

THE CAMBIUM AND ITS DERIVATIVE TISSUES IV. THE INCREASE IN GIRTH OF THE CAMBIUM

I. W. BAILEY

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INTRODUCTION

Since the publication of Nägeli's (1864) "Dickenwachsthüm des Stengels," most botanists, if we may judge from statements in standard textbooks, have assumed that the increase in girth of the lateral meristem, during successive stages in the enlargement of a stem or root, is due to "radial," anticlinal divisions of the cambial initials. Not all investigators, however, have accepted Nägeli's generalization. Robert Hartig (1895) inferred from the structure of the secondary xylem of *Pinus silvestris* L. that the increase in the periphery of the cambium in conifers is due primarily to the elongation of transversely dividing fusiform initials. Klinken (1914) reached a similar inference from the study of serial sections of the phloem of *Taxus baccata* L. He concluded that there are two fundamental types of meristematic activity, one characteristic of the conifers and the other of the dicotyledons. Neeff (1920) subsequently found evidences of Hartig's and Klinken's type of cambial activity in the xylem and phloem of *Tilia tomentosa* which led him to believe that there is no such fundamental distinction between the lateral meristems of gymnosperms and dicotyledons.

There is, of course, a considerable element of uncertainty in ascribing a particular type of meristematic activity to large groups of the vascular plants, either upon the basis of *a priori* deductions or upon that of indirect evidence obtained from the study of the xylem or phloem of one or two supposedly representative species.

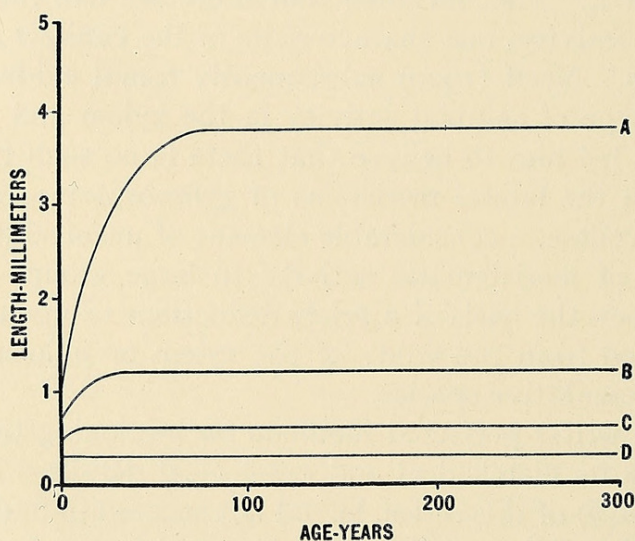
In 1917, the writer perfected methods for sectioning the cambium and for investigating its histological and cytological details. As stated in the third paper (1920 *b*) of this series, he did not succeed in finding evidences of the hypothetical radial, anticlinal divisions which are described and even figured in botanical textbooks. The normal, anticlinal divisions of the fusiform initials, in all of the gymnosperms and less highly specialized dicotyledons examined, were transverse or more or less oblique. That radial longitudinal divisions do occur, at least in certain cases, is suggested however by Kleinmann (1921), upon the basis of the orientation of karyokinetic figures in the cambium of *Raphanus*. In view of these facts, it is evident, on the one hand, that the increase in girth of the lateral meristem is not the simple phenomenon that Nägeli hypothesized, and, on the other

hand, that there may be more than one fundamental type of cambial activity in the vascular plants.

ANALYSIS OF THE PROBLEM

In Nägeli's formulae for computing the frequency of radial divisions, during a given increase in the diameter of a stem or root, the size of the cambial initials is treated as a constant. It is well known, however, that the cambium or lateral meristem is composed of initials of two distinct shapes and sizes: (1) *fusiform initials*, relatively large, elongated elements whose derivatives become differentiated into tracheids, fibers, vessels, sieve tubes, etc.; and (2) *ray initials*, scattered aggregations of small, more or less isodiametric cells which divide to form the horizontal sheets of radially disposed parenchyma, the so-called medullary rays (Plate XXXVI). Therefore, upon the basis of *a priori* considerations, the increase in girth of the lateral meristem might be due to one or more of the following factors:

1. An increase in the tangential diameter of the fusiform initials.
2. An increase in the length of these cells.
3. An increase in the number of these cells.
4. An increase in the diameter of the ray initials.
5. An increase in the number of these cells.



TEXT FIG. 1. Normal curves, showing average lengths of cambial initials at successive stages in the enlargement of a stem. *A*, Conifer or vesselless dicotyledon. *B*, Less specialized type of dicotyledon. *C*, Highly specialized type of dicotyledon. *D*, Highly specialized type of dicotyledon, having a stratified cambium.

In many of the vascular plants, as the writer has shown in previous papers of this series (1920, 1920*a*, 1920*b*), the initials tend to be larger in old stems than in young shoots, but they do not continue to increase in size throughout the entire life of an individual. Thus, in the conifers and

less specialized dicotyledons, where the fluctuations in cell size are considerable, the normal curve of average length of the fusiform initials at successive ages is of the general type illustrated in text figure 1. There is a rapid increase in length for a period of years until a certain size is attained which then remains more or less constant during succeeding growth of the plant. Are these variations in cell size significant factors in the increase in girth of the lateral meristem during the earlier stages in the enlargement of a stem? Some typical measurements taken from *Pinus Strobus* L. are of interest in this connection.

One-year-old stem

Radius of woody cylinder.....	2,000 microns
Circumference of cambium.....	12,566 microns
Average length of fusiform initials.....	870 microns
Average tangential diameter of fusiform initials.....	16 microns
Number of fusiform initials in a cross section of stem.....	724 microns
Average tangential diameter of ray initials.....	14 microns
Number of ray initials in a cross section of stem.....	70 microns

60-year-old stem

Radius of woody cylinder.....	200,000 microns
Circumference of cambium.....	1,256,640 microns
Average length of fusiform initials.....	4,000 microns
Average tangential diameter of fusiform initials.....	42 microns
Average tangential diameter of ray initials.....	17 microns

The increase in width of the original 724 fusiform initials would produce, during the 59-year interval, an arc of 30,408 microns, and the increase in the diameter of the 70 ray initials, during the same interval, an arc of 1,190 microns; or a total circumference of 31,598 microns as compared with the actual circumference of 1,256,640 microns. In other words, the enlargement of the cambial ring, during the 59-year interval, is due primarily to an increase in the number of initials; from 724 to 23,100 fusiform initials and from 70 to 8,796 ray initials.

It is to be emphasized in this connection that such a multiplication of cambial initials—as seen in any given transverse plane or cross section of a stem—is not due necessarily to cell division. For, if the initials elongate and slide by one another, the number which intersect a given transverse plane will be continually augmented. However, if the increase in the number of fusiform initials in *Pinus Strobus* were due entirely to longitudinal sliding growth, the original initials, during the 59-year interval, would have to attain an average length of approximately 26,800 microns instead of 4,000 microns. The ray initials do not elongate to any considerable extent.

In exceptional cases, e.g., *Sequoia*, the fusiform initials may attain a maximum variability in length of 9,000 microns and in width of 60 microns,

but the rate of increase in size during a given period of years is not much in excess of the values recorded for *Pinus Strobus*. Furthermore, the ray initials in certain dicotyledons may have a maximum enlargement in diameter of from 30 to 40 microns, but the variability in the size of their fusiform initials is much less than that which occurs in most conifers.

It is evident, accordingly, that, although the increase in size of the cambial initials, during the earlier stages of the enlargement of certain plants, is by no means a negligible factor, the rapid increase in girth of the lateral meristem must in general be due largely to a progressive increase in the *number*, rather than in the *size*, of its constituent cells.

What then is the relative significance of the increase in the number of the two types of cambial initials? In the young shoot of *Pinus Strobus*, the combined diameters of the 70 ray initials form an arc of 980 microns, whereas those of the 8,796 ray initials in the 60-year-old stem constitute an arc of 149,532 microns, or approximately one eighth of the total circumference of the cambium. Many of the dicotyledons have a much higher percentage of ray initials. Indeed, in extreme cases more than one half of the circumference of the lateral meristem may be occupied by ray initials. Therefore, in discussing the *modus operandi* of the increase in girth of the cambium, it is essential to distinguish between the effects of (1) those anticlinal divisions which are concerned in the origin and multiplication of ray initials, and (2) those which produce an increase in the number of fusiform initials.

The reader should bear in mind in this connection that Nägeli's generalization is based upon the assumption that the divisions in both types of initials are radial, whereas the conclusions of Hartig, Klinken, and Neeff refer to the activity of the fusiform initials. The writer will likewise confine his attention in the following pages to the fusiform initials, reserving further discussion of the ray initials for a subsequent paper of this series.

SIGNIFICANCE OF THE ARRANGEMENT OF FUSIFORM INITIALS

In the gymnosperms and less specialized dicotyledons, the fusiform initials are not arranged in regular rows, whereas in certain of the more highly differentiated dicotyledons they are symmetrically grouped in parallel, horizontal series. The question suggests itself, accordingly, is this striking dissimilarity in the architecture of the lateral meristem indicative of fundamental differences in the growth and division of the fusiform initials, and, if so, what factors are concerned in the transitions from a non-stratified to a stratified arrangement?

As shown in figures 4-6, Plate XXXVI, the "fusiform" initials in stratified meristems are roughly hexangular with long parallel sides and abruptly tapering ends, and the elements of adjacent horizontal series do not overlap to any considerable extent. In other words, the form and the arrangement of the initials indicate very clearly that the increase in girth

of the cambium cannot be due to the *elongation* of transversely dividing cells; for, if it were, the superimposed initials must necessarily crowd by one another and ultimately break up the stratified arrangement. Conversely, if the anticlinal divisions are radio-longitudinal, the products of successive divisions should be grouped in horizontal rows, unless this arrangement is modified by differences in the elongation of adjacent elements. In non-stratified cambia, figures 1-3, the adjacent, overlapping fusiform initials vary considerably in length, but, as the writer has previously stated, the *average* length of these elements does not increase appreciably during the later stages of the enlargement of a stem or root. Thus, the increase in the number of fusiform initials in non-stratified meristems cannot be due solely to radio-longitudinal divisions; for, if it were, there would have to be a general increase in the length of the initials during all stages of the enlargement of the plant.

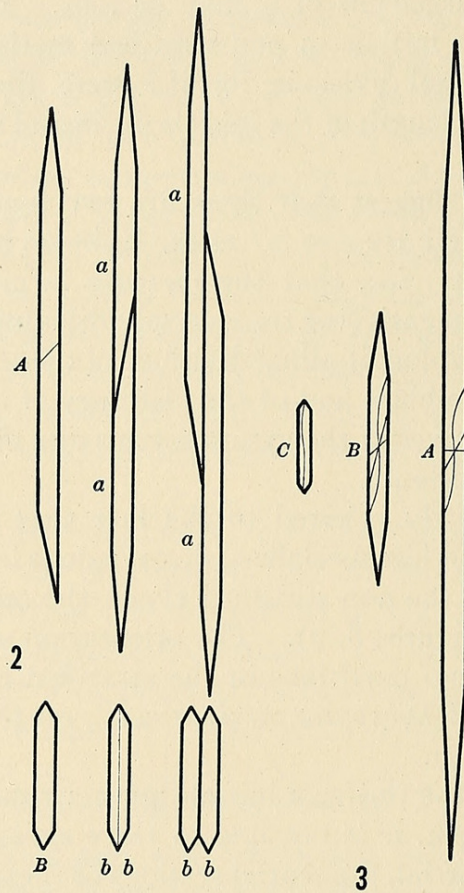
Such facts as these suggest that there are two fundamentally different types of meristematic activity—so far as the fusiform initials are concerned—in the vascular plants; *i.e.*, that the increase in girth of non-stratified cambia is due to the elongation of transversely dividing initials and that of stratified cambia to radio-longitudinal divisions of these elements. Detailed investigations of the cambium and of the histology of its derivative tissues, in numerous representatives of the gymnosperms and dicotyledons, strongly support such an assumption.

The writer has already referred to the fact that in all of the lateral meristems of conifers and less specialized dicotyledons investigated by him—which are, of course, of the non-stratified type—the anticlinal divisions are transverse or oblique (figures 8, 9). The orientation of the cell plates and recently formed anticlinal partitions in the stratified meristems of *Robinia Pseudo-Acacia* L. and of *Diospyros virginiana* L., on the contrary, is radio-longitudinal (figures 6, 7).

Furthermore, since the fusiform initials leave a record of their activities in the xylem and phloem, it is possible to trace successive stages of their growth and division in serial, tangential sections of these tissues.¹ Although this indirect method of studying cambial activity must be applied with a considerable degree of caution, particularly in the case of dicotyledons, it enables one to investigate a large number of plants of which suitable material of the lateral meristem is not readily available. In all of the various genera (62) of gymnosperms and dicotyledons that the writer has examined in this way, the evidence indicates very clearly that the anticlinal divisions in non-stratified meristems are pseudo-transverse, whereas those in stratified cambia are radio-longitudinal. In meristems of the former type, the fusiform initials elongate, sliding by one another, until they attain a certain size. They then divide by means of a more or less oblique partition into

¹For detailed descriptions of this method, the reader is referred to Klinken's and Neeff's papers.

two short halves which in turn elongate and divide (text figure 2, *A*). Owing to the fact that the cells do not divide and elongate in unison, there is a very considerable variability in the length of adjacent initials. In addition, owing to the fact that the frequency of the anticlinal divisions and the elongation of the fusiform elements are not constant, the size of the initials tends to fluctuate more or less in different parts of a given individual; *e.g.*, they tend to be considerably shorter in slender shoots than in robust stems (text figure 1). Thus, the non-stratified arrangement and the variability in size of the fusiform cells are both due primarily to elongation



TEXT FIG. 2. Diagrams illustrating *modus operandi* of the increase in girth of cambium in non-stratified and stratified lateral meristems. *A*, Fusiform initial from non-stratified cambium, dividing pseudo-transversely; *a, a*, products of this division which elongate and slide by one another. *B*, Fusiform initial from stratified cambium; *b, b*, products of the radio-longitudinal division of this initial, which expand laterally but not longitudinally.

TEXT FIG. 3. Types of anticlinal divisions in fusiform initials. *A*, Typical fusiform initial of a conifer. *B*, Fusiform initial of a dicotyledon, having non-stratified cambium. *C*, Fusiform initial of a dicotyledon, having a stratified cambium.

following pseudo-transverse, anticlinal divisions. In meristems of the latter type, on the contrary, the initials divide radio-longitudinally and the products of such divisions expand laterally, but they do not elongate to any considerable extent (text figure 2, *B*). The structure of the secondary

issues in the Calamariales, Sphenophyllales, Lepidophytineae, and Cycadofilices indicates that the cambia in these primitive groups of vascular plants were of the non-stratified type.

In view of these facts, we appear to be justified in concluding that there are at least two distinct, fundamental types of cambial activity in the vascular plants. In the vascular cryptogams, gymnosperms, and less specialized (structurally) dicotyledons, the anticlinal divisions are more or less transverse and the products of these divisions elongate and crowd by one another, producing thereby an increase in the girth of the cambium and a non-stratified arrangement of its cells. In certain of the more highly differentiated dicotyledons, on the other hand, the anticlinal divisions are radio-longitudinal and the products of these divisions expand laterally, thereby increasing the circumference of the cambium, but they do not elongate to any considerable extent, and thus become symmetrically grouped in parallel, horizontal series.

THE TRANSITION FROM THE NON-STRATIFIED TO THE STRATIFIED ARRANGEMENT

In previous papers of this series, the writer (1918, 1920a) has called attention to the fact that in the dicotyledons there is a progressive reduction in the length of the fusiform initials and of their derivatives, which closely parallels successive stages in the differentiation of highly specialized types of vascular tissues. As indicated in table 1, the vesselless dicotyledons (Tetracentron, Trochodendron, and Drimys), whose secondary xylem closely resembles that which occurs in the vascular cryptogams and gymnosperms, have large fusiform initials; fully as large as those of most gymnosperms, for example. Dicotyledons with vessels, on the contrary, are characterized by having much smaller meristematic cells which become shorter and shorter as the tracheary elements become more and more highly specialized. Furthermore, stratified meristems tend, in general, to be composed of smaller fusiform initials than non-stratified cambia. It should be noted, in addition, that, during this sequence of changes, the size-on-age curves (text figure 1) are depressed and ultimately become approximately horizontal; *i.e.*, the length of the fusiform initials is stabilized in plants having stratified meristems.

These facts are of considerable interest in discussing the *modus operandi* of the transitions from one fundamental type of meristematic activity to the other. In most of the non-stratified meristems that the writer has studied, the orientation of the anticlinal partitions fluctuates between a transverse position and varying degrees of obliquity (text figure 3). As the fusiform initials become shorter, the ends of the more oblique partitions tend to approach the extremities of the cells, or, in other words, to become more and more nearly radio-longitudinal. Thus, certain of the more highly differentiated dicotyledons have transitional types of meristems, which show in-

TABLE 1. Length (in microns) of adjacent fusiform initials in random samples of the lateral meristem of old stems

NON-STRATIFIED CAMBIA

Gymnosperms

Species	Max.	Ave.	Min.
<i>Ginkgo biloba</i> L.....	3,000	2,200	1,400
<i>Pinus Strobus</i> L.....	4,000	3,200	2,300
<i>Picea Abies</i> (L.) Karst.....	4,200	3,300	2,400
<i>Juniperus virginiana</i> L.....	3,000	2,200	1,000
<i>Larix decidua</i> Mill.....	5,000	4,000	2,500
<i>Sequoia sempervirens</i> Endl.....	8,700	6,600	4,200
<i>Agathis robusta</i> F. M. Bailey.....	7,700	6,800	4,100
<i>Tsuga canadensis</i> (L.) Carr.....	4,400	3,200	2,200
<i>Podocarpus Nageia</i> R. Br.....	5,000	3,800	2,300
<i>Cedrus libani</i> Barrel.....	4,100	2,900	2,100
Average.....	4,910	3,820	2,450

Dicotyledons

A. Vesselless

<i>Trochodendron aralioides</i> Sieb. et Zucc.....	6,200	4,400	2,800
<i>Drimys Winteri</i> Forst.....	4,500	3,300	2,400
Average.....	5,350	3,850	2,600

B. Vascular tissues not highly differentiated

<i>Betula populifolia</i> Marsh.....	1,160	940	700
<i>Myristica philippensis</i> Lam.....	1,620	1,310	990
<i>Altingia excelsa</i> Noronha.....	2,300	1,900	1,200
<i>Liriodendron tulipifera</i> L.....	1,500	1,100	700
<i>Urandra luzoniensis</i> Merr.....	1,700	1,400	1,100
<i>Dillenia philippinensis</i> Rolfe.....	2,300	1,600	1,000
<i>Gordonia Lasianthus</i> L.....	1,700	1,300	1,000
<i>Cornus florida</i> L.....	1,400	1,100	800
<i>Symplocos tinctoria</i> L'Hér.....	1,400	1,100	600
<i>Halesia diptera</i> L.....	1,100	900	800
Average.....	1,620	1,260	890

C. Vascular tissues highly specialized

<i>Carya ovata</i> (Mill.) C. Koch.....	600	520	420
<i>Litsea glutinosa</i> C. R. Rob.....	700	550	390
<i>Prunus serotina</i> Ehrh.....	590	460	320
<i>Excoecaria Agallocha</i> L.....	870	630	410
<i>Mangifera monandra</i> Merr.....	830	570	390
<i>Acer rubrum</i> L.....	610	490	320
<i>Garcentia dulcis</i> Kurz.....	1,020	740	520
<i>Vatica Mangachapoi</i> Blanco.....	810	610	410
<i>Barringtonia racemosa</i> (L.) Roxb.....	900	720	500
<i>Psychotria luzoniensis</i> F. Vill.....	1,080	700	450
Average.....	800	600	410

STRATIFIED CAMBIA

Dicotyledons

D. Vascular tissues highly specialized

Species	Max.	Ave.	Min.
<i>Grewia multiflora</i> Juss.....	370	250	160
<i>Thespesia populnea</i> (L.) Soland. ex Corr.....	280	250	210
<i>Bombycidendron Vidalianum</i> Merr. et Rolfe.....	430	360	320
<i>Heritiera littoralis</i> Dryand.....	360	300	270
<i>Kleinhovia hospita</i> L.....	480	360	270
<i>Pterospermum niveum</i> Vid.....	430	370	320
<i>Tarrietia sylvatica</i> Merr.....	340	280	210
<i>Sterculia foetida</i> L.....	450	370	320
<i>Robinia Pseudo-Acacia</i> L.....	210	170	140
<i>Diospyros virginiana</i> L.....	520	410	320
Average.....	390	310	250

Basis: 50 measurements of fusiform initials.
Probable errors of individual averages 10-15 percent.

ipient stages of stratification. Furthermore, the variability in the size of adjacent fusiform initials in stratified meristems (table 1) is due, at least in part, to the fact that many of the anticlinal divisions are somewhat oblique.²

How much significance should be attached to the close parallelism in the sequences of changes in the cambium and vascular tissues? Is the progressive reduction in cell size in the lateral meristem due to the increasing specialization of the vascular tissues, or *vice versa*? Many morphologists interpret such correlations as due to cause and effect. There is, however, a very considerable element of uncertainty in so doing, where the basis of comparison is time, as Karl Pearson has so clearly shown. Thus, in the absence of reliable collateral evidence it is not possible to determine whether the changes in the cambium are due to those which occur in the vascular tissues or *vice versa*, or whether the parallel sequences are both due to some third factor or group of factors.

SUMMARY AND CONCLUSIONS

1. There are two fundamental types of cambial activity in the vascular plants: one characteristic of the Calamariales, Sphenophyllales, Lepidophytineae, Cycadofilices, Gymnospermae, and less differentiated (structurally) Dicotyledoneae, and the other of certain highly specialized dicotyledons.

2. In the former type the fusiform initials are not arranged in regular rows. The anticlinal divisions are pseudo-transverse and the products of

² The size and the arrangement of the fusiform initials is also modified by the ray initials, new aggregations of which are periodically carved out of the elongated elements.

these divisions elongate and crowd by one another, thereby producing an increase in the girth of the cambium.

3. In the latter type, in which the fusiform initials are relatively short, of nearly uniform length, and more or less symmetrically grouped in parallel, horizontal series, the bulk of the anticlinal divisions is radio-longitudinal, and the increase in the periphery of the cambium is due primarily to the lateral expansion of the products of these divisions.

4. The transition from the non-stratified to the stratified arrangement closely parallels successive stages in the specialization of the vascular tissues, *e.g.*, the differentiation of vessels, libriform fibers, etc., and appears to be due to a progressive reduction of cell size and of longitudinal sliding growth in the cambium.

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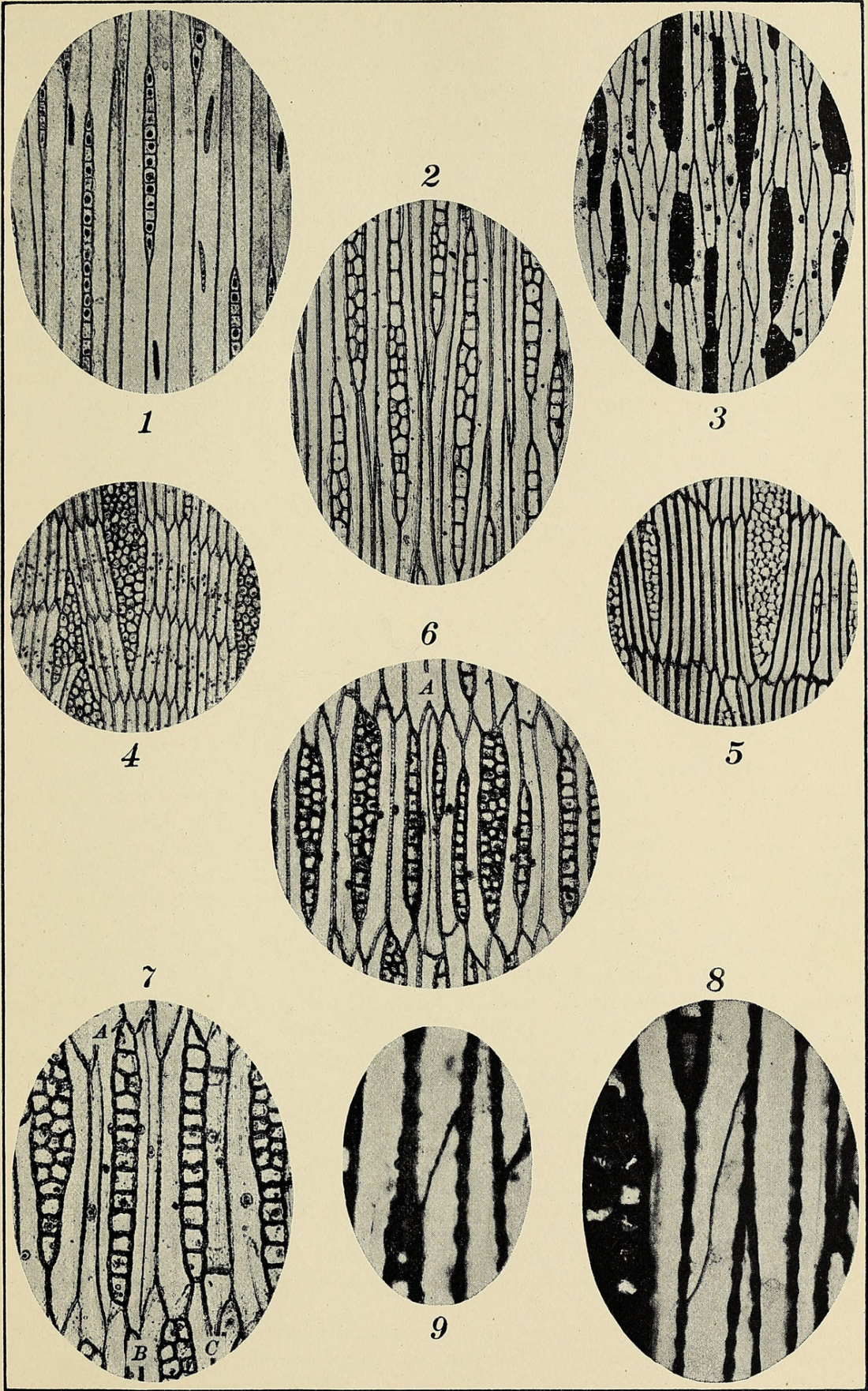
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EXPLANATION OF PLATE XXXVI

FIG. 1. *Pinus Strobus* L. Tangential longitudinal section of non-stratified lateral meristem. The cells are so long that only a portion of each fusiform initial is shown in the photomicrograph. $\times 110$.

FIG. 2. *Myristica philippensis* Lam. Tangential longitudinal section of non-stratified lateral meristem of less highly differentiated type of dicotyledon. $\times 110$.

FIG. 3. *Fraxinus americana* L. Tangential longitudinal section of non-stratified lateral meristem of highly specialized type of dicotyledon. $\times 110$.



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FIG. 4. *Robinia Pseudo-Acacia* L. Tangential longitudinal section of stratified lateral meristem of highly specialized type of dicotyledon, showing parallel horizontal series of fusiform initials. $\times 110$.

FIG. 5. *Heritiera littoralis* Dryand. Tangential longitudinal section of immature phloem, showing stratified elements. $\times 110$.

FIG. 6. *Diospyros virginiana* L. Tangential longitudinal section of stratified lateral meristem. Fusiform initial (A) has divided radio-longitudinally. $\times 110$.

FIG. 7. *Same*. Portion of cambium more highly magnified. Cells A and B have formed radio-longitudinal, anticlinal partitions. Cell C is dividing periclinally. The kinoplasmasomes are approaching the ends of the cell. $\times 148$.

FIG. 8. *Liquidambar Styraciflua* L. Tangential longitudinal section of non-stratified lateral meristem, showing oblique anticlinal division of fusiform initial. $\times 450$.

FIG. 9. *Same*. Oblique anticlinal division. $\times 450$.



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