

ON THE STELAR ANATOMY OF THE PTERIDOSPERMS WITH PARTICULAR REFERENCE TO THE SECONDARY WOOD¹

HENRY N. ANDREWS, JR.

Instructor in Botany, Henry Shaw School of Botany of Washington University

INTRODUCTION

Probably no group of plants, fossil or living, has ever created as much combined interest for the botanist, geologist and layman as the rather heterogeneous assemblage of vegetative and reproductive "species" included within the Palaeozoic Pteridospermae. However, from the time of the publication of Palaeobotany's foundational 'Histoire' of Brongniart (1828) three-quarters of a century was to elapse before the combined efforts of Oliver, Williamson, and Scott gave positive evidence of the seed-bearing habit of the pteridosperms, although the great French palaeobotanists had in the previous decades gathered together highly suggestive evidence. An even longer time was to elapse before new concepts of morphology, based largely on an increased knowledge of these and other fossil forms, began to cast doubt on the concept of a filicinean ancestry of the seed plants.

The relatively abundant primary wood of these plants early attracted considerable attention, and in many cases its taxonomic value seems to have been emphasized at the expense of the secondary wood. No careful survey of the secondary wood has ever been undertaken, an omission which is perhaps partly explicable as a reactionary feeling towards the questionable taxonomic value of the secondary wood in certain other groups.

¹An investigation carried out at Cambridge University, England, and in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

The description of many fossil coniferous and angiospermous woods whose affinities are doubtful has tended to discredit the taxonomic value of the secondary wood in general. Only within recent years has a thoroughly organized study of living angiosperm woods been commenced, and already it is proving of great significance.

It is the purpose of this paper to present the results of a study of the secondary wood of many of the plants included within the Pteridospermae and a comparative analysis of the nature and taxonomic significance of the primary and secondary xylem. It is not intended to present an exhaustive treatise on the stelar anatomy of these plants, much of which would only be repetition, but rather to bring to light those aspects of their structure which have been neglected for one reason or another.

Although Harris wrote in 1932 that, "It should be pointed out, however, that we do not know what constitutes a pteridosperm or what are the morphological limits of this class," it will be shown in the following pages that when the supposed seed plants of the Upper Palaeozoic, especially the secondary wood, are studied with reference to their stelar anatomy, three main types may be distinguished. One of them is exemplified by the very simple, mostly protostelic, Upper Devonian and Lower Carboniferous forms (Type I, p. 71); one includes plants of cordaitan-coniferous affinities (Type IV, p. 82); and the third is characteristic of the plants for which the class Pteridospermae was originally established (Types II, p. 72, and III, p. 77).

At the outset it should be stated that the view that the pteridosperms represent an intermediate group between the ferns and the cycads is no longer tenable. Rather we must look to a common psilophytalean-like ancestor with terminally borne sporangia, a solid protostele and primitive secondary wood for the origin of the ferns and pteridosperms (the secondary wood being usually lacking in the former). In support of this view the following points must be kept in mind:

(1) The evidence supplied by fructifications is overwhelmingly in support of the common origin of the ferns and pteridosperms from plants with terminally borne sporangia. This position has been retained by the latter, whereas in the ferns the sporangia have become dorsally located on the leaf-like structures termed sporophylls. There can no longer be any doubt that sporangia had their origin at or near the tips of branches or telomes¹ as evidenced by such plants as *Rhynia*, *Horneophyton* (Barghoorn & Darrah, '38), *Asteroxylon*, *Hedeia*, *Sporogenites*, *Psilophyton*, and *Taeniocrada*.²

(2) There is no evidence that the position of sporangia superficially on the dorsal surface of leaves (as in the majority of living ferns) is anything other than derived from a terminal position.

(3) It is only in Upper Carboniferous rocks that fructifications closely comparable with, and which may readily have led to, modern ferns become abundant. Among the better-known forms and their probable relationships are: *Oligocarpia* (Gleicheniaceae), *Seftenbergia* (Schizeaceae), *Ptychocarpus*, *Asterotheca*, and *Scolecopteris* (Marattiales).³

(4) Below the Upper Carboniferous these fern-like fructifications are much less abundant, but, beginning in the Lower Carboniferous rocks and extending up through Jurassic times, there runs quite a different line of microsporangiate fructifications. The fundamental similarity of their organization is such as to indicate with little doubt a great and continuous line of development. Some of the better-known members of this group are: *Telangium*, *Crossotheca*, *Aulacotheca*, *Whittleseyia*, *Potoniea*, *Goldenbergia*, *Dolerotheca*, (Kidston, '23-'25, Halle, '33); *Pteruchus* and *Caytonanthus* (Thomas, '25, '33). The members of this line retained their sporangia in a

¹ With the exception of the Lycopod line represented by such members as *Baragwanathia* and *Protolapidodendron*. In the former the sporangia were borne on the stem close to the leaf axil whereas in the latter they were borne in much the same manner as in *Lepidodendron*.

² A few of the more pertinent publications relating to these genera are: Kräusel ('36), Kidston & Lang ('20-'21), Halle ('36), Dorf ('33), Bertrand ('13).

³ See Kidston, '23-'25; Radforth, '38.

terminal position for the most part, although modified by fusion and aggregation of various types. The plants included under (1) above are undoubtedly representative of the complex from which both the fern and pteridosperm lines arose.

It must be emphasized that there is no evidence that the ferns were evolved prior to the pteridosperms. If either has priority the evidence points rather to the pteridosperms. This is by no means an original concept on the part of the present writer but its significance certainly has been overlooked by botanists in general. Robert Kidston, one of the greatest authorities on Carboniferous floras, presented a concise discussion of the matter in his 'Fossil Plants of the Carboniferous Rocks of Great Britain' (pt. 4, pp. 277-8). He considered in particular the value of the presence or absence of an annulus on a sporangium as a means of distinguishing between ferns and pteridosperms and pointed out that its absence, although generally considered indicative of the pteridosperms, must be used with reserve. Kidston's conclusion, that "They [the ferns and pteridosperms] appear as two distinct groups as far back as they can be traced, and from the earliest time seem to have constituted two parallel lines of development," has been more firmly substantiated since it was written.

It may also be pointed out that the cupule, although a morphologically problematical organ, seems to be a distinctive one of the pteridosperms, and it is now well known from the Lower Carboniferous. This will be discussed further in a later paper.

In view of the above evidence and our knowledge of the actual connection or association of the vegetative and reproductive parts of such plants as *Lyginopteris* and *Heterangium*⁴ and the South African pteridosperms (Thomas, '33), Harris's statement that we do not know what constitutes a pteridosperm is not entirely valid. To be sure, we do not know what the exact limits of the group are but we do have a fair knowledge of the characteristic structures of the types for which it was created, such as the terminally clustered sporan-

⁴See Halle, '29, pp. 18-22, for a summary of known seed-bearing species of pteridosperms.

gia, the cupulate seeds, the fern-like foliage and the secondary wood (see pp. 72-82).

Before presenting the results of the study of the secondary wood the primary body will be considered in the light of Prof. Bower's "Size and Form" principles (Bower, '30). Certainly few greater contributions to morphology have been made in recent years than that author's explanation of the relationship between living parenchyma cells and the dead conductive elements of the primary body. It is safe to assert that had 'Size and Form in Plants' appeared twenty-five years earlier considerably less confidence would have been placed in the taxonomic value of the primary body as a means of delimiting species and genera in the Pteridospermae.

VARIATION IN THE ANATOMY OF THE PRIMARY BODY

Anatomical variations have not gone entirely unnoticed. In 1917 Seward pointed out the fact that:

"The external position of the protoxylem is a character to which too much weight may easily be attached; the difference in position between the protoxylem of *Rhetinangium* and *Heterangium* is in some examples of the latter genus hardly perceptible. Kubart (1914) speaks of the stele of his species *Heterangium Sturi* as being almost exarch. The inconsistency in the position of the protoxylem of the osmundaceous stems and in the primary bundles of *Eristophyton* and other Palaeozoic genera is worthy of consideration in this connexion."

In his discussion of "Old Wood and the New," Scott ('02a) wrote:

"Lastly, we come to *Cordaite*s itself, which is anatomically on the same level as recent Cycads; centripetal wood has wholly disappeared from the stem while it still forms the main constituent of the xylem in the bundles of the leaf."

There is, of course, no close relationship between the cycads, on the one hand, and *Cordaite*s and related forms, on the other; if such existed in the past it must be traced to a common ancestor in pre-Carboniferous times. Since in practically all of the earliest vascular plants with secondary wood, the centripetal wood composing the metaxylem was abundant if not predominant, its presence in the more conservative parts

of the later divergent groups would necessarily be expected. Like the seed habit, which had its origin independently in various groups such as the cordaites, pteridosperms, and lycopods, the centripetal or "Old Wood" occurs in widely divergent groups and must be used with caution as a taxonomic character. The same holds true for the position of the protoxylem as will be shown in the following pages.

The primary body of Lyginopteris oldhamia (Binney) Potonié

In view of the abundant remains of this plant in Upper Carboniferous times, its wide distribution, and the many authors through whose hands it has passed, a further consideration may seem superfluous. Although the great range in size and structural details of the stem particularly is generally known, the figures and descriptions are scattered through the literature and many of the more interesting features have never been adequately described. Furthermore, it is only when such figures are presented at the same magnification that a true picture of the variation is realized.

Figures 1 to 10 of plates 5 and 6 represent transverse sections (all shown at a magnification of $\times 7.5$) which have been selected to show variation in size of the stem, the nature of the primary xylem, and the sclerotic "nests" and resin cells.⁵

The limits of publication necessitate the presentation of only the most outstanding features. It must be borne in mind, however, that one of the most significant points in the stelar variation of *Lyginopteris* lies in the fact that no sharp divisions can be drawn separating true forms or varieties. The variation is wide but the almost inseparable intergradations preclude any segregation.

a. Size variation.—The great variation in the size of the primary body of the stems may be seen by comparing figs. 1 and 2 of pl. 5. Although I have observed but few stems smaller than that shown in fig. 2 the larger one shown in fig. 1 is not

⁵ These have been drawn from a study of some few hundreds of slides of this plant contained in the Scott, Williamson, Kidston, Manchester, University College (London), Binney (Cambridge), Cambridge Botany School, and Liège University Collections, in addition to numerous "nitrocellulose pull" preparations and blocks, supplied to the author by Messrs. W. Hemingway and J. R. Lomax.

the maximum that the stems may attain. Aside from its somewhat exceptional size, fig. 1 represents a more or less typical stem with respect to relative extent of primary and secondary bodies, abundance and distribution of primary xylem, and sclerotic "nests." It is quite similar to the type specimen (pl. 6, fig. 5) except that the primary body of the latter is relatively smaller.

b. Parenchyma-sclerenchyma relationship.—There is considerable divergence from the more or less spherical nests as seen in figs. 1 and 5. In addition to such groups there are usually scattered through the pith numerous individual cells (sclerotic or resinous) with dark contents. In some sections the sclerotic nests are absent and the individual secretory cells are more or less uniformly scattered throughout the pith (fig. 4). Particularly small stems (fig. 2) may be almost or entirely lacking in either. That fig. 2 represents a small but mature stem and not merely a young one is evidenced by the prolific secondary xylem.

The distribution and abundance of these pith elements may be highly variable. In figs. 1 and 4 they are quite uniformly distributed, whereas in fig. 8 they form a peripheral cylinder immediately within the secondary xylem, or they may be confined to the central region of the pith as in fig. 7 and to a lesser extent in fig. 10.

c. Primary xylem.—The primary wood, with its mostly centripetally developed elements, generally occurs as five or six rather widely separated eccentrically mesarch bundles in direct connection with the secondary wood. However, the occurrence of a continuous band of primary tracheids in small stems (fig. 3) or of a nearly continuous ring in larger stems (fig. 9) is not uncommon. Various intermediate forms between continuous rings and typically scattered bundles (figs. 1, 5) are to be found. In pl. 8, fig. 17, the primary xylem extends unbroken through approximately 180°, the remainder of the periphery being composed of isolated bundles.

The eccentrically mesarch bundles are well known and need no further description here, but a few of the more interesting

divergences from the normal bundle (shown for comparison in pl. 10, fig. 32) may be briefly noted. Figure 35, a camera-lucida drawing of a bundle in the stem shown in fig. 17, shows abnormally high development of the centripetal elements. Figure 34 shows a very loosely aggregated "bundle" with no readily distinguishable protoxylem. The nature of the specimen whose primary bundle is shown in fig. 35 will be taken up below.

d. Extra-stelar meristematic activity.—The most remarkable stem referable to *Lyginopteris oldhamia* that has come to my attention and which, to my knowledge, has never been described is shown in pl. 7, figs. 11, 14, 15, 16; pl. 10, fig. 33. Its extraordinary feature lies in the presence of a complete medullary cylinder of secondary xylem.

The occurrence in *Lyginopteris* of internal (secondary) xylem in association with the primary bundles (fig. 12) and even irregularly scattered between them (fig. 13) is not uncommon, and as such may be of no phylogenetic significance; at least such was the opinion of Williamson and Scott (1896). But when this internal xylem forms a complete cylinder it most certainly merits careful consideration. The tracheidal cells of this internal secondary xylem are arranged for the most part in radial rows and are of about the same size as the earliest formed centrifugal secondary xylem tracheids; the degree of lignification is the same in both. The amount of associated "ray" or parenchyma cells may be seen to be somewhat greater in the former.

The nature of the tissue between these two bands of secondary xylem is shown in figs. 16 and 33, the latter being a camera-lucida drawing. It will be noticed that there is a striking resemblance to the "partialmark mit primärtracheiden" of the Chemnitz Medullosas (Weber and Sterzel, 1896). No distinct primary bundles are present, the primary tracheids being scattered as individual cells or in small groups throughout the "partialmark." When in small groups they are usually in contact with the tracheids of the normal secondary xylem (fig. 33), but the groups consist of only a few cells and lack a distinct protoxylem.

The ontogenetic origin of such an internal cylinder of xylem is of considerable interest. If it had been laid down in the usual way for secondary wood, by a single row of meristematic cells, one would expect the parenchyma, either on its inner or outer face, to show some indication of crushing. It is, however, for the most part well preserved and there seems to have been no crushing.

Another type of meristematic activity which occasionally occurs in *Lyginopteris* stems may be noted. At *a* in pl. 8, fig. 19, a group of radially arranged cells appears which are almost in contact with the normal secondary xylem and tend to flare out somewhat at the opposite extremity. The cells of such groups are not always radially arranged but may be less regularly oriented as shown in fig. 13. They are unlignified and there is no indication of a true cambium. Whether or not the internal secondary xylem described above represents a later stage (after lignification) cannot be proven but presents an interesting possibility.

It is evident from Miss Esau's studies that the sharp distinction between primary and secondary vascular tissues on the basis of radial arrangement is invalid. She has shown that in *Nicotiana glauca* Graham and *N. tabacum* L. ('38) and in *Apium graveolens* L. ('36) the procambium may lay down radial rows of primary xylem. Of the latter species she states:

"As the layer of dividing procambium cells narrows down to a few rows of cells, the meristem shows an increasing similarity to the cambium of herbaceous dicotyledons. Eventually cells appear with short radial diameters and become arranged, in longitudinal sections, in horizontal tiers. The longitudinal divisions are predominantly periclinal and the resulting cells retain a radial arrangement in the mature state." ['36.]

Since the ontogeny of primary and secondary vascular tissues is a continuous process (except where the primary xylem is entirely centripetal) one must follow Miss Esau's conception of procambium and cambium as two developmental stages rather than as two distinct meristems. In the light of our knowledge of such procambial activity in living plants it appears not impossible that this apparently secondary centripetal growth in *Lyginopteris* may be of like origin.

Williamson and Scott (1896) dismissed these anomalies as lacking significance and in his 'Studies' (1923) Scott writes:

"The most frequent anomaly in *L. oldhamia* is the formation of a medullary cambium, usually arising first inside the primary xylem strands and producing wood and bast with inverted orientation. . . . in extreme instances the wood may become broken up into several distinct masses, each with its own ring of cambium, forming new secondary tissues all around it."

The conclusions of these authors might be accepted without reservation for instances where the internal xylem is associated only with leaf traces (pl. 7, fig. 12), but when it forms a complete ring the similarity to such woods as *Cycadoxylon robustum* or certain of the Permian Medullosas is too striking to ignore any possible phyletic implications.

Although the identification of the specimen may be called into question, there seems to be sufficient evidence in favor of its allocation to *L. oldhamia*. Most of the tissues external to the secondary xylem have been destroyed, although there is a fragment of the characteristic "Dictyoxylon" cortex present. The characteristic sclerotic nests and secretory cells are present in the pith (pl. 7, fig. 11), and the general structure of the centrifugal secondary xylem is typical. Furthermore, this internal secondary xylem occurs in association with leaf traces (fig. 12) and even irregularly scattered between them (fig. 13) in undoubted specimens of *L. oldhamia*.

e. Roots.—The relationship between the tracheids and parenchyma in the roots of *L. oldhamia* in general coincides with the physiological requirements of Bower's "Size and Form" principles. The smaller roots (pl. 8, fig. 22) usually have a solid primary body while in the larger (figs. 20, 21, 23) there is an admixture of parenchyma (these figures are all at a uniform magnification of $\times 23$). The root shown in fig. 22 is about the maximum size that the primary body may attain and still remain purely tracheidal. All roots smaller than this that have come to my attention are likewise composed of tracheids only. When, in the larger roots (figs. 21, 23), the primary body contains an appreciable amount of parenchyma the xylem is broken up into rather regular groups with the protoxylem

outermost; and when the tracheids largely disappear from the central region the roots may present a striking resemblance to the stems (figs. 9 and 20).

f. Foliage.—It has been pointed out in the preceding paragraphs that, although these plants have a wide range of variation in the primary body they form a continuous series. Such is not the case with the foliage “species” associated or in organic connection with the stem remains.⁶ The frond species, on the contrary, are distinct and appear to present a significant example of the varying rate of evolution that different organs undergo.

Sphenopteris Hoeninghausi Brongniart is so well known and has been found so often in contact with the stems having a *dictyoxyllic* cortex that it needs no further mention here. It is, however, not so well known that *Sphenopteris Baumleri* Andrae has been found in organic connection with stems exhibiting the *dictyoxyllic* cortex. Although Gothan ('23), Kidston ('23-'25) and Stur (1885) have figured this it does not seem to have attracted the attention that it merits. While I was studying in Bruxelles, Dr. Stockmans showed me two fine specimens from the Westphalien of Belgium (Nos. 5933, 5930, Mus. d'Hist. Nat., Brux.) in which *S. Baumleri* was associated with the *dictyoxyllic* stems. In the latter specimen (No. 5930) the similarity between the stem compressions associated with *S. Baumleri* and those to which *S. Hoeninghausi* is attached (*Lyginopteris*) extends beyond that exhibited by the hypodermal sclerenchyma, for numerous spines are to be observed quite like those found on the rachis of *S. Hoeninghausi*.

In addition to these two well-defined species of *Sphenopteris* actually in organic connection with the *dictyoxyllic* (*Lygi-*

*Lacking the evidence of internal structure the only characters on which the supposed identity of *Lyginopteris oldhamia* stems is based are the anastomosing strands of hard cortical tissue and in some cases the presence of epidermal spines. Considering the wide distribution and abundance of *L. oldhamia* stem petrifications it is likely that many of the stem and petiole compressions exhibiting a “*Dictyoxylon*,” or perhaps better a *dictyoxyllic* cortex, actually do belong to that species; nevertheless they cannot be proven as such. Paleobotanists have perhaps accepted this external evidence a bit too freely.

nopteris type) stem, others are found in association. A specimen of *S. taitiana* Kidston from the Vendéenne region in France has been figured by Mathieu ('37, II, pl. 7, fig. 6) in association with a fragment of a rachis (or stem?) showing cortical structure characteristic of *Lyginopteris*. Zeiller (1897) described a specimen of *Diploptomena distans* (Sternberg) Stur which, judging from the account, must have been attached to a stem of the dictyoxyllic type:

“Quant à l'axe principal, sa surface est divisée en compartiments fusiformes inégaux et irréguliers, de 4 à 6 millimètres de longueur, circonscrits par des stries longitudinales flexueuses entre-croisées, qui donnent lieu de penser que l'écorce était formée, au voisinage de sa surface externe, de bandes sinueuses résistantes, comprenant entre elles des mailles de tissu plus mou. C'est ce que a lieu dans les écorces du type connu sous le nom de *Dictyoxyton*, où des mailles parenchymateuses sont ainsi encadrées entre des bandes sinueuses de sclérenchyme, organization que Williamson a reconnue notamment chez son *Lyginodendron Oldhamium*.

“Ainsi constitués, ces larges axes charbonneux ressemblent d'une façon frappante à ceux qu'on observe chez le *Sphenopteris Hoeninghausi* Brongt. . .”

The petioles described under the name of *Lyginorachis* likewise present a range in anatomical variation similar to that in the gross external morphology of the fronds. In addition to the petioles of *Lyginopteris oldhamia* five other species of petiole (*Lyginorachis*), for the most part well defined, have been described, namely, *L. taitiana* Kidst. & Crookall, *L. papilio* Kidst. & Scott, *L. Waltoni* Calder, *L. Brownii* Calder, and *L. sp.* (Crookall, R., '31).

Summarizing briefly, it may be seen that the stem anatomy, although highly variable, forms a nearly continuous series, whereas the foliage and petioles, for the most part, represent well-defined species. *Sphenopteris Hoeninghausi* is somewhat of an exception to this in that it is difficult to distinguish from other very closely allied species. Seward in 1917 noted that:

“It is not an easy task even for those most familiar with Carboniferous fronds to distinguish clearly between species agreeing generally with *Sphenopteris Hoeninghausi*, a species regarded by some authors as the type of a group of very similar and closely allied forms all of which were probably borne on stems referable to the genus *Lyginopteris*.”

The Calamopityeae

Of all the supposed pteridosperms preserved as petrified stem remains the assemblage included under the Calamopityeae presents the most difficult taxonomic problems, as is adequately attested by the frequent revisions of members retained within the group.

Calamopitys saturni Unger and *C. annularis* (Unger) Solms are the oldest known members of the Calamopityeae as instituted by Solms-Laubach in 1896, the former species being the genotype. A few years later Scott (1902) described two more species of *Calamopitys* (*C. fascicularis* Scott and *C. beiner-tiana* Scott) after having tentatively assigned them in a previous publication (1899) to *Araucarioxylon*. Zalesky ('11) in turn proposed the genus *Eristophyton* to include these latter two which differ very markedly from either *C. saturni* or *C. annularis* in the structure of the secondary wood and in the structure and arrangement of the primary bundles. Read ('37) has upheld Zalesky's genus and there can be little doubt that this decision is correct. It is, moreover, doubtful whether the very problematical *Calamopitys radiata* Scott, with its highly dilated rays, should remain in the genus. Lastly it may be noted that *Sphenoxylon eupunctata* (D. E. Thomas) Read, originally described as a *Calamopitys*, agrees neither in the nature of its primary or secondary wood with *C. saturni* or *C. annularis*. There can be little doubt that it is generically distinct and for that reason the name *Sphenoxylon* proposed by Read ('37, p. 91) is adopted here.

Judging from the wide divergence of characters in the members of the Calamopityeae, the family can hardly be considered a natural group, as it stands at present. Two points are particularly significant in the history of the group, namely, the early recognition of the similarity of *Calamopitys* (i.e., *C. saturni* and *C. annularis*) to *Lyginopteris*, and Scott's original description under *Araucarioxylon* of the species at present retained in the genus *Eristophyton*.

The close similarity, if not actual identity, of *Calamopitys americana* Scott & Jeffrey, *C. saturni* Unger, and *C. annularis*

(Unger) Solms is well known to those who have dealt with the group. The differences between *C. americana* and *C. annularis* are exceedingly slight, while *C. saturni* is supposed to be unlike these two in having distinctly separate centrally mesarch strands and a primary xylem consisting of a nearly confluent ring with eccentric protoxylem.

Through the kindness of Professor Gothan a considerable number of the type slides of *C. annularis* was obtained from Berlin.⁷ They apparently were not seen by Scott at the time he wrote his "Notes on *Calamopityis* Unger" ('18), since the slides he observed are still in the Scott Collection under the numbers 3676-3681 inclusive.

In the American species, *C. americana*, the primary body is described by Scott and Jeffrey ('14) as follows: "So far the primary structure—pith surrounded by a ring of nearly confluent mesarch xylem strands—is quite similar to that described in the case of *Calamopityis annularis*. In the American species, however, there is strong evidence for the somewhat unexpected conclusion that the pith was a 'mixed' one, containing tracheids." Read ('37) has confirmed the existence of a mixed pith in this plant.

In 1918 Scott notes with regard to the possible presence of medullary tracheids in *C. annularis*: "I have carefully looked into this question. In transverse sections one can distinguish at a few places elements with thicker walls than the ordinary parenchyma, and resembling the tracheids of the xylem ring. But the preservation is not such as to make these indications at all convincing." Now the slides 97(40a) and 101(43I), not

⁷ The slides from Berlin examined by the writer are as follows (the numbers and notations given as they appear on the slides): RADIAL SECTIONS: 97(40R) *Calamop. ann.* Berlin Landesanst; 101(44R) *C. annul.* Culm, Saalfeld, Berlin Landesanst; 49(6R) *Calamop. annular.*, Culm, Saalfeld, Berlin Landesanst; 101(44) *Stigmaria annularis*, Saalfeld, Berlin Landesanst; 49(6R) *Calamop. annularis*, Berlin Landesanst; 100(43I) *Stigmaria annul.* Saalfeld, Berlin Landesanst; 49(6R) *Cal. annul.* Berlin Landesanst; 101(44) *S. annul.* Culm, Saalfeld, Berlin Landesanst. TRANSVERSE SECTIONS: 97(40a) *Calam. ann.* Berlin Landesanst; 74(24) *Stigmaria annul.* Saalfeld, Richt., Berlin Landesanst; 98(41) *Stigmaria annularis*, Saalfeld, Richter, Berl. Landesanst; 100(43I) *Stig. annul.* Saalfeld Richter, Berlin Landesanst. TANGENTIAL SECTIONS: 49(tg) *Calamop. annul.* Culm, Saalfeld, Berlin Landesanst.

seen by Scott, are very well preserved, and I believe there can be no doubt that the pith is mixed, that is, with tracheids scattered through it. Judging from a careful comparison of the slides of *C. americana* and *C. annularis* in the Scott and Berlin collections there seems to be no valid reason for the existence of two species based on this material.

The differences between *C. annularis* (or *C. americana*) and *C. saturni* are primarily the presence of a discontinuous xylem ring in the primary body of the latter and the position of the protoxylem. The primary body is comparatively large in the first two species (7 mm. or more as compared with less than 2 mm. in *C. saturni*), but in view of the size difference in other species of pteridosperms as shown here and the host of plants considered by Bower ('30), that alone can bear little weight. In the Berlin slides 97(40a) and 100(43I) of *C. annularis* primary xylem does not form distinctly continuous rings (pl. 9, fig. 29); at least the variation from a continuous ring is of sufficient significance as regards the supposed distinction of these species.

Perhaps the most interesting slide of all those received from Prof. Gothan is No. 74(24), labeled *Calamopityx annularis*. It is quite likely that it was cut from the same specimen as the section described by Scott ('18, p. 214) which he tentatively assigned to *C. annularis*. Since it has a distinct bearing on the taxonomy of these three species and is better preserved than the slide described by Scott, a detailed description will be given.

The distinctive features in the slide at Scott's disposal may be briefly summarized as follows: primary body only 2.5×1.7 mm.; primary xylem forms a continuous band, while elsewhere there are only scattered tracheids between the primary strands; position of protoxylem not determined; rays of secondary wood narrow.

In my slide the nature of the primary body may be seen in pl. 8, fig. 18, pl. 9, fig. 30. The primary xylem resembles that in the Scott slide but is better preserved, the protoxylem elements being centrally mesarch in most of the bundles—a dis-

tinctive feature of *C. saturni*. It may be noted, however, that in the two bundles shown in fig. 18 the position of the protoxylem varies, that in the bundle at *a* being eccentric. On the other hand, the xylem forms a nearly continuous ring, that part of the primary body between the bundles proper being occupied by tracheids with a few admixed parenchyma cells. There are, however, scattered tracheids within this ring—a feature of *C. americana* and *C. annularis*.

In view of this admixture of characters, it is evident that the distinction between the three “species” is not sharp. A feature of their leaf-trace anatomy may be noted. In slide 3680 (apparently cut from the same block as Berlin slide 98(41)) Scott ('18) described two complete bundles in the cortex or leaf base: “Each is elongated, approximately in the radial plane, and has three internal protoxylem groups, the latter lying toward that side of the strand which faces its neighbor.” In the Berlin slide, however, there are four instead of three protoxylem groups in one of the strands, and their position is eccentric towards the outside rather than on the side adjacent to the other strand. It appears then that as the traces pass out not only does the number of the protoxylem groups change but also their position. This is not surprising in view of the sudden change that may take place in the nature of the vascular supply of many living plants—any one who has taken the trouble to follow the course of the bundles in the basal portion of the petiole of such a plant as *Aesculus Hippocastanum* L. could not fail to be struck by the rapid change through a few millimeters. Such rapid ontogenetic changes give a hint of the caution that must be used in comparing supposedly different fossil species unless equal parts of homologous structures be available for comparison.

Although perhaps these three species of *Calamopityx* should not be merged until further material is obtained, in view of the variable nature of the primary body in this and other groups, combined with the modern concepts of “Size and Form,” the specific distinctions are questionable. An investigator of the present day would certainly describe them as variant of a single species.

Eristophyton Beinertianum (Goeppert) Zalessky and *E. fasciculare* (Scott) Zalessky present certain points of interest which are appropriate to the present discussion. In both species the protoxylem of the leaf-trace bundles, although mesarch at the point of entrance, becomes endarch as it passes down the stem. A further instance of the variation that may be expected in size of the primary body is found in *E. Beinertianum*. First, it may be recalled that the diameter of the primary body of the British specimens varies from 13 to 15 mm., while it is 8 mm. in the Falkenberg specimen (Scott, '18). There are, moreover, four uncatalogued slides in the Scott Collection labeled "*Calamopitys*, Gin Head Vent, near Tantallon Castle, North Berwick." The primary xylem is poorly preserved but in all four the sclerotic "nests" characteristic of *E. Beinertianum* are prominent, and the general appearance of the secondary wood leaves little doubt as to their identity. The dimensions of the primary body and the total diameter (nothing outside of the secondary wood is preserved) of the stems in these four slides are given in table I.

TABLE I
EXPLANATION IN TEXT. ALL DIMENSIONS IN mm.

Slide No.	Primary body	Diameter over all
1	9 × 14	27 × 35
2	4	20
3	3.5	11
4	5	22 × 18

Endoxylon zonatum (Kidston) Scott was segregated from *Calamopitys* (Scott, '24a) primarily on the basis of its endarch primary xylem strands. An examination of the sections in the Kidston Collection has convinced me that this feature is not constant. In slide 803 Kidst. Coll., a strand may be noted that is more mesarch than endarch.

To emphasize further the necessity of caution in the taxonomic use of characters of the primary body a few examples of plants not included within the Pteridospermae may be mentioned.

Although the slides of *Mesopitys Tchihatcheffi* (Goeppert) Zalessky were not available for my examination, Seward's opinion ('17) is of interest: "I am not convinced that the primary xylem-strands are exclusively endarch; in most of the primary groups the protoxylem is clearly on the inner edge, but in a few cases there may be a small amount of centripetal xylem present."

Certainly one of the most remarkable cases of ontogenetic variation in the primary body is that of *Selaginella spinulosa*. Here, according to Gibson (1894), in the upper region of the erect stem seven protoxylem strands occur on the outside of the stele. Farther down these fuse to form three (still exarch), and in their course down the stem they gradually pass toward the center of the stele until, in the trailing axis, they fuse to form a single central protoxylem strand. Not only does the number of protoxylem groups change but there is a complete transition from centrally endarch in the trailing axis to exarch in the stem.

A fine example of the physiological relationship between primary tracheids and parenchyma is shown in the famous fossil hollow trees of Aran, *Lepidophloios Wunschianum* Carruthers. Although it had long been supposed that the steles of other plants had washed into the rotted hollow centers of the trunks, Walton ('35) showed that as the small solid primary xylem enlarged upward the degree of medullation correspondingly increased.

ANATOMY OF THE SECONDARY WOOD

As was pointed out in the introduction, a careful consideration of the characters afforded by the secondary xylem presents an outstanding gap in the literature, particularly in the light of current studies of dicotyledonous woods. This is well illustrated by the original description of *Megaloxylon* in which the secondary wood was described as practically identical with *Cycadoxylon* (*Lyginodendron*) *robustum*. The latter has also been compared closely with *Lyginopteris oldhamia* (Scott, '23). However, if the ray structure of these three be compared

(pl. 13, figs. 39, 40; pl. 14, fig. 42) all three are found to be distinctive.

The secondary xylem in the pteridosperms has been studied in detail to determine what characters, if any, are sufficiently constant to be relied on.

Materials and Methods.—The author has been fortunate in having had access to the type slides of the majority of the pteridosperm woods discussed below, and in many cases the type specimens or additional blocks have been available. The specimens thus dealt with are:

Cycadoxylon robustum (Seward) Scott: portion of the type block from the British Museum (Natural History).

Cycadoxylon anomalum (Will.) Will. & Scott: portion of the type block from the Hunterian Museum, Glasgow University, Glasgow.

Megaloxyton Scotti Seward: portion of the type block from the Binney Collection, Sedgewick Museum, Cambridge.

Lyginopteris oldhamia (Binney) Potonié: numerous blocks supplied by W. Hemingway (Derby) and J. R. Lomax (Bolton); a block from the Binney Collection, Sedgewick Museum, Cambridge.

Medullosa anglica Scott: block supplied by J. R. Lomax.

Medullosa Noei Steidtmann: blocks in the Botany School, Cambridge; blocks supplied by Dr. James Schopf, Illinois State Geological Survey.

Medullosa stellata Cotta, *M. Solmsii* Schenk, *M. Leuckarti* Solms-Laubach: blocks deposited in the Botany School, Cambridge.

Heterangium sp.: block supplied by Prof. W. T. Gordon, King's College, London.

Where the preservation has been particularly good serial tangential sections have been prepared through the secondary wood, using the cellulose-pull technique; when the wood was not sufficiently well preserved to permit this technique ground sections were cut as close together as possible.

The anatomy of the secondary xylem was investigated first to determine whether or not the ray structure is constant

throughout the radius and whether it could be correlated with other characters such as pitting and tracheidal morphology. Since the ray structure presents the most reliable taxonomic character of the secondary wood, the ray types into which most of the pteridosperm woods may be segregated will be described and illustrated. The blocks were in varying states of preservation and in one group the rays were extremely tall. For these reasons uniformly good photographs could not be obtained and drawings were prepared by means of a reflector attached to a vertical photomicrographic camera.

It is not possible to classify these woods on the basis of their ray structure according to the system employed for angiosperm wood by Kribs ('35). Until more extensive studies are made of other groups it seems best to set up an independent classification for the plants discussed here. Four rather distinct ray types are found within the group:

- I. Rays varying from very low (3-4 cells) and uniseriate to tall (usually not over 2 mm.) and 3-4-seriate, the latter not regularly fusiform, heterogeneous. (Chief feature is the uniform gradation between low uniseriate and rather tall irregularly multiseriate). Pl. 12, fig. 37.....
Sphenoxylon, Tetrastichia, Palaeopitys, Aneurophyton.
- II. Rays of great height, up to and exceeding 2 cm.; sides generally parallel but occasionally irregularly dilated; low uniseriate or fusiform rays extremely rare; cell walls very thin, mostly unpitted; cells angular, heterogeneous, intercellular spaces small.
 - A. Rays of first-formed secondary xylem usually narrow, becoming greatly dilated toward the outside. Pl. 14, fig. 42.....*Lyginopteris.*
 - B. Similar to A but less variable in tangential dimensions, usually not more than 4-5 cells wide. Pl. 12, fig. 38; pl. 14, fig. 41..*Heterangium, Stenomyelon, Calamopitys, Rhetinangium, Sutcliffia, Megaloxylon, Medullosa* (in part)—*M. anglica, M. Noei, M. pusila, M. centrofilis, M. distelica, M. Leuckarti.*
- III. Rays elongate-fusiform to nearly circular (that is, with tangential and vertical dimensions nearly equal), heterogeneous, uniseriate rays rare. Pl. 11, fig. 36; pl. 13, fig. 39.....
Cycadoxylon, Colpoxylon, Ptychoxylon, Medullosa (in part)—*M. Solmsi, M. gigas, M. stellata* (?)
- IV. Rays mostly uniseriate, occasionally 2-4-seriate, low, generally not more than 7-10 cells high; heterogeneous; cell walls relatively thicker than in other groups. Pl. 15, figs. 43, 44.....
Eristophyton, Bilignea, Protopitys, Cladoxylon, Endoxylon.

TYPE I.

Type I is illustrated by a camera-lucida sketch (fig. 37) from slide 15T6 Petry Collection (Cornell U.). It is a partial reconstruction in the sense that it represents a composite view of a number of the best-preserved portions of the slide. Other slides were available and as the preservation of the stele of this plant is in general very good the drawing is an accurate generalized reproduction of the ray structure. The secondary woods of *Palaeopitys* and *Tetrastichia* are not as well preserved, particularly the former. However, a careful examination of the slides in the Kidston and Gordon Collections indicates that their ray structure is essentially the same as that of *Sphenoxylon*. Although slides of *Aneurophyton* have not been available for examination, the description given by Kräusel ('36) indicates a close similarity to the other members of this group. Because these early forms are of particular interest as possible forerunners of the Pteridospermae proper a brief summary of the structure of their primary body is included here:⁸

* Although the present treatise involves primarily the stelar anatomy of the pteridosperms, a discussion of the seed or megasporangiate fructifications should be appended in order to present a composite picture of these very early Gymnosperms or "Pro-Gymnosperms." The latter term, originally introduced by Saporta and Marion (1885) to include plants of sigillarian, calamarian, and cordaitean affinities, or the term Hemi-Gymnosperm, is probably more truly descriptive of the plants included under Type I than any other. On the basis of anatomy alone this may appear too speculative but when considered in the light of the fructifications discovered in recent years in these correspondingly early rocks such a belief seems justified. The morphology of the secondary enclosing structure, the cupule, of certain Lower Carboniferous seeds is indeed a pressing problem. Recently an extraordinary large cupule (6.2 cm. long) was discovered in the Lower Carboniferous oil shales of Scotland and will be described in a separate paper. This cupule, as well as *Calathiops Bernhardti* Benson, probably contained in life more than one seed, whereas the smaller forms, such as *Calymmatotheca Kidstoni* Calder (Calder, '38), contained only one seed as in the Upper Carboniferous ones.

In his discussion of the affinities of that extremely interesting plant *Tetrastichia bupatides*, Gordon ('38) has pointed out certain similarities with the petiole base of *Telangium affine*, and it may also be noted that the only foliage (other than that of Lycopods) found in association with the above-mentioned cupule is again *Telangium affine*. The evidence of association is highly suggestive.

Palaeopitys Milleri M'Nab (Kidston & Lang, '23). Solid protosteles 1.5 mm. in diameter, protoxylem elements probably near secondary wood. Mid-Devonian.

Aneurophyton germanicum Kräusel & Weyland (Kräusel, '36). Solid protostele, approximately 1.5–3 mm. in diameter, triarch, the three protoxylem groups near the periphery. Mid-Devonian.

Tetrastichia bupatides Gordon (Gordon, '38). Solid 4- or 5-rayed protostele 1.5–2.5 mm. in diameter, with protoxylem centrally placed in the arms. Lower Carboniferous.

Sphenoxylon eupunctata (D. E. Thomas) Read (D. E. Thomas, '35). Primary body consisting of medullated central column 4×2 mm., with four radiating arms of primary xylem. Upper Devonian.

It is of interest to note that the primary body in three of these four genera is a solid protostele. In *Sphenoxylon*, with its somewhat larger primary body, it is not surprising to find it mixed. Bower has shown that in the Psilotales and Psilophytales the increasing size of a solid protostele is correlated either with medullation (as in *Psilotum*) or stellation (as in *Asteroxylon*), with the result that the xylem-parenchyma ratio remains more or less constant. The same holds true in a general way for these forms with secondary wood. The primary body of *Palaeopitys* is the smallest and is a solid cylindrical protostele. In the other three the primary body is larger and is either more or less stellate as in *Tetrastichia* and *Aneurophyton*, or mixed as in *Sphenoxylon*. It seems evident that the stellate protoxylem (actinostele) had its origin from the protostele at a very early date and that both types independently gave rise to secondary growth.

TYPE II

The woods grouped under Type II constitute a rather uniform assemblage, at least as far as the structure of the secondary wood is concerned. The segregation of *Lyginopteris* from the other members is based on a difference in degree—the

greatly dilated rays as they pass outward seem to be more generally characteristic of this plant than those placed under the sub-type B.

The series of three drawings in pl. 14, fig. 42, represents portions (as the rays of *Lyginopteris* are exceedingly high, often exceeding 2 cm., it is not possible to show complete rays without making an unduly large plate) of a few rays of *Lyginopteris*. At *a* the rays are shown as they appear close to the pith, at *c* as they appear at the outer border of the secondary xylem, while at *b* they are shown midway between. The total radial distance from *a* to *c* was 2.7 mm. The rays do not often attain greater tangential dimensions than those shown in *c*, and it may be noted even here, in the lower left-hand corner of the figure, that the ray is being split at two different points.

The vertical fusion of rays as they pass toward the outside is not an uncommon feature. In fig. 42*c*, the ray at the right now extending the full length of the figure has resulted from the fusion of two separate vertically aligned rays in *a* and *b*.

The question of the phylogenetic origin of the multiseriate ray is one that has long been disputed by anatomists, evidence having been brought forward by Jeffrey and his students in support of an origin from the aggregation of numerous uniseriate rays, and by Bailey and others in support of the widening of a uniseriate ray. In 1914 Bailey and Sinnott wrote:

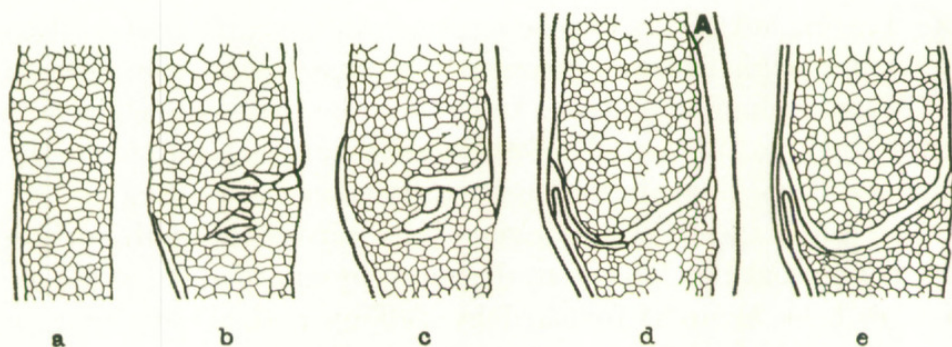
“Multiseriate rays of varying width are well developed in the majority of arborescent or shrubby dicotyledons and may be traced through the Tertiary to the Middle Cretaceous . . . The investigation of the structure and development of rays in the various families of the dicotyledons reveals much evidence that the multiseriate rays originated by the gradual widening of primitive uniseriate rays.”

In view of the evidence presented by both Schools it seems quite likely that the multiseriate rays have had a dual origin. That they were formed ontogenetically in *Lyginopteris* by the dilation of uni- or biseriate rays is well shown in fig. 42 but the bearing that this may have on the origin of homologous structures in more recent seed plants is open to question.

Although the tracheid-ray ratio varies considerably in this

plant these greatly dilated rays are general in occurrence and, although widest when in association with leaf traces, they are by no means confined to this region. In close proximity to the leaf traces the rays, as is usually the case, lose their characteristic shape.

Mechanics of ray division.—It has been possible in two of the pteridosperms to trace individual rays closely enough to determine the manner in which they divide. It was found that in *Cycadoxylon robustum* the actual mechanics of ray division follows essentially the same process as shown for *Cola togoensis* Engler & Kräuse by Miss Chattaway ('37). A single tracheid initial cuts diagonally across the ray, apparently in-



Text-fig. 1. Ray division in *Lyginopteris oldhamia*. Explanation in the text.

creasing in length by sliding growth. The unique anastomosing nature of the tracheids and rays in this wood will be taken up below.

In *Lyginopteris* the case is somewhat different, for the rays do not simply divide by the increasing length of a single tracheid initial. Blocks were selected in which the secondary wood was especially well preserved and a series of tangential sections was prepared by the cellulose-pull technique. Although transverse ground sections of *Lyginopteris* often present remarkably fine cellular details the delicate ray tissue is rarely sufficiently well preserved to produce a uniform series of tangential pulls. Of four especially well-preserved blocks treated in this way one proved to be somewhat superior to the rest (text-fig. 1). Of sixteen sections taken through a radial dis-

tance of 1 mm. those shown in the text-figure have been selected to show the mode of ray division. At *a* the ray may be observed prior to any indication of division; at *b* it has increased its tangential dimensions considerably and ten of the ray cells laid down by the cambial initials have become lignified, their walls being composed of bordered pits as in normal tracheids. Although some of these lignified cells are no larger than the ray-parenchyma cells certain others are distinctly elongated. In *c* the number of lignified cells is smaller but those remaining are considerably larger and the ray has been almost completely dissected.

This increase in size of the lignified ray cells, or "ray tracheids," is apparently due to increase in size of certain cambial initials with resultant crowding out of the others. This increase merges imperceptibly into typical sliding growth as the later-formed lignified cells assume a more distinctly tracheidal shape. If the cell indicated at *A*, text-fig. 1*d* be compared with the corresponding ones in *c* and *e* respectively this becomes apparent; in the latter figure the cell formed from the same initial had so elongated that the end could not conveniently be included in the figure. The resultant U-shaped tracheids are not of uncommon occurrence, and when in association with leaf traces they may assume much more bizarre forms.

Although the division of the rays is primarily due to increase in size and sliding growth of certain initials there remains the possibility of the occasional fusion of the initials themselves.

These lignified cells may occur isolated in the rays unassociated with any later divisions. That is, an initial may lay down a ray cell which becomes lignified while the succeeding cell will remain a normal ray-parenchyma cell. New rays may be formed either by this division of one into two more or less equal parts or by a fragmentation process whereby a small arc-shaped portion of the ray is segmented off followed by a gradual dilation of the newly formed rays as shown in fig. 42.

Williamson and Scott ('96) noted that in *Lyginopteris*, "Ad-

ditional secondary rays appear *de novo* in the later formed layers, as secondary growth proceeds." . . . Their deduction was apparently based on transverse sections in which it is very difficult to ascertain positively the mode of origin of new rays. It is apparent that serial tangential sections present a much more positive means of determining ray origin, and while new rays may arise *de novo* the mode of secondary ray origin as described above is the only one that has been observed in the present investigation.

In subtype B the rays are for the most part very narrow, with nearly parallel sides, and of great height, being as high as 2 cm. or more in *Medullosa Noei* (fig. 41). In *Sutcliffia insignis* Scott (fig. 38) the rays are as high or higher. In slide 71 (0.73), University College Collection (London), three rays were measured having heights of 13.6, 17.6, and 14.0 mm., respectively; a fourth measured nearly 25.0 mm. These figures do not represent extremes but cracks or spots where the preservation is poor prevents the measurement of many rays throughout their entire height.

In *Calamopitys* the rays are very tall, quite uniform in their tangential dimensions, but somewhat broader than the other members of this subgroup (fig. 28).

Tangential sections through the xylem of the large outer steles ("snakerings") of *Medullosa Leuckarti* have been prepared by Mr. Hemingway.⁹ Although the cellular details are not well preserved the general shape of the rays is clearly defined. They are very narrow, most of them probably not more than two cells wide and well over a centimeter high. They are indeed quite similar to the rays of the *Medullosae* of the *anglica* section (Schopf, '39), such as *M. anglica* and *M. Noei*. That this similarity should exist is not surprising for other than being somewhat larger, the general stelar anatomy of *M. Leuckarti* is not vastly different from *M. anglica*. The latter does of course lack the star-rings but this is perhaps not a point of great distinction since there is one present in *M. centrofilis* which Seward ('17) described as forming "a connect-

⁹Slides Nos. 1060, 1061, in the Botany School, Cambridge.

ing link with certain continental Medullosae." The structure of the rays tends to confirm Schopf's tentative inclusion of this species in his subgenus *Anglorota* (Schopf, '39).

Megaloxyton presents somewhat of an exception in that its ray structure is more or less intermediate between subtype IIB and Type III. The rays (fig. 40) do not reach the extreme height characteristic of II and smaller rays are more abundant. The larger rays tend to be fusiform although more elongate vertically and not as broad as the rays of Type III.

TYPE III

The members of Type III possess rays varying from elongate-fusiform to cylindrical. In general they are quite distinct from the high, narrow, parallel-sided rays of the preceding group. The pitting of the tracheids is likewise somewhat different as will be pointed out later. In view of the more or less transitional *Megaloxyton* I am inclined to believe that the members of this group may not be fundamentally different from those of Type II but rather represent an end line of development from the latter, typified in the extreme by the bizarre *Cycadoxyton anomalum*.

Cycadoxyton anomalum.—This remarkable wood has been mentioned a number of times in the literature since its original description by Williamson in 1878. However, inasmuch as certain details of its structure have never been adequately figured and certain questions have arisen with regards to possible identity with *Cycadoxyton robustum* (Seward, 1897) a re-investigation was undertaken. Two fragments of the original block were located in the Hunterian Museum, Glasgow, one of which has been utilized for the study of the rays. A second and somewhat larger fragment is preserved in the Williamson Collection at the British Museum.

The fragment of secondary wood upon which the species is based was collected from the Lower Carboniferous of Arran. It is especially remarkable that such a highly specialized wood should be found in this low horizon, and some doubt has been cast by those familiar with the locality as to its actual derivation from these rocks.

Although originally described by Williamson under the name of *Lyginodendron anomalum* (Williamson, 1878) it became evident that there was no close affinity with *Lyginodendron* (*Lyginopteris*), and it was subsequently placed in Renault's genus *Cycadoxylon* by Williamson and Scott (1896). In his description of *Cycadoxylon robustum* Seward (1897) suggests a similarity between *C. anomalum* and that portion of *C. robustum* where the wood is disturbed by a leaf trace:

"The resemblance between *Lyginodendron robustum* and *Lyginodendron anomalum* as regards the structure of the wood and the form of the medullary rays, which is specially striking in the wood of the former species where the normal form of the rays is modified by the bending of the tracheids to a leaf-trace bundle, points to the possibility of the two forms being closely allied to one another."

In order to check the constancy of the ray structure of *C. anomalum* a small block was studied first by means of serial tangential pulls through a radial distance of approximately 2 mm. When it was found that there was almost no change in the structure of the rays through this distance the block was ground more rapidly and photographs made directly from the etched surface by means of reflected light.¹⁰ This was carried on through a radial distance of approximately 1.5 cm. where there was very little change in the ray structure. It is certain then that there is no close similarity between this constant tracheid-ray relationship and the very irregularly contorted rays in *C. robustum* where they are associated with the leaf traces. A careful comparison of the slides of both species in the Williamson, Scott, and Cambridge Botany School collections, combined with the constant ray structure of *C. anomalum* as shown above, leaves no doubt as to the specific distinction of the two. In fact, it is probable that the distinction is a generic one.

The pitting of the radial walls of the tracheids shows considerable variation from the closely compacted reticulate pitting figured by Williamson (1878). Although the crowded

¹⁰ Very satisfactory photographs were obtained when the silicified block was roughly ground down with #150 carborundum, smoothed with #500, etched for five minutes in 25 per cent hydrofluoric acid, dried, and photographed with reflected light.

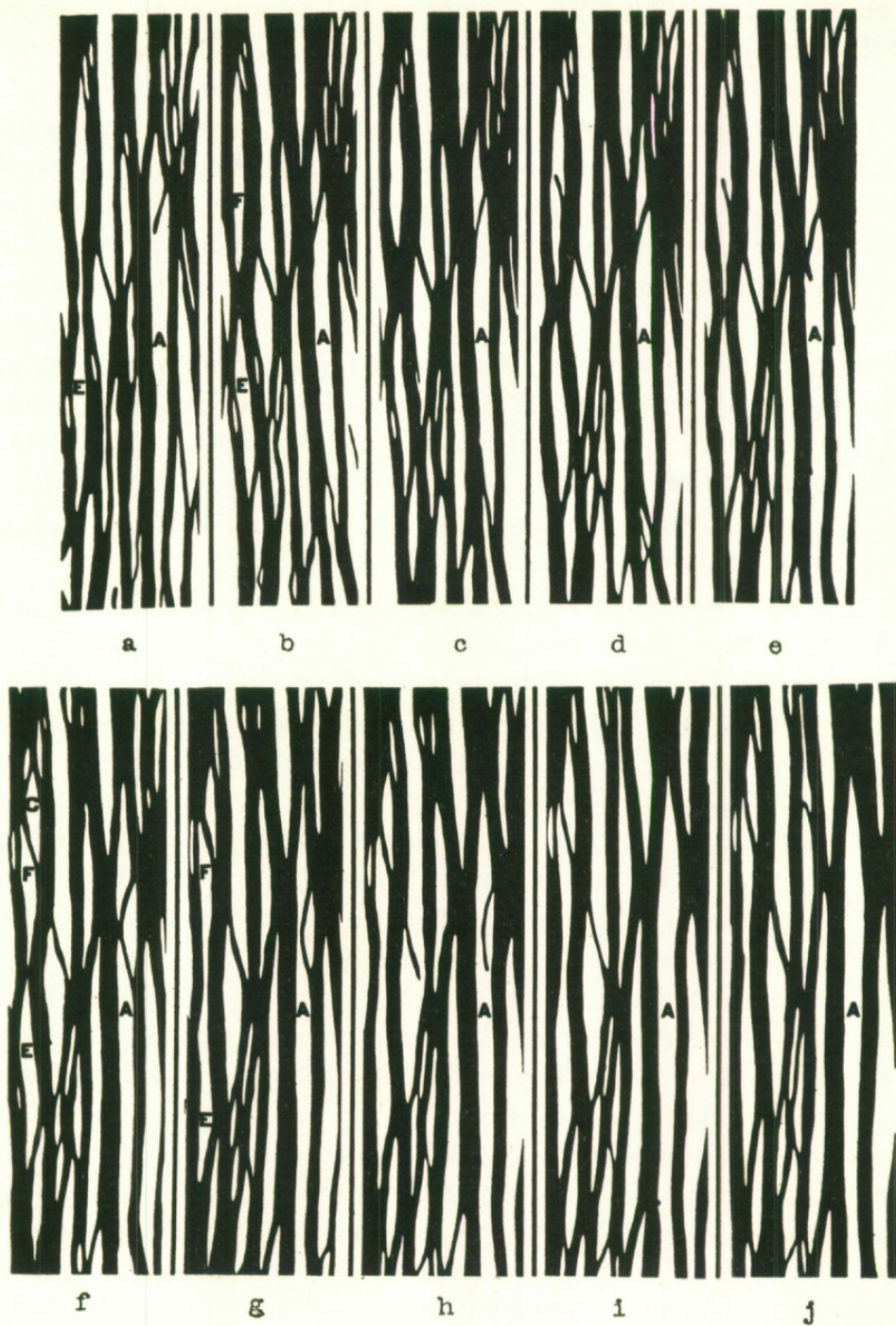
reticulate type (fig. 26) is common it is more often "loose" with the pits irregularly arranged (figs. 25, 27) and in some tracheids they are quite distantly scattered (fig. 24).

Cycadoxylon robustum.—This wood was treated in essentially the same manner as *Lyginopteris*. Although quite well preserved, sufficiently satisfactory preparations could not be obtained by the cellulose-pull technique. A preliminary series of the latter through about 1 mm. of the wood did indicate, however, that ground sections could be prepared sufficiently close together to show the significant features of the anatomy. Consequently, a series of 14 tangential sections extending through a radial distance of 2.5 cm. was prepared by Mr. Hemingway from fragment No. 3 of the original block (V4280 British Museum), the average distance between sections being slightly less than 2 mm.

A region was then selected which was representative and well preserved throughout the entire series. This has been reproduced (text-fig. 2) by means of tracings made with a photomicrographic projector. The drawings correspond to slides 1, 3, 5, 6, 7, 10, 11, 12, and 14, respectively.¹¹ Those sections (Nos. 2, 4, 8, 13) which show no appreciable change over the ones preceding them have been omitted from the series. Text-fig. 2*a* represents the section nearest (2 cm. from) the pith while *j* represents the outermost section. The tracheidal tissue is shown in black and the rays in white.

The most interesting feature of the wood lies in the fact that the new rays cut off from the older ones do not retain their individuality and increase uniformly in size as shown in *Cola togoensis* (Chattaway, '37); rather the rays and the tracheids form an anastomosing network. In order to understand this relationship an individual ray, A in text-fig. 2*a*, will be followed through the series of drawings. In *a* a small portion of the ray is being split off at the top and in *b* this is completed; in *c* a second ray segment is being cut off immediately below the first; in *f* this second division is complete, there being now three distinct rays; in the next figure, *g*, the first of the newly formed

¹¹Preserved in the British Museum (Natural History), London.



Text-fig. 2. *Cycadoxylon robustum*. Series of ray tracings showing the anastomosing nature of the ray-tracheid tissue.

rays has again fused with the "parent" ray, in *h* the second segment follows and is completely fused in *i*, resulting in a single individual ray again.

While these changes have been progressing in the upper portion of the ray A it will be noticed that another division has taken place in *b*, a little above the lower extremity of that portion of the ray shown in the figure; in *d* two small rays are cut off, while in *c* all four have again fused.

As a second example the ray E in text-fig. 2*a* may be followed: this divides to form two equal rays (E and F) in *b*; F divides again (figs. *d* and *e*), producing the two rays F and C in *f*, while F and E fuse again in *g* and remain thus throughout the remainder of the series. Although the structure of any single ray may not remain constant for any great radial distance the general tracheid-ray relationship at any point throughout the secondary wood shows no appreciable variation.

Medullosa Solmsii.—There remains much to be known of the Permian Medullosas of Chemnitz, and it is more than likely that when further knowledge is forthcoming those plants included within the genus must be segregated into a number of different genera. In general, the rays of the Permian forms are lower and more fusiform than those of the English and American species.

The detailed anatomy of the remarkable *M. Solmsii* is but little known, and the structure of the rays has, to my knowledge, never been figured. Weber and Sterzel (1896) figured a tangential cut through the outer ring of meristeles in a specimen of the variety *typica* but it is not sufficiently clear to show the structural details.

Five tangential sections have been prepared from two different meristeles by Mr. Hemingway and two prepared from a third meristele by the author. These sections include both the "internal" and "external" portions of the secondary wood composing the meristeles.

This wood is frequently disturbed by the passage of leaf traces. In the vicinity of the traces the rays are, as is usually the case, broader, lower and less regular in shape. In that

portion of the wood farthest from the traces the rays are quite tall but with a considerable admixture of lower uni- and bi-seriate rays (fig. 46). The rays do not approach the great height found in Type II, although there is no great dissimilarity between them and the rays of *Megaloxylon* which, as previously noted, is more or less intermediate between Types II and III.

Medullosa gigas B.R.—Slides of this species have not been available for study. However, judging from Renault's ('93-'96) description and figures the rays are similar to those of *Cycadoxylon robustum*, clearly justifying its inclusion within this group.

TYPE IV

Those plants included under Type IV have uniformly small rays, only a few cells high and mostly uniseriate, in striking contrast to either Types II or III. The rays of *Bilignea resinosa* (fig. 43) are typical for the group.

Endoxylon zonatum (fig. 44) presents a unique and very striking character in the oblique nature of the horizontal walls of the ray cells. This does not occur in all the rays, as may be seen in the figure, but the majority possess it.

It has been pointed out that the Calamopityeae includes genera which diverge very widely in certain of their characters. The variation in the structure of the secondary wood between certain members of the group is evident if either figs. 43 or 44 be compared with fig. 28 (*Calamopitys annularis*). Scott described such wood as cordaitean and it seems likely that the natural affinities of the following members of the Calamopityeae lie closer to the cordaitean-coniferous complex than to the pteridosperms: *Eristophyton fasciculare*, *E. Beinerianum*, *Endoxylon zonatum*, *Bilignea resinosa*, *B. solida*.

THE TRACHEIDAL MORPHOLOGY OF THE PTERIDOSPERMS

a. *Pitting types*.—The type of pits found in the tracheids of the secondary wood of certain of the pteridosperms is strikingly distinctive. The pits are irregular in size and shape (figs.

50, 51, 52), angular due to their crowded nature, and not arranged in any regular order. This type is characteristic of the following genera: *Heterangium*, *Lyginopteris*, *Rhetinangium*, *Stenomyelon*, *Calamopitys*, and *Medullosa* (*anglica* section). In addition to these, *Palaeopitys* and *Tetrastichia* may be assigned to this group, and also *Aneurophyton* judging from Kräusel and Weyland's description ('29): "die Wände der vierseitigen oder polygonalen Zellen sind in ihrer ganzen Ausdehnung mit netzformig angeordneten Tupfeln bedeckt." Although the pitting occasionally may be typically alternate (fig. 53) it is comparatively rare.

It should be noted, furthermore, that the pits of the metaxylem tracheids of these same woods are universally of this reticulate bordered type, differing from those of the secondary wood only in their often more irregular size and shape (fig. 49). Certain uncatalogued slides of *Stenomyelon tuedianum* Kidston in the Scott Collection show particularly well the rapid transition from scalariform tracheids in the protoxylem to reticulate in the metaxylem (figs. 45, 52, 53).

The great geological age of these plants, the generally primitive nature of the primary body, and this rapid transition, all indicate that this reticulate-bordered pitting is palingenetically the primitive type for the metaxylem and the secondary tracheids of this group; there is no indication in any of the genera from the simplest, such as *Palaeopitys* and *Tetrastichia*, to the more advanced members, such as *Lyginopteris*, that in the secondary wood this type of pitting was ever derived from an annular or scalariform type.

The close correlation of this reticulate-bordered pitting with the ray anatomy of the genera *Stenomyelon* to *Lyginopteris*, as shown in table II, is particularly significant. The range in structure of the primary body from a solid protostele through mixed protosteles to *Lyginopteris*, with a few scattered peripheral bundles, indicates clearly the comparative constancy of the secondary wood throughout the group.

The pits in the secondary wood of those members grouped under ray Types III and IV are either of the typical arauca-

rian-cordaitean type (figs. 54, 56) or are more or less scattered, round or oval. *Protopitys*, with its usually crowded elongate bordered pits, presents a very distinctive type (fig. 48). Such pits occur occasionally in *Mesoxylon multirame* but are not nearly as striking as in *Protopitys*. The figure of *Bilignea resinosa* (fig. 55) is more or less typical for that genus and *Eristophyton*. In *Cycadoxylon robustum* and *Megaloxylon Scotti*, although the pits are closely crowded, the arrangement is more regular (tending to vertical rows) than in those woods with the typical reticulate-bordered type. In *Cycadoxylon anomalum* the pits may be closely crowded (fig. 26) but they are generally more loosely arranged (figs. 24, 25, 27).

TABLE II
EXPLANATION IN TEXT

	Nature of primary body	Ray type	Pitting of radial walls of secondary xylem
<i>Tetrastichia</i>	Solid protostele	I	Reticulate-bordered
<i>Aneuophyton</i>	Solid protostele	I	Reticulate-bordered
<i>Palaeopitys</i>	Solid protostele	I	Reticulate-bordered
<i>Stenomyelon</i>	Solid protostele with 3 narrow "rays" of parenchyma	II	Reticulate-bordered
<i>Heterangium</i>	Mixed protostele	II	Reticulate-bordered
<i>Rhetinangium</i>	Mixed protostele	II	Reticulate-bordered
<i>Medullosa</i>	Mixed protostele	II	Reticulate-bordered
(<i>anglica</i> section)			
<i>Calamopitys</i>	Mixed protostele but more highly medullated than the above three	II	Reticulate-bordered
<i>Lyginopteris</i>	Medullated with distinct scattered peripheral bundles	II	Reticulate-bordered

b. *Pitting in the tangential walls of the tracheids of the secondary wood.*—Judging from accounts in the literature one would conclude that tangential pitting in Paleozoic woods is of rare occurrence. A careful examination of many of the stems of Devonian and Carboniferous seed plants or supposed seed plants reveals a somewhat different story. Reasons will be presented below which seem to indicate that the tangential walls of the secondary wood of all primitive seed plants, or

rather the stock from which seed plants arose, were pitted in the same manner as the radial walls.

In 1935 D. E. Thomas listed the following plants in which tangential pitting was known to occur: *Pitys antiqua*, *Palaeopitys Milleri*, *Callixylon triflve*, *C. Newberryi*, *Volkelia refracta*, *Mesoxylon multirame*, *Bilignea resinosa*, *Sphenoxylon eupunctata*.

Considering first those plants enumerated under ray Type I it may be noted that *Tetrastichia bupatides*, *Palaeopitys Milleri*, and *Aneurophyton germanicum* have all been reported as having tangential pitting. I have been able to examine slides of the first two in the Kidston and Gordon Collections, and for the third, Kräusel and Weyland ('29) write: "Die Mehrzahl der Tracheiden gleicht aber auch hier deren des sekundären Holzes, d.h. die Wände der vierseitigen oder polygonalen Zellen sind in ihrer ganzen Ausdehnung mit netzförmig angeordneten Tüpfeln bedeckt, die in ein bis sechs Reihen stehen können." . . .

The tracheids of these three plants then are pitted alike on the tangential and radial walls. Although the tangential walls of *Sphenoxylon eupunctata* are abundantly pitted, the pits are, as Thomas points out, in many cells scattered and not crowded as in the radial walls. This tendency to lose the tangential pits correlates interestingly enough with the more advanced nature of the primary cylinder of *Sphenoxylon* with its highly medullated primary body.

In addition to the above, I have observed tangential pitting in the following: *Sutcliffia insignis*, slide 71(0.73) University College, London; *Medullosa anglica*, slide A.M.7 Binney Collection, Cambridge; *Heterangium tillaeoides*, slide 1621 Williamson Collection, British Museum (Natural History); *Heterangium (punctatum?)*, Renault Collection, Natural History Museum, Paris; *Stenomyelon tuedianum*, uncatalogued slide in the Scott Collection, British Museum; *Heterangium* sp., slide 91 Gordon Collection, King's College, London, and numerous slides in my own collection.

The most striking occurrence of tangential pitting is found

in the last-mentioned *Heterangium* from Burntisland. Prof. Gordon has kindly allowed me to examine his slides and has placed in my hands a block containing portions of two stems. The excellent preservation of the structure made possible the preparation of a fine series of cellulose pulls through the zone of secondary wood. The latter is quite narrow, being little more than 0.5 mm. wide, but the pitting is *uniform on the tangential walls throughout* as shown in fig. 31. These specimens of *Heterangium* are closely comparable with *H. Grievei*.

It is particularly significant that the most primitive woods possessing secondary xylem (*Tetrastichia*, *Palaeopitys*, and *Aneurophyton*) should be pitted alike on the tangential and radial walls, and that the somewhat more advanced forms (*Sphenoxylon* and *Heterangium*) show a tendency to lose the tangential pitting. The above-noted specimens of *Heterangium* from Burntisland possess uniform pitting on the tangential walls, while in *H. tillaeoides* and *H. punctatum* the pits are scattered. In more highly specialized forms still, such as *Medullosa* and *Sutcliffia*, this character becomes relatively rare.

c. *Tracheid measurements*.—The great length of the tracheids of such pteridosperms as *Lyginopteris oldhamia* and *Medullosa anglica* has been noted by previous workers. Actual measurements have never been made, however, due to the difficulty of obtaining tangential longitudinal sections showing the entire length of the tracheids and the impossibility of obtaining complete serial sections with the older technique. It is surprising to note how few good tangential sections of the relatively common pteridosperms are available in the great English collections, a lack which may be attributed to the emphasis placed on the primary body.

The tracheids were measured by means of complete series of tangential cellulose pulls taken through the secondary wood. Particularly well-preserved tracheids were chosen and traced centripetally and centrifugally through successive pulls in order to check the length accurately.

The tracheid lengths given for *L. oldhamia* are based on two blocks containing exceptionally well-preserved secondary

wood. Although only approximately 25 tracheids were followed in their entirety, the results are representative since the variation in those measured was not great. The average length was found to be 5.8 mm., with a minimum and maximum of 5.1 and 6.7 mm., respectively.

The two species of *Medullosa*, *M. anglica* and *M. Noei*, have tracheids of remarkable length. The figures given in table III are based on only two complete measurements, the length being so great that it is difficult to find a complete cell. In the blocks from which the measurements of both species were obtained many tracheids were traced for well over 1.5 cm. with no termination, and it is almost certain that if figures could be based on more numerous complete cells the average length would be actually greater than that given.

In the following table figures for other gymnosperms are included for comparison, also for the dicotyledons taken from Bailey and Tupper ('18). These latter figures have been compounded from the numerous average measurements of the older wood (not the first annual ring) given for many genera and species included under the six groups.

TABLE III
TRACHEID LENGTHS (mm.)

	Average	Source of data
<i>Lyginopteris oldhamia</i>	5.8	Blocks supplied by J. R. Lomax and W. Hemingway
<i>Medullosa Noei</i>	24.0	Block in the Botany School Collections, Cambridge
<i>M. anglica</i>	17.5	Block supplied by J. R. Lomax
<i>Cycadoxylon robustum</i>	5.6	Block supplied by British Museum (Natural History)
Coniferae	3.6	Bailey & Tupper ('18), average of 35 gen. and 131 sp.
Cordaitales	5.	Bailey & Tupper ('18), average of 2 gen. and 2 sp.
Bennettitales	5.3	Bailey & Tupper ('18), average of 1 gen. and 2 sp.
Cycadales	6.8	Bailey & Tupper ('18), average of 1 gen. and 1 sp.
Ginkgoales	3.5	Bailey & Tupper ('18), average of 1 gen. and 1 sp.
Angiospermae-Dicotyledeae	1.2	Bailey & Tupper ('18), average of 262 gen. and 276 sp.

The great length of the tracheids in *Lyginopteris* and particularly in *Medullosa* is not surprising when one considers their transverse dimensions. In *M. Noei* and *M. anglica* these cells may reach a diameter of 0.25 mm. and, although some few are as small as 40 μ or less, the average diameter is greater than that of any other seed plant that has come to my attention. It is interesting to compare the tracheid diameter of a few representative members of the Carboniferous pteridosperms with the vessels of the earliest known (Lower Cretaceous) dicotyledons:

TABLE IV
TRACHEID AND VESSEL DIAMETERS OF CERTAIN PTERIDOSPERMS AND LOWER CRETACEOUS DICOTYLEDONS RESPECTIVELY

Species	Average diameter in μ^*	
	Vessel	Tracheid
<i>Lyginopteris oldhamia</i>		72.
<i>Medullosa anglica</i>		128.
<i>Rhetinangium Arberi</i>		45. - 85.
<i>Aptiana radiata</i> Stopes	28. - 40.	
<i>Woburnia porosa</i> Stopes	280. - 370.	
<i>Sabulia Scottii</i> Stopes	25. - 60.	
<i>Cantia arborescens</i> Stopes	30. - 50.	
<i>Hythia Elgari</i> Stopes	50. - 70.	

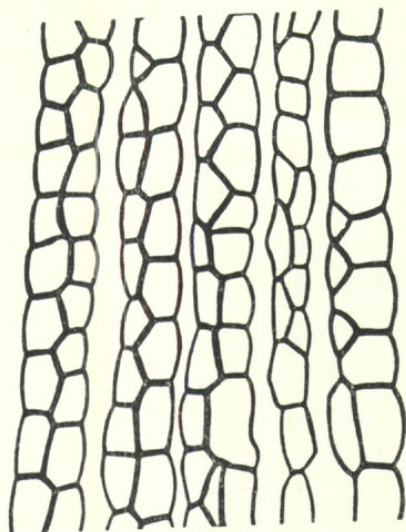
*Although the author has been able to study the slides of the five Lower Cretaceous dicotyledonous woods (*Aptiana*, *Woburnia*, *Sabulia*, *Cantia*, and *Hythia*) the figures are taken directly from Stopes ('12). The measurements for *M. anglica* are from slide 922, Andrews Coll.; for *L. oldhamia*, an average of about 600 cells, from slides 180, 183, Binney Coll., and 1147, 251, Scott Coll.

It is significant that the earliest known dicotyledonous woods described by Stopes ('12, '15) are, with the exception of *Woburnia porosa*, woods with vessels of exceptionally narrow diameter. The tracheids of the above pteridosperms not only equal but in some cases greatly surpass in diameter the vessels of these early angiosperms. The distinction, then, between diameters of tracheids and vessels in the higher plants vanishes when these fossils are taken into consideration.

The angular, irregular shape of the tracheids is particularly noticeable in *Medullosa* (*anglica* section), *Lyginopteris*,

and *Sutcliffia* (text-fig. 3). Tracheids of this shape are found in certain conifers and dicotyledons, and while perhaps of little significance their appearance is striking and has been commented upon by other paleobotanists.

It is significant that there is no trace to be found in the secondary wood of the pteridosperms of tracheids with scalariform pitting on their side or end walls such as has been described in certain families of angiosperms and considered to



Text-fig. 3. *Sutcliffia insignis*. Transverse section of secondary xylem (slide 5(040) Univ. College Coll., London). $\times 50$.

be an indication of a primitive nature. In view of the carefully compiled evidence obtained from living plants by such wood anatomists as Frost ('30, '31) and Kribs ('35) and since we have as yet no proof that the pteridosperms are ancestral to the dicotyledons, it seems best for the present to withhold further phylogenetic considerations in this respect.

LINES OF DEVELOPMENT IN THE PTERIDOSPERM COMPLEX

The discovery in recent years of new psilophytalean and supposed seed-plant stem remains, combined with a more detailed knowledge of the secondary wood of these early plants, materially facilitates a clearer understanding of the natural relationships of this Devonian-Carboniferous complex.

Since *Rhynia* presents the simplest known type of stele it will serve as a starting point in the present discussion. It is evident that two stelar types may have developed from such a protostele. With increase in size the primary body became either medullated or convoluted in order, supposedly, to maintain a more or less constant tracheid-parenchyma ratio. The fossil record clearly indicates that the actinostele arose very early, and like the protostele, acquired secondary wood at a very early date.

In a consideration of what appear to be primitive stelar types in which secondary wood is present, the genera under ray Type I (*Palaeopitys*, *Aneurophyton*, *Tetrastichia*, and *Sphenoxylon*) may be included. It seems reasonable to consider Prof. Harris' very interesting *Schizopodium* as an intermediate form between this group and the simple stelar types of *Rhynia* and *Asteroxylon*, but until more is known of the ontogeny of the "secondary" xylem of *Schizopodium* final judgment must be withheld.

A stele of the *Heterangium* type is not far removed from the above-mentioned group, and from this point a number of lines may have originated. First, with nearly complete medullation as in *Lyginopteris* and the development of extra-xylary rings as shown to occur in that genus the origin of the bizarre medullosas lies close at hand. Secondly, the cycadophytes may quite conceivably be derived from the *Heterangium*¹² type through such a form as *Megaloxyton*. Other than size there is not a great deal of difference between the primary body of the two. The peculiar aggregation of the tracheids to form a leaf trace in *Megaloxyton* is apparently due to the somewhat lower tracheid-parenchyma ratio of the primary body. The secondary wood is in certain respects intermediate between *Heterangium* and the cycadean type.

If it is ever possible to trace dicotyledonous ancestry to the

¹² The writer is quite aware of the danger of employing a few specific plants in building supposed lines of evolution. Names, however, are unavoidable in such a discussion, and it must be borne in mind that they are used only as a matter of convenience to convey *types* of structure represented.

Carboniferous it seems to me that the members of ray Type II present the most plausible group as far as potential plasticity is concerned. It is tempting to consider such phyletic implications with well-known pteridosperms of the *Lyginopteris* type but supporting facts are still notably lacking. As far as the stelar anatomy is concerned there is no sound basis for assuming such a line of development. Further discussion of the angiosperms with reference to the Paleozoic plants considered here could be only in the nature of a review or speculation. The subject has been adequately treated, from the standpoint of reproductive structures, by Dr. H. H. Thomas in his more recent papers.

SUMMARY

1. The distinguishing characteristics of the pteridosperms and their probable relationships to other groups are discussed generally.

2. The primary body of the stem and root of *Lyginopteris oldhamia* is considered in detail with reference to size variation, parenchyma-sclerenchyma relationship of the pith, and the nature of the primary xylem.

3. Medullary meristematic activity is discussed and a remarkable specimen described in which a complete medullary cylinder of supposedly secondary xylem is present.

4. It is pointed out that there are no gaps in the stelar variation of *L. oldhamia* sufficiently wide to permit segregation of varieties, whereas the foliage in organic connection or associated with the stems presents distinct specific segregation. This is explained partly on the basis of character phylogeny and partly on the physiological requirements of the primary body.

5. Evidence is summarized indicating the probable synonymy of *Calamopitys americana*, *C. saturni*, and *C. annularis*.

6. The primary body of certain other fossil and living plants is discussed in relation to "Size and Form" principles.

7. Four ray types are described for those plants generally included within the Pteridospermae.

8. The mechanics of ray division in *Cycadoxylon robustum* is shown to be essentially the same as Miss Chattaway described for *Cola togoensis*. In *Lyginopteris* the method is somewhat different and is described in detail.

9. *Cycadoxylon anomalum* is partially redescribed and is shown to possess a very constant ray structure and it is unquestionably distinct from *C. robustum*. The rays and tracheids are shown to anastomose.

10. Those woods included under Ray Types I and II, particularly the latter, possess a distinctive type of pitting, the pits being irregular in size and shape, closely crowded and irregularly (reticulately) arranged. The woods grouped under Ray Types III and IV possess either loosely arranged circular pits or the araucarian type.

11. It is pointed out that there is no evidence that the secondary tracheids of the pteridosperms ever possessed scalariform pitting. In the earliest known forms only well-developed bordered pitting is found.

12. It is shown that pitting in the tangential walls of the secondary tracheids is of much more common occurrence in these plants than is generally supposed. It is identical with the radial-wall pitting and occurs throughout the secondary wood in *Tetrastichia*, *Palaeopitys*, *Aneurophyton*, and certain specimens of *Heterangium*, and to a lesser extent in others.

13. The lengths of the secondary tracheids have been determined for *L. oldhamia* and *Medullosa Noei*.

14. As a whole it seems clear that the secondary wood offers more stable taxonomic characters than the primary wood, the latter being more readily affected by "Size and Form" factors.

ACKNOWLEDGMENT

For his constructive criticism and an inspiring introduction into modern concepts of morphology I am deeply indebted to Dr. H. Hamshaw Thomas of Downing College, Cambridge.

Although it would not be possible to enumerate all those who have assisted me I wish especially to express my indebted-

ness to Mr. W. N. Edwards and Mr. F. M. Wonnacott, who aided in every way possible during my periods of study at the British Museum (Natural History); to Professor John Walton, for the facilities of his Department and access to the Kidston Collection; to Professor W. H. Lang, for access to the collections of Manchester University; to Dr. R. Crookall and the British Geological Survey, for the loan of study material; to Professor Armand Renier, Professor Suzanne Leclercq and Dr. F. Stockmans, for their very valuable aid during my stay in Belgium.

For the grant of a special Fellowship during the summer of 1938 I wish to thank the Belgium American Educational Foundation not only for financial aid but for the splendid hospitality extended to me while in Belgium.

For aid and continuous encouragement of my paleobotanical studies I am deeply indebted to Dr. Robert E. Woodson. I am also grateful to the staff of the Missouri Botanical Garden for the facilities made available to me.

LITERATURE CITED

- Arnold, C. A. ('38). Paleozoic seeds. *Bot. Rev.* **4**: 205-234.
- Bailey, I. W. ('25). Some salient lines of specialization in tracheary pitting. *Ann. Bot.* **39**: 587-598.
- , and E. W. Sinnott ('14). Investigations on the phylogeny of the angiosperms. No. 2. Anatomical evidences of reduction in certain of the Amentiferae. *Bot. Gaz.* **58**: 36-60.
- , and W. W. Tupper ('18). Size variation in tracheary cells: I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms and angiosperms. *Proc. Am. Acad. Arts & Sci.* **54**: 149-204.
- Barghoorn, E. S. Jr., and W. C. Darrah ('38). *Horneophyton*, a necessary change of name for *Hornea*. *Harv. Bot. Mus. Leaf.* **6**: 142-144.
- Benson, Margaret ('14). *Sphaerostoma ovale* (*Conostoma ovale* et *intermedium* Williamson), a Lower Carboniferous ovule from Pettycur, Fifeshire, Scotland. *Trans. Roy. Soc. Edinb.* **50**: 1-15.
- Bertrand, P. ('13). Psilophytons des Grès de Matringhem. *Ann. Soc. Geol. du Nord* **42**: 157-163.
- Bower, F. O. ('30). *Size and form in plants*. London.
- Brongniart, A. (1828). *Histoire des végétaux fossiles*. Paris.
- Calder, Mary G. ('38). On some undescribed species from the Lower Carboniferous flora of Berwickshire; together with a note on the genus *Stenomyelon* Kidston. *Trans. Roy. Soc. Edinb.* **59**: 309-331.

- Chalk, L. ('35). The phylogenetic value of certain anatomical features in dicotyledonous woods. *Proc. Zesde Int. Bot. Congr.* **2**: 121-122.
- Chattaway, M. M. ('37). On the wood anatomy of the family Sterculiaceae. *Phil. Trans. Roy. Soc. London* **228B**: 313-366.
- Cookson, Isabel C. ('35). On plant remains from the Silurian of Victoria, Australia, that extend and connect Floras hitherto described. *Ibid.* **225B**: 127-148.
- Crookall, R. ('31). The genus *Lyginorachis* Kidston. *Proc. Roy. Soc. Edinb.* **51**: 27-34.
- Dorf, E. ('33). A new occurrence of the oldest known terrestrial vegetation from Beartooth Butte, Wyoming. *Bot. Gaz.* **95**: 240-256.
- Esau, Katherine ('36). Ontogeny and structure of collenchyma and of vascular tissues in celery petioles. *Hilgardia* **10**: 431-467.
- , ('38). Ontogeny and structure of the phloem of tobacco. *Ibid.* **11**: 343-406.
- Frost, F. H. ('30a). Specialization in secondary xylem of dicotyledons. I. Origin of vessel. *Bot. Gaz.* **89**: 67-94.
- , ('30b). *Ibid.* II. Evolution of end wall of vessel segment. *Ibid.* **90**: 198-212.
- , ('31). *Ibid.* III. Specialization of lateral wall of vessel segment. *Ibid.* **91**: 88-96.
- Gibson, R. J. Harvey (1894). Contributions towards a knowledge of the anatomy of the genus *Selaginella*, Spr. *Ann. Bot.* **8**: 133-206.
- Gordon, W. T. ('38). On *Tetrastichia bupatides*: a Carboniferous pteridosperm from East Lothian. *Trans. Roy. Soc. Edinb.* **59**: 351-370.
- Gothan, W. ('23). *Leitfossilien. Dritte Lieferung. Ein Hilfsbuch zum Bestimmen, etc.* Berlin.
- Halle, T. G. ('29). Some seed-bearing pteridosperms from the Permian of China. *Kungl. Svenska Vet. Akad. Handl.* **6**^s: 3-24.
- , ('33). The structure of certain fossil spore-bearing organs believed to belong to pteridosperms. *Ibid.* **12**^c: 1-103.
- , ('36). Notes on the Devonian genus *Sporogonites*. *Svensk Bot. Tid.* **30**: 613-623.
- Harris, T. M. ('29). *Schizopodium Davidi* gen. et sp. nov. A new type of stem from the Devonian rocks of Australia. *Phil. Trans. Roy. Soc. London* **217B**: 395-410.
- , ('32). The fossil flora of Scoresby Sound, East Greenland. *Medd. om Grønland* **85**: Nr. 5.
- Kidston, R. ('23-'25). Fossil plants of the Carboniferous rocks of Great Britain. *Mem. Geol. Surv. Gt. Br. Palaeont.* **2**: 1-681.
- , and D. T. Gwynne-Vaughan ('12). On the Carboniferous flora of Berwickshire. Pt. 1. *Stenomyelon tuedianum* Kidst. *Trans. Roy. Soc. Edinb.* **48**: 263-271.
- , and W. H. Lang ('20-'21). On Old Red Sandstone plants showing structure. *Ibid.* **52**: 603-627, 643-680, 831-854.
- , ———, ('23). On *Palaeopitys Milleri* M'Nab. *Ibid.* **53**: 409-418.
- Kräusel, R. ('36). Neue Untersuchungen zur paläozoischen Flora: Rheinische Devonflora. *Ber. deut. bot. Ges.* **54**: 307-328.

- , and H. Weyland ('29). Beiträge zur Kenntnis der Devonflora III. Abhand. d. Senckenb. Nat. Ges. **41**: 317-359.
- Kribs, D. A. ('35). Salient lines of structural specialization in the wood rays of dicotyledons. Bot. Gaz. **96**: 547-557.
- Mathieu, G. ('37). Recherches géologiques sur les terrains paléozoïques de la Région Vendéenne. Lille.
- Radforth, N. W. ('38). An analysis and comparison of the structural features of *Dactylothea plumosa* Artis sp. and *Senftenbergia ophiodermatica* Goppert sp. Trans. Roy. Soc. Edinb. **59**: 385-396.
- Read, C. B. ('37). The flora of the New Albany Shale. Part 2. Calamopityeae and their relationships. U.S. Dept. Int., Geol. Surv. Prof. Paper 186-E.
- Renault, B. (1893-'96). Bassin houiller et permien d'Autun et d'Épinac. Études des Gîtes Min. de la France. Paris.
- Saporta, G., et A. F. Marion (1885). L'évolution du règne végétal. I. Paris.
- Schopf, J. M. ('39). *Medullosa distelica*, a new species of the anglica group of *Medullosa*. Am. Jour. Bot. **26**: 196-207.
- Scott, D. H. (1899). On the primary wood of certain Araucarioxylons. Ann. Bot. **13**: 615-619.
- , ('02a). The old wood and the new. New Phyt. **1**: 25-30.
- , ('02b). On the primary structure of certain Palaeozoic stems with the *Dadoxylon* type of wood. Trans. Roy. Soc. Edinb. **40**: 331-365.
- , ('17). The Heterangiums of the British Coal Measures. Jour. Linn. Soc. Bot. **44**: 59-105.
- , ('18). Notes on *Calamopitys* Unger. *Ibid.* 205-232.
- , ('23). Studies in fossil botany. Pt. 2 3d ed. London.
- , ('24a). Fossil plants of the *Calamopitys* type from the Carboniferous rocks of Scotland. Trans. Roy. Soc. Edinb. **53**: 569-596.
- , ('24b). Extinct plants and problems of evolution. London.
- , and E. C. Jeffrey ('14). On fossil plants showing structure, from the base of the Waverly Shale in Kentucky. Phil. Trans. Roy. Soc. London **205B**: 315-373.
- Seward, A. C. (1897). A contribution to our knowledge of *Lyginodendron*. Ann. Bot. **11**: 65-86.
- , (1899). Notes on the Binney Collection of coal-measure plants. Pt. II. *Megaloxylon*, gen. nov. Proc. Camb. Phil. Soc. **10**: 158-174.
- , ('17). Fossil plants. Vol. 3. Cambridge.
- Solms-Laubach, H. (1896). Ueber die seinerzeit von Unger beschrieben strukturbietenden Pflanzenreste des Unterculms von Saalfeld in Thüringen. Abhand. d. k. preuss. Geol. Landes. N.F. **23**: 1-100.
- Steidtmann, W. E. ('37). A preliminary report on the anatomy and affinities of *Medullosa noei* sp. nov. from the Pennsylvanian of Illinois. Am. Jour. Bot. **24**: 124-125.
- Stopes, Marie C. ('12). Petrifaactions of the earliest European angiosperms. Phil. Trans. Roy. Soc. London **203B**: 75-100.
- , ('15). Catalogue of the Mesozoic plants in the British Museum. The Cretaceous Flora. Pt. II. 260-294.
- Stur, D. (1885). Die Culm Flora. Abhand. d. k.k. Geol. Reichs. XI.
- Thomas, D. E. ('35). A new species of *Calamopitys* from the American Devonian. Bot. Gaz. **97**: 334-345.

- Thomas, H. H. ('25). The Caytoniales, a new group of angiospermous plants from the Jurassic rocks of Yorkshire. *Phil. Trans. Roy. Soc. London* **213B**: 299-363.
- , ('33). On some pteridospermous plants from the Mesozoic rocks of South Africa. *Ibid.* **222B**: 193-264.
- , ('36). Palaeobotany and the origin of the angiosperms. *Bot. Rev.* **2**: 397-418.
- , ('38a). Palaeobotany and floral morphology. *Compte Rend. du Deux. Congr. de Strat. Carbon. Heerlen* (1935): 1323-1333.
- , ('38b). Pteridosperm evolution and the angiospermae. *Ibid.* 1311-1321.
- Walton, J. ('35). Scottish Lower Carboniferous plants: The fossil hollow trees of Arran and their branches (*Lepidophloios Wunschianus* Carruthers). *Trans. Roy. Soc. Edinb.* **58**: 313-337.
- Weber, O., and J. T. Sterzel (1896). Beiträge zur Kenntniss der Medulloseae. *Ber. d. Naturwiss. Ges. zu Chemnitz*. **13**: 44-143.
- Williamson, W. C. (1878). On the organization of the fossil plants of the coal measures. Pt. II. *Phil. Trans. Roy. Soc. London*.
- , and D. H. Scott (1896). Further observations, etc. Pt. III. *Lyginodendron* and *Heterangium*. *Ibid.* **186**: 703-779.
- Zalessky, M. D. ('11). Étude sur l'anatomie du *Dadoxylon Tchihatcheffi* Goeppert sp. *Mem. Comité Geol. Russe. N.S.* **68^o**: St. Petersbourg.
- Zeiller, R. (1897). Observations sur quelques fougères des dépôts Houillers d'Asie Mineure. *Bull. Bot. Soc. Fr.* **44**: 195-218.

EXPLANATION OF PLATE

PLATE 5

Lyginopteris oldhamia. Transverse sections of stems, all $\times 7.5$.

Fig. 1. Andrews Coll. 1140.

Fig. 2. Manchester Coll. R838b.

Fig. 3. Williamson Coll. 1885HH.



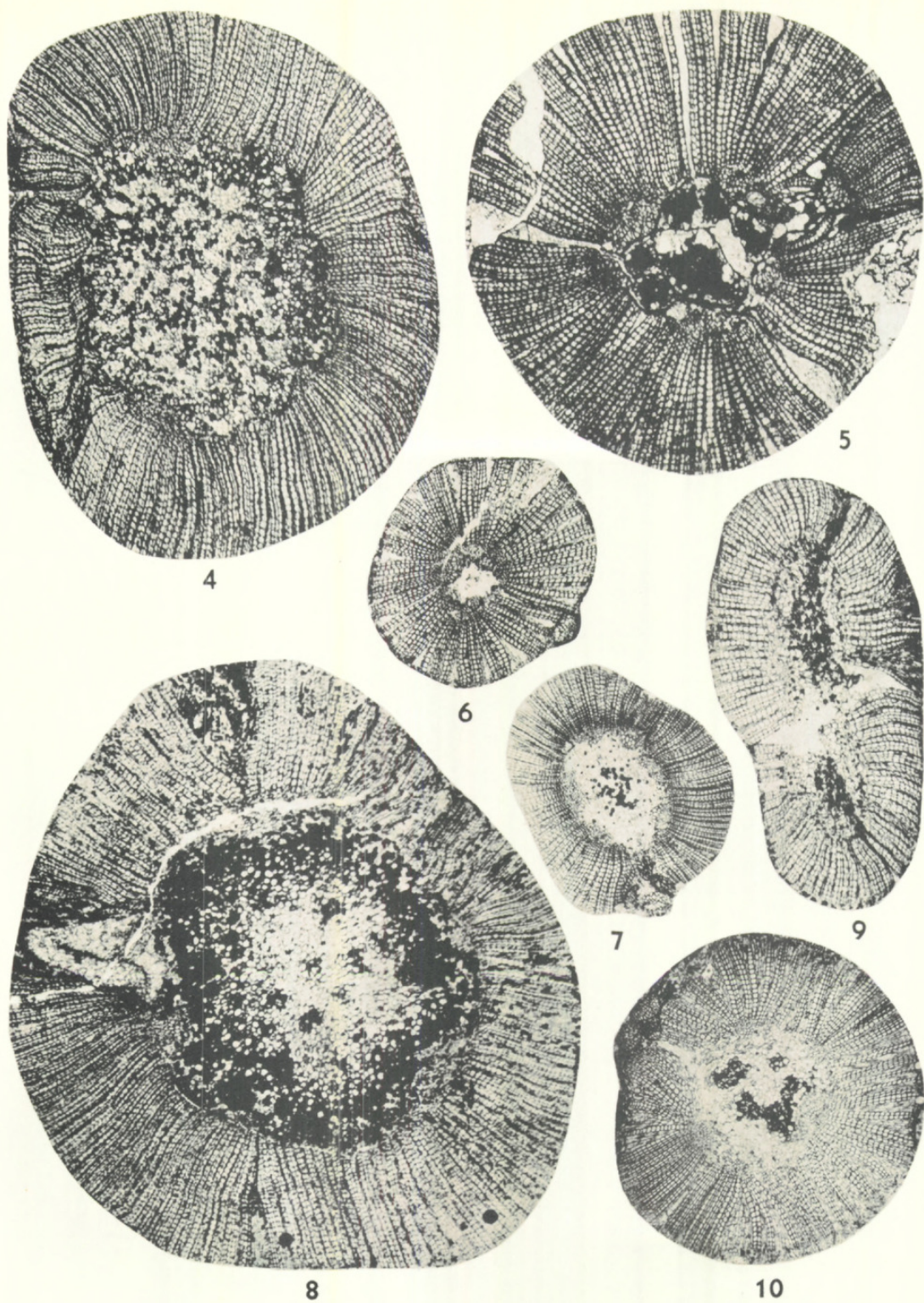
ANDREWS — PTERIDOSPERM ANATOMY

EXPLANATION OF PLATE

PLATE 6

Lyginopteris oldhamia. Transverse sections of stems, all $\times 7.5$.

- Fig. 4. Williamson Coll. 1116.
- Fig. 5. Binney Coll. 180. From the type specimen.
- Fig. 6. Andrews Coll. 611.
- Fig. 7. Scott Coll. 637.
- Fig. 8. Scott Coll. 251.
- Fig. 9. Cash (Manchester) Coll. Q10.
- Fig. 10. Williamson Coll. 1882.



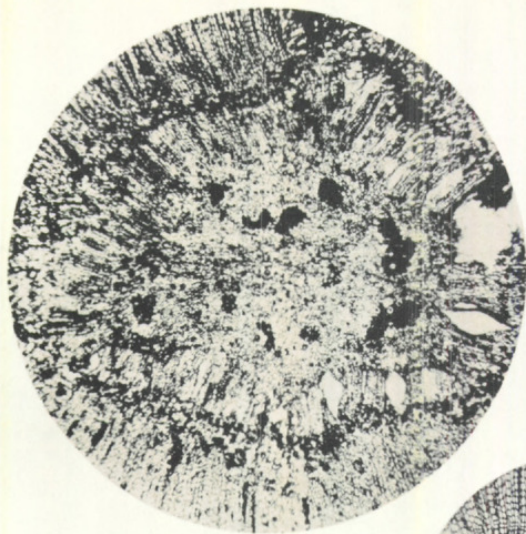
ANDREWS — PTERIDOSPERM ANATOMY

EXPLANATION OF PLATE

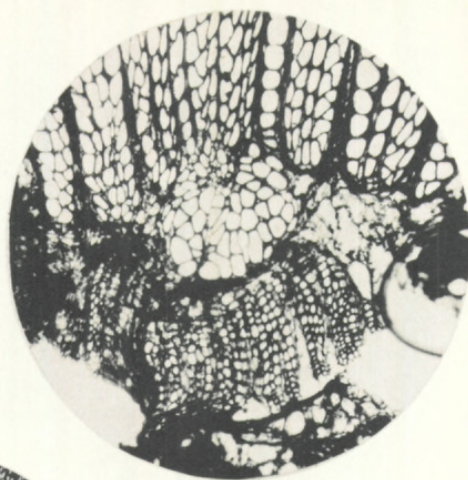
PLATE 7

Lyginopteris oldhamia.

- Fig. 11. Central portion of fig. 14 more highly magnified. $\times 9$.
Fig. 12. Showing secondary centripetal xylem associated with a primary bundle. Manchester Coll. 1625. $\times 27$.
Fig. 13. Anomalous meristematic activity. Manchester Coll. R1059. $\times 8$.
Fig. 14. Stem with complete ring of "centripetal" secondary xylem. Manchester Coll. R1060. $\times 7$.
Fig. 15. Same showing scattered nature of primary xylem adjacent to normal secondary xylem. $\times 26$.
Fig. 16. Portion of fig. 14 shown at magnification of $\times 26$.



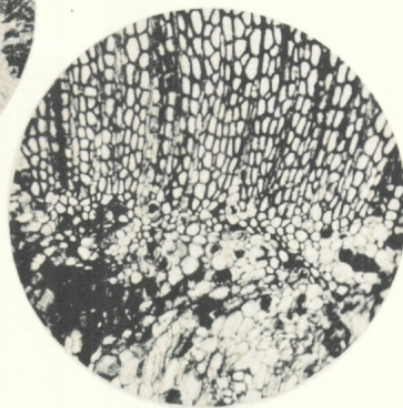
11



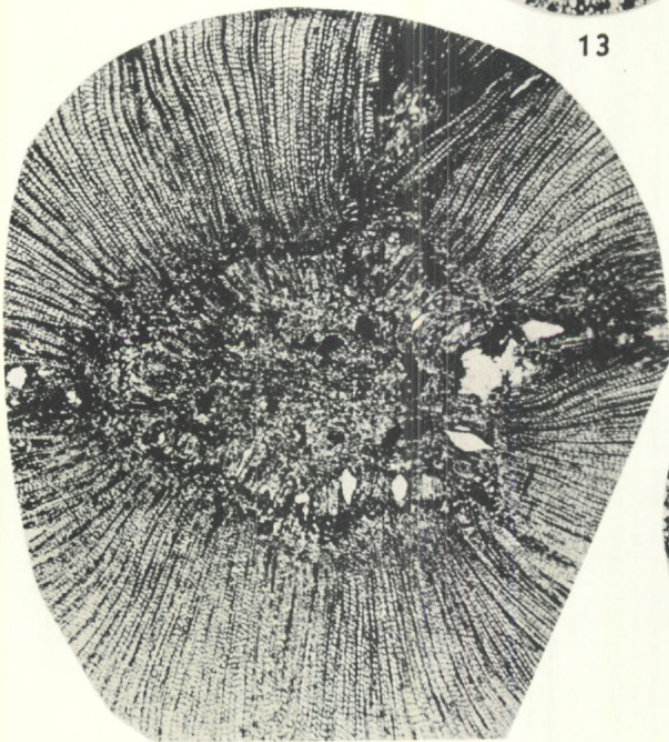
12



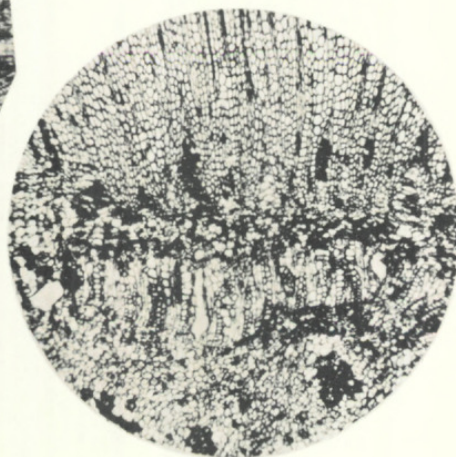
13



15



14

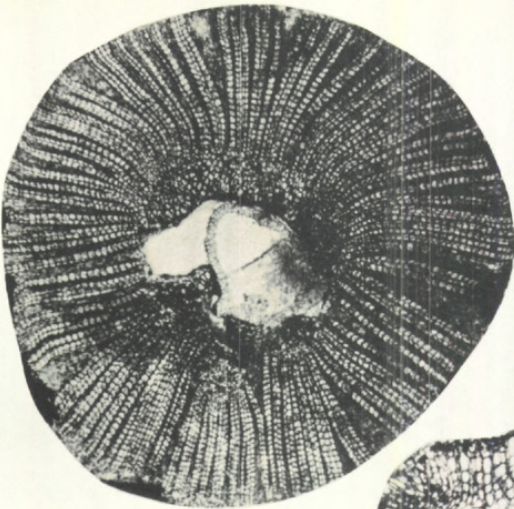


16

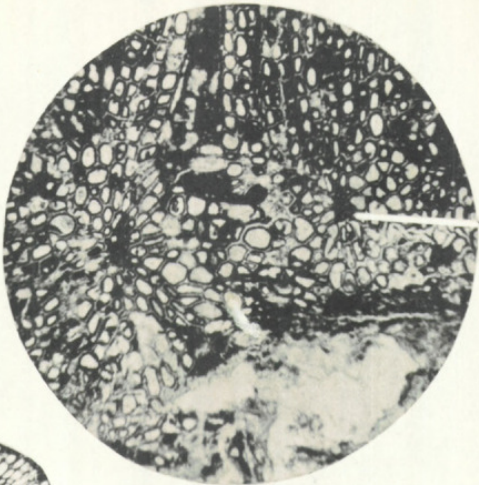
EXPLANATION OF PLATE

PLATE 8

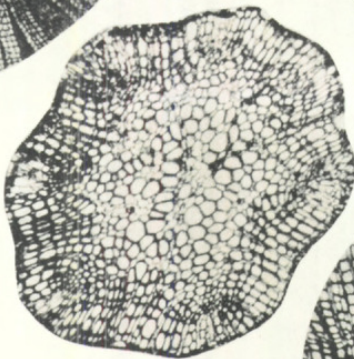
- Fig. 17. *Lyginopteris oldhamia*. Manchester Coll. 1626. $\times 7.5$.
Fig. 18. *Calamopitys saturni*. Berlin Coll. 74. $\times 33$.
Fig. 19. *Lyginopteris oldhamia*. From an uncatalogued slide in the Scott Coll. (labeled 46) showing meristematic activity in the pith, with no lignification. $\times 14$.
Lyginopteris oldhamia. Transverse sections of roots, all $\times 23$.
Fig. 20. Scott Coll. 647.
Fig. 21. Scott Coll. 647.
Fig. 22. Manchester Coll. 1060.
Fig. 23. Scott Coll. 645.



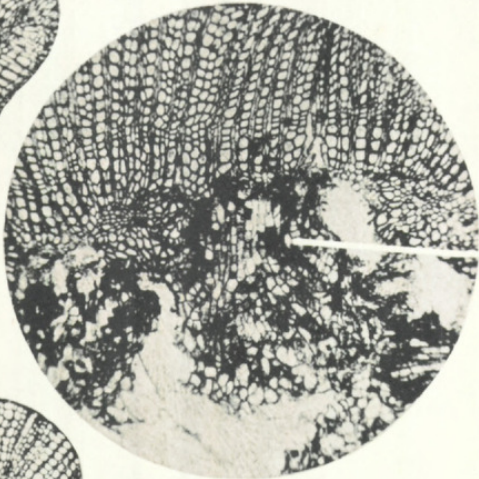
17



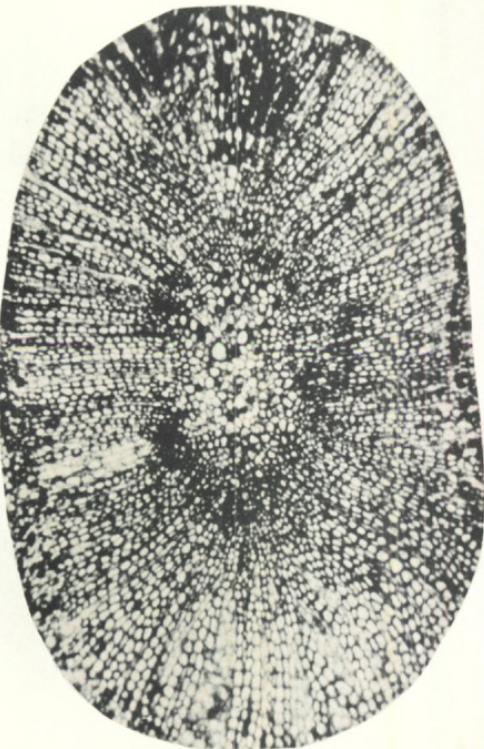
18



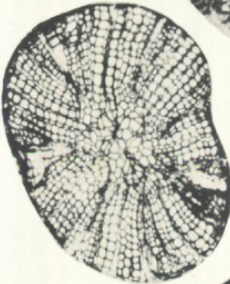
21



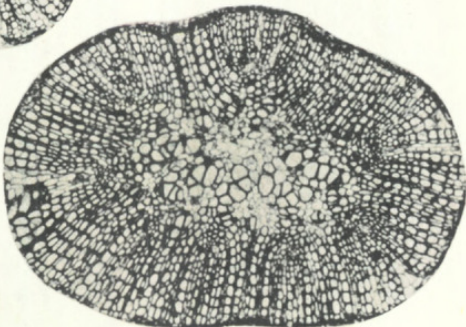
19



20



22



23

EXPLANATION OF PLATE

PLATE 9

Cycadoxylon anomalum. Pitting in the radial walls of the tracheids of the secondary xylem.

Fig. 24. Scott Coll. 651. $\times 185$.

Fig. 25. Scott Coll. 651. $\times 100$.

Fig. 26. Scott Coll. 651. $\times 185$.

Fig. 27. Scott Coll. 651. $\times 146$.

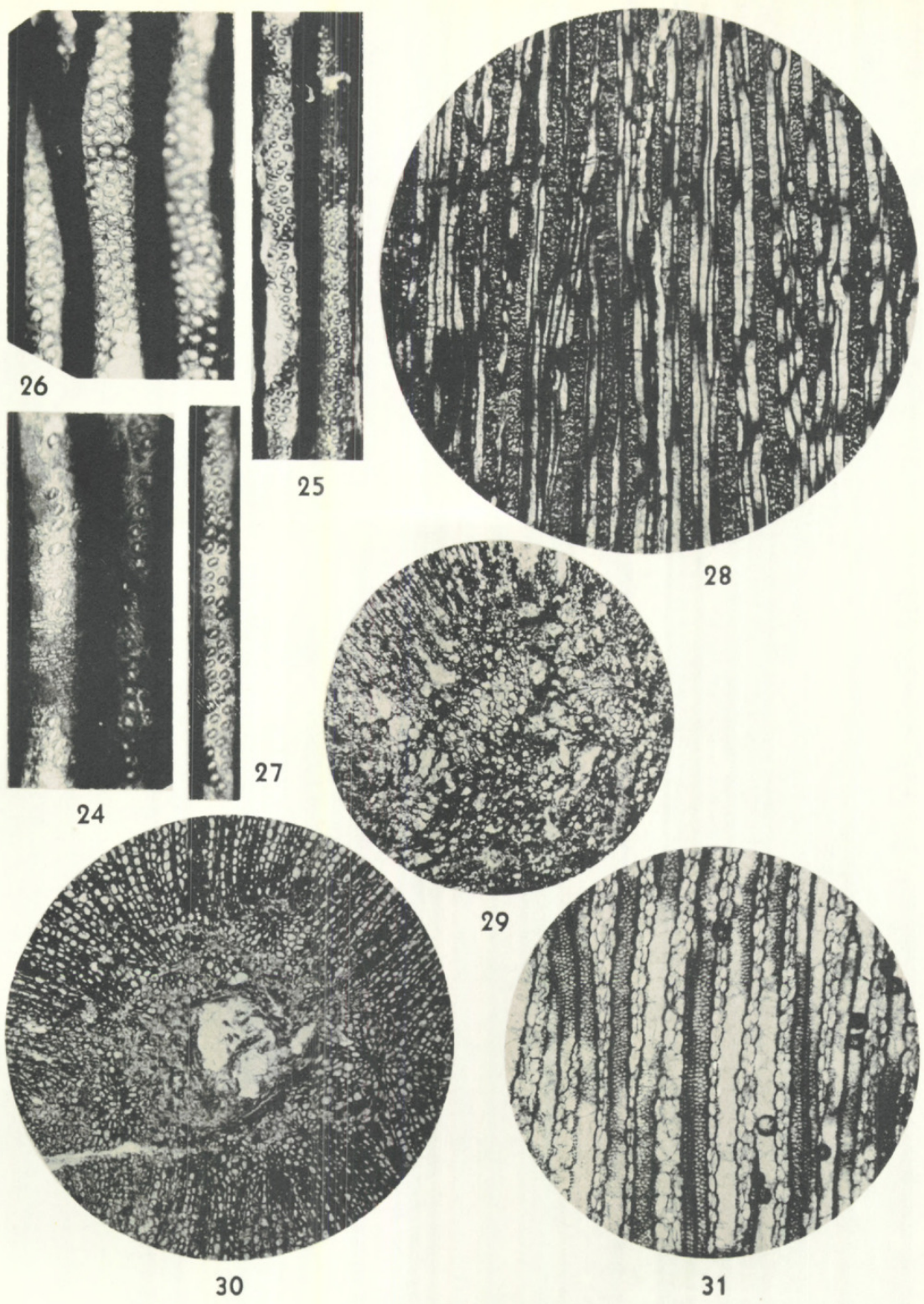
Calamopityx annularis.

Fig. 28. Tangential section through the secondary xylem. Berlin Coll. 49. $\times 17$.

Fig. 29. Showing portion of incomplete primary xylem ring. Berlin Coll. 97.
 $\times 11$.

Fig. 30. Primary body. Berlin Coll. 74. $\times 14$.

Fig. 31. *Heterangium* sp. Showing pitting in tangential walls of secondary tracheids. Gordon Coll. 91. $\times 55$.



ANDREWS — PTERIDOSPERM ANATOMY

EXPLANATION OF PLATE

PLATE 10

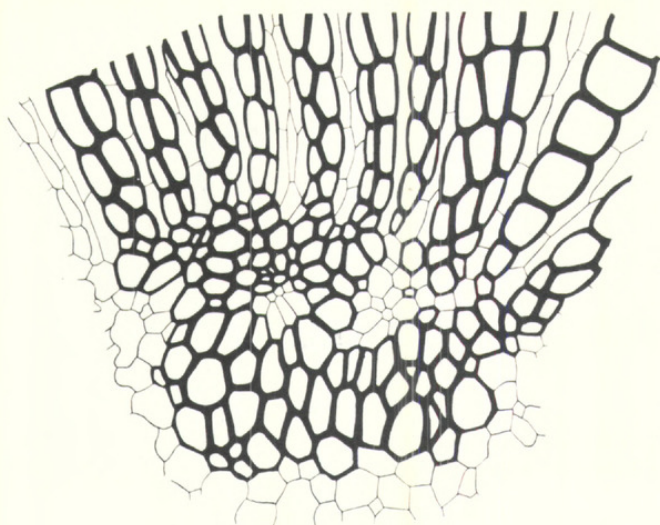
Lyginopteris oldhamia. Transverse sections showing variation in the nature of the primary xylem bundles, all $\times 65$.

Fig. 32. The normal type of bundle. Williamson Coll. 1882.

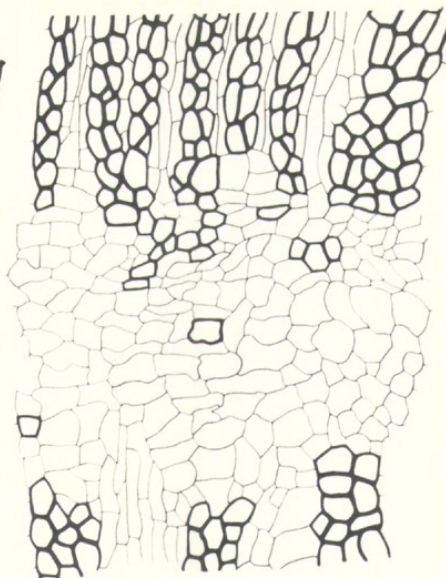
Fig. 33. From the specimen with complete ring of centripetal secondary xylem (fig. 14). The primary xylem is for the most part not aggregated into distinct bundles but consists of a few scattered cells.

Fig. 34. University College (London) Coll. M22V(19).

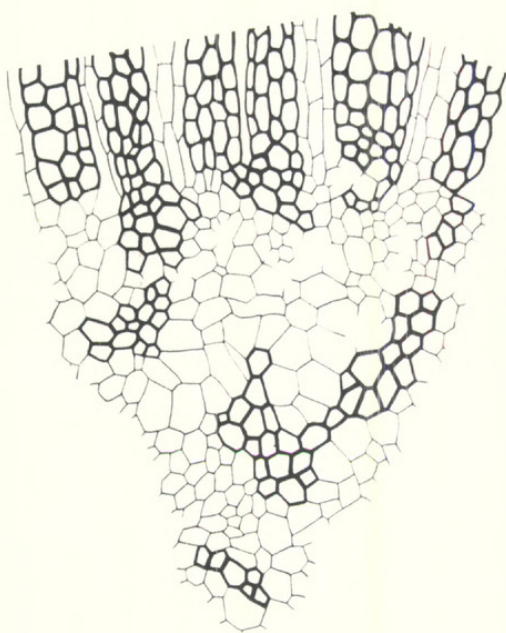
Fig. 35. Manchester Coll. 1626.



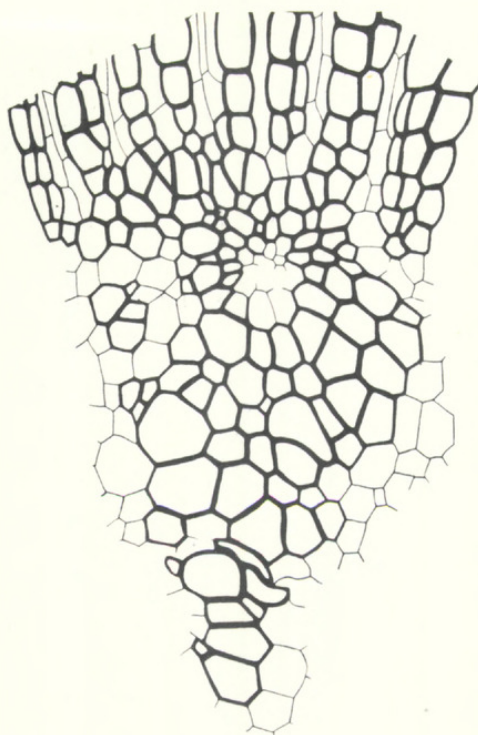
32



33



34

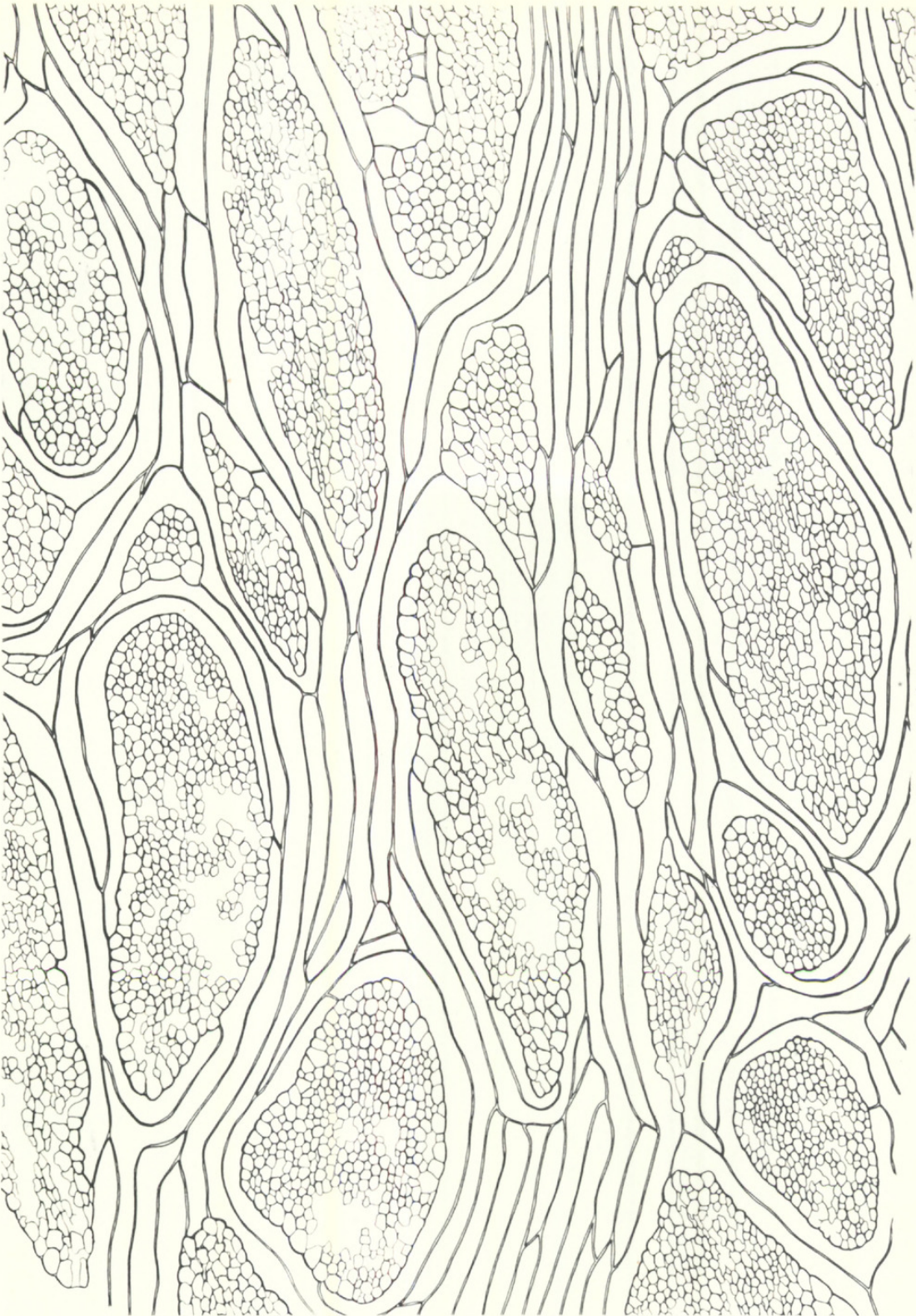


35

EXPLANATION OF PLATE

PLATE 11

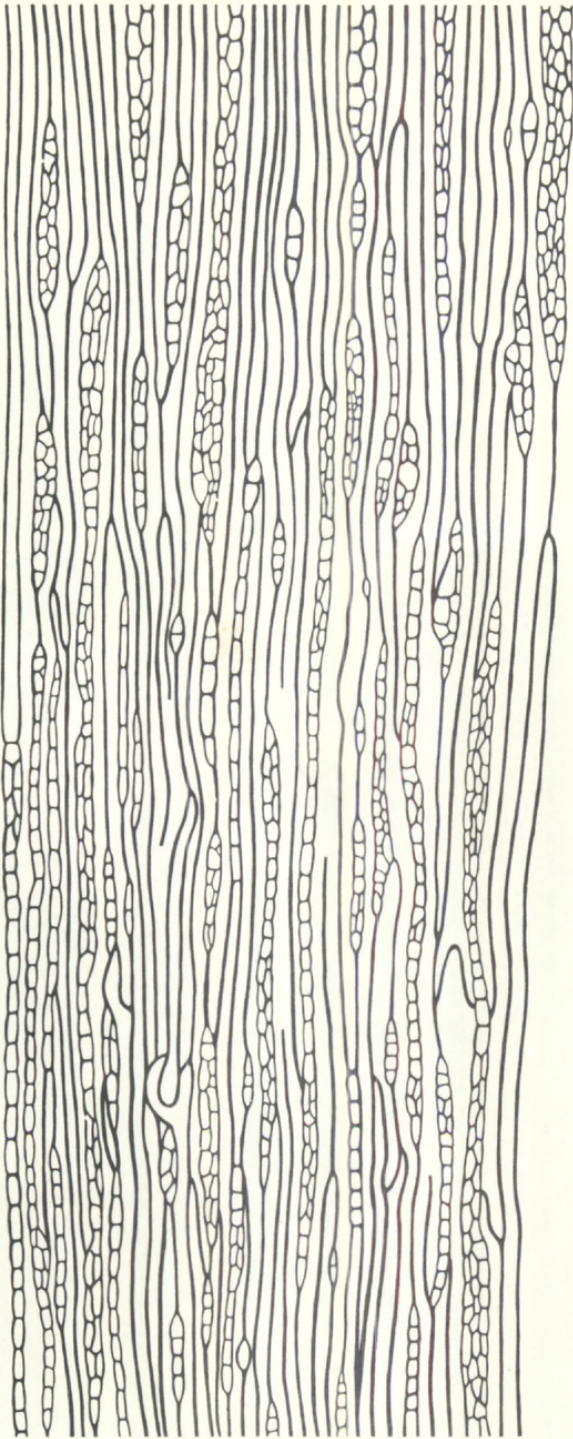
Fig. 36. *Cycadoxylon anomalum*. Tangential section through the secondary xylem. $\times 40$.



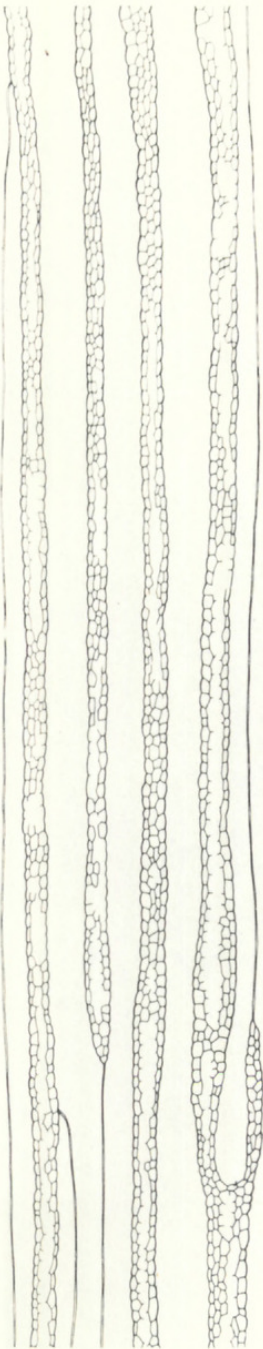
EXPLANATION OF PLATE

PLATE 12

- Fig. 37. *Sphenoxylon eupunctata*. Tangential section through secondary wood.
× 40.
- Fig. 38. *Sutcliffia insignis*. Tangential section through secondary wood. × 40.



37



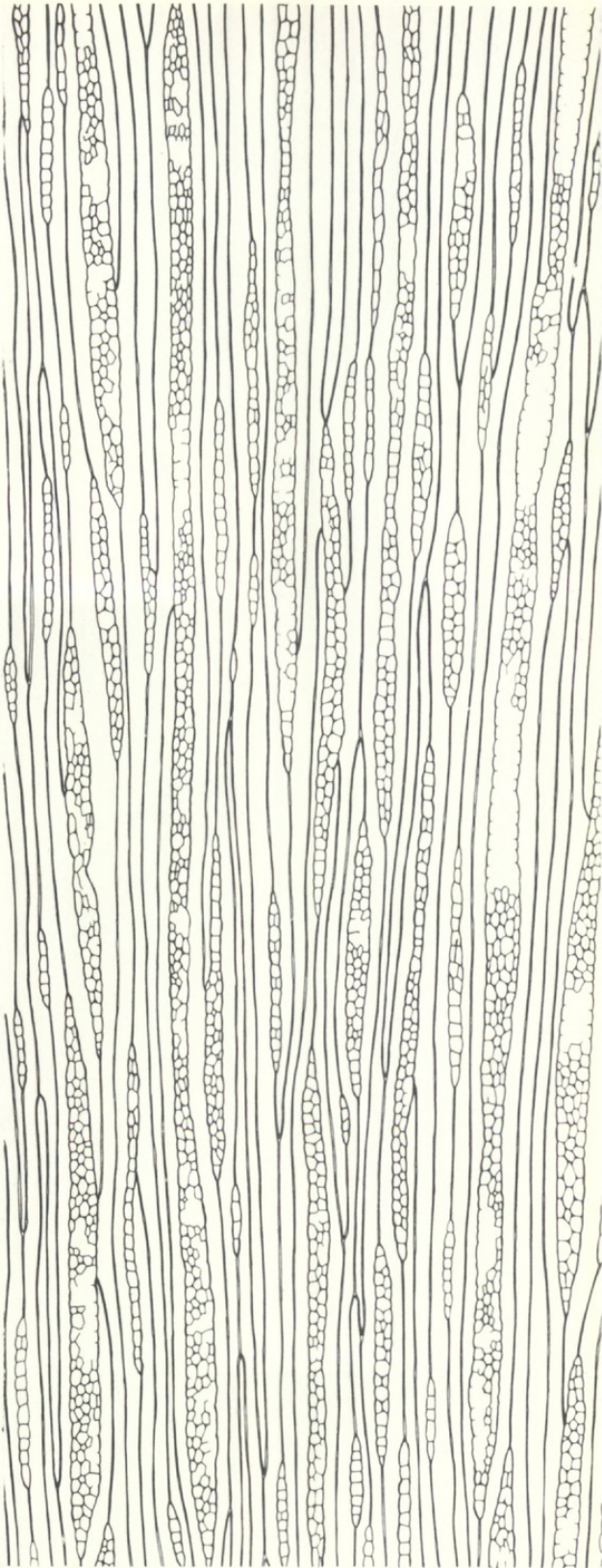
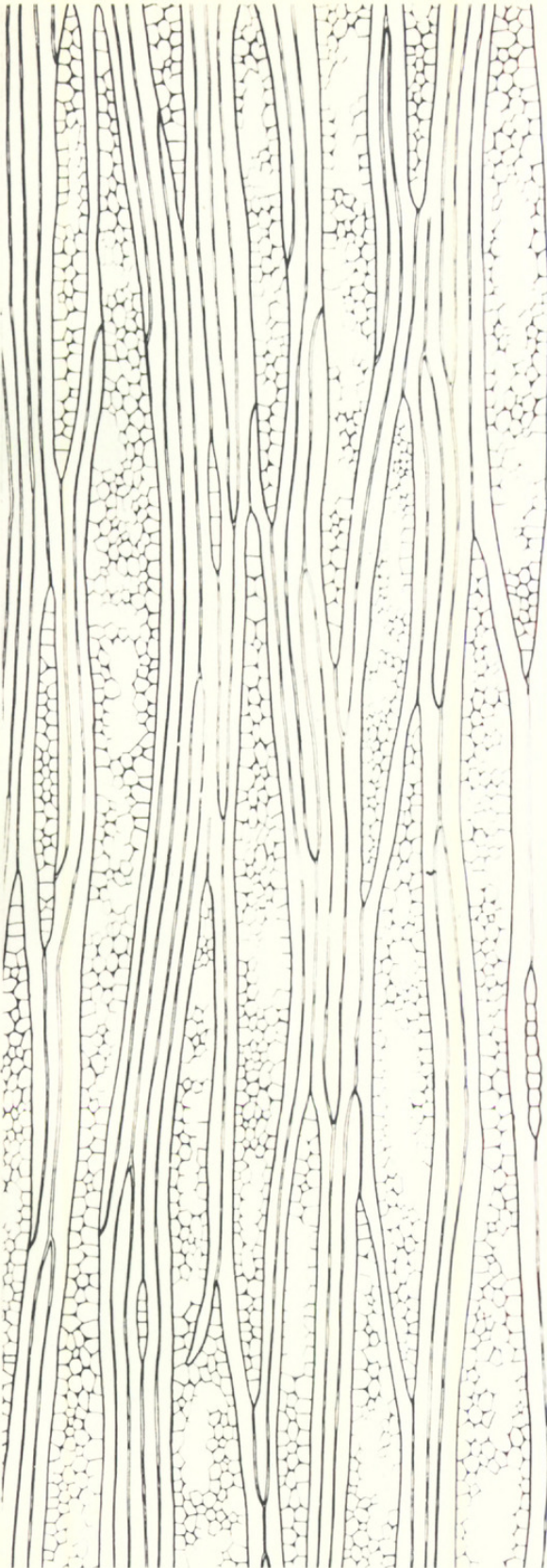
38

EXPLANATION OF PLATE

PLATE 13

Fig. 39. *Cycadoxylon robustum*. Tangential section through secondary xylem.
× 40.

Fig. 40. *Megaloxylon Scotti*. Tangential section through secondary xylem.
× 40.

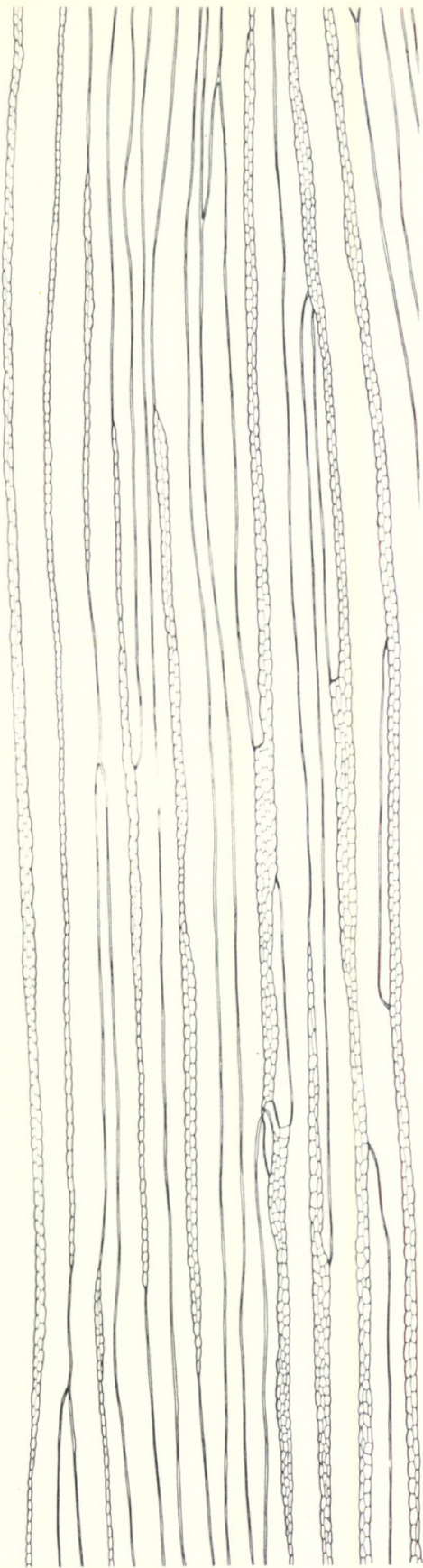


EXPLANATION OF PLATE

PLATE 14

Fig. 41. *Medullosa Noei*. $\times 40$.

Fig. 42. *Lyginopteris oldhamia*. Showing increase in size of two rays in passing from the pith towards the periphery of the secondary xylem; *a*, the rays bordering on the pith; *b*, the rays about half-way out; *c*, the rays near the outside limit of the secondary xylem. $\times 40$.



41



a

b

c

42

EXPLANATION OF PLATE

PLATE 15

- Fig. 43. *Bilignea resinosa*. Tangential section through secondary wood. $\times 40$.
Fig. 44. *Endoxylon zonatum*. Same as above.
Fig. 45. *Stenomyelon tuedianum*. Longitudinal section through primary wood showing transition from protoxylem to metaxylem. $\times 300$.
Fig. 46. *Medullosa Solmsii*. Tangential section through secondary wood. Rays in black. $\times 37$.

Pitting in the tracheids of certain woods included within the Pteridospermae.

All figures of the radial walls of secondary tracheids, except 49, which is a metaxylem tracheid; figs. 49, 50, 51, 52, 53, traced from photographs; figs. 47, 48, 54, 55, 56, from camera-lucida drawings. All approximately $\times 170$.

- Fig. 47. *Mesoxylon multirame*. (Scott Coll. 2360).
Fig. 48. *Protopitys radicans*. (Kidston Coll. 3111).
Fig. 49. *Rhetinangium Arberi*. (Gordon Coll. 1077).
Fig. 50. *Rhetinangium Arberi*. (Gordon Coll. 986).
Fig. 51. *Calamopitys annularis*. (Berlin Coll. 101.44).
Fig. 52. *Stenomyelon tuedianum*. (From uncatalogued slide in the Scott Coll.).
Fig. 53. Same as above.
Fig. 54. *Dadoxylon* sp. (Scott Coll. 1508).
Fig. 55. *Bilignea resinosa*. (Kidston Coll. 2742).
Fig. 56. *Poroxyton Edwardsii*. (Scott Coll. 3336).



Andrews, Henry N. 1940. "On the Stelar Anatomy of the Pteridosperms with Particular Reference to the Secondary Wood." *Annals of the Missouri Botanical Garden* 27, 51–118. <https://doi.org/10.2307/2394284>.

View This Item Online: <https://www.biodiversitylibrary.org/item/54742>

DOI: <https://doi.org/10.2307/2394284>

Permalink: <https://www.biodiversitylibrary.org/partpdf/3099>

Holding Institution

Missouri Botanical Garden, Peter H. Raven Library

Sponsored by

Missouri Botanical Garden

Copyright & Reuse

Copyright Status: In copyright. Digitized with the permission of the rights holder.

License: <http://creativecommons.org/licenses/by-nc-sa/3.0/>

Rights: <https://biodiversitylibrary.org/permissions>

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.