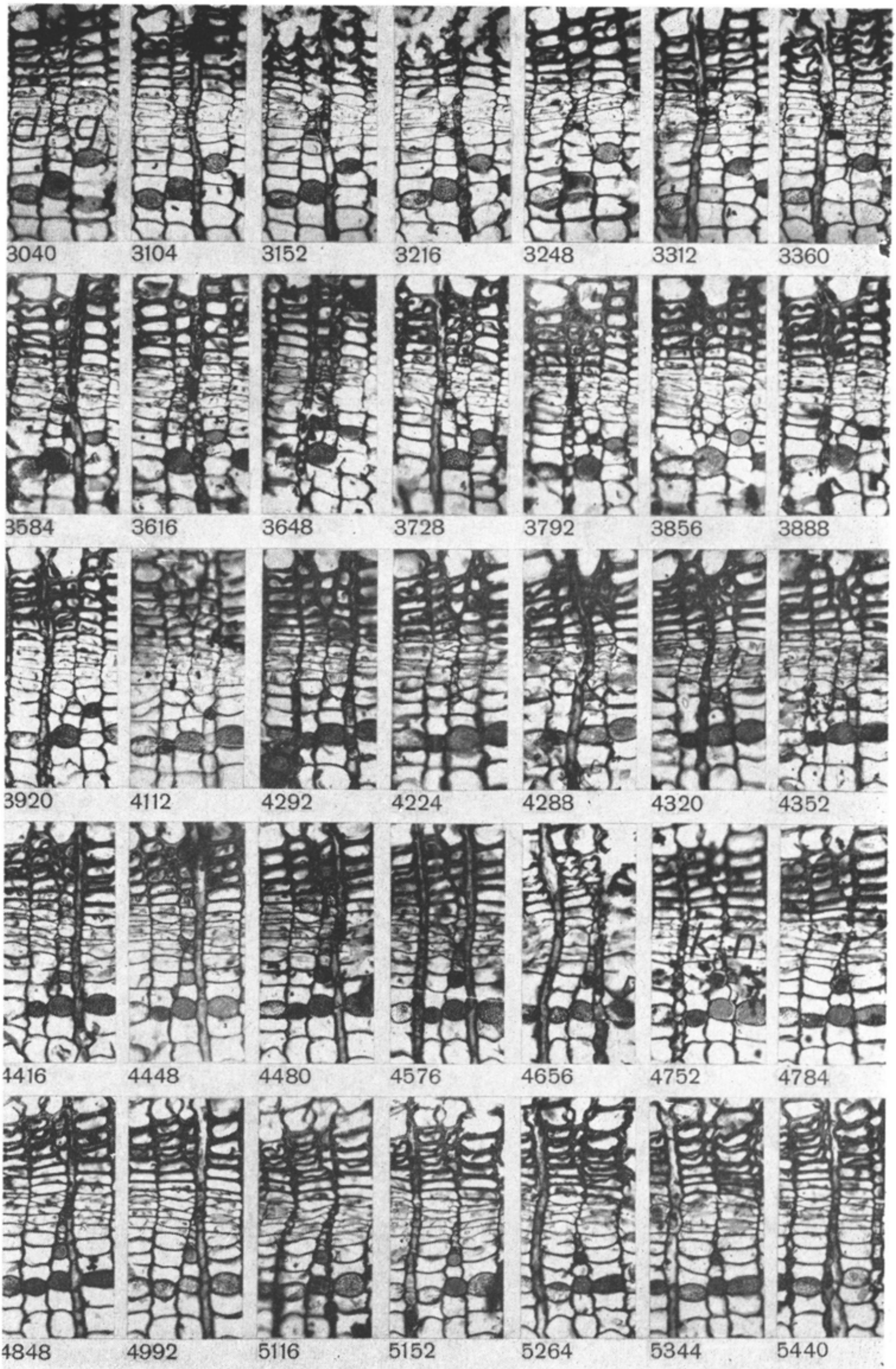


Fig. 11. The same as in fig. 9, but for the series of photographs in Plate II and III. The diagrams illustrate the behaviour of cells at the point where a fusiform initial is being eliminated and in its neighbourhood. Note in particular the intrusive overlapping onto the right side of the cells which the large cell marked "*d*" meets on its way

Plate II and III

A series of photographs of the cambium from an 80-year old tree showing the conditions prevailing in the place where a fusiform initial is eliminated. The reconstructions of the corresponding tangential sections are shown in fig. 11.

Plate III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