SOME CALAMITEAN PLANTS FROM THE LOWER CARBONIFEROUS OF SCOTLAND

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ABSTRACT. Material of the plant previously known as *Protocalamites pettycurensis* Scott is described, and evidence is given for its identity with *Archaeocalamites goeppertii* Solms. New information has been obtained concerning the nodal structure, the root-bearing stems, and root system of the plant. A new petrified cone species (*Protocalamostachys pettycurensis* sp. nov.), probably borne on *Archaeocalamites goeppertii* stems, is described.

THE name *Protocalamites pettycurensis* was proposed by Scott (1920) for some petrified stems which he had previously (1901) named *Calamites pettycurensis*. The stems were from the famous Pettycur Limestone of the Calciferous Sandstone Series (Lower Carboniferous). The stems are characterized by the presence of centripetal wood on the side of the carinal canal towards the pith. Lotsy (1909) distinguished the genus *Protocalamites* Goebel on this character, although Goebel (1906) had originally used it in a wider sense and included in it a number of species based on compressions and casts.

Unpublished investigations on *P. pettycurensis* by the late Dr. M. Benson have been quoted (cf. Scott 1920, Walton 1940) as indicating that the vascular bundles alternate at the node just as they do typically in *Calamites*. On the other hand, however, Dr. J. A. R. Wilson after preliminary examination (unpublished) of stems identified as *P. pettycurensis* from the famous Arran tree-stumps came to the conclusion that there was no alternation at the node. Walton (1940, 1949) states that if both Dr. Benson and Dr. Wilson are right, then *P. pettycurensis* is of the *Mesocalamites* type of Hirmer (1927) and distinct from *Archaeocalamites*. This presupposes that the Pettycur and Arran tree specimens belong to the same plant. As nothing was known about the morphology or detailed anatomy of *P. pettycurensis*, it remained a problematical plant.

Closely associated with some vegetative remains of this plant in a block from Pettycur have been discovered some fertile parts; these are described in the second part of this paper.

Material and methods. The material used in the present investigation is from two localities, viz. the Pettycur Limestone from the Calciferous Sandstone Series of the Lower Carboniferous at Pettycur, Fife, and Arran tree-stumps of the Isle of Arran, again of Lower Carboniferous age.

A large number of serial peel sections were prepared from a number of blocks of both Pettycur and Arran tree material by the well-known peel method of Joy, Willis, and Lacey (1956). The serial peel sections were about 33 sections to 1 mm. For the study of cone specimens the peels were taken at about 40 to 1 mm. The peels were mounted temporarily in xylol for examination.

[Palaeontology, Vol. 6, Part 3, 1963, pp. 408–29, pls. 59–60.]

DESCRIPTIONS

Archaeocalamites goeppertii Solms

Plate 59, figs. 1–10, Plate 60, figs. 1–2; text-figs. 1–5

Comparison. There is no doubt that the material previously identified as *Protocalamites pettycurensis* from the two localities is closely similar except possibly in certain minor details. This will be discussed at the end of the paper.

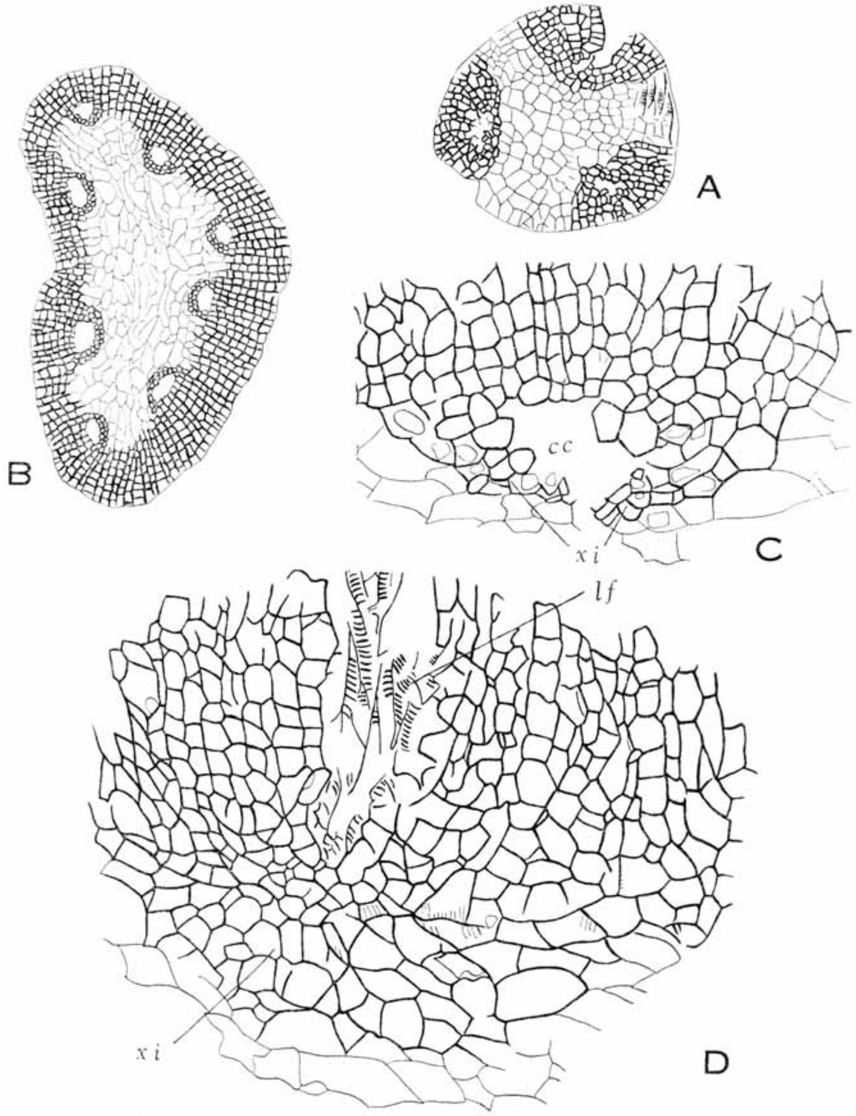
General structure of the internodes. A transverse section of the internode typically shows a ring of primary xylem strands surrounding a pith cavity and a ring of secondary wood developed to the outside of the primary strands. No phloem has been observed. The primary strands are mesarch and the protoxylem is usually represented by carinal canals. The primary medullary rays between the primary strands are continuous with the pith parenchyma; this tissue usually forms a narrow lining around a broad pith cavity. The cortex contains large air spaces.

Altogether some thirty specimens with a more or less complete xylem system have been seen: a much larger number of fragmentary specimens have been observed. The specimens from both Pettycur and Arran show great differences among themselves particularly in the size of the pith and the number of primary strands, in the thickness of secondary wood and in the size of the carinal canals; there is further variation in the size of the primary xylem strands and width of the primary rays.

The number of primary xylem strands varies from three in the smallest specimens (text-fig. 1A) to thirty in the largest ones. A number of mainly slender stems (about 12) showing primary structure with little or no secondary thickening have been seen. Most of these have only a small number of xylem strands, commonly three to seven. These slender stems probably represent the ultimate branchlets of the plant. What were probably the main axes of the plant, however, generally contain more than fifteen primary vascular strands and these nearly always have secondary thickening. In some of these specimens the secondary wood is as thick as 1·5 mm. Only one specimen with as many as thirteen xylem strands has been observed without secondary thickening (Pl. 59, fig. 1).

Most specimens are compressed, but the diameter of the pith has been worked out from the size of the pith circumference; the diameter ranges from 0·1 mm. to 6 mm. The pith is generally hollow, except in some of the slender branchlets where it is solid (text-fig. 1A). In the basal portion of a branch also the pith is typically solid (Pl. 59, fig. 2). In one specimen containing eight primary xylem strands (text-fig. 1B) the pith appears at first sight to be continuous, but it seems likely that there was a small space in the centre, but that this space became closed by compression. The thickness of parenchyma between the primary xylem strands and the edge of the pith cavity varies considerably; sometimes there is none and sometimes this tissue is up to about six cells thick. The variation may be due largely to differences in preservation, but there is some indication that the smaller branchlets had relatively more pith parenchyma than the larger stems. There is no evidence that nodal diaphragms occurred, although in one specimen a slight thickening of the pith parenchyma was observed at the node.

Most of the variation in the size of the primary strands is due to differences in the amount of centripetal metaxylem. Study of series of transverse and longitudinal sections has shown that the amount of centripetal metaxylem which in the internode typically



TEXT-FIG. 1. *Archaeocalamites goeppertii* Solms; Pettycur. A, Transverse section of a very young slender twig showing solid pith and three primary xylem strands; H.C., V35645–3, peel 127, ×80. B, Transverse section of a young twig with a nearly solid pith which is slightly disorganized in the centre; peel 5, ×80. C, One primary xylem strand in the internode showing a carinal canal (*cc*) and very little centripetal metaxylem (*xi*); peel 82, ×210. D, The same strand as in C at the node showing increase in the amount of centripetal metaxylem (*xi*) and emission of a leaf trace (*lf*); peel 139, ×210. (Figures B–D from block V35495, H.C.)

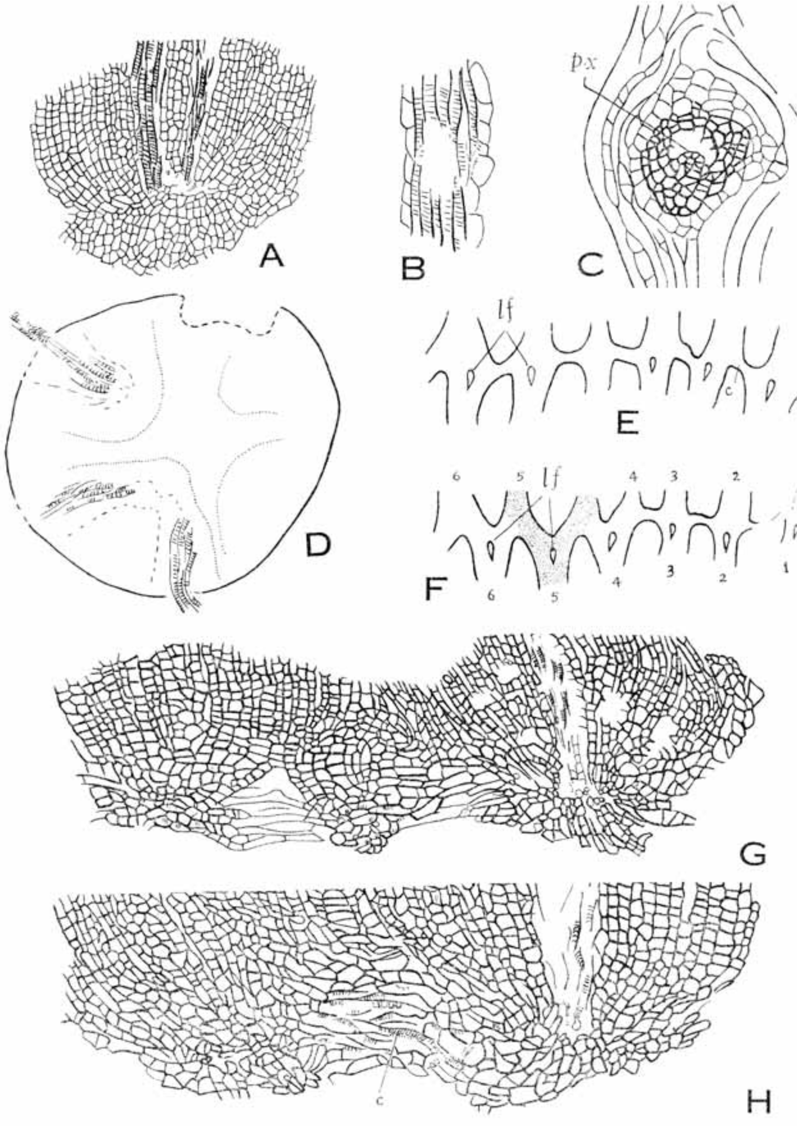
consists of one or two layers of tracheids (text-fig. 1C, Pl. 60, fig. 2) always increases rapidly as a node is approached from either above or below (text-fig. 1D and Pl. 60, fig. 1). The carinal canal in longitudinal section is sometimes seen to contain disrupted protoxylem elements (Pl. 60, fig. 2). The centripetal metaxylem tracheids show scalariform-thickening. In a few of the older, more woody specimens some of the bundles apparently lack centripetal metaxylem; and the carinal canal is sometimes open to the pith cavity. The appearance, however, suggests that this condition is due to poor preservation.

The structure of the primary and secondary xylem is identical in almost every detail to that described in *Archaeocalamites goeppertii* (Solms-Laubach 1897, Walton 1949). The centripetal and centrifugal metaxylem are composed of scalariform elements and the secondary wood tracheids have uni- to multiseriate pitting on their radial walls. The outer part of the wood in larger (woodier) specimens typically has multiseriately pitted tracheids (Pl. 59, fig. 7). The ray cells are generally markedly elongated longitudinally as in *Archaeocalamites* and *Calamites*. The rays are generally uniseriate and evenly distributed except in the interfascicular wood where they are more abundant and grade into the primary medullary rays. Within a distance of about 0·3 mm. from the pith, however, this distinctive structure of the interfascicular wood disappears.

Only a few specimens have been seen in which the cortex is preserved. In the specimen shown in Plate 59, fig. 4, can be seen the epidermis and two to three layers of compact parenchyma. This is followed by the zone of lacunar cortex. The lacunae are traversed by trabeculae which appear to consist of two rows of cells. Some of the small thin walled cells outside the wood (seen near the centre of the photograph) may represent cambial and phloem elements, but it is impossible to prove them as such. There is no evidence of fibrous tissue in the cortex. In *Calamites* the cortex consists of an inner zone of thin walled cells and an outer zone of thick walled cells.

Nodal organization. The leaf traces arise in whorls at the nodes. The number of leaf traces usually equals the number of primary xylem strands in the lower internode. This has been demonstrated by observing close series of transverse sections. Each leaf trace arises from a primary strand, in fact from a core of rather irregularly orientated tracheids which at the level of the node occupy the position of the carinal canal (text-fig. 1D). There is thus no carinal canal for a short distance at the node. As the leaf trace passes through the secondary wood it ascends slightly and is surrounded by a sheath of thin walled tissue. Within the leaf trace xylem there is usually discernible a space which somewhat resembles a carinal canal. As seen in cross-section of the trace (i.e. in tangential section through the stem) this space is seen to be situated nearer to the upper side of the xylem strand (text-fig. 2C). The tracheidal nature of the cells bordering the space is not clear from such sections, but is so from sections passing longitudinally through the space (text-fig. 2B). No definite protoxylem has been observed in the leaf trace, but in one or two well-preserved examples seen in cross-section (text-fig. 2C) a group of small tracheids is present at the lower edge of the canal. Similar canals have been described in the leaf traces of *Calamites* (Williamson and Scott 1894).

Although the leaf traces are usually given out singly from the primary xylem strands, in a few instances they have been observed to arise in pairs (text-fig. 2A). The occurrence of such paired leaf traces is more frequent in slender branchlets (text-fig. 2D) although it



TEXT-FIG. 2. *Archaeocalamites goeppertii* Solms; Pettycur. A, Transverse section through a primary strand to show paired leaf traces; B.C. 213, ×50. B, Longitudinal section through a portion of a leaf trace to show the presence of a space surrounded by tracheids and parenchyma; I.C., block C2, peel 7, ×80. C, Tangential longitudinal section of a node near pith region to show transversely cut leaf trace and associated space. *px*, protoxylem of the leaf trace; (Arran) F.S.C. 856 1/1, ×80. D, Transverse section of a slender branchlet to show one single and one paired leaf trace; H.C., V35645-3, peel 67, ×80. E and F, Diagrammatic figures of tangential longitudinal sections through two nodes near the pith showing course of the vascular bundles, *lf*, leaf traces; F, shows forking of one of the bundles. E, B.C. 299-9; F, B.C. 299-15. G, Part of a transverse section through node to show forking of one of the bundles (on left); I.C. Slide 19, peel 1, ×47. H, Transverse section through node to show linking of the nodal ring strand (*c*) between two bundles; H.C. V35495, peel 177, ×47.

occasionally occurs in larger stems. This is not associated with any increase in the number of cauline strands in the succeeding internode.

The centripetal metaxylem which, as has already been stated, is considerably more massive at the node than in the internode, is undisturbed by the emission of leaf traces.

At the node, strands of primary xylem run across the primary medullary rays linking one primary xylem strand with the next. This linking of the primary xylem strands, constituting a nodal ring, is best seen in tangential longitudinal sections (text-fig. 2 E, F), but it can also be observed by careful study of transverse sections (text-fig. 2H). As can be seen from these figures the linking strand of tracheids often does not run truly horizontally, but somewhat obliquely. These linking or nodal ring strands run from the sides of the vertical strands and connect with both centripetal and centrifugal metaxylem.

The course of the primary strands through the node from one internode to the next is generally straight; that is, there is no regular alternation as there is typically in *Calamites* and *Equisetum*. In the example represented in text-fig. 2E the bundles of the lower internode are continuous with the corresponding bundles of the upper internode across the node. These bundles are interrupted only by leaf traces which are passing outwards from the bundles of the lower internode.

However, in some nodes observed, local alternation of the primary strands takes place as seen in text-fig. 2F. In this example due to forking of the bundle number 5 of the lower internode there is an increase in the number of bundles in the upper internode. The 'new' bundle causes, as it were, displacement of the neighbouring bundles in the upper internode. Thus the bundles 4 and 6 of the lower internode, instead of running straight like bundles 1, 2, and 3, take a slight turn to one side or the other, so accommodating the additional strand. Text-fig. 2G shows a transverse section of part of a node. The left-hand and middle bundles here have arisen by division of one bundle after the emission of a single leaf trace. This figure shows a difference in size, which is quite typical, between the two bundles resulting from the forking.

This interpretation of an occasional alternation by the forking of one of the strands at the node depends upon the correct orientation of the specimen. At first it was rather difficult to determine the correct orientation of sections passing through nodes but careful study has shown that it may be determined from the following characters:

(i) The leaf trace is derived from the protoxylem of the internodal bundle below it and ascends slightly as it passes out into the secondary wood. It almost always lies in the median radial plane through this bundle.

(ii) The leaf trace attachments are always just below the level of the continuous metaxylem ring at the node.

Only four examples (two of which are represented in text-fig. 2F, G) out of twelve studied showed forking of one of the bundles at the node.

Thus, the course of vascular bundles at the node in *Protocalamites pettycurensis* is generally straight, although in a minority of nodes local alternation does occur and is essentially associated with an increase in the number of strands from one internode to the next.

Branching. The branches arise at the node but above the level at which the leaf traces depart. The branch is inserted in the region of the nodal ring. In the three attached branches investigated the insertion has been associated with two or three of the vascular strands of the lower internode of the main stem and has resulted in a loss of one strand from the upper internode. Thus the specimen illustrated in text-fig. 3F, G had seventeen strands in the internode below the branch and only sixteen above.

Text-fig. 3F, G shows two sections of a transverse series passing through the junction of the stem and branch. The pith of the branch tapers towards the point of insertion and is continuous with the stem pith by a narrow neck of tissue. The primary xylem of the branch is directly continuous with that of two bundles of the stem. A series of small strands of scalariform elements depart close together and enter the branch base as seen in text-fig. 3F. In both tangential and transverse sections of the base of a branch the secondary wood of the branch is seen to be continuous with that of the parent stem.

The pith of the branch at the base is probably typically solid. This is seen in one probably charred specimen (Pl. 59, fig. 2) where the delicate cells happen to have been preserved. The pith consists of parenchymatous cells. More usually, however, the base of the branch contains a small cavity in the centre due probably to decomposition of the pith cells. This pith cavity enlarges as the branch emerges and is seen to be surrounded by a ring of primary xylem groups which are separated by medullary rays (text-fig. 3J). The medullary rays are distinct but narrow, consisting of uniseriate or biseriate parenchymatous cells. The branch from which text-fig. 3J was drawn was represented by a short series of rock sections and could not be traced far enough to demonstrate the appearance of carinal canals. This transition has, however, been demonstrated in an isolated branch base. It may not have been genuinely isolated for it was exposed in transverse section on one side of a block, its appearance at this level (text-fig. 3H) suggesting that it was very near its attachment to a parent stem. As the specimen was traced through a series of peels the originally very small pith expanded and gave way to a large pith cavity. The primary xylem strands enlarged and developed carinal canals, thus giving the typical stem structure (text-fig. 3I).

The mode of branching in one observed example of a slender branchlet from Pettycur was somewhat different. The branchlet has five primary xylem strands and bears two laterals. The first lateral arises in the normal way at the node between two of the primary xylem strands (text-fig. 3A). The second branch is given off at a slightly higher level (text-fig. 3C, D). It appears to arise by division of the nodal ring by constriction

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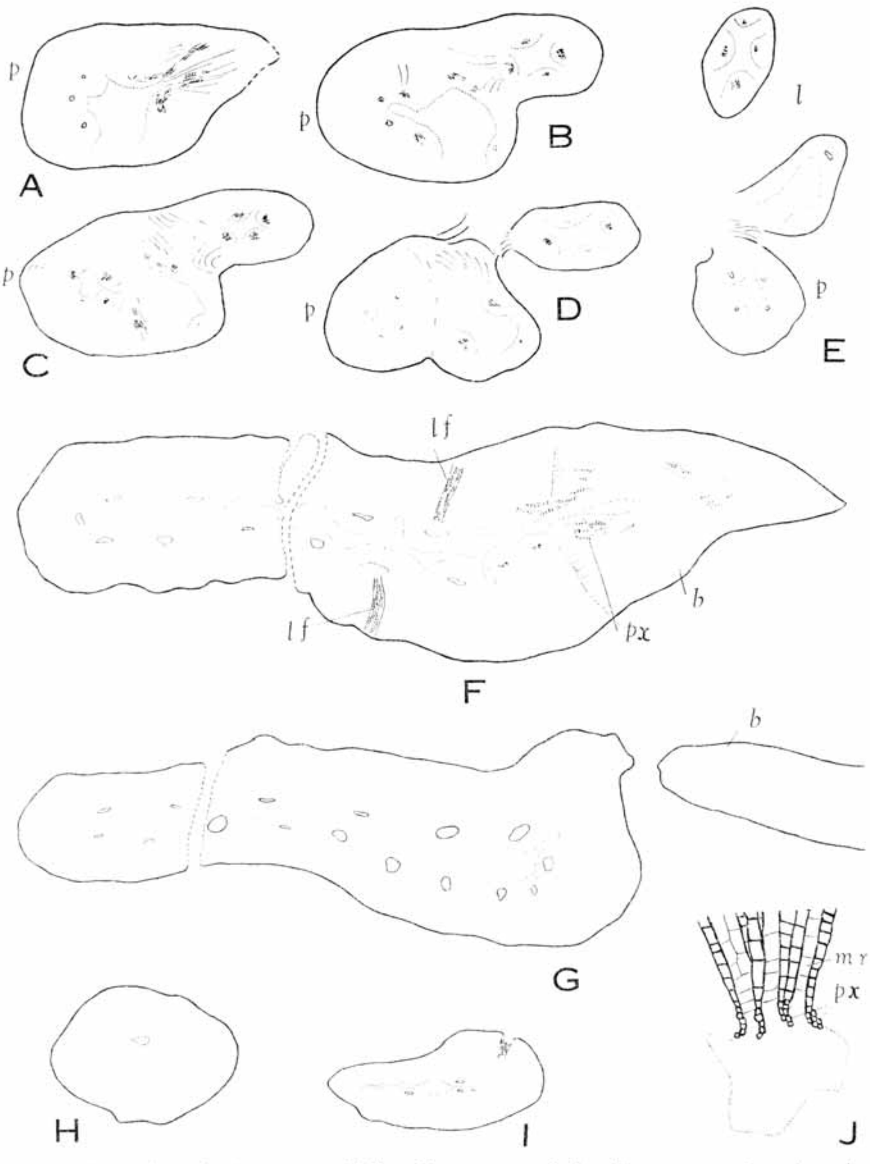
EXPLANATION OF PLATE 59

Figs. 1–10. *Archaeocalamites goeppertii* Solms. 1, Transverse section of a young stem with thirteen primary xylem strands showing primary structure only; Arran, F.S.C. 824, × 45. 2, Transverse section through basal portion of a branch showing solid pith; Arran, F.S.C. 808 2/2, × 20. 3, Transverse section of a rootlet showing dichotomy; Arran, F.S.C. 1702, × 45. 4, Part of a transverse section of stem showing lacunar cortex; Arran, F.S.C. 1704, × 30. 5, Transverse section of central part of the main root to show the absence of pith; Arran, F.S.C. 1700, × 45. 6, Part of transverse section of the root-bearing stem showing bases of three attached roots (*r*); Arran, F.S.C. 814 3/1, × 15. 7, Radial longitudinal section through a part of the secondary wood to show multiseriately pitted tracheids; Pettycur, I.C. Slide 3, peel 10, × 240. 8, Longitudinal section of root showing scalariform tracheids, and towards the outside, imperfectly reticulate tracheids; Arran, F.S.C. 840, × 60. 9, Transverse section of a leaf; Arran, F.S.C. 808 2/2, × 20. 10, Transverse section of a part of the root-bearing stem to show stage in an apparent dichotomy in an attached root; Arran, F.S.C. 815 1/3, × 30.

Note. Plate title: for '*Asterocalamites*' read '*Archaeocalamites*'.



TEXT-FIG. 3. *Archaeocalamites goeppertii* Solms; Pettycur. A–E, Series of transverse sections through a slender stem to show stages in branching. E is orientated at an angle of 90° in relation to A–D. *p*, parent stem and *l*, the laterals; H.C., V35645–3; A, peel 82; B, peel 92; C, peel 93; D, peel 99; E, peel 104. All × 29. F, Transverse section through the junction of the stem and branch showing continuity of pith and primary xylem (*px*), *b*, branch; *lf*, leaf traces; H.C., V35495, peel 125. G, Section of the same specimen as in F to show the departing branch (*b*); peel 161, both × 29. H, I, Transverse sections through base of an isolated branch to show stages in its development into a typical branch structure; H.C., V35594; H, peel 55; I, peel 121, × 29. J, Portion of the base of a branch showing primary xylem groups (*px*) and medullary rays (*mr*); B.C. 199–6, × 80.

(text-fig. 3B, C) and is not obviously associated with any two of the primary xylem strands although these at the level of the nodal ring where the carinal canals are closed are not very distinct. This mode of branching might be interpreted as a sort of dichotomy. In text-fig. 3E the two departing laterals can be seen. The parent branchlet (*p*) now has only four primary xylem strands. Alternatively one might regard the three-bundled axis as the continuation of the main axis and *p* as the second of the two laterals.

Leaves. In the majority of specimens the cortex is not preserved and only xylem elements of the leaf traces are seen as they pass through and sometimes just beyond the zone of secondary wood.

Just below the node the cortex of the stem shows a number of ribs corresponding to the bases of the leaves which are given off from the node. In no specimen have the individual leaves been traced far from the point of attachment before fading out due to poor preservation; thus the form of the leaf could not be determined. There is no evidence of a leaf sheath.

The preserved basal portions of leaves are apparently simple in anatomy. Plate 59, fig. 9, shows a transverse section of a leaf. It is oval in outline; in the centre there is a small bundle which consists of xylem surrounded by a thin-walled tissue, probably phloem. Outside the bundle there is parenchyma which becomes smaller-celled and presumably photosynthetic towards the outside. The epidermis is not clear and no stomata have been observed.

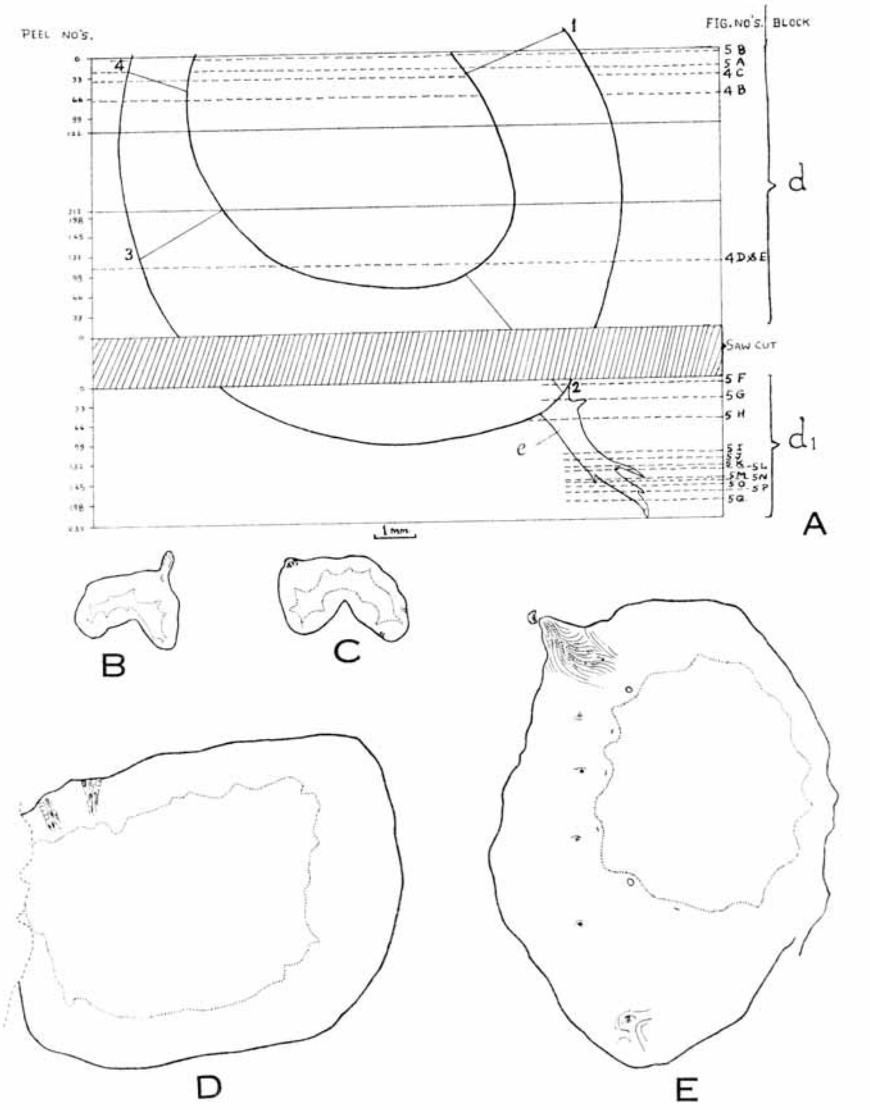
Root-bearing stems. In general anatomy these stems are like the typical stems except for a few minor differences. The pith is hollow and surrounded by a ring of vascular bundles. The carinal canals, however, are comparatively small. Further, the amount of centripetal wood in the internode is generally no more than a single row of tracheids. In some places it disappears completely, though this is likely to be due to poor preservation, since the carinal canal is often open to the pith cavity. There is a thick zone of secondary wood through the greater part of the specimen, but this diminishes considerably towards the top.

Altogether three specimens of root-bearing stems, two from Arran and one from Pettycur, have been seen. The Pettycur specimen was fragmentary and poorly preserved.

The Arran specimen represented in the reconstruction (text-fig. 4A) shows four nodes (1, 2, 3, and 4). This reconstruction was drawn from a model based on camera lucida drawings. The sections passing through the nodal regions of this specimen were studied in detail and the data were recorded as shown in Table 1.

At nodes 1 and 2 the leaf traces are considerably smaller than in typical stems and are in fact difficult to detect in the secondary wood. Text-fig. 5C shows a leaf trace cut nearly transversely from node 2. At node 3 the leaf traces are of more normal size (text-fig. 5D). At node 4 the specimen is somewhat squashed and the preservation is very poor, but there is no doubt that the diameter here is genuinely less and the amount of wood much smaller. Only one root is clearly seen (text-fig. 4B), but it is possible that there was a second feebly developed root (text-fig. 4C). The leaf traces are unfortunately indistinct, the two traces to the right in text-fig. 4C probably represent leaves.

From this it appears that nodes 1 and 2 may probably represent the underground portion of the rhizome as in them the leaf traces are very small and the roots are well developed. Nodes 3 and 4, where the roots are poorly developed and the leaf traces (at



TEXT-FIG. 4. *Archaeocalamites goeppertii* Solms; Arran. A, Reconstruction of the root-bearing stem showing four nodes (1, 2, 3, and 4) and root *e* at node 2. This figure also shows parts of the block peeled and position of the sections figured (text-fig. 4B–E and text-fig. 5A–Q). B, C, Transverse sections through part of node 4, to show one root base in B and three small traces in C, one of which probably represents a root, the others, leaves; B, H.M.Pb., 3504–*d* (upper), peel 171; C, H.M.Pb., 3504–*d* (upper), peel 41. D, Transverse section through a part of node 3 showing two large leaf traces; H.M.Pb., 3504–*d* (lower), peel 112. E, Transverse section through part of node 2 showing one root trace and five very small leaf traces; H.M.Pb., 3504–*d* (upper), peel 112. All ×9.

least in node 3) are larger, probably represent the basal portion of an aerial stem. The curvature of the whole specimen is probably to some extent genuine and not merely an accident of preservation. The woody cylinder is thickest in the middle region.

This specimen is comparable with the curved pith casts of branching rhizomes of *Calamites* (Seward 1898, p. 323, fig. 82), which probably grew underground giving aerial shoots and adventitious roots. It is also comparable with the curved, root-bearing stem base with its thick zone of secondary wood depicted in Eggert's (1962) reconstruction of a calamite based on American material.

TABLE 1

Nodes	*Internodal length*	*Approx. diameter of stem (woody cylinder) at node*	*Approx. thickness of wood in the internode*	*No. of primary xylem strands in the internode*	*No of roots*
Node 1		5·5 mm.			2
	1·6 cm.		1·4 mm.	15	
Node 2		7·9 mm.			5
	1·95 cm.		1·1 mm.	15	
Node 3		4·9 mm.			1 (?)
	0·85 cm.		0·5 mm.	15 (?) 15 (?)	
Node 4		3·0 mm.			2 (?)

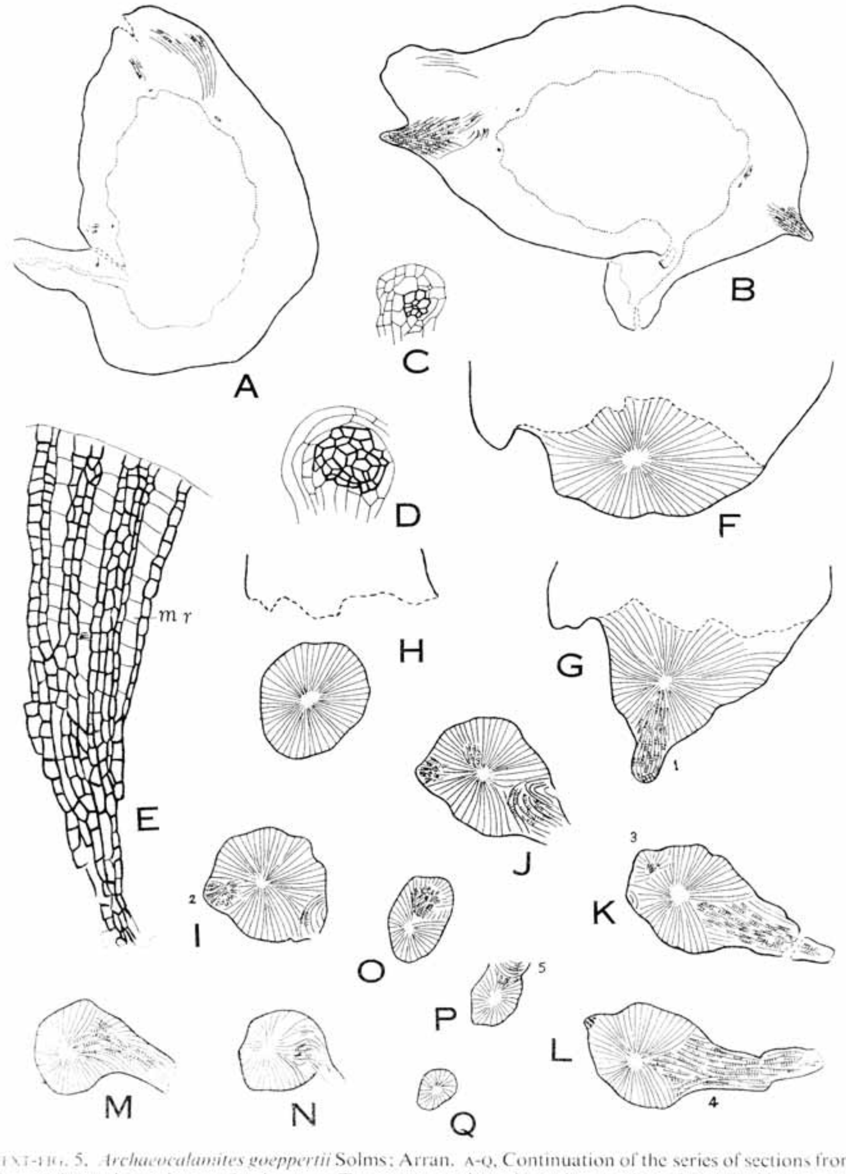
Roots. The roots described here are all from the Arran material. Only a few poorly preserved specimens have been observed in Pettycur material.

The roots are given off in irregular whorls from the nodes of certain stems (Pl. 59, fig. 6). The root traces arise at approximately the same level as leaf traces and are given off from the centrifugal metaxylem either in between the two primary xylem strands (text-fig. 5B) or opposite the primary xylem strand (text-fig. 4E). The primary xylem of the root can be traced through the zone of secondary wood to a point near the primary xylem of the stem, but it does not always join up with it; rather it tends to get lost in the innermost part of the secondary wood. This indicates that the roots were sometimes formed after secondary thickening had started in the stem.

The roots are mostly decorticated and only one or two examples have been seen in which the cortex appears to be lacunar in structure.

In the specimen represented in text-fig. 4A the root marked *e* was traced for a distance of about 7 mm. and the following description is based mainly on this specimen. Other roots on this stem could be traced for only comparatively short distances and some hardly beyond the secondary wood.

The root *e* measures in its decorticated condition about 1·8 mm. in diameter, where it emerges from the wood of the stem. There is no evidence of pith, the centre being occupied by apparently tracheidal (metaxylem) cells. At some levels a small cavity is present in the middle which is probably due to the breaking down of tracheidal cells. In thick peels these cells often show a clear indication of scalariform thickening on their longitudinal walls. The tracheids of the metaxylem core are surrounded by a ring of probably five to six protoxylem groups and a thick zone of wood (Pl. 59, fig. 5).



TEXT-FIG. 5. *Archaeocalamites goeppertii* Solms; Arran. A–Q, Continuation of the series of sections from the specimen shown in text-fig. 4A. A, B, Transverse sections through a portion of node 1 showing two root traces and a few leaf traces; A, H.M.Pb., 3504–*d* (upper), peel 27; B, H.M.Pb., 3504–*d* (upper), peel 3. ×9. C, Leaf trace at node 2 cut transversely; H.M.Pb., 3504–*d* (lower), peel 112, ×50. D, Leaf trace at node 3 cut transversely; H.M.Pb., 3504–*d* (lower), peel 206, ×50. E, Portion of the main root *e* showing medullary rays (*mr*) in the peripheral region of the root; H.M.Pb., 3504–*d*1, peel 146, ×80. I–Q, Series of transverse sections showing stages in the branching of the root *e*. The numbers 1–5 represent the rootlets; H.M.Pb., 3504–*d*1; F, peel 7; G, peel 36; H, peel 68; I, peel 128; J, peel 137; K, peel 146; L, peel 152; M, peel 165; N, peel 168; O, peel 181; P, peel 189; Q, peel 206. All ×9.

Unfortunately the protoxylem groups are not at all distinct and the number could not be determined exactly.

Text-fig. 5G–Q shows the stages in the branching of the root *e*. It gives off five rootlets or secondary roots, which arise in succession and come off at five different points apparently opposite protoxylem groups in the main root. The rootlet number 1 in text-fig. 5G is given off while the main root is still attached to the stem.

The rootlets are smaller in size than the main root. The protoxylem groups, which again are usually rather indistinct, are few in number varying from two to four. The amount of wood is less.

Two cases of apparent dichotomous branching in roots have been observed; one in an attached main root and the other in an isolated rootlet. Plate 59, fig. 10, shows a main root still attached to the stem just before the dichotomy takes place. At this level the primary xylem (*p*) has divided into two nearly equal portions. A little higher, the secondary wood becomes organized around the two primary xylems and the two roots are eventually separated. The true nature of the branching, however, is not perfectly clear because of the plane of section. Plate 59, fig. 3, shows a stage in the dichotomy of an isolated rootlet which, on the evidence of structure (the size and pitting of the tracheids and the form of the primary xylem) belongs to the same plant.

The secondary wood of the root consists of tracheids which are arranged in regular radial series. Rays have only been observed in main roots. Text-fig. 5E shows a portion of the transverse section of the main root *e*. The rays are present in the peripheral zone of the wood and can be distinguished from the tracheids by their larger size and thinner walls. No longitudinal sections were obtained from this particular root, but the tracheids of the outer zone of wood when these are somewhat obliquely sectioned, sometimes show a clear indication of multiseriate pitting on their radial walls. The roots seen in longitudinal section were all more slender than root *e* and only more or less scalariform tracheids were observed (Pl. 59, fig. 8). As with the stem, the first formed secondary wood apparently consisted of uniseriately pitted or somewhat reticulate tracheids, multiseriate pitting occurring in the later formed wood. This has been observed by close examination of slightly obliquely sectioned portions of the wood in attached root *e*.

Discussion. The name *Archaeocalamites* (or *Asterocalamites*) is now generally employed for calamite-like fossils mainly of Lower Carboniferous age which differ from the typically Upper Carboniferous *Calamites* chiefly in the lack of alternation of the vascular bundles at the node. Other characters that appear to differentiate *Archaeocalamites* from *Calamites* are the dichotomous forking of the leaves, and the presence of centripetal metaxylem. Leistikow (1959) has given reason for regarding *Archaeocalamites* Stur as the legitimate name, rather than *Asterocalamites* Schimper or *Asterocalamites* Zeiller.

Some of the species are based on pith casts or compressions, e.g. *A. radiatus* (Bgt.); others are based on petrified material, e.g. *A. goeppertii* Solms.

Petrified material referred to *A. goeppertii* has been studied by a number of authors. In 1852 Goeppert described some details about the secondary wood. Solms-Laubach (1897) described the internodal structure of the primary and secondary xylem and Walton (1949) described the nodal structure.

Renault (1893–6) described two species under the names *Bornia esnostensis* and *B. latixylon* from the Lower Carboniferous of Esnost in France. These species were later referred to *Asterocalamites* and grouped under the family Asterocalamitaceae (Hirmer 1927).

These species of Renault's appear to be genuinely different from *Archaeocalamites goeppertii*, for *A. esnostensis* had much shorter ray cells and wood tracheids with only one or two rows of bordered pits; *A. latixylon* was a larger plant and had wider wood rays.

Walton (1949) in his investigations into a Scottish specimen of *A. goeppertii*, briefly compared this plant with *Protocalamites pettycurensis* and drew the following distinctions:

(i) In *Archaeocalamites* the vascular strands always run straight through the node whereas, according to earlier (unpublished) investigations, there was sometimes alternation in *Protocalamites*.

(ii) In *Archaeocalamites* the centripetal metaxylem diminished (sometimes to nothing) in the internode and increased at the node, whereas in *Protocalamites* the centripetal metaxylem was always massive.

(iii) Rays were evenly distributed in the wood of *Archaeocalamites*, whereas in *Protocalamites* the interfascicular wood contained relatively more rays.

(iv) The pitting of the wood tracheids was regularly multiseriate in *Archaeocalamites* and often uniseriate in *Protocalamites*.

The present investigations into *P. pettycurensis* have shown that the structure of the xylem system of the internode including the structure of the secondary wood is essentially similar to that of *A. goeppertii*.

The nodal structure of *P. pettycurensis* shows that the vascular strands pass straight through without alternation, but that in about one-quarter of the nodes investigated in detail, local alternation does occur and is always associated with the interpolation of an additional strand in the upper internode. Such a local alternation has not been previously reported in *A. goeppertii*, but then few nodes have been studied in detail. It is of interest to note that a few specimens of Lower Carboniferous pith casts have been reported, one in the Goeppert Collection of the Breslau Museum mentioned by Seward (1898), and Feistmantel's specimens from Rothwaltersdorf (1873, p. 491, pl. xiv, figs. 3, 4) which do show a local alternation at the node associated with an increase in the number of bundles from one internode to the next. The same thing has been observed in a specimen labelled *A. scrobiculatus* from the Calciferous Sandstone Series in the Kidston Collection in the Geol. Survey Museum (specimen no. 3190).

With regard to other supposed distinctions between *A. goeppertii* and *P. pettycurensis* mentioned by Walton, the structural distinction between the fascicular and interfascicular wood has been found to disappear in a radial distance of about 0·3 mm. in *Protocalamites*. Thus only in small specimens (i.e. with little secondary wood) is there any general distinction between fascicular and interfascicular wood. Many of the specimens in both Pettycur and Arran tree material are small. Similarly, in small specimens the wood tracheids may not have attained their characteristic multiseriate pitting since there is gradation from the scalariform elements of the centrifugal metaxylem. The outer part of the secondary wood in all larger specimens characteristically has multiseriately pitted tracheids.

The remaining supposed distinction is the marked decrease in the amount of centripetal metaxylem in the internode of *Archaeocalamites*. This has now been demonstrated in *Protocalamites*. It is perhaps especially marked in one root-bearing specimen, and it is therefore noteworthy that Walton's petrified specimen of *A. goeppertii* was probably a root-bearing stem.

There is thus no good case for continuing to separate *A. goeppertii* and *P. pettycurensis*.

The present investigations have added to our knowledge of *A. goeppertii*, chiefly with regard to the root-bearing stems and root system. The root system is simpler than that of *Calamites*, for the main roots are protostelic and probably no more than hexarch, the lateral rootlets have two to four protoxylem groups. There is some evidence of occasional dichotomies in the roots. They compare somewhat with the roots described by Renault (1893–6) in *A. esnostensis;* here the roots were apparently regularly dichotomous, but there was a pith and the number of primary xylem groups was more (about 8).

Protocalamostachys pettycurensis sp. nov.

Plate 60, figs. 3–7; text-figs. 6, 7

Diagnosis. Cone axis slender, with three mesarch xylem strands and six longitudinal series of sporangiophores; three pairs of sporangiophores in each whorl, each pair lying opposite an axial xylem strand. Sporangiophores approx. 1·5 mm. long and 0·15 mm. in diameter. Sporangia approx. 0·9 mm. long and 0·4 mm.wide. Spores about 38 μ in diameter. Sporangium wall cells with peg-like thickenings on the anticlinal walls.

Type specimens. The description is based on twelve specimens clustered in one small portion of the block H.C. V35645.

Horizon. Calciferous Sandstone Series, Lower Carboniferous.

Locality. Pettycur, Fife, Scotland.

Description. The cones described here are all from Pettycur material. Altogether about a dozen specimens have been seen. They are closely associated with vegetative remains of *Archaeocalamites goeppertii*. All the cones were found clustered in one small portion of a block. The preservation of the material is variable; some specimens are quite well preserved.

The cones were probably borne at the extremities of slender branchlets (text-fig. 6M). These contain three mesarch primary xylem strands without secondary thickening.

EXPLANATION OF PLATE 60

Figs. 1–2. *Archaeocalamites goeppertii* Solms; Pettycur. 1, Radial longitudinal section of a primary xylem strand at node showing massive centripetal metaxylem (*cpx*), centrifugal metaxylem (*cfx*), protoxylem (*px*), and a leaf trace (*lf*). 2, The same strand as in 1 in the internode to show one or two layers of centripetal metaxylem (*cpx*) towards the pith (*p*), carinal canal (*cc*) with disrupted protoxylem elements and the centrifugal metaxylem (*cfx*); Pettycur, I.C. Slide 21; 1, × 160; 2 × 200.

Figs. 3–7. *Protocalamostachys pettycurensis* sp. nov.; Pettycur. 3, Oblique longitudinal section of part of cone axis passing through a sporangiophore to show attachment of two of its four sporangia; H.C., V35645–3, peel 22, × 40. 4, Transverse section of cone axis with three mesarch xylem strands and two of its six sporangiophores; several sporangia are seen near it; H.C., V35645–2, peel 18, × 40. 5, Spore, × 900. 6, Transverse section of a sporangiophore; H.C., V35645–2, peel 47, × 160. 7, Part of the sporangial wall in transverse and surface sections; H.C., V35645–3, peel 66, × 200.

Note. Plate title: for '*Asterocalamites*' read '*Archaeocalamites*'.

Several branchlets of this kind, mostly decorticated, and differentiated into nodes and long internodes, are closely associated with the cones. The continuity between one such stem and a typical cone axis has been demonstrated by tracing the specimen through serial peels. The stem is decorticated but as the cone axis is approached (about 1·5 mm. above an observed node) the cortex becomes preserved. The preservation of the cortex in the cone axis may be due to the fibrous nature of some of the cortical cells as seen in one or two of the better-preserved specimens, or perhaps only to the presence of rather closely arranged sporangiophores which might protect the cortical tissues.

The longest portion of cone axis observed was 9 mm. but no definite cone apex has been seen. The diameter of the fertile region of the cone is approx. 4 mm. The cone consists of a slender axis bearing superposed whorls of sporangiophores. There are six sporangiophores in each whorl and each sporangiophore carries four sporangia.

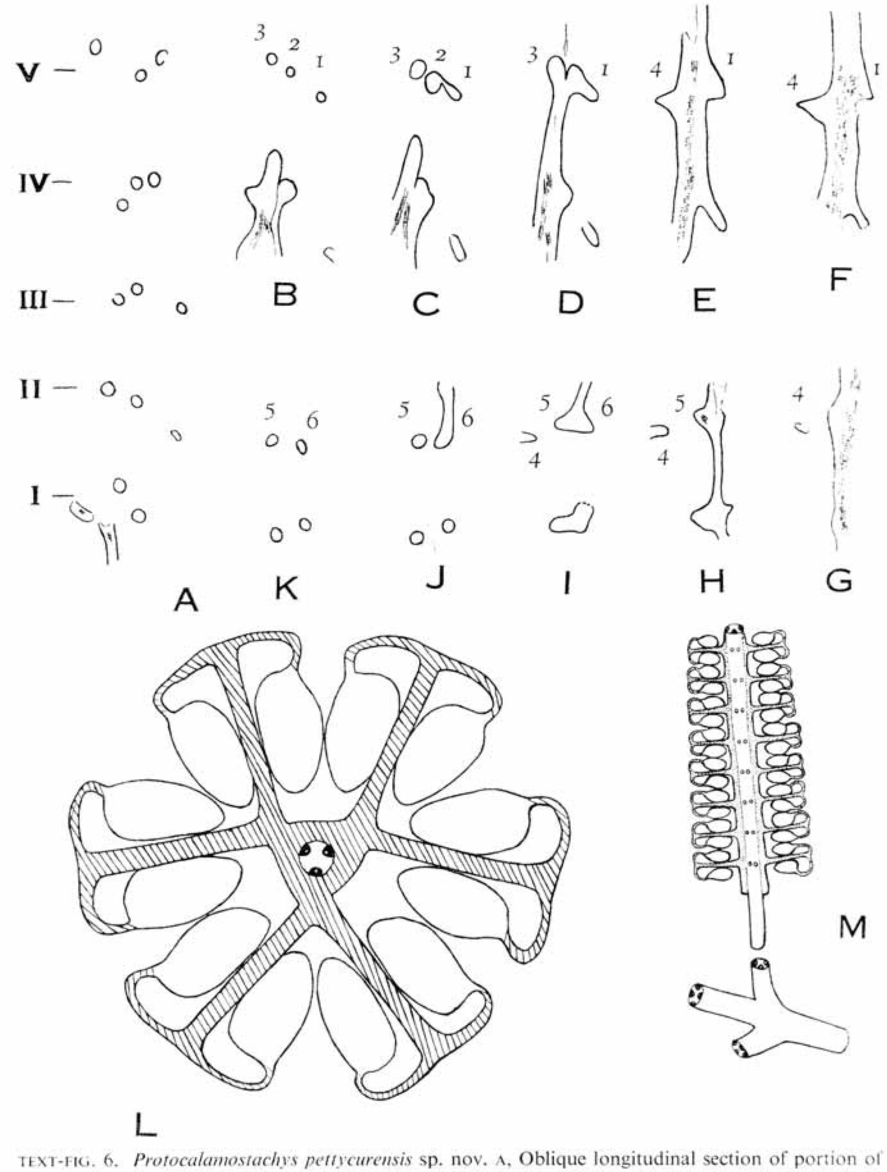
Axis. The diameter of the cone axis based on six specimens is approx. 0·8 mm. As seen in transverse section (Pl. 60, fig. 4) the cone axis is somewhat triangular in shape and consists of a solid pith surrounded by three mesarch primary strands without secondary thickening. Unfortunately the cellular details of the cortex cannot be satisfactorily distinguished. Study of a few transverse and longitudinal sections through the cone axis, however, has shown that in small patches where the cortical cells are preserved, they appear to be fibrous in nature. It is not clear whether the rest of the cortical cells are fibrous or not.

The three xylem strands follow a straight course through the axis without any division or anastomoses, except that at the 'nodes' where the sporangiophores are attached, each strand gives off two weak strands which supply the sporangiophores. There is no nodal ring. Each xylem strand possesses a protoxylem canal surrounded by centripetal metaxylem towards the pith side and centrifugal metaxylem on the outside. The tracheids all show scalariform thickening.

Arrangement of sporangiophores. The sporangiophores are the only appendages on the cone axis. They are arranged in longitudinal series and are attached in pairs. The pairs correspond in position to the three xylem strands of the axis. Text-fig. 6L shows a diagrammatic reconstruction of a transverse section of a cone axis with three pairs of sporangiophores in a whorl. The distal ends of the sporangiophores are shown with two of their four pedicels bearing sporangia.

The distance between successive whorls of sporangiophores is constant and about 1 mm. This is demonstrated well in the series of slightly oblique longitudinal sections passing through a cone represented in text-fig. 6A–K. Text-fig. 6A shows five (I–V) of the eight superposed whorls of sporangiophores observed in this specimen. Text-fig. 6B–K shows only whorls I and II and demonstrates the attachment of the sporangiophores. Whorl II may be taken as a typical example. Text-fig. 6B shows three sporangiophores (1, 2, and 3) of whorl II, out of which 1 and 2 join together (text-fig. 6C) and thus represent the bases of one pair. Next the sporangiophore 3 joins into the axis (text-fig. 6D) and just beyond (text-fig. 6E–G) departs the other member of its pair 4. Lastly the bases of the third pair of sporangiophores (5 and 6) are seen (text-fig. 6H–K).

The sporangiophores. The sporangiophores are long (1·5 mm.) slender, stalk-like structures about 0·15 mm. in diameter. The stalk of the sporangiophore consists of fairly



TEXT-FIG. 6. *Protocalamostachys pettycurensis* sp. nov. A, Oblique longitudinal section of portion of cone to show five (I–V) superposed whorls of sporangiophores. The attachment of sporangiophores in the first two whorls is illustrated in figures B–G. In these figures only sporangiophore bases are shown: H.C., V35645–2; A, peel 79; B, peel 85; C, peel 90; D, peel 91; E, peel 95; F, peel 97; G, peel 100; H, peel 105; I, peel 106; J, peel 108; K, peel 110. All × 18. L, Diagrammatic reconstruction of the cone axis to show three pairs of sporangiophores opposite three xylem strands. The distal ends of sporangiophores are shown with two of its four pedicels bearing sporangia, × 25 approx. M, Diagrammatic reconstruction of a cone to show continuity between the slender stem and cone axis; × 10 approx.

thick-walled cells (Pl. 60, fig. 6) within which is generally present a small space and a strand of tracheidal cells. In some specimens the xylem strand appears to have the form of a ring; the space it contains may be equivalent to the space present in the leaf trace strands of *Archaeocalamites*.

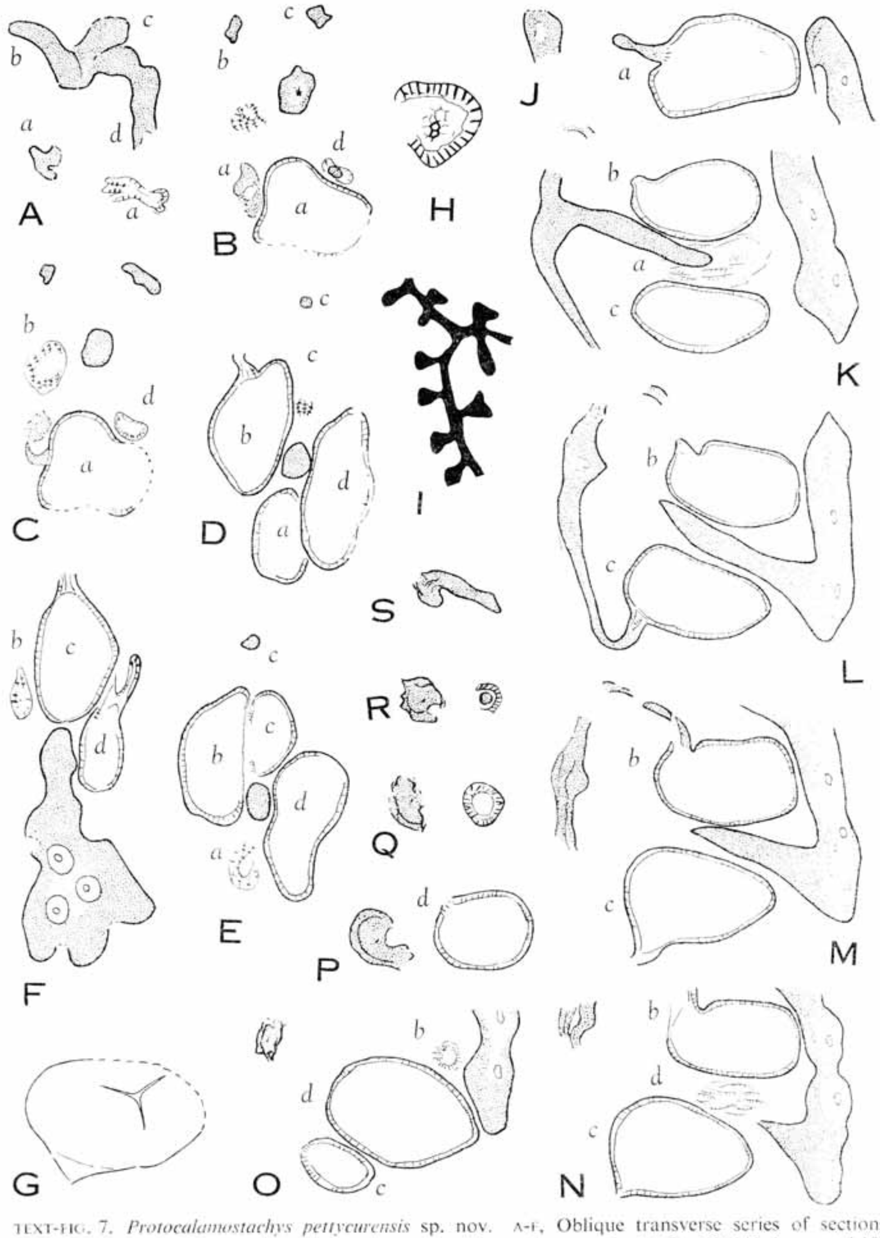
At the distal end of the sporangiophore there are attached four branches or sporangial pedicels. There is some indication (text-fig. 7A) that these may represent two successive dichotomies of the sporangiophore stalk, but the preservation is such that it has not been possible to determine this with certainty. The four pedicels curve towards the axis of the cone and terminate in single sporangia. This general form has been demonstrated from both transverse and longitudinal series of sections through the sporangiophores. An obliquely transverse series is represented in text-fig. 7A–F. Text-fig. 7A shows the distal end of the sporangiophore with its four sporangial pedicels *a*, *b*, *c*, and *d* which are arranged in a cross-wise manner. In text-fig. 7B the stalk of the sporangiophore is seen in the centre surrounded by the four pedicels (*a*, *b*, *c*, and *d*) and parts of two sporangia. Text-fig. 7C shows the attachment of pedicel *a* to its sporangium and text-fig. 7D, F the attachment of pedicels *b* and *c* respectively. Pedicel *d* is seen to continue into sporangium *d* in text-fig. 7B, C. Text-fig. 7E shows the stalk of the sporangiophore with four sporangia and pedicel *c*. In text-fig. 7F the attachment of the sporangiophore to the cone axis is seen.

In the longitudinal series of sections, again the pedicels *a*, *b*, *c*, and *d* with their respective sporangia show the cross-wise arrangement (text-fig. 7J–S). Text-fig. 7J shows pedicel *a* in attachment to its sporangium; on the right is seen part of the cone axis and on the left the base of pedicel *a* near its attachment to the end of the sporangiophore stalk. The attachments of sporangia *b* and *c* are seen in the more medial sections illustrated in text-fig. 7K–N. The sporangia appear to be somewhat tucked in by the pedicels which are attached to the sporangia on the side away from the main shaft of the sporangiophore (Pl. 60, fig. 3). The remaining sporangium *d* and its attachment is seen in text-fig. 7O–S.

The pedicel as seen in transverse section (text-fig. 7H) shows a distinct epidermis consisting of rather large, thick-walled cells. In the centre there is present a minute strand of tracheids. The other tissues are not clear.

Sporangia. The sporangia are about 0·9 mm. long and 0·4 mm. wide. The sporangial wall consists of cells slightly elongated in a direction parallel to the sporangial axis. As seen in transverse section (Pl. 60, fig. 7) the inner walls of these cells are uniformly thickened and the outer walls are thin. The thickness on the anticlinal walls appears to vary considerably; this is mainly due to the presence of projections on the walls which are seen in tangential sections through the cells (text-fig. 7I and Pl. 60, fig. 7). The projections on the walls are swollen at the tips, sometimes with two lobes. In some a light spot or a small hole can be seen in the 'head' which suggests that the projections are really folds of the sporangial wall.

Spores. The spores appear to be very uniform. They vary in size only from 34 μ to 44 μ. The average worked out from fifty individually measured spores is 38 μ. The spore wall appears to be plain or possibly very finely punctate. There is a well-marked triradiate ridge (text-fig. 7G and Pl. 60, fig. 5) the rays of which are 9 μ in length.



TEXT-FIG. 7. *Protocalamostachys pettycurensis* sp. nov. A–F, Oblique transverse series of sections through sporangiophore to show the attachment and form of sporangia: H.C., V35645–2: A, peel 39; B, peel 50; C, peel 51; D, peel 70; E, peel 75; F, peel 84. All ×30. G, Spore, ×810. H, Transverse section of a pedicel showing epidermis and minute strand in the centre; H.C., V35645–3; peel 61, ×80. I, Part of sporangial wall in surface section to show ridges of thickening; H.C., V35645–3; peel 63, ×510. J–R, Longitudinal series of sections through a sporangiophore to show the attachment of sporangia (*a*, *b*, *c*, and *d*): H.C., V35645–3; J, peel 5; K, peel 17; L, peel 21; M, peel 26; N, peel 30; O, peel 40; P, peel 51; Q, peel 56; R, peel 61; S, peel 64. All ×30.

Discussion. This new cone possesses the general characteristics of the genus *Protocalamostachys* which was erected for a single cone from Arran tree material by Walton (1949). The general features of the Pettycur cones fit very well the generic diagnosis published by Walton except for spore size; but this is a character which should probably not be regarded as an important generic criterion. The Pettycur cones however differ in a number of respects from the type species of the genus, *Protocalamostachys arranensis*. They are therefore made the basis of a new species *P. pettycurensis* sp. nov. The following are the main points of contrast between the two species.

The axis of the new cone contains only three mesarch primary xylem strands without secondary thickening, whereas in *P. arranensis* the cone axis contains six mesarch xylem strands with a little secondary xylem on the outside. The distance between successive sporangiophore whorls in the Pettycur cone is 1 mm. whereas in *P. arranensis* this distance is stated to be only 0·8 mm., although in view of the size of the sporangia, it is difficult to see how the sporangiophores could have been quite so closely arranged.

In the Pettycur cones there are six longitudinal series of sporangiophores which are attached in pairs, whereas in the Arran cone there are ten to eleven longitudinal series of sporangiophores which are usually attached in pairs but sometimes singly. The sporangiophores in *P. pettycurensis* are 1·5 mm. long and 0·15 mm. in diameter. The corresponding measurements in *P. arranensis* are 2·7 mm. long and 0·22 mm. in diameter. In both species the sporangia are borne at the extremities of four pedicels which are arranged in a cross-wise manner. The sporangia in *P. pettycurensis* are 0·9 mm. long and 0·4 mm. wide whereas in *P. arranensis* they are 1·2 mm. long and 0·65 mm. wide. The structure of the wall of the sporangium in both species is similar. The spores in *P. pettycurensis* are 38 μ in diameter while those in *P. arranensis* are given as 66 μ.

The cones of *Archaeocalamites* from compressed material have in the past been referred by different authors to various genera, e.g. *Pothocites grantonii* (Paterson 1841), *Asterophyllites spaniophyllus* (Feistmantel 1873) and *Archaeocalamites radiatus* (Stur 1875–7). Kidston (1883*a*, *b*) employed the name *Pothocites* for all these cones. Walton (1949) compared *Protocalamostachys arranensis* with *Pothocites grantonii* and concluded that the petrifaction and the compression cones were probably closely similar in general structure and in size. *Protocalamostachys pettycurensis* probably differs from *Pothocites* in the same ways as it does from *Protocalamostachys arranensis*, i.e. mainly in being smaller, having fewer sporangiophores in a whorl, and fewer vascular strands in the axis. The cone named *Bornia radiata* (Renault 1893–6) differs from *Protocalamostachys* in having its sporangia sessile on what appear to be peltate sporangiophores. It is possible that Renault's figures may be misleading in this, for it is rather surprising that a Lower Carboniferous cone should have sporangiophores almost exactly like those of a modern *Equisetum*.

The evidence that the petrified form of the cone of *Archaeocalamites* was *Protocalamostachys* is now considerable. Both *Protocalamostachys arranensis* and *P. pettycurensis* are probably similar in general organization to *Pothocites grantonii* which is a fructification borne on leafy stems of the *Archaeocalamites* type. Moreover, it is now known that vegetative remains indistinguishable from *A. goeppertii* are frequent at both the Arran and Pettycur localities.

The cone axis in both species of *Protocalamostachys* is similar in general structure to slender axes of *Archaeocalamites*. There is thus good reason to believe that cones of the *Protocalamostachys* kind were borne on *Archaeocalamites* stems.

The association of stems identified as *A. goeppertii* with one kind of cone at the Arran locality and with a specifically different, though generically similar, cone at Pettycur raises the question as to whether the vegetative remains at the two localities do in fact represent the same natural species. Careful comparison has been made between the material from the two localities and no differences worthy of consideration as criteria for specific separation have been discovered. The following two differences should be noted for what they are worth.

(i) The pith cells appear to be somewhat larger in Arran specimens as shown in Table 2. However, the size of the pith cells varies enormously, both in individual specimens and also from one specimen to another. In the latter case the variation apparently depends to some extent on the size of the specimen as determined by the number of primary xylem strands.

TABLE 2

Pettycur specimens		*Arran specimens*	
No. of primary strands	*Size of largest pith cells*	*No. of primary strands*	*Size of largest pith cells*
6	45 μ	7	50 μ
7	50 μ	9	75 μ
8	30 μ	10	75 μ
8	35 μ	11	90 μ
9	65 μ	12	80 μ
12	60 μ	13	75 μ
12	65 μ	14	145 μ
18	75 μ	26	195 μ
23	75 μ		
23	90 μ		

(ii) The smallest stems seen in Arran material have 7 vascular strands, whereas several examples with 6, 5, 4, and 3 have been noted from Pettycur, several specimens with 4 and 3 strands having been seen in close association with the cones at Pettycur.

It is known that amongst living plants different species and sometimes even different genera may be virtually indistinguishable in anatomy. Thus the genera *Quercus* and *Lithocarpus* belonging to Fagaceae are quite distinct on floral characters but the wood of a number of tropical species of *Quercus* is virtually indistinguishable from that of *Lithocarpus*.

Acknowledgements. I am indebted to Professor J. Walton for the loan of slides and cut blocks, to the Trustees of the British Museum (Natural History) for the loan of material, and to the Principal, Royal Holloway College, for the loan of slides from Benson's Collection. I am grateful for the inspiration of Dr. K. L. Alvin who supervised my work. I should also like to thank Dr. K. I. M. Chesters for showing me slides in the British Museum (Natural History).

Location of collections. The slides and peels are preserved at the following Institutions: Hemingway Collection (H.C.), British Museum (Natural History). Benson Collection (B.C.), Royal Holloway College, London. Figured Slide Collection (F.S.C.), Botany Department, University of Glasgow.

Hunterian Museum Palaeobotanical Collection (H.M.Pb.), University of Glasgow. Departmental Collection (I.C.), Botany Department, Imperial College, London.

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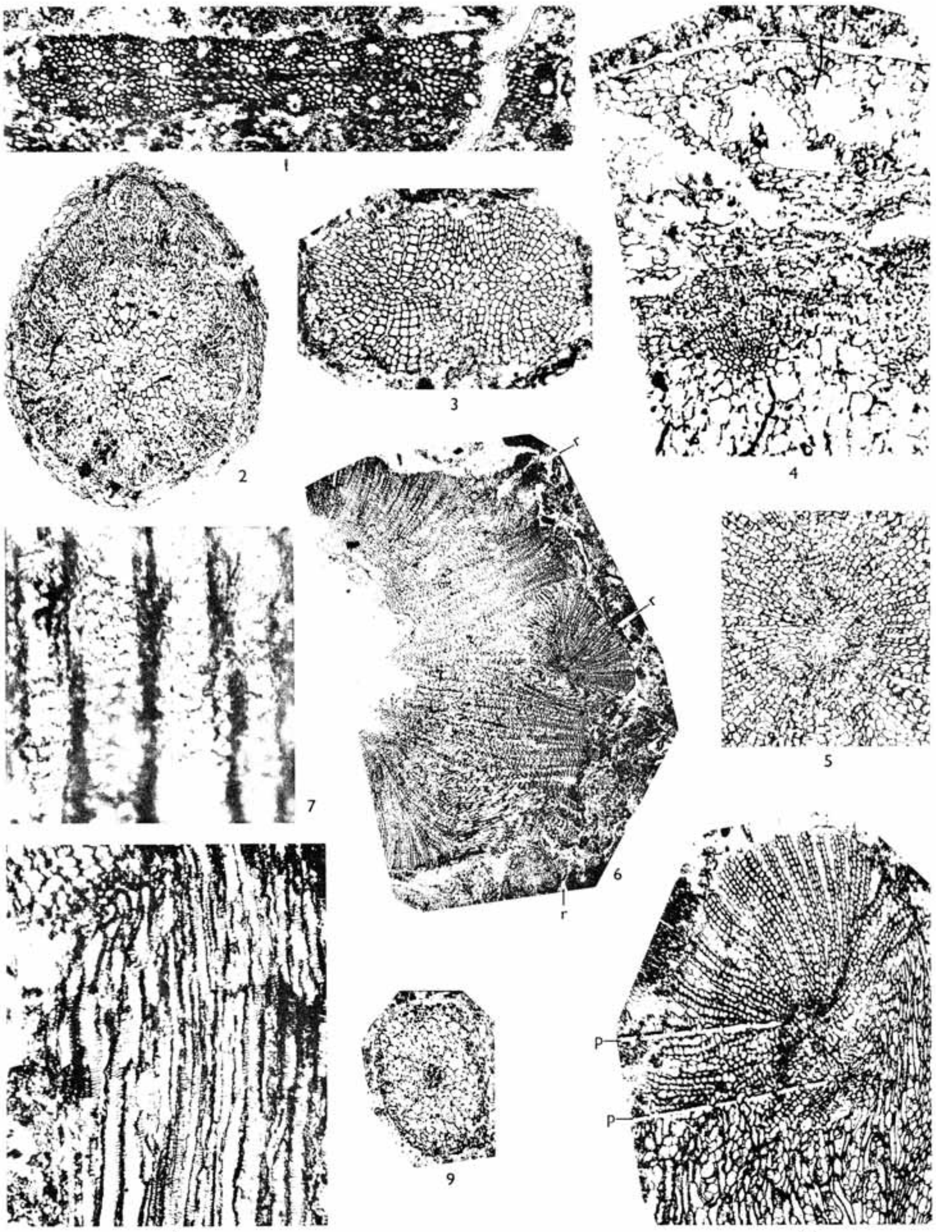
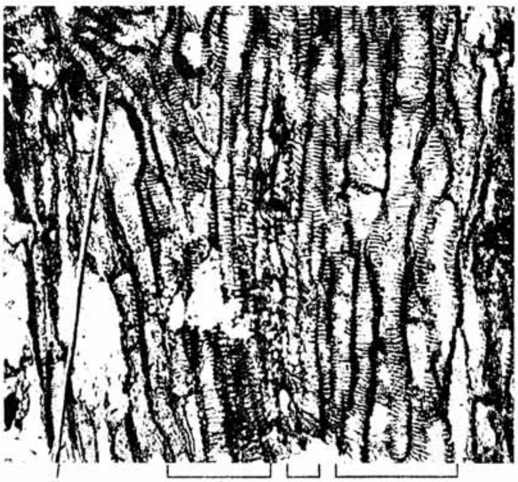
Manuscript received 18 September 1962



CHAPHEKAR, Lower Carboniferous *Asterocalamites*



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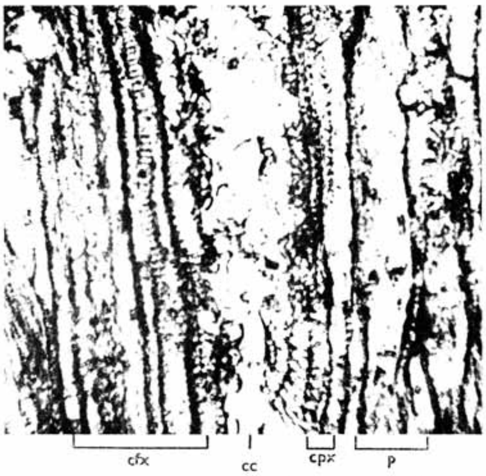

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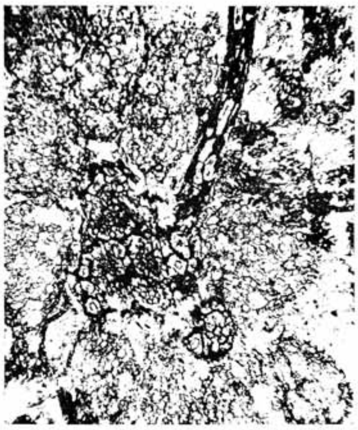

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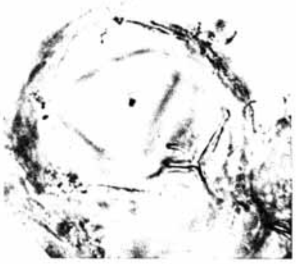

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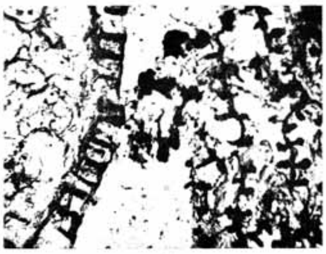

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CHAPHEKAR, Lower Carboniferous *Asterocalamites* and *Protocalamostachys*