REVISION OF THE GENUS *AMYELON* WILLIAMSON

by P. D. W. BARNARD

ABSTRACT. The two new species of root *A. bovius* and *A. equivius* are described from the Cementstone Group of the Scottish Lower Carboniferous. The genus *Amyelon* Williamson is reviewed and an emended diagnosis given. The discussion includes a review of palaeozoic roots and their taxonomic treatment together with some comments on the structure of palaeozoic woods of gymnospermous type.

THE Lower Carboniferous rocks of Scotland contain a series of floras from which a variety of detached petrified plant organs have been recovered. Amongst these remains roots are relatively abundant though only a few have so far been described and figured. Benson (1933) described some adventitious roots attached to *Heterangium* and Gordon (1935) briefly described some which probably belonged to *Pitys dayi*. The two species of root now described possess certain similarities in the structure of their secondary wood, but they probably belonged to quite distinct kinds of woody plant.

The new roots, which are known only as detached organs, have sufficient in common with *Amyelon radicans* (Williamson) to be referred to the same form genus. This was originally erected for the Upper Carboniferous root previously described as *Dictyoxylon radicans* Williamson 1872 and thought to belong to a 'Dicotyledon' (Conifer). In 1874 Williamson revised his conclusions regarding this root for which he then proposed the generic title *Amyelon* and described it as belonging to plants of the genus *Sphenophyllum*. Renault in 1879 described some structurally preserved organs which he referred to Unger's genus *Cordaites*; these included some roots (pl. 15, figs. 13–17).

Later Scott and Williamson (1894) in their revision of Williamson's earlier work on *Sphenophyllum* mentioned that the roots of this pteridophyte had only recently been figured by Renault (1893) and they made no mention of the genus *Amyelon*. It is likely, therefore, that they appreciated that *Amyelon* was more like the root that Renault (1879) had referred to *Cordaites*. In Scott (1900) we find the genus *Amyelon* included in the chapter on the Cordaitales as the root of plants belonging to this group of gymnosperms.

The secondary wood of *A. radicans* and of the two new species of root described here shows the type of ray structure (type iv) which Andrews (1940) distinguished as typical of the Cordaitales and certain pycnoxylic Lower Carboniferous woody stems traditionally assigned to the Calamopityeae (e.g. *Eristophyton*, *Endoxylon*, and *Bilignea*).

The genus *Amyelon* as instituted by Williamson (1874) was not accompanied by a diagnosis. I have examined Williamson's type slides in the British Museum (Natural History). I also prepared some new slides (topotype) from some specimens in an unlocalized coal ball loaned to me by Dr. K. L. Alvin, from the collection in the Botany Department, Imperial College, London. The specimens described here have been investigated by the peel method of Lacey *et al.* (1956).

Organ genus AMYELON Williamson 1874

Type species. A. radicans (Williamson 1872).

Emended generic diagnosis. Roots with small stellate protosteles less than 1 mm. in

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diameter and with two to four arms, each arm ending in an exarch protoxylem. Protoxylem tracheids annular or reticulate, metaxylem reticulate or multiseriate. The secondary xylem compact, composed of small tracheids of an average diameter less than 45 μ, and rays uniseriate. The radial wall pits in one or more series, distant or contiguous, round or hexagonal. Tangential pits present on some tracheids only generally those of the late wood.

Amyelon radicans Williamson

Text-figs. 1G, K; 2E, J, and T

1872 *Dictyoxylon radicans* Williamson, p. 112.
1874 *Amyelon radicans* Williamson, pp. 67–73; pl. 7, fig. 46; pl. 8, figs. 47–52; pl. 9, figs. 53–58.

Emended diagnosis. Primary xylem consisting of a two-, three-, or four-armed protostele about 0·6 mm. in diameter. Secondary xylem possessing growth rings. Tracheids square or polygonal in transverse section, of average dimensions 48×39 μ. Bordered pits on radial walls in 2–5 vertical rows, oval and distant, rarely contiguous and hexagonal. Pits with narrow borders, apertures oval and slightly inclined, opposed at a low angle. Tangential pits not confined to late wood tracheids, distant, scattered, oval. Rays uniseriate, 1–9 cells high, parenchymatous; cross-field pits 6–12, half-bordered, cupressoid.

Material. Syntypes, slide nos. 930 to 974; W. C. Williamson collection, Palaeontology Department, British Museum (Natural History) and topotype, slide nos. 2386–9; Gordon collection, Geology Department, King's College, London. Williamson's specimens being from Oldham, Lancashire, possibly from the Bullion seam (Westphalian A) of the Lower Coal Measures.

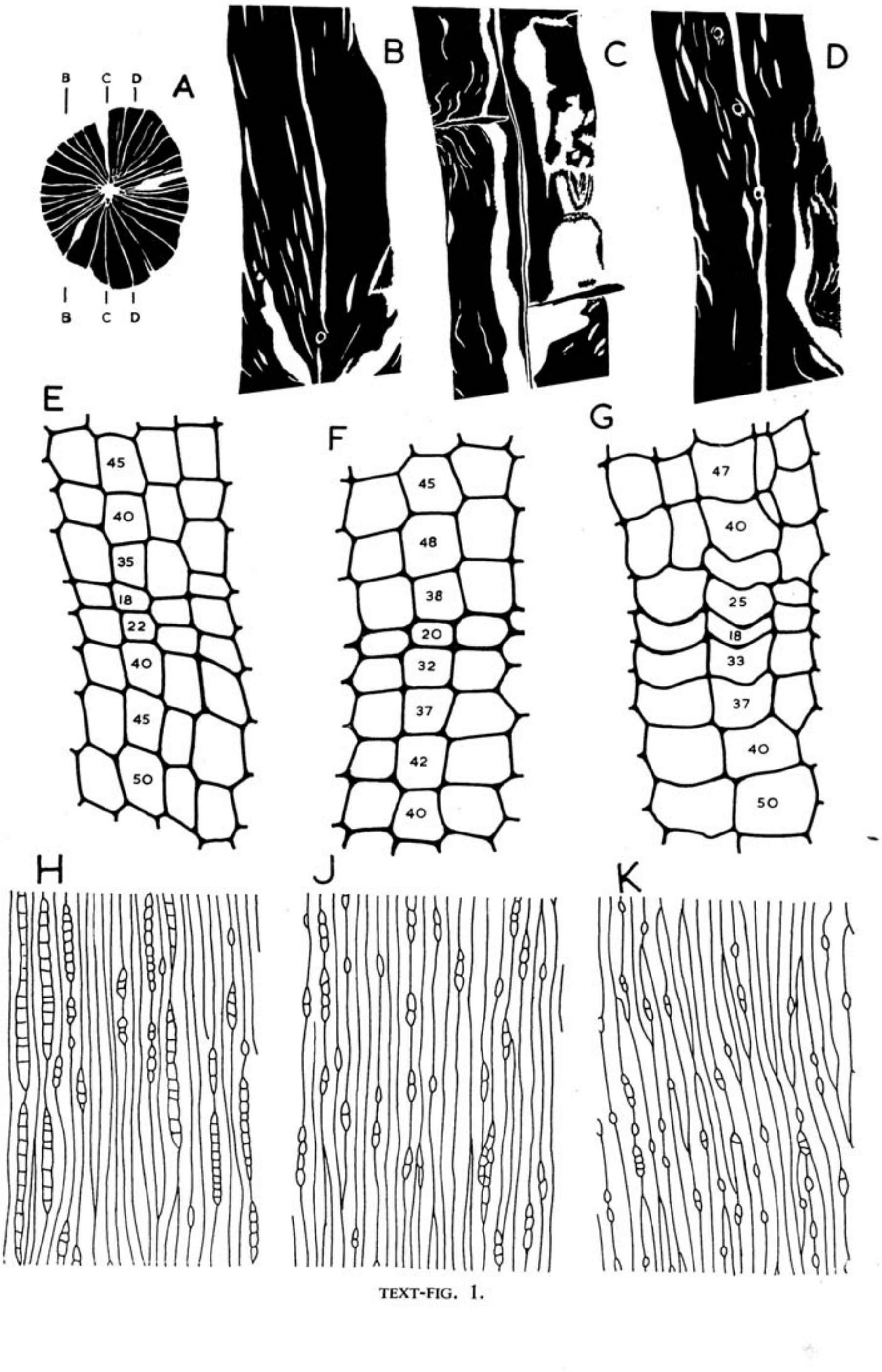
Additional notes. These roots are very variable in certain features, notably in the number of protoxylems, the distribution of the tangential pits, and the height of the rays. In some specimens tangential pits are rare and confined to the late wood tracheids, in others they are of more general occurrence (being found in about 20 per cent. of the tracheids). The ray height in the type specimen and in the one selected for my observations is 1–5 cells (text-fig. 10). In some specimens I have failed to detect rays over 3 cells high, but in one otherwise identical specimen I found rays up to 9 cells high.

The protoxylem consists of annular or reticulate tracheids, whilst the metaxylem is pitted like the secondary wood. There are a few cells of conjunctive parenchyma surrounding the protostele. The secondary wood tracheids appear thin walled and 'soft', they are often rectangular with the tangential sides longer. The growth rings are faint (text-fig. 1G) and easily confused with lines of crushing which occur frequently. The maximum and minimum dimensions of the secondary wood tracheids are 30–70 μ

TEXT-FIG. 1. Camera lucida drawings. A, Transverse section of *Amyelon bovius* to show the position of the three longitudinal sections B, C, and D which have been drawn to show the four rows of lateral root traces. B and D, Tangential sections in which the root traces appear as small knots. C, Median radial section with the laterals seen running horizontally on either side. A, G.C. 2396; B, G.C. 2398 (peel 2); C, G.C. 2398 (peel 17); D, G.C. 2399 (peel 30): all $\times 3$.

E, F, and G, Transverse sections of secondary wood ($\times 200$) to show growth-rings: E, *A. bovius*, G.C. 2425; F, *A. equivius*, G.C. 2431; G, *A. radicans*, G.C. 2387: in each the radial diameters of the tracheids along one file are shown to the nearest micron.

H, J, and K, Tangential longitudinal sections of secondary wood ($\times 40$) to show ray height and frequency: H, *A. bovius*, G.C. 2391 (peel 7); J, *A. equivius*, G.C. 2433; K, *A. radicans*, G.C. 2388 (peel 2).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TEXT-FIG. 1.

tangential by 18–60 μ radially. The pits on the radial and tangential walls are the same size 6–9 μ across. The ray cells are 65–126 μ long radially by 23–56 μ high with from 6–12 pits per cross-field (text-fig. 2E). The tracheid ray cell ratio is 7:1.

Lateral roots are of frequent occurrence and one often finds associated with the larger specimens smaller ones with little or no secondary xylem and a well-preserved cortex. Some roots of this type have been described by Osborn (1909) who figured an associated mycelium thus suggesting a mycorrhizal relationship. In the larger roots the outer cortex is replaced by a deep-seated periderm.

Amyelon radicans may possibly belong to one of the species of stem belonging to the genus *Mesoxylon* Scott and Maslen. I have examined slides of the wood of the four known species of *Mesoxylon* from Lancashire but cannot say that *A. radicans* is the root of one of these stems.

Amyelon bovius sp. nov.

Plate 33, figs. 1, 4, 7; text-figs. 1A-E, H; 2A, B, F, G, K, N, O

Diagnosis. Primary xylem consisting of a four-armed protostele, 0·5–0·8 mm. in diameter. Secondary xylem possessing growth-rings. Tracheids square or polygonal in transverse section, average dimensions 28 × 33 μ. Bordered pits on radial walls, crowded, hexagonal, in 2–4 vertical rows. Pit apertures oval and nearly horizontal. Pits on tangential walls of late wood distant, scattered, round. Rays uniseriate, 1–38 cells high, parenchymatous, cross-field pits 6–12, half-bordered, cupressoid.

Material. Holotype specimen no. 1, slide nos. 2390 to 2393; Gordon collection, Geology Department, King's College, London: and paratypes slide nos. 2394 to 2428; together with peel collection and rock specimens from the Green Ash within the Cementstone Group (Upper Tournaisian) of the Calciferous Sandstone Series (Lower Carboniferous) at Oxroad Bay, in East Lothian, Scotland.

Occurrence. The first of these new species of Lower Carboniferous root comes from a nodule in volcanic ash at Oxroad Bay in East Lothian where it forms one of the most abundant of the plant remains.

The plants from this locality so far described are *Tetrastichia bupatides* Gordon, *Salpingostoma dasu* Gordon, *Eosperma oxroadense* Barnard, and *Calathospermum fimbriatum* Barnard (1960*a*). There are as yet undescribed some four stems, another seed, some clusters of sporangia, and some rachises (*Lyginorachis*). The stems consist of an *Eristophyton sp*., two small protostelic stems of Aneurophytalean or Pteridospermic affinities, and a small herbaceous lycopod. Some account of these remains is given in Barnard (1960*b*).

Description. The primary xylem consists of a stellate tetrarch protostele which is between 0·5–1·0 mm. in diameter. The smallest cells (protoxylem) are exarch, as in most roots. These protoxylem tracheids are less than 10 μ in diameter and conse-

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EXPLANATION OF PLATE 33

Fig. 1. *Amyelon bovius* sp. nov. Transverse section, showing very clearly the four-armed protostele and dense secondary wood with one faint growth-ring; holotype, slide no. G.C. 2390 (peel 8), × 22.

Fig. 2. Transverse section through Gordon's Root of *Pitys*; slide no. G.C. 1826, × 23.

Figs. 3, 5, 6. *Amyelon equivius* sp. nov. 3, Transverse section, secondary wood shows clearly defined growth-rings; slide no. G.C. 2431, × 2. 5, 6, Radial longitudinal section showing tracheids with one row of pits in 5 and two rows in 6; slide no. G.C. 2437, 5 (peel 16), 6 (peel 15), × 640.

Fig. 4, 7. *A. bovius* sp. nov. 4, Tangential longitudinal section showing a lateral root trace passing through the secondary wood; slide no. G.C. 2427, × 60. 7, Radial longitudinal section, to show the pitting; slide no. G.C. 2422, × 640.

quently have proved extremely difficult to trace in longitudinal section. As shown in text-fig. 2K they have annular to reticulate thickenings. The metaxylem consists predominantly of large tracheids up to 70 μ in diameter and hexagonal in transverse section. These tracheids have round distant multiseriate pits on their longitudinal walls, though in some of the central tracheids the pits may be more crowded and hexagonal. The protostele is probably more or less surrounded by a layer of parenchyma, though this is only clearly revealed at the ends of the arms where it sometimes reaches a depth of 2–3 cells.

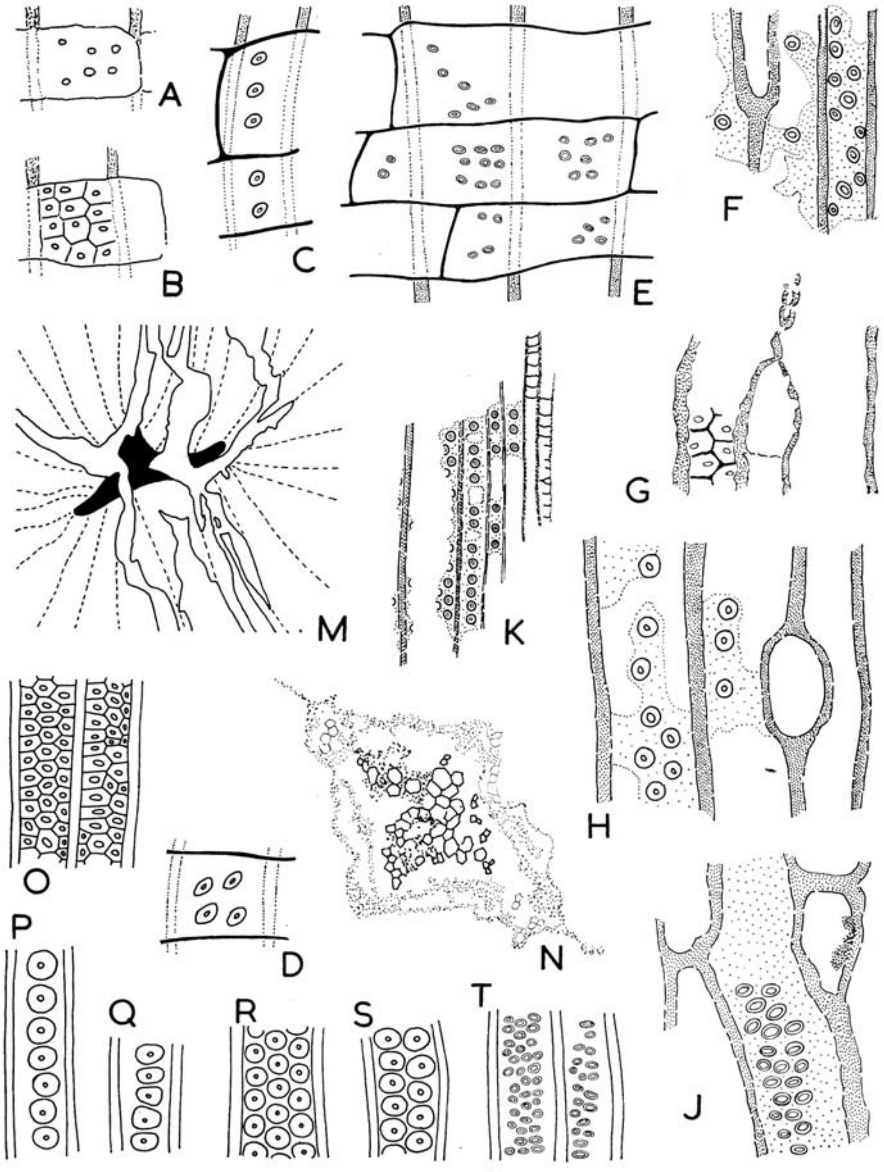
The secondary xylem: the wood in transverse section (text-fig. 1E) shows growth-rings. It is composed of radial files of rectangular or polygonal tracheids, with those of the early wood usually slightly broader radially than tangentially, and uniseriate rays. The wood of the larger roots is generally slightly separated from the primary xylem probably as a result of the breakdown of the conjunctive parenchyma. In many of the specimens further decay has resulted in splits occurring in the rays opposite the protoxylems, and quite isolated wedge-shaped fragments of wood are of fairly frequent occurrence in the matrix.

The secondary wood tracheids, which are smaller than those of the metaxylem, measure 14–48 μ tangentially (average 28 μ) and 10–60 μ radially, with an average for the early tracheids of 33 μ. The smaller tracheids, some one to three of which form the late wood in any growth-ring, have an average radial breadth of 13 μ. In radial longitudinal section the tracheids show 2–4 rows of hexagonal, alternate bordered pits with oval apertures. These pits which cover the radial walls measure 10–14 μ in diameter (text-fig. 2O). In most specimens tangential pits occur only in the late wood tracheids where usually round scattered pits are to be found throughout the length of the tracheids (text-fig. 2F). These pits resemble those found in the primary xylem. In two specimens more extensive tangential pitting was found; in one of these specimens some tracheids were observed with two or more rows of crowded hexagonal pits (text-fig. 2G).

The rays are uniseriate and usually composed of radially elongated thin-walled parenchyma. However, in some of the higher rays the cells may be square. They measure 28–100 μ in length and 36–60 μ in height. The cross-field pitting is not very clearly visible, but there appear to be 6–12 half-bordered 'cupressoid' pits per field (text-fig. 2A, B). The rays are 1–38 cells high, of which those 1–3 cells high are most frequent (text-fig. 1H). As seen in tangential section the ratio of tracheids to ray cells (Gordon's ratio) is 5:1.

In the majority of the specimens there are no tissues preserved external to the wood. In one better-preserved specimen, however, some thin-walled, elongate cells were observed next to the wood; these may be cambial cells or phloem. Separated from the woody cylinder and adjoining cells by an annular mineral-filled cavity there is a black ring of cortical tissue. It consists of 4–6 layers of rectangular cells filled with black contents and is lined by one or two layers of thinner-walled empty cells.

By means of serial longitudinal sections taken through a number of different specimens it has been demonstrated that the lateral roots arise in four rows at irregular intervals of from 1 mm. to several centimetres (text-fig. 1A to D). The primary tissues of the lateral root pass in horizontally or nearly so and fuse with one of the protoxylem groups of the parent root. The lateral roots increase slightly in diameter as they pass out through the secondary wood due to the development of their own secondary wood,



TEXT-FIG. 2.

so that the diameter of the individual laterals as seen in tangential longitudinal sections varies from 0·5–2·0 mm. The lateral roots are all broken off within 0·5–2·0 mm. of their emergence from the main root.

Associated with some of the typical woody roots there are a few specimens without any secondary tissues (text-fig. 2N) which may possibly be small laterals. The larger roots are remarkably straight, one specimen 4 mm. in diameter was almost perfectly straight, throughout a length of 15 cm. Some of the smaller specimens, ones less than 3 mm. in diameter, have a much more sinuose form. No corraloid mycorrhizal forms comparable to those described by Osborne and referred to *A. radicans* have been observed; this may be due to the poorer preservation of the material.

The structure of the wood of *A. bovius* cannot be matched with that of any of the stems found in the flora. It is perhaps suggestive of the genus *Eristophyton*; a specimen referred to this genus in the Oxroad Bay flora, has usually only one or two rows of round distant pits on the radial walls of its tracheids; a few tracheids with crowded hexagonal pits are, however, also present. The rays in this stem are uniseriate, but are only 1–8 cells high.

Amyelon equivius sp. nov.

Plate 33, figs. 3, 5, 6; text-figs. 1F, J; 2C, D, H, M, P–S; 3A

Diagnosis. Primary xylem consisting of a three-armed protostele, 0·7 mm. in diameter, each arm terminated by an exarch protoxylem. Secondary xylem consisting of tracheids and rays and showing clearly defined growth-rings. Tracheids square or polygonal in transverse section, average dimensions $32 \times 38\ \mu$. Bordered pits on the radial walls of the tracheids round and distant, in 1–3 rows. Pit apertures round. Pits on tangential walls of some tracheids only, half the size of the radial wall pits, distant, scattered. Rays uniseriate, 1–9 cells high, parenchymatous, cross-field pits 2–6, half-bordered, cupressoid.

Material. Holotype specimen and slides, nos. 2429 to 2437; Gordon collection, Geology Department, King's College, London, from the shales and cementstones from just above the Old Red Sandstone, the Cementstone Group (Upper Tournaisian) of the Calciferous Sandstone Series (Lower Carboniferous) at Horse Roads Bay, in Berwickshire, Scotland.

Occurrence. The second new species of root is represented by a single specimen (4 cm. in maximum diameter by 6·5 cm. long) in the Gordon collection. It is from Horse Roads Bay in Berwickshire. In the cementstones at this locality, Long (1960, and personal communication) has discovered *Genomosperma latens* Long, *Samaropsis scotica* Calder, and *Stenomyelon*. The plant remains are petrified with carbonate and heavily stained by brown oxides.

TEXT-FIG. 2. Camera lucida drawings. A–E, Radial longitudinal sections showing ray cells and cross-field pitting, all ×350. A and B, *A. bovius*, G.C. 2398 (peel 17), G.C. 2399 (peel 25); C and D, *A. equivius*, G.C. 2437 (peels 15 and 16); E, *A. radicans*, G.C. 2389. F–J, Tangential longitudinal sections showing tracheids with tangential pits, all ×350. F and G, *A. bovius*, G.C. 2391 (peel 7), G.C. 2428 (peel 5); H, *A. equivius*, G.C. 2433: J, *A. radicans*, G.C. 2388 (peel 2). K, radial longitudinal section showing primary xylem in *A. bovius*, annular protoxylem on the right, pitted metaxylem to the left: G.C. 2393 (peel 11); ×350. M, Transverse section showing the centre of *A. equivius*, primary xylem solid black, rays in secondary wood shown by discontinuous lines. G.C. 2431; ×20. N, Transverse section of a small rootlet associated with *A. bovius*, G.C. 2404 (peel 2); ×50. O–T, Radial longitudinal sections of secondary wood tracheids showing pitting all ×250. O, *A. bovius*, G.C. 2399 (peel 25); P–S, *A. equivius*, G.C. 2435; T, *A. radicans*, G.C. 2389.

Description. The primary xylem: unfortunately the small triarch protostele (text-fig. 2M), which measured about 0·7 mm. in diameter, is badly damaged by a large split which passes through the centre of the specimen. The metaxylem tracheids are no larger than the secondary wood tracheids; they are polygonal, and as seen in transverse section measure only 40 μ in diameter. It has not been possible to distinguish the primary xylem in the longitudinal sections.

The secondary xylem: as seen in transverse section (text-fig. 1F) the wood of this species looks very like that of *A. bovius* except that the tracheids are more uniformly square in cross-section. The specimen is badly cracked both radially and along concentric arcs which has resulted in flaking on one side so that the centre is excentrically disposed. This does not, however, reflect the pattern of growth which was clearly regular as may be seen from the growth-rings which form a series of concentric circles.

The secondary wood tracheids measure 20–65 μ tangentially, average 32 μ; and 15–66 μ radially, average 31 μ. The size of the tracheids usually shows some decrease from the beginning to the end of the growth-ring (text-fig. 1F) though the first tracheids in any one increment are not always the largest. In radial longitudinal section (text-figs. 2P–S) the tracheids have from one to three rows of round bordered pits with round pores. The pits are 14–18 μ in diameter, and most commonly occur in a single row; two rows of alternate pits are fairly common but the tracheid with three rows of pits is exceptional. The tangential walls of the tracheids are usually devoid of pits; however, tangential pits occur widely in peels from the end of the growth-rings. These pits are smaller than those on the radial walls, 7–9 μ in diameter, round and irregularly scattered (text-fig. 2H).

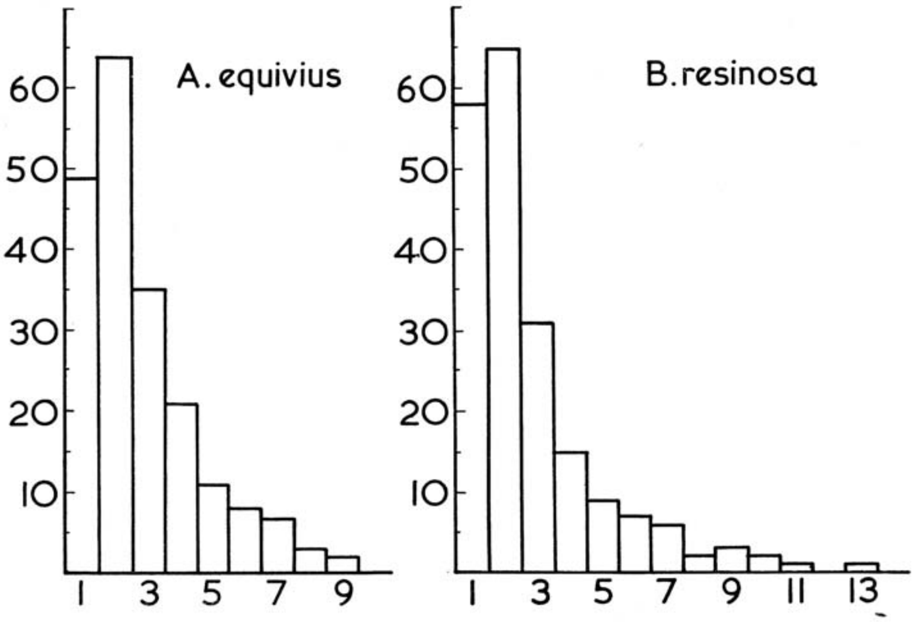
The rays are homogeneous, uniseriate or very rarely biseriate (text-fig. 1J), and are composed of radially elongated cells which measure 35–70 μ in height by 45–90 μ in length. The cross-field pits have been observed only occasionally. There are from two to six pits in the field and they are half-bordered and again of the cupressoid type (text-fig. 2C, D). The rays are 1–9 cells high; their frequency is shown in the histogram (text-fig. 3). The tracheid ray ratio is 6:1. No tissues have been observed external to the wood. A lateral root trace has been observed opposite a protoxylem group in a portion of the specimen peeled tangentially.

The secondary wood of this root is remarkably like that of the stem *Bilignia resinosa* Scott (1924). I have prepared peels from a paratype of *B. resinosa*, labelled in Kidston's handwriting in the Gordon collection, and have been able to compare it with this root. The size of the tracheids, the size and distribution of the pits, agrees perfectly. In *B. resinosa* the rays, especially in the inner part of the wood, are higher but the ray height frequency for the stem 13 mm. from the pith is almost identical to that of the wood 15 mm. from the centre of the root. No other Lower Carboniferous stem possesses so much similarity in the histology of its secondary wood. These two organs may possibly belong to one plant species. However, as so far they are only known from separate localities from rocks of about the same age, the root can at present only be referred to an organ genus for roots.

DISCUSSION

Authors have differed in their treatment of petrified palaeozoic roots; some, like Williamson, have described roots as separate entities, the rest have only described them in relation to the supposed stems that bore them. This has resulted in a very uneven presentation of the facts concerning these organs. I think the creation of clearly defined organ genera for the reception of roots is highly desirable. All the roots so far described may be placed in six major anatomical classes: *Amyelon*, roots of *Callixylon*, *Kaloxylon*, *Astromylon*, roots of *Sphenophyllum*, *Rhizonium* sensu Williamson (1889).

As now revised the genus *Amyelon* is regarded as a repository for Palaeozoic roots



TEXT-FIG. 3. Histograms to show the frequency distribution of the height of 200 rays; A, *Amyelon equivius*, B. *Bilignea resinosa*. The height is expressed as the number of cells seen in tangential longitudinal section.

having the kind of secondary wood structure broadly characteristic of *Dadoxylon*. Besides the three species described here other examples can perhaps be included in the genus. One such example is the root described by Renault (1879) as belonging to *Cordaites* and coming from the Stephanian of Autun and which, as stated in a later work (1896), has a diarch protostele.

Our knowledge of the roots of *Callixylon* is based on *C. petryi* described by Beck (1953). The secondary wood of this root showed the characteristic radial alignment of pit groups on the radial walls of the tracheids, a feature so far found only in this genus of Devonian stems. The protostele in these roots has the form of a maltese cross with two protoxylems at the end of each arm.

The genus *Kaloxylon* Williamson (1876) is typified by *K. hookeri* Williamson; it has a large, three- to eight-armed protostele (0·8–1·5 mm. in diameter) which contains tracheids together with extensive conjunctive parenchyma. The secondary wood in this species contains both uniseriate and multiseriate rays, the latter arising near the protoxylem. This root has been shown to belong to the pteridosperm stem *Lyginopteris oldhamia* Binney. The roots of other pteridosperms are similar in structure and could be classified as organ species in the genus *Kaloxylon*. Thus, the roots associated with *Heterangium lomaxi* Scott have a tetrarch protostele (about 0·9 mm. diameter) and very little conjunctive parenchyma. The secondary wood contains multiseriate rays opposite the protoxylems (Williamson and Scott 1895, pl. 27, fig. 27). The roots of *H. grievii* Williamson were briefly described by Benson (1933); they possessed a two- to three-armed protostele, and the secondary wood contained multiseriate rays. The roots of *Medullosa anglica* Scott (1899) are triarch (protostele up to 3 mm. in diameter) and contain conspicuous conjunctive parenchyma. The secondary wood contained rays up to three cells wide and was very extensively developed.

The roots associated with *Pitys dayi* Gordon (1935) have a tetrarch protostele (0·8–1·0 mm. diameter) with very little conjunctive parenchyma. The secondary wood contains low uniseriate rays together with high rays up to four cells wide which run out from the protoxylem groups. The structure of the secondary wood of these roots has more in common with that found in *Kaloxylon* than that of *Amyelon*. Should these roots in fact belong to *P. dayi* as Gordon suggests, then in the form of its roots this species of *Pitys* shows yet another structural similarity to the pteridosperms in addition to those enumerated by Gordon.

Bertrand and Renault (1887) described some roots from Autun, which they referred to *Poroxylon edwardsi*. These have a diarch protostele, and the secondary wood contains broad rays opposite the protoxylems which gives these roots the appearance of a *Kaloxylon*. Like *Pitys*, *Poroxylon* possesses a number of other pteridosperm-like features. Small diarch rootlets without secondary tissues, called *Radiculites reticulatus*, were described and figured by Lignier (1906) from the Stephanian of Grand 'Croix. In a subsequent paper (1911), he described without figures a further specimen possessing secondary tissues and compared it to the root of *Poroxylon*. Thus, the name *Radiculites* has come to be regarded by some authors as a form genus for the roots of *Poroxylon*. There is probably very little that distinguishes *Radiculites* from *Kaloxylon*. This already uncertain taxonomic situation has been further confused by Zalessky (1937) by his erection of a new genus for some compressions or impressions of root-like organs of unknown structure from the Stephanian of the Donetz basin which he called *Radiculites luganicus*.

The genus *Astromyelon* Williamson (1878) is typified by *A. williamsoni* (Cash and Hick) Williamson, which possesses from two to twelve or more exarch protoxylem groups which, in all except the finest rootlets, are found surrounding a solid pith. Thus all the larger woody specimens resemble a calamite stem lacking carinal canals. These roots are further distinguished by their lacunar cortex. They are associated with the stems of *Calamites* from the Westphalian and Stephanian.

The roots of *Sphenophyllum* are superficially very like *Amyelon* as seen in transverse sections. Thus Williamson originally catalogued two species of *Amyelon*; one, *A. radicans*, he described fully, but of the other only one specimen was figured (1874, fig. 59) and its name *A. reticulatum* appears only in his catalogue. This inadequately described and figured root was no doubt rightly referred to *Sphenophyllum*. Renault (1893–6) is regarded as the first person to describe and figure the roots belonging to *Sphenophyllum*; his roots from Autun were diarch. The English, Westphalian A, root specimens of *Sphenophyllum* possess a small, two- or three-armed exarch protostele (0·3–0·5 mm. diameter) surrounded by secondary wood. The wood shows uniform structure unlike that of the stem in which a differential development occurs opposite the protoxylems. It consists of tracheids with multiseriate bordered pits on their radial walls only; between them there is parenchyma in the form of short discontinuous rays connected by vertical columns of cells. The secondary wood is thus quite unlike that in *Amyelon*. The first clear original figure of the English *Sphenophyllum* root appeared in Scott (1920, fig. 43).

The genus *Rhizonium* Corda (1845) was founded on specimens of stigmarian rootlets. Williamson (1889), however, though recognizing the true nature of the species in the original description, used the genus as a form genus for small roots without any secondary tissues. He described as species of this genus three forms from English coal measures (Westphalian) the relationships of which are unknown.

Growth-rings occur in the secondary wood of the three specimens of *Amyelon*. They have also been reported in the root *Callixylon petryi*. The presence of growth-rings has also been recorded in a number of Carboniferous and Devonian woody stems, *Mesopitys tchihatcheffi* (Goeppert), *Bilignia resinosa* Scott, *Endoxylon zonatum* (Scott), *Eristophyton waltoni* (Lacey), *Megalomyelon myriodesmon* Cribbs, *Pitys* and *Callixylon* in which genus it was studied by Arnold (1929). So far secondary wood showing growth-rings has only been recognized in forms possessing Cordaitalean features.

The three specimens of *Amyelon* have all been found to possess tangential pits on the secondary wood tracheids. These tend to be confined to the late wood though they may occasionally be more widely distributed. The fairly extensive occurrence of tangential pits in palaeozoic woods has been noted by Andrews (1940). To the species listed in that work the following may be added, *Pitys dayi* Gordon, *Eristophyton waltoni* Lacey, and *Callixylon petryi* Beck, so that including the species described here this character has been recognized in a total of twenty-one species from thirteen genera. The evidence suggests that tangential pitting is a palaeomorphic character and that the absence of pits on the tangential walls of early wood tracheids is a neomorphic character in the secondary wood, this being the reverse of Jeffery's (1917, p. 49) hypothesis on the origin of tangential pits.

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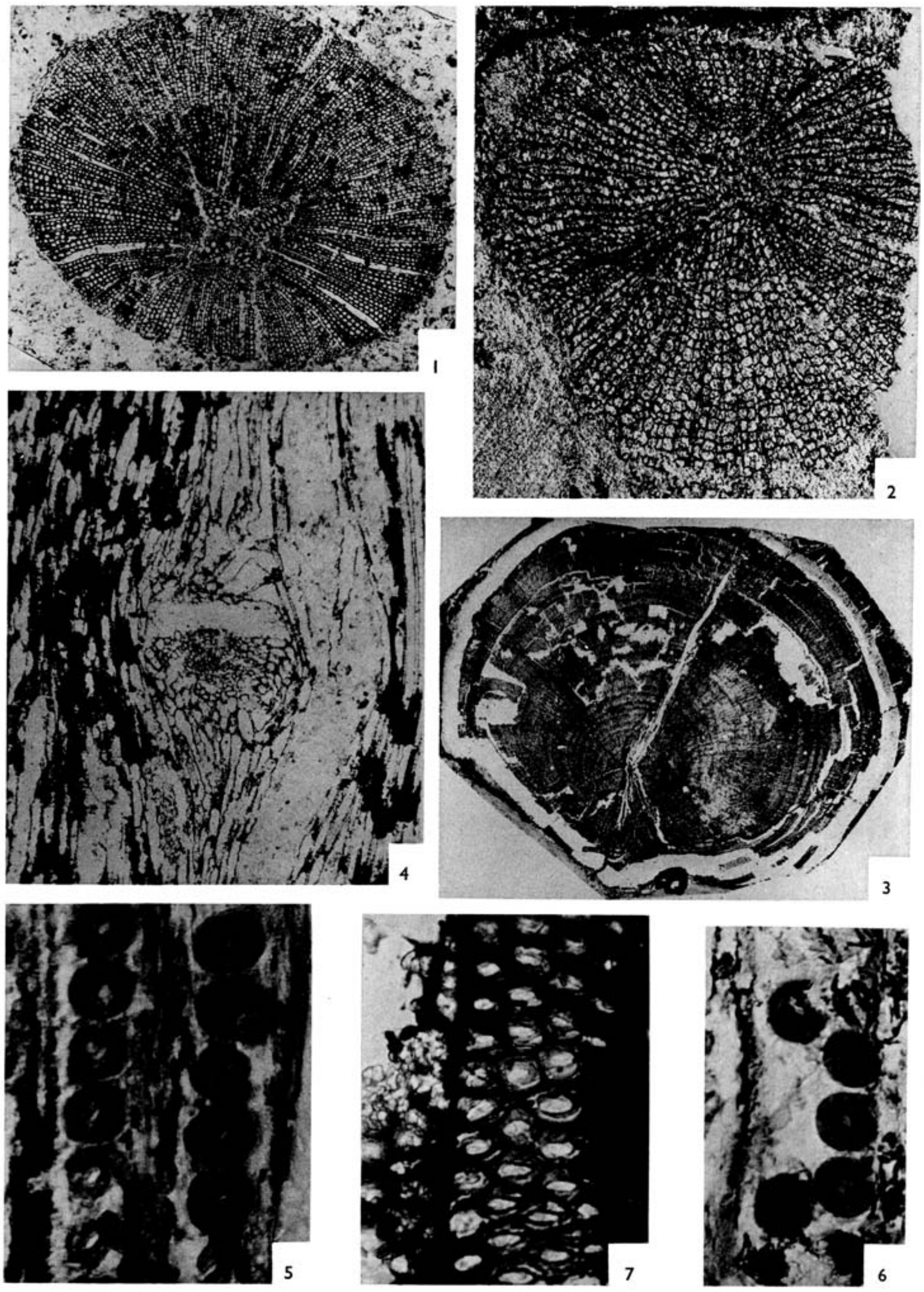

BARNARD, *Amyelon*