THE WOOD ANATOMY OF THE PROTEACEAE

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[*Manuscript received May* 28, 1948]

Summary

This paper contains a general description of the wood anatomy of 26 genera of the Proteaceae. The genera described are those which produce timber trees or large woody shrubs. A map is given to show the geographical distribution of the woody genera of the Proteaceae. The relationship of the wood anatomy to the botanical classification is discussed, with special reference to those genera in which there are marked anatomical differences within the genus.

The wood anatomy is discussed in relation to that of other woods with large rays and the means of distinguishing between them are detailed.

I. Introduction

The family Proteaceae includes about 54 genera and over 1,000 species. The members consist of shrubs and trees, very rarely herbs, usually with spirally arranged, more or less leathery leaves, subdivided or entire, without stipules. The flowers are often clustered in large spikes or heads; the fruit is a dehiscent capsule or follicle, or an indehiscent stone fruit or nut (Ewart 1930). Most members of the family are markedly xerophytic.

The family shows two main centres of development: Australia where over 600 species occur, many genera of which are endemic, and South Africa which has about 300 species. The family extends from eastern Asia, China, and Japan down through Malaya to New Guinea. Members are also found in New Caledonia, Tahiti, New Zealand, and South America.

The family is subdivided, according to Engler and Prantl (1889) as follows:

A. Persoonioideae

1.	Persoonieae	*Bellendena, Symphyonema, Agrastachya, Garnieria, Dilobeia, Beauprea, Cenarrhenes, Persoonia,* Brabeium.**
2.	Franklandieae	*Franklandia.*
3.	Proteeae	*Isopogon, Petrophila, Sorocephalus, Nivenia, Serruria, Mimetes, Spatalla, Adenanthos, Faurea,* Protea,* Leucospermum, Leucadendron,* Aulax, Simsia.*
4.	Conospermeae	*Synaphea, Conospermum.*

B. Grevilloideae

1.	Grevilleae	*Darlingia,* Buckinghamia, Grevillea,* Carnarvonia,* Hakea,* Orites,* Helicia,* Xylomelum,* Lambertia, Roupala,* Panopsis,* Macadamia,* Hicksbeachia,* Kermadecia, Guevina,* Euplassa.*
2.	Embothrieae	*Embothrium,* Telopea,* Lomatia,* Knightia,* Cardwellia,* Stenocarpus.**
3.	Banksieae	*Banksia,* Dryandra.**

The genus *Musgravea* is now placed between *Darlingia* and *Buckinghamia*, and *Finschia* is placed near *Grevillea*.

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* Genera with species producing trees or large shrubs.

The family contains few plants of economic value, and most of the species are small or medium sized shrubs. Many, however, are handsome flowering trees well adapted for ornamental plantations, while nearly all are rich honey yielders and hence of value to apiarists. A few representatives form large trees, some of which produce valuable timber. Timbers of the silky oaks *Cardwellia sublimis, Orites excelsa,* and *Grevillea robusta* are used extensively in furniture and panelling. Satin oak (*Embothrium wickhami*) is used for the same purposes and also *Knightia excelsa* (rewa rewa of New Zealand). *Banksia serrata* has been used for boat knees, bullock yokes etc., and *B. verticillata* is used for carriage finishing etc. of railways in Western Australia as well as for furniture. *Hakea leucoptera* and *H. vittata* have been used for ornamental turnery and smoking pipes.

Of the extra-Australasian genera, *Faurea, Protea,* and *Leucadendron* occur from tropical to South Africa, and in Madagascar, but only *Faurea* is of commercial importance as a timber (Sim 1921; Scott 1927, 1935). *F. macnaughtoni* is a furniture wood and *F. saligna* can be used as a constructional timber. *Embothrium, Guevina, Lomatia, Panopsis,* and *Roupala* occur in the New World but do not grow to a great size; only *Roupala* is of any importance though the other genera are used locally for furniture etc. (Record and Hess 1943).

The accompanying map (Fig. 1) shows the geographical distribution of the woody members of the family according to Gardner (1941-2).

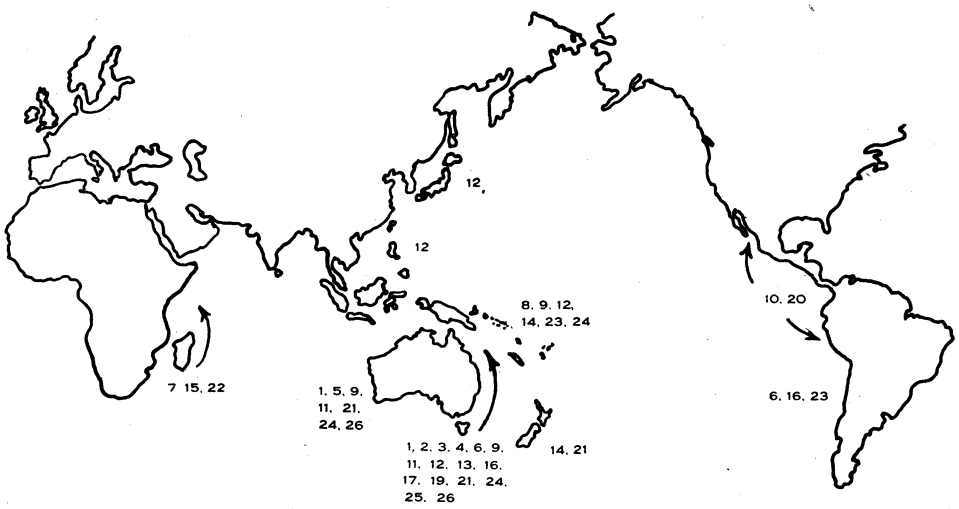

Fig. 1.—Map showing geographical distribution of the woody members of the Proteaceae.

Key to Genera (in alphabetical order):

1. *Banksia*
2. *Cardwellia*
3. *Carnarvonia*
4. *Darlingia*
5. *Dryandra*
6. *Embothrium*
7. *Faurea*
8. *Finschia*
9. *Grevillea*
10. *Guevina*
11. *Hakea*
12. *Helicia*
13. *Hicksbeachia*
14. *Knightia*
15. *Leucadendron*
16. *Lomatia*
17. *Macadamia*
18. *Musgravea*
19. *Orites*
20. *Panopsis*
21. *Persoonia*
22. *Protea*
23. *Roupala*
24. *Stenocarpus*
25. *Telopea*
26. *Xylomelum*

II. Description of Wood Anatomy of the Proteaceae

(*a*) *General Properties*

The truewood of timbers of the Proteaceae varies in colour from a very light creamy brown (e.g. many *Persoonia* and *Helicia* spp.) through those tinted with pink (*Stenocarpus sinuatus*), pink-brown, and red-brown to the very deep red-brown tinted with purple of *Xylomelum occidentale;* sapwood is light coloured and contrasts sharply with the heartwood in those timbers which have deeply coloured heartwood. Pink and red tinted timbers are commonest in this family. Some timbers (e.g. *Cardwellia sublimis* and *Embothrium wickhami*) are very lustrous and this feature in company with others makes them highly suitable for use in furniture and interior finish.

In weight there is a range from the light timbers of *Cardwellia* and *Embothrium* with air-dry densities of 36 and 34 lb./cu.ft. respectively to *Hakea leucoptera,* a hard heavy timber with an air-dry density of 60 lb./cu.ft.

All timbers of this family, except some species of *Persoonia,* are characterized by a more or less well-marked ray figure due to the presence of broad rays which may, as in *Xylomelum,* reach a height of over 2 cm. and a width of over 1 mm. and form about 50 per cent. of the substance of the wood (Plate 1, Fig. 1). Vertical and intercellular canals (probably of traumatic origin) have been observed in *Grevillea robusta, G. striata, G. stenobotrya, Hakea macraena.* and *Musgravea stenostachya;* they have been reported in *Banksia* and *Cardwellia* (Record 1936; Record and Hess 1943).

(*b*) *The Tissues*

(i) *Vessels.*—The pore arrangement in the family varies from predominantly solitary (*Faurea macnaughtoni,* Plate 4, Fig. 6; Plate 2, Fig. 2) and solitary and short tangential and radial multiples (*Roupala dielsii,* Plate 1, Fig. 3) to a marked tangential arrangement (*Knightia excelsa,* Plate 1, Fig. 5). This tangential pattern is often closely connected with the arrangement of the parenchyma, and the two together, as seen on the cross section, may form festoons which extend tangentially from ray to ray, and are looped with the concavity towards the periphery (*Telopea oreades,* Plate 1, Fig. 4). The tangential bands of vessels may be only one or two deep radially as in *Knightia* (Plate 1, Fig. 5), or massed into wide bands which form the dominant pattern of the wood, as in many species of *Banksia* and *Hakea* (Plate 1, Fig. 6; Plate 5, Fig. 6). Other pore patterns occur within the family, though less commonly: an irregular scattered distribution of solitary or grouped pores as in *Cardwellia* (Plate 2, Fig. 1) and an irregular formation of tangential bands as in *Leucadendron argenteum* (Plate 3, Fig. 4). The vessels may vary much in size from the few large vessels of *Cardwellia* and *Carnavonia* to the small, closely ranked and quite uncountable vessels of *Banksia* and *Hakea.* Differences in pore size are common throughout the growth rings and are sufficiently marked in some species of *Hakea,* and occasionally in *Persoonia toru,* for the woods to be classed as semi-ring-porous. Microscopically the vessel elements have some features that serve to distinguish the genera. Although simple perforation plates predominate throughout the family, reticulate and

foraminate multiple perforation plates are common in the smaller vessels of *Lomatia* and *Telopea* (Plate 2, Fig. 3; Plate 6, Fig. 3). Spirals occur in *Banksia, Hakea, Dryandra, Grevillea,* and *Guevina,* but are not invariably present and are more conspicuous in some species than in others (Plate 2, Fig. 4). The inter-vessel pits vary in size from genus to genus; pits to parenchyma and ray cells are similar to the inter-vessel pits; in *Musgravea* and *Faurea* they are commonly, and in *Helicia, Panopsis,* and *Stenocarpus* occasionally, unilaterally compound in the parenchyma walls. Brown resinous deposits are common in the vessels of some species of *Banksia, Grevillea, Xylomelum* etc., and white deposits are sometimes conspicuous in the pores of *Cardwellia sublimis.* Tyloses have not been observed.

(ii) *Parenchyma.*—The parenchyma is commonly plentiful, apotracheal or paratracheal or both; three types of parenchyma arrangement can be distinguished within the family, though there is some overlapping between the types. *Reticulate parenchyma,* fine narrow lines, 1-3 cells wide, running from ray to ray and forming a typical reticulate pattern on the cross section, occur in *Musgravea, Hicksbeachia, Panopsis,* and some species of *Stenocarpus* and *Helicia* (Plate 3, Figs. 1, 2, and 6). In all these woods the parenchyma lines appear to be apotracheal and the narrow lines are approximately parallel and continuous. The vessels and vessel groups are rather few and lines of parenchyma are often completely independent of the vessel groups for a considerable distance across the wood. Vasicentric parenchyma is commonly also present around the vessel groups. *Banded parenchyma* (probably paratracheal), associated with the vessels and vessel groups distinguishes the majority of the other genera, and is characteristically on the abaxial side of the pores and pore groups. The parenchyma may be in narrow lines 1-3 cells wide (*Helicia ferruginea, Finschia* sp., Plate 3, Figs. 3 and 5) or bands of 4 and more cells wide (*Xylomelum pyriforme, Grevillea robusta,* Plate 1, Fig. 2; Plate 5, Fig. 2). Where the parenchyma lines are narrow and numerous, as in *Hicksbeachia* sp., *Darlingia,* and *Finschia* (Plate 3, Fig. 5), the fundamental distinction between this type and the reticulate is a little obscure, though the distinction is clear to the eye, and it is possible that the linking of every parenchyma line with one or more vessel groups and the absence of independent parenchyma lines is due to the greater number of vessel groups and not to a fundamental difference in the parenchyma type. It serves, however, as a useful diagnostic feature for distinguishing the woods (cf. Plate 3, Figs. 5 and 6). The lines and bands of parenchyma tend to curve from one large ray to another, and this, with the arrangement of the pore groups on the axial side of the parenchyma, gives the "festoon" or "pendant" pattern so characteristic of many Proteaceae. *Paratracheal parenchyma,* vasicentric and associated with apotracheal lines, or aliform and confluent to give irregular bands. This is characteristic of *Cardwellia,* some species of *Stenocarpus, Carnarvonia* (where it is sometimes associated with diffuse parenchyma), *Xylomelum,* and *Embothrium wickhami* (where it is predominantly aliform) (Plate 5, Fig. 3). It is also common in the species which have lines of reticulate parenchyma and, in *Helicia,* its presence aids the distinction between the two groups into which the species can be divided.

(iii) *Rays.*—Large rays are characteristic of most genera, and it is only in the section Persoonioideae that really small rays occur. In this section, however, the rays are very variable in size and all the genera examined show species with some very large rays. In *Persoonia* the seven species examined showed a series from *P. quinquenervis,* with uniseriate rays, to *P. linearis* and *P. elliptica* in which the rays are of two distinct sizes and resemble closely those of some of the Grevilloideae. In *Faurea* (three species) there was again a gradual difference between the species, *F. macnaughtoni* approaching very closely the structure of some of the Grevilloideae. In the Grevilloideae the rays are commonly of two distinct types, large multiseriate rays and small uniseriate ones. It appears unlikely that the uniseriate rays all increase in size and become multiseriate, but the increase in ray tissue which is made necessary by the increasing perimeter of the stem seems to be brought about, as in the Sterculiaceae (Chattaway 1937) either by the formation of new uniseriate rays through the change from fusiform cambial initials into ray initials, or by the subdivision of multiseriate rays through the reverse change taking place. In some genera this subdivision produces only large rays, but in others (notably those of the *Banksia* type) the rays seldom attain such enormous proportions and the subdivision results in a graded series of rays, all distinct from the uniseriate rays, but often only 5 or 6 cells wide and not very high. The uniseriate rays are often formed only of erect cells, and in many woods are only 1 or 2 cells high (*Banksia grandis,* Plate 2, Fig. 5). The rays of *Banksia* and *Dryandra* are characterized by the presence of vascular tissue. On tangential sections these appear to have the structure of small stems, and on radial sections vessels and tracheids can be seen running radially along the rays. Some of these have the characteristic pitting and thickening of protoxylem elements (Plate 7, Figs. 1-4), others resemble small vessels and have simple perforation plates. Further details of this tissue will be published in a subsequent paper. Stone cells occur in the rays of species of *Persoonia* (Plate 6, Fig. 1), *Faurea, Stenocarpus* (Plate 6, Fig. 2), *Roupala,* and *Hakea* and have been observed in one species of *Grevillea* and one of *Panopsis.* Crystals are present in the stone cells of *Stenocarpus salignus* and in the ray cells of some species of *Hakea.*

(iv) *Fibres.*—In most genera the ground mass of the wood is formed of libriform fibres with simple or indistinctly bordered pits. In some species of *Stenocarpus,* and in *Xylomelum, Persoonia, Protea,* and *Faurea,* however, the ground mass of the wood is formed of fibre tracheids with conspicuously bordered pits. The walls are thin to moderately thick in the majority of the genera; where they are thick, the thickness of the wall is much greater than the diameter of the lumen. Septa have not been observed.

(v) *Tracheids.*—These occur in some genera, and appear to be of three different kinds: (i) tracheids of independent origin and probably the only true tracheids within the family; (ii) tracheids which are variants of the ground mass of fibre tracheids; (iii) tracheids which are variants of the small angular vessel segments.

In *Macadamia* the ground mass of the wood is formed of libriform fibres, but bands of tracheids occur at irregular intervals, possibly delimiting the growth

zones. This feature serves to distinguish *Macadamia* from all other members of the family examined (Plate 6, Figs. 5 and 6).

In some species of *Stenocarpus* and in *Xylomelum*, tracheids occur around and among the vessels and seem to be a development from the ground mass of fibre tracheids. In the vicinity of the vessels the fibre tracheids tend to have thinner walls and wider lumina and more numerous pits with large borders. In macerated material differences in length can be observed from the long fibre tracheid which forms the ground mass of the wood to the typical blunt-ended tracheid which is always associated with vessels or groups of vessels and which is identical in length with the vessel members.

In many of the genera with the *Banksia* type of structure there is great variation in vessel size, the smaller ones being little larger in diameter than the surrounding fibres and parenchyma cells. Among these small elements all gradations will be found from small vessel members with minute perforation plates, to imperforate elements which are indistinguishable from true tracheids. Tracheids of this type have also been found in *Persoonia*.

III. Relation of Wood Anatomy to Botanical Classification

The family Proteaceae has been divided into two groups, the Persoonioideae and the Grevilloideae. The wood anatomy suggests that though some members of the Persoonioideae are quite distinct from the members of the Grevilloideae variations in structure can be found within this group, leading to the structure characteristic of most of the Grevilloideae.

Persoonia quinquenervis is unlike any other member of the Proteaceae in having small solitary vessels, often independent of any parenchyma or capped abaxially by a few cells, and low predominantly uniseriate rays. Within this genus there is, however, a series leading to *P. elliptica* which has irregular bands and clusters of vessels, backed by irregular bands of parenchyma, and rays of two distinct sizes, with the large rays subdividing in the manner typical of other members of the family. In *Faurea* the structure approaches that of the Grevilloideae.

Within the Grevilloideae two main types of structure stand out, but these do not separate the genera according to the botanical classification given above; they actually split several of the genera, but they appear to be constant and serve usefully in separating the woods according to the following key:

Key

Type 1. Parenchyma lines apotracheal, reticulate, *Musgravea, Helicia* (in part), *Panopsis, Stenocarpus* (in part).

Type 2. Parenchyma lines or bands paratracheal.

(2*a*) Vessels usually surrounded by parenchyma and often in the middle of wide bands of parenchyma, *Carnarvonia, Xylomelum,* and occasionally *Cardwellia* and *Grevillea.*

(2*b*) Vessels on the axial side of parenchyma lines or bands, solitary or in clusters, or tangential multiples, *Cardwellia, Darlingia, Embothrium* (in part), *Finschia, Grevillea, Helicia, Hicksbeachia, Macadamia, Roupala, Stenocarpus* (in part).

(2*c*) Vessels on the axial side of the parenchyma lines or bands; in tangential arrangement, usually from ray to ray, often forming bands several vessels deep, *Banksia, Dryandra, Embothrium* (in part), *Guevina, Hakea, Knightia, Lomatia, Telopea.*

In Type 1 the parenchyma is arranged predominantly in close apotracheal lines, usually 2 or 3 cells wide, and the vessels do not occur solely on the axial side of the parenchyma as in the rest of the family, but are usually surrounded by a thin layer of vasicentric parenchyma. The fibres have rather thin walls in all the genera examined. It is occasionally a little difficult to distinguish between this type and woods such as *Hicksbeachia* in which the lines of paratracheal parenchyma are very numerous and narrow, but the size and position of the vessels, the vasicentric parenchyma and the thinner walled fibres should give the necessary clues. The genus *Helicia* serves to show both types of structure, the division of the genus in this respect being also noted by Janssonius (1934). A similar division of *Stenocarpus* has been noted by the author.

Type 2 is based on woods with paratracheal parenchyma which may be mainly aliform (as in *Embothrium*), but is more commonly confluent, forming narrow lines or broad bands which curve from ray to ray, concave towards the periphery, the vessels and vessel groups seeming to depend from the parenchyma as pendants from a chain. The pendant vessel arrangement is often obscure in Type (2*a*) where the vessels are sometimes completely surrounded by vasicentric parenchyma and even by the wide bands of parenchyma or by irregularities in confluent bands. It is sometimes obscure also in Type (2*c*) where the pattern is given to the wood on cross sections by the massed bands of vessels which tend to obscure the narrower lines of parenchyma.

In all except three genera the wood is, in spite of variations from species to species, and sometimes even within a species, of the same fundamental type. But in *Helicia, Embothrium,* and *Stenocarpus* there are very distinct and apparently fundamental differences, which might, if found also in the flowers and leaves, warrant division of each of these genera.

Helicia

H. ferruginea and *H. glabriflora* examined by the author, *H. serrata, H. attenuata,* and *H. javanica* described by Janssonius (1934), and *H. formosana* figured by Kanehira (1940) have wood of the typical *Grevillea* type, with small vessels, solitary or in clusters, appearing on cross sections as pendants from the parenchyma lines, touching the parenchyma only on the abaxial side, moderately numerous to numerous; parenchyma in narrow concentric paratracheal lines; rays often over 5 but less than 10 mm. high; fibres with very thick walls and small lumina and few simple pits (Plate 3, Fig. 3).

H. diversifolia and *H. montana* examined by the author and *H. incisa* and *H. lanceolata* described by Janssonius (1934) are of the *Musgravea* type, with vessels which are almost always surrounded by a narrow rim of vasicentric parenchyma, and are fewer and larger than in the other species; the parenchyma lines are apotracheal but are less numerous and less regular than in *Musgravea;* the rays usually less than 5 mm. high; the fibres thin walled, with small indistinctly bordered pits (Plate 3, Fig. 6).

According to Janssonius (1934) a division of the genus on these anatomical points is in accordance with the classification of Koorders and Valeton (1900) in their "Flora Javanica."

Embothrium

E. wickhami from Australia has a quite distinct structure from the three American species examined and it seems possible that these should be distinct genera. The wood shows clusters of vessels which lack the characteristic tangential pattern; the parenchyma is aliform and confluent, when confluent tending to form broad bands which enclose the vessel groups (Plate 5, Figs. 3 and 4).

Of the three American species, *E. coccineum* and *E. grandiflorum* show structure of the *Banksia* type, with bands of pores extending tangentially from ray to ray, often several pores deep radially with the parenchyma on the abaxial side of the bands. In the one available specimen of *E. weberbaueri* the tangential arrangement is less marked and this species seems (as in some species of *Banksia* and *Hakea*) to link the others to the *Grevillea* type. The pores of all three species are smaller and more numerous than those of *E. wickhami* and the rays smaller, lower, and less conspicuous.

Stenocarpus

The distinction between the two groups in *Stenocarpus* is similar to that observed in *Helicia,* but *Stenocarpus laurinus, S. reticulatus,* and *S. salignus,* which have woods of the *Grevillea* type, show a tendency for the parenchyma to be aliform as well as in regular concentric bands. In *S. salignus* there is a considerable variation from aliform parenchyma to broad bands which may enclose the pores (Plate 2, Fig. 6).

In *S. sinuatus* and *S. umbellatus* the wood is of the *Musgravea* type with clustered, irregularly spaced pores surrounded by vasicentric parenchyma and also with numerous fine concentric lines of apotracheal parenchyma (Plate 3, Figs. 1 and 2).

IV. Description of the Genera*

A. Persoonioideae

(*a*) *Faurea*

A genus consisting of about 15 species confined to tropical South Africa and Madagascar (Sim 1921; Scott 1927, 1935). Four species were available for examination: *F. discolor* Welw., *F. macnaughtoni* Phillips, *F. saligna* Harv., and *F. speciosa* Welw. (see Plate 2, Fig. 2, and Plate 4, Figs. 3, 5, and 6).

(i) *General Properties of the Timber.*—Light brown to dark brown in colour, moderately heavy (*F. macnaughtoni* 52-60 lb./cu.ft. air-dry†; cutting moderately evenly, rather fine in texture. Match-size splinters burn to a full white or buff ash.

(ii) *Structure.—Growth rings* not marked. *Pores* mostly solitary, sometimes in short chains and clusters but with a tendency to tangential arrangement; white deposits sometimes present; pits to parenchyma and ray cells sometimes unilaterally compound. *Parenchyma* usually abundant, in close association with the pores, occasionally vasicentric (Scott 1927) but more often aliform and confluent,

* In alphabetical order.

† Density figures given in this paper are on the air-dry basis at 12 per cent. moisture content.

on the abaxial sides of the pores, forming 1-8 seriate bands, sometimes broken, but sometimes continuous from ray to ray, sometimes anastomosing and somewhat concave towards the periphery. *Rays* large except in *F. speciosa* where they are usually not more than 5 mm. high; stone cells of very irregular shape have been observed in the large rays of one sample of *F. speciosa* and in *F. discolor*. *Fibre* wall thickness slightly greater than the diameter of the lumen; pits with small but distinct borders. *Tracheids* (and small imperfectly perforated vessel members) often associated with the vessel groups.

(*b*) *Leucadendron*

Only one species was available for examination, *L. argenteum* R.Br. The genus consists of about 70 species, confined to South Africa. *L. argenteum* is the best known and is cultivated, not for its timber but for the ornamental flowers and silvery silky leaves from which it gets its common name of "silver tree" (Plate 3, Fig. 4).

(i) *General Properties of the Timber.*—Light brown in colour and moderately light in weight. Fine and uniform in texture. Match-size splinters burn to a full dark grey ash.

(ii) *Structure.—Growth rings* not clearly defined but sometimes marked by slight differences in pore size. *Pores* moderate in size and moderately numerous; in pore multiples and clusters, seldom solitary, commonly arranged in loose concentric somewhat irregularly spaced bands. *Parenchyma* inconspicuous with a lens, paratracheal, sometimes, but not regularly on the abaxial side of the pore groups, forming bands 1-3 cells wide. *Rays* variable in size but seldom more than 1-5 mm. high, of all sizes from 1-10 cells wide. *Fibre* wall thickness much less than the diameter of the lumen; pits bordered but the borders small and indistinct.

(*c*) *Persoonia*

A genus consisting of shrubs and small trees which, with the exception of a single New Zealand species, is limited to Australia, which has 60 species. Seven species have been examined, but only one sample was available of each, viz. *P. elliptica* R.Br., *P. lanceolata* Andr., *P. longifolia* R.Br., *P. linearis* Andr., *P. media* R.Br., *P. quinquenervis* Hook., and *P. toru* A.Cunn. (Plate 5, Fig. 5; Plate 6, Fig. 1).

(i) *General Properties of the Timber.*—Sometimes tinged with pink or red, bark varying from brown and fine textured in some specimens to thick and flaky and red. Moderately light to heavy in weight, with air-dry densities of from 33-58 lb./cu.ft. (67 lb./cu.ft in *P. quinquenervis*). Texture fine and even; match-size splinters burn to a full or partial buff or black ash.

(ii) *Structure.—Growth rings* not clearly defined. *Pores* from 20 to more than 50 per sq.mm. not visible to the naked eye and not always clearly defined with a lens; solitary (*P. quinquenervis*) and in multiples of 2-6, with tangential arrangement in irregular concentric bands often with scattered pores and pore multiples between the bands; the typical proteaceous pattern with lines of pores curving from ray to ray and concave towards the periphery is absent from this

genus, and in some specimens the lines of pores may be convex, following the curve of the stem; spiral thickening was observed in all species except *P. longifolia*, but varied in frequency and distinctness in different species. *Parenchyma* associated with the pores, on the abaxial side of the pores and pore groups, not clearly visible with a lens and scarce in all species except *P. longifolia*. *Rays* variable in size in the different species; in *P. quinquenervis* uniseriate, very occasionally partially biseriate; in *P. lanceolata* and *P. media* usually 1-4 and in *P. toru* 1-6 wide, the larger rays uncommon in *P. media;* in *P. toru* the small rays are predominantly uniseriate and 1-3 cells high; *P. elliptica, P. linearis,* and *P. longifolia* have the more typical proteaceous rays of two distinct sizes. Stone cells were observed in the rays of *P. elliptica, P. lanceolata* (Plate 6, Fig. 1), *P. linearis,* and *P. longifolia*. *Fibre* wall thickness less than the diameter of the lumen; pits bordered except in *P. toru* and *P. quinquenervis*. *Tracheids* in all species examined, the larger vessels and vessel groups being surrounded by small elements which show all transitional stages between vessel elements and tracheids.

(*d*) *Protea*

The genus consists of about 75 species of small trees and ornamental shrubs, confined to South Africa and cultivated more for their flowers than for the timber. Three species were examined: *P. elliottii* C. H. Wright, *P. grandiflora* Thunb., and *P. lepidocarpon* R.Br.

(i) *General Properties of the Timber.*—The wood is light brown in colour with a pinkish tinge and moderately light in weight. Match-size splinters burn to a full or partial ash.

(ii) *Structure.—Growth rings* feebly marked by slight difference in pore size. *Pores* frequently solitary, occasionally in short tangential multiples, moderately numerous. *Parenchyma* moderately abundant, rather irregular in distribution, paratracheal, aliform and confluent, in 1-4 seriate bands. *Rays* of two distinct sizes, the larger rather low, usually less than 5 mm. high, with many uniseriate rays in *P. grandiflora* but varying from uniseriate to many cells wide in *P. lepidocarpon*. *Fibre* wall thickness less than the diameter of the lumen; pits numerous, bordered.

B. Grevilloideae

(*a*) *Banksia*

A large genus of about 50 species widely distributed through Australia, to which they are endemic. They vary in habit from shrubs to large trees; several grow to about 50-60 ft. and produce timber of commercial value. The woods of different species are very similar and no attempt has been made here to separate them. The following species were examined: *B. aemula* R.Br., *B. attenuata* R.Br., *B. collina* R.Br., *B. dentata* Linn., *B. ericifolia* Linn., *B. grandis* Willd., *B. ilicifolia* R.Br., *B. integrifolia* Linn., *B. latifolia* R.Br., *B. littoralis* R.Br., *B. marginata* Cav., *B. menziesii* R.Br., *B. serrata* Linn., *B. verticillata* R.Br. (Plate 1, Fig. 6; Plate 2, Figs. 4 and 5; Plate 7, Figs. 1-4).

(i) *General Properties of the Timber.*—Pink to a deep red-brown, sometimes with a purplish tinge, with interlocked and sometimes wavy grain; moderately light (29-50 lb./cu.ft.), moderately fine but of uneven texture. Match-size splinters burn to a full or partial ash. Vertical gum canals have been reported by Record (1936).

(ii) *Structure.—Growth rings* not defined. *Pores* not visible to the naked eye (except in *B. latifolia*) but distinct with a lens (except in some specimens of *B. integrifolia, B. marginata,* and *B. menziesii*); in crowded tangential bands, concentric, up to about 7 pores deep radially, often looped from ray to ray, concave towards the periphery; spiral thickenings sometimes conspicuous, but often faint and very sporadic in occurrence; deposits occasionally present in some species. *Parenchyma* in narrow lines or bands, 1-4 cells wide on the abaxial side of the pores. *Rays* often inconspicuous on the cross section owing to their colour being the same as that of the fibres, of two distinct types; the larger usually less than 5 mm. high, except in *B. aemula, B. ilicifolia,* and *B. grandis* (in the last-named often more than 10 mm. high), the smaller seldom more than 4 or 5 cells high and mostly only 1 or 2, composed entirely of upright cells (Plate 2, Fig. 5). *Vascular tissue* (see p. 283) observed in the rays of all species, but variable in frequency. *Fibre* wall thickness variable in different species, greater than the diameter of the lumen in *B. aemula, B. attenuata, B. grandis, B. ilicifolia,* and *B. menziesii,* and occasionally in *B. collina, B. dentata, B. latifolia, B. marginata,* and *B. serrata.*

(*b*) *Cardwellia*

A monotypic Australian genus, *C. sublimis* F.Muell., occurring in north Queensland, and attaining a height of 100-150 ft. with a diameter at breast height of about 4 ft. (Plate 2, Fig. 1).

(i) *General Properties of the Timber.*—Pink or light brown to reddish-brown, often with a golden sheen, moderately light (31-39 lb./cu.ft.); grain often interlocked; rather coarse and irregular in texture. Match-size splinters burn to a charcoal, without leaving any ash. Vertical gum ducts reported by Record (1936). It is often very difficult to distinguish between *Cardwellia sublimis* and *Grevillea robusta,* the best distinguishing features are the burning splinter test, in which *G. robusta* gives a full ash; the pore size, which is somewhat larger in *C. sublimis;* the presence of white deposits in *C. sublimis;* and the presence of spiral thickenings in *G. robusta.*

(ii) *Structure.—Growth rings* not defined. *Pores* usually large, clearly visible to the naked eye, few to moderately numerous, 3-6/sq.mm. in clusters and short tangential multiples, usually enclosed in the parenchyma bands, white deposits very common. *Parenchyma* abundant, vasicentric, aliform and confluent, forming broad bands up to 12 cells wide, commonly enclosing the pores. *Rays* of two distinct types, the larger usually more than 5 but less than 10 mm. high; the smaller uniseriate or often partially biseriate, up to 12 cells high, composed of erect, square and procumbent cells. *Fibre* wall thickness less than the diameter of the lumen, but rather variable.

(c) *Carnarvonia*

A monotypic Australian genus, the one species, *C. araliaefolia* F.Muell., occurs in the tropical mixed jungles of north Queensland.

(i) *General Properties of the Timber.*—Dark reddish-brown with a purplish tinge, moderately heavy (35-45 lb./cu.ft.), grain often interlocked, texture rather coarse and uneven. Match-size splinters burn to a full brown ash with smoke and a brown exudation streaming from the pores (Swain 1928).

(ii) *Structure.—Growth rings* not defined. *Pores* sometimes solitary but usually in clusters of tangential multiples; sometimes individually distinct to the naked eye, but more often only distinct with a lens, about 6-10 per sq.mm.; commonly filled with reddish-brown deposits. *Parenchyma* occasionally aliform, usually confluent, in broad bands 2-6 cells wide, sometimes surrounding the pores and pore groups but more often touching them on the abaxial side and partially surrounding them; apotracheal parenchyma abundant, diffuse, as scattered cells and short tangential lines. *Rays* of two distinct types, the larger usually more than 5 but less than 10 mm. high and up to 0.5 mm. wide; the smaller few, uniseriate, mainly composed of square or procumbent cells. *Fibre* wall thickness greater than the diameter of the lumen.

(d) *Darlingia*

Specimens from one species, *D. spectatissima* F.Muell. from Queensland, a tree attaining about 100 ft. in height and 18 in. diameter, were available for examination.

(i) *General Properties of the Timber.*—Truewood pink-brown, moderately heavy (44-47 lb./cu.ft.) texture rather coarse. Match-size splinters burn to a partial cream or grey ash.

(ii) *Structure.—Growth rings* not defined. *Pores* barely visible to the naked eye but individually distinct with a lens; about 6-10/sq.mm., predominantly solitary but occasionally in pairs or short tangential multiples, deposits not observed. *Parenchyma* in fine curved concentric bands on the abaxial side of the pores; 1-8 (commonly 2-4) cells wide; in one specimen occasional short tangential lines occurred without obvious connection with any pores. *Rays* of two distinct sizes, the large rays commonly over 5, but less than 10 mm. high, and about 0.25 mm. wide, rather uniform in size; the small ones uniseriate, of erect cells only. *Fibre* wall thickness rather variable but usually less than the diameter of the lumen; pits with small but distinct borders.

(e) *Dryandra*

A genus of 50 species confined to the south of Western Australia. Most of the species are small shrubs; only two, which attain tree size, viz. *D. floribunda* R.Br. and *D. nobilis* Lindl., were available for examination. The timber has no known uses. The wood is structurally indistinguishable from that of some of the smaller species of *Banksia*. Vascular tissue, similar to that in the rays of *Banksia*, was observed.

(*f*) *Embothrium* (in part see p. 286)

A genus which occurs in South America, with one species, *E. wickhami* Hill and F.Muell., in eastern Australia (Plate 5, Fig. 3). The wood of the Australian species is very different from that of the American, and it is possible that the genus is ill-defined. *E. wickhami* is a tree of about 70-90 ft. high with a diameter of 13-28 inches; it occurs in Queensland and New South Wales.

(i) *General Properties of the Timber.*—Pink-brown with a golden sheen, moderately light (about 31 lb./cu.ft. air-dry, Swain 1928), with slightly interlocked grain, coarse and uneven in texture. Match-size splinters burn to a dark buff ash (Swain 1928).

(ii) *Structure.—Growth rings* not defined. *Pores* just distinct to the naked eye, about 4/sq.mm., solitary or in short tangential multiples and clusters; red deposits filling many pores; white deposits sporadic, present in some samples. *Parenchyma* not very abundant, vasicentric, often forming eccentric or incomplete sheaths around the vessels, aliform with short tangential wings, occasionally, though rarely forming curved bands from ray to ray and giving the looped appearance typical of the Proteaceae. *Rays* of two distinct types, the larger seldom more than 5 mm. high, the smaller uniseriate, composed almost entirely of upright cells. *Fibre* wall thickness less than the diameter of the lumen.

(*g*) *Embothrium* (in part see p. 286)

Three American species were available: *E. coccineum* Forst., *E. grandiflorum* Lam., and *E. weberbaueri* Perkins (Plate 5, Fig. 4). There are considerable differences in structure between the two parts of the genus, *E. coccineum* and *E. grandiflorum* having the *Banksia* type of structure, whereas *E. weberbaueri* is transitional between this and the *Grevillea* type. The American species of *Embothrium* are shrubs and small trees distributed throughout the Andean region of South America. They produce an attractive good quality timber, but the smallness of the tree prevents it being of any commercial value (Record and Hess 1943).

(i) *General Properties of the Timber.*—Light greyish-brown with a high lustre, moderately heavy and hard with straight grain.

(ii) *Structure.—Growth rings* ill-defined, sometimes showing, microscopically, differences in pore size. *Pores* in clusters and short tangential multiples (*E. weberbaueri*); extending from ray to ray and forming continuous bands, often several pores deep radially (*E. coccineum, E. grandiflorum*); numerous, not visible to the naked eye, but distinct with a lens. *Parenchyma* in lines and bands 2-4 cells wide on the abaxial side of the pore groups and bands. *Rays* of two distinct sizes; the larger seldom more than 5 mm. high in *E. coccineum* and *E. weberbaueri* but often over 10 mm. high in *E. grandiflorum,* rather variable in width; the smaller uniseriate, often low, and composed of square or upright cells. *Fibre* wall thickness less than the diameter of the lumen.

(*h*) *Finschia*

A small to moderate sized tree from New Guinea; two species, *F. densiflora* C.T.W. and *F. ferruginea* C.T.W. (Plate 3, Fig. 5) were examined. The wood is very similar to that of some species of *Grevillea* but has thinner fibre walls, and, in some specimens, uniseriate rays composed predominantly of upright cells.

(*i*) *Grevillea*

A large genus of about 170 species of trees and shrubs distributed throughout Australia. *G. robusta* gives one of the timbers known as silky oak. The following species were available for investigation: *Grevillea barklyana* F.Muell., *G. heliosperma* R.Br., *G. hilliana* F.Muell., *G. pinnatifida* F.Muell., *G. polystachya* R.Br., *G. robusta* A.Cunn., *G. stenobotrya* F.Muell., *G. striata* R.Br., and *G. subargentea* C.T.W. (Plate 4, Fig. 4; Plate 5, Fig. 2).

(i) *General Properties of the Timber.*—The heartwood is pinkish and lustrous, moderately light to rather heavy (37-66 lb./cu.ft., mostly 38-45 lb./cu.ft. air-dry), grain commonly interlocked; texture coarse and uneven. Match-size splinters burn to a full white or buff ash. Red deposits frequent in some specimens.

(ii) *Structure.—Growth rings* not defined, but occasionally there is a slight difference in pore size in early and late wood in some specimens of *G. robusta* and *G. stenobotrya. Pores* usually 6-10/sq.mm.; some solitary but usually in irregular clusters or short radial or tangential multiples, on the axial side of the parenchyma bands; vessel members sometimes with spiral thickening. *Parenchyma* predominantly in rather broad concentric bands, often looping from ray to ray, concave towards the periphery, 2-8 (commonly 4-6) cells wide, on the abaxial side of the pores and pore groups; often aliform and occasionally vasicentric; a few scattered cells or short tangential lines of diffuse parenchyma are sometimes present, especially in *G. robusta. Rays* of two distinct kinds, the larger variable in height and width, seldom more than 5 mm. high but sometimes up to 1 mm. wide, the small ones predominantly uniseriate, 5-15 cells high, usually of square or procumbent cells and very rarely of upright ones. *Fibre* wall thickness almost always greater than the diameter of the lumen except in some samples of *Grevillea pinnatifida, G. robusta,* and *G. subargentea.*

(*j*) *Guevina*

A monotypic genus, represented by *G. avellana* Molina from Chile. A small to medium-sized tree, occasionally growing to 65 ft. with a diameter of 30 in. The timber is used locally (Record and Hess 1943).

(i) *General Properties of the Timber.*—Heartwood pale brown with a pinkish tinge; lustre high but broken by the bands of pores and parenchyma; rather light; texture medium to rather coarse.

(ii) *Structure.—Growth rings* not defined. *Pores* indistinct to the naked eye but clearly visible with a lens, numerous, in clusters and tangential bands, irregular and parallel, curving from ray to ray, slightly concave towards the periphery; deposits not observed; vessel members with spiral thickening. *Parenchyma* in narrow bands 1-3 cells wide on the abaxial side of the pore bands. *Rays* of two distinct types, the larger commonly more than 5 but less than 10 mm. high; the smaller uniseriate, usually only 1-3 cells high, of upright cells only. *Fibre* wall thickness less than the diameter of the lumen.

(*k*) *Hakea*

A large Australian genus of about 100 species, mostly shrubs or small trees, seldom attaining a great size. The following species were available for examination: *H. cycloptera* R.Br., *H. eriantha* R.Br., *H. flexilis* F.Muell., *H. laurina*

R.Br., *H. lorea* R.Br., *H. leucoptera* R.Br., *H. macraena* F.Muell., *H. multilineata* Meissn., *H. pedunculata* F.Muell., *H. preisii* Meissn., *H. recurva* Meissn., *H. saligna* Knight, *H. subulata* A.Cunn., *H. vittata* R.Br. (Plate 5, Fig. 6).

(i) *General Properties of the Timber.*—Woods usually rather dark in colour, reddish-brown; sometimes rather heavy (46-60 lb./cu.ft.) and hard to cut, very fine but uneven in texture. Match-size splinters burn to a full white or buff ash. Vertical gum canals were observed in *H. macraena.*

(ii) *Structure.—Growth rings* often marked by a distinct difference in pore size between the beginning and end of the growth zone, sometimes amounting to definite semi-ring porosity. *Pores* usually visible, but sometimes indistinct with a lens; densely clustered in tangential bands from ray to ray, often several pores deep radially; commonly round in outline, with rather thick walls, except in *H. eriantha, H. laurina,* and *H. saligna;* in isolated clusters rather than in bands in *H. pedunculata, H. preisii,* and *H. subulata;* extremely numerous and very difficult to count; spirals sometimes very conspicuous, but not observed in all species, and often sporadic within a sample. *Parenchyma* sparse around the pores and usually in narrow bands on the abaxial side of the pore bands. *Rays* rather small and not very conspicuous in *H. laurina, H. lorea, H. subulata,* and *H. vittata;* of two distinct sizes, the larger usually less than 5 mm. high, varying in size and often with very thick walls to the individual ray cells, the smaller often rather few, sometimes of erect cells only; stone cells, often containing crystals observed in *H. laurina, H. leucoptera, H. recurva, H. subulata, H. vittata;* a few crystals were observed in ordinary ray cells in *H. pedunculata* and *H. preisii. Fibre* wall thickness much greater than the diameter of the lumen. *Tracheids*: all stages of transition can be found in the broad bands of vessels, between very small perfect vessels, small vessels with imperfect perforations, and imperforate vessel members that are difficult to distinguish from true tracheids (see p. 283).

(*l*) *Helicia* (in part see p. 285)

The genus is represented by about 50 species scattered throughout the Pacific Area from Australia to Japan. Two species of this section of the genus were available, *H. ferruginea* F.Muell. and *H. glabriflora* F.Muell. Both are Australian, but appear to be identical in structure with *H. serrata* Blume, *H. attenuata* Blume, and *H. javanica* Blume from Java, and to *H. formosana* Hemsl. from Formosa.

(i) *General Properties of the Timber.*—Light grey-brown with pinkish rays; moderately light (about 36 lb./cu.ft.); texture rather fine and uniform. Match-size splinters burn to a full grey ash.

(ii) *Structure.—Growth rings* not defined. *Pores* numerous (about 20/sq. mm.), not individually visible to the naked eye, but distinct with a lens; some solitary but predominantly in short tangential multiples on the axial side of the soft tissue; spirals absent from all specimens examined, though cited for this genus by Record (1936). *Parenchyma* in fine regular concentric lines from ray to ray, concave towards the periphery and on the abaxial side of the vessel groups; 1-4 (but usually 2) cells wide. *Rays* of two distinct sizes, the larger sometimes less than 5 mm. high in *H. ferruginea* but usually between 5 and 10 mm. high; the

smaller uniseriate, few and composed of erect cells only; a few small crystals were observed in the ray cells of *H. glabriflora*. *Fibre* wall thickness greater than the diameter of the lumen.

(*m*) *Helicia* (in part see p. 285)

The species with the *Musgravea* type of structure are described here; the specimens available were *H. diversifolia* C.T.W. and *H. montana* Sym. (Plate 3, Fig. 6). The trees are indistinguishable botanically from other species of the genus and are of similar distribution; species with this type of structure occur in Java as well as on the mainland of Australia.

(i) *General Properties of the Timber.*—The differences between these species and the rest of the genus lie chiefly in the distribution of the vessels and parenchyma and the thinner fibre walls.

(ii) *Structure.—Growth rings* not well defined. *Pores* few and scattered, solitary, clustered and in short radial and tangential multiples. *Parenchyma* paratracheal, vasicentric, surrounding the pores and pore groups; apotracheal, in concentric lines usually 1 or 2 cells wide. *Rays* of two distinct kinds, the large ones usually less than 5 mm. high, small ones uniseriate, few, commonly of erect cells only. *Fibre* wall thickness considerably less than the diameter of the lumen.

(*n*) *Hicksbeachia*

This is a monotypic genus from eastern Australia. *H. pinnatifolia* F.Muell., a small tree with edible nuts, provided material for examination.

(i) *General Properties of the Timber.*—Very light or straw-coloured, with conspicuous ray figure; moderately light (about 37 lb./cu.ft.), texture very fine but uneven owing to the large rays. Match-size splinters burn to a full grey ash.

This wood is structurally of interest as it is intermediate between woods such as *Helicia* and *Macadamia* with the *Grevillea* type of structure, and the *Musgravea* type (see p. 285). The fibres are very thick walled, the vessels small and on the axial side of the parenchyma lines as in the *Grevillea* type, but there are many parenchyma lines which seem entirely unconnected with any vessel or vessel group and suggest the development of lines of a definitely apotracheal type. Some of these lines are short and broken, giving diffuse parenchyma. The vasicentric parenchyma that accompanies the pore groups of the *Musgravea* type is entirely absent.

(ii) *Structure.—Growth rings* not defined. *Pores* indistinct even with a lens, solitary and in short multiples and clusters, on the axial side of the lines of parenchyma. *Parenchyma* abundant, as fine narrow lines 1 or 2 cells wide, irregularly concentric and often broken or anastomosing; some paratracheal on the abaxial sides of the vessels and vessel groups and some apparently apotracheal, without any connection with the vessels. *Rays* of two distinct sizes, the larger seldom more than 5 mm. high and up to 2 mm. wide, the smaller uniseriate, few, consisting entirely of upright cells. *Fibre* wall thickness greater than the diameter of the lumen.

(*o*) *Knightia*

The genus consists of 3 species, occurring in New Zealand and New Caledonia (Gardner 1941-2).. Only one, *K. excelsa* R.Br. from New Zealand, was available for study. It forms a tree up to 100 ft. high, with a diameter of 3 ft. (Plate 1, Fig. 5; Plate 4, Fig. 1).

(i) *General Properties of the Timber.*—Light brown with darker and conspicuous ray fleck, moderately heavy (46 lb./cu.ft. air-dry), grain straight or slightly wavy. The wood is used for furniture veneers, as well as cabinet work, turnery etc. It is also in demand for brake shoes, and, being easily split, for shingles and fence rails.

(ii) *Structure.—Growth rings* not defined. *Pores* not visible to the naked eye but distinct with a lens, numerous; regularly arranged in tangential multiples, generally only 1 pore wide, forming concentric lines, curved and concave towards the periphery and extending from ray to ray. *Parenchyma* forming bands 2-3 cells wide on the abaxial side of the pores. *Rays* of two distinct types: the larger conspicuous on all faces though seldom more than 5 mm. high; the smaller up to about 5 cells high, formed predominantly of upright cells. *Fibre* wall thickness less than the diameter of the lumen.

The structure of *Knightia* is very similar to that of *Orites* (p. 296). Both can be separated from *Grevillea* by the straighter lines of pores and parenchyma and the more regular tangential arrangement of the pores from ray to ray.

(*p*) *Lomatia*

This genus with 13 species is widely distributed through eastern Australia, the Pacific islands, and South America. Four species were available for examination: *Lomatia dentata* R.Br. and *L. obliqua* R.Br. from Chile and *L. ilicifolia* R.Br. and *L. longifolia* R.Br. from Australia (Plate 2). The species are structurally indistinguishable. They grow to large shrub size or small trees, and the wood is only of local importance. In gross structure the wood is indistinguishable from *Guevina* (p. 292); microscopically, however, it can be distinguished by the absence of spiral thickenings from the vessels and the presence of irregularly reticulate multiperforate perforation plates (Plate 2, Fig. 3). If the origin of a specimen is known this too will serve to distinguish the genera.

(*q*) *Macadamia*

This genus of 5 species is confined to eastern Australia. Two species were available, *M. praealta* Bailey and *M. ternifolia* F.Muell. (Plate 6, Figs. 5 and 6).

(i) *General Properties of the Timber.*—Deep pinkish-brown; moderately heavy (44 lb./cu.ft. air-dry) with interlocked grain; said to have an unpleasant odour when green. Match-size splinters burn to a thin white ash.

(ii) *Structure.—Growth rings* not visible to the naked eye but defined microscopically by bands of tracheids (Plate 6, Fig. 6). *Pores* indistinct to the naked eye but visible with a lens, about 20-25/sq.mm., solitary and in short tangential multiples arranged rather regularly on the axial side of the lines of parenchyma. *Parenchyma* paratracheal, usually 2 cells wide in regularly spaced concentric

lines, on the abaxial side of the vessels and vessel groups. *Rays* of two distinct sizes, the larger usually more than 5 but less than 10 mm. high, the smaller, uniseriate, few, seldom more than 3 or 4 cells high, composed entirely of upright cells. *Fibre* wall thickness greater than the diameter of the lumen.

(*r*) *Musgravea*

The genus consists of one species endemic to Queensland, *M. stenostachya* F.Muell. (Plate 6, Fig. 4). It is one of the smaller of the jungle trees, about 60-80 ft. high. It has a limited range in north Queensland. The tough lobed leaves may be a foot or more in length (Swain 1928).

(i) *General Properties of the Timber.*—Heartwood brown and lustrous, moderately light in weight (30-37 lb./cu.ft. air-dry), texture fine and even, sometimes with vertical gum canals. Match-size splinters burn to a full grey ash.

(ii) *Structure.—Growth rings* not defined. *Pores* of the larger size just visible to the naked eye; 3 or 4/sq.mm., some solitary but mostly in clusters and short radial and tangential multiples. *Parenchyma* to some extent paratracheal and vasicentric, surrounding the pores and pore groups; but predominantly apotracheal, in narrow curved parallel bands, usually 2 or 3 cells wide, and about 4/mm. *Rays* of two distinct sizes, the large ones up to 5 mm. high and about 0.50 mm. wide, the uniseriates rather few and mostly of upright cells. *Fibre* wall thickness usually less than the diameter of the lumen; pits few, indistinctly bordered.

(*s*) *Orites*

This is a small genus of about 6 species confined to eastern Australia. One species was available for examination, *Orites excelsa* R.Br. (Plate 4, Fig.2).

(i) *General Properties of the Timber.*—Light pink-brown with a golden sheen; moderately light (31 lb./cu.ft.), grain sometimes slightly interlocked; moderately fine but uneven. Match-size splinters burn to a full buff ash.

(ii) *Structure.*—The wood is structurally indistinguishable from that of *Knightia* (p. 295), but deposits were occasionally observed in the pores.

(*t*) *Panopsis*

The genus consists of a few species widely distributed through tropical South America. The trees are small to medium-sized; the best known, *P. rubescens* Pohl., attaining about 50 ft. The timber is used locally for cabinet work but is of no commercial importance (Record and Hess 1943). The only material available was *P. sessilifolia* (Rich) Sandwith and two samples of unnamed species.

(i) *General Properties of the Timber.*—Heartwood pinkish-brown with very conspicuous lighter coloured rays. Lustrous, varying in weight and hardness, with rather coarse and uneven texture given by the ray tissue.

(ii) *Structure.—Growth rings* not defined. *Pores* visible to the naked eye, about 2 or 3/sq.mm., some solitary, but mostly in clusters and short radial and tangential multiples. Pits to ray cells and parenchyma occasionally unilaterally compound. *Parenchyma* to some extent paratracheal, vasicentric surrounding the pores and pore groups, but predominantly apotracheal, in narrow concentric lines

usually 2 or 3 cells wide, somewhat convex from ray to ray, the concavity towards the bark, about 6-8/mm. *Rays* of 2 distinct sizes, the large ones often more than 10 mm. high and about 1-1.5 mm. wide, the uniseriates rather few and consisting almost entirely of upright cells. *Fibre* wall thickness less than the diameter of the lumen.

This timber is the only American member of the Proteaceae with this type of structure: *Andriapetalum* is now considered synonymous with *Panopsis*.

(*u*) *Roupala*

A genus of about 60 species, most abundantly represented in Central and South America, but also occurring in New Caledonia. Six species were examined: *R. angustifolia* Diels, *R. brasiliensis* Klotzsch, *R. complicata* Linden, *R. dielsii* Macbride, *R. loranthoides* Meissn., *R. montana* Aubl.; the wood structure of all is very similar (Plate 1, Fig. 3). *R. brasiliensis* is a rain-forest tree attaining a height of 100 ft. or more with a trunk 24-30 in. diameter and about 50 feet free of branches. The timber is highly durable and is employed locally in exposed structures, railway sleepers, and to a small extent for furniture and cabinet work (Record and Hess 1943).

(i) *General Properties of the Timber.*—Brown to reddish-brown, sometimes with a purplish tinge, sometimes lustrous, texture rather coarse. Match-size splinters burn to a full black ash.

(ii) *Structure.*—Similar to that of many species of *Grevillea* from which it can be distinguished microscopically by the finer texture, the presence of stone cells in the rays, and by the uniseriate rays which are low, usually 1 or 2 cells high and consisting entirely of upright cells.

(*v*) *Stenocarpus* (in part see p. 286)

A genus distributed through eastern Australia, New Guinea, and the Pacific Islands. Three species with the *Grevillea* type of structure were examined: *S. laurinus* Panch and Sebert, *S. reticulatus* C.T.W., *S. salignus* R.Br.; of these only *S. salignus* has any commercial value (Plate 2, Fig. 6; Plate 6, Fig. 2).

(i) *General Properties of the Timber.*—Red-brown, moderately heavy (about 50 lb./cu.ft.), grain wavy and interlocked. Match-size splinters burn to a full buff ash.

(ii) *Structure.—Growth rings* not defined. *Pores* variable in size in different species, in *S. laurinus* visible only with a lens, in the other two species with the naked eye, usually few (*S. reticulatus*) to moderately numerous, solitary or in short tangential multiples; white deposits sometimes observed in *S. reticulatus* and *S. salignus*. *Parenchyma* on the abaxial side of the pores, rarely surrounding them in *S. salignus*, predominantly aliform in *S. reticulatus* and in bands 3-7 cells wide in the other species. *Rays* of two distinct sizes, the larger commonly over 5 but usually under 10 mm. high, the smaller uniseriate, up to 15 cells high, of square and procumbent cells; stone cells commonly present in the large rays, sometimes containing crystals. *Fibre* wall thickness greater than the diameter

of the lumen; pits rather conspicuous, bordered. *Tracheids* present, probably transitional stages between true tracheids and fibres, around the vessels and sometimes at the limits of the growth rings; with larger lumina than the fibres and more numerous pits.

The wood of *S. laurinus* and *S. salignus* resembles *Grevillea* in its gross structure, but the two genera can be distinguished microscopically by the presence of stone cells in *Stenocarpus,* by the fibre pitting, and by the tracheids that accompany the vessels and vessel groups.

(*w*) *Stenocarpus* (in part see p. 286)

Two species with the *Musgravea* type of structure are described here: *S. sinuatus* Endl. and *S. umbellatus* Schlechter (Plate 3, Figs. 1 and 2). The structure of these two species of *Stenocarpus* is almost identical with that of the species of *Musgravea* described above (p. 296). Vertical gum canals have not been observed in *Stenocarpus,* but as these are not a regular feature of *Musgravea* their absence cannot be taken as indicative of *Stenocarpus.*

(*x*) *Telopea*

This is a genus of three species, confined to eastern Australia and Tasmania. Only one species, *T. oreades* F.Muell., was available for examination (Plate 6, Fig. 3). It is a small tree 30-40 ft. high and 1½-2 ft. in diameter. It is often cultivated for its ornamental flowers.

(i) *General Properties of the Timber.*—Light pink-brown, moderately light (39-46 lb./cu.ft.), grain interlocked, texture moderately fine. Match-size splinters burn to a buff ash.

(ii) *Structure.*—In gross structure the wood of *Telopea* is not distinguishable from that of *Guevina* (see p. 292). Microscopically, however, it can be distinguished by the absence of spiral thickenings from the vessels and the presence of irregularly reticulate multiperforate perforation plates. If the origin of a specimen is known this too will serve to distinguish the genera, as *Guevina* occurs only in South America.

(*y*) *Xylomelum*

This is a small genus of Australian shrubs and small trees. Three species were available for examination: *X. occidentale* R.Br., *X. pyriforme* Knight, and *X. salicinum* A.Cunn. (Plate 1, Fig. 1).

(i) *General Properties of the Timber.*—Dark red-brown, moderately light (about 40 lb./cu.ft. air-dry), very brittle, coarse and uneven in texture, with a marked figure due to the enormous rays. Match-size splinters burn with difficulty to a charcoal or to a charcoal stump and thin white ash.

(ii) *Structure.—Growth rings* not defined. *Pores* indistinct to the naked eye but distinct with a lens, about 5-8/sq.mm.; solitary and in clusters, sometimes tangentially aligned; usually with abundant reddish deposits and with sporadic white deposits in *X. pyriforme. Parenchyma* very abundant, aliform, and confluent in broad bands which may be up to 20 cells wide in *X. occidentale,* usually

enclosing the pores (*X. occidentale*), but sometimes (especially in the other two species) only on the abaxial side of the pores and partially surrounding them. *Rays* of two distinct types, the larger enormous (in *X. occidentale*, probably the largest in the Proteaceae and sometimes forming 50 per cent. of the bulk of the wood); the smaller up to about 16 cells high, composed almost entirely of square or procumbent cells. *Fibre* wall thickness of the walls greater than the diameter of the lumina; pits bordered. *Tracheids*, which are probably transitional stages between true tracheids and fibres, present around the vessels.

V. Distinction between Proteaceae and Other Families with Large Rays

The greatest distinguishing features of the Proteaceae are the large rays and the tangential pattern formed on the cross section by the parenchyma and vessels. Where this pattern is well marked it is sufficiently characteristic to distinguish the Proteaceae from all other woods with large rays. Where it is not so marked confusion may arise. This is most likely to occur between some of the *Grevillea* type, in which the predominance of aliform parenchyma, or broad bands containing the vessels, disturbs the characteristic "festoon" or "necklace" pattern. A macroscopic examination might not bring out the points of difference between *Cardwellia* and *Embothrium* and some of the Rhizophoraceae (for example *Carallia* and *Pellocalyx*). The scalariform perforation plates and pitting of the Rhizophoraceae will, however, serve to separate these two families without difficulty.

Hoheria (Malvaceae) is easily confused macroscopically with some of the Proteaceae of the *Banksia* type, although even with a lens it is possible to see that in *Hoheria* the parenchyma occurs on both sides of the curved pore bands and not, as in *Banksia* etc., on the abaxial side. Reference to a radial section does not give the clue to the identity as spiral thickenings occur on the vessel walls in both *Hoheria* and many of the Proteaceae of the *Banksia* type, but the storeyed parenchyma which can be seen on the tangential section of *Hoheria*, and the absence of uniseriate rays, should serve to distinguish them.

The *Musgravea* type of structure might be confused with some of the woods with reticulate parenchyma and large rays, but the ray width of the Proteaceae is usually sufficient to distinguish these woods. Where confusion might arise, as with a few of the Anonaceae, the characteristic proteaceous curving of the parenchyma from ray to ray should serve as a distinction, even though the characteristic "pendant" vessel pattern is absent.

In the few members of the family in which only small rays are present, there may be difficulty in distinguishing the woods, as the range of possible families is extended. Only by use of all available features and microscopic study can such woods be identified.

VI. Key to Proteaceae

A key for the identification of the Proteaceae based on the card sorting method has been prepared, and though designed primarily for use with a hand lens (x10) it is supplemented by a few features which can only be observed by

the use of a prepared slide and a microscope. It has not been found practicable to separate species, and each card represents a genus; where some species can be distinguished by the presence of any special feature a note has been added on the back of the card.

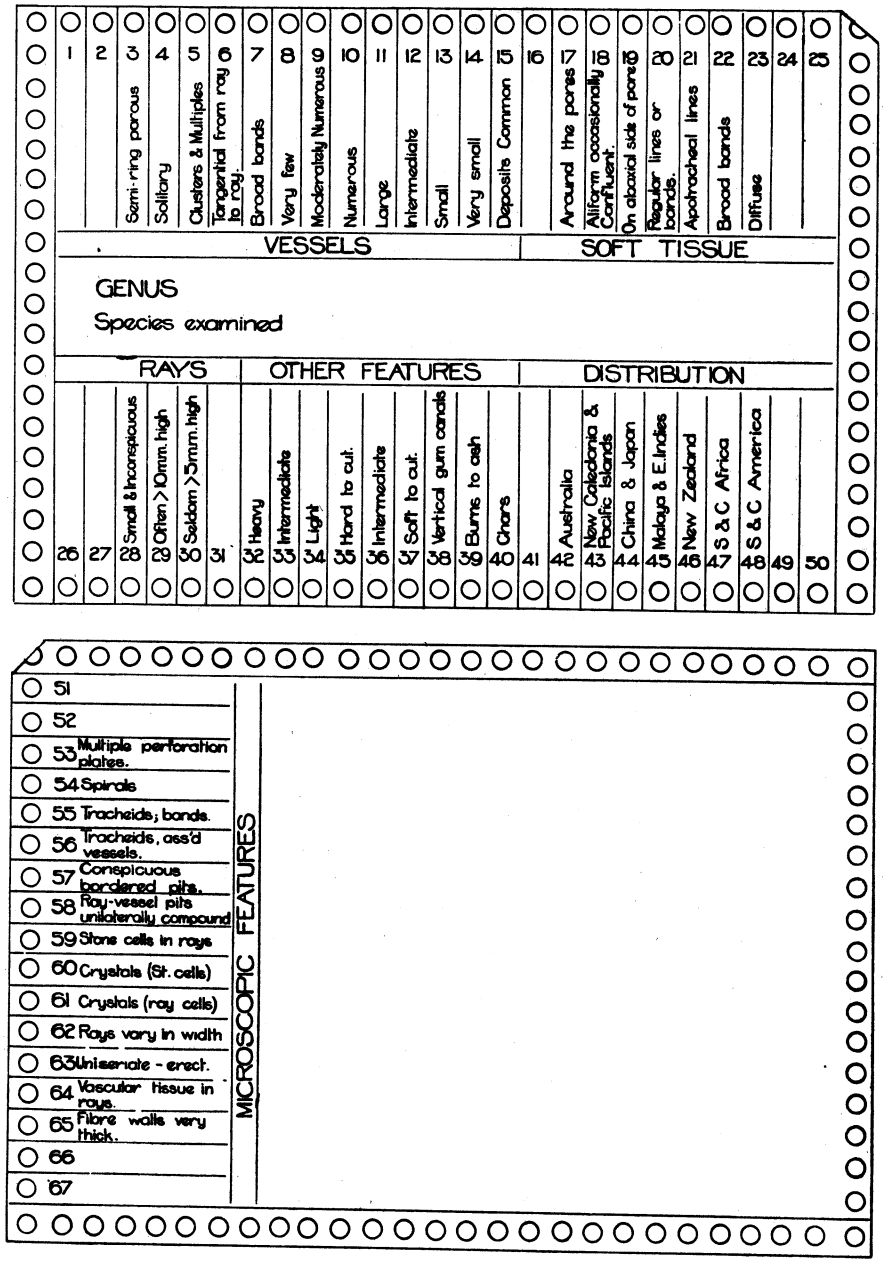

Fig. 2.—Front (upper) and back (lower) of card suggested for card sorting key to the Proteaceae.

As the principle lying behind the use of this type of key has already been explained (Clarke 1938) it will not be described in detail here, but a specimen card is shown in Figure 2. The details of the genera of the Proteaceae for use with such a card-sorting key can be extracted from the foregoing descriptions of the genera, or may be obtained from the author.

VII. Acknowledgments

The author specially wishes to express her thanks to Miss A. M. Eckersley by whom much of the preliminary data were collected, and whose descriptions have often been used as a basis for the text; to Dr. L. Chalk and the late Professor S. J. Record for material of the South African and South American genera; to Dr. H. E. Dadswell for advice in the preparation of the manuscript; and to Mr. H. D. Ingle for assistance in taking many of the photographs.

The work described in this paper was carried out as part of the research programme of the Division of Forest Products, C.S.I.R.

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Explanation of Plates 1-7

Plate 1

Fig. 1.—*Xylomelum pyriforme* Knight. Transverse surface of wood. x 10.
Fig. 2.—*Xylomelum pyriforme* Knight. Transverse section. x 64.
Fig. 3.—*Roupala dielsii* Macbride. Transverse section. x 64.
Fig. 4.—*Telopea oreades* F.Muell. Transverse surface of wood. x 10.
Fig. 5.—*Knightia excelsa* R.Br. Transverse section. x 64.
Fig. 6.—*Banksia marginata* Cav. Transverse section. x 64.

PLATE 2

Fig. 1.—*Cardwellia sublimis* F.Muell. Transverse surface of wood. x 10.
Fig. 2.—*Faurea macnaughtoni* Phillips. Transverse section. x 75.
Fig. 3.—*Lomatia ilicifolia* R.Br. Radial longitudinal section. Multiple perforation plate. x 400.
Fig. 4.—*Banksia marginata* Cav. Radial longitudinal section. Spirally thickened vessel members. x 200.
Fig. 5.—*Banksia grandis* Willd. Tangential longitudinal section. Uniseriate rays of erect cells only. x 65.
Fig. 6.—*Stenocarpus salignus* R.Br. Transverse section. x 75.

PLATE 3

Fig. 1.—*Stenocarpus sinuatus* Endl. Transverse surface of wood. x 10.
Fig. 2.—*Stenocarpus sinuatus* Endl. Transverse section. x 75.
Fig. 3.—*Helicia ferruginea* F.Muell. Transverse section. x 75.
Fig. 4.—*Leucadendron argenteum* R.Br. Transverse section. x 75.
Fig. 5.—*Finschia* sp. Transverse surface of wood. x 10.
Fig. 6.—*Helicia* sp. Transverse surface of wood. x 10.

PLATE 4

Fig. 1.—*Knightia excelsa* R.Br. Transverse surface of wood. x 10.
Fig. 2.—*Orites excelsa* R.Br. Transverse surface of wood. x 10.
Fig. 3.—*Faurea saligna* Harv. Transverse surface of wood. x 10.
Fig. 4.—*Grevillea robusta* A.Cunn. Transverse surface of wood. x 10.
Fig. 5.—*Faurea speciosa* Welw. Transverse surface of wood. x 10.
Fig. 6.—*Faurea macnaughtoni* Phillips. Transverse surface of wood. x 10.

PLATE 5

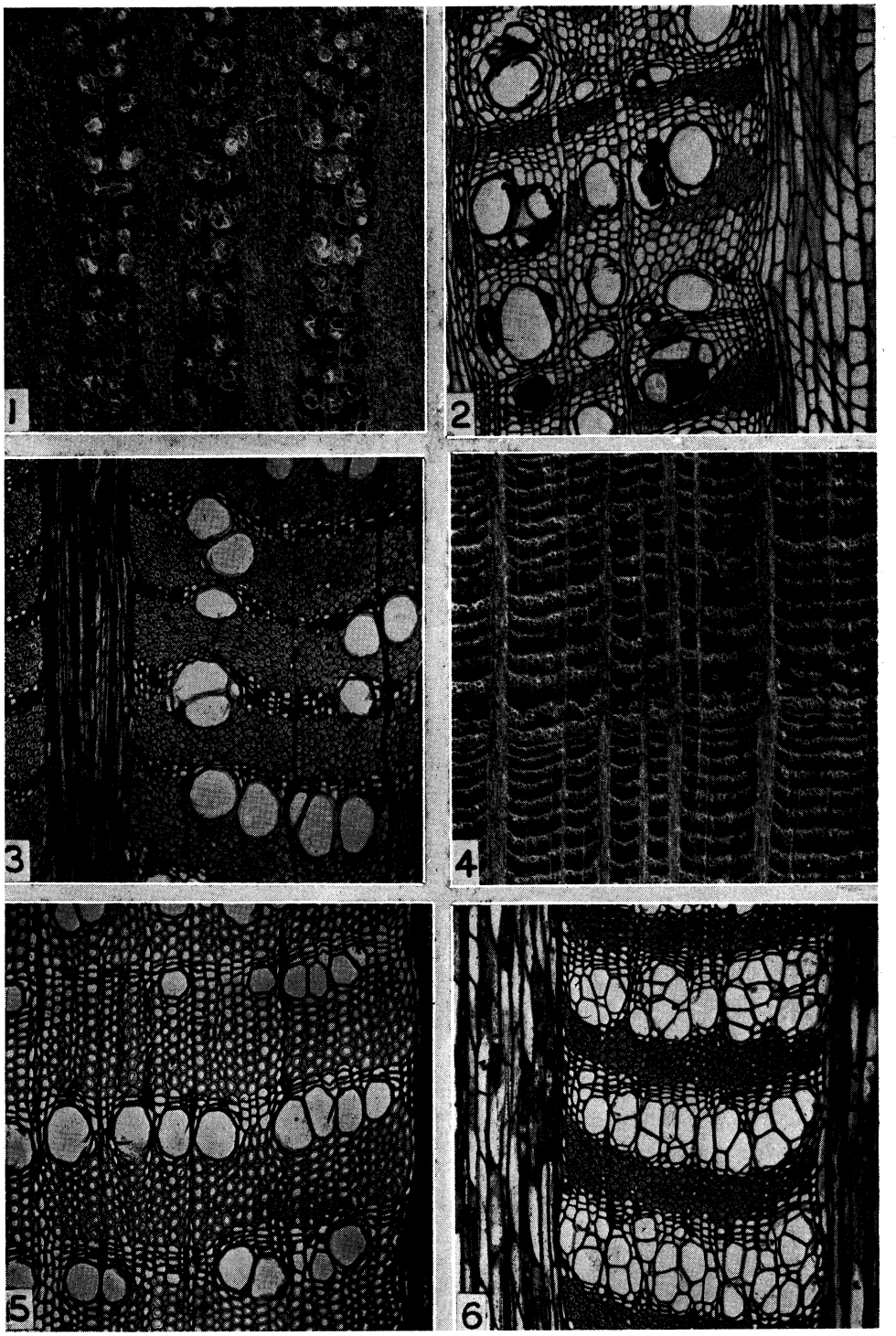
Fig. 1.—*Protea lepidocarpon* R.Br. Transverse section. x 64.
Fig. 2.—*Grevillea robusta* A.Cunn. Transverse section. x 64.
Fig. 3.—*Embothrium wickhami* Hill and F.Muell. Transverse section. x 75.
Fig. 4.—*Embothrium coccineum* Forst. Transverse section. x 75.
Fig. 5.—*Persoonia longifolia* R.Br. Transverse section. x 75.
Fig. 6.—*Hakea leucoptera* R.Br. Transverse section. x 75.

PLATE 6

Fig. 1.—*Persoonia lanceolata* Andr. Tangential longitudinal section. Stone cells in rays. x 75.
Fig. 2.—*Stenocarpus salignus* R.Br. Tangential longitudinal section. Stone cells in rays. x 400.
Fig. 3.—*Telopea oreades* F.Muell. Irregularly reticulate perforation plate. x 400.
Fig. 4.—*Musgravea stenostachya* F.Muell. Transverse surface of wood. x 10.
Fig. 5.—*Macadamia ternifolia* F.Muell. Transverse section showing band of tracheids. x 225.
Fig. 6.—*Macadamia ternifolia* F.Muell. Transverse section. x 75.

PLATE 7

Fig. 1.—*Banksia grandis* Willd. Tangential longitudinal section. Vascular tissue in large ray. x 65.
Fig. 2.—*Banksia grandis* Willd. Radial longitudinal section of large ray, with vascular tissue. x 120.
Fig. 3.—*Banksia ilicifolia* R.Br. Tangential longitudinal section. Vascular tissue in large ray. x 48.
Fig. 4.—*Banksia grandis* Willd. Elements of vascular tissue from ray, isolated by maceration. x 140.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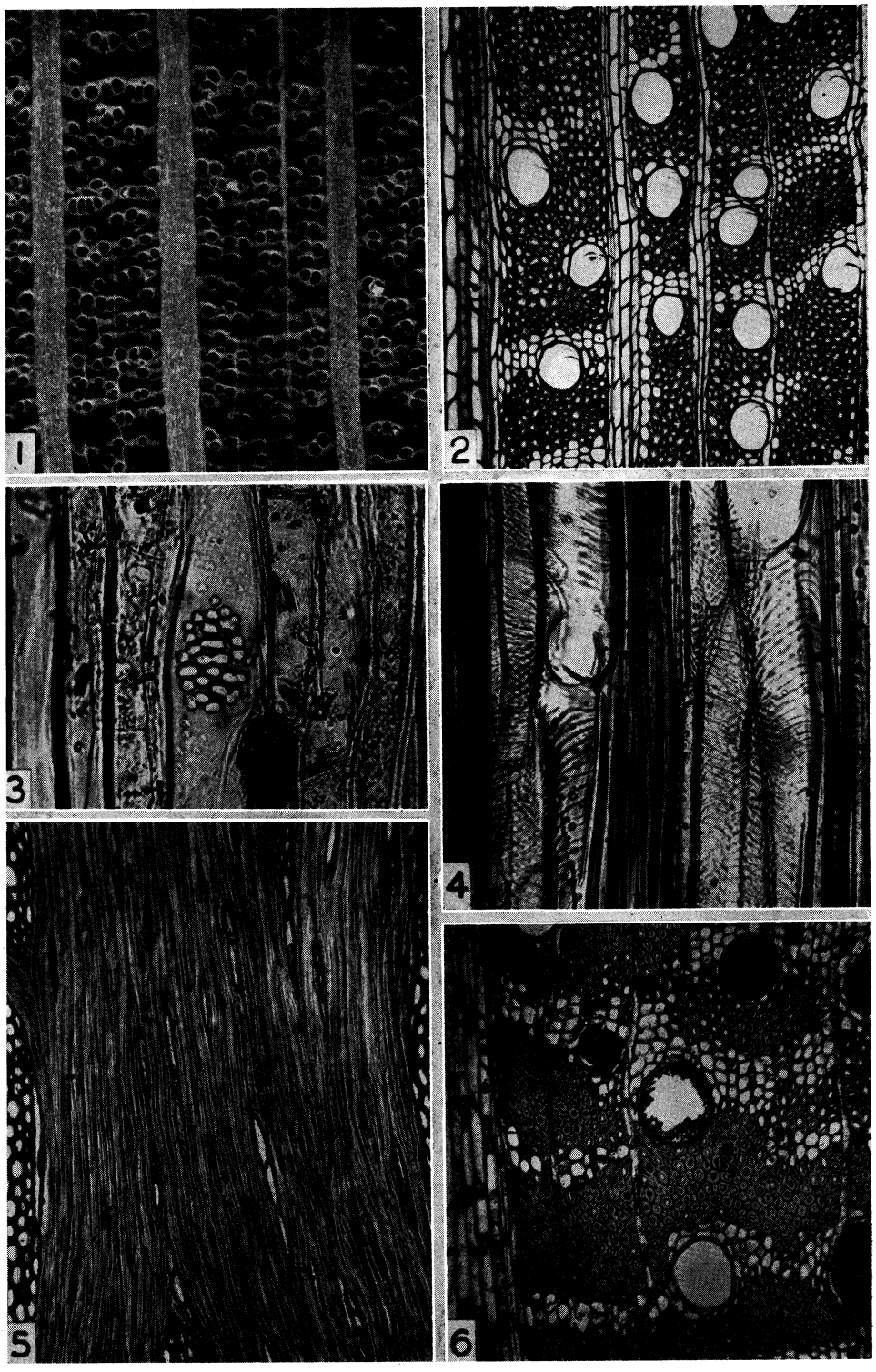
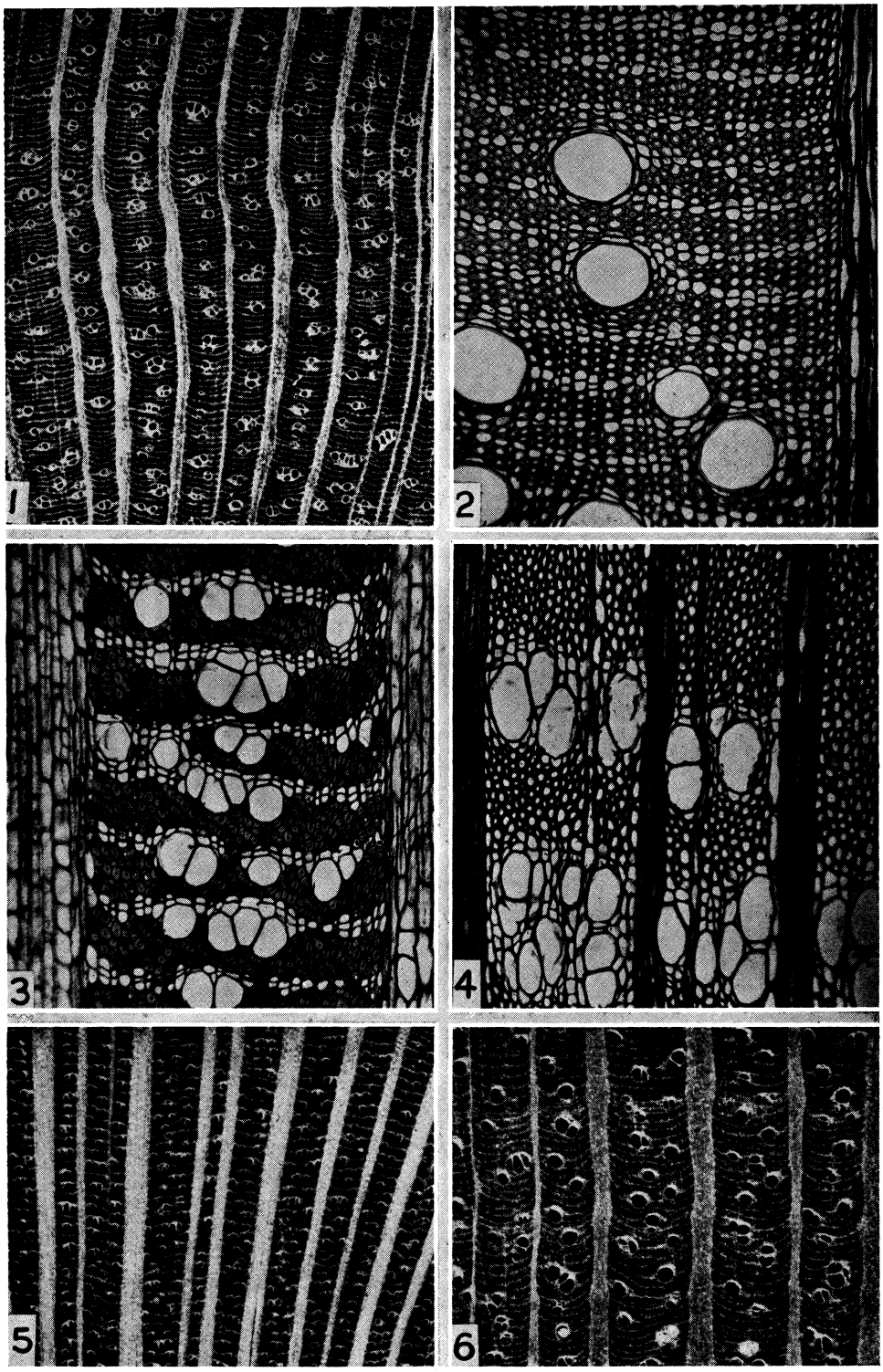


CHATTAWAY.—THE WOOD ANATOMY OF THE PROTEACEAE



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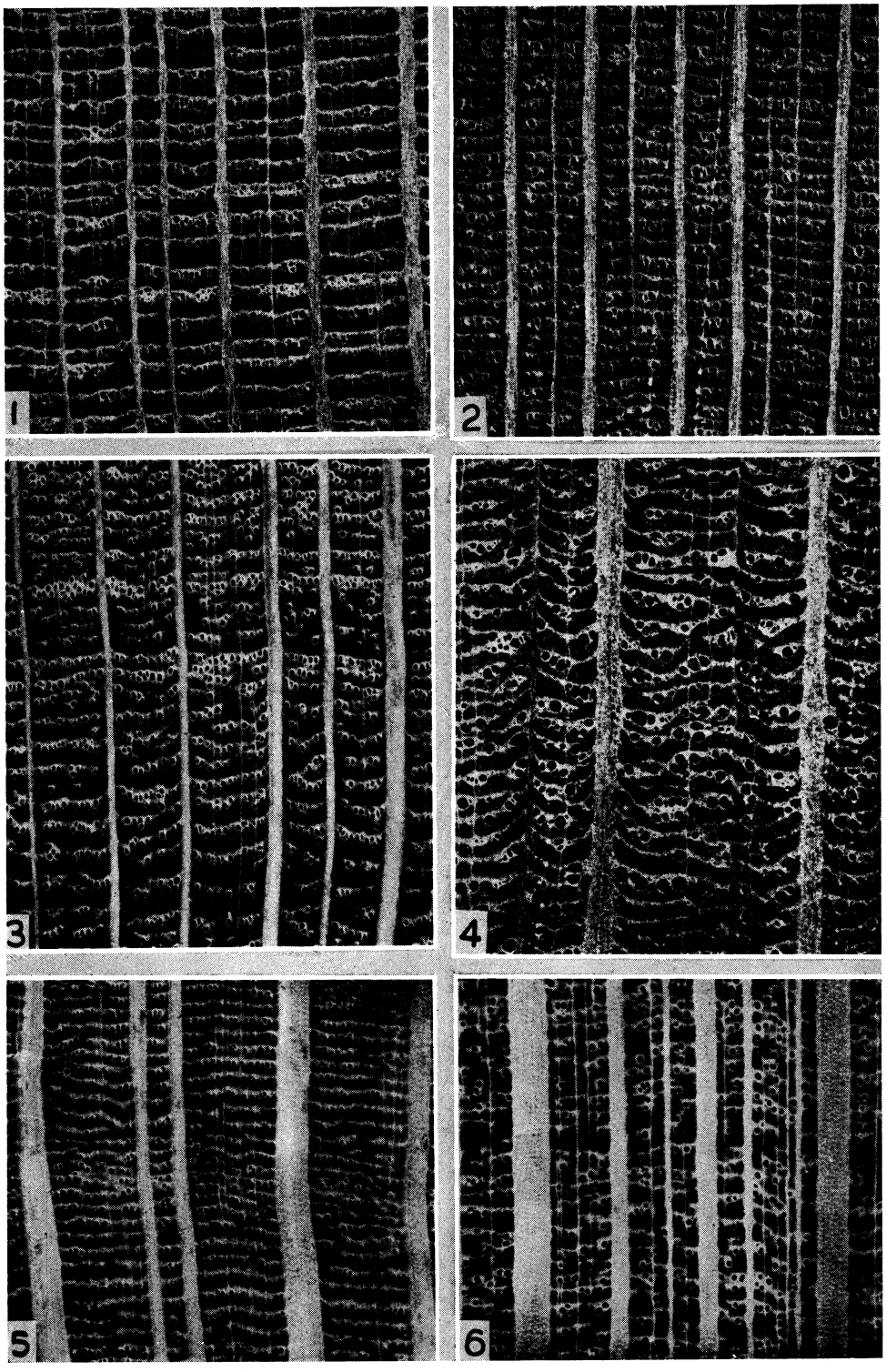

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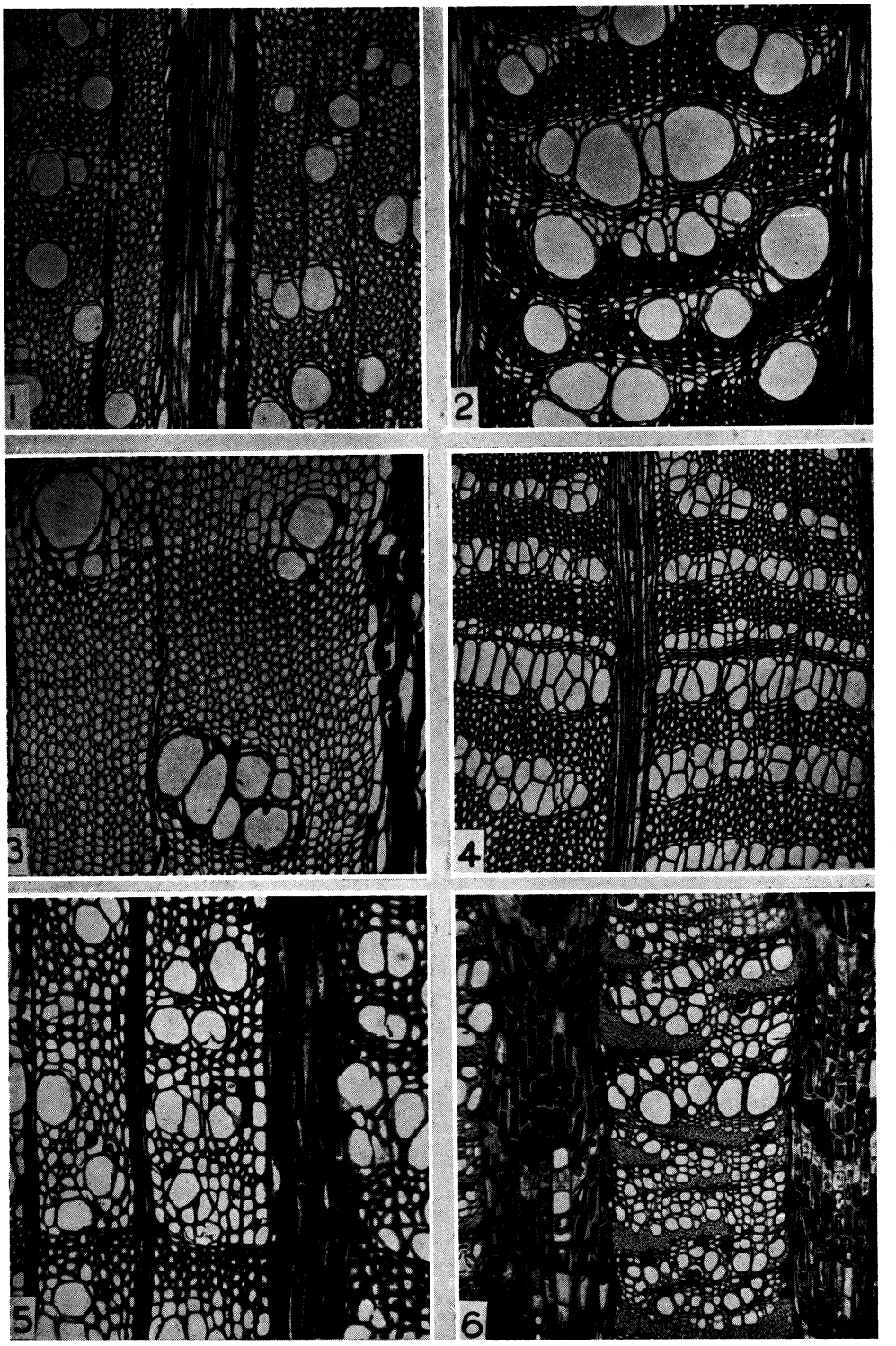
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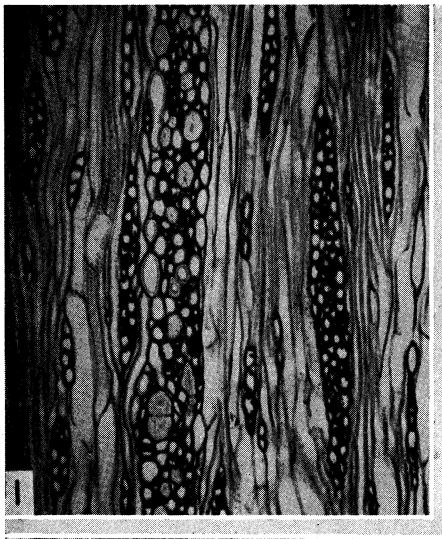
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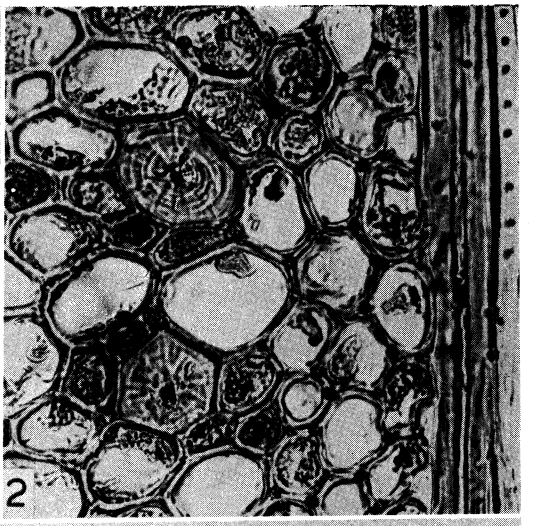
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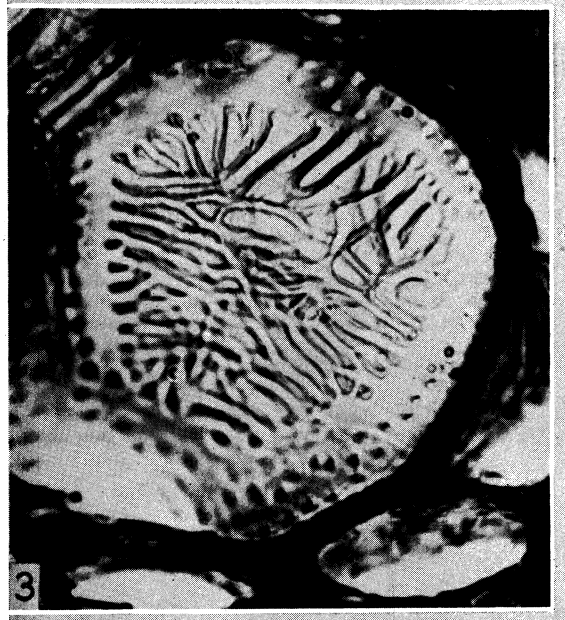
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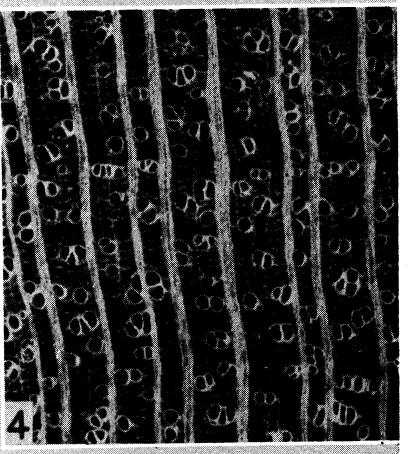
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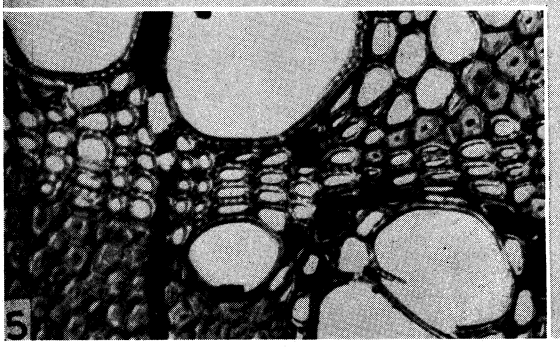
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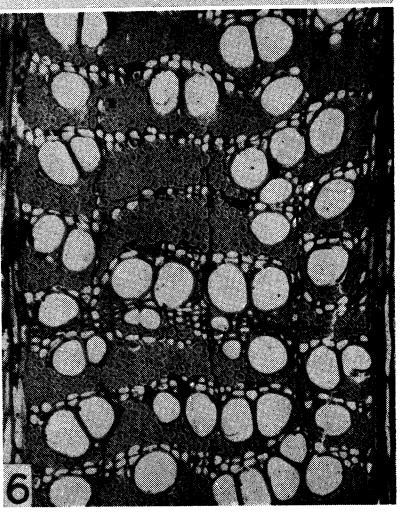
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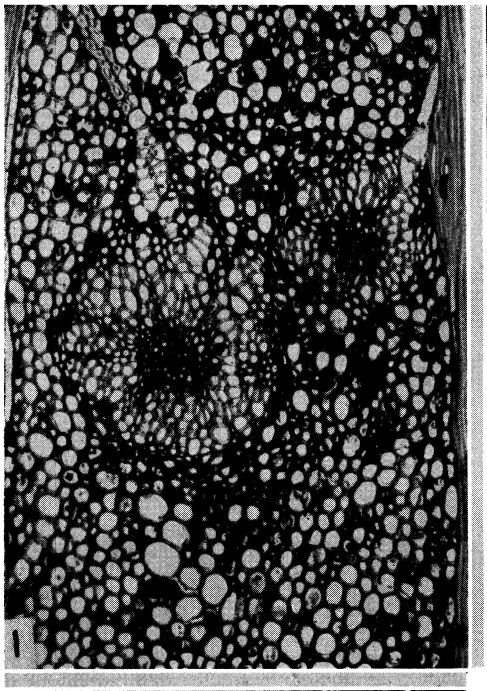
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