THE DEVELOPMENT OF TYLOSES AND SECRETION OF GUM IN HEARTWOOD FORMATION

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(Plates 1-7)

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Summary

The origin of both the tyloses and the gum† which are commonly observed in the heartwood vessels of numerous species has been traced to the ray cells.

Tyloses are developed in the heartwood of species in which the width of the aperture of the pits from vessels to ray cells exceeds approximately 10 μ; in woods in which the width of the pit apertures is less than approximately 10 μ gum is secreted into the heartwood vessels.

There is thus considerable evidence that the activity of the ray cells is a very important factor in the blockage of vessels at heartwood formation, and it is suggested that one of the clues to the development of heartwood may lie in the length of life of the ray cells.

I. Introduction

Gerry (1914) summarized the literature on the occurrence of tyloses, and this and her own observations showed that although tyloses have in the past been considered one of the characteristics of heartwood, they are in fact quite common in the sapwood of many trees, occurring even in the outermost rings near the bark. Gerry found tyloses in the sapwood of all species in which they occurred in the heartwood. Furthermore, Klein (1923) showed that tyloses could be produced artificially in sapwood by allowing air to enter the vessels following an injury, and he concluded that the formation of tyloses in heartwood was due to the same cause, namely, the contiguity of an air-filled vessel to a living cell of the wood. It has been found that injury to the sapwood of mountain ash (*Eucalyptus regnans* F.v.M.) causes tyloses to form above and below the injury, and that, as in the experiments of Klein, the tylosed area corresponds closely with the area of damage, and consequently with air-filled vessels. In *Acacia* spp. the gum which blocks the vessels both in the heartwood and around an injured area appears to be excreted into the vessels under the same conditions as those which cause tyloses to form in *Eucalyptus regnans*.

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† It is recognized that the secretions into the vessels of the heartwood are of a very varied nature, and that they may be gums, resins, or kinos. This paper is not concerned with the chemical composition of the secreted substances, but only with the details of their secretion, and the term "gum" will therefore be used throughout the article to cover all forms of secretion into heartwood vessels.

These conditions may afford some clue to the factors which cause the change from sapwood to heartwood, and will be the subject of further investigations.

Little work appears to have been done on the actual formation of tyloses or on the secretion of gum. The literature on the subject of both tyloses and gum in wood seems mainly concerned with two aspects, the opposition offered by tyloses to the penetration of preservatives, and the chemical nature of gums and resins. The occurrence of tyloses in heartwood of some species and of gum in that of others seems to have received little attention. The present survey has been undertaken as a result of observations on tyloses in many different woods. These have cast doubt on the common statement that tyloses are a product of ray *or* parenchyma cells. This may be true as regards the tyloses which form in wholly parenchymatous parts of the plant, such as the leaves (for tyloses may occlude intercellular spaces as well as vessels), but it is not true with regard to their occurrence in wood. During this survey the correlation of vessel-ray pit size with tylosis formation became very apparent, and it is surprising to find only one reference to it in literature. H. von Alten (1909) states that "we were able to show a relationship between the form of the vessel walls and the formation of tyloses, and this seemed to depend especially on the size of the pits." As will be shown, the important feature is not the pitting of the vessel wall in general; it is the size of the pit aperture between vessels and ray cells which determines whether tyloses can form or not.

II. Experimental Results

(*a*) *Correlation between the Size and Type of Vessel-ray Pitting and the Occurrence of Tyloses*

A survey has been made of the occurrence of tyloses in the wood of over 1,100 genera, using both the material at the Division of Forest Products and the descriptions of woods published by about 47 other wood anatomists. The result of this survey shows that, given the necessary physiological conditions, the presence of tyloses depends on the anatomical structure of the wood itself, and that while tyloses occur almost universally in woods with large vessel-ray pitting (Plate 1, Fig. 1), in which the apertures are large and the borders narrow or insignificant, they are rarely observed in woods with smaller bordered pits (Plate 1, Fig. 2) and never in those in which the vessel-ray pitting is very small or minute. In woods with small bordered vessel-ray pits the occlusion of the vessels in the heartwood is brought about by the secretion of the gum.

Table 1 shows the families in which tyloses occur regularly in all or most of the genera, and Table 2 those in which tyloses have never or very rarely been observed. The measurements have been taken from the available descriptions of woods and checked and added to by measurements made on material at the Division of Forest Products. The closeness of the correlation is immediately apparent. Table 3 shows the families in which tylosis formation occurs in some subfamilies and not in others; here, too, the occurrence of tyloses and the type and size of vessel-ray pits show the same close correlation. In families in which there is no clear correlation with the botanical subdivision, the pit size is marked for individual species.

TABLE 1

CORRELATION OF OCCURRENCE OF TYLOSES WITH SIZE AND TYPE OF VESSEL-RAY PITTING (FAMILIES WITH TYLOSES*)

Family	Approx. Pit Size (μ)	Pit Type	Family	Approx. Pit Size (μ)	Pit Type
AKANIACEAE	Up to 40	Simple†	LAURACEAE	12-80	Simple
ANACARDIACEAE	16-40	„	LECYTHIDACEAE	Up to 20	„
ARALIACEAE	10-35	„	LYTHRACEAE	15	„
BURSERACEAE	Up to 23	„	MAGNOLIACEAE	Up to 50	„
CAPRIFOLIACEAE	„ „ 15	„	MONIMIACEAE	„ „ 30	„
CARYOCARACEAE	Large‡	„	MORACEAE	„ „ 24	„
COCHLOSPERMACEAE	Up to 16	„	MYRISTICACEAE	„ „ 45	„
CORNACEAE	15-45	„	OLACACEAE	„ „ 40	Wide apertures usually simple
CUNONIACEAE	Up to 50	„			
DATISCACEAE	„ „ 50	„			
DIPTEROCARPACEAE	„ „ 25	„			
ELAEOCARPACEAE	„ „ 25	„	OLEACEAE	5-10	Wide apertures
ELEAGNACEAE	„ „ 12	Wide apertures occasionally simple	PLATANACEAE	Up to 12	Simple
			RHIZOPHORACEAE	„ „ 65	„
			SALICACEAE	12-15	„
			SAPOTACEAE	Up to 30	„
EUCRYPHIACEAE	„ „ 32	Simple	SCROPHULARIACEAE	„ „ 12	„
FAGACEAE	17-20	„			
HAMAMELIDACEAE	20-70	„	SONNERATIACEAE	„ „ 20	„
HERNANDIACEAE	20	„	THEACEAE	„ „ 40	„
JUGLANDACEAE	8-15	Wide apertures often simple	ULMACEAE	12-18	„
			URTICACEAE	15-30	„
			VITACEAE	Up to 25	„
JULIANACEAE	Large‡	Simple	VOCHYSIACEAE	10-12	Wide apertures occasionally simple

* Tyloses recorded for all or most of the genera; their absence from records may mean that no mature wood was available for examination.

† "Simple" is used to denote pits in which the border is almost absent; a very narrow border is usually present in some part of the pit.

‡ Recorded, no measurements available.

It will be seen from these tables that there is an overlap between the largest pits in which tyloses do not occur and the smallest in which they do, and that this lies in the region of 8-10 μ. In the Leguminosae (Mimosaceae, Caesalpiniaceae, and Papilionaceae) generally, tyloses are absent except from one subgroup of the Papilionaceae – the Galegeae. It is to this subgroup that *Robina* L., the most tylosed member of the family, with pits up to 16 μ, belongs. Record (1943) has noted tyloses in *Lennea* Klotzsch, *Hebestigma* Urb., and *Gliricidia* H.B. et K. No material was available at the Division of Forest

TABLE 2

CORRELATION OF OCCURRENCE OF TYLOSES WITH SIZE AND TYPE OF VESSEL-RAY PITTING (FAMILIES WITHOUT TYLOSES*)

Family	Approx. Pit Size (μ)	Pit Type	Family	Approx. Pit Size (μ)	Pit Type
ACERACEAE	8-10	Bordered	MORINGACEAE	8	Bordered
ANONACEAE	4	,,	MYOPORACEAE	3-4	,,
APOCYNACEAE	4-9	,,	MYRICACEAE	8	,,
BALANOPSIDACEAE	4	,,	NYSSACEAE	5-7	,,
BERBERIDACEAE	4	,,	OCHNACEAE	2-6	,,
BUXACEAE	3	,,	OLINIACEAE	3	,,
CAPPARIDACEAE	5	,,	OPILIACEAE	V. Small	,,
CASUARINACEAE	4	,,	PITTOSPORACEAE	8	,,
CELASTRACEAE	2-7	,,	POLYGALACEAE	8-10	,,
COMPOSITAE	3-8	,,	PROTEACEAE	5-6	,,
CRYPTERONIACEAE	6-7	,,	RHAMNACEAE	4-8	,,
EBENACEAE	3-4	,,	RUBIACEAE	3-8	,,
EPACRIDACEAE	2-4	,,	RUTACEAE	2-5	,,
GONYSTYLACEAE	3	,,	SABIACEAE	8-9	,,
GOODENIACEAE	6-8	,,	SAPINDACEAE	3-7	,,
HIPPOCASTANACEAE	6	,,	STYRACACEAE	5-8	,,
HIPPOCRATACEAE	3	,,	TAMARICACEAE	3	,,
MALVACEAE	8-10	Bordered often with wide apertures	THYMELIACEAE	5-7	,,
			ZYGOPHYLLACEAE	2-4	,,
MELIACEAE	2-8	Bordered			
MIMOSACEAE	4-8	,,			

* Isolated records of tyloses in occasional specimens or by one of several observers have been disregarded.

Products for measurement of pit size in these genera, nor does Record give them, but it is significant that they all belong to the subfamily Galegeae. Tyloses have occasionally been recorded for other genera of the Leguminosae, but such sporadic tyloses may be traumatic, or may occur in woods with pits of the borderline size. As a whole, the Leguminosae, with the exceptions noted, have the heartwood vessels plugged with gum and have small bordered pits, only occasionally reaching 10-12 μ. The tyloses recorded by other observers in occasional species almost invariably occur in woods with pits of the larger size in which there are occasionally vessel-ray pits with unusually narrow borders and wide apertures.

Gerry (1914) has mentioned and figured gum droplets which simulate tyloses, and care has to be taken, in examining slides for tyloses, not to be deceived by artefacts which may resemble tyloses so closely as to mislead even an experienced observer. The only way to be certain in such cases is to use solvents which remove gums but leave the walls of true tyloses intact; such an

TABLE 3

CORRELATION OF OCCURRENCE OF TYLOSES WITH SIZE AND TYPE OF VESSEL-RAY PITTING (FAMILIES WITH BOTH TYLOSED AND UNTYLOSED GENERA)

	Tyloses		No Tyloses	
Family	Subfamily or Genus	Pit Size and Type	Subfamily or Genus	Pit Size and Type
BETULACEAE	Coryleae	9-10 μ simple†	Betuleae	3-7 μ bordered
BOMBACACEAE	12 genera	Up to 25 μ simple†	6 genera	3-6 μ ,,
CAESALPINIACEAE	Reported in 3 genera	Up to 12 μ coalescent apertures	43 genera	4-8 μ ,,
ERICACEAE	Andromedeae	Up to 16 μ simple†	Other subfamilies	5-7 μ ,,
EUPHORBIACEAE*	36 genera	Up to 60 μ simple†	7 genera	4-6 μ ,,
GUTTIFERAE*	9 genera	Up to 20 μ often simple†	2 genera	6-8 μ ,,
ICACINACEAE*	2 genera	Up to 30 μ simple†	5 genera	5-8 μ ,,
LOGANIACEAE*	*Fagraea*	Up to 25 μ often simple†	Other genera	4-5 μ ,,
MYRTACEAE*	11 genera	Up to 30 μ simple†	9 genera	3-4 μ ,,
PAPILIONACEAE	Galegeae	Up to 16 μ wide apertures	Other subfamilies	6-10 μ ,,
ROSACEAE	Chrysobalanoideae	Up to 30 μ simple†	Other subfamilies	3-6 μ ,,
STERCULIACEAE*	4 genera	Up to 50 μ often simple†	13 genera	4-8 μ ,,
TILIACEAE*	5 genera	Up to 16 μ often simple†	4 genera	3-6 μ ,,
VERBENACEAE	Viticeae	Up to 15 μ often simple†	Other subfamilies	2-7 μ ,,

* No correlation with division into subfamilies.

† "Simple" is used to denote pits in which the border is almost absent; a very narrow border is usually present in some part of the pit.

artefact is shown in Plate 1, Figure 4, in *Eremophila Mitchelli* Benth. After treatment with 1 per cent. sodium hydroxide the "tyloses" in this wood disappeared. The bordered vessel-ray pits measuring only 3-4 μ in diameter gave the clue, but the deception was absolute on superficial examination.

(b) The Formation of Tyloses or Secretion of Gum by the Ray Cells

Examination of a large number of sections has shown that in every wood where early stages of tylosis formation or gum secretion could be observed, both tyloses and gum came from the ray cells, even when the vessels were also bordered by parenchyma. In all, many hundreds of budding tyloses and early stages in gum secretion were examined. In only three woods were four or five examples found in which tyloses emerged definitely and unmistakably from parenchyma cells (Plate 4, Fig. 1) and only one in which the secretion of gum could similarly be undoubtedly traced to the parenchyma.

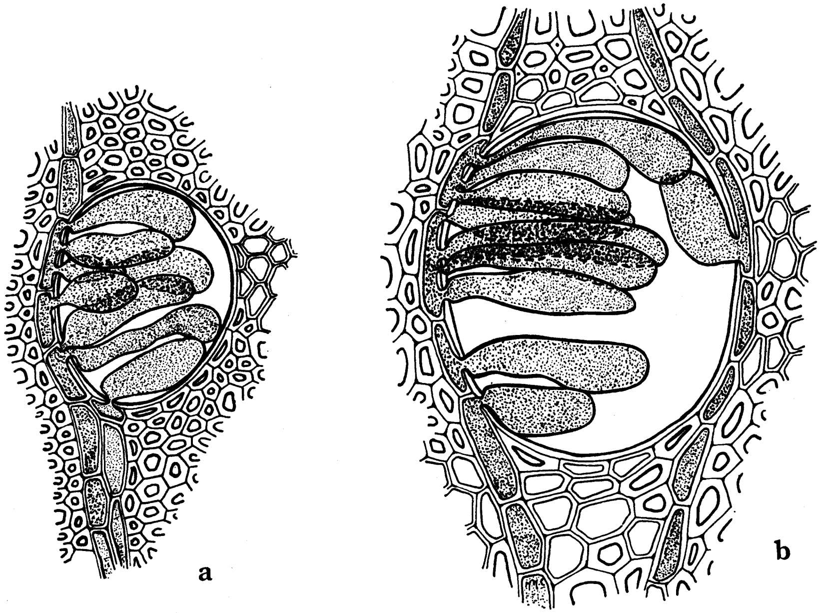

Fig. 1.—Development of tyloses from ray cells.
a. Hopea ferruginea Parijs. x approx. 155.
b. Quercus sundaica Blume. x approx. 170.

Plate 2, Figures 1-4, and Plate 3, Figures 1 and 2, show that even when the vessels are surrounded by a parenchymatous sheath and are contiguous to a ray for only part of their circumference, the tyloses emerge from the ray cells and not from the parenchyma. In these Plates, early stages in the development of tyloses from the ray cells of *Eucalyptus Dalrympleana* Maiden, *Dipterocarpus retusus* Blume, and *Quercus pseudo-molucca* Blume are shown. In these species of *Eucalyptus* and *Quercus,* the vessels are for the most part bordered with fibres and tracheids, and the tylosis formation from the rays alone might be attributed to the sparsity of parenchyma cells, but this is not the case in *Dipterocarpus retusus,* where the vessels are often bordered almost entirely by rays and parenchyma, and yet the tyloses still arise only from the ray cells. Figure 1 shows the same tissue distribution in *Hopea ferruginea* Parijs and

Quercus sundaica Blume, in which the origin of the tyloses is from the rays, although many parenchyma cells border the vessel. Plate 4, Figure 2, shows part of a vessel in *E. miniata* A. Cunn. in which young tyloses arise from a pair of superposed rays.

When vessels which are completely blocked throughout their length by tyloses are examined, it may at first seem impossible that all the tyloses have come from the rays. Further examination of tangential sections shows, however, that the centre of tylosis formation, where the burst pits can be seen, is always in the rays. Figure 2 (*a-f*), which has been reconstructed from actual photographs of various Dipterocarpaceae, shows how the growth and proliferation of the tyloses has caused them to spread from the immediate neighbourhood of their parent ray and fill the whole of the intervening space between that ray and rays above and below. In (*a*) a single tylosis from a cell of a uniseriate ray has met with no obstacle except the opposite wall of the vessel, and has grown to enormous size, doubling back on itself and effectively blocking the vessel cavity; (*b*) shows a uniseriate ray from every cell of which tyloses have emerged, extending above and below the ray for a considerable distance; (*c*), (*d*), and (*e*) show further examples of the extent to which tyloses from a single ray can proliferate and fill the vessel cavity, while (*f*) shows a vessel similarly blocked, but the tyloses have grown from the cells of four different rays. From these diagrams it will be seen that even when the vessel is flanked by parenchyma, the tyloses arise from the ray cells alone. In Figure 1 (*a* and *b*), cross-sections of earlier stages of similar development are shown.

In woods with small bordered pits between the vessels and the ray cells, in which the secretion of gum replaces the development of tyloses at heartwood formation, the gum may completely fill the cavity of the vessel and extend far above the ray from which it has been secreted; and, as in the case of the tyloses, it is only by examining the very early stages at the junction of sapwood and heartwood that the origin of this gum can be accurately traced. Occasionally, however, when the secretion of gum has gone on for some time, the fresh gum is of a different colour from that previously secreted and the origin from the ray cells is clearly shown. Plate 5, Figure 4, shows a tangential section of *Swartzia tomentosa* D.C., in which the sapwood vessels contained some dark amorphous deposits; on heartwood formation the gum secreted by the ray cells has pushed aside the deposits, giving a characteristic pattern of gum droplets down the vessel wall.

In Plate 6, Figure 1, a vessel of *Albizzia toona* F.M. Bail. is passing through one of the wide parenchyma bands which characterize that wood. The gum, shown enlarged in Plate 6, Figure 2, arises from the ray and not the parenchyma cells; similar examples of early stages in gum formation are shown in Plate 3, Figure 5, and Plate 4, Figures 3-7. In only one example found during an examination of hundreds of slides could the gum be traced with certainty to the parenchyma.

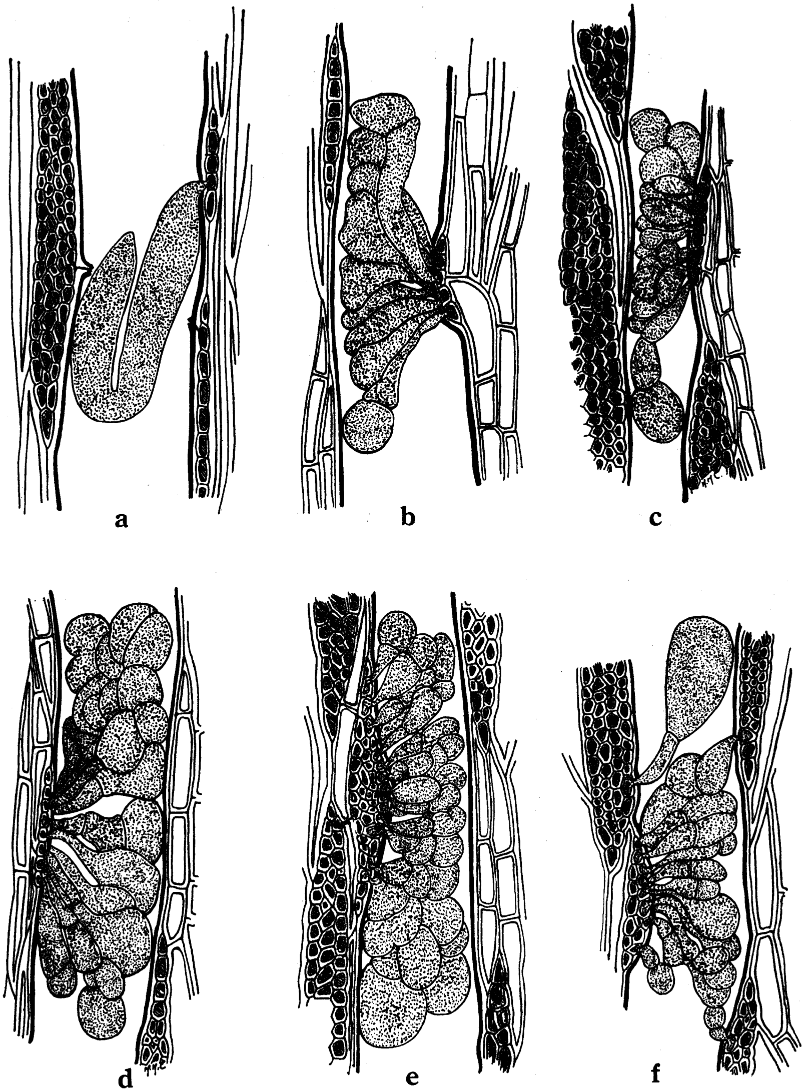

Fig. 2.—Growth and proliferation of tyloses.

a. *Shorea* sp. Large single tylosis filling the vessel cavity. x approx. 110.

b. *Hopea ferruginea* Parijs. Tyloses arising from every cell of a ray, growing and filling the whole vessel cavity. x approx. 110.

c. *Anisoptera marginata* Korth. Tyloses arising from every cell of a ray, growing and filling the whole vessel cavity. x approx. 60.

d. *Anisoptera marginata* Korth. Tyloses arising from every cell of a ray, growing and filling the whole vessel cavity. x approx. 60.

e. *Hopea odorata* Roxb. Tyloses arising from every cell of a ray, growing and filling the whole vessel cavity. x approx. 80.

f. *Hopea odorata* Roxb. Tyloses arising from four different rays to fill the whole vessel cavity. x approx. 80.

In Plate 6, Figure 3, the gum droplet at "A" may at first sight appear to come from a parenchyma cell, but a closer examination shows that a very small uniseriate ray is present (Plate 6, Fig. 4).

Figure 3 (*a-c*) is made from photographs of some Proteaceae. In each case, the gum can clearly be seen to have come through pits of the ray cells, and not from the surrounding parenchyma; Plate 4, Figures 3-7, shows similar early stages of gum secretion from uniseriate and multiseriate rays. In some

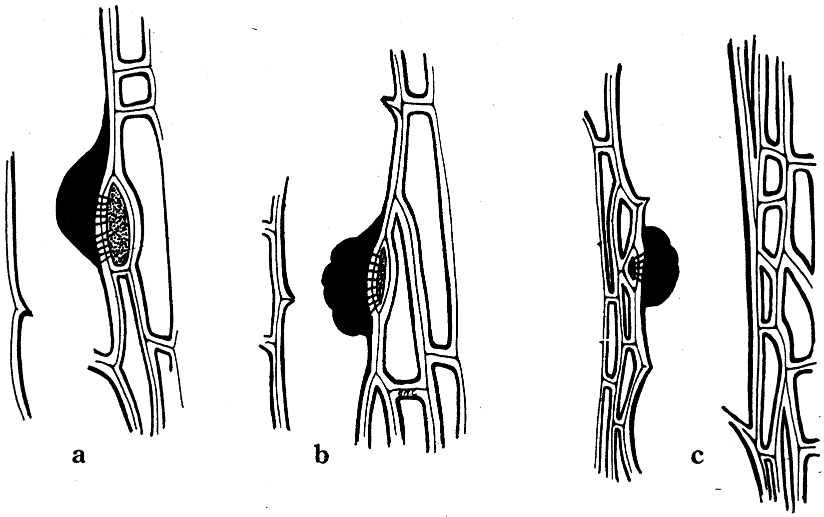

Fig. 3.—Secretion of gum from uniseriate rays which are only one cell high.
a. Faurea saligna Harv. x approx. 250.
b. Faurea Macnaughtoni Phillips. x approx. 250.
c. Cardwellia sublimis F.v.M. x approx. 110.

woods gum and tyloses occur together, generally in the form of gum-filled tyloses (Plate 5, Fig. 3), but occasionally, in addition to gum-filled tyloses, gum may be secreted directly into the vessels. As far as can be seen, the development differs in no way from that in other woods in which only gum or tyloses occur.

III. Discussion

It will be seen from the above that both gum and tyloses in wood appear to have the same origin, namely, the *ray* cells, and to be formed under similar conditions, i.e. when conduction ceases in the vessels, either as a result of injury or in the normal life of the tree, at the time of heartwood formation.

It was stated by Klein (1923) that tyloses were formed when a living parenchyma cell was in contact with an air-filled vessel, and Gerry (1914) in a résumé of earlier literature on the subject defined them as prolongations of wood or medullary ray parenchyma. These statements should be amended because it has been found that, except in one or two rare instances, both tyloses and gum are formed in the woody parts of trees when a cell of a *medullary ray* is in contact with a vessel. Both tyloses and gum have been observed to have been produced from wood parenchyma cells, but such an origin appears to be extremely unusual. From this it would appear that it is the ray cells which play an important and active role in the formation of heartwood, while the wood parenchyma is purely a storage tissue.

In much of the early work on tyloses their origin was attributed to the alteration in pressure in the vessels at the time of truewood formation, allowing the turgid ray or parenchyma cells to push through the pit openings into the vessels. This view is supported by the frequency of tyloses in woods with large simple* vessel-ray pits and the absence of tyloses from woods in which these pits are small and typically bordered. Tyloses appear to be the result of active growth on the part of the ray cells, and to occur not because of, but in spite of, the states of tension and compression that occur in stems. This view accords with those of Winkler (1906) and Klein (1923). The latter reviewed the whole subject and proved to his own satisfaction that tyloses resulted from a vessel which is full of air bordering on a living cell. His experiments were made on injured material, and he considered that he had disproved the tension theory of tylosis formation and proved conclusively that tyloses occurred in his material wherever an air-filled vessel touched upon a living ray or parenchyma cell, and that they did not occur even in injured vessels if these were kept filled with water. On these grounds he denied the existence of a wound stimulus, and suggested that the drying of the pit membrane was sufficient to cause the protrusion and growth of the ray cell.

Gerry's statement that tyloses can occur in the sapwood of all species in which they are present in the heartwood agrees well with Klein's theory. Even in the sapwood occasional vessels may occur in which, through injury or other cause, the sap stream has ceased to function, and in which the conditions postulated by Klein are present.

It does not appear, however, that the work of Klein and Winkler rules out the possibility that an internal stimulus may activate the growth of a ray cell. It is possible that the change from a water-filled to an air-filled vessel may alter the concentration of the growth hormones in the ray cell and thus release an increase of activity within the cell, but it is difficult to imagine that this physical change is of itself sufficient to cause the enormous amount of growth that may be involved in tylosis formation, or the active secretion of large quantities of gum. How great this activity may be is seen from Plate 5, Figure 4, and Plate 7 as well as from Figures 1, 2, and 4. In the formation of a large tylosis such as that shown in Plate 7, the ray cell may have grown to about 40 times its original size, and the secondary wall may have increased from no thickness at all to fill almost the whole of the tylosis.

The growth involved in forming tyloses appears to be exactly similar to that by which secondary thickening of fibres and vessels is laid down. Budding

* The term "simple" is used here to denote pits in which the aperture is very large and the border is almost absent; a border of variable width is usually present in some part of the pit.

tyloses of *Eucalyptus Dalrympleana* Maiden, thin-walled full-grown tyloses of *E. rubida* Deane and Maiden, and sclerosed tyloses of *Gymnacranthera Farquhariana* Warb. were delignified by standard procedure. The budding tyloses of *E. Dalrympleana* and the full-grown tyloses of *E. rubida* are thin-walled, and proved on delignification to consist largely of lignin and to have undergone only very slight secondary thickening. The heartwood of *Gymnacranthera Farquhariana,* on the other hand, contains tylosed vessels in which sometimes almost the whole lumen of the vessel is filled by a "sclerosed tylosis" (Record 1925) in which the wall thickness of the tylosis is many times that of the containing vessel wall. On delignification these tyloses proved to have a wall structure similar to that of adjacent fibres, and to have similar optical and chemical properties. These tyloses are of particular interest as they show clearly the extent of the growth which has resulted from the stimulation of a single ray cell. On account of their very thick walls it is easy to see the limits of a single tylosis both in macerated material and in longitudinal sections (Fig. 4

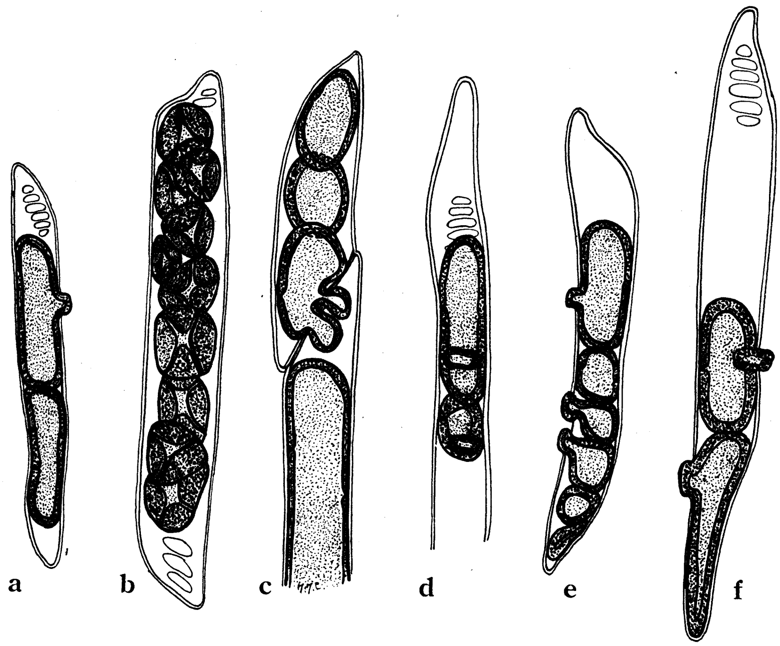

Fig. 4.—Macerated material. Vessel members enclosing sclerosed tyloses. (See text for details.) *Gymnacranthera Farquhariana* Warb. x approx. 72.

and Plate 7). On maceration the vessel members and the tyloses they contain separate from the surrounding tissues (Fig. 4, *a-f*), but, owing to the continuity of the cell wall, the tyloses remain connected with the thickened wall of the ray cell from which they originated. Figure 4 (*d* and *f*) shows these tylosis mother cells in surface view, lying on the vessel member into which the tyloses protrude; (*a*), (*e*), and (*f*) show similar ray cells and their daughter tyloses as they appear in side view and on tangential sections of the wood (see also Plate 7).

Although the secretion of gum by the ray cells does not involve any actual enlargement of the cell, it must represent a considerable increase of cell activity, resulting not in cell wall formation as in the growth of tyloses, but in the production of an equally large amount of new material in the form of gum.

It is suggested that when the vessels cease to function, whether as the result of injury or on the formation of heartwood, changes of a relatively violent nature occur within the living ray cells, resulting ultimately in the death of the nucleus and complete cessation of all metabolic activity in the cell. But there appears to be a phase before the final dissolution of the nucleus, during which it is stimulated to greater activity. Such activity shows itself in growth, and causes the cell to try to expand. The only part of the cell in which expansion can take place is the unthickened part of the intercellular membrane which stretches across the pits. In woods with large vessel-ray pitting this unthickened membrane may occupy a considerable portion of the part of the ray cell which is contiguous to the vessel, and consequently growth takes place in these areas, forcing the intercellular substance into the vessel, where it forms a tylosis. Further growth may cause the tylosis to proliferate (as in *Dipterocarpus* spp.) or to increase in cell-wall thickness (as in *Gymnacranthera Farquhariana*). In woods with small vessel-ray pitting only a very small portion of the cell wall remains in the unthickened condition, and the consequent resistance of the cell to expansion must be increased. For some reason, not as yet fully investigated, this results in the activity of the cell taking another form, and substances are secreted by the cell into the vessel cavity. On contact with the air in the vessels these substances solidify to form the gum with which vessels of the heartwood or of damaged areas in the sapwood become blocked. Thus the blocking of the vessels by gum and tyloses appears to be a manifestation of the reaction of living ray cells to a stimulus which causes increased activity. Wherever tyloses and gum occur, whether in sapwood, wound wood, or heartwood, they are formed because a *living* cell borders on an air-filled one. Air-filled vessels may exist in the centre of all mature trees, yet not all trees have recognizable heartwood. In past attempts to explain the formation of heartwood the stress has been on the air-filled vessel, and it may be because the problem has always been regarded from this angle that information on it is so meagre. It is possible that a real understanding of the problem of heartwood formation will follow investigations of the living ray cells that occur deep within the tree trunk.

IV. Acknowledgments

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Explanation of Plates 1-7

Plate 1

Fig. 1.—*Hedycarya arborea* Forster. Radial longitudinal section showing large vessel-ray pitting. x 225.

Fig. 2.—*Entandrophragma angolense* Welw. Radial longitudinal section showing small vessel-ray pitting. x 225.

Fig. 3.—*Eucalyptus Dalrympleana* Maiden. Transverse section of vessel showing budding tyloses. x 470.

Fig. 4.—*Eremophila Mitchelli* Benth. Tangential longitudinal section of vessel showing oil droplets which may easily be confused with tyloses. x 1000.

Plate 2

Fig. 1.—*Eucalyptus Dalrympleana* Maiden. Transverse section showing development of tyloses from ray cells. x 180.

Fig. 2.—*Eucalyptus Dalrympleana* Maiden. Transverse section showing development of tyloses from ray cells. x 85.

Fig. 3.—*Dipterocarpus retusus* Blume. Transverse section showing tyloses of various sizes developing from ray cells. x 170.

Fig. 4.—*Quercus pseudo-molucca* Blume. Transverse section showing young tyloses developing from ray cells. x 170.

Plate 3

Fig. 1.—*Eucalyptus Dalrympleana* Maiden. Transverse section showing one-sided development of tyloses where the vessel is contiguous to a ray on one side only. x 160.

Fig. 2.—*Dipterocarpus retusus* Blume. Transverse section showing young tyloses arising from ray cells although the vessel is also touched by vasicentric parenchyma. x 170.

Fig. 3.—*Faurea saligna* Harv. Transverse section. Gum secretion on side contiguous to ray cells. x 400.

Fig. 4.—*Carnarvonia araliaefolia* F.v.M. Transverse section. Gum secretion on side contiguous to ray cells. x 125.

Fig. 5.—*Melia Azedarach* Linn. Tangential longitudinal section showing gum secretion from ray cells. x 180.

Fig. 6.—*Carapa moluccensis* Lamk. Transverse section showing small gum drop and vessel-ray pitting. x 400.

Plate 4

Fig. 1.—*Antiaris* sp. Transverse section showing exceptional case of tylosis development from parenchyma. x 500.

Fig. 2.—*Eucalyptus miniata* A. Cunn. Tangential longitudinal section showing tyloses developing from pair of superposed rays. x 180.

Fig. 3.—*Melia Azedarach* Linn. Tangential longitudinal section showing secretion of gum from ray cells. x 70.

Fig. 4.—*Khaya anthotheca* D.C. Tangential longitudinal section showing secretion of gum from ray cells. x 40.

Fig. 5.—*Carnarvonia araliaefolia* F.v.M. Tangential longitudinal section showing secretion of gum from cells of multi-seriate ray. x 150.

Fig. 6.—*Carnarvonia araliaefolia* F.v.M. Gum secretion from cells of uniseriate ray. x 150.

Fig. 7.—*Acacia mollissima* Willd. Tangential longitudinal section. Secretion of gum by ray cells. x 225.

PLATE 5

Fig. 1.—*Grevillea robusta* A. Cunn. Transverse section showing gum-filled vessels occurring only along the ray. x 75.

Fig. 2.—*Faurea saligna* Harv. Transverse section showing gum-filled vessels occurring only along the ray. x 75.

Fig. 3.—*Eucalyptus Blakleyi* Maiden. Transverse section showing gum in tyloses. x 700.

Fig. 4.—*Swartzia tomentosa* D.C. Tangential longitudinal section showing secretion of fresh gum into a vessel already filled with black amorphous deposits. x 110.

PLATE 6

Fig. 1.—*Albizzia toona* F.M. Bail. The vessel is surrounded by parenchyma but the gum is secreted by the ray cells. x 43.

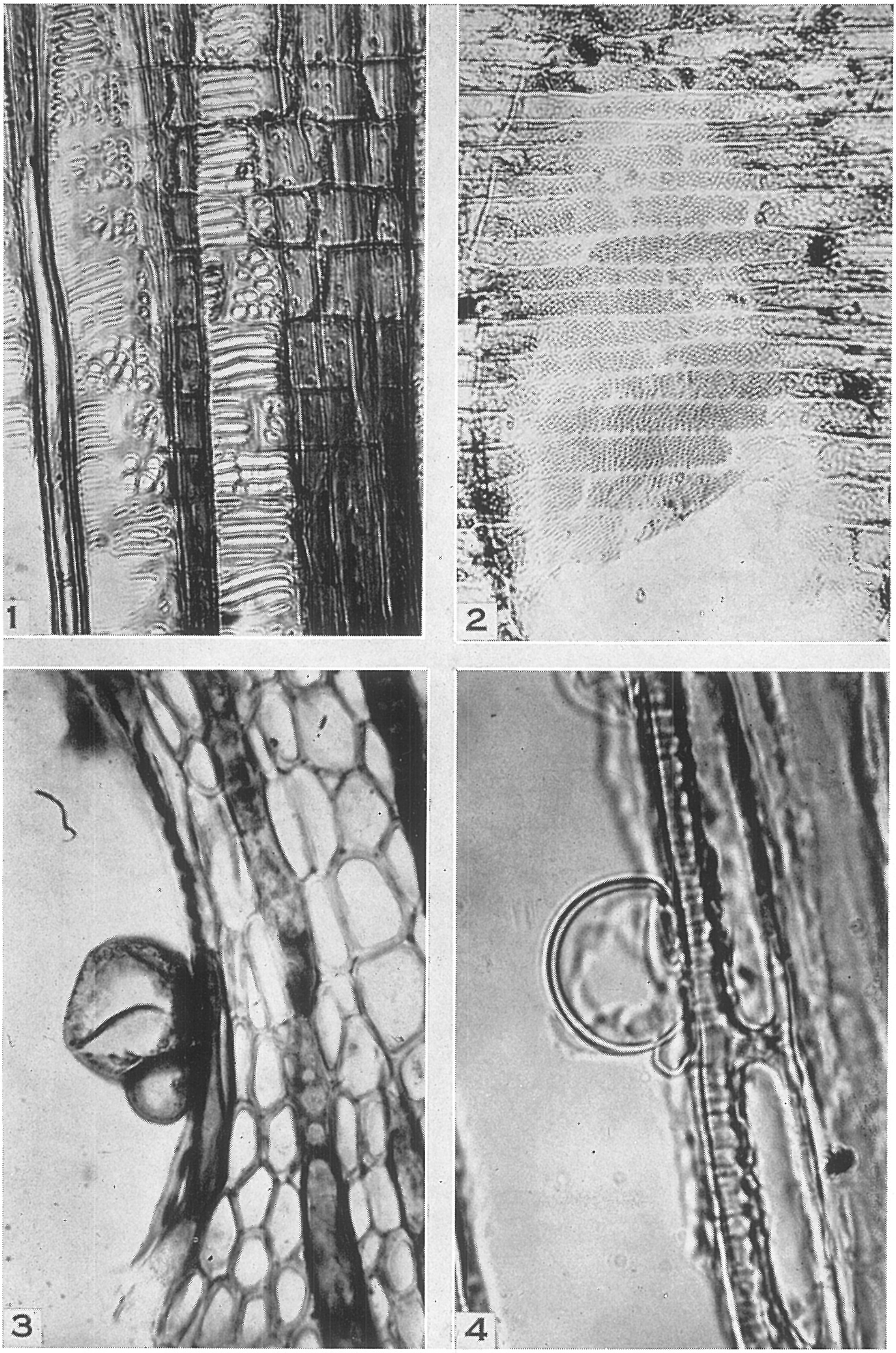
Fig. 2.—*Albizzia toona* F.M. Bail. Part of the above enlarged. x 125.

Fig. 3.—*Melia dubia* Hiern. At "A" the gum is secreted by a small unicellular ray. x 115.

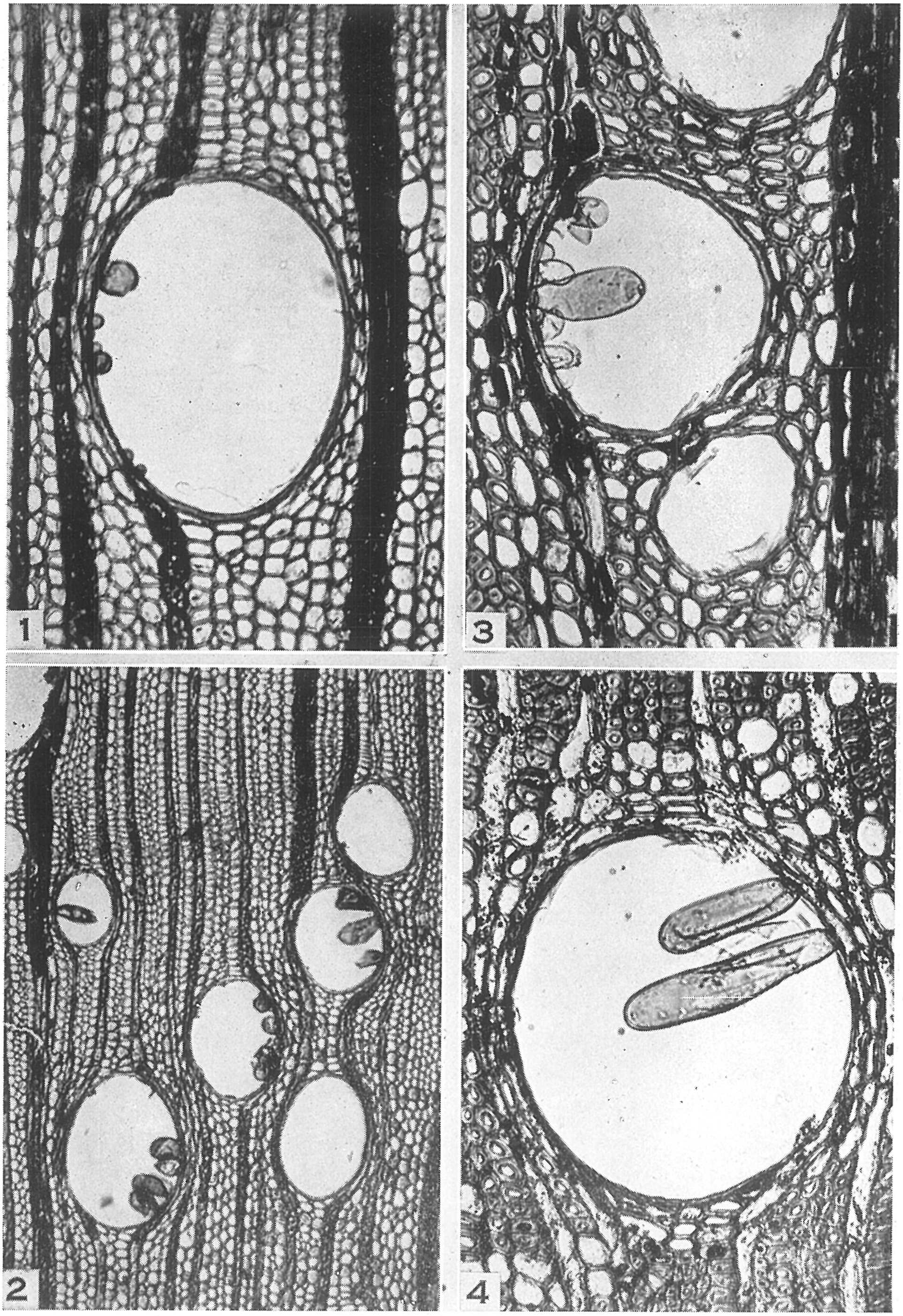
Fig. 4.—*Melia dubia* Hiern. "A" enlarged. x 600.

PLATE 7

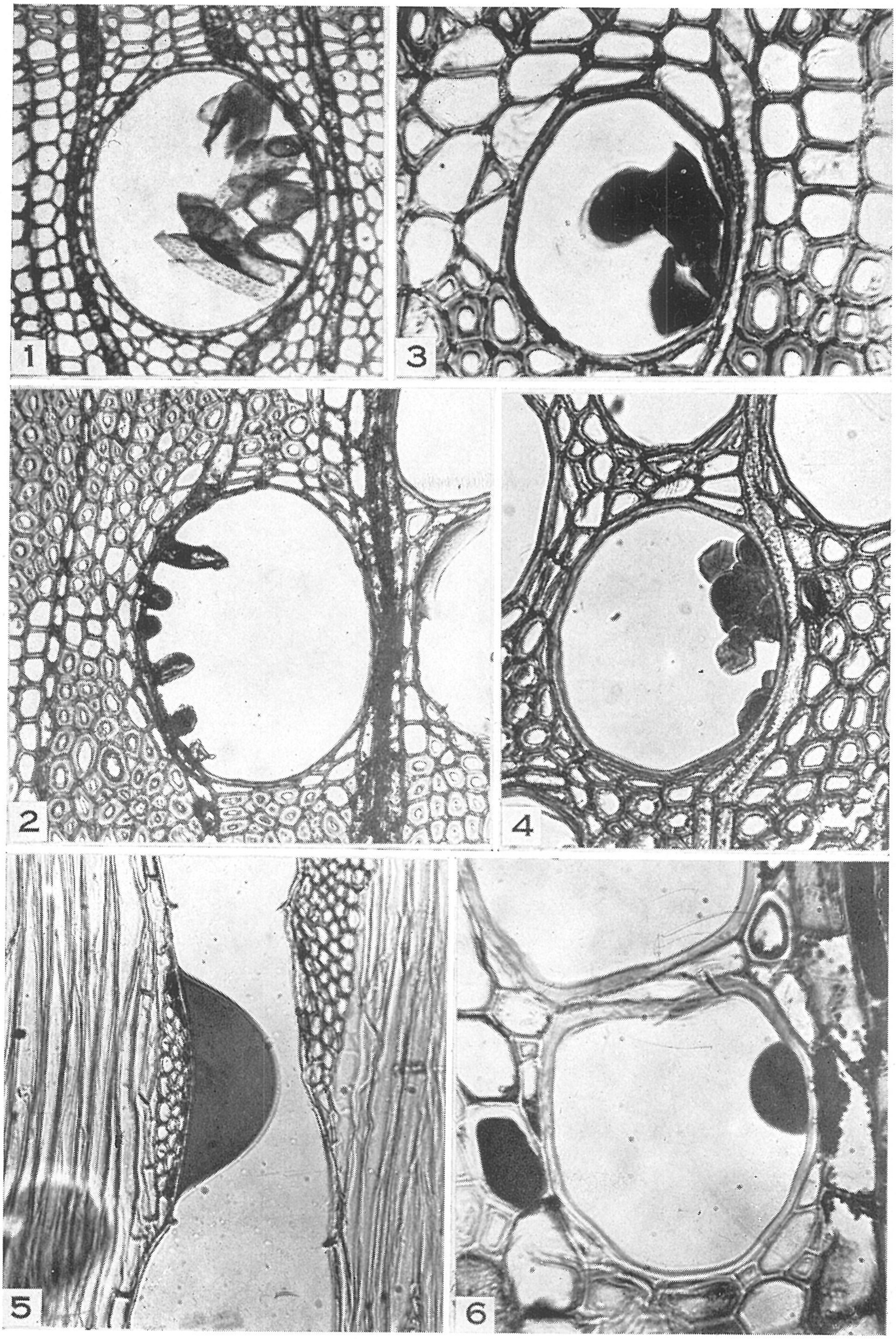
Gymnacranthera Farquhariana Warb. Tangential longitudinal section of sclerosed tylosis, showing the ray cell from which it originated. x 280.



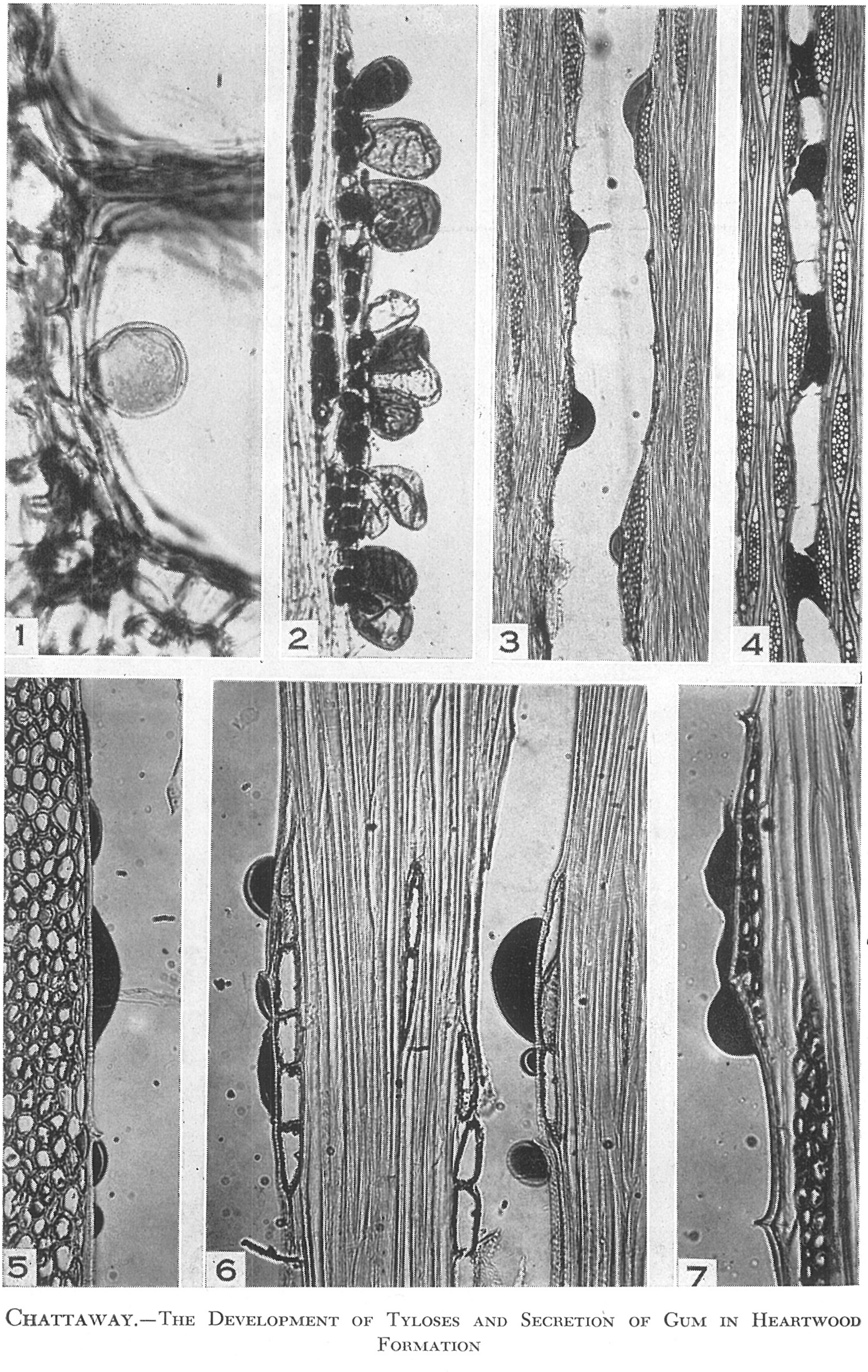
Chattaway.—The Development of Tyloses and Secretion of Gum in Heartwood Formation



Chattaway.—The Development of Tyloses and Secretion of Gum in Heartwood Formation



CHATTAWAY.—THE DEVELOPMENT OF TYLOSES AND SECRETION OF GUM IN HEARTWOOD FORMATION



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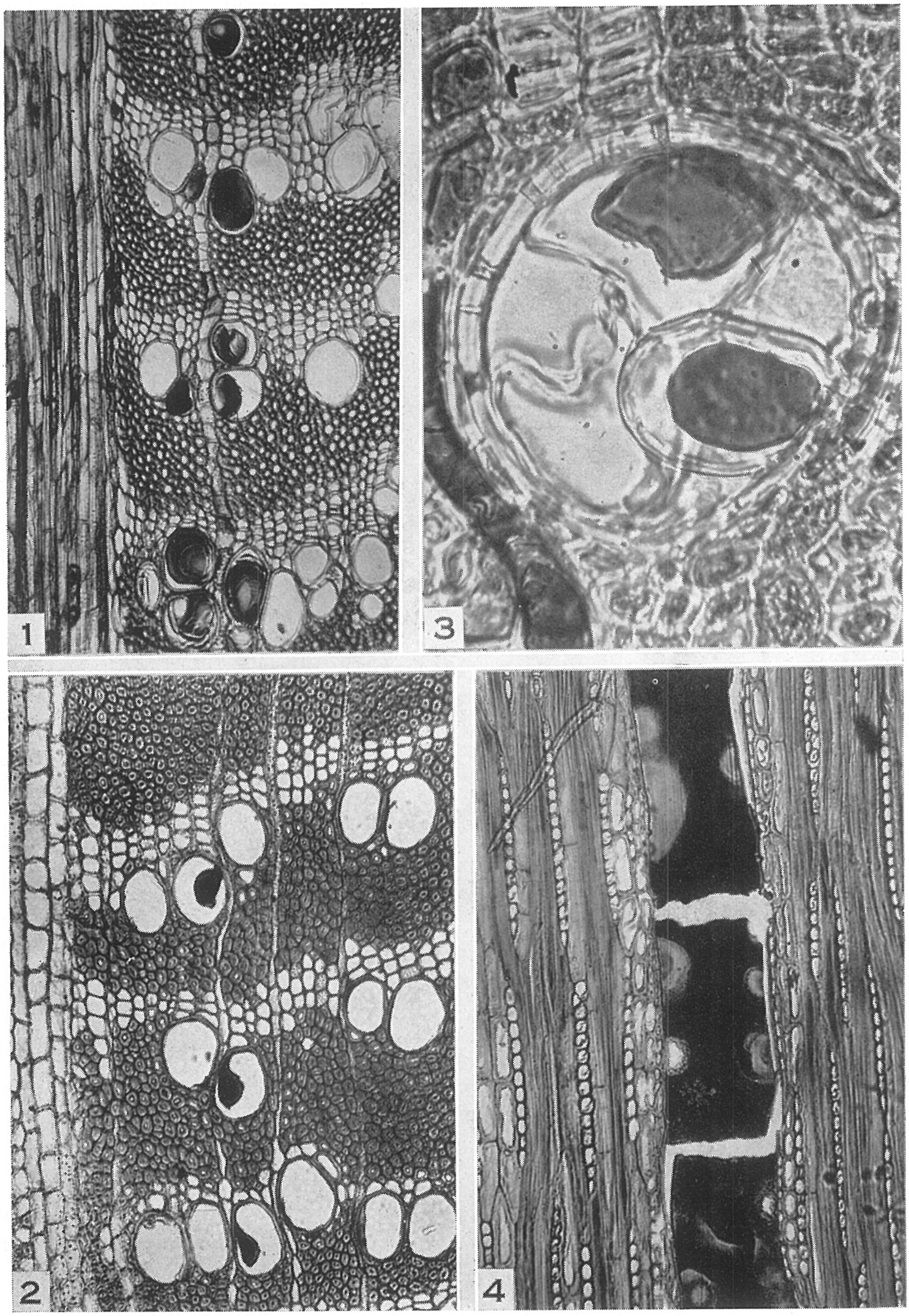

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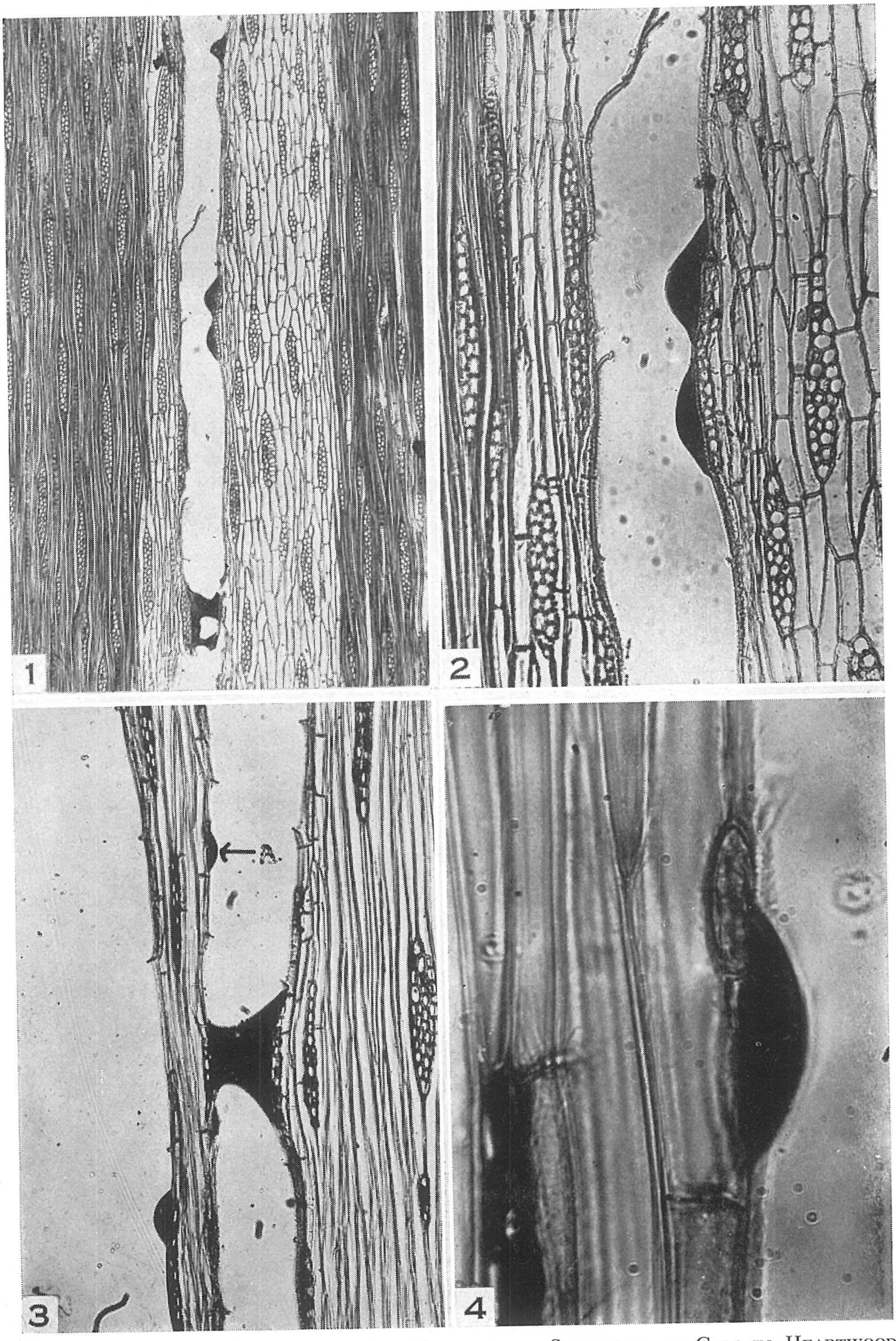
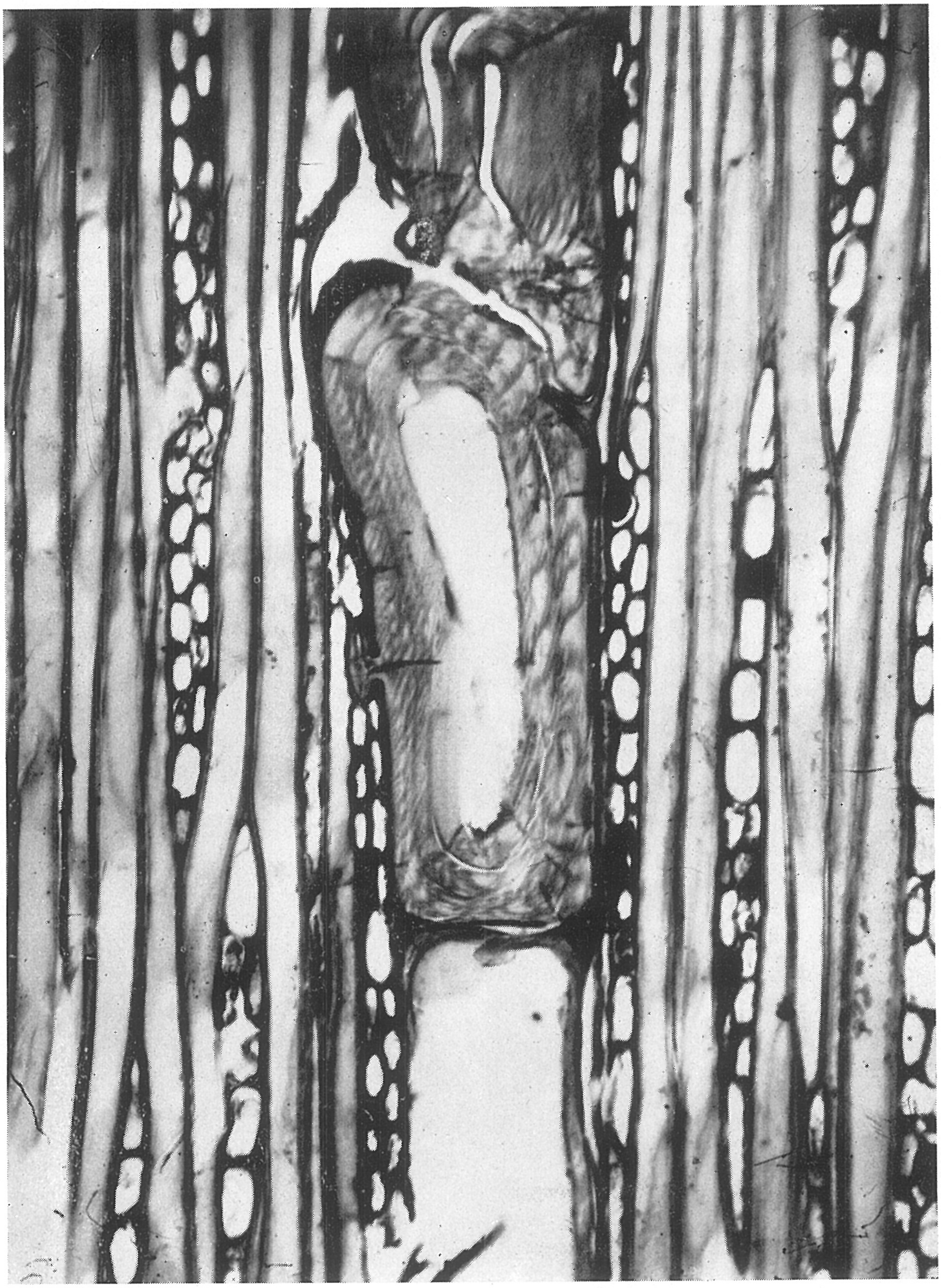


CHATTAWAY.—THE DEVELOPMENT OF TYLOSES AND SECRETION OF GUM IN HEARTWOOD FORMATION



Chattaway.—The Development of Tyloses and Secretion of Gum in Heartwood Formation