VII—THE WOOD ANATOMY OF THE FAMILY STERCULIACEAE

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[Plates 29–31]

CONTENTS

I—Introduction

The group Malvales is moderately well defined, both taxonomically and in the anatomy of the wood, but, to judge by the frequency with which the limits of the families are constantly being revised, its division into families and subfamilies is still a matter of some difficulty to taxonomists. A similar state of affairs exists in regard to the wood, for, although it is comparatively easy to recognize a specimen as one of the Malvales, it is often extremely difficult to decide to which family it belongs. This is possibly due in large part to faults in the systematic grouping, and the present investigation was undertaken to find out whether the groups suggested by the wood anatomy can be used to clarify the taxonomic position. In one family in particular, the Sterculiaceae, the wood anatomy suggests a heterogeneous group that needs revising, and this family has therefore been selected for detailed study. Two aims have been kept in view: the first, to find out how far the wood anatomy is in agreement with the present taxonomic classification, and what changes it suggests; the second, to try to ascertain which features in the wood are peculiar to a family, and imply relationship, and which are to be encountered in unrelated families, and represent stages in phylogenetic development.

The need for a revision of the existing classification of the family became evident at an early stage in the investigation, for the family Sterculiaceae, as established by

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Bentham and Hooker (1867), includes a group of woods with a very wide range of structure; and, in spite of having given its name to the family, the genus *Sterculia* is by no means typical of it. Further investigation led to the conclusion put forward by the author (Chattaway 1932), that not only is *Sterculia* not typical of the family as a whole, but that the entire subfamily to which it belongs differs considerably from all the other subfamilies of Bentham and Hooker's Sterculiaceae. The anatomical differences are indeed so great that it seems inappropriate to retain for so large a family as the one they delimited a name that is associated with an isolated group within it. This conclusion, based upon anatomical characters, supports that which Edlin (1935) drew from the floristic characters, namely, that the family name should be restricted to the Sterculieae. In the past, various authorities have suggested that this subfamily stands apart from the others, but none of them raised it to the status of a separate family, although, as Edlin states, the differences between the Sterculieae and the related subfamilies (under the old classification) are quite as sharp as those separating many other families. This idea was indeed put forward by Dumont (1887), who concludes from the general anatomy that the Sterculieae is "a group parallel to the primary families Malvaceae, Bombacaceae and Tiliaceae".

Within the subfamily Sterculieae itself there has been further confusion in the classification of the genera. The genus *Sterculia* has often been reclassified and redivided; for example, the genera *Brachychiton*, *Ebribroma*, *Firmiana*, *Pterygota*, *Pterocymbium* and *Scaphium* have all at one time or another been classified as *Sterculia*. Edlin (1935) is unable to find any satisfactory means of distinguishing these genera floristically, and states (p. 9) that within the tribe Sterculineae the *Colas*, confined to Africa, are not easily distinguished from the more widely distributed *Sterculias*, and, with the exception of *Tetradia* and *Octolobus*, the other genera have all at one time or another been accounted *Sterculias*. He therefore divides the family into two tribes, containing only seven genera, as follows:

Sterculineae: *Sterculia* L.; *Cola* Schott; *Tetradia* R.Br.; *Octolobus* Welw.

Tarrietineae: *Tarrietia* Bl.; *Heritiera* Ait.; *Argyrodendron* F. von Muell.

Edlin concludes, "until this group, numbering at least 150 species scattered throughout Asia, Africa, Australia and South America, has been revised monographically by one investigator, it will be impossible to say with finality what genus should or should not stand....It is possible that a careful consideration of the wood structure of the Sterculiaceae may throw light on the value of the generic divisions". The present author has made such a study, and has been able to suggest changes in regard to some of the difficult genera.

The second aim of the investigation is to study the relative values of the anatomical characters that are commonly used for diagnostic purposes, by examining their occurrence within a group of closely allied woods. Research by other workers upon vessel-member length (Frost 1930*a*, *b*), pitting (Frost 1931) and ray type (Kribs 1935), has established a sequence of development for each of these features, so that it is possible to say whether a wood is primitive or advanced in regard to them. By using these established characters it is possible to decide upon the level of development attained by any family, such as the Sterculiaceae, and also to arrange the genera within the family in order, representing an advancing series of specialization in regard to vessel-member length, pitting or ray type. The evidence obtained from such a series can then be used to test the other features in the wood. This method has been applied to the Sterculiaceae, for vessel diameter, vessel number, the percentage of solitary vessels, fibre length and the type of parenchyma, but the conclusions that are drawn can only be applied within this family. Probably some of the developmental series will be found to apply only to single families or groups of families, and to have no general application, while others apply to all woods, irrespective of their family. The former may imply relationship, the latter must be regarded as "stage features" (Chalk 1935), representing stages of development passed through by members of totally unrelated groups. The great difficulty in this part of the work has been that the anatomist must use the genera, as established by the taxonomists, to find out what are reliable generic characters, while, as will be shown in § XII, the taxonomists are not unanimous as to the constitution of the different genera.

In handling the material assembled for this investigation two alternative methods of presenting the facts were considered. The first, that of treating each genus separately and then reviewing the anatomical characteristics of the family as a whole, was discarded; it would involve much repetition, because the genera are very much alike in several of the features examined. The second method, which is the one adopted, is to consider each anatomical feature separately, establishing so far as possible the position of each genus in regard to that feature, and finally to give an abbreviated description of the genera, picking out the particular features by which each can be distinguished from the rest. The position of the genera is discussed and the proposed changes explained and justified in § XII. By this means the material relating to the systematic position of the genera can be placed together and can be read without the necessity of disinterring it from a mass of anatomical detail. Similarly, each separate anatomical feature has as far as possible been treated comprehensively in the appropriate section, so that the facts relating to any particular tissue can be found together.

II—Terminology

The technical terms used in this paper are for the most part those approved by the International Association of Wood Anatomists, and published in the "Glossary of Terms used in Describing Woods" (1933). Where these terms are new, or differ from those previously in use, they are explained in footnotes.

III—MATERIAL AND METHODS

The material examined is as follows (the species are given in § XII):

Argyrodendron F. VON MUELL.	17	specimens of	3	species.
Brachychiton SCHOTT and ENDL.	10	,,	3	,,
Cola SCHOTT	29	,,	13	,,
Eribroma PIERRE	1	,,	1	,,
Firmiana MARSIGLI	9	,,	5	,,
Heritiera AIT.	16	,,	4	,,
Octolobus WELW.	1	,,	1	,,
Pterocymbium R.BR.	9	,,	2	,,
Pterygota ENDL.	7	,,	3	,,
Scaphium ENDL.	7	,,	4	,,
Sterculia L.	72	,,	32	,,
Tarrietia BL.	27	,,	7	,,

In all 205 specimens of seventy-eight species, representing twelve different genera, were examined. Of these *Cola*, *Eribroma* and *Octolobus* are confined to tropical Africa, and *Brachychiton* and *Argyrodendron* to Australia; *Scaphium*, *Pterygota*, *Firmiana* and *Pterocymbium* occur in tropical Asia; *Tarrietia* occurs in tropical Asia and Australia, and *Heritiera* in tropical Asia and tropical Africa; *Sterculia* has a very wide range of distribution throughout the entire tropics. *Tetradia* is now extremely rare, and it has not been possible to obtain material of this genus.

Transverse, tangential and radial sections of the wood, cut at 10–15μ, have been used for the general investigation of the family, but special sections, cut at about 5μ and mounted in glycerine jelly, were used for the investigations of the pitting, and sections treated with various solvents for the investigation of the crystals.

A special technique was used for the study of the rays, in order to follow their development from the cambium, and to trace the changes that take place in the cambial initials. The method that has been employed here is similar to that by which BEIJER (1927), KLINKEN (1914) and NEEF (1920) studied the structure of stratified cambium, and is a modification of that which ZIJLSTRA (1909) employed in his macroscopic study of ray structure. A wedge of wood, extending if possible from the pith to the cambium, was cut out with each side parallel to the rays, and deep enough to contain the tallest ray. Serial tangential sections were cut at 30μ; this distance was determined by the radial dimensions of the ray cells, so as to ensure that each ray cell should be represented on at least one section. By following these sections from the pith towards the periphery a picture of the cambium could be obtained as it was at different stages of development.

IV—MEASUREMENTS

Only three features have been measured for the purposes of this paper, fibre length and vessel-member* length, both measured on slides of macerated material, and vessel diameter, measured from transverse sections.

Fibre length involves little difficulty in measuring, except that of avoiding broken fibres, and of distinguishing between libriform fibres and fusiform wood parenchyma cells† in woods like *Pterocymbium* sp. and *Sterculia crassiramea* MERRIL.

Vessel-member length has been measured on macerated material, as advocated by CHALK and CHATTAWAY (1934), and the measurements were made from tip to tip of the vessel member and not from perforation plate‡ to perforation plate as before. For this reason the figures given here are occasionally slightly higher than those given in the earlier paper (CHATTAWAY 1931), because, although "tails" are exceptional in woods such as these with almost horizontal perforation plates and marked storeys, there is often a tendency for the vessel to take a lateral rather than a vertical course, and for the perforation plate to be formed in the side wall rather than in the end wall of the vessel member (CHALK and CHATTAWAY 1934).

In measuring vessel diameter, only the tangential diameter has been used. The committee of the International Association of Wood Anatomists has not yet issued any definite recommendation in regard to vessel diameter, and the terms of size used here are those proposed by CHATTAWAY (1932). It is, however, very likely that when more data have been collected from special investigations such as this, the classes may need considerable readjustment. Formerly only solitary vessels were measured, but for this investigation all the vessels have been measured, and, although this increases the range of size in any one sample, especially in woods with groups and clusters of vessels, it probably gives a truer picture of the wood than the method previously used.

Variation within a single species always presents a difficulty, and it is unwise to base the mean value for any feature on less than five or six samples from different trees. Measurements alone are seldom sufficient to distinguish between the different species of a genus even where the mean is based upon adequate material. The measurements used in this paper are expressed as the mean of each genus, and the range of the different samples is indicated by plus and minus twice the standard deviations of the means. Measurements from immature wood have been excluded so far as possible.

In a recent issue of "Trees and Timbers of the British Empire" (CHALK, CHATTAWAY, BURTT DAVY, LAUGHTON and SCOTT 1935), a new method of expressing the mean

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* *Vessel member* or *vessel element*: one of the cellular components of a vessel.—To replace *vessel segment.* Further use of the term segment is discouraged, since it implies the reverse of the actual process of vessel formation.

† *Fusiform wood parenchyma cell*: a wood parenchyma cell derived from a cambial initial without subdivision.—To replace *substitute* and *intermediate wood fibre*, which are inappropriate since they obscure the fact that the cells are parenchyma.

‡ *Perforation plate*: the area of the wall (originally imperforate) involved in the coalescence of two members of a vessel.

and range of a genus diagrammatically was used, and the same method is employed here.

Vessel number was, so far as possible, counted on 25 sq. mm., but occasionally, where only a small block was available for sectioning, a smaller area was used; in every case complete growth periods were covered so as to include vessels from both early and late wood.

V—Storeyed Structure

The genera of the Sterculiaceae are all characterized by regular storeyed structure, which produces distinct ripple marks on the tangential surface of the wood. Storeyed structure only occurs in rather highly specialized woods which have short cambial initials, and is due to the method of multiplication of the cambial initials, by longitudinal instead of by transverse divisions (Bailey 1923; Beijer 1927). This regular arrangement of the initials is reflected in the tissues formed from them, affecting the shape of the vessels, fibres and parenchyma strands (Chalk and Chattaway 1934, 1935; Janssonius 1931). A further result of this method of division is that the range of length in the vessel members decreases. Chalk and Chattaway (1935) investigated this, and showed that in storeyed woods the shortest vessel member is usually more than half the length of the longest, while in non-storeyed woods it is always less than half. This affects the coefficient of variation (Rendle and Clarke 1934); for non-storeyed woods it was found to be 0·188, and for storeyed woods 0·111. In the Sterculiaceae the storeys are very regular, and the range in cambial initial length within the family and the coefficient of variation (0·102) are very small. The higher coefficient of variation for storeyed woods generally is due to the inclusion of woods in which both methods of division occur. The marked regularity of the storeys in all the genera of the Sterculiaceae and the low coefficient of variation suggest that in this family transverse or oblique divisions of the cambial initials are uncommon.

As storeyed structure is due to short cambial initials it indicates that the woods are advanced, but apart from this it has no phylogenetic significance. It is, however, a very useful diagnostic feature, and the height of the storeys provides a simple means of estimating the length of the cambial initials. If the rays are short they too may be storeyed, and this combination of features is of still further use in recognizing woods. In the Sterculiaceae, the uniseriate rays are often storeyed, but, owing to their peculiar method of growth, the large rays are often quite independent of the storeys.

VI—Vessels

(a) *Vessel-Member Length*

The study of vessel-member length throughout a large number of families has shown (Bailey 1920) that the length of a vessel member is approximately the same as that of the cambial initial from which it was derived, and the significance of vessel-member length lies in the fact that it provides a measure of the length of the cambial initial where the initials themselves are not available. In hardwoods generally a wide range in vessel-member length may be encountered, and FROST (1930*a*, *b*, 1931) has shown that there is a relation between the length of the vessel members, the type of perforation plate and the type of intervascular pitting. He has also established the fact that, on the whole, woods with long vessel members, scalariform perforation plates and scalariform intervascular pitting are more primitive than those with shorter vessel members, simple perforation plates and alternate intervascular pitting. Subsequent research has confirmed his conclusions, and it is now possible to use vessel-member length to deduce the relative positions of woods from different families; and also as a guide to the relative position of the genera within a family, and to assess the significance of other features in the wood.

The vessel-member length for the different genera in the Sterculiaceae is shown in fig. 1. There is considerable overlapping between the ranges for the different genera (especially for *Firmiana*), but nevertheless there is a significant* difference between the values at the top and bottom of the series. The means were based on all the named species of each genus available, but in some cases this was not very many, and the means might be liable to some slight alteration if more material were available.

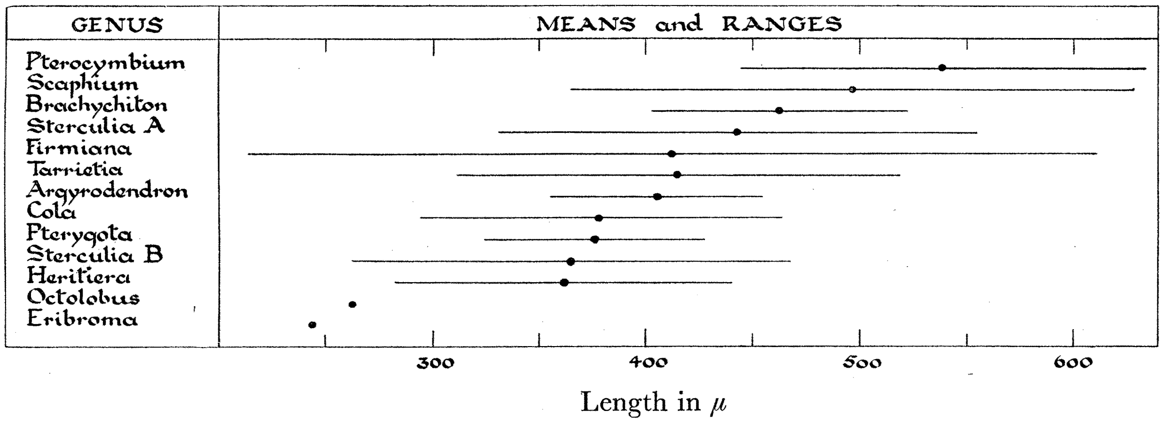

FIG. 1—Diagram to show vessel-member length in the Sterculiaceae.

It will be seen that the genus *Sterculia* appears twice in this list. A greater difference in structure was found between some of the species of this genus than between some of the other genera, and the *Sterculia* species were accordingly separated into two groups, one with narrow lines of parenchyma and one with broad bands of parenchyma. The former is referred to as *Sterculia* A, the latter as *Sterculia* B. The difference in vessel-member length between the two groups appears to be significant.

Following FROST's (1930*a*, *b*) assumption that the more primitive woods have the

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* Calculated from the formula $Ed = \sqrt{(Ea^2 + Eb^2)}$, where $Ed =$ the standard error of the difference and Ea and Eb the standard errors of the means compared. To be significant the difference between the means should be more than three times the standard error of the difference.

longest vessel members, there is some likelihood that the woods at the top of the series given in fig. 1 are slightly more primitive than those at the bottom of the series, although there is so little range throughout the whole family that no extreme differences would be expected. Furthermore, although it is quite possible that further material of any genus might alter its mean to some extent, and that changes in position between adjacent members of the series might be necessitated, it is nevertheless very unlikely that further measurements would cause changes in position between the top and bottom of the series, or between widely separated members of the series. The series into which the genera may be arranged for any one feature is not intended to be regarded as fixed or unalterable, especially when it is based upon measurements, but rather as indicating the general trend of development in that feature.

From a consideration of vessel-member length it seems probable that woods such as *Pterocymbium*, *Scaphium*, *Brachychiton* and *Sterculia* A might be expected to be more primitive than *Cola*, *Pterygota*, *Heritiera* and *Sterculia* B; but the range met with in the different genera suggests that the family as a whole is a specialized one, and the mean vessel-member length of the entire family is short ($398\mu \pm 80{\cdot}5$).

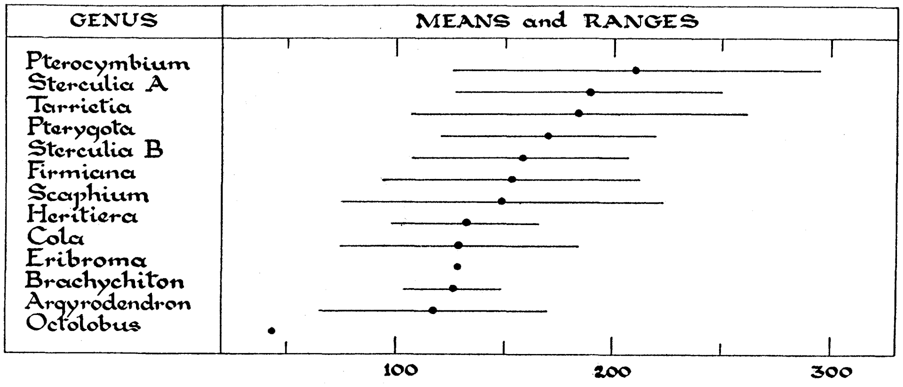
(*b*) *Vessel Diameter*

Unfortunately very little research has yet been done upon the significance of vessel diameter, but BROWN (1921) and FROST (1930*a*) have both suggested that vessels tend to be smaller in primitive woods than in specialized ones. CHALK and CHATTAWAY (1935) found no general relation between vessel diameter and vessel-member length, though they found that the maximum widths recorded all occurred in woods with relatively short vessel members. The woods measured by these authors were classified according to the type of perforation plate and the presence or absence of storeyed structure, and it was then found that within a limited range of length, such as occurs in any of these groups, the longest vessel members tend to be broader than the shortest.

The vessels in the Sterculiaceae are usually of moderate size; small vessels occur in a few species of *Cola* and in *Octolobus*, and rather large ones in *Pterocymbium* and some species of *Sterculia*. The range in size within any one sample is often very great, especially in woods that have a large proportion of clusters and groups of vessels. In these woods there may be, within a single group, vessels varying from 30 to 200μ in tangential diameter.

The means and ranges for the different genera are shown diagrammatically in fig. 2. Excluding *Octolobus*, of which only one sample was available, there is only 84μ difference between the largest and the smallest mean, and the ranges overlap very much. Nevertheless the difference between both *Cola* and *Brachychiton* at the bottom of the series and *Pterocymbium* at the top appears to be significant. *Brachychiton* and *Sterculia* A are very much alike in all other features, and the vessels of *Brachychiton* are unexpectedly small.

The chief interest in this series lies in the support it gives to the conclusions of CHALK and CHATTAWAY (1935) mentioned above. The woods of the genera of the Sterculiaceae form a series within the limits of vessel-member length associated with storeyed structure, similar to those examined before, but not including any of the same genera. The correlation coefficient between vessel-member length and vessel diameter for these woods is $+ 0{\cdot}655 \pm 0{\cdot}107$, but the relation is probably masked to some extent by the relations that may exist between these two features and the percentage of solitary vessels and the number of vessels. This will be further discussed at the end of this section.



Diameter in μ

FIG. 2—Diagram to show vessel diameter in the Sterculiaceae.

(c) *Distribution*

The author was unable to find any evidence from the work of other investigators for assigning any phylogenetic significance to vessel number, and the results given below show that within this group the number of vessels is not significantly related to the degree of specialization of the wood as inferred from the length of the cambial initials. The extreme variability of vessel number under the influence of external conditions renders it a somewhat unsatisfactory feature to work with, and there appears to be great variation, not only between the different samples of the same species, but occasionally even in different parts of the same sample. In spite of this, however, it is possible to arrive at an estimate that is sufficiently accurate to show whether the vessels are few or numerous, solitary or grouped.

The vessels in the Sterculiaceae are never numerous, and the entire range encountered was only 1–13 sq. mm. There is only a slight difference in vessel number between the different genera, but there is a difference between the two subfamilies. In the Sterculineae the vessels are (with the exception of *Octolobus*) fewer than in the Tarrietineae.

The relative frequency of solitary vessels and vessel groups was computed at the same time as vessel number; the results of both counts are shown in Table I.

The high percentage of solitary vessels in *Pterocymbium*, *Sterculia* A and *Tarrietia* are useful in helping to distinguish the woods of these genera, and the difference in the percentage of solitary vessels between *Sterculia* A and *Sterculia* B serves to emphasize the difference in structure between the two sections of the genus.

A study of the figures obtained for vessel diameter, vessel-member length, the number of vessels per unit area and the percentage of solitary vessels suggested that these features are to some extent interdependent, and that correlation coefficients between any two of them may be misleading. The method of partial correlation coefficients was therefore adopted. The primary purpose of these measurements was to find out whether the size and distribution of the vessels is in any way related to their degree of specialization, as indicated by the vessel-member length. It was observed that the vessels tended to be more solitary in the woods with long vessel members, and a correlation coefficient between vessel-member length and the percentage of solitary vessels of + 0·564 ± 0·127 confirmed this impression. But this relation disappears if a partial correlation coefficient (— 0·062) is calculated, eliminating vessel number and diameter. It is suggested therefore that the apparent relation between vessel-member length and the percentage of solitary vessels can be traced to diameter. For example, within this group, woods with long vessel members tend to have wide vessels, and wide vessels are characteristically solitary. But specialization of the wood appears to have no direct relation to the percentage of solitary vessels. Similarly it was found that there is no relation between the degree of specialization and the number of vessels. There does, however, appear to be a relation between specialization of the wood and the diameter of the vessels; such a relation has already been indicated (Brown 1921; Chalk and Chattaway 1935; Frost 1930 *a*). In the Sterculiaceae the simple correlation between these features was + 0·655 ± 0·107; the partial coefficient, eliminating the percentage of solitary vessels and vessel number, was rather lower (+ 0·408).

Table I—The Percentage of Solitary Vessels and the Number of Vessels per sq. mm.

	% of solitary vessels			No. of vessels per sq. mm.		
Genus	Mean of means		S.D. of means	Mean of means		S.D. of means
Pterocymbium	65·9	±	14·6	1·2	±	0·50
Sterculia A	63·2	±	14·5	3·2	±	1·58
Tarrietia	53·0	±	15·5	5·2	±	1·71
Scaphium	44·6	±	17·1	2·4	±	1·06
Firmiana	41·4	±	16·5	3·2	±	1·04
Eribroma	41·0			1·4		
Brachychiton	40·9	±	9·7	3·2	±	0·91
Heritiera	39·2	±	14·3	5·1	±	1·83
Pterygota	38·9	±	19·0	2·6	±	1·69
Cola	35·4	±	15·7	3·1	±	1·68
Sterculia B	32·3	±	14·6	2·5	±	0·99
Octolobus	25·0			11·0		
Argyrodendron	20·7	±	11·4	4·7	±	2·09

One striking relation emerged from these figures—between the diameter and the percentage of solitary vessels. The simple correlation coefficient was $+ 0{\cdot}922 \pm 0{\cdot}028$, which has increased to $+ 0{\cdot}938$ in the partial correlation coefficient eliminating vessel-member length and vessel number. This relation does not appear to have any significance beyond the fact that where groups are common the number of small vessels is increased, and the mean diameter correspondingly reduced.

Making use of FROST'S (1930*a*, *b*) conclusions regarding vessel-member length, one is led to the conclusion that *Pterocymbium* is the most primitive genus, and that, allowing for some slight interchange in position between the genera, there is a gradual progressive specialization through a series running as follows: *Pterocymbium*, *Scaphium*, *Brachychiton*, *Sterculia* A, *Firmiana*, *Tarrietia*, *Argyrodendron*, *Cola*, *Pterygota*, *Sterculia* B, *Heritiera*, *Octolobus*, *Eribroma*.

Specialization of the wood within this group of genera does not seem to be related to the distribution of the vessels, but there is a slight positive relation to diameter.

VII—PITTING

Research by FROST (1929) upon the pitting of dicotyledonous woods has shown that the shortening of the vessel members that indicates phylogenetic specialization is accompanied by changes in the sculpturing of the lateral walls, and that there is a parallel sequence of types of pitting from scalariform, through opposite to alternate arrangement. Alternate pits are usually associated with simple perforation plates, and are probably characteristic of the majority of dicotyledonous woods. Within this large group of woods there is considerable variation in the shape and size of the pitting, but no attempt appears to have been made to study the significance of these variations.

In the majority of woods with alternate pitting the intervascular pit-pairs* are arranged in such a way that number and size are complementary features. In a few woods the pit-pairs are widely and irregularly spaced, but in most woods the pits are so close together and so regular that their size can be conveniently estimated by the number in a given area. Using this method of estimating size the genera in the Sterculiaceae have been arranged in three groups, according to the size of their intervascular pit-pairs:

Group I: 3–6 pits per $275\mu^2$. *Brachychiton*, *Pterocymbium*, *Pterygota*, *Sterculia* A.

Group II: 6–10 pits per $275\mu^2$. *Cola*, *Eribroma*, *Firmiana*, *Scaphium*, *Sterculia* B (except *S. quinqueloba* and *S. coccinea*), *Tarrietia*.

Group III: 10–16 pits per $275\mu^2$. *Argyrodendron*, *Heritiera*, *Octolobus*.

The genus *Sterculia* occurs in two groups; in the species included in *Sterculia* A the pits are few and large, and are very similar to those of *Brachychiton*; in *Sterculia* B they

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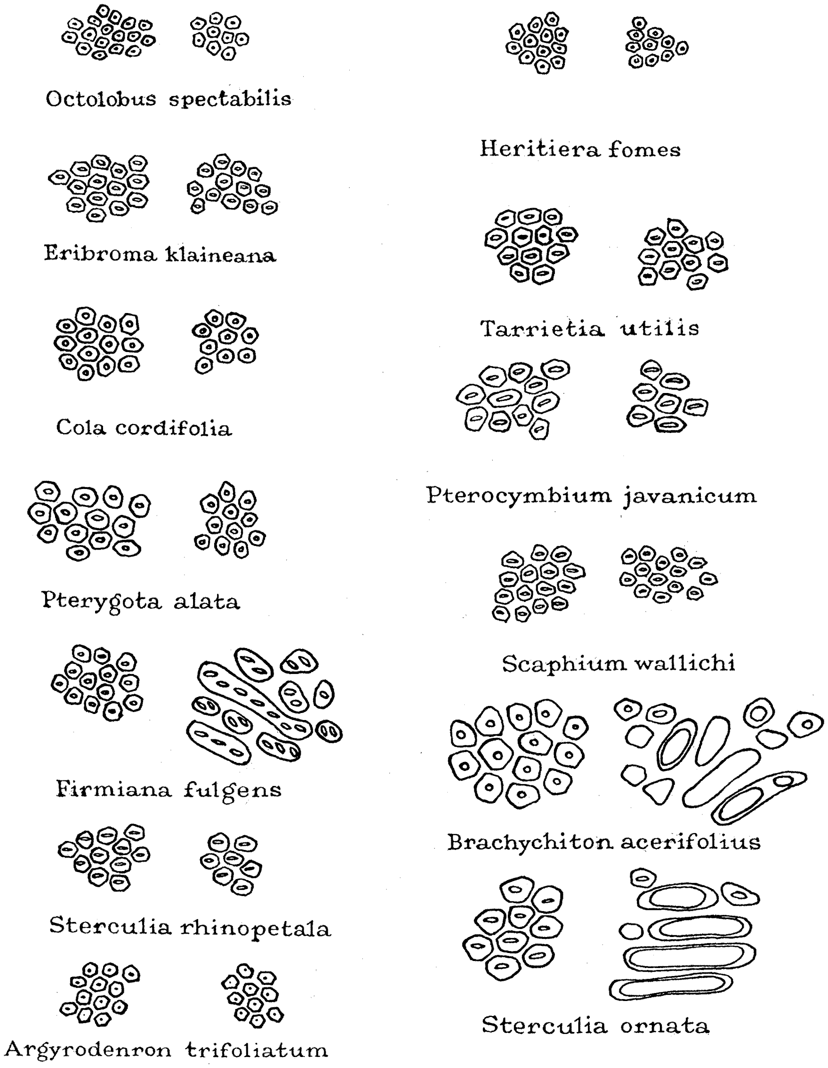
* *Pit-pair*: two complementary pits of adjacent cells.

are smaller and more numerous, like those of *Cola*; the only exceptions to this are *S. quinqueloba* K. Schum. and *S. coccinea* Roxb., which have larger and fewer pits than would be expected, and show the type of pitting otherwise restricted to *Sterculia* A.


Octolobus spectabilis

Eribroma klaineana

Cola cordifolia

Pterygota alata

Firmiana fulgens

Sterculia rhinopetala

Argyrodenron trifoliatum

Heritiera fomes

Tarrietia utilis

Pterocymbium javanicum

Scaphium wallichi

Brachychiton acerifolius

Sterculia ornata

Fig. 3—Intervascular and vessel-parenchyma pit-pairs. In each pair the intervascular pitting is on the left and the vessel-parenchyma pitting on the right. (× approx. 500.)

Fig. 3 illustrates some of the types of vascular pitting in the different genera. In each case the group of pits on the left represents pits to other vessels, and the group on the right pits to parenchyma cells. The difference in size between the intervascular pit-pairs in *Sterculia ornata* Wall. (*Sterculia* A) and *S. rhinopetala* K. Schum. (*Sterculia* B) is clearly shown.

The pits to other vessels are always alternate, commonly hexagonal in outline, and the apertures are round or elliptical, and frequently coalescent.* Fig. 4 illustrates two intervascular pit-pairs, similar to one another in shape, but with coalescent apertures towards one vessel. These coalescent apertures occur where the thickness of the wall between the pits is less than the thickness of the rest of the vessel wall. Drawings of similar pits in *Sterculia quinqueloba* K. Schum. are illustrated in fig. 5. Fig. 5 (1) corresponds to fig. 4*a*, but in the example drawn the apertures are coalescent in both vessels. Fig. 5 (3) is similar to fig. 4*c*, but the walls of the contiguous vessels differ in thickness.

The vessels never touch the rays, but are always separated from them by at least one cell of paratracheal parenchyma.† There are therefore no pits from vessels to ray cells, but only from vessels to wood parenchyma. In all the genera of the Sterculiaceae except *Brachychiton*, *Firmiana* and *Sterculia* the vessel-parenchyma pit-pairs are similar in size and shape to the intervascular pit-pairs, but consist of one simple pit in the parenchyma, and one bordered one in the vessel. Such a pit-pair is shown diagrammatically in fig. 12. The surface view is very similar to that of the intervascular pit-pairs, but the sectional elevations show a bordered pit on one side only of the middle lamella; the other pit, in the parenchyma cell, is simple. A pit-pair of this type, from the wood of *Sterculia quinqueloba* K. Schum., is illustrated in fig. 6.

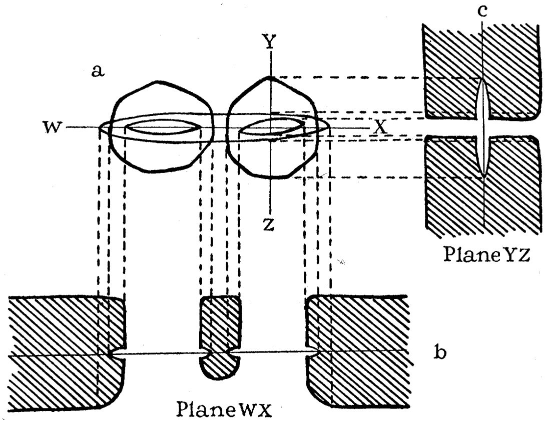


Fig. 4—Diagram of two intervascular pit-pairs, with coalescent apertures in one wall. *a*, tangential section; *b*, cross-section; *c*, radial section.

In all the bordered pits so far described the secondary wall arches over the primary pit field, producing a pit in which there is a sudden narrowing of the pit chamber towards the outer aperture. If the apertures of two or more pits coalesce, this inner aperture is very large, as in figs. 4 and 5. The pit canal, however, is not always of equal width throughout its length, and though it most commonly widens towards the inner aperture, it may occasionally narrow or curve. This is possibly due to the later deposits of the secondary wall being laid on in such a way as to arch over the earlier

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* *Coalescent apertures*: slit-like inner apertures united into spiral grooves.

† *Paratracheal parenchyma*: see footnote, p. 331.

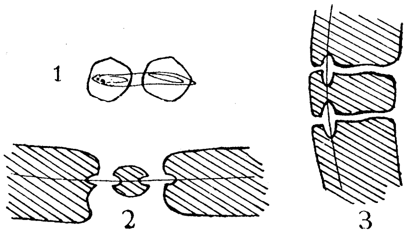

FIG.5

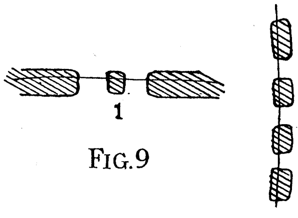

FIG.9

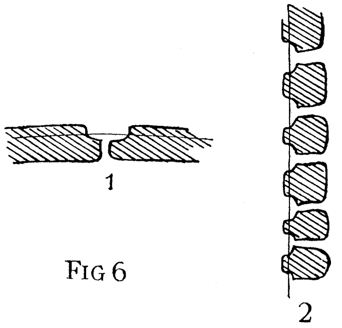

FIG 6

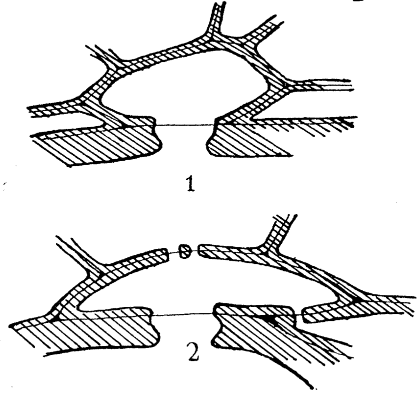

FIG.10

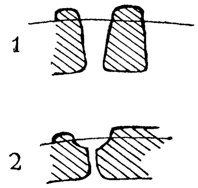

FIG.7

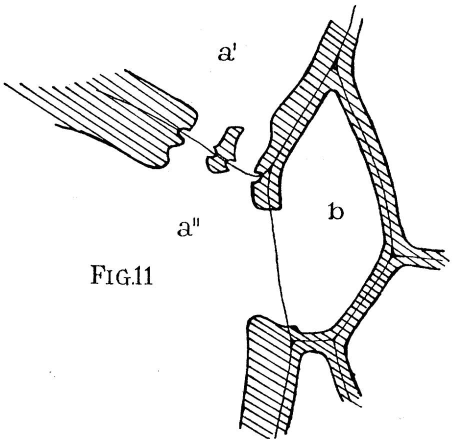

FIG.11

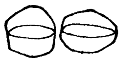

FIG.8

FIGS. 5–11—Intervascular and vessel-parenchyma pit-pairs. (All approx. × 650.)

FIG. 5—*Sterculia quinqueloba* K. SCHUM. Intervascular pit-pairs. 1, surface view; 2, cross-section; 3, longitudinal section.

FIG. 6—*S. quinqueloba* K. SCHUM. Vessel-parenchyma pit-pairs. 1, cross-section; 2, longitudinal section.

FIG. 7—*S. urens* ROXB. Vessel-parenchyma pit-pair. 1, simple pit in vessel wall; 2, bordered pit in vessel wall; 1 and 2, both in cross-section.

FIG. 8—*S. quinqueloba* K. SCHUM. Intervascular pit-pair, with wide aperture extending as far as the outline.

FIG. 9—*S. ornata* WALL. Simple vessel-parenchyma pit-pairs. 1, cross-section; 2, longitudinal section.

FIG. 10—*S. quinqueloba* K. SCHUM. Simple vessel-parenchyma pit-pairs. The vessel wall arches over the primary pit field, but no distinct pit chamber is formed. 1 and 2, cross-section.

FIG. 11—*S. quinqueloba* K. SCHUM. Group of vessel-parenchyma pit-pairs in cross-section. *a'* and *a''* are vessels, and *b* is a parenchyma cell; the pits from *a''* to *a'* are bordered, the pit from *a''* to *b* is simple.

ones. This overarching of the later deposits of the secondary wall is clearly shown in fig. 5 (2). It may also occur when the pits are simple, and it is easy to confuse the resulting simple pit with one that has a true border. The pit-pairs of *Sterculia ornata* WALL. illustrated in fig. 9 are simple, and so are those of *Sterculia quinqueloba* K. SCHUM. shown in fig. 10. These pit-pairs become more understandable when they are examined at a high magnification; seen with a low-power lens they appear bordered, but with a higher magnification it becomes clear that there is no distinct pit chamber, and that the apparent border is really an overarching secondary wall. A simple and a bordered pit from *Sterculia urens* ROXB. is illustrated in fig. 7; in each case the pit leads to a parenchyma cell, and the distinction between the two types is clear.

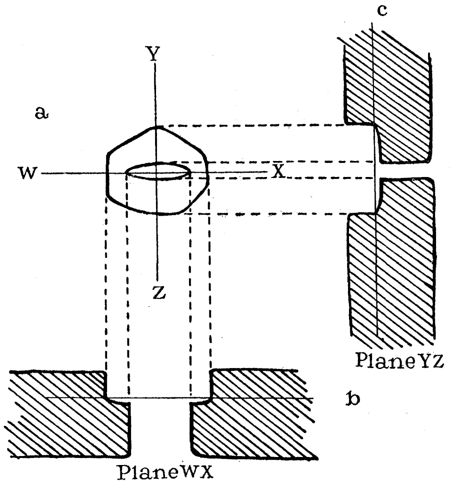

FIG. 12—Diagram of vessel-parenchyma pit-pair. *a*, tangential section; *b*, cross-section; *c*, radial section.

In *Firmiana* the majority of the vessel-parenchyma pit-pairs are similar to those described above, but unilaterally compound* pits also occur. A single oblong pit in the parenchyma cell may subtend several pits in the vessel wall (fig. 3). This type of pit is very common in *Firmiana*, and occurs occasionally in species of *Sterculia* A and in *Brachychiton*. In the last two genera there are both unilaterally compound pits and vessel-parenchyma pit-pairs that are much larger than the intervascular pit-pairs; these are illustrated in fig. 3; they are characteristic of all the species of *Sterculia* A of *S. quinqueloba* and of all the species of *Brachychiton*.

An interesting group of pit-pairs was seen in cross-section in *S. quinqueloba*; it is illustrated in fig. 11. The section passes through the junction of three cells, *a′* and *a″* are vessels, and *b* is a parenchyma cell. The pit-pairs between the vessels are bordered, and one of the pits in *a″* has an overarching wall as well as a marked border. The pit-pair between the vessel *a″* and the parenchyma cell is simple, though there is again some overarching of the vessel wall. The apertures of all three pits in the vessel *a″* are

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* *Unilaterally compound pitting*: a type of pitting in which one pit subtends two or more smaller pits in the cell adjacent.

coalescent. In *S. quinqueloba*, although a great number of apparently simple pits from vessels to parenchyma cells are seen on cross-sections of the wood, fewer are to be found on longitudinal sections. The explanation of this appears to be that even when the pits from vessels to parenchyma cells are the same size as the pits to other vessels, the apertures are often much larger than those in the intervascular pit-pairs, especially horizontally. In extreme cases the aperture extends as far as the outline, with the result that the pit may appear simple when cut through transversely, although when it is cut longitudinally a large border can be seen. Fig. 13 shows a surface view and sectional elevations of two such pits. In *b* both pits appear simple, but in *a* and *c* a border can be seen. Fig. 8 illustrates two such pits from *Sterculia quinqueloba*.

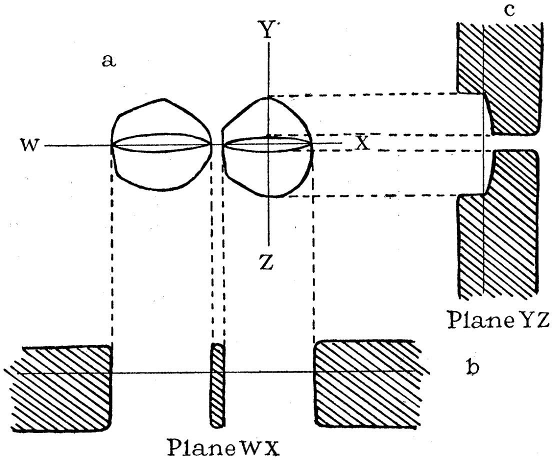

FIG. 13—Diagram of vessel-parenchyma pit-pair with wide aperture extending as far as the border. *a*, tangential section; *b*, cross-section; *c*, radial section.

In a study of large pit-pairs between vessels and parenchyma cells recently made at this Institute, Ross (1936) has attempted to estimate their significance. From his work, as well as from this investigation, one fact emerges clearly, that large vessel-parenchyma pit-pairs do not occur unless the intervascular pitting is large. Ross states that they only occur in "those woods whose intervascular pits are round, alternately arranged and have a diameter greater than about six microns". In the Sterculiaceae, too, they only occur where the pit-pairs are large, but even then they are not universal in all genera. From a superficial survey of their occurrence in other families the author has been led to the conclusion that they are usually developed with some regularity throughout a family (Lauraceae) or throughout certain sections of a family (Bombacaceae, Rosaceae), and that it is less common to find them, as here, in single genera and not in closely related genera.

RECORD (1934) states that in woods with storeyed structure the vessel-parenchyma pit-pairs are mostly small and half-bordered. *Sterculia* and *Brachychiton* are exceptions to this, and so are many genera of the Bombacaceae and some genera of the Tiliaceae. There are also a few exceptions in other families (one in the Amarantaceae, two in the

Caesalpiniaceae and one in the Ulmaceae), but only very few, and it may be significant that of the genera with large vessel-parenchyma pit-pairs and regular storeyed structure, by far the majority belong to families of the Malvales. The main tendency in the phylogeny of pitting has been for a reduction in the size of the pits, and FROST'S (1931) series from scalariform to alternate is supported by correlation with the vessel-member length. Large vessel-parenchyma pit-pairs do not fit into any such series. They do not conform to any of the accepted types of pitting, and their frequent orientation with the long axis vertical or oblique suggests that their scalariform shape is of secondary origin, and not related to primitive scalariform pitting. ROSS (1936) reviewed this type of pitting in several different families, but was unable to suggest any very definite correlations with other features.

In the Sterculiaceae the pitting is moderately constant in size and shape throughout each genus, and the smaller intervascular pit-pairs occur on the whole in the genera with the shortest vessel members. In the *Sterculia* A group there are no exceptions, and in the *Sterculia* B group *Sterculia pallens* WALL. has unilaterally compound vessel-parenchyma pit-pairs similar to those of *Firmiana*. This species is also exceptional in other respects, and its systematic position will be discussed later.

The two genera with large vessel-parenchyma pit-pairs are *Brachychiton* and *Sterculia* A, and these two genera have also many other features in common. The two sections of *Sterculia* are quite distinct in regard to the size and number of the pits, except for *S. quinqueloba* K. SCHUM. and *S. coccinea* ROXB.; these species are also intermediate between the two sections of the genus in the distribution of the parenchyma, and must be considered borderline types.

VIII—FIBRES

The fibrous tissue in all the genera of the Sterculiaceae is consistently *libriform*, with simple pits, and, with the exception of the crystal-bearing fibres, never *septate*. The fibres differ considerably in length, in the regularity with which they are storeyed, and in wall thickness, both from genus to genus, and occasionally within the genus.

The fibre length for the different genera is shown in fig. 14, in which the genera are arranged with the fibre length decreasing from top to bottom of the list. If this figure is compared with the one for vessel-member length (fig. 1) it will be seen that the position of many of the genera is reversed; for example, *Cola* and *Sterculia* B have very long fibres but short vessel members, while *Pterocymbium* and *Scaphium* have short fibres and long vessel members. The difference between the two sections of *Sterculia*, however, is not significant, and the fibres of *Sterculia* A are actually very slightly longer than those of *Sterculia* B.

One interesting feature of the fibre length is the relation between the ultimate length of the fibres and the length of the cambial initials from which they were formed, as inferred from the vessel-member length. The author has recently shown (CHATTAWAY

1936) that among woods selected at random from a very wide range of families the shortest cambial initials are associated with the greatest amount of extension in the fibres; for example, in woods with initials 350 μ long, the fibres tend to be three times that length, while in woods with cambial initials of 1000 μ and over, the fibres are rarely more than one and a half times the length of the initials, consequently the same fibre length may occur in woods with different lengths of cambial initial, and it is possible that the amount of extension may serve to distinguish the fibres of two woods where the actual length will fail.

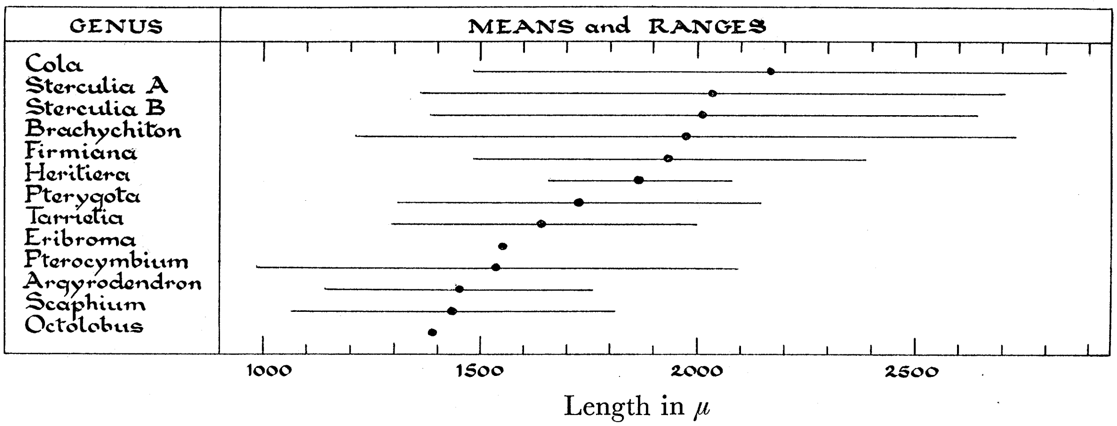

FIG. 14—Diagram to show fibre length in the Sterculiaceae.

The data given in figs. 1 and 14 for vessel-member length and fibre length have been combined in Table II to show the amount of fibre extension for different vessel-member lengths, and it will be seen that the amount of extension increases as the vessel-member length becomes shorter.

TABLE II—FIBRE LENGTH EXPRESSED IN TERMS OF VESSEL-MEMBER LENGTH

	Fibre extension $\frac{\text{Fibre length}}{\text{Vessel-member length}}$			
Genus	Mean of means		S.D. of mean	Vessel-member length
Pterocymbium	2·88	±	0·44	Approx. 500 μ
Scaphium	2·93	±	0·56	
Argyrodendron	3·60	±	0·41	400–500 μ
Tarrietia	3·95	±	0·56	
Brachychiton	4·24	±	0·58	
Pterygota	4·62	±	0·43	
Sterculia A	4·63	±	0·85	
Firmiana	4·81	±	1·01	
Heritiera	5·12	±	0·57	Below 400 μ
Octolobus	5·25			
Cola	5·70	±	0·71	
Sterculia B	5·73	±	0·91	
Eribroma	6·45			

Distinctions that can be drawn between the genera on the length of their vessel members are confirmed. In addition to this, although there is no significant difference between the actual fibre lengths of *Sterculia* A and B, these two groups show a significant difference in the extension of their fibres.

The figures given in Table II were compared with those for fibre elongation generally (Chattaway 1936); it was found that the values in the Sterculiaceae are consistently higher than those for a random selection of woods covering several families, though not higher than values met with in some other advanced families. Furthermore, they agree well with values calculated for this family from the data given by Bailey (1920).

Unfortunately very little appears to be known about the causes of fibre extension, and consequently it is impossible to offer any explanation of the above phenomenon. But it is interesting to notice that in a recent discussion on libriform fibres and fibre tracheids (Bailey 1936; Reinders 1935), Bailey comments on the fact that tracheids elongate less during differentiation than either fibre tracheids or libriform fibres. Many of the lowest values for elongation given by the present author (Chattaway 1936) occur in woods with fibre tracheids, while high values predominate in families such as this, in which the fibres are libriform. This confirms the idea that there may be some phylogenetic significance to be attached to the type of pitting of the fibre walls, in spite of the overlapping of types that occurs in many families.

The fibres in some genera (*Cola*, *Sterculia* B, *Heritiera*, *Eribroma* and *Octolobus*) may show little sign of being storeyed, even where the parenchyma is regularly storeyed, the individual fibres being thin and thread-like, with little or no indication of a "bauchig" middle portion. These fibres show a greater amount of extension than the fibres of other genera that are "bauchig" and retain their storeyed arrangement. This suggests that the extreme amount of extension is only attained when the whole cell is involved. There are noticeably fewer pits in these very long fibres, which may be the result of the great extension they have undergone; in the regularly storeyed fibres the pits are almost all on the wider middle portion, and not on the attenuated tips, and they are often quite numerous; in the very long and thread-like fibres that are not storeyed the few pits that occur are not localized in any particular part of the fibres, but are scattered throughout their length.

Crystal-bearing fibres, which will be described in the section on crystalliferous cells, occur in *Sterculia* sp. and in *Eribroma*.

IX—Vertical Wood Parenchyma

The three main types of parenchyma, terminal, metatracheal and paratracheal,* are all represented in the Sterculiaceae; the terminal parenchyma occurs sporadically

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* *Terminal parenchyma*: aggregated wood parenchyma, forming a more or less continuous layer of variable width at the close of the season's growth. *Metatracheal parenchyma*: aggregated wood parenchyma forming concentric laminae, mostly independent of the vessels and vascular tracheids. *Paratracheal parenchyma*: aggregated wood parenchyma in association with the vessels or vascular tracheids.

in many of the genera, and both metatracheal and paratracheal parenchyma occur together in all the genera except *Scaphium*.

Terminal parenchyma offers little that is of interest in this family; where it is well developed it forms lines on the cross-section, that are often continuous, and if the growing periods are short, these terminal bands may follow one another closely, and may be difficult to distinguish from broad bands of metatracheal parenchyma, as for example in some species of *Sterculia* and in *Argyrodendron*. Terminal parenchyma often occurs sporadically, and may be present in one sample of a species and absent from another.

The distribution of the metatracheal and paratracheal parenchyma shows considerable variation in different genera. Certain types can be distinguished which are linked together by intermediate forms. For example, the metatracheal parenchyma varies in distribution from narrow discontinuous lines one cell wide (the "diffuse"* type of the International Association of Wood Anatomists) to broad bands several cells wide, and there appears to be a sequence of development in these types that runs parallel to that for vessel-member length (CHATTAWAY 1932). The narrow lines occur in the genera with the long vessel members, and the broad bands in those with the shorter ones; and this sequence is accompanied by a parallel sequence in the type of cell of which the strands are composed. The cells of the narrow lines are often two per strand, and are then quite easy to distinguish from those of the paratracheal parenchyma (RECORD 1934); the cells of the broad bands are usually four per strand, and the individual cells of the metatracheal and paratracheal parenchyma are often quite indistinguishable from one another, and it is sometimes difficult to decide whether the bands are truly metatracheal, or are aliform and confluent, and consequently wholely paratracheal.

Pterocymbium javanicum R.BR. or *P. tinctorium* K. SCHUM. may be taken as an example of one end of the series. In these woods the fibres are very thin-walled and have large lumina, so that it is often difficult to distinguish between the fibres and parenchyma on the cross-section (fig. 25, Plate 29). It is, however, usually possible to distinguish the sheath of paratracheal parenchyma from the short tangential lines of metatracheal parenchyma. On tangential section the storeyed structure of the wood is clearly marked, the pointed ends of the parenchymatous elements interlocking with characteristic gabled ends (BEIJER 1927; RECORD 1934). The cells of the parenchyma are easy to recognize on the longitudinal sections (fig. 28, Plate 29) on account of their cross-walls, and the sheaths of paratracheal parenchyma are seen to consist of from four to eight cells (usually four), while those of the metatracheal parenchyma are usually subdivided into only two cells. Other strands can be seen that are clearly not fibres; they are of the same length as the parenchyma strands, and have similar gabled ends, but are not subdivided by cross-walls. These are the intermediate or substitute fibres of the

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* *Diffuse parenchyma*: single parenchyma strands or cells distributed irregularly among the fibrous elements of the wood as seen on cross-section.

older writers (DE BARY 1884; SOLEREDER 1908), now called fusiform wood parenchyma cells,* as, in spite of their shape and their lack of cross-walls, they are certainly parenchymatous and not fibrous in nature. They may possibly represent a more primitive condition than the strands of two cells, before septation of the strands occurred at all. They are present in considerable numbers in some species of *Pterocymbium*, but the more usual condition throughout the genus is for the strands of metatracheal parenchyma to be formed of two cells, gabled at their extremities, and separated from one another by a cross-wall that meets the side walls at right angles, without any intercellular spaces. Three species of *Sterculia*, *S. crassiramea* MERRIL, *S. villosa* ROXB. and *S. cariboea* R.BR., are very similar to *Pterocymbium*, but as the fibre walls are slightly thicker in the two last-named species, it is easier to distinguish the tissues on cross-sections of these woods.

Cola (fig. 27, Plate 29) may be taken as representing the other end of the sequence. Here the broad bands of parenchyma are so conspicuous as to be visible to the naked eye on a cross-section of the wood. These bands, which are sometimes broad enough to include many of the vessels and their surrounding paratracheal parenchyma, are sharply marked off from the fibres, which form a solid mass, usually without any scattered parenchyma strands among them. The bands are composed of strands that are usually subdivided into four cells; the cells at the extremities of the strands have gabled ends that interlock with the strands of the storeys above and below; the middle cells of the strands have rounded corners and conspicuous intercellular spaces between them (fig. 30, Plate 29). There is no appreciable difference between the cells surrounding the vessels and those of the rest of the band, but the cells actually contiguous to the vessels are sometimes disjunctive,† and occasional strands on the edges of the bands may be formed of two cells instead of the usual four.

Intermediate forms exist between the two extreme types that have been described. The following genera have conspicuous lines of metatracheal parenchyma: *Brachychiton*, *Heritiera*, *Sterculia* A, *Tarrietia*; in these the fibres and parenchyma are more distinct on the cross-section than in *Pterocymbium*, and strands of four cells are of more frequent occurrence (figs. 26, 29, Plate 29). *Argyrodendron*, *Eribroma*, *Firmiana*, *Octolobus* and *Sterculia* B are very similar to *Cola*. *Firmiana* and *Pterygota* are usually very similar to *Cola*, but the bands sometimes appear as if they were wholly paratracheal. Thus, although in one part of a section the bands may be very regular, and appear to be formed independently of the vessels, merely including them where they interrupt the course of the bands, there may be other parts of the wood, even on the same section, where the direction of the bands seems to be influenced mainly by the position of the vessels.

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* See footnote, p. 317.

† *Disjunctive parenchyma cells*: wood or ray parenchyma cells partially disjoined during the process of differentiation; contact is maintained by means of tubular processes. To replace "conjugate" parenchyma, which implies development in the wrong direction.

In a few species of *Sterculia* B, in which broad bands predominate (*S. coccinea* Roxb.; *S. quinqueloba* K. Schum.; *S. urens* Roxb.), there is also a considerable amount of scattered metatracheal parenchyma, and the general appearance of the wood is intermediate between the two types.

The strands that form the narrow lines of parenchyma are often less subdivided than those of the broad bands, and the cells fit tightly together and lack the intercellular spaces that occur between the cells in the broad bands. The position of the different genera in respect of these details is shown in Table III, from which *Scaphium* is omitted, as it has no metatracheal parenchyma.

Table III—The Vertical Wood Parenchyma

	Metatracheal parenchyma predominantly in			
Genus	Narrow lines	Broad bands	Intercellular spaces	Number of cells per strand
Pterocymbium	+	−	−	1–2
Brachychiton	+	−	−	2–(4)
Sterculia A	+	−	−	2–(4)
Firmiana	−	+	+	4
Tarrietia	+	−	−	2–4
Argyrodendron	−	+	(+)	(2)–4
Cola	−	+	+	4
Pterygota	−	+	(+)	4
Sterculia B	−	+	+	4
Heritiera	+	−	−	2–4
Octolobus	−	+	+	4
Eribroma	−	+	+	4

Brackets indicate that the feature or number occurs, but is uncommon.

In this table the genera are arranged according to vessel-member length, *Pterocymbium* having the longest, and *Eribroma* the shortest. It will be seen that broad bands, intercellular spaces and strands of four cells are on the whole characteristic of the genera with short-vessel members, while narrow lines, the absence of intercellular spaces and two cells per strand are characteristic of the genera with longer vessel members. Making use of Frost's (1930*a*, *b*) conclusions that the woods with shorter vessel members are the more advanced, the sequence given above suggests that in this family broad bands of parenchyma are a sign of specialization, and that this is accompanied by greater subdivision of the parenchyma strands and cells with rounded corners.

Two genera occupy anomalous positions as regards their parenchyma. *Scaphium* has relatively long vessel members and no metatracheal parenchyma, and is unlike the other genera of the Sterculiaceae in regard to this tissue, as it has narrow sheaths of vasicentric parenchyma* in most species, and only a little aliform parenchyma* in one

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* *Vasicentric parenchyma*: paratracheal parenchyma forming a vascular sheath of variable width, and circular or oval in cross-section. *Aliform parenchyma*: vasicentric parenchyma with wing-like extensions. *Confluent parenchyma*: coalesced aliform parenchyma, forming irregular tangential or diagonal bands.

species, *S. wallichii* R.BR. *Heritiera*, on the other hand, has very short vessel members, but has nevertheless very abundant metatracheal parenchyma, in lines one cell wide. As will be shown later there are advanced features in other tissues in this genus, and advance in one tissue may have been accompanied by a lag in another.

Paratracheal parenchyma is considered by some writers to be a more advanced condition than metatracheal parenchyma, and EAMES and MACDANIELS (1925, p. 68) sum up the situation as follows: "In highly specialized woods, where the tissue consists largely of fibers, and where water-conducting cells—in such cases porous vessels—are relatively few, each vessel is ensheathed with parenchymatous cells, and no parenchyma cells occur among the non-conducting fibers." JEFFREY (1922, p. 59) also suggests that the gradual loss of conducting functions in the fibres, through the sequence tracheids—fibre-tracheids—libriform fibres, is accompanied by a gradual change in parenchyma arrangement, the concentration of parenchyma around the vessels replacing cells scattered among the fibres.

This idea of the relation between the parenchyma and the conducting tissues suggests that the development of homogeneous masses of parenchyma in connexion with the vessels is the most advanced type. As conduction has become localized in the vessels, contact of the parenchyma with the main conducting system has been retained by the development of the scattered cells into continuous bands, and the tendency appears to have been for these bands to have become wider and to enclose the vessels completely. But definitely paratracheal parenchyma, without any diffuse parenchyma, can be found associated with primitive vessel characters in many families (CHALK 1935), though in such cases it is never very abundant. Further specialization seems to have led to the development of more abundant paratracheal parenchyma, such as aliform and confluent; for example, in the Leguminosae the parenchyma is mainly vasicentric in the Mimosaceae, which is generally regarded as the least advanced subfamily, and mainly confluent in the Papilionaceae, which can be regarded as the most advanced. The study of parenchyma in the Sterculiaceae suggests that the greatest specialization is reached in the woods with broad bands that enclose the vessels, and that these have been derived partly from metatracheal and partly from paratracheal parenchyma.

Crystalliferous parenchyma strands occur in some of the advanced species of *Sterculia*, in *Eribroma*, *Argyrodendron*, and in some species of *Heritiera* and *Tarrietia*. They will be discussed in a later section.

X—RAYS

In two earlier papers on the Sterculiaceae (CHATTAWAY 1933*a*, *b*) the author published the results of investigations upon the rays of all the genera included in the family before its revision by EDLIN (1935). Two features were specially studied, tile cells* and sheath cells.† At that time the Sterculiaceae included several genera with tile cells, but since the revision of the family by Edlin, these genera have been transferred to the Buettneriaceae, and therefore do not come within the scope of this paper. Tile cells (Chattaway 1934; Moll and Janssonius 1906) occur in the nearly related families Bombacaceae, Malvaceae and Tiliaceae, but have not yet been observed outside this group. Sheath cells (Moll and Janssonius 1906) are rather more widely distributed, though by no means common, and occur in several other families. They are absent from the Buettneriaceae, but are present in the rays of all the genera of the Sterculiaceae except *Heritiera.* As a whole, with this exception, the rays of all the genera are markedly heterogeneous, having not only sheath cells, but also marginal cells, or marginal rows of cells, that are different in size and shape from the rest of the ray. As seen on the radial section both marginal cells, sheath cells and the cells of the uniseriate rays are upright, while the central cells of the multiseriate parts are procumbent. The rays thus conform to the type described by Kribs (1935) as "heterogeneous II". The erect cells are usually without contents, but the procumbent cells in *Sterculia* sp., *Tarrietia, Argyrodendron* and *Heritiera,* are often full of dark contents, and in the other genera, although they are apparently without contents in the mature heartwood, there is often a distinction between the two types of cell in the sapwood, and the procumbent cells are often filled with starch, while the marginal cells appear quite empty.

In the evolutionary sequence of ray types that is given by Kribs, this type of heterogeneous ray is less advanced than the homogeneous ray, uniformity of cell size and shape throughout the ray representing the highest form of ray development. *Heritiera* is interesting in this connexion. The ray type is more advanced than that of any other genus in the family; sheath cells are almost entirely absent, and the erect marginal cells that are so characteristic of the other genera are confined to relatively few rays, the majority of the rays having only a very slight difference between the marginal and central cells. In the other genera the uniseriate rays are formed of cells that are similar to the marginal and sheath cells of the multiseriate rays, thus conforming to Kribs's type "heterogeneous II", while in *Heritiera* the cells of the uniseriate rays are usually small, and are similar to the procumbent cells of the multiseriate rays, thus conforming to Kribs's (1935) definition of "homogeneous II". The marginal cells in *Heritiera,* if they differ from the central cells, do so in their radial dimensions rather than their height, so that they are often indistinguishable on the tangential section, though on the radial section they appear to be narrower radially than the central cells. There is, however, some variation throughout the genus, an heterogeneous rays are more common in *H. fomes* Syme., while homogeneous rays predominate in

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* *Tile cells*: special type of apparently empty upright or square ray cells of approximately the same height as the procumbent cells and occurring in indeterminate horizontal series usually interspersed among the procumbent cells.

† *Sheath cells*: upright ray cells tending to form a sheath about the smaller cells of a multiseriate ray or the multiseriate part of a ray.

H. littoralis DRY. This specialization of the rays is confirmed by the vessel-member length, which points to *Heritiera* being a rather advanced type, although the parenchyma is less advanced, and consists of metatracheal lines one cell wide, and the paratracheal parenchyma is often very scanty.

Although the rays of the Sterculiaceae appear to offer little that is of interest in regard to the phylogeny of the family, there are two features of their development that are of general interest and have been followed in some detail. These are the method of increasing the number of rays as the girth of the stem increases, and the rather unusual method of growth of the individual ray initials that gives rise to sheath cells.

As the stem increases in girth there is a proportional increase in the amount of ray tissue, but this is not merely by the growth of existing rays which must become farther and farther apart, but by the formation of new rays to maintain the even distribution of the ray tissue. It has already been shown by BEIJER (1927) and others that new uniseriate rays arise by subdivision of the fusiform initials, which normally give rise to vertical wood elements, and this process is common in the Sterculiaceae; but in this family the spread of the ray tissue is also achieved by branching of the large rays. This breaking up of a large ray into smaller ones is brought about by the change of ray initials into fusiform ones. These two methods of spreading the ray tissue involve contradictory processes, in one instance the conversion of fusiform initials to ray initials, in the other the reversion of ray initials to the fusiform condition.

The multiseriate rays that are found in an old stem are not all primary in origin; some of them are derived from the new uniseriate rays, that have subsequently grown considerably in size. This increase in the number of cells is usually the result of the division of the ray initials, but it has been found that this process is augmented in some of the Sterculiaceae by absorbing adjacent fusiform initials into the rays. These new ray initials are at first larger than those of the rest of the ray, and give rise to the sheath cells.

In order to understand the structure of the rays in the mature wood, it is necessary to see how they have arisen, and to be able to visualize them as ribbons of tissue set edgeways in the wood, extending from pith to cortex, or starting in the mature wood, and usually extending to the cortex, but occasionally fading away again in the wood. It is clear that to achieve such a picture of the rays it is not enough to study the cambium alone, as it is essential to trace the history of individual cambial initials throughout the development of a multiseriate ray from its inception. Sections of the cambium show any particular cell at one stage only, and are therefore inadequate. Special methods were used for following the course of the rays from the pith outwards. They have already been described in § III. These methods are only suitable for a study of tissues in which there is little extra-cambial growth, that is to say, in which the individual cells undergo little change in size or shape after their formation from the cambium, and consequently there are limits to their use in the study of vessels or fibres, or of woods without a rather regular arrangement of the tissues. They are, however, entirely suitable for an investigation of ray cells, in which extra-cambial growth is slight, except in a radial direction, and in which the cells retain their shape, and change so slowly in relative position that the products of any particular ray initial can be traced on serial tangential sections for a long distance through the wood, while any change of shape in the cambial initial is immediately mirrored in the daughter cell. Furthermore, it is easy to distinguish between intra-cambial subdivisions that affect the initials, and extra-cambial ones that take place in the daughter cells. The former will be seen in all subsequent daughter cells, and will permanently affect the appearance of the ray, while the latter occur only in one cell, and the changes they cause will be seen only in one section.

(*a*) *Increase in the Number of Rays*

Examination of very young stems shows that the primary wood of the Sterculiaceae forms a completely closed ring round the stem, and the primary rays, though they may be high, do not extend for the full internode, and are seldom more than two or three cells wide. During the formation of the first few rows of secondary cells the primary rays become much wider, as the result of radial divisions of their initials, and in some species they may be extremely large at maturity.

As secondary growth proceeds and the stem increases in girth the primary rays become widely separated, and the need arises for additional ray tissue; this is provided for in two ways. The most usual method is by the formation of new ray initials from fusiform initials, so that a great many small uniseriate rays appear between the large ones. The formation of a new ray initial from a fusiform cambial initial has been described before (Haberlandt 1914), but there appears to be very little record in literature of the development of the newly formed uniseriate ray into one of the different types of multiseriate ray. The first stage of ray growth is the transverse division of a fusiform initial, and the resultant uniseriate ray may at first closely resemble a parenchyma strand, but the cells soon become slightly more rounded. As the usual procedure throughout the family Sterculiaceae is for only one, or occasionally two or three superposed fusiform initials to be used up in the formation of the new ray, and as the fusiform initials are storeyed, it is common to find numerous short uniseriate rays arranged in regular horizontal rows. In many genera these uniseriate rays are very numerous, and they often form such a conspicuous feature of the tangential section of the wood as to give the impression of two distinct ray sizes, as if the uniseriate rays belonged to a different system from the multiseriate ones. In very young stems this is the case, and the rays are either primary and multiseriate, or secondary and uniseriate, but some of the uniseriate rays soon grow, and this condition is rapidly succeeded by one in which the multiseriate rays are both primary and secondary in origin, and represent all gradations in size from the biseriate condition upwards.

Although this method of spreading the ray tissue evenly through the stem is the most usual it is not the only one. There are some woods in which uniseriate rays are only sparingly developed, and the spread of ray tissue occurs mainly by the breaking up of the larger rays into smaller ones, which continue to grow and then again divide. This splitting up of large rays has already been described by Zijlistra (1909) and Jost (1901) for the primary rays of the Cupuliferae, for *Aristolochia* and *Clematis*, and for the secondary rays of *Fagus*, but the process has not been followed in great detail, and no adequate explanation has been offered for its occurrence. Jost suggests that it occurs by the return of ray initials to the fusiform condition, but gives neither diagrams nor further explanation, and later refers to adjacent fusiform initials pushing in between the ray cells by sliding growth.

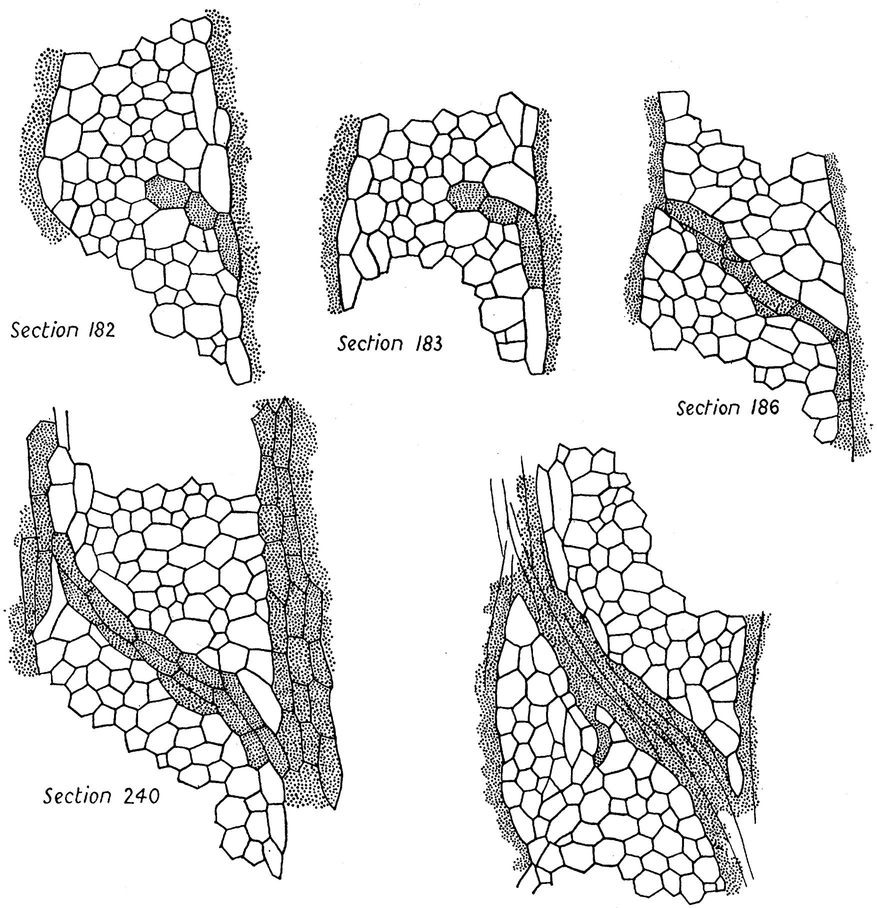

Fig. 15—*Cola togoensis* Engl. and Krause. Reversion of ray initials to fusiform initials, causing separation of a large ray into two parts. In section 240, the ray lies among wood parenchyma, in section 256, among fibres. (× 85 approx.) Reproduced by permission from *Forestry*, **7** (2).

This process has been followed in different genera of the Sterculiaceae, especially in *Cola togoensis* Engl. and Krause. Details of the changes are given in fig. 15. The figure shows camera lucida drawings selected from serial sections 30μ thick passing through approximately 2·2 mm. of wood at a distance of 5·5 mm. from the pith. In sections 182 and 183 from the pith the first stages are seen. They involve a slight swelling and elongation of the ray cells; they are made more conspicuous in the drawing by the cross-hatching, which does not imply a difference in the cell contents, but merely indicates the cells in which any change is recognizable. They might not be recognized as the preliminaries to a split if they were seen only on isolated sections, but can be recognized easily where the later stages can be traced backwards to their inception. In section 186, the line of slightly elongated cells is clearly seen across the ray; in section 240, the ray is passing through one of the layers of wood parenchyma, and is seen to be cut right across by a layer of cells that is almost identical with the parenchyma on the right; in section 256, the ray is in a region of fibres, and the separating layer is fibrous too. Thus it is clearly seen that initials that were producing ray cells are now forming alternating bands of fibres and vertical wood parenchyma; and this is the normal sequence for fusiform initials in this wood. It should be quite clear from this diagram that there is no question of adjacent initials pushing in between the ray cells, for the individual cells can be recognized in all sections, and they themselves are changed, not pushed aside by intruding cells.

Similar breaking up of the larger rays has been observed in species of *Cola*, *Sterculia*, *Eribroma* and *Pterygota*. In *Cola togoensis* it occurs with extraordinary frequency, and appears to be the chief way of providing the amount of ray tissue necessitated by the increasing perimeter of the stem, and of disseminating it through the stem. New uniseriate rays which provide for this increase in other woods are infrequent. Fig. 16 shows a series of diagrams selected from a series of 1500 sections at intervals through approximately 8 cm. of stem, starting from the pith. The wood has moderately numerous primary rays that often extend some distance vertically, though not through the whole primary internode. Five such rays are shown in fig. 16 (1); they are marked by various signs and cross-hatchings to enable each to be followed in successive sections, and they are marked A to E. At the stage shown in (1), which is near the pith, the wood is not yet storeyed, but tangential growth is very rapid, and storeys are established within a few hundred sections of the centre of the stem. Fig. 16 (2) shows the first indication of any splitting, where the changes already described in fig. 17 occurred, and the rays A^1 and A^2 are seen to be cut off from A; by (5) these three rays are seen to be separated by a considerable mass of ground tissue. In (5) ray B begins to split, and similar splits can be followed in the other rays in succeeding sections. Ray F appears first as a small uniseriate ray in (3); it grows till (14), when it undergoes its first split into F and F^1. Ray C splits for the first time in (7); some of the rays derived from it are pushed out of the section by the tangential growth of the wood, and do not appear in the diagrams, but nevertheless by the end of the series ray C can be seen to have given rise to ten rays, and to have spread through a considerable tangential area of the wood.

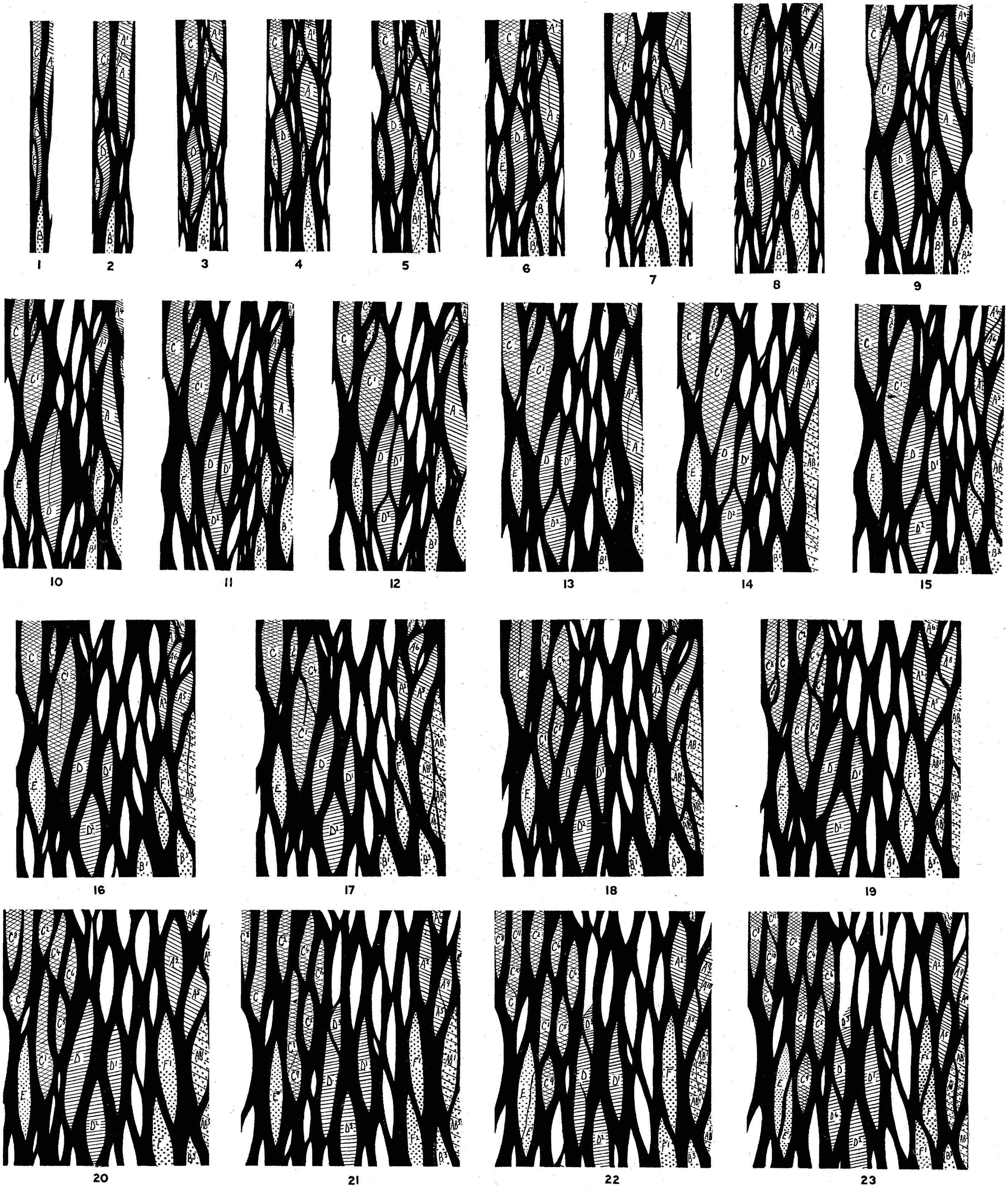

FIG. 16—*Cola togoensis* ENGL. and KRAUSE. Development of the rays through 8 cm. of wood, showing increase in number by splitting. No. 1 from a section near the pith. The cross-hatching of each ray shown in No. 1 is retained throughout the series for that ray and its derivatives. (× 5.) Reproduced by permission from *Forestry*, **7** (2).

(*b*) *Increase in the Size of Individual Rays*

The two methods by which the rays are spread through the wood are thus seen to be by the formation of new uniseriate rays, and by the splitting up of large ones. Growth in size may also take place in two different ways. Rays usually increase the number of their cells by the swelling and division of the ray initials, the peripheral ones being larger and dividing more actively than those in the middle. This type of ray growth adds to the width of the ray, and at the same time to the circumference of the stem by the production of new cells. Rays may grow in height by the cells at the apex swelling, pushing up between adjacent fusiform initials, and then dividing. Occasionally growth in height may take place more suddenly by a fusiform initial above or below the growing ray changing into a series of ray initials. This is shown in fig. 17 for *Tarrietia utilis* SPRAGUE. The newly added initial usually remains attached to the existing ray, and grows with it, but occasionally, as in the ray figured, it may become

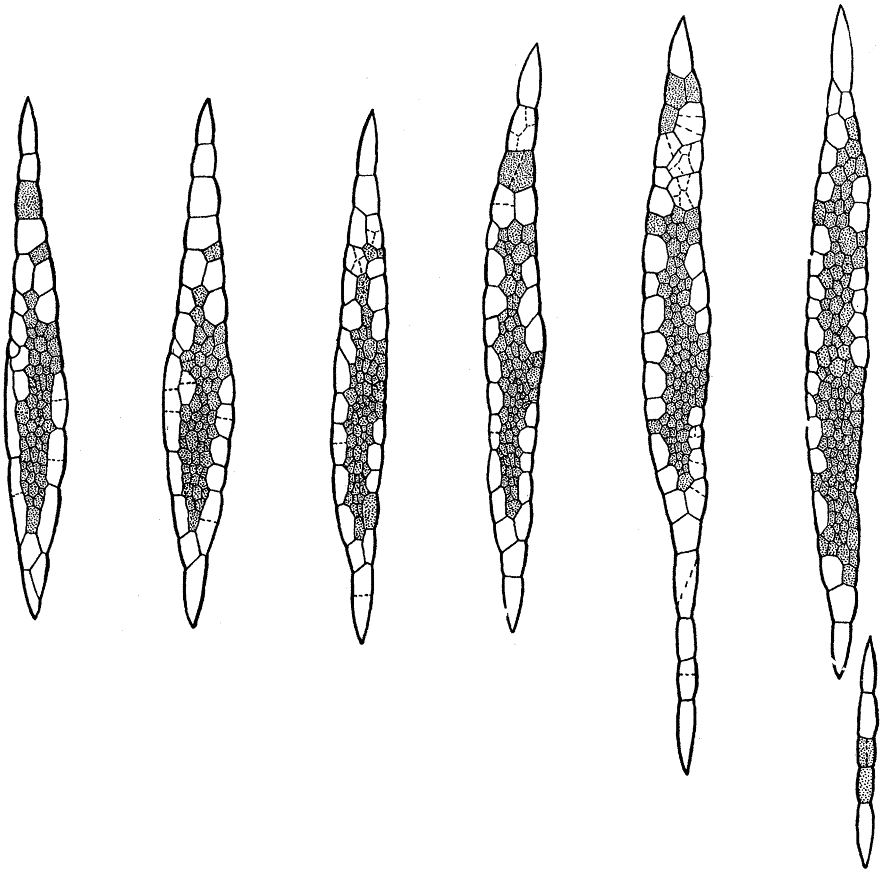

FIG. 17—*Tarrietia utilis* SPRAGUE. Gradual subdivision of added initials, forming sheath cells, and ultimately procumbent cells. The fusiform initial which is added to the bottom of the ray in section 330 is subsequently separated from it, and gives rise to an independent uniseriate ray (section 460). (× 85.) Reproduced by permission from *Forestry*, **7** (2).

separated from the larger ray while it is still in the uniseriate condition, in which case it continues to grow as an independent ray.

This method of growth by converting adjacent fusiform initials to ray initials and their addition to an existing ray is the second method of growth already referred to. The addition of a whole fusiform initial to increase the height of a ray is of moderately common occurrence; less common is the addition of new initials to the sides of the rays, resulting in rays with sheath cells. These new initials are at first only subdivided into three or four cells, and are very similar to parenchyma strands, which may indeed easily be mistaken for newly added ray initials. Once they have been added to the ray, however, these initials persist, and appear in all subsequent sections, whereas a parenchyma strand, which results from extra-cambial subdivision of a daughter cell of an initial, is only transitory, and gives place in subsequent sections to the usual radial sequence of fibres and parenchyma.

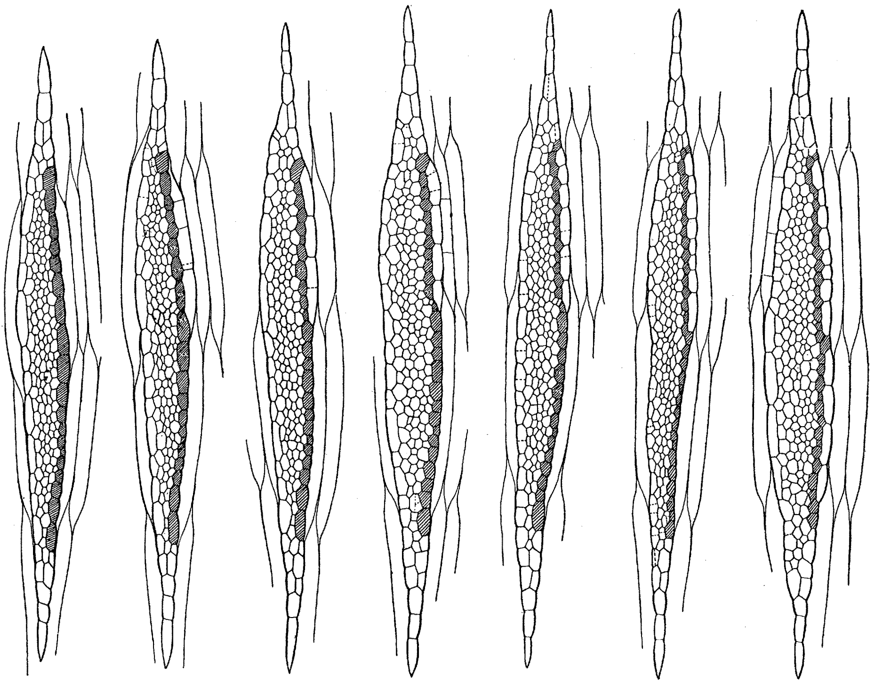

FIG. 18—*Pterocymbium javanicum* R.BR. Formation of sheath cells by the addition and subdivision of adjacent fusiform initials. (× approx. 45.) Reproduced by permission from *Forestry*, **7** (2).

It is this process of adding a layer of cells down the side of the ray that gives rise to the marginal sheath of larger cells by which the rays of this family are so often surrounded. Details of their formation have been studied in *Pterocymbium javanicum* R.BR., in which there is often a very conspicuous layer completely surrounding the rays. Fig. 18 shows a series of camera lucida drawings selected from serial sections 30μ thick through approximately 1·5 cm. of mature wood. In order to follow the changes in size and position more easily all the peripheral cells on the right of the ray are cross-hatched in the first drawing, and the same cells are similarly marked in all the subsequent ones. These cells are larger than the central cells of the ray, and are bordered by successive fibrous or parenchymatous cells of the ground tissue of the wood. In section 35, the cell lying immediately to the right of the ray in the upper storey is subdivided, and looks like a parenchyma strand. This subdivision has, however, taken place in the initial, and not extra-cambially, and it persists through all subsequent sections. This new cell layer is now the peripheral layer of the ray, which has increased in width, and it replaces the former peripheral layer, the cells of which are undergoing further subdivisions, and becoming smaller. The newly added cells are at first large, but they become smaller through the formation of transverse walls, and ultimately assume much the same proportions as the cell row to which they were added. Meanwhile, similar changes have been taking place in the lower part of the ray. The shaded peripheral cells in the lower part of the ray have undergone subdivision, and in section 307 a new initial is added to the ray in the lower storey, and at the same time another initial is added to the opposite side of the ray. In section 222 the lower part of the ray appears much narrower than it was in section 144, which may possibly correspond with the change from erect to procumbent cells. It is not possible to check this fact, as it would necessitate being able to see both radial and tangential sections of the same cell, but the slight shrinkage in tangential area that is frequently seen in the initials at this stage of ray growth is probably associated with extra-cambial radial elongation of the ray cells. It is quite distinct from the swelling and shrinking in ray width that commonly occurs when a ray is passing through a parenchymatous or fibrous layer in the wood respectively. The decrease in width mentioned here occurs irrespective of the tissue which surrounds the ray at the time. It will be seen that in both section 144 and section 222 the cells adjacent to the ray are fibrous.

Fig. 19 shows a more general view of ray growth in the same wood. The sections from which the drawings in fig. 18 were made occurred between fig. 19 (3) and (4) in this figure. The whole range of diagrams in this figure represents sections at intervals of approximately 1·5 cm. through 9 cm. of wood. Fig. 19 (1) shows two rays, one three storeys high, and the other, only partly shown, thirteen storeys high. These large rays are separated from one another by one fibre, and each is surrounded by a conspicuous sheath of large cells. On their left are two uniseriate rays, each of which has arisen through the change of a fusiform initial into a series of ray initials, and subsequently grown by division of the cells till it exceeds its original storey in height. The growth of these rays can be traced through the whole 9 cm.; at the end of the series they are seen to be 4 and 5·5 storeys high respectively, and to have acquired a complete layer of sheath cells. The increase in size has taken place in two ways, by cell division and by the conversion of fusiform initials to ray initials, and their addition to the existing cell complex. Growth in height has been gradual, except in Fig. 19 (3), by swelling and subsequent division of the apical initials, which push their way in among the surrounding elements. This accounts for the fact that increase in height is, for the most part, independent of the storeys. The exception to this is between Figs. 19 (2) and (3), where one of the small rays is seen to have jumped a complete storey by the addition of a whole converted fusiform initial.

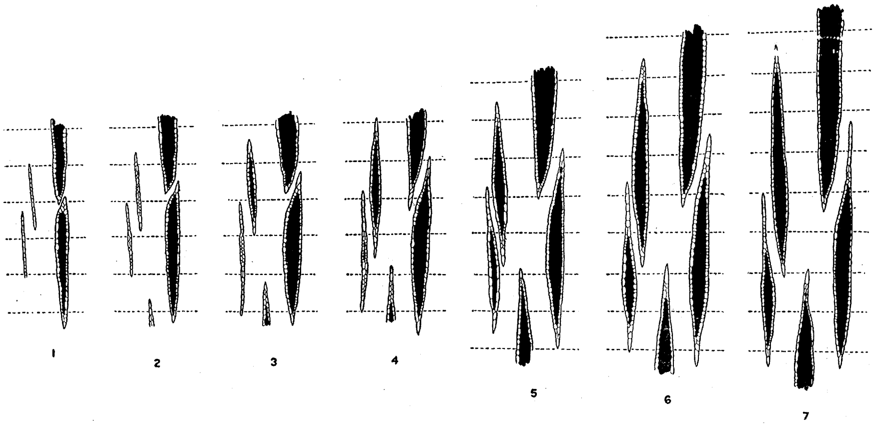

FIG. 19—*Pterocymbium javanicum* R.BR. Successive sections at 1·5 cm. intervals, showing the development of two uniseriate rays. The dotted horizontal lines represent the limits of the storeys in the other elements. (× 10.) Reproduced by permission from *Forestry*, **7** (2).

Figs. 17 and 20 show similar stages in the addition of a layer of sheath cells to a ray of *Tarrietia utilis* SPRAGUE. The distinction between the marginal and sheath cells is very noticeable in this species, as the procumbent cells of the ray are usually filled with dark contents. In figs. 17 and 20 the cross-hatching represents the dark contents of the cells, and it is clear that the contents appear in the peripheral cells after the large sheath cells have been subdivided, and this is probably also the time at which the cells elongate radially and become procumbent. The author showed (CHATTAWAY 1933*a*) that in rays with tile cells there is probably some connexion between the elongation of the procumbent cells and their dense contents, and that lack of contents and a different appearance in the cell contents of the initials is associated with the erect tile cells. It has not been possible to examine fresh cambial material of *Tarrietia*, but the sudden change from empty cells to cells filled with dense contents in the mature wood may possibly reflect some fundamental difference in the initials from which the cells have been derived.

These sheath cells, which are so conspicuously developed in *Pterocymbium* and *Tarrietia*, are present in all the genera except *Heritiera*. In some genera they are much less regular than in others, notably in *Cola*, *Sterculia* B, *Eribroma* and *Octolobus*, and often form only a partial sheath around the ray. In this case growth takes place mainly by division of the existing initials, supplemented by the occasional addition and conversion of fusiform initials.

This method of growth is evidently at the expense of the fusiform initials that form the ground tissue of the stem, and it contributes nothing to the increase in perimeter.

In rare cases—as, for example, in ray D^3 in fig. 16 (22, 23)—it may use up all the fusiform initials between the rays, so that they fuse into one. But this is unusual, because the fusiform initials generally multiply by radial division more rapidly than they are absorbed by the rays.

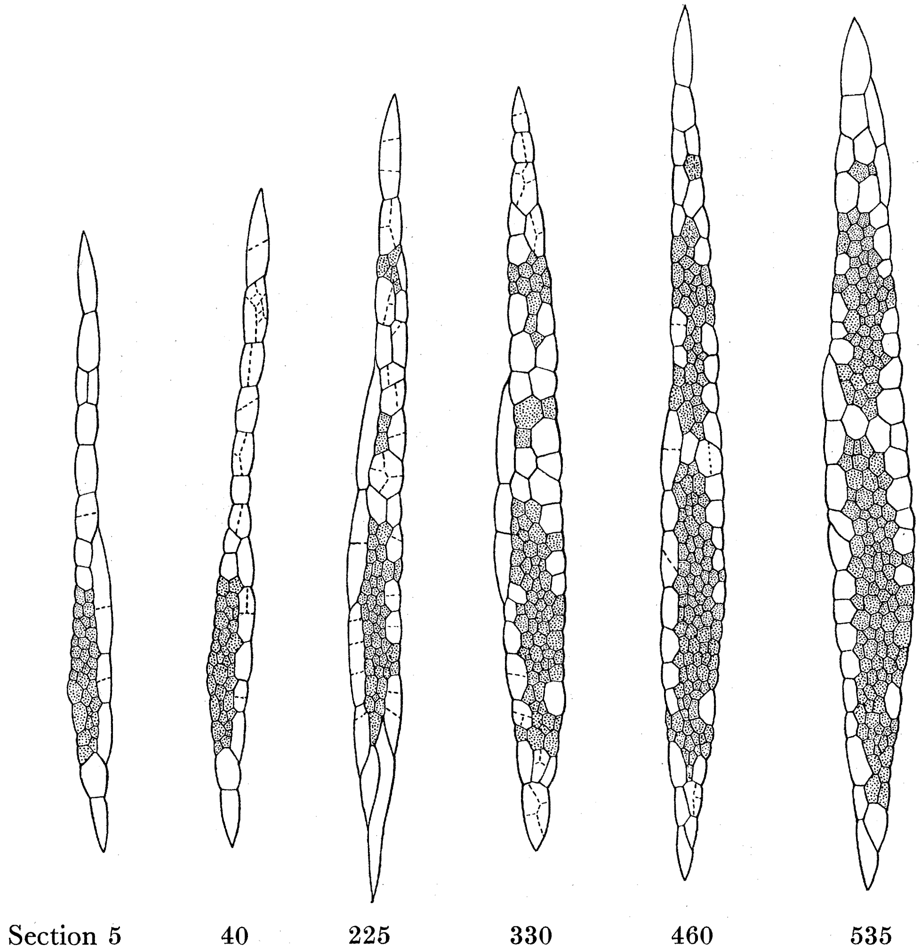

FIG. 20—*Tarrietia utilis* SPRAGUE. Gradual subdivision of added initials, forming sheath cells, and ultimately procumbent cells. The shading represents the cell contents that appear in the peripheral cells after the large sheath cells have been subdivided. (× 60.)

The phenomenon of splitting rays in this family appears to have little systematic importance, and to depend almost directly upon ray size. The concentration of growth into a few very large rays has two results: first, it produces a very uneven distribution of ray tissue through the stem, large patches of ray tissue and large spaces without any, and, secondly, it produces rays in which the peripheral cells that are in contact with other elements of the wood are few compared with the number of inner cells that are surrounded only by other ray cells. Thus the splitting up of a ray has two effects, the ray tissue is spread more evenly through the stem, and the surface of the rays is increased in proportion to the bulk. A study has been made of the ratio of ray surface to mass in the Sterculiaceae, using the perimeter and the area of the ray as seen on the tangential section, but it is impossible to say more than that it confirms the view that the splitting process is closely related to a low ratio. In the species with smaller rays, and in the small rays of all species, this ratio is very high; with slight increase in the size of the rays it falls very rapidly, since the area is approximately doubled when a uniseriate ray becomes biseriate, while the increase in surface is small. In the larger rays the ratio decreases more slowly, and the result is a curve that is steep at first, but finally flattens out, a common form of growth curve. For each species there seems to be a "danger zone" on this curve, and when this ratio is reached the ray is liable to divide.

In *Sterculia quinqueloba* K. Schum., although the rays were traced through nearly 3000 sections—representing approximately 9 cm. of wood—no complete splitting was observed. Several times a ray began to split, and several ray initials reverted to the fusiform condition, but the split was never completed, and the ray either remained in this condition permanently, or, more frequently, the reverse process took place and the split closed up. During this time the ray did not grow in size. Similarly in *Sterculia urens* Roxb., rays began to split, often in considerable numbers; these rays were followed in sections through about 15 cm. of the wood, and the initials that had changed always reverted to fusiform initials. Finally, however, some factor must have intervened to upset the balance, for within a few millimetres several rays were found to have completed the split. In both woods it was very noticeable that the splits almost always started from the same end and side of the different rays, which suggests a physiological impulse passing up or down the tree. It has not been possible yet to procure material in which the top could be distinguished from the bottom of the specimen, so this point remains unsettled.

Reviewing this family as a whole, it appears that the more primitive method of ray growth is by the addition of new fusiform initials, since the woods with the longest vessel members have the more regular layers of sheath cells (*Pterocymbium*, *Brachychiton*, *Scaphium* and *Sterculia* A). Growth by subdivision of existing initials is always present, and in the more advanced species it appears to predominate, sheath cells being formed only sporadically, and forming a very irregular layer as seen on the tangential section (*Cola*, *Sterculia* B, *Eribroma* and *Octolobus*). It is possible that the excessive growth of few rays is also a primitive feature, since the smaller rays seem to become the rule in some of the more advanced genera, but there is no evidence to confirm that this holds true throughout other families.

XI—Crystalliferous Tissue

At the end of the last century investigations upon the occurrence of calcium oxalate in plants were very frequent, but the authors appear for the most part to have confined themselves to descriptive studies of the formation of crystal druses and calcium oxalate crystals in leaves and meristems, and the formation of these crystals in woody tissues were usually omitted from their investigations.

There has been much discussion as to the importance of calcium oxalate in plant metabolism, and the conclusion usually arrived at is that it is almost always an excreted waste product, and that it has no active function in the plant tissues. Some authors—Meyer, Combes, quoted by Milanez (1932)—suggest that the crystals are formed during the synthesis of proteins, but this would hardly account for their occurrence in the woody parts of plants. Schimper (1890) has suggested that calcium oxalate is accumulated in the plant as the result of the withdrawal of phosphorus from the calcium phosphate of the crude sap, and that this accumulation would have fatal results if it were not rendered innocuous by combination with the oxalic acid left from respiration. Thus calcium and oxalic acid, both toxic to the plant, are withdrawn from the cell sap in the form of crystals, and are often further removed from all active contact with the plant by being surrounded by an impermeable membrane. Haberlandt (1914, p. 533), too, considers that crystals are an excretory product, and suggests that their occurrence in the marginal strands of banded parenchyma may be merely putting them in a place where they can have least effect on the metabolism of the plant, since these strands abut only on one side on the parenchyma, and on the other touch the fibres, with which there is little communication. Milanez (1932) has recently stated that crystals of calcium oxalate in the wood of plants result from the activity of the cambial meristem, and has suggested that their frequent occurrence in terminal parenchyma (as in many of the Caesalpiniaceae) may be the result of the accumulation of excreta from the activity of the whole growing season. This appears to be a very probable explanation of the crystals in the chambered parenchyma, but does not seem equally applicable to the solitary crystals that are often found scattered irregularly through rays and parenchyma.

In the Sterculiaceae crystals appear to be absent altogether from certain genera, for example, *Pterocymbium* (a few solitary crystals were observed in one sample of *P. tinctorium* Merril), *Scaphium*, *Firmiana* and *Octolobus* (one sample only available). They were found to be constant in occurrence in both rays and parenchyma in *Pterygota*, *Brachychiton* and *Eribroma* (one sample only); sporadic in *Cola*, and present in the rays or parenchyma or both, in most species of *Sterculia*, *Tarrietia*, *Heritiera* and *Argyrodendron*. Crystalliferous fibres are present in *Sterculia* spp. and *Eribroma*.

The solubility of the crystals in HCl without effervescence and their solubility, though only after prolonged action, in copper sulphate, show them to be calcium oxalate. Bargagli-Petrucci (1903) mentions the occurrence of silica in the wood of *Heritiera littoralis* Dry. and *Sterculia* sp., but says that it is sporadic in occurrence; the author has not found silica in any of the samples of *Heritiera littoralis* examined.

The crystals are always surrounded by a membrane, and are isolated by it from the rest of the cell. Wittlin (1896) describes the formation of this type of crystal sheath; it seems to be very similar to the Rosanoffian membrane that surrounds crystal druses (Rosanoff 1865, 1867), but the trabeculae are lacking. Wittlin states that "one is almost tempted to assume that every crystal is surrounded by a membrane, and that unenclosed crystals hardly ever occur". The author finds that this is true for all the genera of the Sterculiaceae examined, although there is very much difference in the thickness and visibility of this membrane. In some cases it is extremely thick and has so closely invested the crystal as to give the impression that the crystal is still present, even after its solution in HCl; or it may be so thin as to be obscured by the crystal, and even after the crystal has been dissolved out it can only be seen with critical illumination. Some such variability in the thickness of the membrane is shown in all the figures illustrating this section, but especially in fig. 21 (1), which illustrates adjacent ray cells from *Pterygota alata* Roxb. containing crystals with both thin and thick membranes.

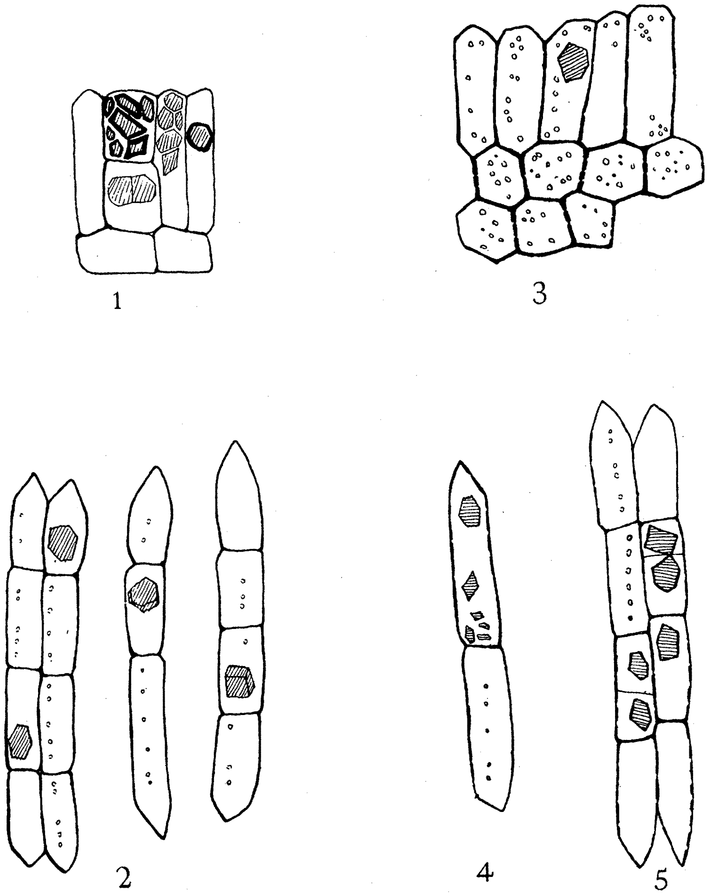

Fig. 21—Crystals in ray and parenchyma cells. 1, *Pterygota alata* Roxb.; crystals in upright ray cells. In the cell on the left the crystals are surrounded by thick membranes, while in the adjacent cells the membranes are very thin. 2, *Sterculia hypochra* Pierre; solitary crystals in parenchyma strands. 3, *S. ornata* Wall.; solitary crystal in upright ray cell. 4, *S. hypochra* Pierre; parenchyma strand, the upper cell of which contains several crystals. 5, *S. hypochra* Pierre; parenchyma strands with paired crystals separated by thin septa. (All × 140.)

The crystals may occur either as large solitary crystals, or as groups of small crystals, in unchanged cells of the parenchyma or rays, or in specialized cells. The latter may be cells of the vertical parenchyma (the chambered parenchyma of the older writers), special septate or subdivided cells of the rays, or crystalliferous fibres.

Where the crystals lie free in unspecialized cells of the parenchyma or rays they are often conspicuous only in sections that have been prepared from unsoftened material, since they may be dissolved out by the action of the softening reagent, and leave only a very thin membrane, and no modification of the shape of the cell to tell of their presence. Figs. 21 (2) and (3) show such solitary crystals in parenchyma and ray cells respectively, while fig. 21 (4) illustrates a collection of smaller crystals within a single parenchyma cell. This figure may be compared with fig. 21 (5) which illustrates a pair of parenchyma strands from the same wood, where two crystals lying in a single parenchyma cell are seen to be separated from one another by a thin septum. This condition may be intermediate between the usual condition in this wood, and the more specialized types with true chambered parenchyma.

Chambered parenchyma strands occur scattered sparsely among the metatracheal parenchyma in *Heritiera* spp. and *Tarrietia* spp., but they are very common in *Argyrodendron trifoliatum* F. von Muell., *Eribroma klaineana* Pierre, *Sterculia appendiculata* K. Schum., *S. elegantiflora* Hutch. and Dalz., *S. oblonga* Mast., and *S. rhinopetala* K. Schum. In the last-named wood crystalliferous tissue is especially abundant, and special subdivided crystal cells occur in the rays as well as in the parenchyma (fig. 31, Plate 30). The crystalliferous tissue has two very characteristic features in all the above woods. The sheaths surrounding the crystals are always conspicuous, and it is extremely rare to find more than one crystal per cell.

Fig. 22—*Sterculia quinqueloba*. K. Schum. Apical cell of crystalliferous parenchyma strand, showing crystal sheath and thickened wall. (× 500.)

The extra deposition of thickening in crystalliferous cells is not always confined to the crystal sheath, but also affects the wall of the cell, which may become much thicker than is usual for parenchyma (fig. 22). This is also illustrated in figs. 23 and 24, which show that the thickening is laid down more on one side of the cell than on the other. This particular manner of thickening is very noticeable in all the *Sterculia* species that have chambered parenchyma. They all have broad bands of parenchyma, and the crystalliferous strands are confined to the margins of the bands, and the thickening is always more marked on the side that is towards the fibres. Sometimes the crystal membrane itself, as well as the cell wall, is much thinner towards the parenchyma. Figs. 23 (1–5) and 24 (1–3) and (6–7) show such strands viewed from the tangential direction; the thickening of both the wall and the crystal sheath is more regular, and usually thinner, on the radial than on the tangential walls.

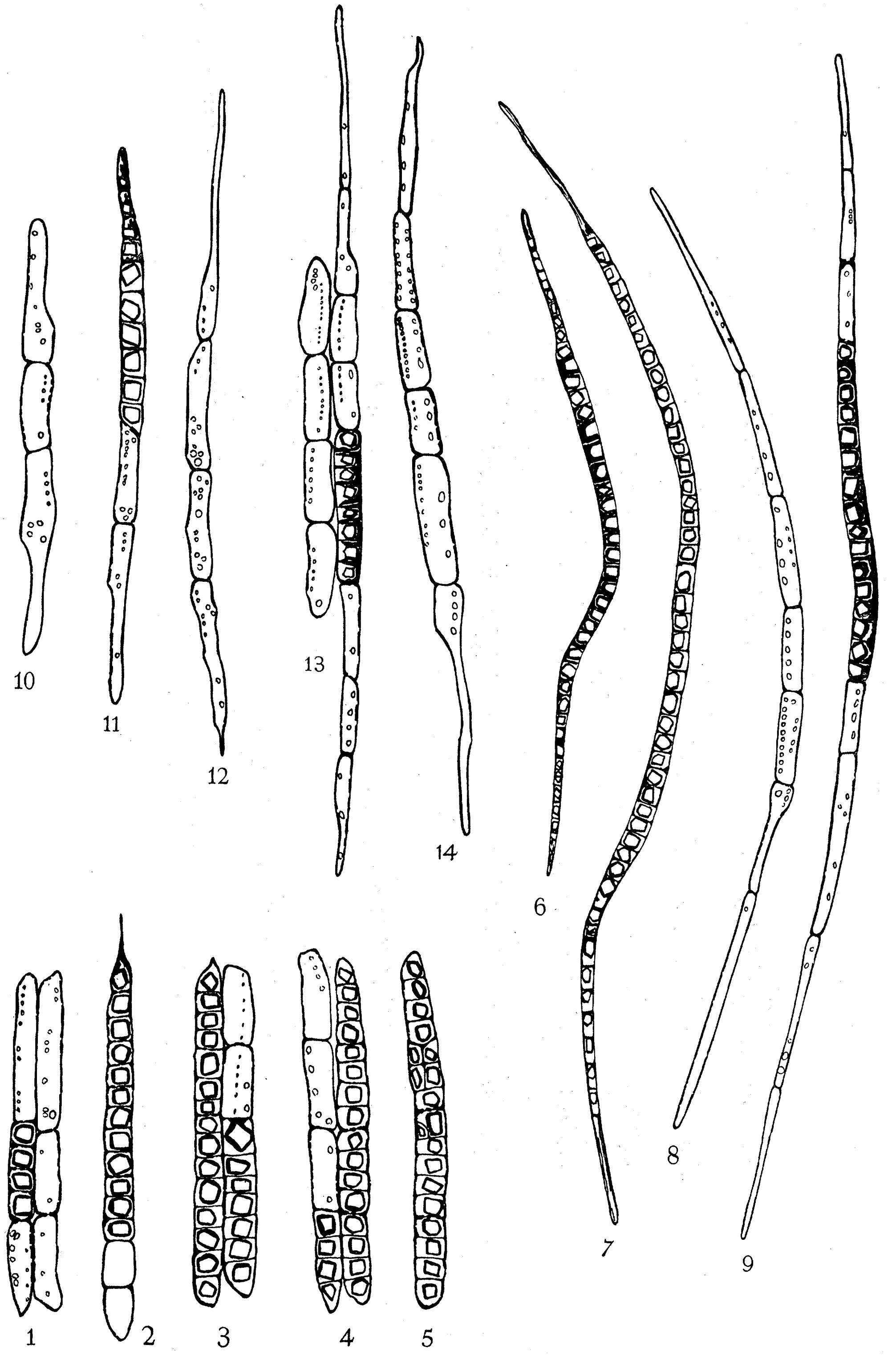

FIG. 23—*Sterculia oblonga* MAST. Crystalliferous tissue. 1–5, chambered parenchyma strands, containing solitary crystals. 6 and 7, crystalliferous fibres. 8–14, elongated strands, subdivided by cell walls, and occasionally also septate; the septate portions containing crystals. (All × 140.)

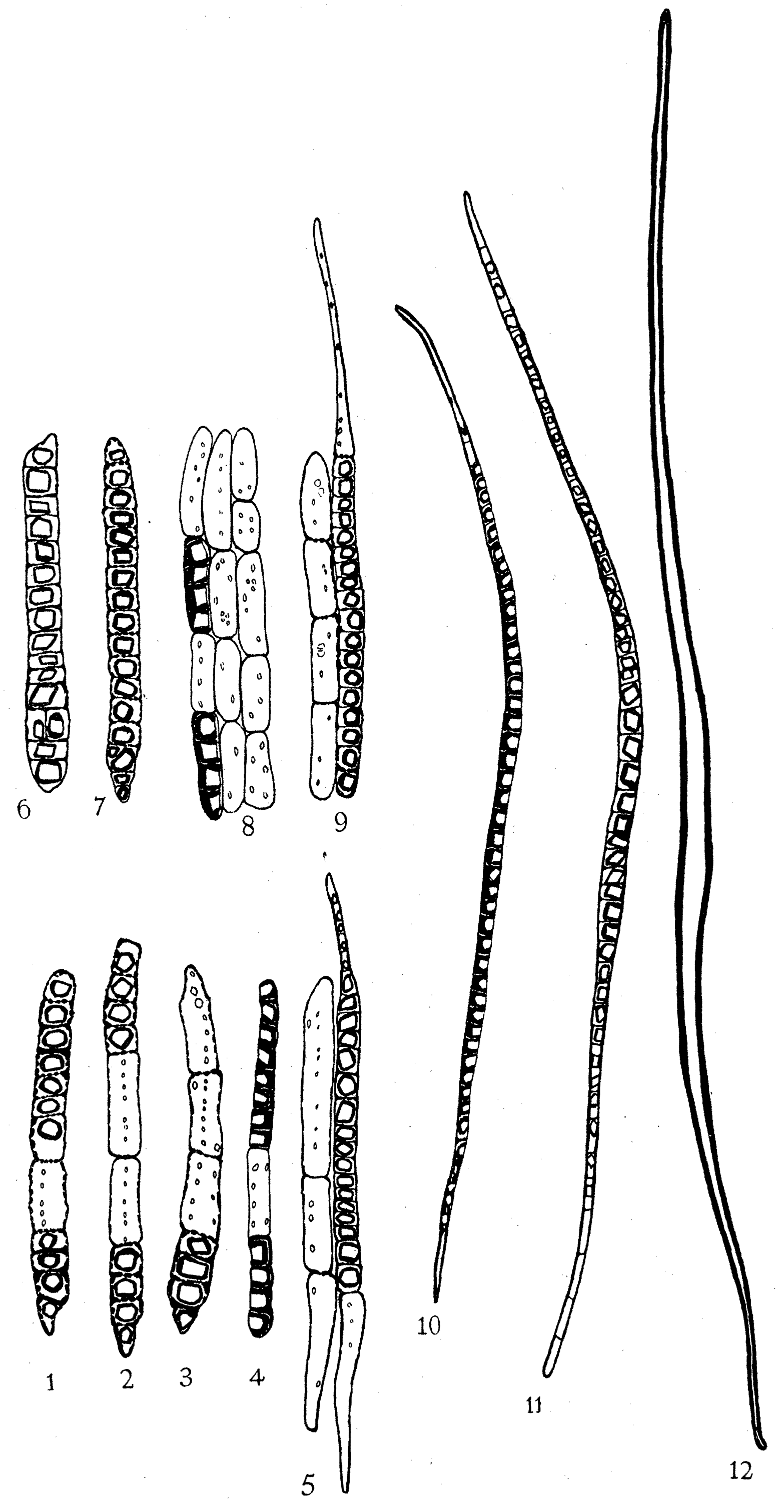

FIG. 24—*Sterculia elegantiflora* HUTCH. and DALZ. Crystalliferous tissue. 1–4 and 6–8, chambered parenchyma strands, containing solitary crystals. 5 and 9, elongated strands, subdivided by cell walls, and also septate; the septate portions containing solitary crystals. 10–12, libriform fibres; 10 and 11, containing crystals. (All × 140.)

Milanez (1932) has described this type of parenchyma very fully, and has given names—hemi-crystalliferous, holo-crystalliferous, etc.—to the different parenchyma strands. Such terms appear to the author to be both unnecessary and confusing. The cells are essentially the same in all cases; they are parenchyma cells that have been further subdivided to contain crystals, and the distinction drawn by Milanez merely refers to cases where one, two, or more cells of a parenchyma strand are so divided. Figs. 23 (1–5), and 24 (1–4) and (6–8) illustrate such series of crystalliferous parenchyma strands from *Sterculia oblonga* Mast. and *S. elegantiflora* Hutch. and Dalz. respectively, and show that in each instance the cells of the strand have been regularly divided into four crystalliferous cells. Sometimes the subdivision is by walls and sometimes by septa; in the former case the pits in the dividing wall can be seen. Owing to the thickening of the cell wall that commonly occurs in these cells, and to the thick membrane that surrounds the crystal, the distinction between wall and septum is often difficult to see, but may sometimes be made more easily on slides of macerated material. The action of the macerating fluid causes the strands of parenchyma to disintegrate into their component cells, but the cells themselves have not disintegrated in the same way, as they are only divided by septa, and each cell still consists of four compartments.

Milanez (1932) states that the "crystal fibre of certain authors is almost always a simple series of crystalliferous parenchyma cells", and adds that he has not succeeded in finding crystals of calcium oxalate in authentic wood fibres. The author cannot agree with this statement. In the *Sterculia* species that have chambered parenchyma, undoubted crystalliferous fibres are often present. Stages intermediate between parenchyma and fibres can be found in *S. elegantiflora* and *S. oblonga.* In the latter, strands of four or more cells that are parenchymatous in nature can often be found; they are thin-walled, and are subdivided by walls and not by septa, and have simple pits similar to those of the normal parenchymatous cells, but the series does not conform to the definition of a wood parenchyma strand, since it is often considerably longer than the cambial initial from which it was derived (International Association of Wood Anatomists 1933). In the *Sterculia* species illustrated in figs. 23 and 24, the length of the parenchyma strand probably corresponds very closely with the length of the cambial initial, and shows little variation from strand to strand; such strands are illustrated in fig. 23 (1) and (13), and in fig. 24 (8) and (9). The chambered strands are usually the same length, and again there is little variation in length between them. But there are also strands that are half-parenchymatous and half-fibrous; such strands occur also quite commonly in other woods. In *S. oblonga* and *S. elegantiflora* there are also very long strands which still retain the form of parenchyma, but which seem to have undergone some, often considerable, elongation. Such strands are illustrated in figs. 23 (8–14), and fig. 24 (5) and (9). The cells are divided by walls and not by septa, and the pitting corresponds to that usually found in parenchyma, and not to that found in fibres. Usually some of these long parenchyma strands are subdivided to contain crystals (fig. 23 (9), (11) and (13)). Crystalliferous strands that are much longer than the parenchyma strands are illustrated in fig. 23 (6) and (7) and fig. 24 (10) and (11). These are subdivided, and contain crystals throughout their length, and are probably the "crystal fibres" of other writers (HARTIG, quoted by HABERLANDT 1914). It is difficult to see whether the cells are divided by walls or by septa, but from their appearance in slides of macerated material, the latter seems more probable, as they seldom disintegrate during maceration. They are usually slightly shorter than the longest fibres, but approximate more closely to them in length than to the parenchyma strands. In fig. 24 (11) and (12), two fibres are shown side by side for comparison, one a crystalliferous fibre, the other a normal libriform fibre of average length. This is the only occurrence of septation of the fibres within the Sterculiaceae.

It seems doubtful whether any phylogenetic importance can be attached to the occurrence of crystals. Solitary crystals in unspecialized cells are certainly sporadic in occurrence, and may be present in some samples of a species, but not in others. But the author has found, both in the Sterculiaceae and in other families that she has examined, that chambered parenchyma is much more constant in its occurrence. Until a review of the distribution of chambered parenchyma, and that of crystalliferous fibres in the different families of dicotyledons has been made, it is impossible to decide whether they are a primitive feature or a specialized one. Within the Sterculiaceae chambered parenchyma and crystalliferous fibres are confined to the more advanced genera, though they are not universal in these—for example, they are absent altogether from *Cola*; and the absence of crystals from the wood of *Pterocymbium* and *Scaphium* cannot be considered as a sign of primitive structure, as they are also absent from species of *Cola* and *Firmiana* and from the sample of *Octolobus* examined. Both isolated crystals and chambered parenchyma are however very useful diagnostic features, and may serve to establish the affinities of doubtful genera.

XII—THE GENERA

In the following account of the genera the author has not attempted to give a detailed description of each genus, but rather to pick out the particular features by which each can be distinguished from the rest. Details of the elements and tissues have already been given for each genus, and all that will now be attempted will be to show how far the present classification of the species is consistent with the wood anatomy. Several of the species have already appeared in different genera at different times, and though some of them still remain a puzzle, it is possible that the wood anatomy may in some cases suggest the appropriate relationships.

The tribe Sterculineae (EDLIN 1935)

1—*Brachychiton* SCHOTT. and ENDL.

B. acerifolius A. CUNN.; *B. discolor* F. VON MUELL.; *B. rupestris* K. SCHUM.

The first two species of this genus appear to be indistinguishable from species of *Sterculia* A, except as regards vessel size and distribution. The species have all at one time or another been included in the genus *Sterculia*, and there appears to be no adequate reason for separating them, on the grounds of wood anatomy; they have in common, the arrangement of the parenchyma, and the type of vessel-parenchyma pit-pairs.

Brachychiton rupestris K. SCHUM. (fig. 32, Plate 30) is different from all the other material of the Sterculiaceae examined, in having large cavities in the parenchyma. These are possibly for water storage, and the name "Australian bottle tree" may owe its origin to this, or to the curious shape of the trunk. Owing to these cavities the wood is extremely spongy, and of an irregular texture, the cavities alternating with masses of harder fibrous tissue. Apart from this peculiarity it has much in common with the species of *Sterculia* B, having very short vessel members, broad bands of parenchyma, four cells per parenchyma strand, with intercellular spaces between the cells, and chambered crystalliferous parenchyma. Only one small sample of this species was available, and it has been considered advisable to omit it from the table of measurements in view of its somewhat anomalous structure. Such measurements as are available, however, show much closer agreement with *Sterculia* B than with the other species of *Brachychiton*.

The author finds that, on anatomical evidence, there is little distinction between the genera *Brachychiton* and *Sterculia*; for *Brachychiton acerifolius* and *B. discolor* agree closely with the section A of that genus, and *B. rupestris* with the section B. There appears also to be very little morphological difference between *Brachychiton* and *Sterculia*, and BENTHAM and HOOKER (1867) did not consider the differences sufficient to separate the two genera.

2—*Cola* SCHOTT.

C. acuminata SCHOTT. and ENDL.; *C. buntingii* BAK. f.; *C. caricifolia* K. SCHUM.; *C. chlamydantha* K. SCHUM.; *C. cordifolia* R.BR.; *C. heterophylla* SCHOTT. and ENDL.; *C. lateritia* K. SCHUM.; *C. laurifolia* MAST.; *C. lepidota* K. SCHUM.; *C. mirabilis* A. CHEV.; *C. nitida* A. CHEV.; *C. togoensis* ENGL. and KRAUSE; *C. verticillata* STAPF.

This genus appears to be very homogeneous, and the species are often indistinguishable from one another. They are also very similar to species of *Sterculia* B, from which they can only be distinguished by the absence of chambered crystalliferous parenchyma. Solitary crystals appear sporadically in the rays and parenchyma of a few species, but neither crystalliferous fibres nor chambered parenchyma have been observed in any species.

3—*Eribroma* Pierre.

E. klaineana Pierre.

Only one sample of this genus was available. The species was previously placed in the genus *Sterculia,* and from its wood anatomy there appears no reason why it should not be included in this genus. All the features measured fell within the range for the different species of *Sterculia* B, though they are below the average. Some of the species of *Sterculia* B cannot be distinguished from *Eribroma.* The presence of chambered crystalliferous parenchyma and crystalliferous fibres in the wood of *Eribroma* serve to distinguish this genus from *Cola,* which it otherwise resembles. Neither Harms (Dalla Torre and Harms 1900–7) nor Thonner (1915) recognizes *Eribroma* as a distinct genus, but both sink it in *Sterculia.*

4—*Firmiana* Marsigli.

F. barteri K. Schum.; *F. colorata* R.Br.; *F. fulgens* Wall.; *F. populifolia* Terrac.; *F. simplex* W. F. Wight.

The species of this genus are very similar to one another in structure, with the exception of *F. simplex* W. F. Wight, which differs only in being ring-porous.

The bands of parenchyma that occur in this genus are often apparently composed mainly of paratracheal parenchyma, and may occasionally be entirely confluent in nature.

Firmiana can be distinguished from the other genera that have broad bands of parenchyma by the absence of crystals (occasional crystals were observed in one sample), and by the unilaterally compound vessel-parenchyma pit-pairs.

In 1932 the author (Chattaway 1932) suggested that *Sterculia pallens* Wall. was related to *Firmiana,* through *F. wallichii* R.Br. This species, and also *F. affinis* Mast., have now been transferred to the genus *Scaphium,* with which they have much in common. *Sterculia pallens,* however, closely resembles some of the other species now remaining in the genus *Firmiana,* having parenchyma that is apparently confluent, and it shares with them the unilaterally compound vessel-parenchyma pit-pairs. The author suggests that this species of *Sterculia* should be transferred to *Firmiana* (fig. 33, Plate 30).

In a recent paper, Ridley (1934) transferred *F. colorata* R.Br., *F. fulgens* Wall. and *Sterculia pallens* Wall. to another genus, *Erythropsis.* These woods cannot be distinguished from one another, or from the other species of *Firmiana,* and the wood anatomy suggests that the correct solution lies in transferring *Sterculia pallens* to *Firmiana,* rather than in the use of another generic name—*Erythropsis*—for all three woods.

5—*Octolobus* Welw.

O. spectabilis Welw.

Only one sample of this species was available. It is indistinguishable from *Cola,* except for the extremely small intervascular pit-pairs.

6—*Pterocymbium* R.Br.

P. javanicum R.Br.; *P. tinctorium* K. Schum.

The two species included in this genus are indistinguishable from one another in their wood structure. They are very similar in type to *Brachychiton* and *Sterculia* A, from which they can, however, be separated by the absence of crystals, and by the vessel-parenchyma pit-pairs. These are similar in size and shape to the intervascular pit-pairs, and are quite distinct from the large simple pits to parenchyma cells that characterize the vessels of *Brachychiton* and *Sterculia* A.

The strands of metatracheal parenchyma are commonly one- or two-celled, and owing to the thinness of the fibre walls the distinction between the fibres and parenchyma, as seen on the cross-section, is never very sharp.

Bentham (Bentham and Hooker 1867) found that there was occasionally a tendency to the hermaphrodite condition in *Pterocymbium javanicum*, and suggested that this was a primitive condition. The present author has already pointed out that *Pterocymbium* has certain primitive features in the wood.

7—*Pterygota* Endl.

P. alata Roxb.; *P. macrocarpa* K. Schum.; *P. kamerunensis* K. Schum.

The species of *Pterygota* examined are rather similar in their general features to *Cola* and *Sterculia* B. The genus has been considered a synonym for *Sterculia*, but is maintained as a distinct genus by Dalla Torre and Harms (1900–7). The main difference from *Cola* lies in the abundance of solitary crystals in the rays and parenchyma of all the material examined. The absence of chambered parenchyma and crystalliferous fibres serves to distinguish *Pterygota* from some, though not all, of the species of *Sterculia* B.

8—*Scaphium* Endl.

S. affinis Mast.; *S. lincaricarpum* Ridl.; *S. macropodium* Miq.; *S. wallichii* R.Br.

The species of *Scaphium* examined have almost all at one time or another been considered as members of some other genus. *S. macropodium* has been transferred from *Sterculia*; *Scaphium wallichii* was once *Sterculia scapigera*, and was thence transferred to *Firmiana* as *F. wallichii* and finally to *Scaphium*, where it appears to fit best, at least so far as the anatomy is concerned; *S. affinis* has also been transferred from *Firmiana*, and in this case too the wood appears to resemble the other species of *Scaphium* much more than any species of *Firmiana* examined.

The genus differs from *Sterculia* mainly in the absence of metatracheal parenchyma. The paratracheal parenchyma is often rather scanty, sheathing the vessels, but occasionally it is distinctly aliform (fig. 34, Plate 30). This is interesting in view of the affinity with *Firmiana*. There is obvious confusion between the two genera, as is shown by the various changes that have been made in their classification. In both *Scaphium* and *Firmiana* the parenchyma, though banded in the latter, is probably paratracheal, and it is possible that the two genera represent a somewhat different line of development from the rest of the family.

9—*Sterculia* L.

Sterculia A. Metatracheal parenchyma predominantly in lines one cell wide (fig. 35, Plate 31).

S. angustifolia Roxb.; *S. cariboea* R.Br.; *S. carthaginensis* Cav.; *S. columbiana* Sprague; *S. crassiramea* Merril; *S. foetida* L.; *S. harmanda* Pierre; *S. hypochra* Pierre; *S. javanica* R.Br.; *S. macrophylla* Vent.; *S. montana* Merril; *S. oblongata* R.Br.; *S. ornata* Wall.; *S. parviflora* Roxb.; *S. philippinensis* Merril; *S. recordiana* Standl. (Standley 1935); *S. rubiginosa* Vent.; *S. spangleri* R.Br.; *S. tragacantha* Lindl.; *S. urceolata* Smith; *S. villosa* Roxb.

There is great similarity in general features between the species of this section of the genus. Occasional samples may show sporadic bands of parenchyma, and occasionally abnormalities such as wide regions of very thin-walled tissue may be found, but the parenchyma is usually paratracheal, in wide sheaths around the vessels, and metatracheal, in lines one cell wide. These woods are often indistinguishable from *Brachychiton.* They often have large simple pits from vessels to parenchyma cells. Crystals are often present, in the rays and parenchyma, but are usually solitary, in unspecialized cells, and the crystal sheath is usually rather thin.

Sterculia B (fig. 36, Plate 31). Metatracheal parenchyma and paratracheal parenchyma often indistinguishable, predominantly in broad bands three or four cells wide.

S. appendiculata K. Schum.; *S. blancoi* Rolfe; *S. blumei* G. Don.; *S. cinerea* A. Rich.; *S. coccinea* Roxb.; *S. elegantiflora* Hutch. and Dalz.; *S. oblonga* Mast.; *S. pallens* Wall.; *S. quinqueloba* K. Schum.; *S. rhinopetala* K. Schum.; *S. urens* Roxb.

It has already been suggested that the wood of *S. pallens* resembles that of *Firmiana* more than that of the other species of *Sterculia* B. As Ridley (1934) has already suggested affinities with *Erythropsis* (indistinguishable from *Firmiana*), the author suggests that it should be transferred from *Sterculia.*

The other species of *Sterculia* that have broad bands of parenchyma are often very similar in general structure to *Cola*, from which they can be distinguished by the presence of chambered parenchyma. Four species, however, *Sterculia cinerea*, *S. coccinea*, *S. quinqueloba* and *S. urens*, are sometimes intermediate in type between the two sections of the genus, and they may occasionally have a considerable amount of metatracheal parenchyma scattered between the bands, either as isolated strands or as short lines. The vessel-parenchyma pit-pairs may occasionally be simple (constantly in *S. quinqueloba*), and chambered parenchyma strands and crystalliferous fibres are absent. They thus appear to be borderline cases, and it is difficult to assign them to either section of the genus with certainty. On the whole, in the majority of samples examined, there appears to be more similarity to this section of the genus than to section A.

The tribe Tarrietineae (EDLIN 1935)

1—*Argyrodendron* F. v. MUELL.

A. actinophyllum (MOORE) EDLIN; *A. trifoliatum* F. v. MUELL.; *A. actinophyllum* var. *peralatum* (F. M. BAILEY).

The genus *Argyrodendron* was founded by F. VON MUELLER, for *Tarrietia argyrodendron*. This genus was referred back to *Tarrietia* by BENTHAM and HOOKER (1867), but has been revived by EDLIN (1935) to include *T. argyrodendron* and *T. actinophylla*. These two species are quite distinct anatomically from the other species of *Tarrietia* examined, having broad bands of parenchyma, whereas the species of *Tarrietia* have narrow lines, and it seems proper that the two species should be kept in a separate genus.

The author has also received material from Australia bearing the designation *T. argyrodendron* var. *peralata*. From the wood structure these specimens are clearly allied to *Argyrodendron*, and the material undoubtedly represents *Tarrietia trifoliata* var. *peralata* F. M. BAILEY. The author suggests that as it cannot be separated from *Argyrodendron* from the same source, *A. actinophyllum* var. *peralatum* is a better designation for it.

2—*Heritiera* AIT.

H. elata RIDLEY; *H. fomes* SYME.; *H. littoralis* DRY.; *H. macrophylla* WALL.

The genus *Heritiera* is very homogeneous, and the species are very similar anatomically. They can be distinguished from *Argyrodendron* by the narrow lines of metatracheal parenchyma one cell wide, and from *Tarrietia* by the rays, in which there is often only a very slight distinction between marginal and central cells, by the absence of sheath cells and by the occasional presence of chambered strands in the metatracheal parenchyma. This feature and the occurrence of dark gum-like deposits in the rays and parenchyma distinguish species of *Heritiera* from the species of *Sterculia* A. It is probable that *Heritiera* represents a more advanced type of structure than most woods with narrow lines of metatracheal parenchyma, and possibly an advance in ray structure, and in the parenchyma strand itself, has been accompanied by a lag in the type of parenchyma and its distribution.

3—*Tarrietia* BL.

T. cochinchinensis PIERRE; *T. javanica* BL.; *T. perakensis* KING; *T. simplicifolia* MAST.; *T. sumatrana* MIQ.; *T. sylvatica* MERRIL; *T. utilis* SPRAGUE.

The species now placed (EDLIN 1935) in the genus *Tarrietia* are very similar to one another anatomically. *T. utilis* SPRAGUE was formerly placed in the genus *Heritiera* as *H. utile*. The woods of *Heritiera* and *Tarrietia* have many points of similarity, especially when seen in cross-section but the rays of *T. utilis* are markedly heterogeneous, and often have a very conspicuous sheath of erect marginal cells, while the rays of *Heritiera* often have little distinction between marginal and central cells, and are almost always without sheath cells. The wood anatomy thus confirms the transference to *Tarrietia*.

Suggested changes

The following changes in classification are suggested:

Sterculia pallens WALL. to be transferred to *Firmiana*; *Brachychiton* and *Eribroma* again to be sunk in *Sterculia*; the genus *Sterculia* to be subdivided into two subgenera.

The rearrangement of these genera is reflected in the dimensions of the elements. The alterations in the mean values for vessel-member length, vessel diameter and fibre length are given below.

Vessel-member length. *Sterculia* A is altered from 441 ± 55·2 to 446 ± 54·8μ; *Sterculia* B from 353 ± 51·4 to 337 ± 32·8μ; *Firmiana* from 414 ± 99·5 to 420 ± 95·5μ. The changed position of *Sterculia pallens* WALL. from *Sterculia* B to *Firmiana* makes a significant difference to the mean lengths of the former genus, but not to that of the latter. This is not unexpected, for *Sterculia pallens* is the only species in *Sterculia* B with vessel members much above the average length for that group, but they are very little different from the average length for *Firmiana*, and the addition of this species to the genus *Firmiana* does not make a significant difference to the mean length of the genus.

Vessel diameter. *Sterculia* A is altered from 187 ± 31·0 to 176 ± 37·4μ; *Sterculia* B from 156 ± 25·0 to 155 ± 25·6μ; *Firmiana* from 153 ± 29·5 to 153 ± 29·7μ. The addition of the specimens of *Brachychiton* to *Sterculia* A reduced the average diameter by a significant amount. The vessels of *Brachychiton* were much smaller than was expected for this type of wood, but as this was the only feature in which *Brachychiton* differed from *Sterculia* A it was not considered sufficient to warrant keeping the two genera separate.

Fibre length. *Sterculia* A is altered from 2029 ± 334 to 2009 ± 335μ; *Sterculia* B from 2017 ± 317 to 2008 ± 326μ; *Firmiana* from 1939 ± 226 to 1920 ± 221μ. None of these changes is significant.

XIII—CONCLUSION

The most interesting feature of the wood of the Sterculiaceae lies in the unusual relations of the metatracheal and paratracheal parenchyma, and in the development of the rays. The latter show two different ways of solving the problem of spreading the ray tissue through the wood, neither of them apparently leading on to any further advance, but probably representing side-lines of specialization, since the main line of development is towards the formation of small rays. The splitting up of large rays would have the effect of forming numerous small rays, if the rays so formed did not grow and split and grow again. As it is there is always a large number of big rays present in the wood, and the trend of development towards smaller rays is not achieved in this way. The only genus in which there appears to be any advance along the main line of the phylogenetic sequence established by KRIBS is *Heritiera*, in which the rays are reduced in size, and sometimes approach the homogeneous condition.

The most characteristic anatomical features of the Sterculiaceae are as follows: Both paratracheal and metatracheal parenchyma occur in the same wood, either independently as sheaths round the vessels and narrow metatracheal lines, or combined as broad bands. The parenchyma and small rays are storeyed, but the larger rays are higher than, and independent of, the storeys, and are surrounded by sheath cells. Other characters that are consistent throughout the family are vessels with simple perforation plates, alternate intervascular pitting, libriform fibres that are never septate, and the absence of tracheids. Within the family, the genera can be distinguished by the type of parenchyma, the size of the intervascular and vessel-parenchyma pitting, the grouping of the vessels, and the occurrence of chambered parenchyma and crystalliferous fibres, or solitary crystals. Within the genera it is seldom possible to distinguish the species, except *Firmiana simplex* which is ring-porous, and *Brachychiton rupestris* which has anomalous structure.

The family Sterculiaceae is similar in many respects to the other families of the Malvales—Bombacaceae, Malvaceae and Tiliaceae; it is most easily confused with the Bombacaceae. In the Bombacaceae there is only one genus with broad bands of parenchyma—*Catostemma*—and the vessel arrangement and the purely paratracheal nature of the bands serves to distinguish it from those Sterculiaceae which have broad bands of parenchyma. The other genera of the Bombacaceae can be distinguished from the Sterculiaceae which have narrow lines of parenchyma by the presence of tile cells (Durioideae), by the more continuous lines of metatracheal parenchyma, which often alternate with great regularity with layers of fibres one cell wide, by the rather scanty development of the paratracheal parenchyma and by the absence, or irregular development, of sheath cells. In the Sterculiaceae only *Brachychiton* and *Sterculia* A. regularly have large vessel-parenchyma pit-pairs, but in the Bombacaceae they are present in all the genera that are without tile cells, except *Maxwellia* and *Montezuma*.

EDLIN (1935), basing his conclusions upon the floral morphology of the different families, was led to the conclusion that the Tiliaceae is the most primitive family of the Malvales, and he suggested that the three families Bombacaceae, Buettneriaceae and Sterculiaceae have been derived from the Tiliaceae upon mutually independent lines. He further suggested that the Malvaceae have arisen from the Bombacaceae as a result of further specialization.

The author has not studied the other families of the Malvales in as much detail as the Sterculiaceae, but examination of the wood appears to confirm the view that the Buettneriaceae, Bombacaceae and Sterculiaceae may have been derived from the Tiliaceae, but have developed along independent lines. EDLIN suggested that the unisexual and apetalous flowers and apocarpous ovary that separate the Sterculiaceae so clearly from the other Malvales represent a side-line of evolutionary development, and do not lead to other alliances. The author has already suggested that the ray development in this family represents such a side-line, and it is also possible that the combination of paratracheal and metatracheal parenchyma in broad bands, such as occur in *Cola*, *Sterculia* B, etc., represents the end of a series that does not give rise to any other forms. Bands of parenchyma are found occasionally in the other families of the Malvales, but these are much less regular, and appear to be entirely paratracheal.

EDLIN suggests that this family has been derived from the Tiliaceae through the genus *Christiana*. This genus differs from the Sterculiaceae, particularly in regard to the wood parenchyma and rays, but it is not easy to be certain whether these differences render such a derivation impossible. Diffuse parenchyma is absent from *Christiana*, and as this is probably a primitive feature, it seems unlikely that it should originate in woods derived from *Christiana*. The rays in *Christiana* are smaller, and though of the same general type (heterogeneous II), probably represent a more advanced type than those found in the Sterculiaceae. It seems more likely therefore that if the Sterculiaceae are derived from the Tiliaceae they have come through some other genus, perhaps no longer living. Until more is known of the development of the different tissues, the evidence supplied by the wood is insufficient to decide whether the Sterculiaceae have been derived from the Tiliaceae, or whether both have come from a common ancestor.

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XIV—SUMMARY

1—The Sterculiaceae must be considered a rather advanced family; the genera all have storeyed structure, vessel members less than 550μ long, simple horizontal perforation plates, and alternate pitting.

2—The vessels vary from narrow to wide in the different genera, and vessel diameter appears to have little systematic significance. A positive relation was observed between diameter and vessel-member length, but there is no relation between vessel-member length and vessel distribution.

3—The size and frequency of the intervascular pitting is constant throughout each genus, with the exception of *Sterculia*, and the genera with the longest vessel members have the largest pits. Large simple pits between vessels and parenchyma cells, that occur in *Brachychiton* and *Sterculia* species, have been studied in detail.

4—The fibres are libriform and non-septate throughout the family, except for the crystalliferous fibres in *Eribroma* and *Sterculia* species. There is a negative relation between vessel-member length and the relative amount the fibres have extended during differentiation, the greatest relative extension occurring in the woods with the shortest vessel members.

5—The different forms of parenchyma are discussed, and the anatomical characters of the cells. The most advanced type of parenchyma in the family appears to be broad bands that include both metatracheal and paratracheal parenchyma. This form appears to represent the ultimate stage of two separate lines of development, one represented by the series diffuse—narrow metatracheal lines—broad metatracheal bands, and the other by the series vasicentric—aliform—confluent.

6—The rays show very little difference in type throughout the family, and cannot be used, except in the case of *Heritiera*, to separate the genera, but sheath cells are slightly more regular in the woods with the longest vessel members and narrow lines of parenchyma, than in those with shorter vessel members and broad bands of parenchyma. The occurrence and development of sheath cells and the increase in the number of rays by splitting up of the larger rays has been studied in detail.

7—Crystals are of frequent occurrence throughout the family, and appear to have little phylogenetic significance; they are, however, useful diagnostic features. Chambered parenchyma and crystalliferous fibres have been studied in *Eribroma* and *Sterculia* species.

8—The taxonomic position of the genera is discussed, and the following changes in classification suggested: *Sterculia pallens* WALL. to be transferred to *Firmiana*; *Brachychiton* and *Eribroma* again to be sunk in *Sterculia*; and the genus *Sterculia* to be subdivided into two subgenera.

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DESCRIPTION OF PLATES

PLATE 29

FIGS. 25–27—Distribution of parenchyma. FIG. 25—*Pterocymbium tinctorium* K. SCHUM., scattered cells and short tangential lines. FIG. 26—*Sterculia carthaginensis* CAV., abundant paratracheal parenchyma, and narrow metatracheal lines. FIG. 27—*Cola caricifolia* K. SCHUM., broad metatracheal bands. (All × 33.)

FIGS. 28–30—Types of parenchyma cell. FIG. 28—*Pterocymbium javanicum* R.BR., two cells per strand, without intercellular spaces. FIG. 29—*Sterculia recordiana* STANDL., two to four cells per strand, without intercellular spaces. FIG. 30—*Sterculia appendiculata* K. SCHUM., four or more cells per strand; cells with rounded corners and intercellular spaces. (All × 155.)

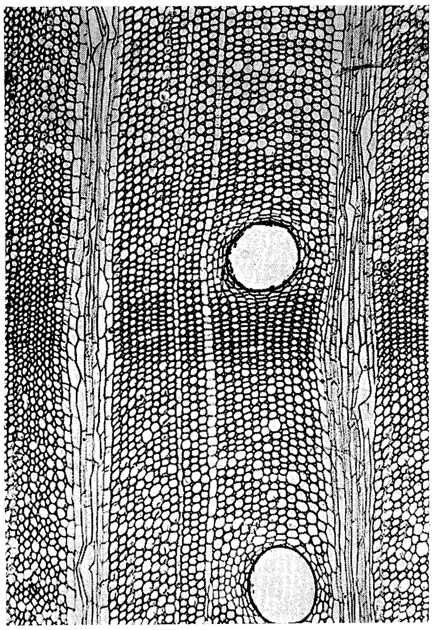


FIG. 25

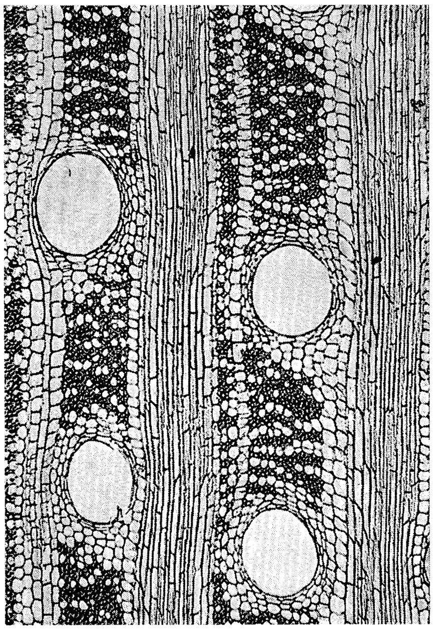


FIG. 26

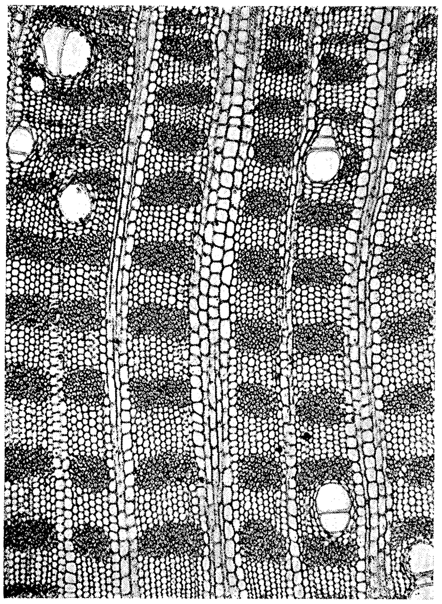
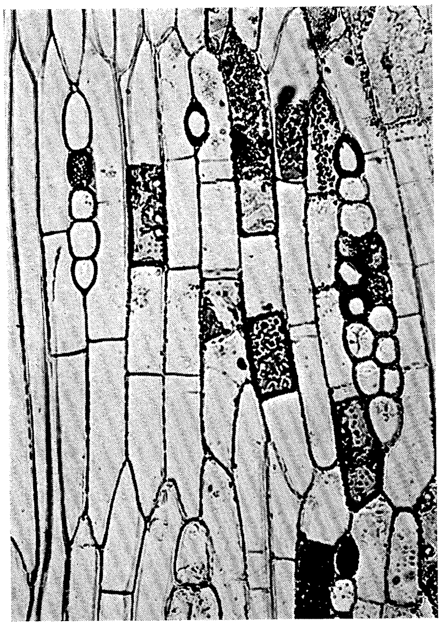


FIG. 27

FIG. 28



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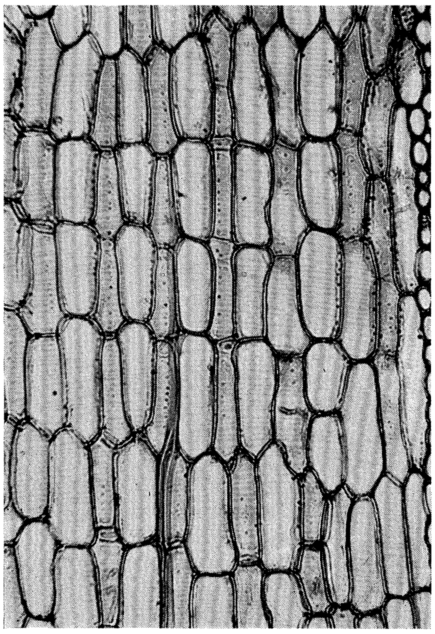

FIG. 30

PLATE 30

FIG. 31—*Sterculia rhinopetala* K. SCHUM. Radial section; solitary crystals in rays, parenchyma and fibres. (× 175.)

FIG. 32—Transverse section of *Brachychiton rupestris* K. SCHUM.; showing broad bands of parenchyma and large cavities. (× 10.)

FIG. 33—Transverse sections of: *a*, *Sterculia pallens* WALL.; *b*, *Firmiana fulgens* WALL.; showing the similarity of structure in the two woods. (× 33.)

FIG. 34—Transverse sections of *Scaphium* spp. *a*, *S. macropodium* MIQ. parenchyma terminal and vasicentric; *b*, *S. wallichii* R.BR. parenchyma terminal and aliform, occasionally confluent. (× 33.)

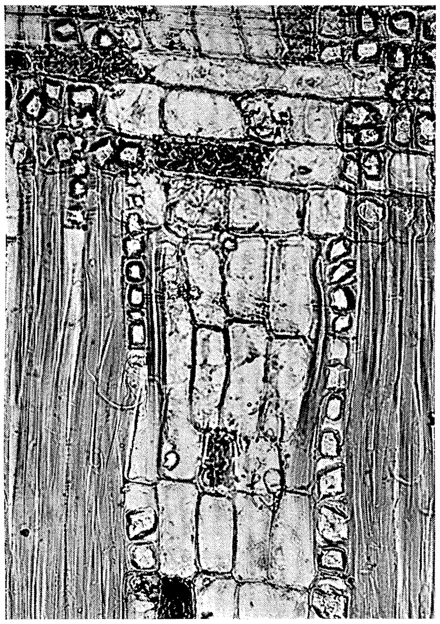

Fig. 31

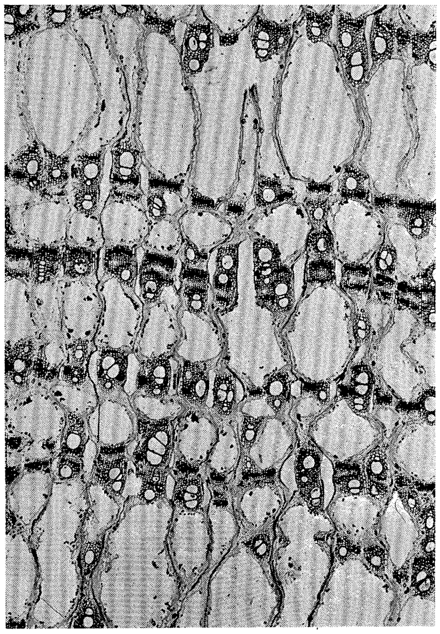

Fig. 32

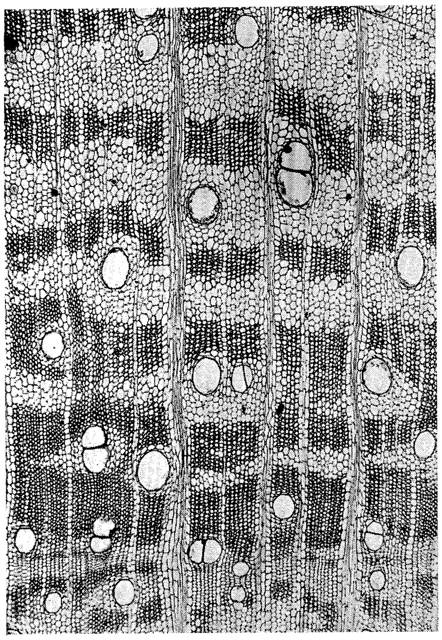

Fig. 33
a

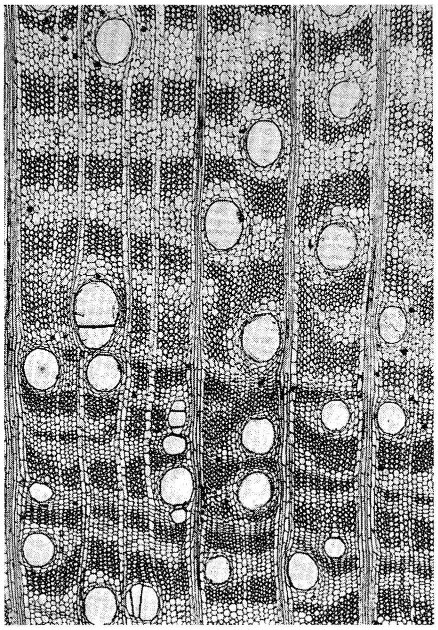

Fig. 33
b

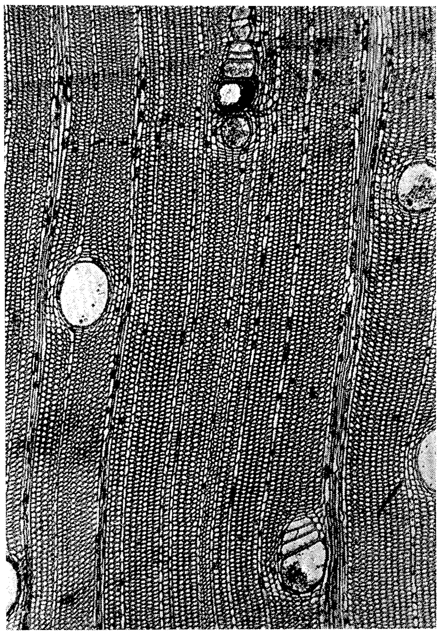

Fig. 34
a

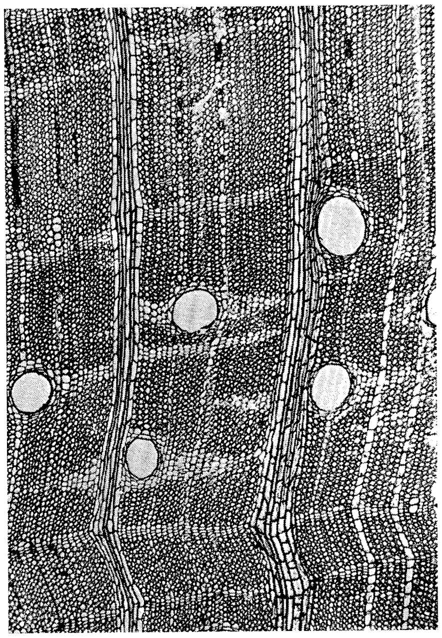

Fig. 34
b

PLATE 31

FIGS. 35, 36—Comparison of *Sterculia* A and *Sterculia* B. 1, transverse sections: A, *S. carthaginensis* CAV. B, *S. blancoi* ROLFE. 2, tangential sections: A, *S. recordiana* STANDL. B, *S. appendiculata* K. SCHUM. 3, radial sections: A, *S. foetida* L. B, *S. oblonga* MAST. (All × 33.)

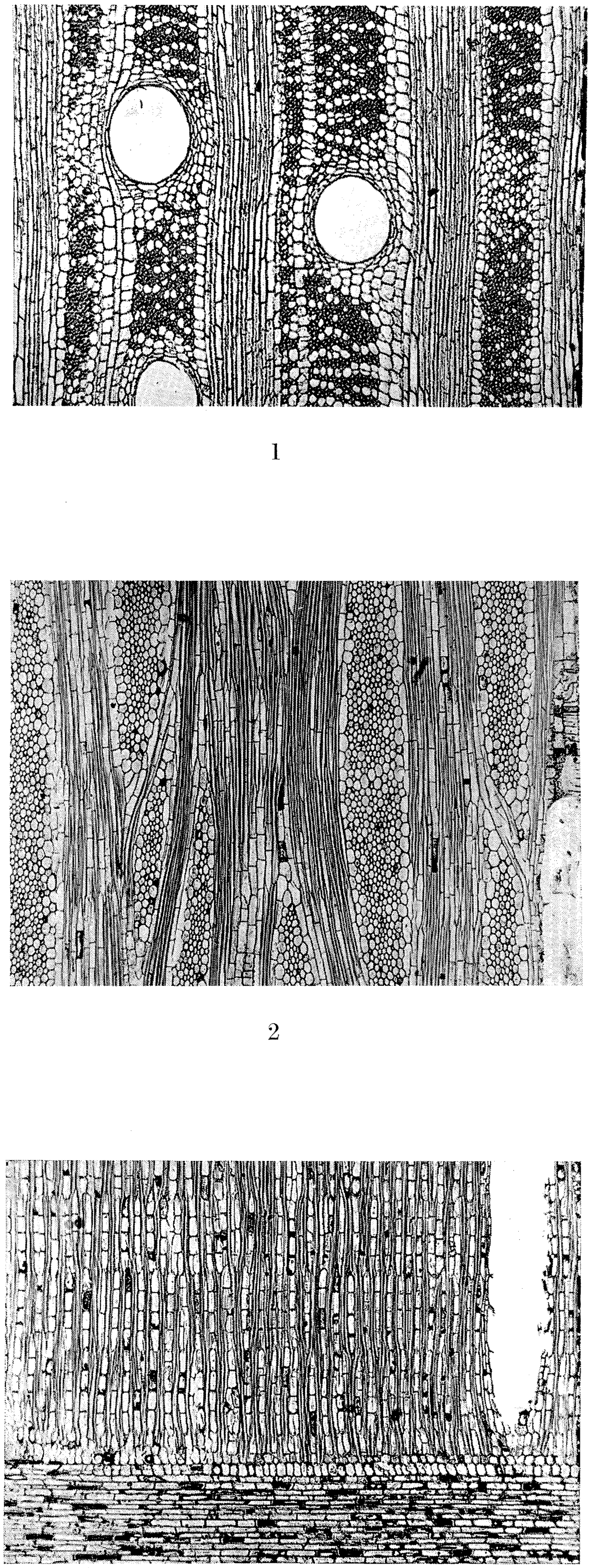

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FIG. 35. *Sterculia* A

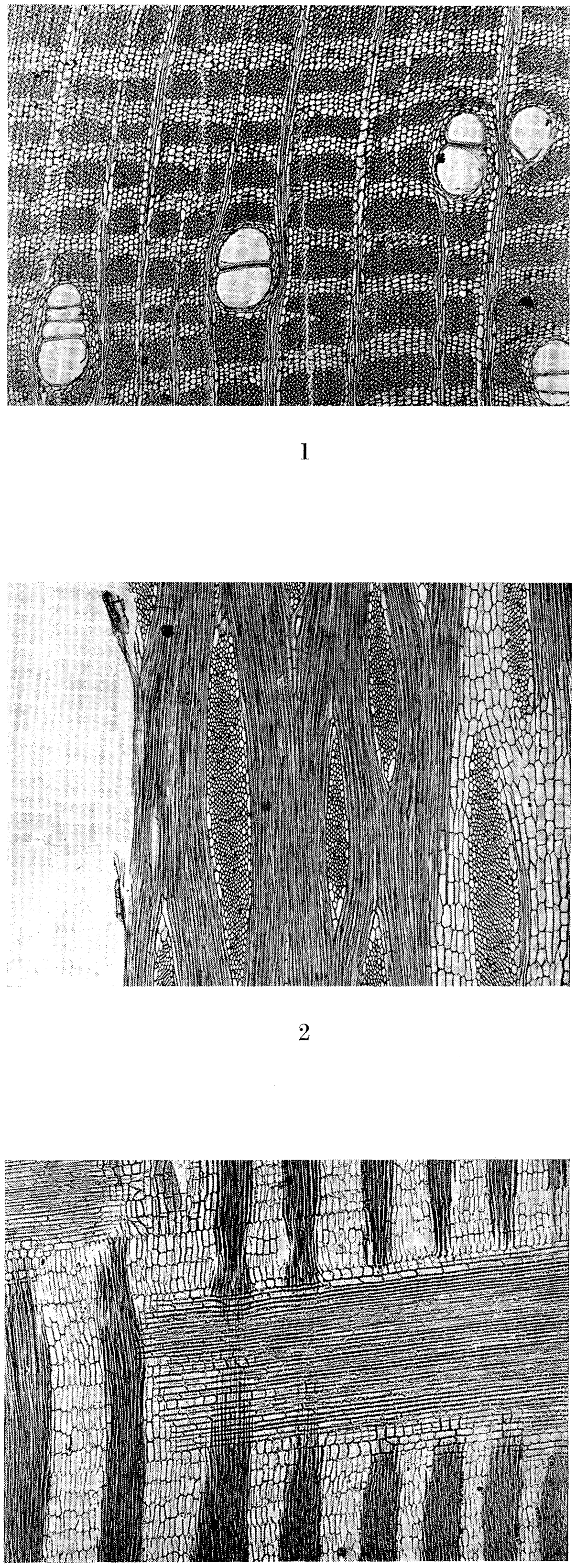

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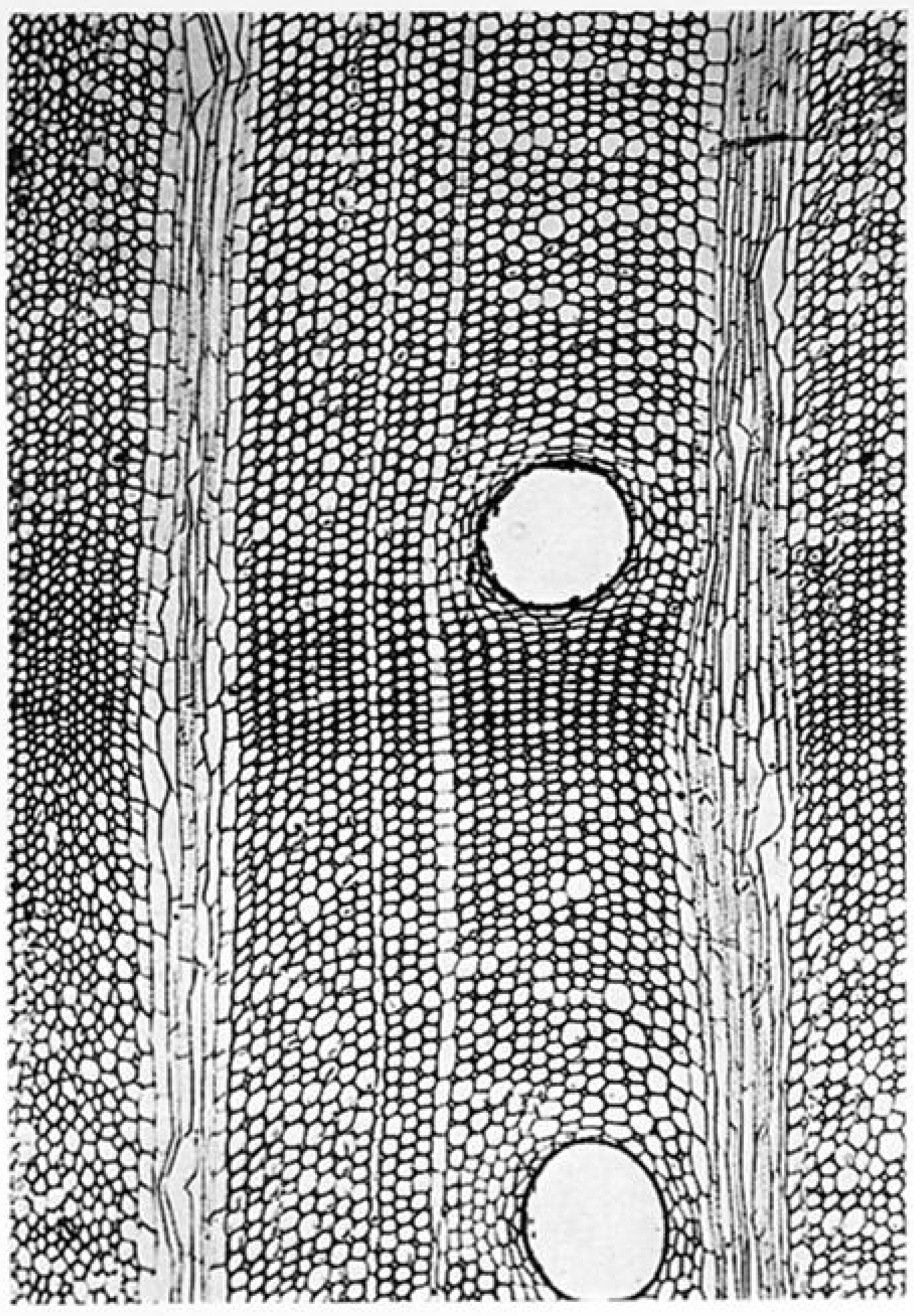
FIG. 36. *Sterculia* B

FIG. 25



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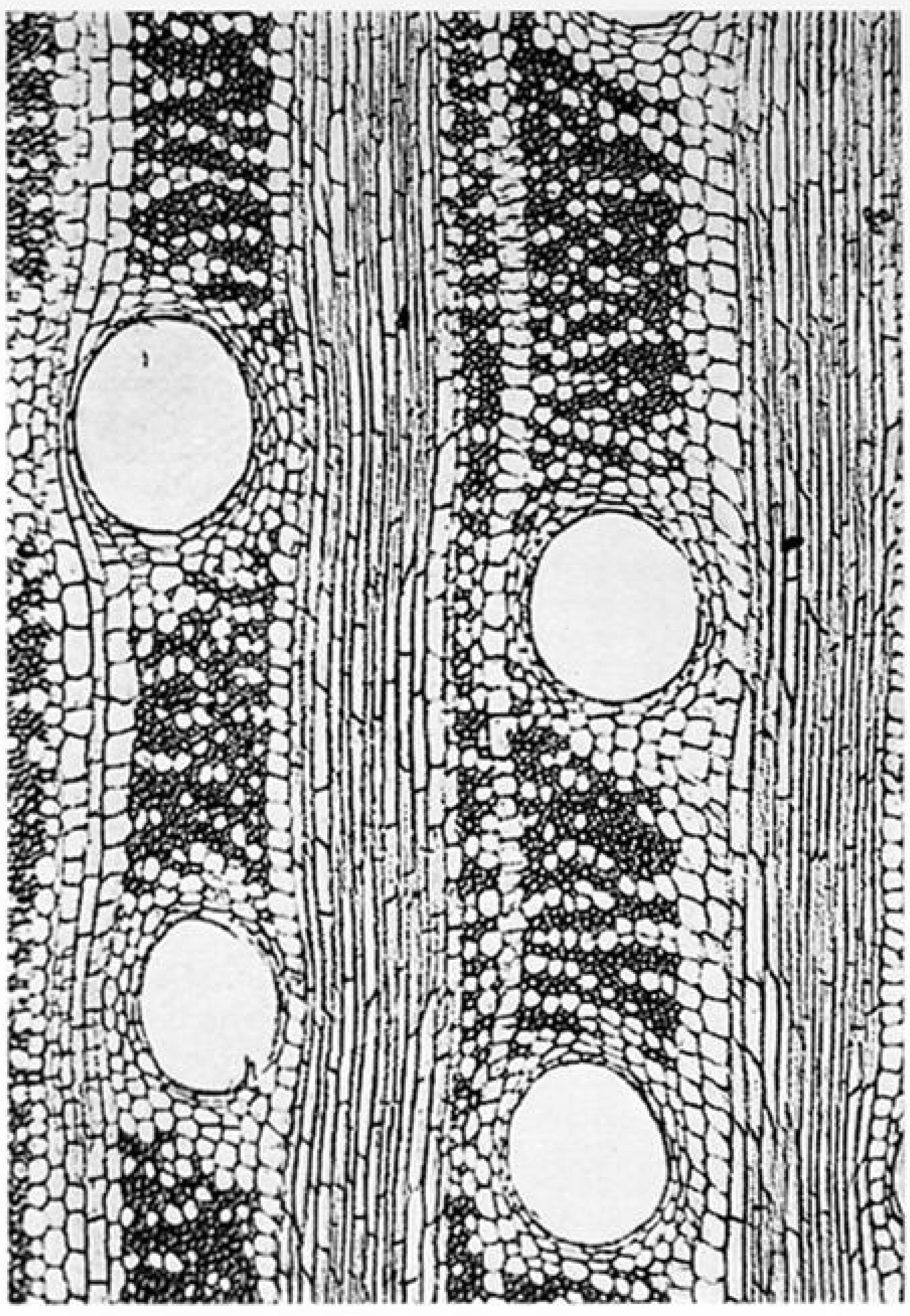

FIG. 27

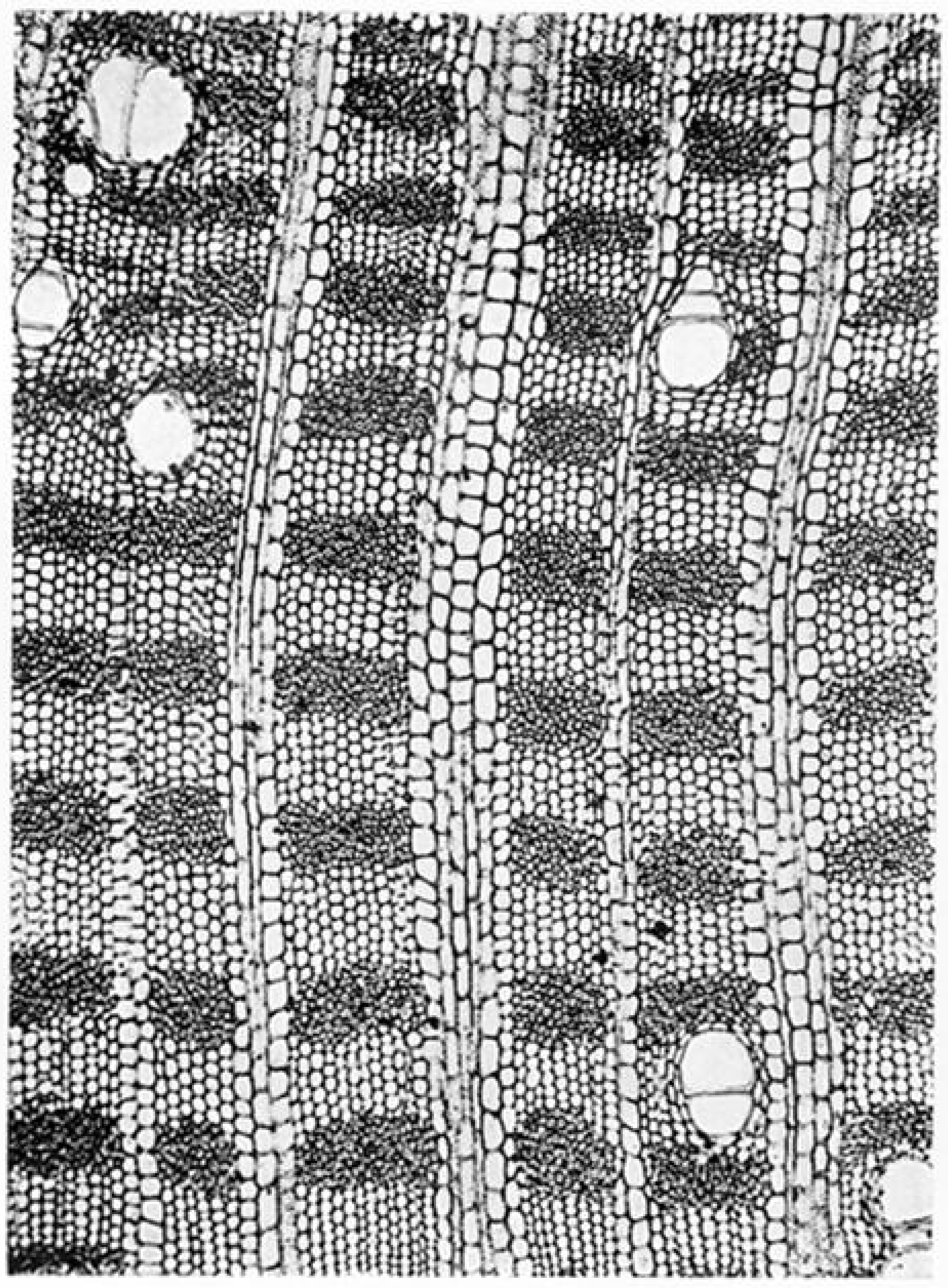

FIG. 28

FIG. 29

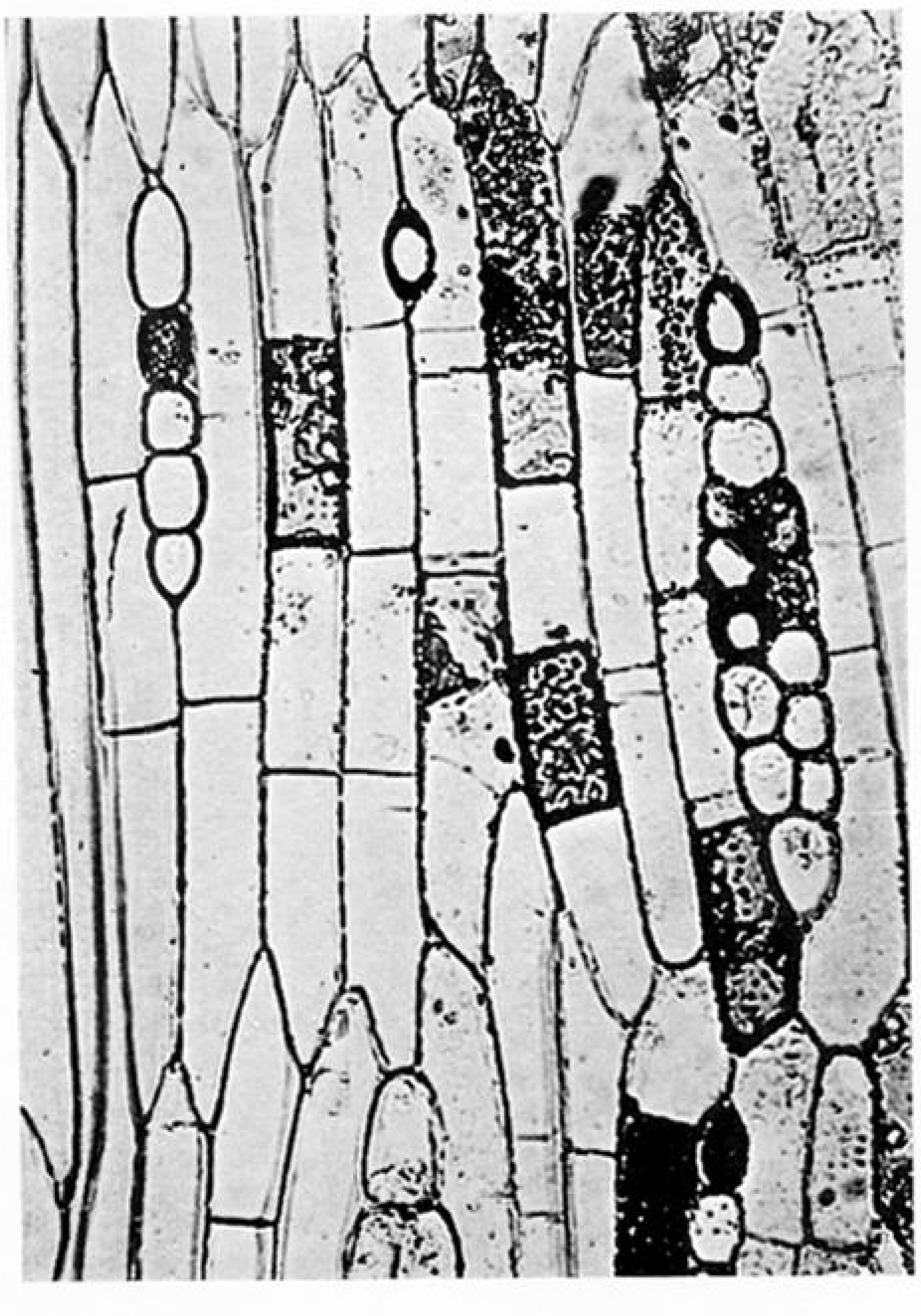

FIG. 30

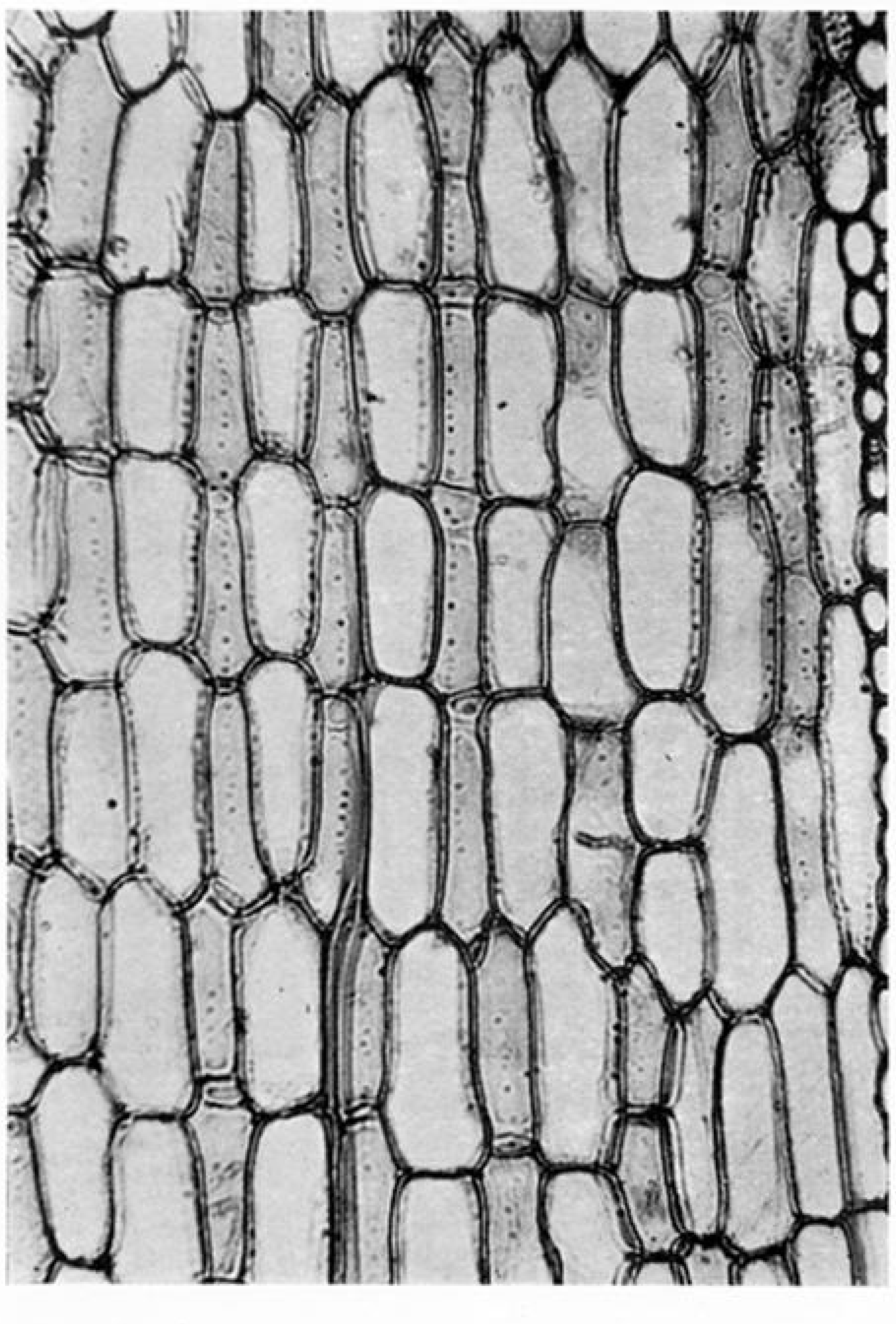

PLATE 29

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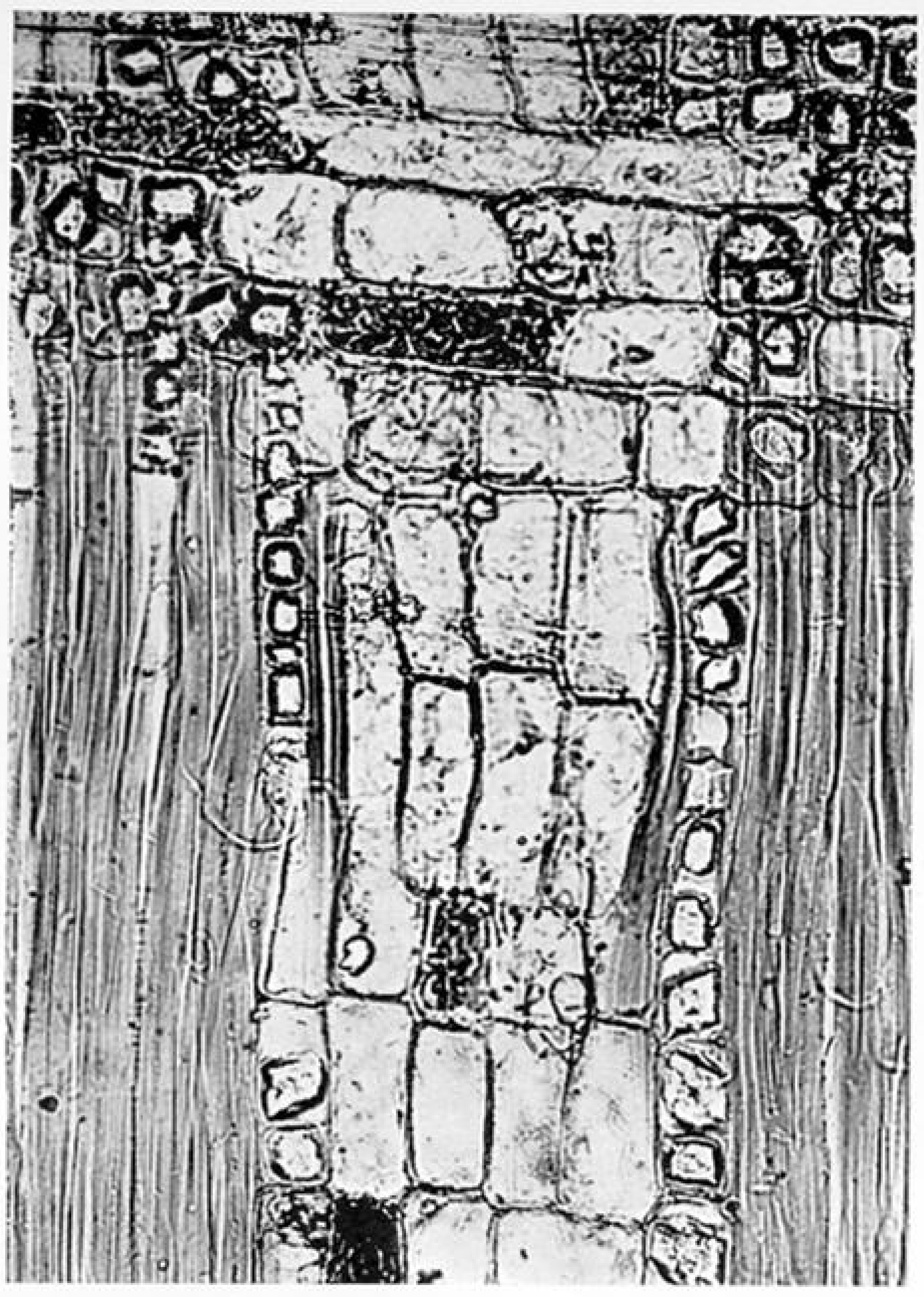
FIG. 31



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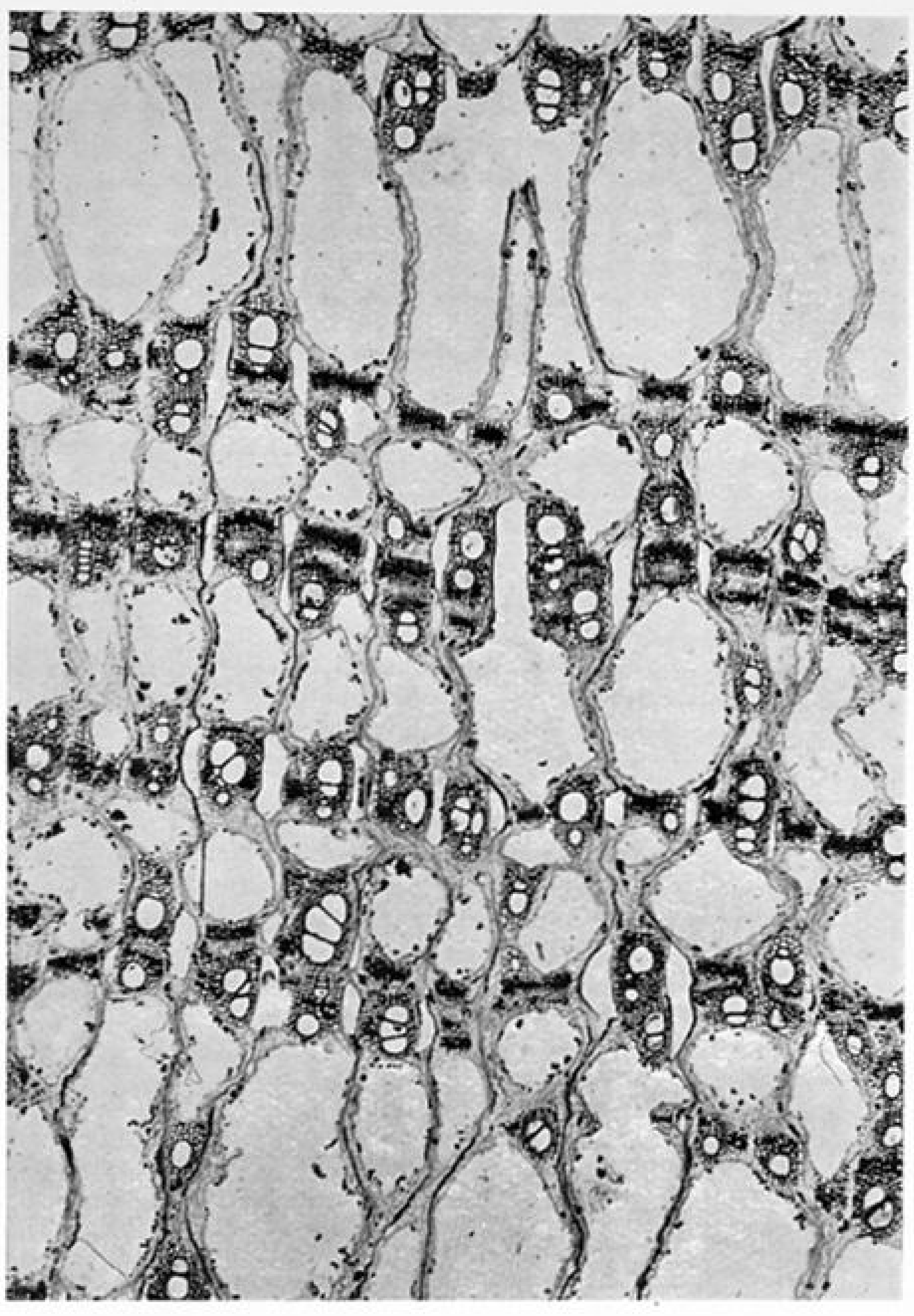

FIG. 33 *a*

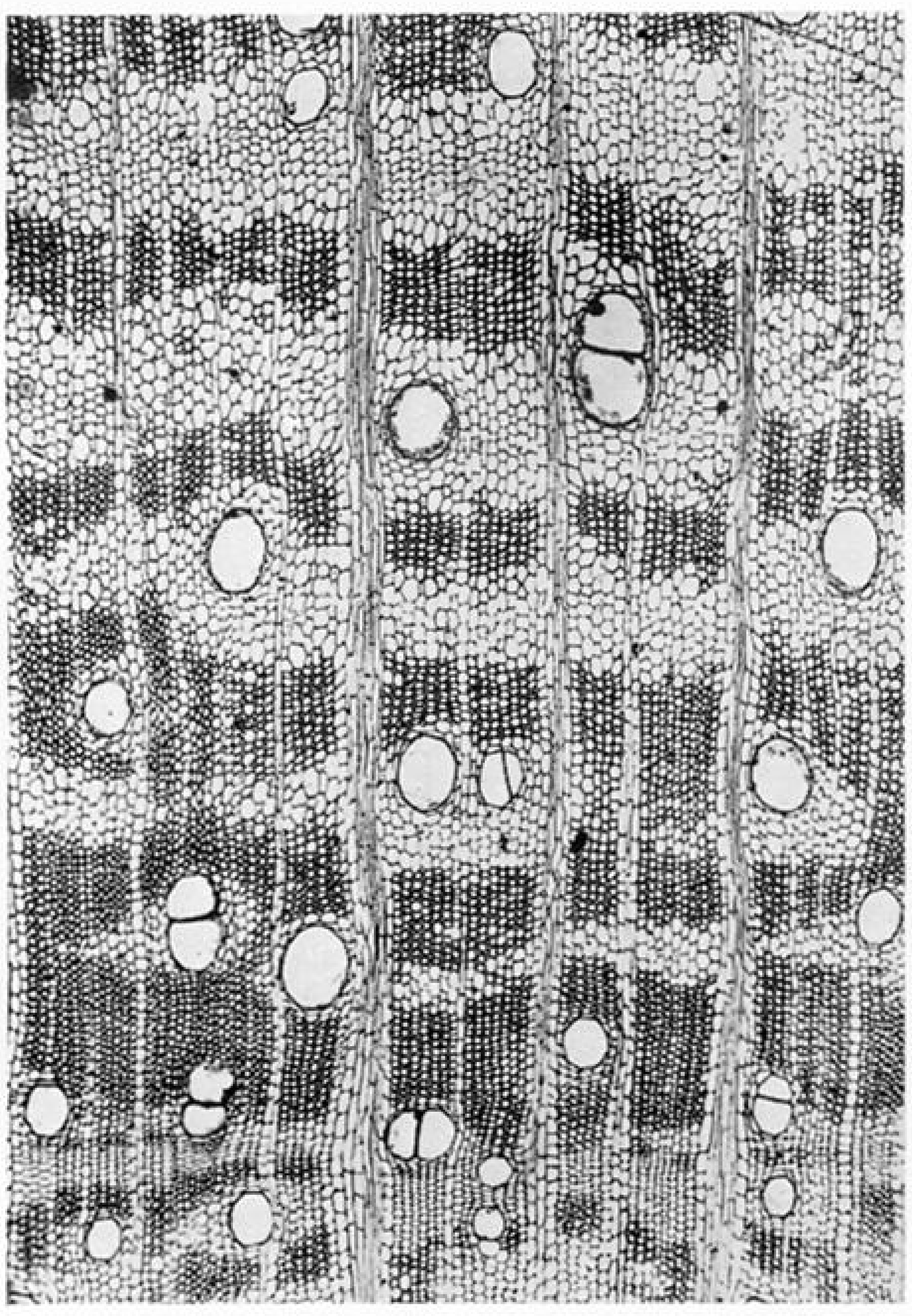

FIG. 33 *b*

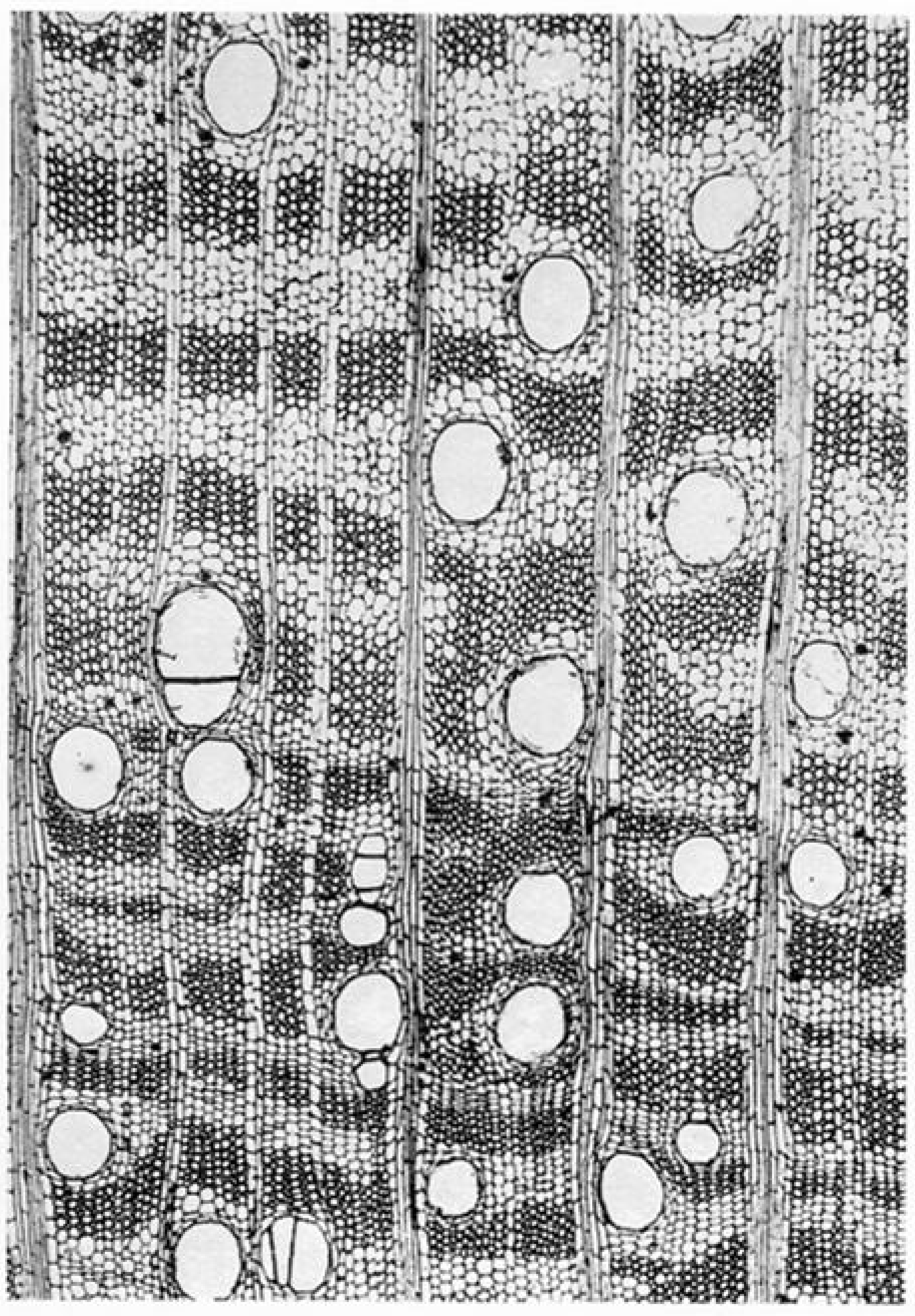

FIG. 34 *a*

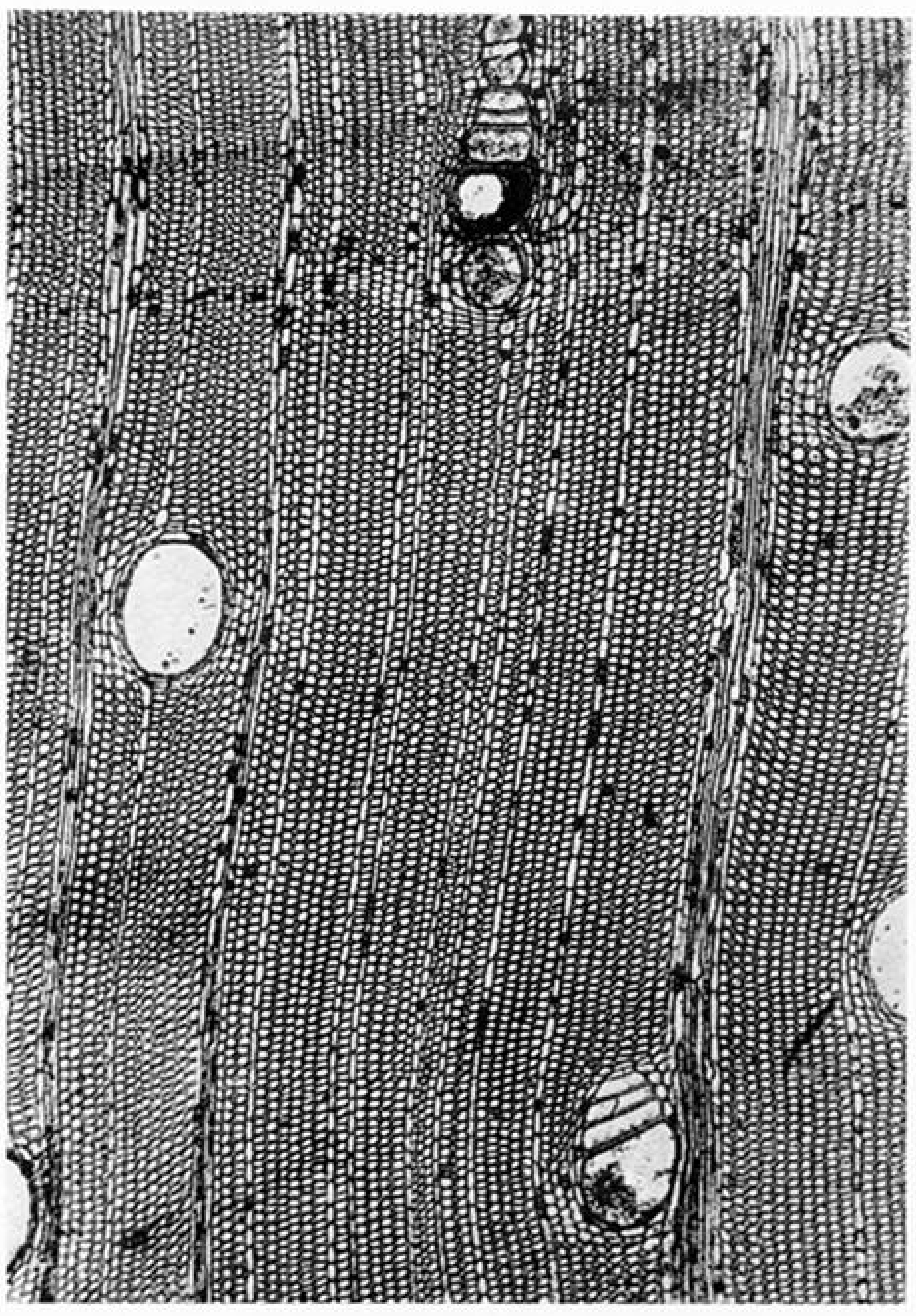

FIG. 34 *b*

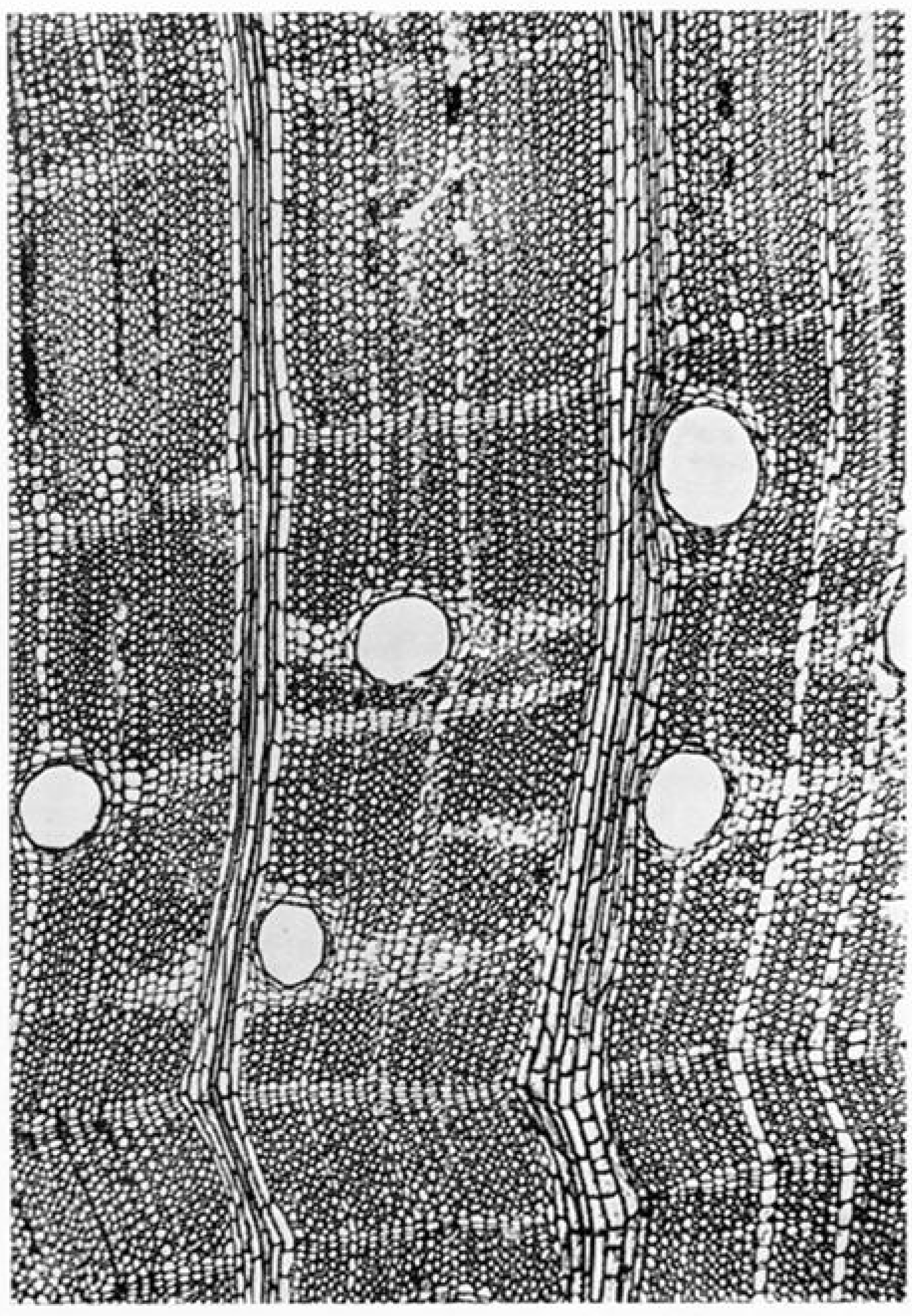

PLATE 30

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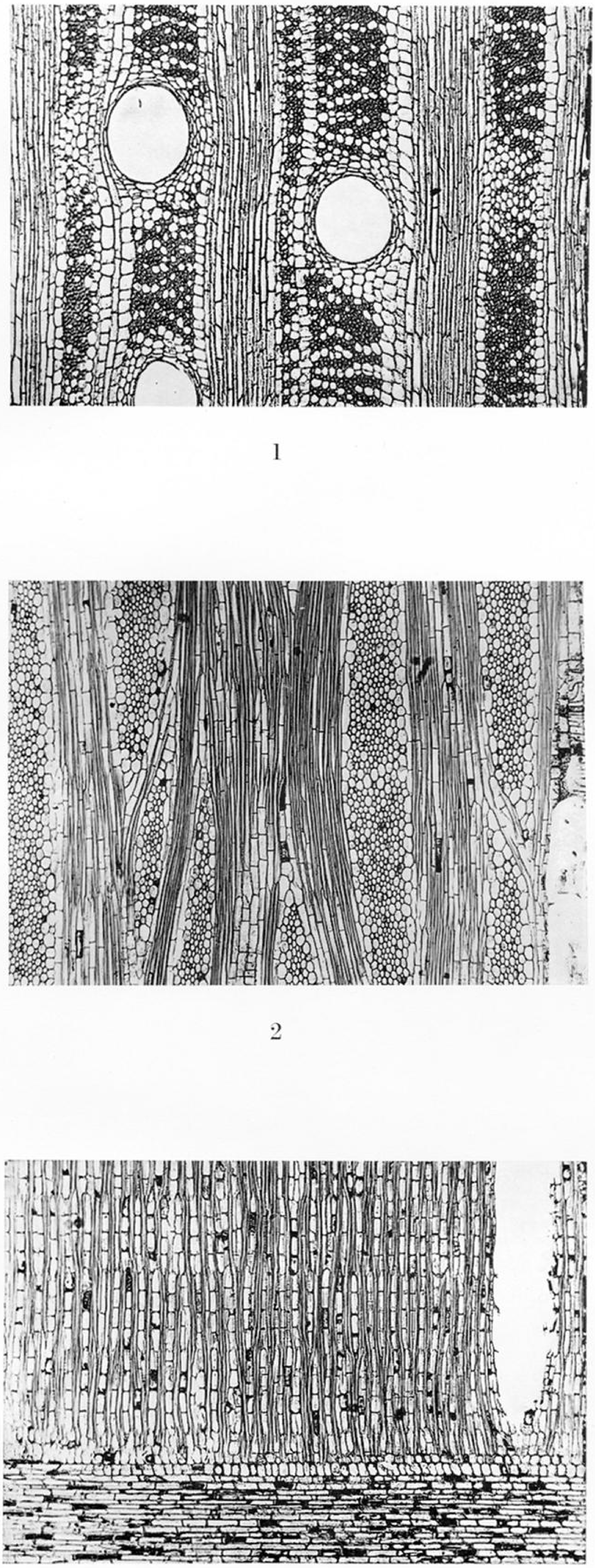

Fig. 35. *Sterculia* A

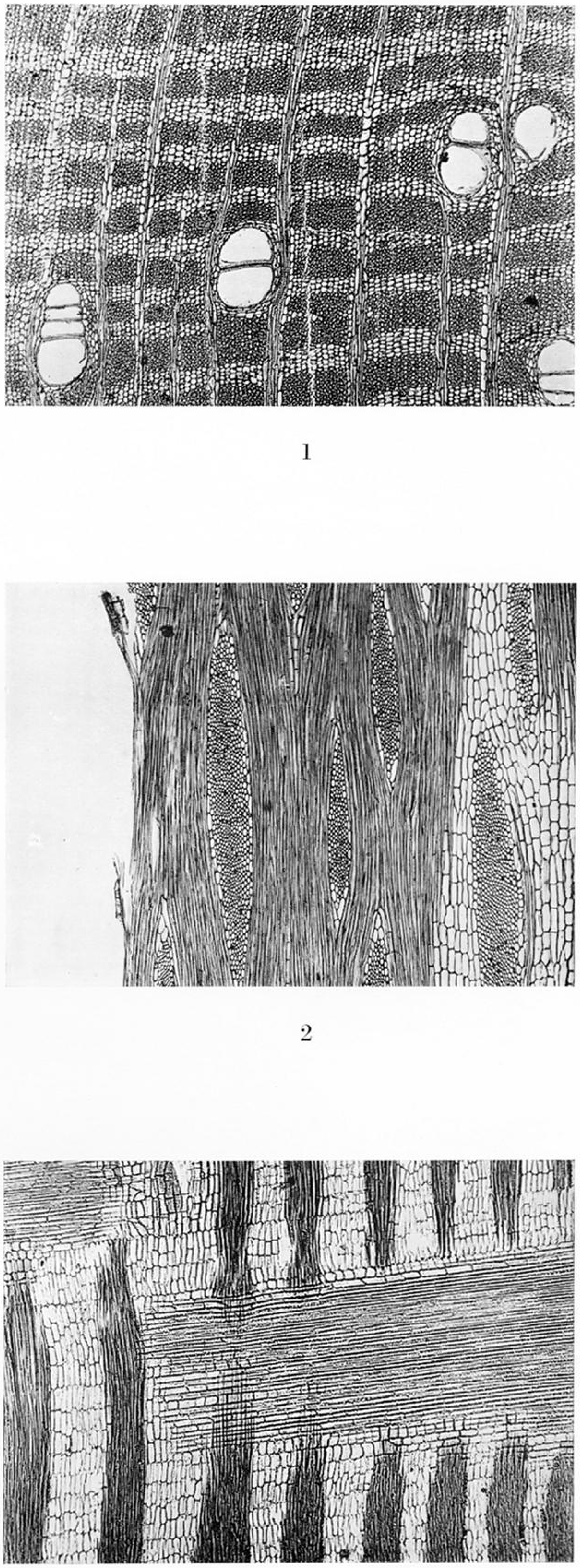

Fig. 36. *Sterculia* B

Plate 31

Figs. 35, 36—Comparison of *Sterculia* A and *Sterculia* B. 1, transverse sections: A, *S. carthaginensis* Cav. B, *S. blancoi* Rolfe. 2, tangential sections: A, *S. recordiana* Standl. B, *S. appendiculata* K. Schum. 3, radial sections: A, *S. foetida* L. B, *S. oblonga* Mast. (All × 33.)