AMYELON IN AMERICAN COAL-BALLS

by ARTHUR A. CRIDLAND

ABSTRACT. *Premnoxylon iowense* Pierce and Hall is recombined as *Amyelon iowense*. These cordaitean roots resemble the stilt roots of modern mangroves. They are usually siphonostelic and possess aerenchyma composed of phloem and phelloderm. Increase in circumference of a deep-seated periderm distended the outer part of the phloem. Aerenchymatous phelloderm was laid down and cortex was sloughed, leaving periderm the outermost tissue. Lenticels flank clusters of lateral rootlets.

DURING the Pennsylvanian Period, cordaitean plants dominated some American coal swamps and their roots are often overwhelmingly abundant in coal-balls. Knowledge of these specimens provides new details of anatomy and morphology and leads to speculation on the biology and environment of deposition of American cordaitean plants. The American roots show similarities to *Amyelon radicans* (Williamson) Williamson, and I refer them to the genus *Amyelon*. Nevertheless, they show distinctive characters necessitating recognition of a different species. I propose to call this species *A. iowense* (Pierce and Hall) comb. nov., since the material studied shows agreement with *Premnoxylon iowense* Pierce and Hall (1953), but indicates that the differences between *A. radicans* and *P. iowense* are not as fundamental as previously supposed.

THE GENUS *AMYELON*

A. radicans is the type species of the genus *Amyelon* (Barnard 1962). Since there is substantial agreement between this root and a root attached to an American cordaitean stem (Andrews 1942) there is no doubt of the natural affinities of *Amyelon*. It can unhesitatingly be referred to the family Cordaitaceae of the Cordaitales. That is to say, *Amyelon* should be considered an organ-genus (Lanjouw *et al.* 1961, art. 3). Therefore, to refer additional specimens to *Amyelon*, an investigator should present evidence of their correct assignment to the Cordaitaceae. A recent revision of *Amyelon* (Barnard 1962) includes roots not proven as members of the Cordaitaceae. One, named *A. bovius*, is perhaps suggestive of a root of *Eristophyton* (Barnard 1962); the other, *A. equivius*, is possibly the root of *Bilignea resinosa* (Barnard 1962). I believe they should be excluded from *Amyelon*.

Genus *Amyelon* Williamson 1874

Type species. A. radicans (Williamson) Williamson 1874.

Emended diagnosis. Cordaitean roots bearing clusters of rootlets on conspicuous protuberances. Roots protostelic or siphonostelic. Primary xylem exarch; frequently tetrarch or triarch, sometimes diarch; tracheids spiral, annular, scalariform, reticulate, and multiseriate. Secondary xylem composed of radially arranged tracheids and uniseriate rays. Tracheids usually with three to five rows of bordered pits on their radial walls, pits crowded and hexagonal or oval and separate. Tangential pitting occasional.

[Palaeontology, Vol. 7, Part 2, 1964, pp. 186–209, pls. 33–37.]

Cross field pitting uniseriate and oblique. Only cambium, phloem, and periderm outside the xylem of mature roots. Periderm deep in origin, cortex sloughed early in development. Periderm divisible into phelloderm and phellem. Rootlets usually diarch, primary xylem tracheids with spiral and annular thickening, sometimes with hexagonal pitting in the metaxylem. Some phloem cells with dark contents; endodermis thick-walled. Cells of inner cortex thin-walled, with dark contents or colourless. Outer cortex of thin-walled colourless cells. Root hairs absent.

Amyelon radicans (Williamson) Williamson 1874

Holotype and synonymy. See Barnard (1962).

Remarks. The following should be added to Barnard's (1962) emended diagnosis: Protoxylem touching the secondary xylem. Excentric growth-rings present in the secondary xylem of all but young specimens. Phloem compact. Phelloderm extensive and compact, no cells with brown contents. Rootlets usually diarch or triarch with spiral or annular thickening or hexagonal pitting.

Amyelon iowense (Pierce and Hall) comb. nov.

1942 Root attached to *Mesoxylon nauertianum*, Pyramid Mine, Perry County, Illinois. Coal No. 6, Kewanee Group. Andrews, pl. 4, figs. 13–16 only (text-fig. 1; pl. 3, figs. 8, 9, show coenopterid rootlets).

1953 *Premnoxylon iowense* Pierce and Hall, Ellis Mine, SW¼ sect. 7, T. 74 N., R. 15 W., Mahaska County, Iowa. Desmoinesian Stage.

Emended diagnosis. Large roots protostelic or siphonostelic, pith entire, or with a lacuna at the centre, some pith cells filled with brown contents. Primary xylem exarch, usually tetrarch, sometimes triarch or diarch. Protoxylem touching the secondary xylem or separated from it by several parenchymatous cells. Protoxylem tracheids with spiral, annular, or scalariform thickening. Metaxylem tracheids with uniseriate or biseriate simple pits, or with crowded, hexagonal, bordered pits. Secondary xylem composed of radially arranged tracheids and uniseriate rays. Tracheids with one to five rows of bordered pits on their radial walls. Uniseriate bordered pits occurring on the tangential walls rarely. Rays, one to eight cells high, some cells with brown contents. Cross field pitting uniseriate and oblique. Phloem consisting of sieve elements, phloem parenchyma, phloem rays and phloem fibres. Outermost part of the phloem usually aerenchymatous, with phloem rays greatly stretched radially. Phelloderm extensive, usually aerenchymatous, some cells very long, with brown contents. Phellem cells rectangular, tangentially elongated. Lenticels present. Lateral rootlets borne in clusters on conspicuous protuberances of the main root, protuberances always occurring between two lenticels. Rootlets 500 μ in diameter. Primary xylem usually diarch, rarely triarch or tetrarch. Cells with brown contents present in phloem and inner cortex. Endodermis thick-walled. Outer cortex composed of colourless, thin-walled cells. Cortex of young main roots sloughed by development of periderm arising from a deep-seated phellogen. Phellogen arising before extensive development of secondary xylem and phloem.

Syntype specimens. Coal-ball UM 110 and a series of unnumbered slides, Paleobotanical Collection, University of Minnesota, Minneapolis.

Other material studied

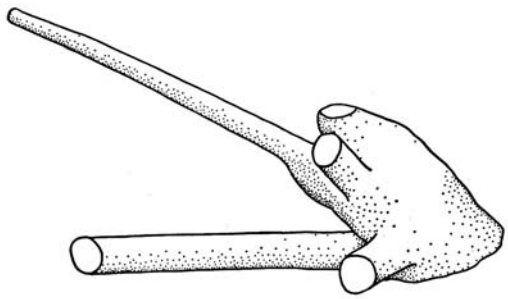
Locality 1. Pittsburg and Midway Coal Company's open strip mine, 2 miles north of Halowell, Kansas. Sect. 4, T. 33 S., R. 22 E., Cherokee County. Mineral and/or Fleming Coal, Cabaniss Formation of the Cherokee Group, Desmoinesian Stage. Coal-ball KU 1021, Botany Department, Kansas University, Lawrence. Coal-ball KU 1016, Botany Department, Kansas University, Lawrence. Coal-ball KU 1044, Botany Department, Kansas University, Lawrence.

Locality 2. Kruger Coal Company's abandoned shaft mine, ¼ mile north of Cherokee, Kansas. S½ SW¼ Sect. 7, T. 31 S., R. 24 E., Crawford County. Weir-Pittsburg Coal, Cabaniss Formation of the Cherokee Group, Desmoinesian Stage. Coal-ball KU 1115, Botany Department, Kansas University, Lawrence.

Locality 3. Atlas Coal Mine, 2·9 miles north and west of Eddyville, Iowa. W½ SW¼ Sect. 18, T. 74 N., R. 15 W., Mahaska County. From a part of the Desmoinesian Stage including the Seahorne Limestone and the Bevier Coal. Coal-ball IU 1755, Botany Department, Illinois University, Urbana.

Locality 4. Mine on a 40-acre plot belonging to Tom Elsloo *et al.*, on east side of State Highway No. 137, north-east of Givin and 3·9 miles south of Oskaloosa, Iowa. NW¼ NE¼ Sect. 12, T. 74 N., R. 16 W., Mahaska County. From a part of the Desmoinesian Stage including the Seahorne Limestone and the Bevier Coal. Coal-ball IU 1823, Botany Department, Illinois University, Urbana.

Peels were prepared using the cellulose acetate film technique (Joy *et al.* 1956). These were supplemented by occasional poured peels (Darrah 1936) and a few ground sections.



TEXT–FIG. 1. Reconstruction of a large specimen with five branches. Extra-xylary tissues omitted. KU 1021, ×0·5.

LARGE ROOTS

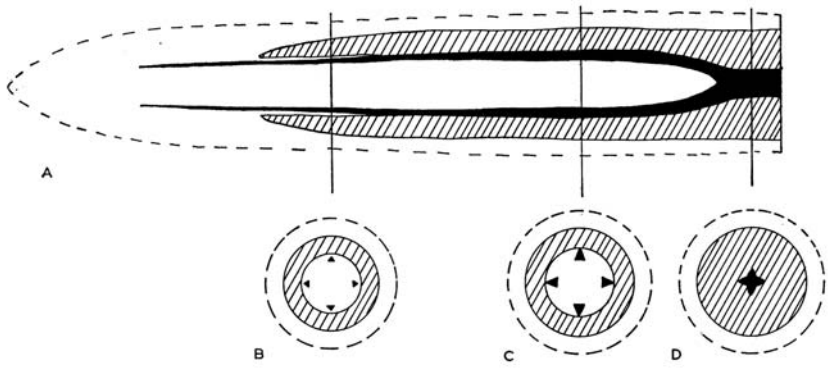
The mode of branching of large roots is shown in text-fig. 1 and their general organization is shown in Plate 33, fig. 1. A central pith with four exarch primary xylem poles at its periphery is surrounded by a cylinder of secondary xylem. Cambium occurs at the edge of the secondary xylem and there is a zone of compact secondary phloem. Aerenchymatous tissue, partly secondary phloem and partly phelloderm, accounts for the largest volume of root. Phellogen and fairly thick, compact phellem occur outside the aerenchymatous phelloderm.

Pith. In transverse section, pith cells are rounded and thin-walled (Pl. 33, fig. 1), measuring 70–160 μ, while in longitudinal section they are rectangular, 95–260 μ long, and are arranged in axial rows. Some of them have light brown contents. Frequently the pith is

entire, but in larger specimens there is a central lacuna. There is absolutely no indication of the chambered pith so characteristic of cordaitean stems.

Some specimens have no pith, but serial sections through several roots show a transition from a protostelic condition near the point of attachment to a supraordinate root (Pl. 33, fig. 2, text-fig. 2A, D), to a siphonostelic condition further away (Pl. 33, fig. 1; text-fig. 2A, B, C).

Primary xylem. There are from two to four exarch primary xylem poles, with the protoxylem either touching the secondary wood or separated from it by several rows of parenchymatous cells (Pl. 34, fig. 1). Where diarch primary xylem plates occur they



TEXT–FIG. 2. A, Theoretical radial section through an entire root. Attachment to a supraordinate root to the right, root apex to the left. B–D, Transverse sections at levels indicated by the lines passing through A. B, Tetrarch siphonostele; primary xylem separated from the secondary xylem by parenchyma cells. C, Tetrarch siphonostele; primary xylem in contact with the secondary xylem. D, Tetrarch protostele; primary xylem in contact with the secondary xylem. Conventions: primary xylem, solid black; secondary xylem, diagonal lines; outer limit of root, broken line; parenchymatous tissues left blank. Not to scale.

measure about 600 μ from protoxylem to protoxylem. Where the primary xylem is triarch or tetrarch, isolated primary xylem poles are triangular in transverse section and measure about 250 μ along the base and 275 μ radially. Protoxylem cells are about 23 μ in transverse section, while metaxylem cells are about 57 μ. Wall sculpturing of protoxylem tracheids is spiral, annular (Pl. 34, fig. 2) and scalariform, while the region transitional from protoxylem to metaxylem has tracheids with simple, uniseriately arranged pits on their radial walls (Pl. 34, fig. 3). These simple pits are transversely elongated and look intermediate between scalariform thickening and true pitting. Many metaxylem tracheids have uniseriate, or alternately arranged biseriate, simple pits about 8 μ in diameter on their radial walls (Pl. 34, fig. 4). Those furthest from the protoxylem poles have alternately arranged, crowded and hexagonal bordered pits with slightly oblique slit apertures on their radial walls, as in secondary xylem tracheids.

Secondary xylem. The secondary xylem is composed entirely of tracheids and xylem rays (Pl. 34, fig. 8). In transverse section the tracheids are square and measure 35–70 μ across,

while the ray cells are elongated radially and measure about 60×16 μ. The tracheids are pitted almost exclusively on their radial walls with one to five rows of pits, although three rows are typical. The pits are of the crowded, hexagonal type (Pl. 34, fig. 5), or else they are less crowded, but still flattened above and below by contact with each other (Pl. 34, fig. 6). Where the pits are crowded and hexagonal they measure 23 μ radially $\times 12$ μ axially and the almost transverse or slightly oblique pit apertures measure 16×2 μ. There is no torus in any pit pair.

Uniseriate pits occur on the radial walls of tracheids adjacent to the cambium of one specimen (Pl. 34, fig. 6). These pits measure 23 μ radially $\times 12$ μ axially and are flattened by contact above and below. Their apertures are diagonal slits (measuring 16×2 μ), in contrast to the nearly horizontal slits in other pits, but none are crossed. A tracheid of the same root shows uniseriate bordered pits on a tangential wall (Pl. 37, fig. 5). This tracheid is 26 μ across, the pits are 18×14 μ, are flattened where they contact above and below, and have obliquely orientated slit-like apertures which are 12×1 μ. Hence it is both narrower and bears smaller pits than the tracheids with pitting on their radial walls.

Xylem rays are uniseriate and are from one to eight cells high (Pl. 34, fig. 8) with individual cells measuring 60 μ radially $\times$ 50–80 μ axially. Some have brown contents. The cross field pitting (Pl. 37, fig. 4) is uniseriate and in each ray cell there are at least three simple oblique cross pits, measuring 16×2 μ.

Cambium. The cambium and its immediate derivatives form a well-defined zone about six cells deep, surrounding the secondary xylem (Pl. 35, figs. 1, 3, 4). These cells are tangentially elongated and measure about 28×12 μ in transverse section. Plate 35, fig. 3

EXPLANATION OF PLATE 33

The following abbreviations are used in Plates 33–37: *c*, cambium. *pa*, aerenchymatous phloem. *pc*, compact phloem. *pd*, aerenchymatous phelloderm. *pe*, periderm. *pf*, phloem fibre. *ph*, phloem. *pm*, phellem. *pp*, phloem parenchyma. *pr*, phloem ray. R.S., radial section. *s*, sieve cell. T.L.S., tangential section. T.S., transverse section. *x*, xylem.

Figs. 1–4. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, General features of a root. KU 1021 F, $\times 15$: T.S. 2, Root near its attachment to a supraordinate root. At the centre there is a poorly preserved tetrarch protostele. Note the growth ring in the secondary xylem. KU 1021 j, 513; slide 727, $\times 10$: T.S. 3, Part of the root in Plate 37, fig. 2 showing a xylem pole, phloem, periderm, and part of the inner cortex; $\times 60$. 4, Rootlet showing thick-walled endodermis. Vascular tissue to the right and cortical tissue to the left. KU 1021 F, 76; slide 361, $\times 250$: R.S.

EXPLANATION OF PLATE 34

Figs. 1–9. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, Primary xylem pole separated from secondary xylem by several parenchymatous cells. IU 1755 F, 2, $\times 100$: T.S. 2, Protoxylem tracheid with annular thickening. KU 1021 *G*, 7; slide 421; $\times 300$: T.L.S. 3, Uniseriate simple pits. Primary tracheids in a region transitional between protoxylem and metaxylem. IU 1755 *C*, $\times 600$: R.S. 4, Metaxylem tracheids, one with uniseriate simple pits, another with biseriate, alternate simple pits. IU 1755 *C*, 4, $\times 600$: R.S. 5, Radial wall of a secondary tracheid. KU 1021 *G*, 11; slide 425, $\times 300$. 6, Secondary tracheids with uniseriate pits. KU 1021 *G*, 14; slide 428, $\times 200$: R.S. 7, A root near its attachment to a supraordinate root. Its growth has been restricted by adjacent roots and no aerenchyma has developed. The convolutions at the lower right-hand side are lenticels. KU 1021 j, 357; slide 703, $\times 8$: T.S. 8, Tracheids and uniseriate rays of secondary xylem. KU 1021 *G*, 3; slide 417, $\times 100$: T.L.S. 9, Phloem fibre with uniseriate simple pits. KU 1021 *G*, 7; slide 421, $\times 250$: R.S.

probably shows an actual cambium cell, while in Plate 35, fig. 4 the gradual transition between phloem and cambium is clear.

Phloem. There are two regions of phloem (Pl. 33, fig. 1; Pl. 35, fig. 1; Pl. 37, fig. 7); an inner compact region, about 200 μ thick with radially arranged rows of cells and an outer aerenchymatous region, about 1·5 mm. thick, with cells less regularly arranged. Externally, the aerenchymatous phloem abuts against an aerenchymatous phelloderm.

Several types of cells can be recognized in the compact phloem. Those with thick dark walls are most conspicuous and I interpret them as phloem fibres. In transverse section they are rectangular, tangentially elongated, measure approximately 35×16 μ and occur in tangential rows (Pl. 35, figs. 1, 4, 6). Cases of poor preservation demonstrate them as the phloem cells most resistant to decay. These dark, thick-walled, phloem fibres are conspicuous in longitudinal sections (Pl. 35, fig. 2). Some have a single row of simple pits about 9 μ in diameter on their radial or tangential walls (Pl. 34, fig. 9). Fibres of similar structure occur in the secondary phloem of *Taxodium distichum* where they have a comparable arrangement in tangential rows, characteristic of the living Taxodiaceae and some Cupressaceae (Chang 1954).

Transverse sections also show rounded or square thin-walled cells of two sizes in the phloem (Pl. 35, fig. 4). Those of larger diameter measure 30–40 μ across, while those of smaller diameter measure about 20 μ across. Radial sections show that the thin-walled cells of larger diameter are rectangular, have horizontal end walls and are only 105 μ long (Pl. 35, fig. 2) and occasionally have brown contents. I interpret them as phloem parenchyma cells. Radial sections also show that the thin-walled cells of smaller diameter have transverse end walls, but are longer. I suggest that they are sieve elements, but no unequivocal details support this view. Phloem rays are present and in transverse section their radially elongated cells measure approximately 35×58 μ, except near the edge of the compact phloem where they are frequently conspicuously enlarged (Pl. 35, figs. 1, 4) and measure 70 μ radially $\times$ 46 μ tangentially.

At the edge of the compact phloem there is a transition to aerenchymatous phloem (Pl. 35, figs. 1, 7; Pl. 37, fig. 7). Phloem fibres persist for some distance beyond the edge of the compact phloem and the enlarged ray cells extend through the aerenchyma as tortuous chains. The distribution of phloem fibres is well illustrated in Plate 35, fig. 6, where the general preservation is poor and only the resistant xylem tracheids and phloem fibres are preserved. Here the phloem fibres occur for a considerable distance beyond the zone of compact phloem, occupying a zone corresponding to the inner part of the aerenchyma in better-preserved specimens. Interpretation of the inner part of the aerenchyma as phloem is supported by radial sections. In Plate 36, fig. 1 there are two prominent rays. That in the upper left-hand part of the photograph extends as an organized unit for some distance into the aerenchyma, an anatomical feature not found in aerenchymatous cortex. The ray cells furthest from the xylem are longer radially than the ray cells in the xylem, and two of them, at the bottom of the ray, have distinct projections of varying lengths. At the lower right-hand side of Plate 36, fig. 1 there is a ray with conspicuously radially elongated cells. A similar ray in the aerenchymatous phloem is shown in Plate 36, fig. 2. In this case, although the ray is still organized as a distinct unit, the cells are considerably radially elongated and measure 250×40 μ. I interpret this radial elongation as a result of stretching during secondary growth.

Phelloderm. Externally the aerenchymatous phloem abuts directly against aerenchyma of different structure, about 1·3 mm. across (Pl. 33, fig. 1; Pl. 37, fig. 7). Since this outer aerenchyma is apparently derived from the same meristematic region giving rise to the phellem (Pl. 35, fig. 8), I regard it as phelloderm. Its cells look similar in transverse and longitudinal sections. They are frequently rounded, measuring about 90 μ across, with short projecting arms, but are sometimes larger and more or less rectangular, measuring about 200×90 μ. These larger cells are often constricted at the middle and thus shaped like a peanut fruit. The phelloderm cells tend to be arranged in axial rows. In addition, the phelloderm has some large cells, up to 150 μ across, with brown contents (Pl. 33, fig. 1). Plate 35, fig. 5 shows these cells in longitudinal section, one measuring over 8 mm. with no traces of cross walls. In radial sections the aerenchymatous phelloderm can be readily differentiated from the aerenchymatous phloem by the presence of these cells and by the absence of phloem fibres and phloem rays (Pl. 37, fig. 7).

The aerenchymatous phloem and phelloderm described above are typical of mature roots, but there are some variations in structure. Plate 34, fig. 7 shows the same root illustrated in Plate 33, fig. 1, but is a transverse section close to the point of attachment to a larger root. In this region the root lies between two other roots, its more or less triangular shape suggesting that growth was restricted. No aerenchyma is present. Instead, the phloem is compact and up to 500 μ thick, over twice as thick as the compact phloem in the region of the same specimen shown in Plate 33, fig. 1, and the phelloderm is a fairly compact tissue with only small intercellular spaces. Both these facts suggest that restriction of growth by the adjacent roots inhibited normal distension of phloem and phelloderm to form aerenchyma. Further variation in the structure of tissues between

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EXPLANATION OF PLATE 35

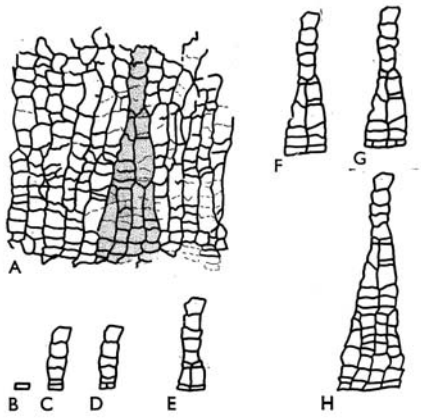
Figs. 1–8. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, Root showing secondary xylem, cambium, and phloem with a transition from compact phloem to aerenchymatous phloem. KU 1021 F, 2; slide 338: T.S. 2, Compact phloem. Short rectangular cells are interpreted as phloem parenchyma and narrower, longer cells with transverse end walls may be sieve cells. At the right, a dark phloem fibre is visible. KU 1021 *G*, 17; slide 431, ×400: R.S. 3, Cambium and its immediate derivatives: phloem above, xylem below. KU 1021 E, 2; slide 318, ×350: T.S. 4, The outer edge of the secondary xylem, the cambium, and its immediate derivatives. KU 1021 E, 2; slide 318, ×350: T.S. 5, Aerenchymatous phelloderm containing long wide cells with dark contents, and aerenchymatous phloem with much thinner phloem fibres. KU 1021 *H*, 4; slide 503, ×10: T.L.S. 6, Poorly preserved specimen with only secondary xylem and phloem fibres preserved. KU 1021 j, 83; slide 640, ×20: T.S. 7, Aerenchymatous phloem showing the stretched and meandering phloem rays, phloem fibres, and phloem parenchyma. KU 1021 E, 2; slide 318, ×50: T.S. 8, Aerenchymatous phelloderm, phellogen, and phellem. KU 1021 f, 3; slide 409, ×100: T.S.

EXPLANATION OF PLATE 36

Figs. 1–5. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, Outer part of the secondary xylem, cambium, compact phloem, and the inner part of the aerenchymatous phloem. KU 1021 *G*, 16; slide 430, ×100: R.S. 2, Aerenchymatous phloem with radially stretched phloem rays, phloem fibres, and a vertical chain of parenchyma. KU 1021 *G*, 15; slide 429, ×50: R.S. 3, Rootlet showing diarch primary xylem surrounded by brown debris. The outer cortex has large colourless cells. KU 1021 F, 45; slide 351, ×100: T.S. 4, Root in which the only aerenchyma developed is phelloderm. Phloem is a compact tissue which has been torn away from the internal tissues. Note the growth-ring in the secondary xylem. IU 1755 B, 2, ×10: T.S. 5, Root showing ten clusters of lateral rootlets. KU 1115 *C*, 12; slide 744, ×2: oblique longitudinal section.

xylem and phellem is shown by the specimen in Plate 36, fig. 4. In this case, the aerenchyma is exclusively phelloderm and the phloem is a compact zone of tissue about 250 μ across.

Phellem. Smaller mature roots are surrounded by phellem composed of thin-walled cells, rectangular in transverse section, measuring 150 μ tangentially $\times$ 80 μ radially. These cells are arranged in simple radial rows, reflecting their derivation from the phellogen. In larger roots the phellem is more extensive, attaining a thickness of up to 3 mm., with parts exhibiting cell arrangements reflecting a growth pattern where phellogen cells divided radially and increased the diameter of the root (text-fig. 3A, stippled area).



TEXT-FIG. 3. Phellem of a mature root and hypothetical stages in its development. A, Phellem of a mature root. Poorly preserved thin cell walls indicated by broken lines, all other cell walls indicated by bold lines. B–H. Hypothetical stages in the development of the stippled area. H is comparable to the stippled area in A. A is based on KU 1021 E, 2; slide 318, $\times$30.

Theoretical stages in this growth process are shown in text-fig. 3B–H. At first (text-fig. 3B) a single phellogen cell cut off a single row of phellem cells (text-fig. 3C). Then there was a radial division in the phellogen cell (text-fig. 3D), tangential enlargement of each daughter phellogen cell to the normal size and subsequently two rows of phellem cells were cut off (text-fig. 3E, F). This process continued (text-fig. 3G, H) until the root had a greater circumference. There was evidently little or no compensating growth of soft tissues inside the phellogen, and the expansion of the phellogen led to the development of radially acting tension, causing the formation of aerenchymatous phloem and phelloderm. Radial subdivision did not occur in every phellogen cell. If it had done so the phellem would have rapidly developed large cracks and would have been of little protective value. Even so, in older specimens quite large cracks sometimes developed in the phellem, but by this time it was about to be sloughed and a new phellem was usually being differentiated.

Lenticels. Many transverse sections show that the phellem has an irregular outline, with distinct convolutions (Pl. 34, fig. 7; Pl. 37, fig. 1; text-fig. 4A) which bear resemblances

to the lenticels of some modern plants. These lenticel-like convolutions occur in pairs, and clusters of lateral rootlets arise between them (text-fig. 5B). In transverse section the convolutions measure as much as 3 mm. across the base, project approximately 3·5 mm. They are 2–3 mm. long. In the distal part of the convolution the phellem is noticeably thinner than elsewhere. Transition between numbers of rows of cells is abrupt and the additional rows are reflexed as prominent lips, often with several such lips on each

TEXT-FIG. 4. Lenticel. A, See Plate 37, fig. 1, ×20. B, Transverse section through part of a lenticel. There is a burst closing layer to the right. Above and to the right of the intact closing layer there are some large cells, some containing gum (indicated in solid black). KU 1021 E, 60; slide 327, ×100.

convolution. Analogy can be made between the thin region of phellem in these convolutions and the closing layer in modern lenticels, and the lips can be compared to burst closing layers.

Phelloderm inside the lenticels is composed of cells rounded in transverse section and measuring about 75 μ across, some with brown contents. These cells have occasional, very small intercellular spaces between them, and there is a gradual transition from this kind of phelloderm to the aerenchymatous phelloderm described previously. Occasionally there are phellem convolutions where the distal part is no thinner than the rest of

EXPLANATION OF PLATE 37

Figs. 1–7. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, Lenticel showing a thin area at the top of the convolution of phellem. Several lip-like flaps comparable to broken closing layers are visible. 1_1 was probably once joined to 1_2. KU 1044 B; slide 736, ×20: T.S. 2, Small tetrarch root. KU 1021 j, 165; slide 646, ×25: T.S. 3, Phellem and an aerenchymatous part of the phelloderm. Slide 1109, Henry Shaw School of Botany, St. Louis, ×50: T.S. 4, Xylem rays showing the cross field pitting. KU 1021 *G*, 14; slide 428, ×500: R.S. 5, Uniseriate pits on the tangential wall of a tracheid. There are xylem rays to the right and left of this tracheid. KU 1021 *G*, 3; slide 417, ×400. 6, Root with several immature lenticels. IU 1877 B, 2, ×6: T.S. 7, Xylem, compact phloem, aerenchymatous phloem with radially elongated phloem rays and phloem fibres, aerenchymatous phelloderm with vertical chains of peanut-shaped cells and large cells with dark contents, and phellem. KU 1021 *G*, 6; slide 420, ×15: R.S.

the phellem and there are no prominent lip-like flaps (Pl. 37, fig. 6). These may be immature lenticels.

ROOTLETS

Clusters of up to twenty rootlets are borne on conspicuous phellem-covered protuberances of the large roots, and each cluster of rootlets is associated with two flanking lenticels (text-figs. 5B, L, O; 6A, F, G). Each protuberance protrudes about 3 mm. from the main part of the root, measures 3 mm. tangentially, and just over 3 mm. axially. The bulk of the protuberance is compact phelloderm, composed of rounded cells measuring 85 μ, some with dark contents. Externally the protuberance is covered by phellem.

In most specimens the clusters of lateral rootlets show no regular taxy, but one specimen (Pl. 36, fig. 5) is a notable exception. Here the clusters of rootlets are much more abundant than usual (there are ten of them on a piece of root 10 cm. long) and they are all borne along one side of the root. Perhaps this root ran over the surface of the soil, with the clusters of rootlets borne on its lower surface.

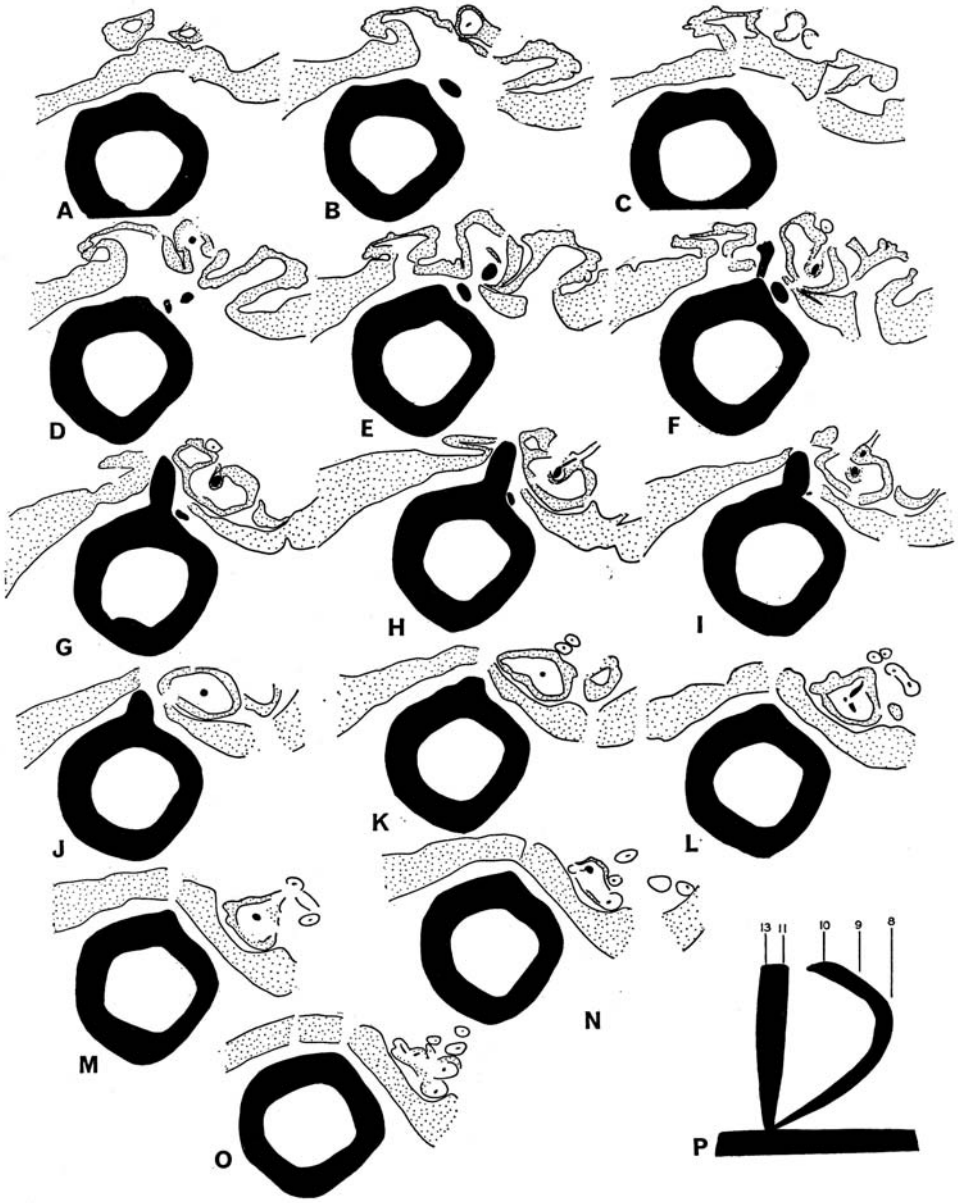
Xylem. Plate 36, fig. 3 is a transverse section of a rootlet approximately 500 μ in diameter. There is a diarch primary xylem plate composed of only a few tracheids. The central tracheid, which I interpret as a metaxylem tracheid, is largest and measures 22 μ across. Two adjacent tracheids, which may be metaxylem or protoxylem, are only 14 μ across, while at the ends of the xylem plate some smaller, but very poorly preserved tracheids must certainly be interpreted as protoxylem.

In longitudinal sections of rootlets the only xylem elements recognized were protoxylem tracheids with spiral and annular thickenings, but none is preserved well enough to be illustrated. The narrowness of the primary xylem plate in the rootlets, combined with the frequent imperfect preservation of the cells, makes it difficult to study the tracheids adequately.

Phloem and inner cortex. Two regions can be recognized in the tissues surrounding the diarch plate. An inner region, 140 μ thick, representing the phloem and the inner part of the cortex, is poorly preserved and contains much brown debris. In some rootlets preservation is favourable enough to determine that cells of the inner cortex are about 32 μ across, but no details of phloem cells can be distinguished.

Outer cortex. Surrounding the inner cortex there is a region of thin-walled cortical cells, up to 150 μ thick, composing the rest of the root. These cortical cells are rounded to hexagonal in transverse section and have no dark contents. They measure about 45 μ across and are at least 100 μ long. There is some suggestion that the peripheral walls of the outermost layer of cells are slightly thickened, as in an epidermis, but no cell is piliferous.

Endodermis. No attached rootlet shows the endodermis clearly, but in a radial section of a detached rootlet a row of cells with greatly thickened walls can be seen close to the xylem (Pl. 33, fig. 4). These cells, which measure 46 μ radially and 100–160 μ axially, probably represent a thick-walled endodermis. Although detached rootlets lack distinctive characters and are easy to misassign, I am confident that this rootlet is correctly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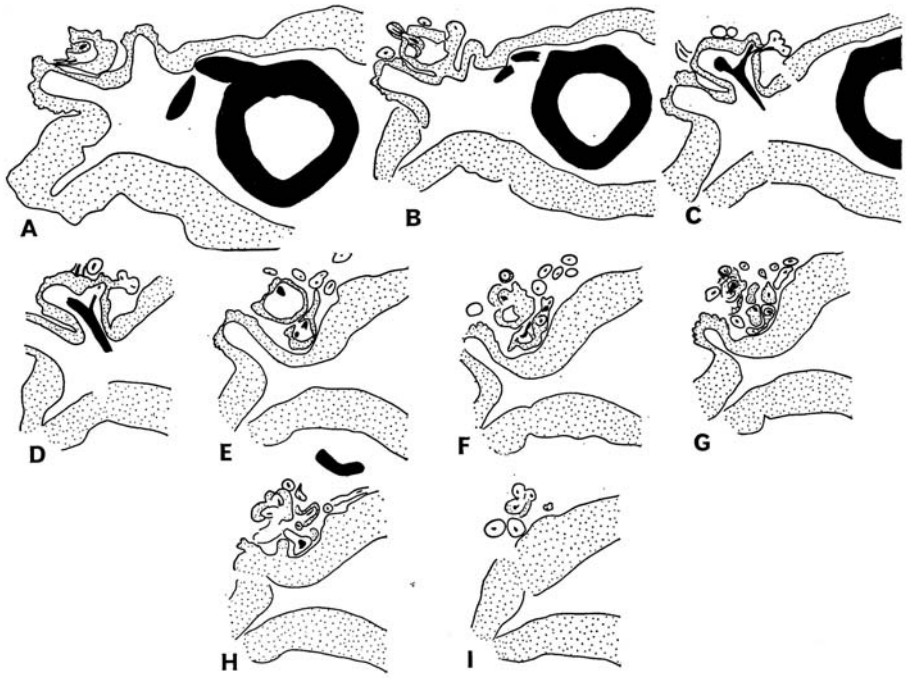
referred to *A. iowense*, since similar cells were seen in some attached rootlets, but were too poorly preserved to photograph.

Periderm. The rootlet in Plate 37, fig. 2, and Plate 33, fig. 3 calls for special comment since although a deep-seated periderm has arisen, the cortex has not been sloughed. Part of the outer cortex is still present, but not the epidermal layer. Part of the inner cortex is moderately well preserved and many of its cells have brown contents (Pl. 33, fig. 3). It is impossible to verify the presence of an endodermis, because the cells immediately outside the periderm have decayed. Periderm, about 200 μ thick, is composed mainly of radial rows of cells measuring 35–40 μ tangentially by 12–23 μ radially, but some cells are nearly square and measure just over 40 μ across. Periderm cells are slightly thicker-walled than cortical cells and thinner-walled than xylem tracheids. The periderm of this rootlet was not seen in longitudinal sections, but in some peels it was cut obliquely. These oblique sections help verify the identification of the tissue, because they show no evidence of pitting on any of its cell walls. On the other hand, tracheids in the same oblique sections have clear indications of pitting on their walls. Within the periderm there is a tetrarch protostele with exarch primary xylem poles. Although the position of the phloem is indicated in Plate 33, fig. 3, no structural details can be determined.

Possession of a deep-seated periderm suggests that this specimen will eventually develop into a large root bounded by periderm, comparable to those already described. Another indication that this rootlet will develop into a large root comes from the number of protoxylem poles. It is uncommon to find rootlets with more than two protoxylem poles, while most large roots are triarch or tetrarch. A similar situation exists in *A. radicans*, where Osborn (1909) suggested that small triarch and tetrarch specimens are immature primary roots.

TEXT-FIG. 5. Representative transverse serial sections through two lenticels and a basal protuberance bearing a cluster of lateral rootlets. All ×3. Xylem, black; phellem, stippled.
A, Stele, phellem, part of a lenticel and part of the protuberance. KU 1021 I, 73; slide 546. B, As in A, but with part of a second lenticel. KU 1021 I, 104; slide 570. C, As in B, but the protuberance has vascular tissue and part of the trace supplying it is seen in oblique longitudinal section. KU 1021 I, 115; slide 571. D, Two parts of a curved trace supplying the protuberance are present (cf. text-fig. 5P). KU 1021 I, 132; slide 573. E, Parts of the curved trace supplying the protuberance are present (cf. text-fig. 5P). KU 1021 I, 162; slide 579. F, Vascular supply within protuberance partly enclosed by a few layers of phellem cells continuous with those covering the protuberance. The trace supplying the protuberance is near the xylem of the main root and another well developed trace is present. KU 1021 I, 172; slide 580. G, Vascular supply of protuberance is near the base of the large trace. The protuberance is subdivided and rootlets lie close to it. KU 1021 I, 186; slide 580. H, As in G, but showing the departure of a rootlet devoid of phellem. KU 1021 I, 189; slide 583. I, As in H, but the section is from a region past the subdivision of the protuberance and nearly past the lenticels. Only part of one lenticel is seen to the right of the protuberance. KU 1021 I, 199; slide 585. J, Only the large trace is visible. The vascular supply in the protuberance is devoid of phellem. Part of a lenticel is shown to the right. KU 1021 I, 211; slide 587. K, As in J, but with two rootlets present. KU 1021 I, 222; slide 588. L, Note the rootlets derived from the protuberance and the branching vascular tissue within the protuberance. KU 1021 I, 244; slide 590. M–O, Further branching of the protuberance into rootlets. M, KU 1021 I, 252; slide 591. N, KU 1021 I, 267; slide 594. O, KU 1021 I, 275; slide 595. P, Theoretical longitudinal section of the traces shown in text-fig. 5C–J.



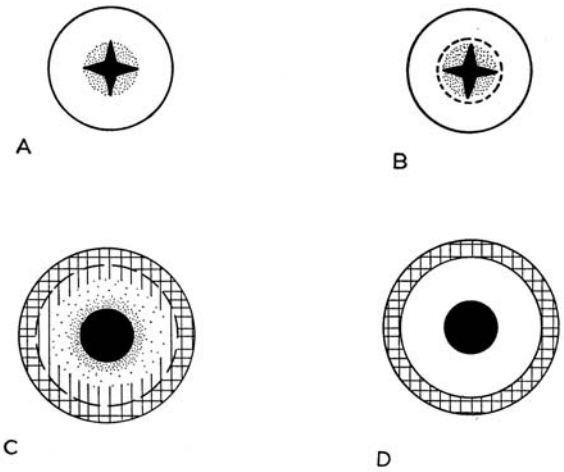
TEXT-FIG. 6. Representative transverse serial sections through a cluster of lateral rootlets, their basal protuberance and its two associated lenticels. Xylem, black; phellem, stippled. All ×3.
A, Note the protuberance, with its vascular supply, between two lenticels. Two parts of a large trace supplying the protuberance are also visible. KU 1021 I, 3; slide 534. B, As in A, but with the protuberance giving rise to several rootlets. KU 1021 I, 44; slide 539. C, Vascular supply entering the protuberance, which has given rise to several rootlets. KU 1021 I, 73; slide 546. D, As in C. KU 1021 I, 85; slide 557. E–I, Sections showing rootlets departing from the protuberance, ultimately passing into a region showing few rootlets. E, KU 1021 I, 132; slide 573. F, KU 1021 I, 148; slide 576. G, KU 1021 I, 161; slide 578. H, KU 1021 I, 174; slide 583. I, KU 1021 I, 198; slide 584.

SPECIMENS OF *AMYELON IOWENSE* SHOWING ANOMALOUS STRUCTURE

Two specimens showing anomalous features were studied critically. The features judged to be anomalous are: growth-rings in the xylem, outer part of xylem C-shaped in transverse section and associated with a knob-like protrusion showing tracheids cut obliquely, intraxylary phellem and callus, and, prominent nodular projections from the surface of the root. Most probably these represent wound reactions, but I am unable to interpret them unequivocally. In these circumstances presentation of a detailed record of these features is a tedious and elaborate affair, fit rather for archives (Cridland 1961) than for publication.

DISCUSSION

Pith is a feature unknown in other cordaitean roots. Evidently when roots of *A. iowense* were small they were protostelic, but as they grew the apical meristem increased its size, and its functioning was modified so that a siphonostele was laid down (text-fig. 2). This common type of change in function of apical meristems is called epidogenesis



TEXT-FIG. 7. Stages in the development of secondary tissues in *Amyelon iowense*. A, Young rootlet before the inception of secondary thickening. Xylem indicated by solid black, phloem by stippling, cortex shown in white with no attempt to differentiate inner and outer cortex. B, Later stage, after the inception of a deep-seated phellogen (shown by a broken circle). C, Still later stage, after much activity by the phellogen and the vascular cambium. The xylem (solid black) is surrounded by a cambium and a zone of compact phloem (closely spaced stippling) recently derived from the cambium. Outside the compact phloem there is a zone of aerenchymatous phloem (sparse stippling), aerenchymatous phelloderm (vertical lines), phellogen (broken circle), and phellem (cross hatching). D, Specimen comparable to that shown in diagram C, in which the aerenchymatous phloem and phelloderm have decayed before preservation, leaving a space between phellem and xylem.

(Eggert 1961). Further variation in the structure of *A. iowense* was presumably controlled by changes in function of the apical meristem. In some roots the primary xylem contacts the surrounding secondary xylem cylinder, but in others there are several intervening rows of parenchymatous cells. Different specimens have different numbers of parenchymatous cells, suggesting a gradual transition between these two conditions (text-fig. 2).

The extensive aerenchyma of mature roots and its absence in rootlets is best considered in relation to depth of origin of the phellogen and subsequent development of phellem and phelloderm. Changes in structure, and the manner in which I believe they occurred, are shown in text-fig. 7. Text-fig. 7A shows a rootlet with four primary xylem poles. In text-fig. 7B, a deep-seated phellogen has arisen outside the phloem. I have not

seen a specimen with a single row of deep-seated phellogen cells, but in Plate 37, fig. 2, radial rows of deep-seated periderm can be seen adjacent to the stele. This deep origin agrees with *A. radicans* (Osborn 1909; Scott 1909, p. 531; Halket 1930) and *Radiculites reticulatus* (Lignier 1911). In text-fig. 7C there has been considerable secondary growth. Conspicuous phellem has developed, which delimits the outer surface of the root, all tissues outside being sloughed. Patterns made by the phellem cells when seen in transverse section suggest that as a result of radial divisions of the phellogen, and perhaps of radial subdivisions of phellem cells, the phellem increased the circumference of the root markedly (text-fig. 3). Evidently there was no comparable compensating growth in diameter of soft tissues within the phellem and the tangential expansion of the phellem must have placed a considerable radially acting tension upon them. The outer part of the phloem was distended to form aerenchyma (Pl. 36, figs. 1, 2), while aerenchymatous phelloderm was laid down (Pl. 37, fig. 7). This view that tangential expansion of phellogen and consequent increase in diameter of the root has caused the development of aerenchyma is supported by the lack of aerenchyma where part of the root has been prevented from expanding by its proximity to other roots (Pl. 34, fig. 7). In some roots, there is no aerenchymatous phloem, only an aerenchymatous phelloderm (Pl. 36, fig. 4). Again this may be a result of submaximal tangential expansion of the phellogen and its derivatives.

If radial sections of specimens at the stage of development shown in text-fig. 7C were not studied critically, it would be easy to misinterpret the aerenchyma as cortex. Text-fig. 7D shows a root at a comparable stage of development, where the aerenchyma has decayed. Many specimens of *A. iowense* are preserved thus, and if there were no knowledge of the aerenchyma from other specimens it would be logical to assume that the space represents a decayed cortex. This hypothesis of a deep-seated phellogen, but with the phellem derived from it eventually delimiting the surface of the root, has implications in the interpretation of other cordaitean roots. It resolves the different views regarding depth of origin of periderm in cordaitean roots. Some were believed to develop periderm superficially (Williamson 1874; Renault 1879, 1896), while in others, a deep-seated phellogen has been demonstrated (Osborn 1909; Scott 1909, p. 531; Lignier 1911; Halket 1930). In my opinion the phellogen of all known cordaitean roots was deep-seated and any apparently different position results from distension of phelloderm and/or phloem.

Aerenchymatous phloem is unusual in vascular plants, but is precedented in the pneumatophores of *Laguncularia racemosa* (Schenck 1889*b*). As in *A. iowense* the phellogen is deep-seated; it expands tangentially by radial cell divisions and the outer part of the phloem is eventually stretched to form aerenchyma. Where elm trees grow in excessively moist conditions, abnormal radial cell elongation in the phloem may also lead to the formation of aerenchymatous phloem (Sorauer 1909, p. 327). Large pieces of bark are shed and whole branches may be decorticated (Graebner 1924, p. 356). As far as I am aware, aerenchymatous phelloderm is not recorded in modern plants, but it has a parallel in aerenchymatous phellem (Schenck 1889*a*; Eames and MacDaniels 1947, pp. 390–1).

In *Psaronius*, near the stem, roots are narrow and occur in a compact zone, joined to each other by parenchymatous tissue. Farther away they are much larger, have conspicuous aerenchyma, and are free. Reed (1949) postulated that the aerenchyma is

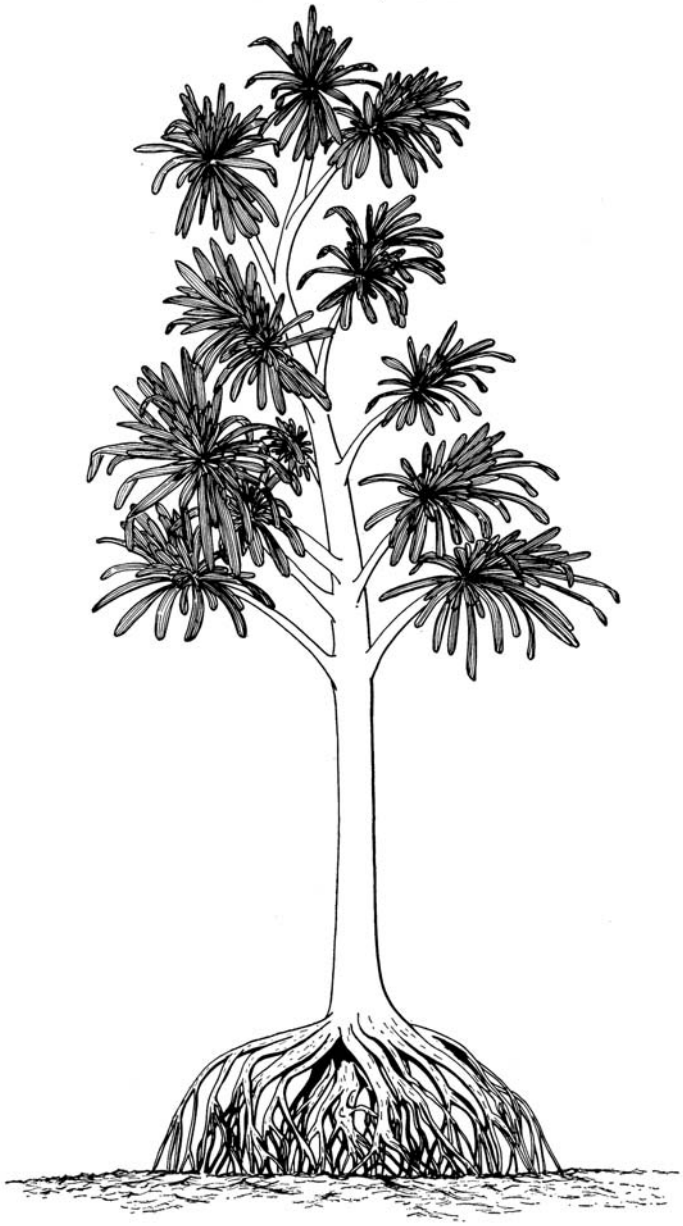
phelloderm derived from phellogen, which also gave rise to four or five rows of phellem cells (called periderm by Reed, 1949) to the outside. Such interpretation shows substantial agreement with the development of *A. iowense*, but the critical reader should be aware that Morgan (1959) has denied the validity of Reed's interpretations.

Roots of *Medullosa noei* Steidtmann are reported to have aerenchymatous cortex and superficial periderm (Baxter 1949, Stewart 1951). They should be worth re-examining in the light of the developmental stages of *A. iowense*.

Beck's (1958) observations on *Levicaulis* and other fossil lycopods may also be discussed with reference to *A. iowense*. In *Levicaulis* several zones of periderm (called secondary cortex by Beck) develop. Increase in circumference of the stem is apparently effected by intrusive growth of new radial rows of cells. There is no comparable increase in the size of the cortex, which is pulled outwards from the stelar tissues. Wedge-shaped tears occur at its inner margin and a lacuna is formed between cortex and stele. Other fossil lycopods show comparable periderm development and have a lacuna between stele and outer cortex resulting from decay of a fragile parenchyma. In several specimens this delicate tissue (often described as hyphal or trabecular tissue) is composed of radially orientated, stretched cells, with numerous intercellular spaces. According to Beck the trabecular tissue represents an intermediate stage in the formation of the lacuna. Based on the sequence of events in *A. iowense*, the trabecular tissue might easily be the normal condition in these lycopods.

Although there is not absolute agreement between the supposed lenticels of *A. iowense* and the lenticels of a given modern plant, there is a general approximation in structure. Further, the arrangement of the lenticels upon the roots of *A. iowense* has a parallel in modern plants. They occur in pairs and a cluster of lateral rootlets arises between them (text-fig. 5E, L, O). In dicotyledons, lenticels on roots are invariably paired, one on either side of the base of each rootlet (Devaux 1900; Wetmore 1926). Although in *A. iowense* it is a case of clusters of rootlets borne on a protuberance between the lenticels, and in dicotyledons it is a case of a single rootlet, the general arrangement is quite similar.

Possession of lenticels communicating with aerenchyma is particularly significant in connexion with two other features of these roots; the possession of pith and clusters of lateral rootlets. Because they have a pith it is possible that the roots were aerial organs. Pith occurs in some subterranean roots, but is not a common feature. On the other hand, many aerial roots possess pith, particularly those growing in mangrove swamps (Schenck 1889*b*; Liebau 1914; Bowman 1921; Buscialoni 1921; Ernould 1922; Mullan 1932–3; Ogura 1940). I know of no plants other than mangroves whose roots have lenticels, aerenchyma, pith, and clusters of lateral rootlets occurring together. The mode of branching of the mature roots (text-fig. 1) is more like that seen in stilt roots than in negatively geotropic pneumatophores. I believe the habit of the cordaitean plants in American coal-balls was something like that of the genus *Rhizophora*, a view expressed in the reconstruction (text-fig. 8), where the cordaite shown is a small tree, like specimens of *Rhizophora* growing closest to the sea. The suggested mangrove habit of *A. iowense* has implications in considering the environment in which these fossils grew. Modern mangroves with stilt roots are restricted to tropical or subtropical saline swamps of sheltered marine shores and estuaries, and *A. iowense* may have grown in a similar habitat. If this were so, a clue is provided to the environment of deposition of the



TEXT-FIG. 8. Reconstruction of a cordaitean plant bearing stilt roots. No attempt has been made to include lenticels and clusters of lateral rootlets. 1/28th natural size.

Mineral, the Fleming and the Weir-Pittsburg coals of Kansas, some of the Desmoinesian coals of Iowa and the No. 6 coal of Illinois, which all have coal-balls containing *A. iowense*. It may well be that the debris forming many other coals of the mid-continental U.S.A. and other parts of the world, accumulated under similar conditions.

COMPARISON WITH PREVIOUSLY DESCRIBED CORDAITEAN ROOTS

Premnoxylon iowense

When Pierce and Hall (1953) described *Premnoxylon*, similarities to *Amyelon* were pointed out, but the following differences were noted: (1) *Premnoxylon* possesses a pith. (2) The pith contains scattered tracheids, i.e. it is a mixed pith comparable to that of *Lepidodendron vasculare*. (3) Primary xylem is separated from secondary xylem by several rows of parenchymatous cells. (4) There is a complex method of trace formation.

The significance of the differences between *Premnoxylon* and *Amyelon* is weakened by reference to text-fig. 2. The transverse section illustrated in text-fig. 2D is referable to *Amyelon*, while that shown in text-fig. 2B, with its pith and its primary xylem poles separated from the secondary xylem by several rows of parenchymatous cells, has some of the attributes of *Premnoxylon*. Text-fig. 2C shows an intermediate condition in which the root has a pith, but the primary xylem poles are in contact with the secondary xylem. In the cordaitean roots I studied there is no mixed pith, but some longitudinal sections pass through a few metaxylem cells and their presence gives an illusion of a mixed pith. Lateral traces in the syntypes of *P. iowense* show no essential differences from the lateral traces of other cordaitean roots. I conclude that *P. iowense* and the specimens of *Amyelon* described in this paper should be identified together. *Premnoxylon* is a synonym of *Amyelon*, but since *P. iowense* is not specifically identical with *A. radicans*, I propose the new combination *A. iowense* (Pierce and Hall) Cridland.

Roots of Mesoxylon nauertianum

Andrews (1942) described a protostelic *Amyelon* root attached to a specimen of *Mesoxylon nauertianum*. It is bounded by phellem within which there is phelloderm containing many large cells with dark contents (a tissue Andrews (1942) interpreted as cortex). There is a slightly thinner zone of compact phloem outside the secondary xylem. In a region of this root there is slight development of aerenchymatous tissue, but a root associated with *M. nauertianum* in another coal-ball shows much better aerenchyma (Pl. 37, fig. 3).

Although the root attached to *M. nauertianum* is probably identical with *A. iowense*, Andrews's paper should not be used to modify the nomenclature. The attached root never received a separate name, and it is useful to have a specific name for the detached organs. While it would no doubt avoid the use of an excess and somewhat superfluous name to refer to both attached and detached roots simply as the roots of *M. nauertianum*, this simple and straightforward course is not open. *M. nauertianum* is not clearly differentiated from other species of *Mesoxylon* (Andrews 1942) and unless further study indicates otherwise, this name cannot be applied to any but the type specimen.

Andrews (1942) also described some detached rootlets with abundant root hairs, which he suggested may belong to the genus *Amyelon*. I have re-examined these beautiful

rootlets, and it is my conclusion that they cannot be correctly attributed to *Amyelon*, but instead, a closer comparison can be made between them and the roots of coenopterid ferns. I cite the rootlets of *Psalixochlaena cylindrica* (Holden 1960) as comparable organs, but I do not imply generic identity. The following points should be considered: (1) Andrews's (1942, figs. 8, 9) rootlets and other comparable rootlets (especially Slides 1114–18) have a piliferous layer with extremely long and abundant root hairs, looking like those of *P. cylindrica* (Holden 1960, Pl. 10, fig. 4). In contrast no undoubted cordaitean rootlet has root hairs. (2) Andrews's (1942, figs. 8, 9) specimens have a layer of cells with dark contents beneath the piliferous layer and a similar layer of cells surrounding the stele, corresponding to the exodermis and endodermis of *P. cylindrica*. Although there is an endodermis in other cordaitean rootlets (Lignier 1906; Osborn 1909; Carpentier 1924; Halket 1930; Zimmermann 1933) there is no exodermis. (3) Cortical cells in Andrews's rootlets are larger (60 μ) in transverse section than those in cordaitean rootlets (45 μ). (4) Secondary xylem was beginning to form in a rootlet Andrews (1942) illustrated in text-fig. 1*b*, and its tracheids are polygonal in transverse section, as in coenopterid rootlets (Holden 1955). Comparable tracheids in *Amyelon* are more or less square.

Amyelon radicans (*Williamson*) *Williamson*

A. radicans occurs exclusively in European coal-balls of Lower Westphalian or equivalent age. This root is well known (Williamson 1872*a*, 1872*b*, 1874; Felix 1886; Osborn 1909; Scott 1909; Thomson 1914; Coulter and Chamberlain 1917; Seward 1917; Leclercq 1928; Koopmans 1928; Halket 1930; Cridland 1962). Rootlets are similar to those of *A. iowense*, and they are borne in similar clusters on conspicuous protuberances ('large globular masses' of Williamson, 1874; 'parenchymatous roots' of Halket, 1930) from the parent root. There are no lenticels beside the protuberances. In addition to the clusters of lateral rootlets, occasional rootlets are attached directly to the main axis (Halket 1930), a feature not observed in *A. iowense*. As in *A. iowense*, in most rootlets of *A. radicans* the walls of the endodermal cells are uniformly dark brown and are thicker than the walls of adjacent cells. Halket (1930) recognized two younger developmental stages, but neither is illustrated, and I have been unable to relocate them on those of her slides I have examined (Cridland 1962).

There are two regions of tissue outside the xylem in large roots of *A. radicans*. Because of the deep-seated phellogen in *A. radicans* (Osborn 1909; Halket 1930) and the developmental stages of *A. iowense*, I believe that the inner region of parenchyma (Williamson's (1874) 'inner bark') is phelloderm, and that the outer region (Williamson's (1874) 'outer bark') is phellem. The compact phelloderm in *A. radicans* presents a striking contrast to the aerenchymatous phelloderm of *A. iowense*. Similarly, in contrast to *A. iowense*, *A. radicans* evidently developed no aerenchymatous phloem. One result of this lack of aerenchyma is that in *A. radicans* the phloem and the phelloderm account for only about one-tenth of the root diameter, much less than in *A. iowense*, where these tissues account for about six-tenths of the root diameter. Unlike *A. iowense*, mature roots of *A. radicans* are always protostelic (Williamson 1874, figs. 46, 56, 57; Scott 1909, fig. 191; Seward 1917, fig. 477; Coulter and Chamberlain 1917, fig. 203; Leclercq 1928, fig. 7; Koopmans 1928, fig. 61). While the protosteley of the roots in Leclercq's (1928, fig. 7) may perhaps be attributed to the proximity of the roots to the point of

branching, this explanation surely cannot be applied to all the specimens cited above. I have searched carefully through several collections of European coal-balls and have not succeeded in finding a siphonostelic specimen of *A. radicans*. It is remotely possible that siphonosteley occurs in specimens described by Felix (1886). Several have an empty space at the middle, or at least a break occurs between the central tracheids, but it is not clear whether this space resulted from decay of parenchyma cells or tracheids. These specimens are not illustrated, and it is difficult to be sure how significant the space is, but it is probably inconspicuous.

Excentric growth-rings occur with high frequency in the xylem of *A. radicans*. In contrast, while growth-rings do occur in some specimens of *A. iowense*, they are rare and are usually associated with other anomalous features.

Roots of Cordaites *described by Renault (1879, 1896)*

In both publications Renault described petrified plants from the Permian at Autun and the Stephanian Assise de St. Etienne near Grand Croix. He did not specify the locality of the unnamed cordaitean roots, but since he stressed the abundance of cordaitean remains in the Assise de St. Etienne, I presume they came from that stratum. Based on a textbook account of similar roots (Renault 1881), Osborn (1909, p. 603) claimed that the roots are from Autun, but I can find nothing to support this assumption in Renault's text.

Detached rootlets were described scantily, but large roots were described in detail. They have an exarch protostele and secondary xylem with hexagonal pitting. Phloem is preserved, and surrounding it there is a layer Renault interpreted as cortex and then a somewhat sinuose and convoluted layer he interpreted as periderm.

In most specimens, the inner part of the tissue Renault called cortex has decayed, but in some it is preserved and proves to be aerenchyma composed of ramose cells (Renault 1896). Unfortunately the aerenchyma is not illustrated.

Renault's roots can be reinterpreted in the light of *A. iowense*. I suggest that no cortical tissue is preserved. Instead, a deep-seated phellogen arose and produced radial rows of phellem towards the outside and less regularly organized phelloderm towards the inside. As a result of the development of periderm and the subsequent increase in root diameter, the cortex was sloughed, and I presume that aerenchyma was formed by distension of phloem and/or phelloderm. Contorted areas of phellem (Renault 1879, Pl. 15, fig. 14), which Renault considered were formed when part of the tissue he called cortex decayed, show a surprising agreement with immature lenticels of *A. iowense*. A fair analogy can be made between the specimen in Renault's (1879) Plate 15, fig. 13 and *A. iowense*, particularly the regions of *A. iowense* close to their attachment to a supraordinate root (Pl. 34, fig. 7), where there is no aerenchyma and the primary xylem is protostelic, but I do not imply that Renault's specimen is close to its attachment to a supraordinate root.

Radiculites reticulatus *Lignier*

Cordaitean rootlets from the Assise de St. Etienne were described by Lignier (1906, 1911) as *R. reticulatus*. An identical rootlet from the same horizon was described by Zimmermann (1933) and Permian specimens which I identify with *R. reticulatus* were

described by Carpentier (1924). *Radiculites* Zalessky (1937), a later homonym for compressed roots of uncertain affinity, has no relationship to *Radiculites* Lignier (1906).

The relationship of *R. reticulatus* was established by a case of attachment to a larger, definitely cordaitean rootlet (Lignier 1911), which unfortunately is not mature enough for close comparison with Renault's (1879, 1896) roots. A reticulum of thickening material in the cortex of *R. reticulatus* is a striking and unusual feature not known in *Amyelon*. Nor is it known in *Kaloxylon*, lyginopterid roots which Barnard (1962) suggests are difficult to differentiate from *Radiculites*. The network in *R. reticulatus* compares favourably with the lignified cortical network in the roots of many living gymnosperms and dicotyledons (Van Tieghem 1870–1, 1888; Scott and Whitworth 1928; Guttenberg 1940, pp. 121–2, 1941, pp. 20–31; Van Fleet 1948). Halket (1930) suggested that the cortical thickenings are artifacts of preservation, but she did not examine specimens. Had she done so, I am confident she would not have made this suggestion. The network is strikingly clear, and Zimmermann (1933), apparently unaware of the works of Lignier (1906, 1911) and Halket (1930), described and illustrated this feature independently.

In *R. reticulatus* periderm arose within the pericycle and the cortex was ultimately sloughed (Lignier 1911). This deep origin of periderm is consistent with Halket's (1930) observation of phellogen in the pericycle of *A. radicans* and with the deep origin of phellogen in *A. iowense*.

Other Cordaitean roots

Amyelon in a coal-ball from the Desmoinesian of Iowa, was figured by Wilson and Johnston (1940, fig. 6), but no details of its anatomy were described. This figure, which shows only xylem in transverse section, is insufficient for comparison with *A. iowense*.

There is a record of *Amyelon* from the Calhoun Coal of Illinois (Underwood 1934). This report is in an unpublished thesis which I should not consider had not Fischer and Noé (1938) already drawn attention to it. I have re-examined the specimens which Underwood studied and conclude that none can be confidently assigned to *Amyelon*. Those she illustrated in figs. 72–75 are medullosan roots; while the rootlets she illustrated in figs. 76 and 77 are poorly preserved and have no special characters.

There is no basis for comparison of *A. iowense* with other presumed cordaitean roots. Williamson's catalogue name, *A. reticulatum*, refers to *Sphenophyllum* (Barnard 1962). The little known about the specimens of *A. radiatus* (Spencer 1881, 1882) carries no conviction that they are cordaitean roots. Gordon's (1914) Lower Carboniferous record of *Amyelon* is excluded since there are no described or illustrated specimens, while Barnard's (1962) Lower Carboniferous species are excluded because there is no evidence that they are members of the Cordaitaceae. No comparison can be made with the roots attached to *Rhizocordaites* and similar stumps (Grand'Eury 1877, 1890) since their anatomical structure has not been studied. Likewise, no anatomical details are known concerning the South African root-bearing stumps assigned to *Cordaites hislopi* by Seward (1917, p. 263).

Acknowledgements. This paper was written under the direction of Dr. R. W. Baxter, as part of a study of the Coal-Age Flora of Kansas supported by the National Science Foundation. I am indebted to Dr. J. Hall for the loan of the type specimens of *Premnoxylon*, to Dr. Fredda Reed for the loan of comparative material of *Psaronius* and to Prof. P. J. Sedgwick for the loan of slides studied by Miss

M. E. Underwood. I am similarly indebted to Dr. J. Franks, Dr. F. Rose, Mr. T. West, Prof. A. Pitot, and Prof. W. Zimmermann for the loan of slides. Dr. H. G. Hershey was kind enough to supply information on some coal-mines in Iowa. I owe a special debt of gratitude to the Society of the Sigma Xi for a grant-in-aid which enabled me to further this work through visits to laboratories and museums, and to Dr. H. N. Andrews, Prof. C. A. Arnold, Dr. E. S. Barghoorn, Dr. S. H. Mamay, Dr. J. M. Schopf, and Dr. W. N. Stewart who kindly made facilities available to me. Finally, I am grateful to Prof. T. M. Harris and Dr. T. Delevoryas for much helpful criticism.

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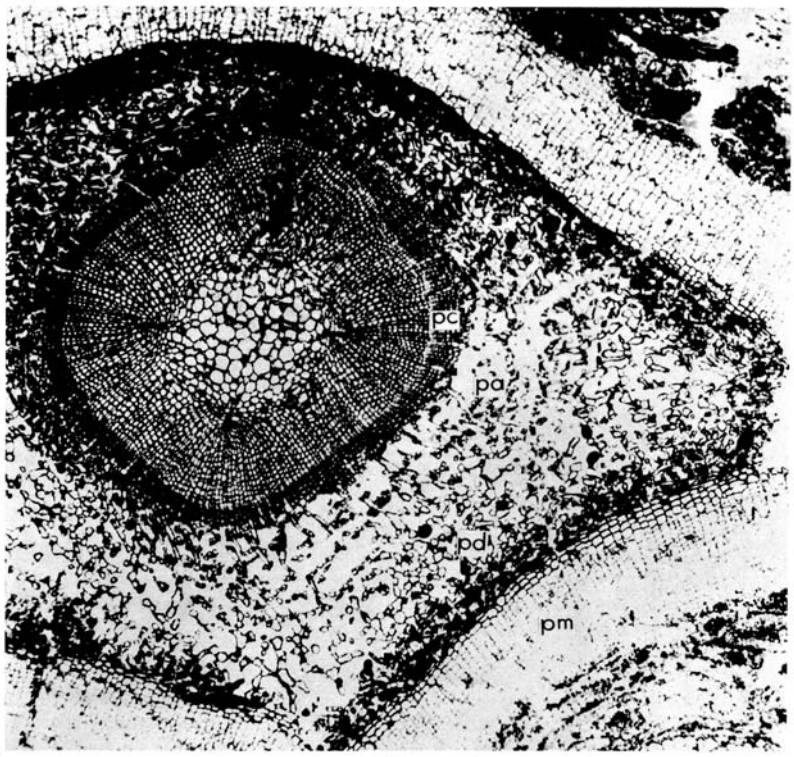
Revised manuscript received 9 September 1963



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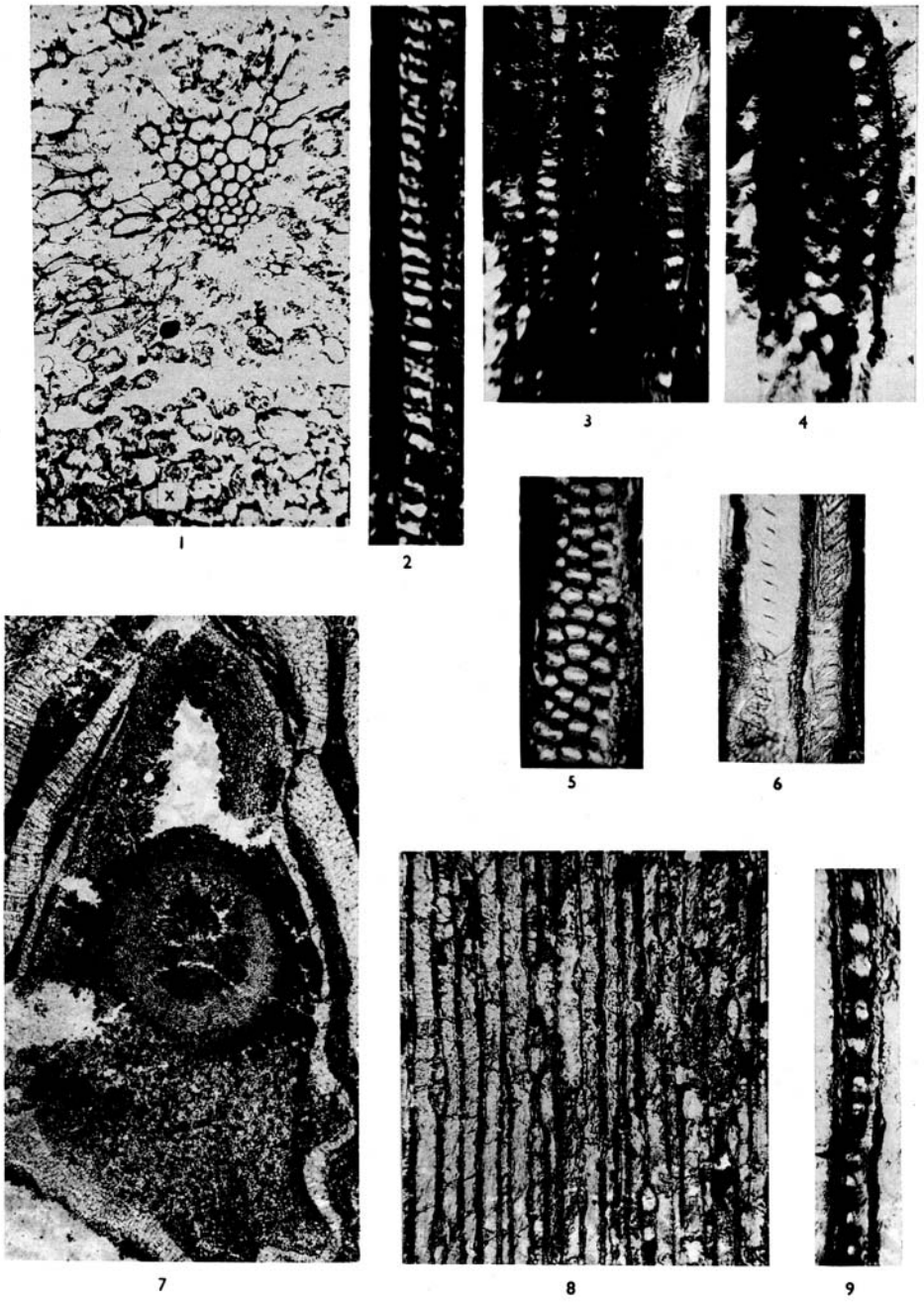

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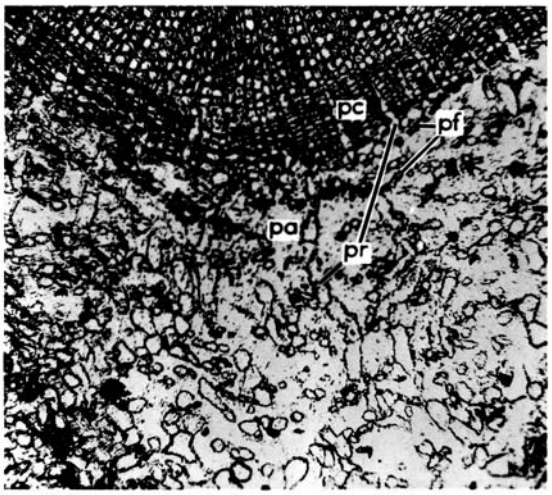

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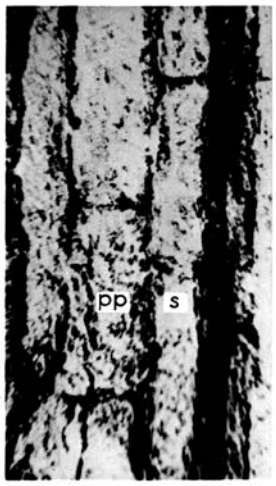

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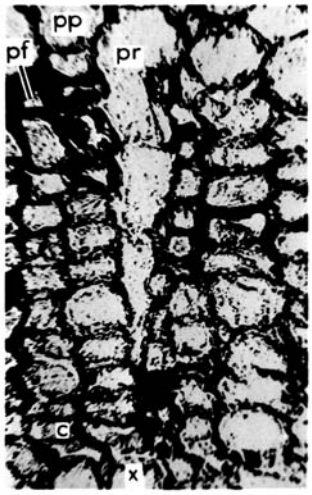

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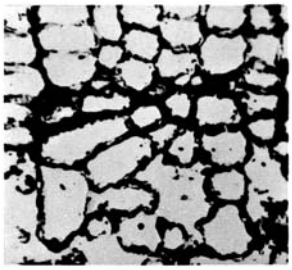

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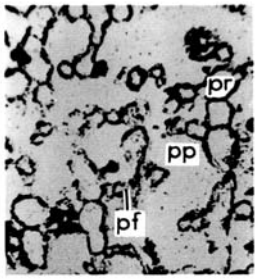

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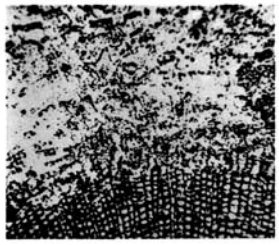

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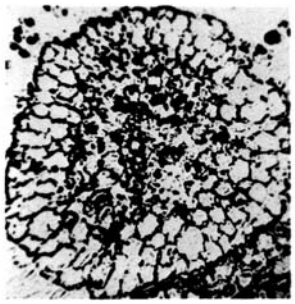

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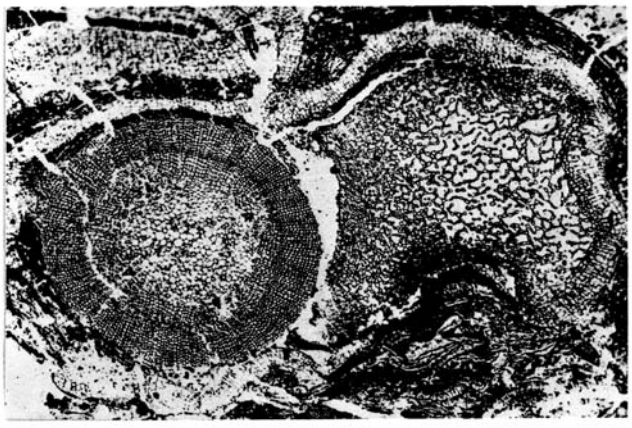

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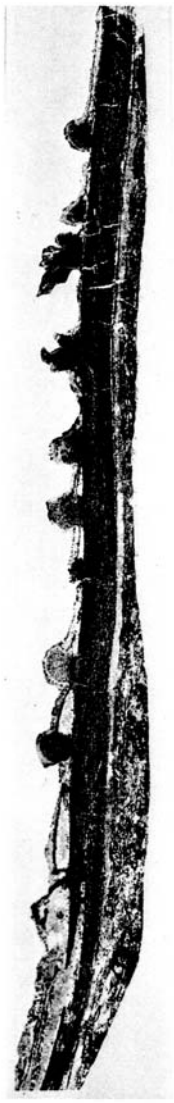

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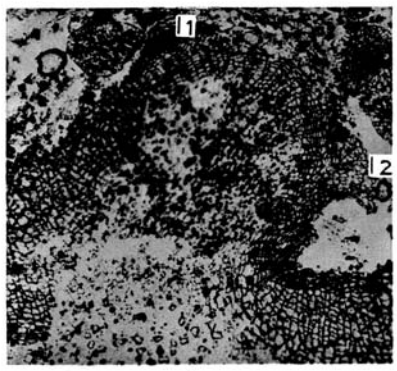

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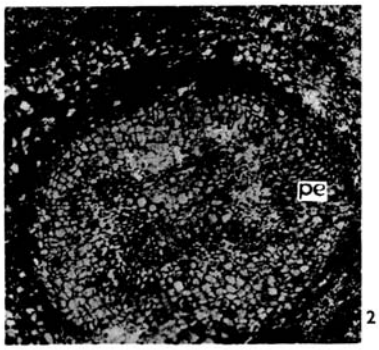

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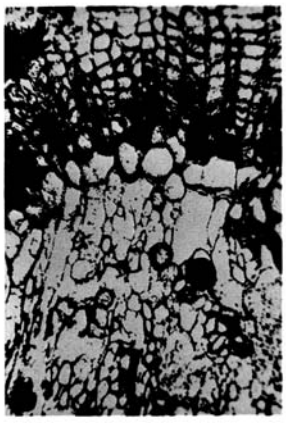

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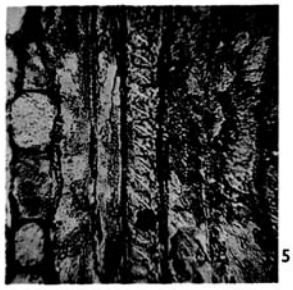

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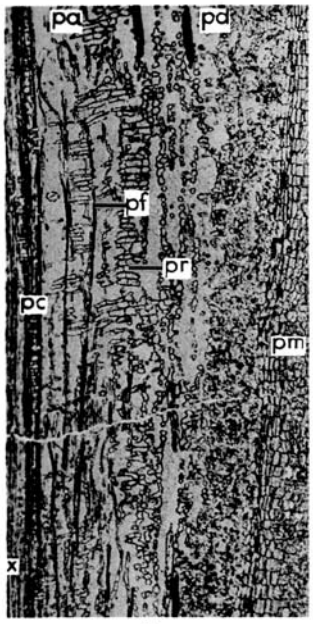

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