FOSSIL OAK WOOD FROM THE BRITISH EOCENE

by DONALD W. BRETT

ABSTRACT. The circumscription of the organ-genus *Quercinium* Unger is discussed in relation to the wood structure of the Recent oaks and emended so as to include fossil wood conforming to the wood of the living species of *Quercus* L. and *Lithocarpus* Blume, since the wood of these genera is anatomically indistinguishable. *Quercinium quercoides* (Goepp.) Edwards is designated type species, and the name *Quercinium* Unger recommended as a *nomen conservandum* against the earlier valid name *Kloedenia* Goeppert. Two fossil woods, each with a type of structure found today in species of tropical evergreen oaks, are described and figured: *Quercinium porosum* sp. nov. from the Woolwich Beds (Landenian), Herne Bay, Kent; *Quercinium pasanioides* sp. nov. from the London Clay (Ypresian), near Ipswich, Suffolk.

FOSSIL wood resembling that of recent *Quercus spp.* has generally been referred to the genus *Quercinium* Unger (1842). Unger based this genus upon three very briefly described specimens of fossil wood which agreed in gross structure with the wood of oaks of the ring porous type with rays of two distinct sizes: 'Ligni strata concentrica distincta. Radii medullares biformes ("heteromorphi" in Unger 1850) . . . Vasa porosa . . . in uno v. in duobus stratis coacervata, in reliquis multo minora, fasciculatim aggregata.' The diagnosis was emended slightly by Mercklin (1855) who added a description of the wood parenchyma.

Felix was the first to deviate much from the original circumscription of the genus when he described under *Quercinium* a species, *Q. knowltoni*, in which the pores decrease in size gradually through the growth ring (Felix 1896). In this respect it resembled a wood previously described by Conwentz as *Quercites transiens*. Subsequent authors have used *Quercinium* as 'merely a form-genus for fossil wood closely resembling the recent *Quercus*' (Edwards 1931, p. 66), with neither type species nor generic diagnosis. Unfortunately a situation similar to this exists in respect of many genera created for fossil wood of dicotyledons. Furthermore, *Quercinium* is to be regarded as an organ-genus since its affinity with the Recent oaks is undoubted.

It would in fact be impracticable to restrict the genus to Unger's diagnosis since the growth ring in the wood of *Quercus* and allied genera is very variable, and all grades occur between ring porous and diffuse porous types, with and without a seasonal decrease in pore size. It is equally certain that this organ-genus cannot be regarded as comprising fossil wood of *Quercus* alone.

The major trends of specialization in the structure of the wood of the oaks appear to be closely associated with the differentiation of the growth ring with distinct early and late wood, and parallel grades are to be found in each of the large genera *Castanopsis* Spach., *Lithocarpus* Blume, and *Quercus* L.

The boundary of the growth ring is often difficult to trace in species from the humid tropical regions but in many evergreen oaks from temperate regions the ring is clearly marked by a more or less gradual diminution in diameter of the vessels in the late wood. In the truly ring porous types the radial pattern, which is a characteristic feature of transverse sections of wood throughout the oak–chestnut alliance, is often altogether lost

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from the early wood and the large pores of this zone form a tangentially continuous ring. In many species of *Quercus*, where this is the mature arrangement, the first few rings of secondary wood possess the radial, diffuse porous pattern.

Examination of a large number of ring porous woods led Metcalfe and Chalk (1950) to conclude that 'it would appear unwise . . . to rule out the possibility that ring porousness may represent an ecological specialization, which occurs in wood at very different levels of general specialization and in widely separated taxonomic groups' (op. cit., p. xlviii). The oaks furnish an instructive illustration of a trend to ring porousness within several closely related species groups, which has apparently gone hand in hand with their general adaptive radiation from tropical centres.

The wood rays are basically of two distinct sizes in the Fagaceae but, as in *Castanea* and *Nothofagus*, specialization has led to the elimination of the very broad rays from *Castanopsis*, and a few species of *Lithocarpus*, e.g. *L. fenestratus* (Roxb.) Rehd., *L. pachyphyllus* (Kurz) Rehd. (Gamble 1881), *L. lappaceus* (Roxb.) Rehd. (Gamble 1881; Tippo 1938), and *L. sieboldii* (Makino) Nakai (Metcalfe and Chalk 1950). Broad rays may also be absent from the young stems and branches of several *Quercus spp.*

Wood parenchyma, typically banded in the oaks, may vary between individual species from regular and continuous bands of one to four cells in radial extent to discontinuous and wavy tangential strings of cells, in some forming a sort of reticulate arrangement and in yet others the parenchyma is rare and diffuse. In some *Quercus spp.* at least there is considerable variation between different samples and this appears often to be related to the width of the growth rings.

CIRCUMSCRIPTION OF THE ORGAN-GENUS

Fossil wood ascribable to the recent *Castanea* and *Castanopsis* will be excluded from the organ-genus *Quercinium* if this latter be restricted to wood with rays of two distinct sizes.

The two genera *Lithocarpus* and *Quercus* are not distinguishable on the basis of wood anatomy alone. Types of structure found in one genus grade insensibly into those of the other at all levels of specialization of the growth ring. The evergreens in the genus *Quercus* have wood indistinguishable from that of many species of *Lithocarpus*, and it would hardly be possible to distinguish the ring porous wood of *L. uraianus* (Hay.) Hay., for example, from many other *Q. alba*-type woods.

I propose to emend the organ-genus *Quercinium* to include fossil wood conforming to that of the Recent genera *Quercus* L. and *Lithocarpus* Blume. The two new species described in this paper have a structure found today in species of evergreen oaks from the tropics, and are thus included in the organ-genus as now understood.

Family FAGACEAE
Organ-genus QUERCINIUM Unger

Emended diagnosis. Fossil secondary wood, or stems or roots with some secondary wood. Rays of two distinct sizes; uniseriate rays numerous, multiseriate rays often very broad and high and appearing compound or aggregate. Wood parenchyma commonly in tangential bands or strings, but may be diffuse. Vessels mostly large and solitary except in the late wood of ring porous species, and showing some radial pattern in transverse sections; often accompanied by tracheids (vasicentric); vessel members with simple perforations, exceptionally scalariform when very narrow; intervascular pitting alternate to sub-opposite. Ray to vessel pits large, gash-like, usually vertically or obliquely elongated. Remainder of wood tissue of fibre-tracheids and/or fibres.

Type species. The selection of a type species for *Quercinium* is desirable since one has never been designated. The three species originally included in the genus by Unger (1842) were given such inadequate description that it would be impossible to recognize any of them again, and the specimens do not appear to have been preserved. At that time, however, Unger observed that *Kloedenia quercoides* Goeppert (1839) could probably be included in *Quercinium*, and in 1845 he cited this earlier name as synonymous with *Quercinium sabulosum*, one of his three original species, ignoring the priority of Goeppert's name. Thus, on Unger's own admission, *Q. sabulosum* may be accepted as a synonym of *K. quercoides*. Meanwhile Goeppert had described another specimen apparently identical with his *Kloedenia* material, under a new name *Quercites primaevus* Goeppert (1845), abandoning completely his previous name. Felix (1883) re-examined some of Goeppert's original *Kloedenia* material, provided a full description, and used a new combination, *Quercinium primaevum*, which is invalid, since the earlier name for this material, *K. quercoides* Goepp., was validly published. The valid name for this species remains *Kloedenia quercoides* Goepp. If this be accepted into the organ-genus diagnosed above, the name *Quercinium* should, according to the International Code, be abandoned in favour of *Kloedenia*. This latter name has been used only once and has

EXPLANATION OF PLATE 21

Figs. 1, 2. *Q. porosum.* 1, Transverse section of secondary wood showing the close arrangement of the large vessels, the broad rays, and absence of growth rings. ×16. The two light areas are caused by a dark gum-like infiltration of the tissue. 2, As fig. 1, but showing origin of a broad ray by aggregation of fine rays and elimination of the intervening tracheary tissue. ×37.

Figs. 3, 4. *Q. pasanioides.* 3, Transverse section for comparison with fig. 1. The vessels are arranged in radial strings, and the banded parenchyma shows as light, wavy lines. Tangential compression during fossilization has reduced the tangential diameter of most of the vessels here. ×16. 4, Transverse section of a radial cluster of vessels accompanied by vasicentric tracheids. The tangential bands of parenchyma are visibly differentiated from the fibres of the ground tissue, as are the numerous fine rays. ×37.

EXPLANATION OF PLATE 22

Figs. 5, 6, 11. *Q. porosum.* 5, Radial section. Part of a broad ray is shown on the left, and to the right of centre some intervascular pitting of a vessel. Tyloses fill the vessels and wood parenchyma is abundantly represented. ×50. 6, Tangential section, showing part of a broad vertically compound ray of some twelve cells in width, and uniseriate rays. ×50. 11, Radial section, part of a vessel with tyloses and ray cells showing the simple, elongated pits to the vessel. ×135.

Figs. 7–10. *Q. pasanioides.* 7, Tangential section, showing uniseriate rays and a broad ray with fibrous inclusions. ×50. 8, Radial section to show appearance of the regularly banded wood parenchyma; some chambered crystalliferous cells are visible in the strand to the left of centre. ×50. 9, Radial section, to show ray to vessel pitting of elongated simple pits; small, bordered pits of the fibre-tracheids are also shown. ×135. 10, Radial section, showing the richly pitted walls of the ray cells ×135.

since been generally abandoned by authors. I would therefore recommend that *Quercinium* Unger be added to the list of *nomina conservanda.*

Edwards (1931) drew attention to the confusion in the nomenclature of this species and used the combination *Quercinium quercoides* (Goepp.) Edwards. Under this name I designate this species as the type species of the organ-genus *Quercinium* Unger.

Synonymy of type species. Kloedenia quercoides Goeppert 1839. *Quercinium sabulosum* Unger 1845. *Quercites primaevus* Goeppert 1845. *Quercinium primaevum* (Goepp.) Felix 1883.

SYSTEMATIC DESCRIPTIONS

Quercinium porosum sp. nov.

Plate 21, figs. 1, 2; Plate 22, figs. 5, 6, 11

Holotype. No. V 26291 and slide preparations in Dept. of Palaeontology, British Museum (Nat. Hist.), London. Silicified wood from the sands of the Woolwich and Reading Series, Herne Bay, Kent. Eocene (Landenian).

In transverse sections the vessels are abundant, almost always solitary, and show no special pattern, 6–10 per sq. mm., tangential diameter 80μ–270μ (average 237μ); members short, around 0·6–0·8 mm., perforations simple, transverse or slightly oblique. Intervascular pitting mostly alternate, of circular bordered pit pairs. Tyloses fill all the vessels. Imperforate tracheary cells with walls of moderate thickness, numerous large, circular bordered pits with crossed, elliptical inner apertures. Parenchyma abundant, diffuse; half-bordered pit pairs from the tracheary cells distinguish the parenchyma in transverse sections. Rays of two distinct sizes; uniseriate rays abundant, deflected by the vessels, eight to twelve per mm., two to thirty cells high in tangential section. In transverse section some very broad rays appear to be formed by aggregation of many uniseriate rays. Broad rays occur every 2–3 mm. and are up to twenty cells in width, and may be over 5 mm. high. Pits from the vessels to the ray cells are large, gash-like, and mostly elongated obliquely to the vertical.

Viewed in radial section the ray cells are mostly slightly elongated radially but more or less square to upright at the margins, they are abundantly pitted. Growth rings are not discernible. There are slight suggestions of periodicity in the ground tissue, often accompanied by occasional very small pores, but there is no obvious overall difference in pore size or distribution here.

The combination of the following characters distinguishes this species from all those previously described: the almost complete absence of periodicity in growth, and the crowded, large pores which show little or none of the radial pattern typical of the oaks in general. These characters were found to be closely matched in a sample of the wood of the living species *Quercus* (*Cyclobalanopsis*) *lamellosa* Sm., although the sample also showed areas with fewer pores in radial/oblique arrangement.

Quercinium pasanioides sp. nov.

Plate 21, figs. 3, 4; Plate 22, figs. 7–10

Holotype. No. V 25808 and slide preparations in Dept. of Palaeontology, British Museum (Nat. Hist.), London. Calcified wood from the London Clay 5 feet below the surface in the valley of the river Finn between Tuddenham and Rushmere, near Ipswich, Suffolk. This is from the lowest portion of the formation. In this region the London Clay has been found to be at the most about 100 feet thick (Boswell 1927). Eocene (Ypresian). Presented to the British Museum by Mr. H. E. P. Spencer in 1938.

In tranverse section the vessels are mostly solitary but occasionally in radial or oblique pairs, about nine per sq. mm. and disposed in a radial flame-like pattern; tangential diameter from 60 μ for the rare small vessels to 200 μ, average about 130 μ (estimated from measurements of apparently undistorted pores in the transverse sections). Average member length around 0·460 mm., perforations simple, horizontal or slightly oblique. Pitting to tracheids is alternate, circular bordered pits with elliptical apertures. Tyloses fill all the vessels. Imperforate tracheary cells are of two kinds: vasicentric tracheids with wide lumen and bordered pitting on all walls in single or alternating longitudinal rows, half-bordered pitting to the parenchyma; fibre-tracheids of smaller diameter and with narrow lumen, bordered pitting rather small and sparse. Parenchyma mostly in regular bands one to four cells in width, about three to four bands per mm., but these are not always tangentially continuous; vertically the strands may consist of up to twelve cells, these cells being three to five times the height of the ray parenchyma. The strands commonly include one or several chambered cells, each containing usually four crystals. Rays of two distinct sizes: uniseriate rays numerous, up to 15 per mm., multiseriate rays mostly not less than 1 mm. apart. The cells are elongated radially in both types of ray, except for the marginal rows in which they are square or even upright. The multiseriate rays may be as much as twenty cells broad, up to 1 cm. in height in tangential section and traversed by fibres, often contorted, thus appearing to be compounded of narrower units. Height of the uniseriate rays is commonly eight to twelve cells but varies from three or four to as many as twenty cells. All the ray cells are richly pitted; the ray to vessel pits are large, usually elliptical with the long axis vertical. Growth rings are barely distinguishable but may be traced in places by a slight difference in character of what is taken as late wood. In such zones, which do not always coincide on opposite sides of the broad rays, the parenchyma bands appear slightly closer and there are more of the smaller, rounder vessels.

In all its general features the fossil is remarkably like the wood of several evergreen oaks but differs from many of the Recent species and from the few similar species of *Quercinium*, chiefly in the characters of the indistinct growth ring and the more or less regular banded parenchyma. Thus it is set apart from the fossils *Quercinium anomalum* Platen, *Q. wardi* Platen (both Platen 1908), and *Q. ricardensis* (Webber) Boeshore and Jump (Webber, 1933), to which it otherwise shows most resemblance. Among the specimens of Recent wood compared with the fossil species, that of *Lithocarpus* (*Pasania*) *hystrix* (Korth) Rehd., in the Kew collection from Malaya, stands out as a very close match in all details: in more general terms this is a type of wood found in the oaks of the rain forests of south-east Asia.

DISCUSSION

The wood of many plants growing in tropical and subtropical regions often shows little or no evidence of periodicity in radial growth. The lack of sharp distinction between growth increments in wood is more particularly a feature of trees, mostly evergreens, growing in the rain forests where the environment is little affected by a seasonal régime, and periodicity in cambial activity is apparently more directly controlled by inherent factors (see Richards 1952, ch. 8).

The presence in the London Clay of a wood of this character, when considered in association with the taxonomic affinities of the fruits and seeds described by Reid and Chandler (1933), lends firm support to these authors' conclusions regarding the living conditions of the 'tropical' element in the flora of the London Clay. I believe there is sufficient evidence to regard the L.C. flora as consisting of more than a single vegetation type. There are several woods and small twigs from the Clay with structural and taxonomic affinities quite different from those of the wood (*Q. pasanioides*) described above; these include both dicotyledonous and coniferous types. It is difficult to escape the conclusion that they grew under quite different conditions. I have described one such wood previously (*Cercidiphyllum*) and at the same time stressed the presence in this flora of a temperate element, which is presumed to be part of an earlier flora in the region under consideration (Brett 1956; Reid and Chandler 1933, p. 60). As such, this element must be regarded as representative of one or more plant associations ecologically distinct from the rain forest and littoral vegetation types which are also represented in the London Clay flora. Disregarding for the present the possibility that the wood and small twigs have drifted in the sea from higher latitudes, the alternative explanation for their occurrence in the London Clay must be that they have been carried down river from some region inland where a more temperate climate prevailed and seasonal differences in rainfall and/or temperature were greater. Thus, together with those fruits and seeds whose taxonomic affinities are with Recent temperate genera, they may represent the vegetation of some cooler upland valleys.

The flora of the Woolwich and Reading Series immediately precedes that of the London Clay but is unfortunately still little known. Miss M. E. J. Chandler, who has recently been working on the Woolwich and Reading fruits and seeds, is of the opinion that conditions during this period were probably very little different from those of London Clay times, i.e. the lowlands had a tropical climate; several of the London Clay genera are in fact represented (Chandler, personal communication). The nature of the wood described above (*Q. porosum*) certainly suggests a tropical environment, and I have another wood from the same locality which also supports this view and is a member of the Anacardiaceae, a family well represented in the London Clay flora. As in the London Clay, however, there are other woods, fruits, &c., the conifers in particular, which suggest the temperate (? montane) element.

A species of *Quercinium* from beds of similar age to the Woolwich and Reading in the Paris Basin has been described by Fritel and Viguier (1911). From their description the wood appears to be of the red-oak type, at any rate distinctly ring porous, and therefore quite different from *Q. porosum*.

The identification of these two woods as belonging to the Fagaceae extends the earliest record of the occurrence of that family in British deposits back from the Brackelsham Beds (Cuisian/Lutetian) to the Ypresian and Landenian. On the continent of Europe and also in North America, oaks and other Fagaceae have been recorded from leaf remains from the early Cretaceous onwards. Some of the leaves from the Lower Eocene (Landenian) of Belgium and France have been referred to the genus *Pasaniopsis* on account of their resemblance to tropical oaks, while others are referred to *Quercus* and *Dryophyllum* (Saporta and Marion 1878; Depape 1925).

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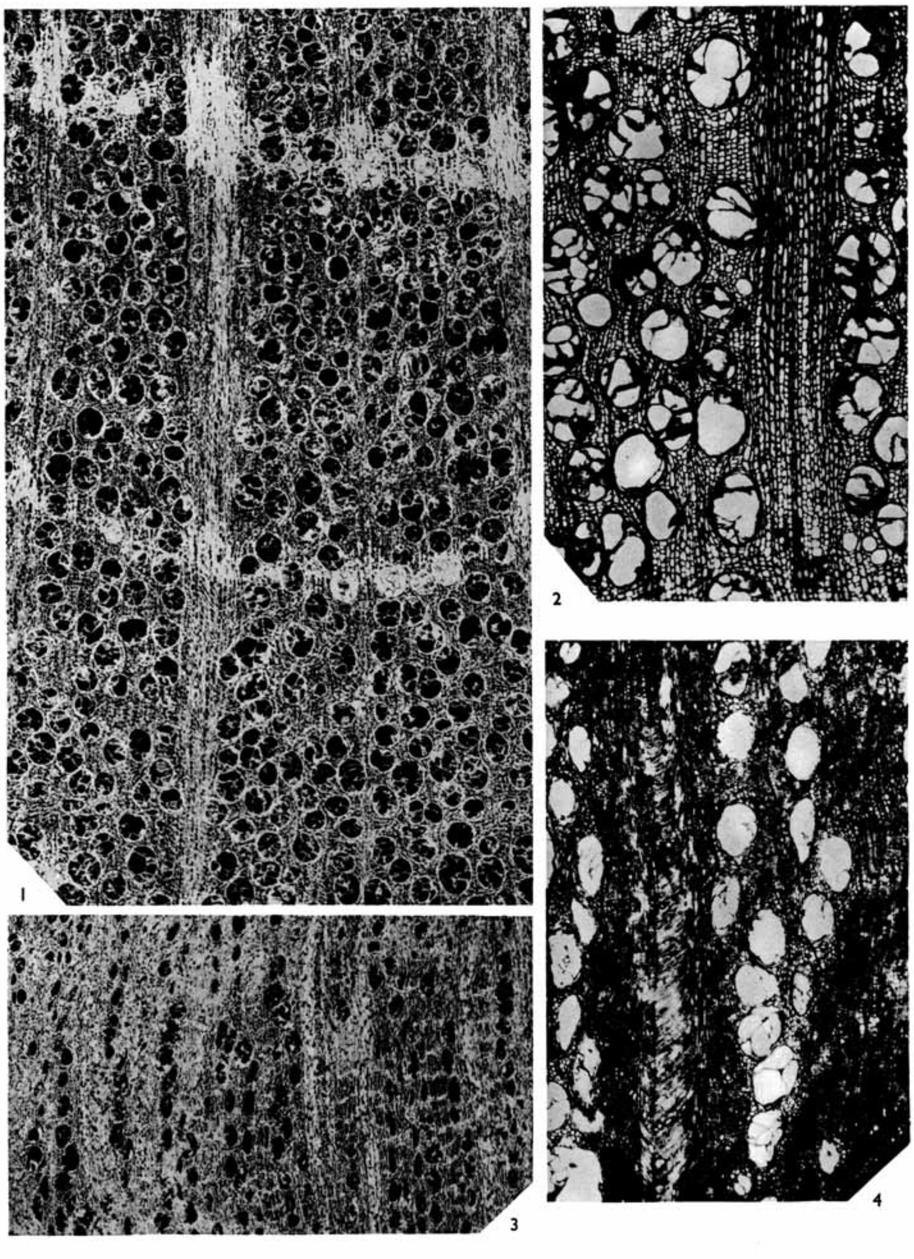
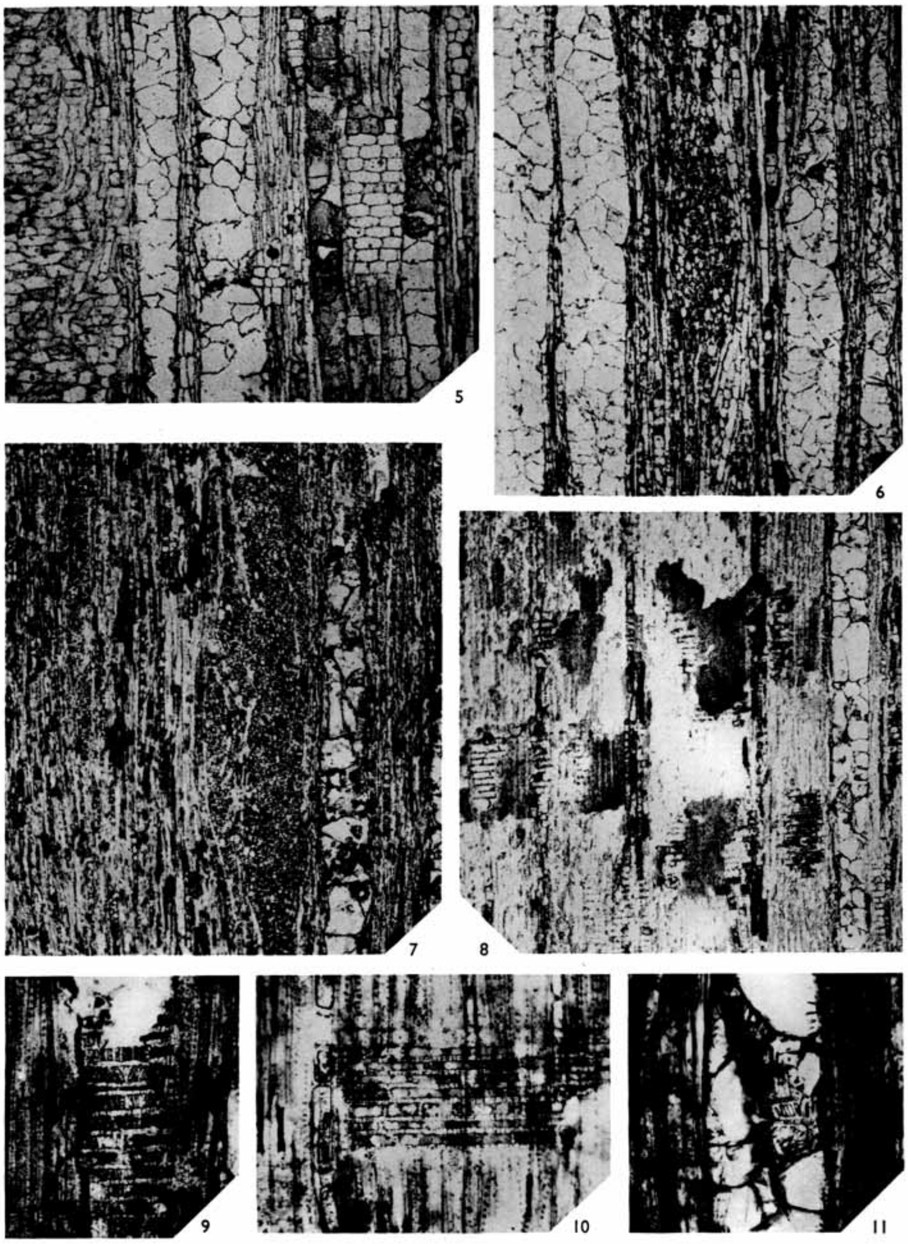


BRETT, *Quercinium*



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