THE CELL WALL STRUCTURE OF XYLEM PARENCHYMA

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Summary

The fine structure of the cell wall of both ray and vertical parenchyma has been investigated. In all species examined secondary thickening had occurred. In the primary cell wall the micellar orientation was approximately transverse to the longitudinal cell axis. Using optical and X-ray methods the secondary cell wall was shown to possess a helical micellar organization, the micelles being inclined between 30° and 60° to the longitudinal cell axis.

The distribution of the various cell wall constituents was studied, and it was observed that most of the lignin occurred in the intercellular layer and primary wall. The layered structure of the cell wall of sclerosed parenchyma cells was also investigated and it was demonstrated that these cell walls possess both structural and chemical heterogeneity.

I. INTRODUCTION

In previous investigations of the cell wall structure of tissue elements of the xylem, attention has centred mainly on elements of mechanical or conducting function. The fine structure of xylem parenchyma—ray and vertical parenchyma—has received little attention. In form, the individual parenchyma cells are isodiametric or elongated with truncated ends and are usually thin-walled in comparison with the prosenchyma elements. They possess simple pitting. The fine structure of ray parenchyma appears to have been first studied by Tuszon (1903) who observed helical fractures in the walls of isolated cells. These he considered to be evidence of a helical micellar organization in the cell wall. A similar conclusion was reached much later, from optical (Ritter and Mitchell 1939) and X-ray (Gross, Clarke, and Ritter 1939) studies of the ray parenchyma of gymnosperms. So far as the writers are aware, no study has been made of the distribution of the cell wall constituents in ray or vertical parenchyma nor has any direct evidence of their cell wall organization been presented, apart from the work of Tuszon. Accordingly, the investigations described below were undertaken.

II. MATERIALS AND METHODS

Various species with comparatively thick-walled ray and vertical parenchyma cells were selected for investigation, particular attention being paid to the 'sclerosed' cells in vertical parenchyma and 'stone' cells in rays where these occurred. Such cells have unusually thickened cell walls and are similar in

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some features to the stone cells of phloem. Sclerosed tyloses were also examined since they are developed from parenchyma cells (Chattaway 1949). The species forming the main basis of the investigations reported here were:

Dialium laurium Baker (Leguminosae)—sclerosed and thin-walled ray and vertical parenchyma.

Fagus atropunica Sudw. (Fagaceae)—ray parenchyma.

Grevillea robusta A.Cunn. (Proteaceae)—ray parenchyma.

Gymnacranthera farquhariana Warb. (Myristicaceae)—sclerosed tyloses.

Hodgkinsonia ovatiflora F.Muell. (Rubiaceae)—ray and vertical parenchyma.

Persoonia lanceolata Andr. (Proteaceae)—'stone' cells in rays.

Podocarpus amara F.M.Bailey (Podocarpaceae)—ray parenchyma.

Pongamia pinnata L.Merr. (Leguminosae)—vertical parenchyma.

Tsuga canadensis L.Carr (Pinaceae)—ray parenchyma.

Using thin sections of this material the distribution of lignin in the cell wall was examined by the staining technique of Coppick and Fowler (1939) and the 72 per cent. sulphuric acid method (Dadswell 1931). The presence of polyuronide substances in the cell wall was demonstrated by treatment of carefully delignified sections with cuprammonium solution (Kerr and Bailey 1934), the delignification being effected by alternate treatments with chlorine water and 3 per cent. alcoholic monoethanolamine (van Beckum and Ritter 1937).

In cell walls with helical micellar organization it is customary to describe the micellar orientation by reference to the angle made by a tangent to the helix and the major morphological axis of the cell. This angle is referred to in the remainder of this paper as the 'micellar angle,' and can be determined by a number of methods to which further reference will be made. From species with wide rays, e.g. *Grevillea robusta,* or with wide bands of parenchyma, e.g. *Pongamia pinnata,* it was possible to dissect out bands of ray or vertical parenchyma tissue free from other elements. These were used for direct X-ray examination. For species with narrow rays or narrow bands of parenchyma the technique of building up a composite specimen from thin sections was employed (see Gross, Clarke, and Ritter 1939) before X-ray examination.

The X-ray diagrams obtained in the present study varied considerably. From *Grevillea robusta* ray cells, good although faint 4-point diagrams were obtained, permitting reasonably accurate determination of the micellar angle. Usually, however, 2-point diagrams consisting of two diffuse arcs were obtained as in *Pongamia pinnata.* Estimates of the micellar angle from these diagrams would be over-estimates compared with values obtained by other methods. The diffuseness of these diagrams may arise because of the extremely thin specimens used, and the existence of angular dispersion of the micelles about the direction of preferred orientation.

By optical methods the micellar angle can be determined from the position of the major extinction position (see, for example, Hartshorne and Stuart 1950) or from the value of the birefringence of the cell wall in transverse section. The second method was of particular value when the cell wall was very thick and the micellar orientation varied in the different layers, when the pitting of the cell wall made the determination of the major extinction position difficult, or when the X-ray diffraction pattern was too diffuse to permit measurement. It must be emphasized, however, that the results obtained by the birefringence method were only approximate as several assumptions were necessary in the calculations.

The birefringence, $(n'_\gamma - n_\alpha)$, of the cell wall in transverse section was determined using the de Senarmont compensator (Ambronn and Frey 1926; see also Hartshorne and Stuart 1950) and was calculated from the relation

$$n'_\gamma - n_\alpha = \phi\lambda/360d, \quad .. \quad .. \quad .. \quad (1)$$

where

ϕ is the phase difference (°),

λ is the wavelength of the light (μ) (0.59 for the Na line),

and d is the section thickness (μ).

After measuring the phase difference the section thickness was determined. This was done by macerating the section on a slide and turning the cells on their sides for direct measurement by gently sliding the cover glass (Preston 1946).

As the cell wall is not entirely composed of cellulose, the birefringence of which must be known in order to calculate the micellar orientation, it is necessary to make an estimate of the birefringence of a body the composition of which is approximately that of the parenchyma cell wall. Harlow and Wise (1928) have published figures for the cellulose content of ray parenchyma varying from 32 to 42 per cent. In the calculations made in this investigation it was assumed that the cellulose content was 40 per cent. If this assumed value is too high in comparison with the actual value for the specimen examined, then the calculated micellar angle will be too small, and conversely if the assumed value is too low the calculated angle will be too high.

The birefringence of a body containing 40 per cent. cellulose can be calculated from the mixture formula of Hermans (1949):

$$v_m (n_m - 1) = v_1(n_1 - 1) + v_2 (n_2 - 1) + \quad .. \quad (2)$$

where v_1, v_2 . . . . . are the volumes; n_1, n_2 . . . . . the refractive indices of the components; and v_m and n_m the corresponding quantities for the mixture. Thus, if $n_{\gamma 1}$ and $n_{\alpha 1}$ are the major and minor refractive indices of cellulose, n_γ and n_α the corresponding quantities for a body containing 40 per cent. cellulose, and n_R the refractive index of the non-crystalline components of the cell wall, then, by applying equation (2) separately to each of the refractive indices of cellulose, the following equations are obtained:

$$v_m (n_\gamma - 1) = v_1 (n_{\gamma 1} - 1) + v_2 (n_R - 1) \quad .. \quad (3)$$

$$v_m (n_\alpha - 1) = v_1 (n_{\alpha 1} - 1) + v_2 (n_R - 1). \quad .. \quad (4)$$

Subtracting equation (4) from equation (3) and rearranging:

$$n_\gamma - n_\alpha = \frac{v_1 (n_{\gamma 1} - n_{\alpha 1})}{v_m} \quad .. \quad .. \quad (5)$$

Taking the density of the cellulose as 1.56 and that of the cell wall as 1.46 (Stamm and Hansen 1937), $v_1 = 0.4/1.56$, $v_m = 1/1.46$, and $n_{\gamma 1} - n_{\alpha 1} = 0.07$ (Hermans 1949), then $n_\gamma - n_\alpha = \frac{0.4 \times 1.46}{1.56} \times 0.07 = 0.026$. For a cell wall containing 40 per cent. cellulose and a birefringence of $n'_\gamma - n_\alpha$ in transverse section, it can be seen from the section of the index ellipsoid shown in Figure 1 that $OA = n_\gamma$, $OB = n_\alpha$, $OC = n'_\gamma$ (Preston 1946; Preston and Wardrop 1949).

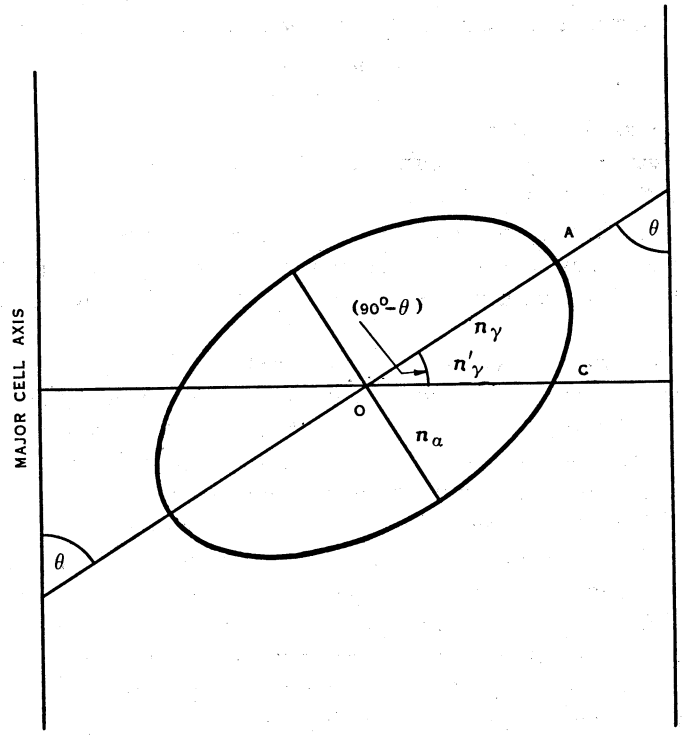

Fig. 1.—For explanation, see text.

From the geometry of the ellipse,

$$\frac{n'^2_\gamma \sin^2 \theta}{n_\gamma^2} + \frac{n'^2_\gamma \cos^2 \theta}{n_\alpha^2} = 1,$$

whence

$$\cos \theta = \frac{n_\alpha}{n'_\gamma} \left[\frac{(n_\gamma - n'_\gamma)(n_\gamma + n'_\gamma)}{(n_\gamma - n_\alpha)(n_\gamma + n_\alpha)} \right]^{\frac{1}{2}}. \quad .. \quad (6)$$

As pointed out by Meredith (1946), n_α is regarded as being approximately unchanged at different values of θ as the micelles are oriented in layers parallel

to the cell surface. Values of θ for various specimens obtained by using equation (**6**) are given in Table 1.

TABLE 1

BIREFRINGENCE IN TRANSVERSE SECTION AND MICELLAR ANGLES OF XYLEM PARENCHYMA

Species	Birefringence in Transverse Section ($n'_\gamma - n_\alpha$)	Micellar Angle (degrees)
Dialium laurium		
Ray parenchyma	0.013	45
Grevillea robusta		
Ray parenchyma	0.007	32
Hodgkinsonia ovatiflora		
Ray parenchyma	0.007	32
Vertical parenchyma	0.007	32
Pongamia pinnata		
Vertical parenchyma	0.015	50

III. Results and Discussion

(*a*) *Distribution of Cell Wall Constituents*

In all specimens examined the cell wall of both vertical and ray parenchyma had undergone secondary thickening. This was very slight in *Podocarpus amara,* especially in the vertical parenchyma, and was poorly developed in *Pongamia pinnata,* but in the other species the secondary wall was readily recognizable. The primary wall was discernible only with great difficulty in cross sections of cells *in situ,* but could be detected when carefully delignified (holocellulose method) sections were examined between crossed nicols. Plate 1, Figure 1, shows the primary wall of the ray cells of *Grevillea robusta* after this treatment.

Using the staining technique of Coppick and Fowler (1939) on sections cut transverse to the long axis of ray and vertical parenchyma cells, the lignin was observed to be situated mainly in the intercellular zone and the primary wall, although the secondary wall was also strongly stained. However, when the sections were treated with 72 per cent. sulphuric acid no coherent lignin residue from the secondary wall was obtained, but the primary wall and intercellular zone were so heavily lignified that they left a lignin framework undistorted by the considerable swelling of the secondary wall by the acid. The lignin framework so obtained from ray parenchyma of *Grevillea robusta* is shown in Plate 1, Figure 2, and from the vertical parenchyma of *Pongamia pinnata* in Plate 1, Figure 3.

The presence of polyuronide or pectic substances in the primary wall was demonstrated by treating carefully delignified sections with cuprammonium solution following the method adopted by Kerr and Bailey (1934). Plate 1, Figure 4, shows the result of this treatment on the ray parenchyma of *Grevillea*

robusta. It is of interest to note that the polyuronide residual layer is much thicker than that obtained by similar treatment of cross sections of fibres. The pectic or polyuronide nature of the framework was established from the fact that no residue was observed when the delignified sections were extracted with ammonium oxalate, or hydrolysed by dilute acid, before treatment with the cuprammonium solution. These observations on xylem parenchyma, together with those of Kerr and Bailey (1934) on fibres and tracheids, demonstrate the essential similarity in chemical composition of the different cells of the xylem.

(*b*) *Cell Wall Organization*

The micellar orientation in the primary wall of the ray parenchyma of *Grevillea robusta* was determined from the direction of the major extinction position and was found to be inclined at an angle of 80°-90° to the long axis of the cell. Material for examination in this way was obtained by gently tearing delignified radial longitudinal sections along the direction of the rays when fragments of the primary wall remained adhering to the untorn cells. Using this technique the micellar orientation of the primary wall of vertical parenchyma cells in *Pongamia pinnata* was also found to be 80°-90° to the long axis of the cell. Thus the micellar orientation of the primary wall of parenchyma is similar to that in the primary wall of tracheids (Preston 1947).

In sections cut at right angles to the length of the parenchyma cells the secondary wall of both vertical and ray parenchyma when viewed between crossed nicols appeared optically homogeneous in the species of *Pongamia, Grevillea, Hodgkinsonia,* and *Podocarpus* examined; this was also the case in the vertical parenchyma of *Fagus* and the ray parenchyma of *Tsuga.* Examples of this are shown in Plate 1, Figures 5 and 6, for the ray parenchyma of *Grevillea robusta* and vertical parenchyma of *Pongamia pinnata* respectively. However, in the ray parenchyma of *Dialium laurium* (Plate 2, Fig. 2) and of *Fagus atropunica* (Plate 2, Fig. 1) there was evidence of a layered structure in the secondary wall. This was also apparent in the vertical parenchyma of *Dialium laurium* (Plate 2, Fig. 3) and was greatly pronounced in 'sclerosed' vertical parenchyma cells of this species (see Plate 4, Fig. 1).

As indicated earlier, Tuszon (1903) referred to the presence of a helical organization of the cell wall of rays. Direct demonstration of this type of organization was attempted using the technique of crushing isolated cells previously described by the authors (Wardop and Dadswell 1948). The application of this technique was more difficult with parenchyma cells than with fibres because of the presence of numerous pits in the relatively thin cell wall. However, in *Grevillea robusta* it was found to be possible and from Figure 4 of Plate 2 the helical organization of a ray parenchyma cell is quite apparent. It was assumed that the cell wall tended to cleave parallel to the direction of micellar orientation, because of the 'fibre-like' texture of the secondary wall in which there exists little dispersion of the micelles about their direction of orientation. The angle of the striations so produced was found to be approximately 38°. In view of the distortion which inevitably occurs when using

this technique the result is in quite good agreement with the angle of 40° obtained for the micellar orientation by X-ray methods, and the angle of 33° from the birefringence measured on cross sections of ray parenchyma cells from the same source.

Further information on the helical organization of ray parenchyma cells from *Grevillea robusta* was obtained from a study of the end walls of the cells. This was accomplished by cutting a series of sections 8 μ in thickness, at right angles to the long axis of the ray cells, from which two sections containing the end walls of contiguous cells were selected. In the first section the end wall of the cell under investigation, and that of the next cell nearer the bark, were obtained, whereas in the second section the other end wall of the cell studied and that of the next cell near the stem centre were obtained, so that both end walls of the cell investigated were available. These sections were carefully delignified, taking care that their orientation relative to each other in the ray was not altered. Upon subsequent treatment with 0.1 per cent. sodium hydroxide the end walls of the contiguous cells were separated by gently sliding the cover glass and the two end walls of the one cell were available for examination.

The optical behaviour of the end walls was complicated by the presence of numerous pits. When viewed between crossed nicols the micelles in some walls were apparently oriented uniformly in one direction. In most walls studied, however, there was evidence that the micellar orientation was not uniform. Thus, on rotation of the specimen through 360° there were four positions of maximum brightness (Plate 2, Fig. 5) indicating the presence of strands of cellulose of uniform orientation. Upon reorienting the specimen so that these strands were in a position of extinction, extinction of the whole field did not occur, but the area between the strands appeared bright (Plate 2, Fig. 6). This indicated the presence of more than one direction of micellar orientation in the end walls. This could be demonstrated further when the specimen was examined between crossed nicols with the addition of a retardation plate (first order). When the specimen was placed so that the strands of cellulose, shown in Plate 2, Figure 5, were parallel to the direction of the slow ray of the plate, the strands gave a blue addition colour, whereas the regions between them gave an orange-red subtraction colour. These colours were reversed on rotating the stage 90°.

In these end walls it is necessary to consider whether the heterogeneity arises as a result of a gross distortion by the pits of an otherwise uniform orientation or whether in fact there exist several directions of micellar orientation in the wall, i.e. a crossed fibrillar type of structure. Evidence of the latter possibility is contained in the observation that when viewed between crossed nicols the points where the different micellar directions apparently cross do not undergo complete extinction, and also the direction of elongation of the pits in the end walls is not uniform (Plate 2, Fig. 7). Confirmation of this evidence was sought by crushing isolated end walls after staining with

congo red in the manner described for the lateral walls. This was unsuccessful as the walls tended to fragment on crushing and no conclusive observations were made. However, some evidence of a crossed fibrillar structure was observed in some cases near the edges of the end wall where there were two sets of striations intersecting at an acute angle (Plate 2, Fig. 8).

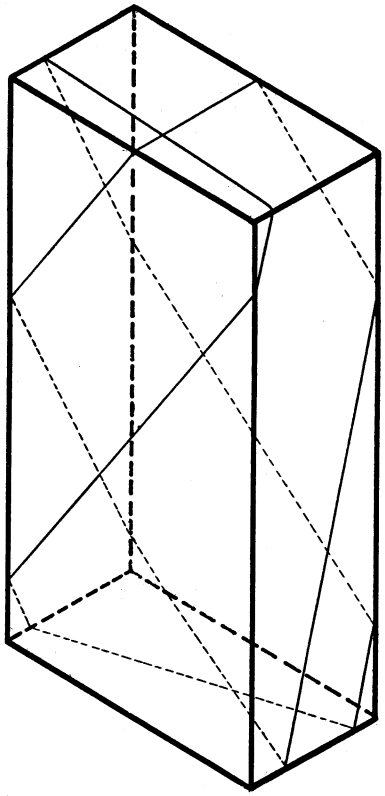

Fig. 2.—A diagrammatic representation of the supposed micellar orientation in ray parenchyma. Two loops are considered to have been wound on a rectangular prism to give a uniform helical arrangement on the lateral walls and to cross on the end walls.

Admittedly the evidence of a crossed micellar orientation of the end wall is inconclusive. However, such a structure must be considered in relation to the way in which it can be reconciled with the uniform helical micellar organization of the lateral walls. In this respect the model proposed by Preston (1934) made by winding a series of loops on a rectangular prism is of assistance. The loops may be wound so that they are parallel to each other on the end walls (as considered by Preston) and this would correspond to the examples observed with apparently uniform orientation on the end walls; or they may be wound with the loops crossing on the end walls as shown diagram-

matically in Figure 2. This would correspond to the examples with an apparently crossed fibrillar type of structure. Such models are essentially similar and possess no centres of organization or 'poles,' as observed by Preston and Astbury (1937) in *Valonia,* and thus seem to represent an essentially different type of organization.

The helical organization of the secondary wall in ray parenchyma cells was further demonstrated in cells isolated from a specimen of *Hodgkinsonia ovatiflora* which had been attacked by fungus. Cells of ray and vertical parenchyma and a vessel element from the specimen are shown on Plate 3, Figures 1-3. In these phase-contrast photomicrographs the light areas are those from which cellulose had been removed. The direction of the cavities in the cell wall was parallel to that of the major extinction position in each case. For the ray cell in Plate 3, Figure 1, the inclination of the cavity to the longer cell axis was approximately 40°, which is in fair agreement with the angle of 33° calculated from the birefringence of the intact cell wall in cross section. Bailey and Vestal (1937) have described fungal penetration of the cell wall parallel to the direction of micellar orientation, the cavities so produced having pointed ends (cf. Plate 3, Fig. 2).

Using the birefringence method the micellar orientation in normal ray parenchyma cells of *Dialium laurium* has been calculated to be 50°, and of *Podocarpus amara* to be 40°. Thus in the ray cells investigated the micellar angle in the secondary wall varied between 30° and 50°.

The organization of the primary wall in vertical parenchyma was demonstrated in the manner described earlier for ray parenchyma and similar results were obtained. The organization of the secondary wall was again studied by optical and X-ray methods but, because of its thinness, attempts to demonstrate the helical organization by the technique of crushing isolated cells were unsuccessful. However, the presence of a helical organization was clearly demonstrated in cells of *Hodgkinsonia ovatiflora* which had been attacked by fungus. The cavities in the cell walls were inclined at an angle of 30° to the longer cell axis, and these cavities were parallel to the major extinction position. From the birefringence of unattacked cells in transverse section the angle was calculated to be 33°.

The micellar angle in parenchyma cells of *Pongamia pinnata* was found to be 60° to the longitudinal cell axis from the measurement of the major extinction position, and 54° by birefringence measurements on cross sections. X-ray methods, using carefully isolated strands containing parenchyma cells only, gave a value of 55°. The micellar angle of normal parenchyma cells in *Dialium laurium* was 55° calculated from birefringence measurements.

In the various examples studied the cell wall organization of both ray and vertical parenchyma cells is essentially the same in distribution of chemical constituents, helical micellar arrangement in the secondary wall, and magnitude of the micellar angle. The relatively large micellar angles observed are of interest, particularly in the ray parenchyma, in relation to the influence attributed to these cells in governing the shrinkage in wood (Greenhill 1936). The

difficulty of determining the exact micellar angle in individual cells militated against the establishment of any relationship between length and micellar angle such as has been established for conifer tracheids by Preston (1934, 1948).

(*c*) *Sclerosed Parenchyma*

In addition to the cells with comparatively thin walls the investigation of which has been referred to above, there occur in both rays and vertical parenchyma of certain species some cells with greatly thickened cell walls. These cells are similar in some features to the 'stone' cells of phloem and other tissues; they have in fact been referred to under this name when observed in xylem ray tissue. The more general term, however, is 'sclerosed parenchyma.' Sclerosed parenchyma cells selected for investigation were from the vertical parenchyma strands of *Dialium laurium* and the ray tissues of *Persoonia lanceolata.* The presence of the primary wall was demonstrated in the manner described above for normal ray cells of *Grevillea robusta.*

In the vertical parenchyma of *Dialium laurium* it was observed that the secondary wall consisted of a number of layers distinctly visible when thin cross sections were viewed in the polarizing microscope between crossed nicols (Plate 4, Fig. 1). Each layer was composite and in cross section appeared to consist of an outer, thicker, birefringent part and an inner, narrower, less birefringent or isotropic part. The layers were separated from each other by delignifying longitudinal sections cut sufficiently thin to include no whole cells (8 μ), and then gently crushing the section by sliding a cover glass over it (Plate 3, Fig. 4). When these transverse sections were treated with 72 per cent. sulphuric acid the secondary wall of the sclerosed parenchyma cells swelled greatly, revealing that each layer consisted of a number of lamellae 0.1-0.2 μ in thickness and of varying lignin content (see Plate 3, Figs. 5 and 6). In addition, between the individual layers was a thin isotropic lamella consisting mainly of lignin (Plate 3, Fig. 5). The presence of a non-cellulosic lamella separating physically discrete layers of the cell wall has also been recorded for fibres of bamboo by Lüdtke (1931, 1934) and for *Pandanus* by Bailey and Kerr (1935).

As well as variations in the chemical nature of the walls of sclerosed parenchyma cells there are also variations in their physical nature. This can be seen from the optical heterogeneity in transverse section (Plate 4, Fig. 1), and in longitudinal section (Plate 4, Fig. 2). From these photomicrographs it is apparent that the part of the wall appearing birefringent in transverse section is isotropic or feebly birefringent in longitudinal section, and the part isotropic in transverse section appears birefringent in longitudinal section. From these observations it was concluded that within each layer the optical heterogeneity observed can be attributed to a difference in micellar orientation. That each layer consists of a number of lamellae may be attributed to variations in micellar texture such that in the lignin-rich lamellae the volume of the intermicellar system is greater than in the lignin-poor lamellae.

Further information concerning the differences in micellar orientation between layers as distinct from the differences within them described above can be obtained from the study of birefringence or phase difference in successively formed layers. Changes observed when examining cross and longitudinal sections of typical cells with thickened secondary walls are shown in Table 2. It will be noted that in the transverse section the phase difference of the birefringent layers decreased in successively formed layers (i.e. in each layer nearer the lumen) and that in the longitudinal section the phase difference also decreased towards the lumen. Assuming this change in phase difference reflects a change in orientation rather than in composition then the micellar angle would be expected to decrease in each successively formed layer appearing birefringent in transverse section.

TABLE 2

EVIDENCE OF DIFFERENCES IN MICELLAR ORIENTATION IN VARIOUS LAYERS OF THE CELL WALL OF SCLEROSED VERTICAL PARENCHYMA OF *DIALIUM LAURIUM*

Layer Number From Lumen		Transverse Section			Longitudinal Section
		Phase Difference	Birefringence ($n'_\gamma - n_\alpha$)	Micellar Angle	Phase Difference
3	Outer	68	0.019	59	—
	Inner	—	—	—	40
2	Outer	56	0.016	52	—
	Inner	—	—	—	20
1	Outer	48	0.014	48	—
	Inner	—	—	—	14

The micellar angle of each of these successive birefringent layers was calculated from the magnitude of their birefringence (Table 2). On the other hand, the decrease in phase difference in successive birefringent layers in longitudinal section would be expected to reflect an increase in micellar angle with respect to the longitudinal cell axis. Unfortunately no calculation of these angles was possible because the section thickness could not be determined accurately. Thus the changes in micellar orientation between layers correspond to those that would occur if there were a constant angle between the two directions of orientation within each layer of the wall such that any decrease in the micellar angle of one orientation would imply an increase in the other.

It is of particular interest that the layered structure described above appears to resemble closely that of the cell wall in fibres of *Pandanus* (Bailey and Kerr 1935) and bamboo (Lüdtke 1931, 1934; Preston and Singh 1950). Preston and Singh concluded that in bamboo the micellar angle decreased in the successive layers appearing birefringent in transverse section but did not determine the orientation of the non-birefringent layers. A similar type of structure also appears to exist in the fibres of *Calamus* and *Cocos*, and von Mohl in 1844 (see Braun 1853) described the way in which the cell wall layers in these fibres

could be separated from each other by treatment with dilute sulphuric acid. He pointed out further that each layer consisted of an outer, broader, softer part; and an inner, thinner, firmer part.

The structure of the sclerosed parenchyma cells of *Dialium* differs from that of *Pandanus* in that the lignin is distributed in lamellae throughout each of the cell wall layers which in turn are separated by an isotropic layer of lignin, whereas in *Pandanus* the lignin is confined for the most part to the region between layers. Since the meristem giving rise to monocotyledonous fibres develops from cells which have already become parenchymatous, it is interesting to consider whether the layered type of structure observed in *Dialium* parenchyma is characteristic of all thick-walled cells of parenchymatous origin. Examination of the sclerosed ray cells (stone cells) of *Persoonia lanceolata* (Plate 4, Fig. 3) and of the sclerosed tyloses in *Gymnacranthera farquhariana*, which are of parenchymatous origin (Chattaway 1949), shows that in these cases a similar layered structure is to be found. It may be noted further that intermediate stages between the extreme simplicity of the cell wall organization of normal parenchyma cells in *Grevillea*, *Podocarpus*, and *Pongamia* on the one hand, and the extreme complexity of structure in the sclerosed cells of *Dialium* and *Persoonia* on the other hand, have been observed in *Fagus* (Plate 2, Fig. 1), *Dialium* (Plate 2, Figs. 2 and 3), and other genera.

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EXPLANATION OF PLATES 1-4

PLATE 1

Fig. 1.—*Grevillea robusta.* A transverse section of a ray after delignification and gentle tearing. Parts of the feebly birefringent primary wall (*P*) can be seen adhering to the more strongly birefringent secondary walls. x980.

Fig. 2.—*Grevillea robusta.* Part of a transverse section of a ray after treatment in 72 per cent. H_2SO_4 showing the rigid lignin framework of the middle lamella and primary wall. x430.

Fig. 3.—*Pongamia pinnata.* A transverse section of vertical parenchyma after similar treatment to the section shown in Figure 2. x430.

Fig. 4.—*Grevillea robusta.* Transverse section of a ray after delignification and treatment with cuprammonium hydroxide solution showing the polyuronide frame of the primary wall and middle lamella. x980.

Fig. 5.—*Grevillea robusta.* Transverse section of a ray between crossed nicols. x430.

Fig. 6.—*Pongamia pinnata.* Transverse section of vertical parenchyma between crossed nicols. x430.

PLATE 2

Fig. 1.—*Fagus atropunica.* Transverse section of a ray between crossed nicols. x980.

Fig. 2.—*Dialium laurium.* Transverse section of ray parenchyma between crossed nicols. x980.

Fig. 3.—*Dialium laurium.* Transverse section of vertical parenchyma between crossed nicols. x980.

Fig. 4.—*Grevillea robusta.* An isolated cell of ray parenchyma after staining with congo red and crushing. Photographed in green light. x980.

Fig. 5.—*Grevillea robusta.* The end wall of a ray cell, photographed between crossed nicols, showing several strands of cellulose in the position of brightness. x1080.

Fig. 6.—*Grevillea robusta.* As in Figure 5 with the strands of cellulose appearing bright in Figure 5, in extinction. x1220.

Fig. 7.—*Grevillea robusta.* The same end wall as shown in Figures 5 and 6, stained with congo red, showing pits. x1080.

Fig. 8.—*Grevillea robusta.* The edge of an end wall after staining with congo red and crushing. Photographed between crossed nicols. x980. Total enlargement x2670.

PLATE 3

Fig. 1.—*Hodgkinsonia ovatiflora.* A cell of ray parenchyma isolated by maceration showing the helical course of fungal attack. Phase contrast. Photographed x400. Total enlargement x870.

Fig. 2.—*Hodgkinsonia ovatiflora.* A cell of vertical parenchyma viewed as in Plate 3, Figure 1. Photographed x400. Total enlargement x870.

Fig. 3.—*Hodgkinsonia ovatiflora.* Part of a vessel element viewed as in Plate 3, Figures 1 and 2. Photographed x400. Total enlargement x740.

Fig. 4.—*Dialium laurium.* A single cell wall of a cell of sclerosed vertical parenchyma after delignification and separation of the various layers. x430.

Fig. 5.—*Dialium laurium.* Part of a transverse section of sclerosed vertical parenchyma after treatment with 72 per cent. H_2SO_4 showing lamellae present in each of the cell wall layers, which are separated by an isotropic layer of lignin. x980.

Fig. 6.—*Dialium laurium.* As in Plate 3, Figure 5. x980.

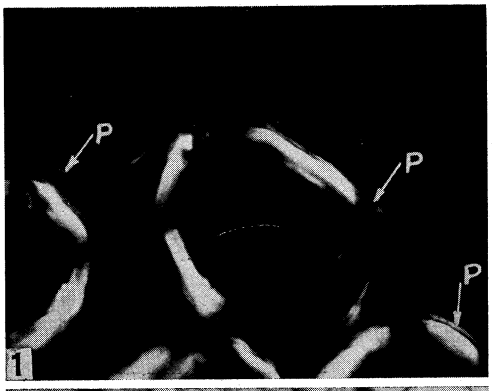
PLATE 4

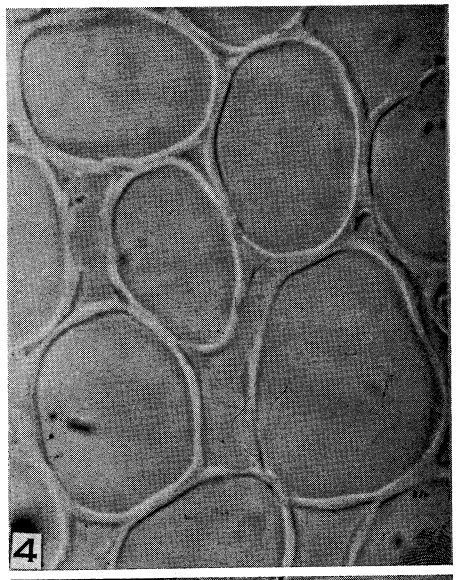
Fig. 1.—*Dialium laurium.* Sclerosed vertical parenchyma in transverse section between crossed nicols. Photographed x980. Total enlargement x2250.

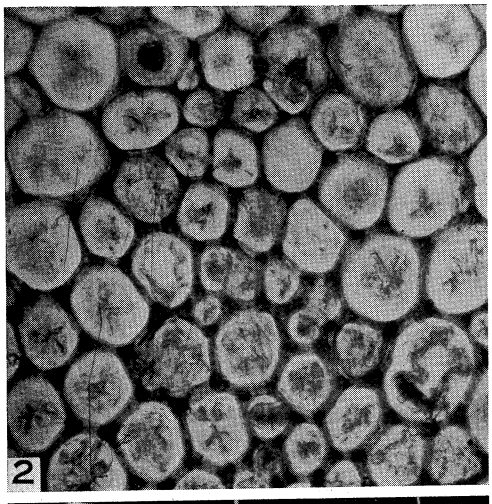
Fig. 2.—*Dialium laurium.* Sclerosed vertical parenchyma in longitudinal section between crossed nicols. Photographed x980. Total enlargement x2250.

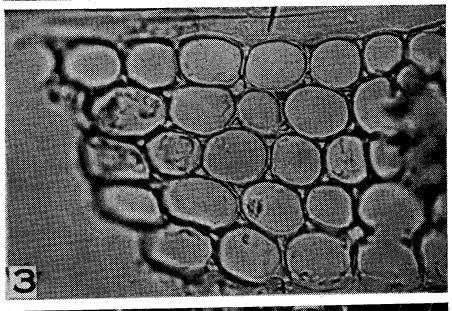
Fig. 3.—*Persoonia lanceolata.* Transverse section of a sclerosed cell of ray parenchyma between crossed nicols. x980.

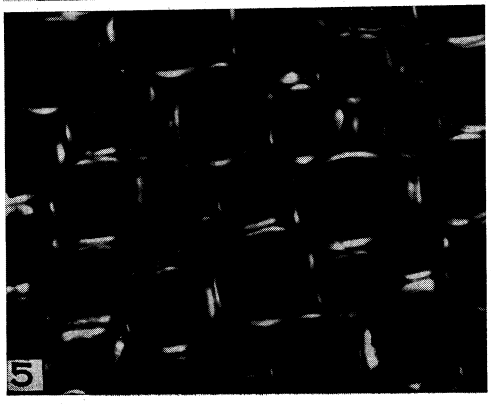
CELL WALL STRUCTURE OF XYLEM PARENCHYMA

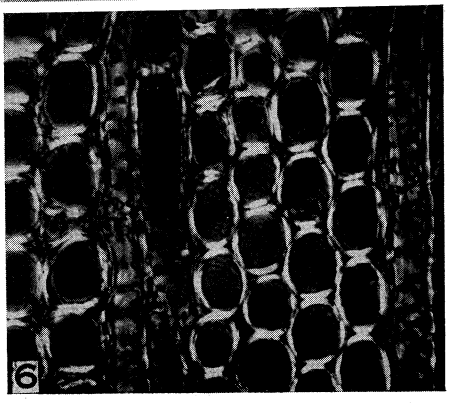












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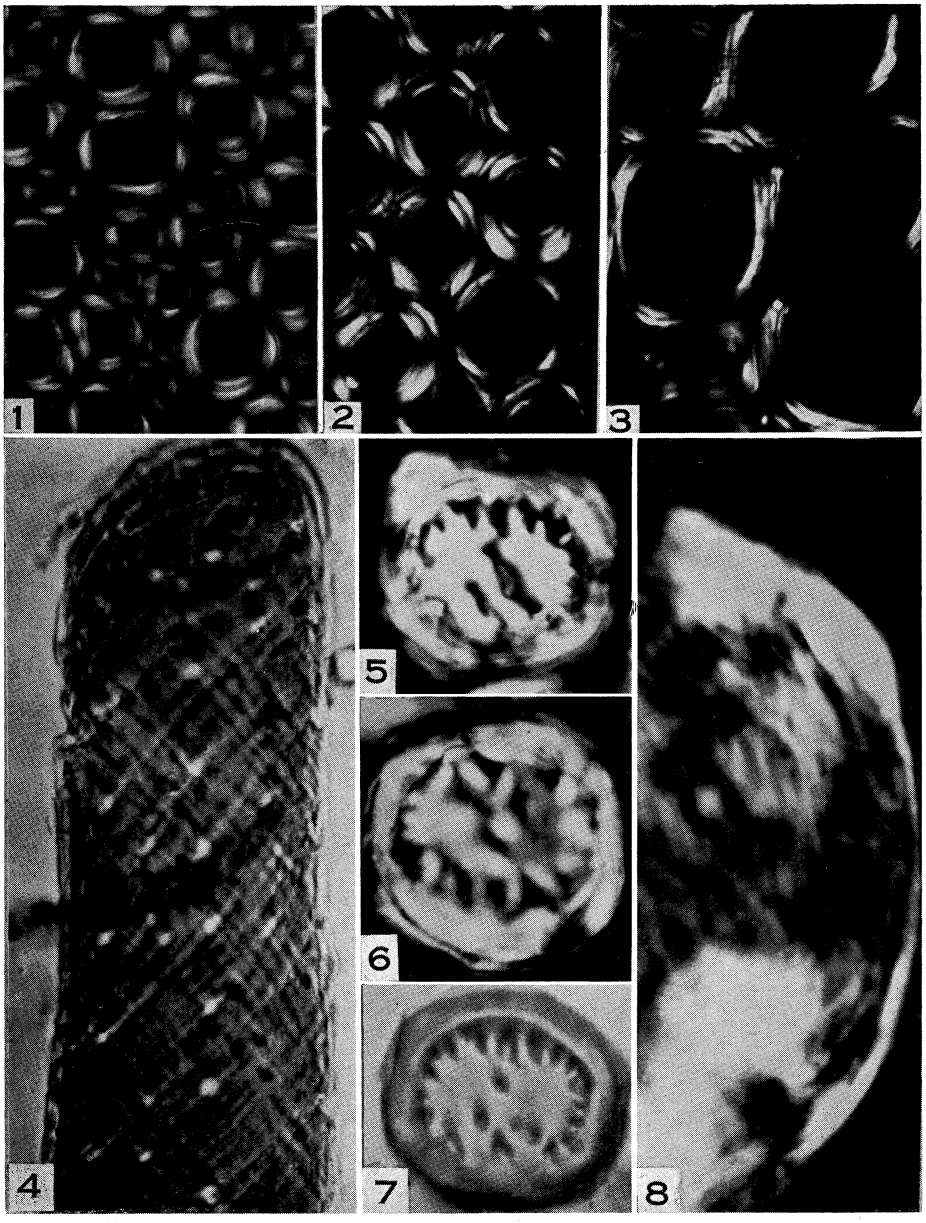

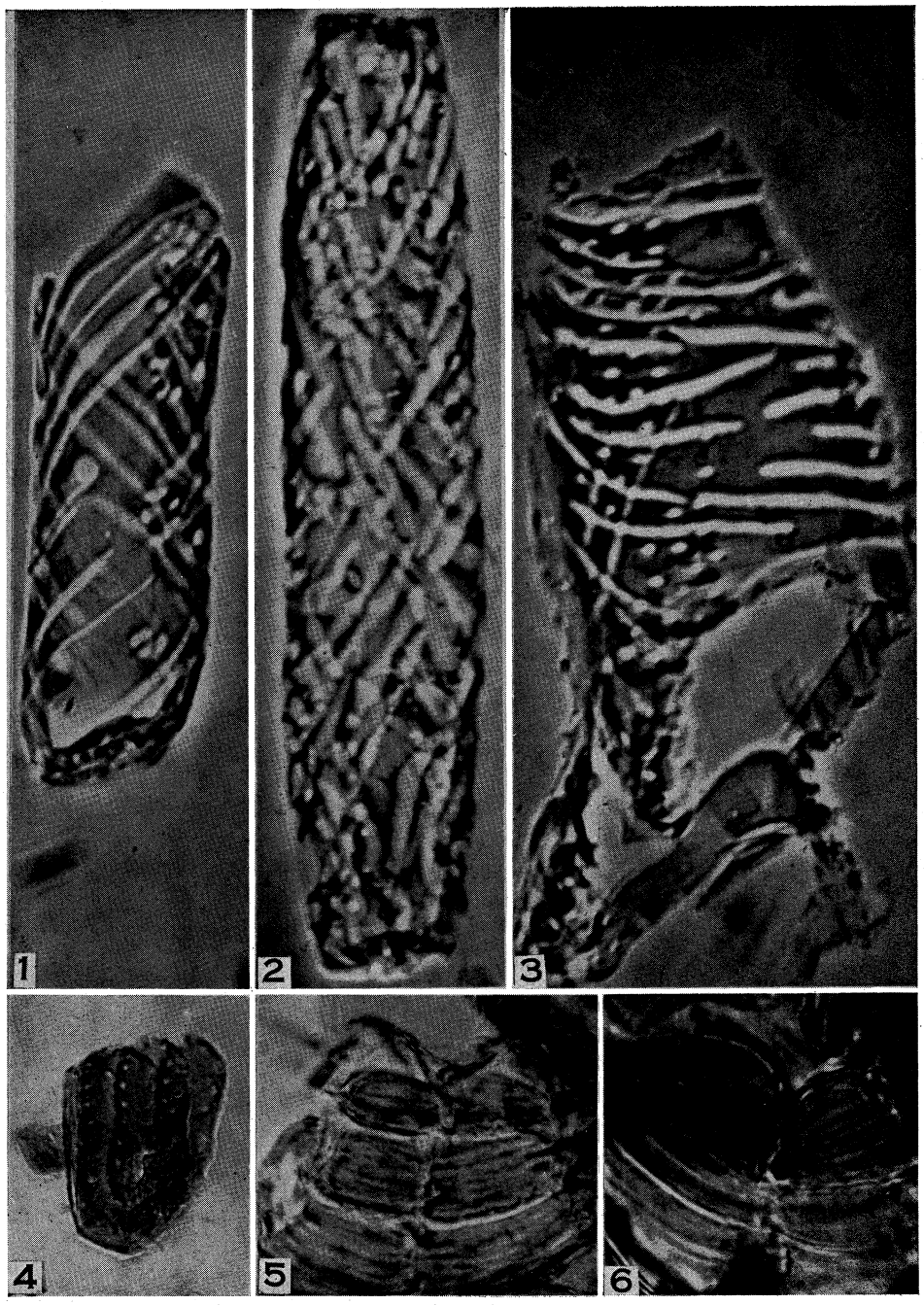
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CELL WALL STRUCTURE OF XYLEM PARENCHYMA