LEPIDODENDRON JOHNSONII, SP. NOV., FROM THE LOWER PENNSYLVANIAN OF CENTRAL COLORADO

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THE occurrence of petrified plant remains in the lower Pennsylvanian rocks of central Colorado was first announced by J. H. Johnson (9) in 1932. In 1938 the writer, accompanied by D. B. Gould, visited the locality mentioned by Johnson, and spent several days collecting material. It is in the eastern part of Chaffee County, about four miles southwest of Trout Creek Pass in the Mosquito Range. The erosion of the Weber (?) formation in this region has produced a broad valley known as Chubb Gulch, at the southern end of which the plant remains are exposed not far above the base of the formation. Beginning at the site of the abandoned town of Newett near the place where the highway crosses Trout Creek the plant-bearing horizon may be followed in a northwesterly direction for a distance of about two miles, and along this exposure large quantities of plant material are scattered over the grassy terrain within a zone approximately one hundred yards wide. Near the southern end of this strip, where the highway and the creek cross the plant horizon, the material consists mainly of a compressed fibrous substance having the appearance of indurated lignite. Although the organic origin of the remains at this place is quite evident, preservation is insufficient for identification of any of the constituent plants.

As the outcrop continues northwestward preservation improves, and the remains of *Lepidodendron* may be definitely recognized.

GEOLOGICAL AND PALEOECOLOGICAL FEATURES

The Weber (?) formation in central Colorado lies unconformably upon the Leadville limestone of Mississippian age. In the Trout Creek section of Johnson (10) the plants occur about 155 feet above the base of the Weber (?), and the plant bed is referred to as a definite horizon about fourteen feet above the base of a twenty-one-foot layer of black shale (which is layer No. 8 of his Trout Creek section). Therefore the plant bed is at about the middle of the lower zone of the Weber (?) formation, which consists mainly of dark shale with scattered sandstone and limestone layers. The large fauna of the Weber (?) indicates an age approximately equivalent to the middle and upper Pottsville. Read (13) has described a small middle Pottsville flora, from the vicinity of Leadville, which is situated at about the same level as the *Lepidodendron* bed at Trout Creek.

The determination of the age relations of the Paleozoic rocks in central Colorado is complicated by folding, faulting, igneous intrusions, and widespread unconformities. The sediments range from pre-Cambrian to Pleistocene, with unconformities occurring at the bases of all the Paleozoic formations except the Ordovician and Permian. That at the base of the Pennsylvanian is the most pronounced (Lovering and Johnson, 12). Not only were large amounts of the Leadville limestone removed previous to Pennsylvanian deposition, but it was irregularly eroded, so that the overlying Weber (?) rests upon a very uneven surface. This erosion interval is believed to have continued throughout most or all of early Pennsylvanian time. According to Ver Wiebe (17), none of the land areas in central Colorado were mountainous during this period of early Pennsylvanian erosion, but immediately thereafter a marked uplift was started which was maintained throughout the remainder of the Pennsylvanian. These highlands occupying the approximate position of the present Front Range supplied the sediments which make up the Pennsylvanian and Permian strata in the present Mosquito Range. The deposition

of the dark shales of the Weber (?) formation took place during the early part of this uplift, when the source of supply was some distance away. The terrain over which deposition occurred was one of low relief with numerous swamps, in which there grew thick stands of *Lepidodendra* and other Pennsylvanian plants
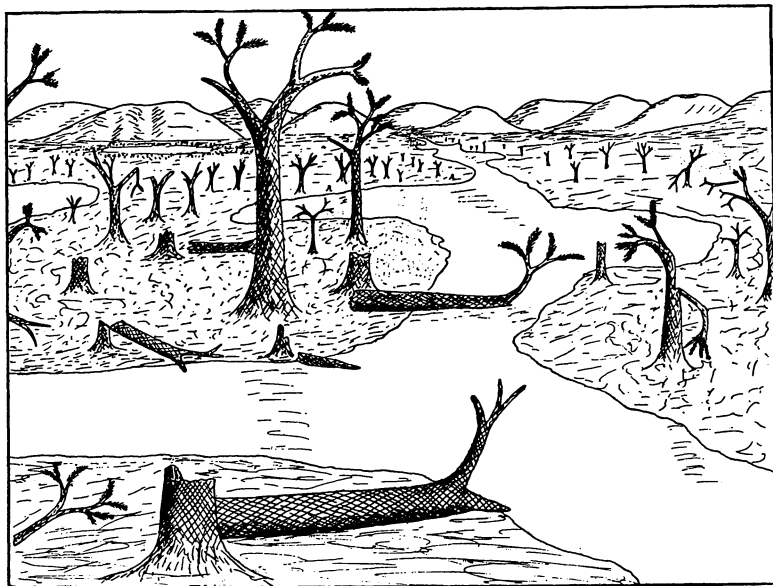

FIG. 1. Reconstruction of lower Pennsylvanian landscape in central Colorado during deposition of early Weber (?) sediments. The swampy lowland in the foreground, which supports the *Lepidodendron* forest, is being built up by mud carried by the sluggish streams. In the background are low hills occupying the approximate position of the present Front Range

(Fig. 1). With the continuation of Weber (?) deposition coarser sediments were laid down at intervals, and in the shallow waters of the shifting embayments calcareous algae flourished, producing occasional thin zones of algal limestones. In the succeeding Coffman conglomerate land plants are rare and fragmentary, although in the lowest member Gould (7) found imprints of *Calamites* and *Lepidodendron*. In the overlying Chubb siltstone and the Bath submember of the Maroon formation, which is generally placed

in the Permian, *Calamites* persists along with coniferous types
such as *Walchia* and *Lecrosia*. These coniferous types probably
spread over the drier uplands, although in the Chubb siltstone
Lecrosia exists in such quantities as to indicate a dense growth
close to the site of deposition.

PRESERVATION

Preservation of the plant remains at the Trout Creek locality
was the result of siliceous infiltration. The plant tissues are em-
bedded within a dense dark gray cherty rock which breaks into
irregular masses (Pl. I, Figs. 1–2). Some portions of the silicified
trunks contain pieces of the vascular axes wholly or partly en-
closed by the outer periderm tissue. In all the specimens exam-
ined the primary cortex (that between the periderm and the
vascular cylinder) has completely disappeared, and the remaining
space has been filled with débris and stigmarian rootlets. Pieces
containing vascular tissue are not so abundant as those consist-
ing entirely of periderm, which, to the unaided eye, look like
petrified wood, but microscopic examination of thin sections re-
veals their true nature. A typical block showing the woody
appearance of a broken surface has been figured by Johnson (10,
Pl. 7, Fig. B). Most of the broken trunk fragments are strewn
over the ground, where they weathered out from the shale, but
a few were noticed which are partly embedded in the soil and
which may be the bases of trunks still standing in the positions
in which they grew. In them the exposed portions are badly
broken as a result of long exposure. The majority of the blocks
are wholly or partly encrusted with a limy deposit of secondary
origin, which obscures the surface rather badly and renders diffi-
cult the selection of good specimens in the field. No leaf cushions
are present on any of the trunk surfaces, although numerous small
shale fragments bearing characteristic imprints of *Lepidodendron*
and *Lepidophloios* occur in intimate association. The silica which
served to cement the shale particles and petrify the plant tissues
was probably derived from highly charged waters issuing from
hot springs. The preservation is of much the same type as that
which usually results from burial in volcanic ash, but in which

replacement of the cellulose and lignin of the walls is not carried to completion. Lack of evidence of vulcanism in central Colorado during the Pennsylvanian precludes the possibility of the derivation of the silica from volcanic eruptions of any sort.

Although in many of the trunks histological details are preserved with a surprising degree of perfection, the trunks are badly broken, and most of them appear to have been subjected to considerable weathering previous to burial. Many of the enclosed vascular cylinders are split or crushed, or preserved only in part, but in all cases the tissues immediately surrounding them have decayed. Frequently pieces of two or more axes occupy the interior cavity of a single trunk (Fig. 2, p. 26). This situation is similar to that found in some of the hollow trees embedded in the volcanic ash beds of Lower Carboniferous age on the island of Arran. Walton (18), who described them at some length, concluded that such occurrences are due to the breaking of the slender vascular axis into short lengths after it had been left standing unsupported within the hollow cylinder. He also discusses the alternative explanation which proposes that the short lengths are fragments that floated into open cavities of submerged upright trunks. Which of these explanations can best be applied to the Colorado trees cannot be decided at present because difficulties arise with either. It seems probable, however, that most of the trunks had fallen before burial, although a few were observed which may represent the basal trunk portions that were still standing at the time they were encased in the rapidly accumulating black mud. In the case of horizontal trunks, the débris in the interior could be attributed to both flotation and collapse. With respect to the "collapse" theory it may be pointed out that frequently the contained vascular axes appear too well preserved to have been broken into short pieces under their own weight alone. On the other hand, nothing has been identified within the trunk cavities except fragments of *Lepidodendron* and *Stigmaria*, and it seems that, if the contents accumulated by flotation, they would include remains of other plants as well. The invading stigmarian rootlets have penetrated not only the inner cortical zones but also the pith; in some places they may be seen in cracks in the secondary
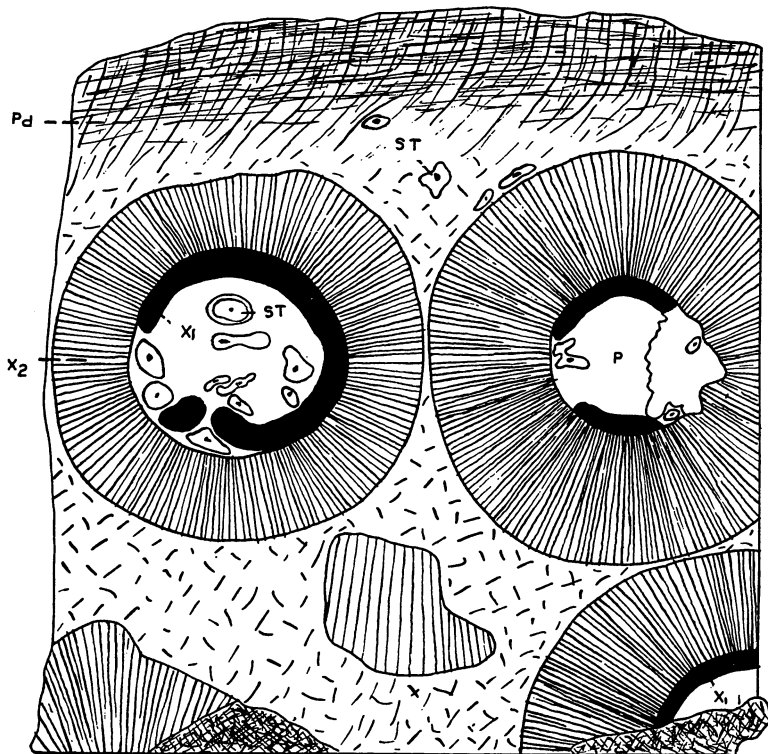
FIG. 2. Sketch of a portion of a silicified trunk of *Lepidodendron Johnsonii*, showing two complete central cylinders and fragments of others. P, pith; Pd, periderm; ST, stigmarian rootlets; X_1, primary xylem; X_2, secondary xylem. $\times \frac{2}{3}$

wood. Of course, these invading rootlets came from other plants nearly contemporaneous geologically which grew in the overlying soil after burial of the plants in question.

INTERNAL STRUCTURE

The tissues preserved are the pith, the primary and secondary xylem, and the cortex or periderm. The phloem and the inner and middle cortex have decayed, and must perforce be omitted from consideration. The remaining structure is typical of those

of other medullated species of *Lepidodendron* and *Lepidophloios*, so that the necessity of describing a new species arises principally from the combination of features present rather than from anything distinctly new. The possibility of there being more than one species among the numerous specimens examined must be taken into account, but if others exist they are as yet unrecognized.

In cross section the trunks of *Lepidodendron Johnsonii* are large, being sometimes as much as two feet in diameter. The outer shell, or periderm, is six inches or more thick, and surrounds a large inner portion from which all structure has disappeared except the slender central cylinder (Fig. 3, p. 28).

The Central Cylinder

In most of the specimens examined the central cylinders are rather uniform in size. Some of them are as much as 10 cm. in diameter, although they average about 7.5 or 8 cm. (Fig. 2 and Pl. II, Fig. 1).

Pith. — In most of the axes the pith accounts for a fourth or more of the total diameter of the central cylinder. It usually measures from 2.5 to 3 cm. (Pl. II, Fig. 1), although in one specimen it is quite small, being only 5 mm. (Pl. III, Fig. 1). In the axes with the large pith the cellular structure has mostly disappeared, and the space is filled with a mass of invading stigmarian rootlets and structureless débris. In that with the small pith there may be observed some structural details, upon which the following comments are based.

In the specimen shown in Plate III (Figs. 1–2) the pith is differentiated into two zones. The central part is made up of small thin-walled cells, which are rounded or slightly irregular and probably similar to the so-called "hyphal" cells present in the pith of some species. A few of these cells appear to contain dark material. In the outer part of the pith the cells are more regular and are arranged in longitudinal series with transverse end walls, so that they appear square or rectangular in longitudinal section (Pl. V, Fig. 1). The cross diameters of the cells vary considerably in both zones, but in general they are noticeably smaller than those in the adjacent primary xylem. There

are no tracheids or other thick-walled elements visible in the pith, and the transition to the primary xylem is abrupt.

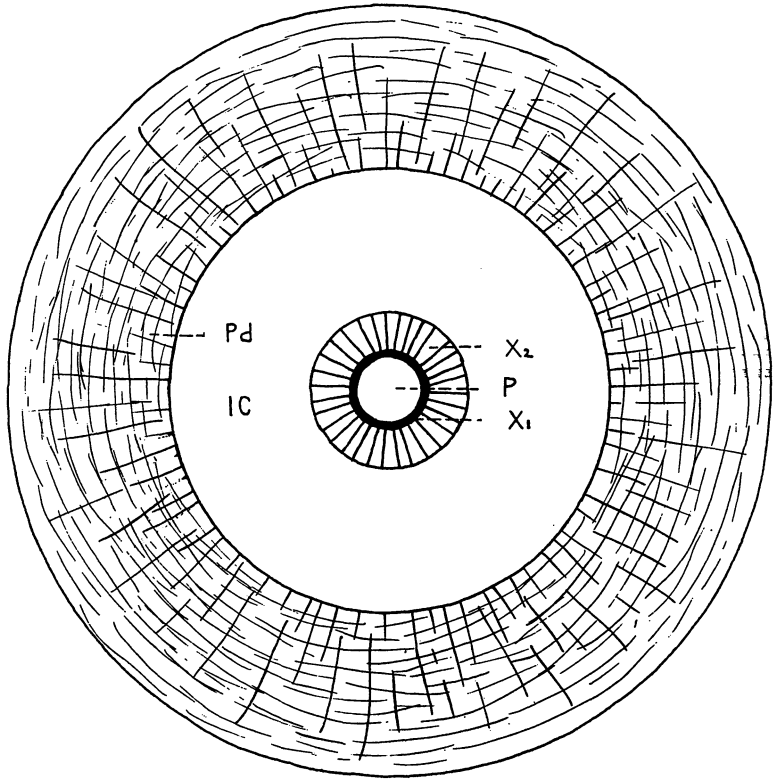*Primary xylem.* — The primary xylem forms a continuous cyl-

FIG. 3.   Reconstruction of cross section of trunk of *Lepidodendron Johnsonii*, showing the tissues restored to their approximate original proportions. IC, inner and middle cortex (decayed); P, pith; Pd, periderm; X_1, primary xylem; X_2, secondary xylem. $\times$ about $\frac{1}{4}$

inder around the pith, the only interruptions being the large ramular openings where the branches depart. In many axes the primary cylinder has undergone considerable alteration, either from decay of the tissues or from displacement due to crushing or the invasion of stigmarian rootlets.

In most of the axes the primary xylem core is 30 or 40 mm. in diameter (Pl. II, Fig. 1), although in one specimen (that mentioned above with the small pith [Pl. III, Figs. 1–2]) it is only 7 mm. The thickness of the tissue ranges from about 1 mm. in the specimen with the small core to 4 or 5 mm. in the larger ones (Pl. II, Fig. 2). It consists almost entirely of tracheids of fairly large size, in which the radial diameter slightly exceeds the tangential one. The tracheids are largest next the pith, where they are about 200 micra in radial diameter, but they diminish very gradually toward the outside. It is only just beneath the corona teeth that they suddenly become much smaller (Pl. IV, Figs. 1–2). The crenulated outer margin of the primary cylinder (the corona) is typically lepidodendroid (Pl. III, Fig. 2; Pl. IV, Figs. 1–2), and the indentations are separated by a series of slightly irregular rounded teeth with the protoxylem at the apices. The teeth are so spaced that three or four occur within the length of a millimeter. Those giving rise to traces are slightly larger and more pointed than the others. The indentations between adjacent teeth are smoothly rounded.

These so-called teeth of the corona are simply the longitudinal ridges of the protoxylem on the outer surface of the primary cylinder as seen in transverse section. Because of poor preservation along the zone of contact between the primary and the secondary wood it has not been possible to ascertain accurately the exact course followed by the protoxylem ridges, but they seem to divide at intervals of several centimeters, at which points the traces depart. Beyond the point of division the two ridges continue along a parallel course as reparatory strands. The traces appear to depart from the crests of the ridges (Pl. IV, Fig. 1) at or slightly below the point of division, and then to bend abruptly outward. At places in the transverse sections a trace may be seen opposite the sinus between the separating ridges (Pl. IV, Fig. 2). The manner of trace departure is believed to be essentially similar to that described by Bertrand (2) for *Lepidophloios Harcourtii*. The traces appear to form at rather long intervals, which may indicate somewhat distant spacing of the leaves upon the stem. The irregularities in the size of the corona teeth are the result of the spiral

sequence of leaf insertion. The larger and more prominent teeth are those nearer the point of trace departure, whereas the more rounded and less conspicuous ones belong to traces leaving at higher levels.

In longitudinal section the primary tracheids show as long, straight conducting tubes with pronounced scalariform sculpturing of the walls. Near the ends the tracheids taper gradually to a point. Although exact measurements of the length of these tracheids are difficult to obtain owing to their tendency to pass from the plane of section, a single one was followed for more than 12 mm. Others are probably longer.

The transverse bars of the tracheid walls extend completely across the wall face and at the corners merge into a continuous secondary layer. The bars of one face tend to alternate with those on adjacent faces. They extend across in a transverse direction or they may become interconnected in such a way as to produce a reticulate pattern, and occasionally a close approach to hexagonal multiseriate pitting is locally produced. A similar occurrence has been observed by Calder in *Lepidodendron Brownii* (3) and in *Lepidodendron brevifolium* (5). It may be noted that this appearance of hexagonal pitting and reticulation does not occur in the parts most remote from the protoxylem, but in those near it, and the condition is therefore not homologous with the spiral-scalariform-reticulate-pitted sequence commonly present in the more advanced groups of vascular plants. In *Lepidodendron* any stages beyond the scalariform type of thickening are entirely sporadic and local.

The transverse bars are about 7.5 micra in width, and are spaced at a distance slightly greater than their diameter. They broaden a little toward the corners of the tracheids, and are narrowest at the middle. Where well preserved, the bars appear to consist of a light translucent substance surrounding darker material in the interior. This inner darker substance may sometimes make up the greater part of the inside of the bar, it may consist merely of a thin irregular thread, or in places it may even be absent entirely. Because of the irregular distribution of this substance inside the bars it is believed that the appearance is the

result of irregular chemical action during petrifaction. The translucent outer part is probably caused by more complete replacement of the cellulose and lignin by silica. That chemical action has advanced well toward the point of complete replacement is indicated by the fact that practically all structure breaks down under treatment with hydrofluoric acid. Consequently, in this case cellulose peels which can be successfully made from coal-ball material and some other types of petrifactions are of little value.

Extending vertically across the slitlike openings between the transverse bars is a series of numerous fine threads, which appear to consist of the same substance as the translucent matter of the bars themselves (Pl. VII, Fig. 1). These threads have been observed in several species of *Lepidodendron* and *Lepidophloios* and have been variously interpreted. Seward and Hill (16) explain them as post-mortem changes during which the pit-closing membrane contracted and became torn. In our material this explanation seems unsatisfactory because the threads show most clearly in the better-preserved portions of the tracheids. Were these threads the result of contraction and tearing, it would seem that occasional larger pieces of wall material would remain. None have been found, however, and although some of the threads are broken, they produce a pattern of striking regularity. Preservation has doubtless altered their appearance somewhat and may even have accentuated them, but they can hardly be interpreted otherwise than as the result of definite structural features within the secondary wall. Contraction alone would almost certainly cause the formation of cross cracks as well as vertical ones. When cut crosswise, the bars appear as a double row of beads (Pl. VII, Fig. 2), and preservation is often sufficient to show that the vertical threads traversing the spaces between them connect the upper and the lower sides of adjacent bars. The threads appear to have lain against the primary wall layer and to have bridged the pit cavity (if the transverse slit may be so designated) on the inside. There is no indication whatsoever that the threads are a part of the primary wall. Calder gives a detailed account of these threads in *L. Brownii*, and arrives at a conclusion some-

what different from that reached here. She states that the threads "do not impinge directly on the dark brown bars above and below the pit areas, but merge first of all in a continuous pale yellow band, apparently of the same material as the threads themselves" (Calder, 3). In *L. Johnsonii* it is likewise evident (as stated) that the threads are a continuation of the outer substance of the transverse bars, but the essential difference is that in our material this lighter outer layer makes up the bulk of the substance of the bars, and, furthermore, it is believed that this apparent differentiation in the structure of the bars may be due mostly to preservation. In the tracheids of *L. Brownii* studied by Calder the walls are apparently preserved in a darker and less translucent state.

If spiral or annular thickenings exist in this species, they are confined to a very few cells at the extreme tips of the xylem points. Unfortunately, preservation is generally unsatisfactory along this zone, but even in the smallest tracheids in which the structure is visible nothing but scalariform sculpturing can be definitely recognized.

Secondary xylem. — The secondary xylem forms a sheath 3 cm. or more thick around the primary cylinder (Pl. II, Fig. 1). It consists for the most part of large scalariform tracheids (Pl. VI, Figs. 1–2) quite similar to the larger ones in the primary xylem, although locally they may appear more bent or twisted owing to outward passage of traces and rays between them. Radial seriation due to cambial origin (a feature not present in the primary tissue) is quite evident.

Along the contact zone between the two xylem layers the secondary tissue conforms to the outline of the primary cylinder. The secondary xylem, however, does not lie directly against the primary, but is separated from it by a very thin parenchymatous layer, from which most of the cell structure has disappeared. The innermost secondary xylem cells are rather small and delicate (Pl. V, Fig. 2), and those of a single radial series are separated from those of the adjacent series for a short distance from the primary xylem by narrow raylike extensions of parenchyma (Pl. IV, Fig. 1). Outwardly the tracheids enlarge gradually over a dis-

tance of fifteen or twenty elements, but beyond this point they attain their full size (Pl. V, Fig. 2). This inner zone of rather delicately constructed secondary tracheids contrasts strongly with the more robust ones of the primary cylinder. Histologically the secondary tracheids are similar to the primary ones.

Most of the xylem rays are small structures showing considerable range in height. The largest ones consist of twenty or more superimposed cells, although few of them exceed ten. The majority are one cell wide, but a few are wider. They are all narrow, being usually less than one quarter as wide as the tracheids that flank them. Cell structure in the rays has mostly disappeared, although occasionally narrow but widely spaced scalariform bars may be detected.

After departure from the primary cylinder the traces bend outward rather sharply and pass in a horizontal direction through the secondary xylem (Pl. VI, Fig. 1). In the inner part of the xylem layer they pass through large raylike masses of parenchyma of considerable vertical extent. These large "rays" diminish rapidly, and at a short distance outward the amount of parenchyma accompanying the trace is so reduced that the trace appears as a small spindle-shaped object about equal to the width of two tracheids (Pl. VII, Fig. 3). Owing to decay and accumulations of opaque material within the traces the internal structure is not well shown. The presence in them of a few serially arranged cells indicates, however, that secondary growth has added slightly to the diameter.

The xylem tissue of *Lepidodendron* apparently served only for water conduction; the function of support was taken over by the thick periderm layer at the outer part of the trunk. The plant is, therefore, an excellent example of physiologic specialization. That the xylem was a negligible factor in the support of the trunk is indicated not only by the small size of the central cylinder but by the consistency of the xylem as well. To judge from the size of the tracheids composing it, the tissue was porous and, because of the structure of the secondary walls, must have been very soft. The secondary xylem seems characteristic of a tissue which grew rapidly. *L. Johnsonii* agrees with the majority of Pennsylvanian

plants producing secondary wood in showing a complete lack of seasonal layering. Rather than assume strict climatic uniformity as an explanation of the lack of seasonal responses in the wood of these trees, the writer makes the alternative proposal that in *Lepidodendron* the entire amount of secondary xylem formed was produced within a single growing season, probably the first one. Secondary periderm formation, however, doubtless continued year after year. The secondary periderm was probably added slowly and may not have been subject to seasonal variation. On the other hand, the rather evenly distributed tangential bands of secretory structures may have been annual additions. The periderm differs in appearance from the secondary xylem, which is certainly indicative of rapid and uninterrupted growth.

The Extravascular Tissues

The tissues surrounding the vascular cylinder in most species of *Lepidodendron* and related genera are usually rather strongly differentiated into a hard, resistant outer layer and a soft inner zone, which is seldom preserved. This inner part consisted originally of the cambium, phloem, pericycle, endodermis, and at least a part of the cortex. The outer layer is often preserved as a hollow shell, within which is the somewhat misplaced central cylinder embedded in a mass of stigmarian rootlets and other débris that fills the space remaining after the decay of the softer parts. In many species, as in *L. Johnsonii*, secondary growth has added materially to the thickness of the outer layer.

The morphology of this outer layer of *Lepidodendron* has been variously interpreted, and its exact nature remains somewhat of a question because of the difficulty of determining the position of the meristematic tissue from which it was derived and also its relation to the more destructible tissues beneath it. Some writers divide the extravascular tissues into inner, middle, and outer cortex; the last generally applies to the zone of secondary origin. In his account of *L. Hickii* Watson (19) goes even further and recognizes an inner, a middle, and an outer cortex and a periderm. He thus follows certain others in regarding the secondarily formed zone as extracortical. Scott (14) designates the entire thickness

of extravascular tissue as cortex, and considers the secondary layer a part of it. Whether the periderm layer is to be classed as secondary cortex or as apart from it is probably a matter of definition, but in the present account Scott's practice will be followed, and the terms "periderm" and "secondary cortex" will be construed as having the same meaning.

The periderm of *L. Johnsonii* is remarkable for its great thickness; large blocks consisting entirely of this tissue may be found in abundance at the Trout Creek locality. At first these blocks of silicified tissue were thought to be portions of large woody cordaitean trunks, an error soon apparent upon microscopic examination. The periderm is probably the thickest ever recorded for any Paleozoic lycopod. Kisch (11), who gives a comprehensive account of this tissue in *Lepidodendron*, *Sigillaria*, and *Stigmaria*, says that it may attain a thickness of 7 or 8 cm. In *L. Johnsonii* a thickness of 15 cm. has been measured, and it is probable that in the largest trunks a thickness of 20 cm. was a common occurrence.

When the periderm of *L. Johnsonii* is cut or broken transversely the radial alignment of the cells is apparent even to the unaided eye. The mass of the tissue has a dark gray color, although there are scattered throughout it irregularly spaced lighter lines that extend radially and superficially resemble rays. These lines are either narrow silica-filled cracks through which the traces pass outward or strips of tangentially elongated cells (Pl. IX, Fig. 1). They never contain radially elongated cells such as commonly make up true vascular rays. Closer inspection of the periderm reveals very narrow, slightly irregular lines extending tangentially and spaced approximately 2 or 3 mm. apart (Pl. IX, Fig. 2). Except for their waviness they bear some resemblance to the late wood of a growth ring. The periderm splits readily along the radial plane, and the exposed surface resembles that of secondary xylem.

The outermost periderm is always lacking, so that it has not been possible to examine the leaf cushions or the surface layer. Most of the inner periderm is preserved (Pl. IX, Fig. 1), but because of complete disappearance of all structure between this and

the central cylinder the transition from primary to secondary cortex cannot be studied. It is believed (although the evidence is indirect) that in this plant the phellogen, or meristematic, layer was to the outside and that the preserved tissue was built up by addition to the exterior, and hence was of the nature of phelloderm.

The following description of the periderm is based upon detached fragments and portions ensheathing the concavities containing the central cylinders. Since almost all the periderm material is similar in structure, there is no reason to doubt that it may all be attributed to one species. Only a few small fragments are of questionable affinity. It is difficult to associate any particular piece of periderm tissue with the central cylinder of the same stem because several cylinders are usually present within the stem cavities.

The periderm of *L. Johnsonii* is a complex tissue consisting of fibers, "chambered" cells, and glands. The fibrous part, to which the generally obsolete term "prosenchyma" may be applied, resembles secondary xylem in its grosser aspects, although differing markedly from it where details of cell structure are concerned. The fibers are vertically elongated cells arranged in radial series and with rather thick walls. In transverse section they measure about 60 micra in radial diameter and appear broadly oval. The thickened walls are dark-colored. The fibers in adjacent rows tend to alternate with each other, and between them, at the corners, are small intercellular spaces. In tangential section these cells, which are irregularly arranged with tapering ends, may be twenty or thirty times as long as they are wide. The radial section shows that the cells in a series are of equal length, with the square ends evenly placed (Pl. X, Fig. 1); they thus present a superficial resemblance to the storied structure present in certain dicotyledonous woods. No pits are visible on any of the walls. At places in the transverse section a rather striking appearance results when the inner layers of the radial walls have become pulled inward as if shrinkage had occurred, although at the same time remaining firmly attached to the tangential surfaces (Pl. VII, Fig. 4). This separation of the layers of the walls is believed to

have been effected by preservation and by the structure of the wall.

For a depth of a centimeter or more the innermost periderm is less compact than that farther out, and the solidarity of the fibrous ground tissue is broken by groups of cells having very peculiar shapes. These cells are the same as the "chambered" cells described by Kisch (11), although they differ considerably in details from any she has figured. In transverse section they have the same radial diameter as the fibers, but they are enlarged tangentially to three or four times this dimension (Pl. IX, Fig. 3). They fit together in radially placed rows of a dozen to thirty or more, with their flat tangential faces adjacent. The cells are broadest at the mid-portion of a band; they diminish gradually toward either extremity, where they finally continue as a row of ordinary fiber cells. Owing to the orderly arrangement of all the cell types in the periderm and the nearly complete absence of displacement which almost certainly would have resulted had these "chambered" cells undergone tangential enlargement subsequent to their formation, it is believed that they were formed from especially broad cambial initials. Frequently several of these bands are arranged side by side in large compound bands, which may extend in a radial direction for a considerable distance (Pl. IX, Fig. 3). In these as well as in the fibers the inner layer of the wall has sometimes been pulled away, although here the separation has taken place along the tangential face, which happens to be the longer one. At places the separated portions bulge inward and almost fill the cell cavity. The effect thus produced may be the same as that which is figured by Kisch in *Lepidodendron selaginoides* and *Lepidophloios sp.* and which is explained as due to swelling of the wall.

The peculiarities of these chambered cells show best in tangential section. Viewed in this plane they appear somewhat oval, with rounded or taper-pointed ends (Pl. X, Figs. 2–4). Some of them (about one half) are divided by transverse septa into two parts, and are thus true "chambered" cells. The others are undivided; for this reason the term "chambered" is not so appropriate to them. Since, however, they are morphologically alike,

the same designation will be used for all of them, regardless of the fact that some are cell pairs resulting from the transverse division of a larger initial.

These "chambered" cells are arranged in vertical series, with each cell slightly oblique to the one directly above, so that the taper-pointed end of the lower cell fits snugly against the curved outline of the cell or cells next above. These cells (or cell pairs) are broadest at the mid-portion, and occasional ones show division by a vertical septum. Although they probably arose from special cambial initials, the ends apparently underwent elongation after cambial division and pushed their way in between the adjacent cells for a short distance in a manner similar to the attenuation of wood fibers during their development. Little resistance had to be overcome during this elongation because the enlarging elements were easily forced apart. Instead of forming a sharp point the elongated ends frequently remained broadly acute or even rounded (depending upon the amount of resistance encountered). Adjoining the end there is often a fairly large intercellular space (Pl. X, Fig. 4). The transverse septa are slightly thinner than the side walls, although careful examination shows less difference in thickness than at first appears upon casual observation. The proximity of the side wall to the thicker-walled fibers tends to give the false impression of a greater thickness than actually exists.

"Chambered" cells differing somewhat in form and arrangement from those described here have been reported in the periderm of a number of Paleozoic lycopods, but, so far as has been observed, they are not present in the better-known species of *Lepidodendron* or *Lepidophloios*. In *Sigillaria*, however, Kisch (11) figures these cells arranged in slightly oblique vertical groups resembling those of *L. Johnsonii* to some extent, although the initial cell may be divided by four or five septa.

The function of these chambered cells cannot be fully explained. From their shape and general appearance one might readily conclude that they are nothing but cells which have proliferated into spaces formed during lateral expansion of the trunk. This explanation, however, does not fit the facts well because in the

transverse sections there is no evidence of displacement among the radially seriated fibers. Moreover, these cells appear to have arisen directly from the phellogen along with the other elements of the periderm. A more likely reason for their presence is that they gave elasticity to the cortex; by permitting a certain amount of movement within the tissues, either during development or in response to the bending of the trunk by the wind, cracking of the otherwise hard and resistant tissue was lessened. The arrangement may be a simplification of the Dictyoxylon structure in several other groups of Paleozoic plants.

The secretory tissue which makes up the tangential bands already referred to is arranged in complex glandular structures placed in slightly irregular rows (Pl. IX, Fig. 2). Laterally the glands are nearly contiguous, although they are frequently separated from each other by a few intervening fibers (Pl. VIII, Figs. 1–2).

The individual structures extend vertically in the periderm for an undetermined distance, with groups of thin-walled cells with dark contents arranged at intervals of about 1 mm. (Fig. 4). The dark contents of these cell masses tend to obscure details within, but from all appearances they form slightly elongated or oval masses, which probably served to manufacture and store waxy or gummy substances. Completely surrounding and connecting these masses of secretory cells in the vertical direction is a jacket of thin-walled cells with colorless contents. In longitudinal section these jacket cells are rectangular with transverse ends. A slight constriction occurs between adjacent masses of dark cells. In transverse section the glands show as groups of twelve or fifteen cells arranged more or less around a center (Pl. VIII, Fig. 2). The

FIG. 4. Glandular structure as seen in longitudinal section. The pockets of thin-walled cells with dark contents are surrounded by a jacket of transparent cells with transverse end walls. × about 35

appearance of a gland in transverse section depends upon whether the section happens to pass between the secretory cell masses or through them. Sections cut through the storage compartments are slightly larger than those cut between.

As the periderm increased in thickness the phellogen periodically produced tangential rows of gland initials, and as new periderm accumulated on the inside additional bands of glands were formed at regular intervals. These glands probably secreted the waxy or gummy substances which were deposited on the outer surface of the trunk and thus rendered the tissues resistant to decay. The secretions also permeated the cell walls throughout the periderm. This periodic formation of secretory structures was probably due to the inability of the older glands to function efficiently after they had become deeply buried in the periderm.

The foregoing interpretation of the formation and function of the glands is based upon the assumption that the initiating layer, the phellogen, was outside the preserved portion. It also assumes a certain amount of permeability throughout the entire thickness of the periderm, which permitted the transfer of food and water to the meristematic layer on the outside. Although the innermost periderm may have become relatively inactive, it nevertheless remained alive during the life of the plant.

A similar tangential arrangement of the glands occurs in several species of *Lepidodendron* and *Lepidophloios*, but preservation is not always adequate to reveal their exact structure. These glands had been observed long before their function as secretory organs was known. Seward and Hill (16), studying *L. Wünschianus*, were apparently the first to suspect their true function. They believed them to be lysigenously developed ducts because in the material they studied the cellular composition had broken down. Seward (15) later attributed a like function to similar tangential bands in *Lepidodendron vasculare*. Scott (14) refers to these glands but casually, and Kisch (11), in her somewhat inclusive treatment of the subject of fossil lycopodiaceous periderm, mentions their probable secretory function, but describes them very inadequately as "zones formed by regular or irregular lines of cells which may be crushed or completely disorganized." From

Kisch's description it is evident, however, that these zones are identical with the tangentially banded glands of *L. Johnsonii*. Walton (18, Pl. V, Fig. 39) figures a secretory strand of *L. Wünschianus* in which the cells in the interior have broken down. It is impossible to entertain reasonable doubt that the structures described by Seward, Kisch, and Walton are imperfectly preserved. Our material shows conclusively that the secretory organs are not open ducts, but solid strands arranged in tangential bands, and that each strand contains vertically arranged masses of cells with dark contents.

SPECIFIC DIAGNOSIS

Lepidodendron Johnsonii, sp. nov. — Arborescent, with large trunks attaining a diameter of 50–60 cm.; central cylinder of main trunk averaging 7–8 cm. in diameter but smaller in branches; pith large, cells in center rounded and loosely arranged and surrounded by compactly placed angular cells with transverse end walls; primary xylem cylinder 1–5 mm. thick; cells largest adjacent to pith but diminishing slightly toward outside, becoming abruptly smaller just inside protoxylem region, scalariform or rarely reticulate; outer surface of primary cylinder ornamented with low protoxylem ribs from which leaf traces depart; traces departing steeply from angle formed by bifurcation of ribs; ribs appearing in transverse section as small points, 3–4 per millimeter; secondary xylem 3 or more centimeters in thickness, composed of scalariform tracheids and small rays; innermost tracheids small but gradually enlarging outwardly; course of traces horizontal; traces with very slight secondary development; periderm a thick woody outer zone of secondary origin and consisting of fibers, "chambered" cells, and glands; fibers radially seriated, thick-walled, vertically elongated with transverse ends when seen in radial section but pointed in tangential view; "chambered" cells in radial and vertical series and confined mostly to inner part of periderm, laterally broadened and slightly oblique vertically, and with rounded or taper-pointed ends, some divided by transverse septa; secretory organs appearing in transverse section as slightly wavy tangential bands and resembling growth rings when seen by

the naked eye; individual glands vertically elongated and consist-
ing of a series of groups of thin-walled cells with dark contents
surrounded by a jacket of cells with transverse end walls.

Locality. — Southern end of Chubb Gulch, about four miles
southwest of Trout Creek Pass, Mosquito Range, Chaffee County,
Colorado.

Horizon. — Lower Weber (?), about 155 feet above the base
of the Trout Creek section (according to Johnson, 9), Pennsylva-
nian system.

The species is named after J. Harlan Johnson, who discovered
the locality.

COMPARISONS WITH OTHER FORMS

Most of our knowledge of the internal anatomy of *Lepido-
dendron* and *Lepidophloios* is based upon twigs only a few centi-
meters in diameter. There are often marked differences in the
size of the primary cylinder between the smaller twigs and the
main trunks of the same plant and in the relative extent of the
tissues. In *L. Wünschianus*, for example, Walton (18) has found
that, although the main stem contains a large pith, the smaller
branches possess a solid xylem strand unaccompanied by secondary
accretion. Furthermore, he has shown that there is a marked
decrease in the size of the primary cylinder as the transition to
the root zone is approached. Had the trunks and small branches
of this species originally come from separate localities, they would
have received separate specific names. Because of the discrepancy
in structure of different parts of the plant it is impossible to make
accurate comparisons between *L. Johnsonii*, of which only the
trunk is known, and the numerous species described entirely from
small stems or branches. Of the large number of *Lepidodendron*
and *Lepidophloios* species only three, *Lepidophloios Wünschianus*,
Lepidodendron brevifolium, and *Lepidophloios Harcourtii*, can be
satisfactorily compared with it. All of these contain a large cen-
tral pith with a comparatively thin primary xylem ring and, if
the specimen assigned by Calder (4) to *L. Harcourtii* is correctly
identified, all possess a well-developed layer of secondary wood in
the older parts.

Lepidophloios Wünschianus

The similarity in the preservation of the Colorado. trunks and those from the Lower Carboniferous ash beds of Scotland has been mentioned. The resemblance pertains to the state of preservation, however, rather than to conditions which prevailed at the time of deposition. In Colorado there is no evidence of volcanic activity at that time, and the trees were overwhelmed by a rapid accumulation of black mud instead of by an ash fall. Another difference is that in Colorado the preserving medium is silica, not calcium carbonate. The silica, probably contained in the water from hot springs, served to cement the black shale particles as well as to infiltrate the trunks.

When comparing a form such as *L. Johnsonii* with other species of the same or related genera, one can hardly avoid laying emphasis on the size of the trunks. Environmental conditions are seldom so favorable for the preservation of large trunks as for smaller parts of the plant body because of the tendency of the former to become stranded in shallow water, where they are then subjected to various destructive forces. It is for this reason that the majority of the known structurally preserved species of *Lepidodendron* and *Lepidophloios* are based upon small branches not more than a few centimeters in diameter. In this respect *L. Johnsonii* and *L. Wünschianus* are rather exceptional and, consequently, one is inclined to be unduly impressed by size, a character which is not necessarily fundamental in relationships and which should be used with caution. Misinterpretations due to size difference cannot always be avoided, especially when organs belonging to the same plant show marked variation in structure.

L. Wünschianus is known mostly from the account by Seward and Hill (16) of a well-preserved trunk from the Lower Carboniferous beds at Dalmeny, near Edinburgh, and from the work of Walton (18) and others on the hollow trunks of the island of Arran off the west coast of Scotland. The trunk described by Seward and Hill was 33 cm. in diameter and contained a central cylinder 6.5 cm. in diameter. A central hollow was surrounded by 11 mm. of pith tissue; around it was the mantle of primary

xylem, which was 3 mm. thick. The thickness of the secondary wood was 22 mm.; that of the periderm layer, 70 to 80 mm. These dimensions indicate a tree comparable in size to *L. Johnsonii*.

The structure of the central cylinder is very similar in both species. The "hyphal" cells mentioned as being in the pith of *L. Wünschianus* have not been recognized with certainty in *L. Johnsonii*, although in the smallest specimen observed the pith is definitely divided into two regions, an inner one of rounded cells and an outer zone, where the cells are rectangular (Pl. V, Fig. 1). The thickness and structure of the primary xylem is similar in both species. Seward and Hill also comment upon the fact that definite protoxylem elements cannot be recognized. Both species possess a similar corona and, as nearly as can be determined, the leaf traces depart in a similar manner. The trace of *L. Johnsonii* is unknown outside the secondary wood. Within the secondary wood the traces of the two species closely resemble each other, but it is not known whether in *L. Johnsonii* the trace shows the marked secondary addition in the inner cortex figured for *L. Wünschianus*.

The secretory glands in the periderm of *L. Wünschianus* are arranged in tangential rows similar to those of *L. Johnsonii*. They are not described in longitudinal section, and Seward and Hill state that they appear to be of lysigenous origin. This appearance, however, is certainly due to faulty preservation. Seward and Hill also mention tangential broadening of some of the periderm cells, but whether these broadened cells are the same as the "chambered" cells of *L. Johnsonii* is unknown. Walton (18) mentions the marked thickening on the radial walls of the periderm cells. To judge from his descriptions and figures, these thickenings are probably the same as those in *L. Johnsonii* that resulted from the partial detachment of the layers of the inner part of the radial wall (Pl. VII, Fig. 4).

Lepidodendron brevifolium

L. brevifolium was first described by Williamson (20, pp. 288–291) from the Calciferous Sandstone in 1872, but the specific

name was not applied until later. The original specimen had a pith about 1 cm. in diameter, surrounded by about 2 mm. of primary xylem. An additional centimeter of secondary wood gave to the slightly compressed axis a diameter of about 3 cm. Williamson estimated that the original trunk was about 14 inches in diameter.

L. brevifolium is distinguished from *L. Johnsonii* by the absence of outwardly projecting teeth on the periphery of the xylem cylinder, but aside from this the two species have several features in common. Rather little seems to be known of the periderm of *L. brevifolium*, although apparently it attained considerable thickness. Williamson (20, Pl. XLIII, Fig. 17) illustrates the periderm in radial section, where it is seen to be made up principally of square-ended prosenchymatous cells such as are described for other species, but says nothing of "chambered" cells or glands.

Calder (5) has added a few details to our information on this species, and has shown the presence of scattered reticulately thickened tracheids in the xylem. Her figures (Pl. II, Fig. 10) indicate a layer of secondary wood thicker than that originally described by Williamson.

An unnamed species of *Lepidodendron* described by Barnard (1) from the Lower Carboniferous of New South Wales, and compared by him to *L. brevifolium*, may be mentioned. The xylem cylinder, the only part preserved, is about 6.5 cm. in diameter. The pith cavity, which is 3.1 cm. in diameter, is surrounded by 7 mm. of primary wood. The dimensions of this stem compare well, therefore, with those of *L. Johnsonii*, *L. brevifolium*, and *Lepidophloios Wünschianus*.

Lepidophloios Harcourtii

This species probably bears less resemblance to *L. Johnsonii* than does either of the two previously discussed, but a brief comparison seems appropriate because of approximate age equivalence. *L. Harcourtii* is commonly assigned to the Lower Carboniferous (Scott, 14, p. 120; Hirmer, 8, p. 238), but Crookall (6) has given satisfactory evidence that all specimens of *L. Harcourtii* of known source came from Upper Carboniferous levels

and that the usual reference to the Lower Carboniferous is unfounded. As a result of the general supposition that *L. Harcourtii* and *L. Wünschianus* are of the same age, the two species are often confused. Seward and Hill (16), for example, assigned the Dalmeny tree (*L. Wünschianus*) to *L. Harcourtii* in the belief that it merely represented an older trunk which had developed secondary wood. Scott (14) and Walton (18) recognized the two forms as distinct, but Hirmer (8) considered them one species. Calder (4) appears to have been the first to identify an Upper Carboniferous specimen bearing secondary wood as *L. Harcourtii*.

Between *L. Harcourtii* and *L. Johnsonii* there are some strong points of resemblance as well as some marked differences. The primary xylem of both consists of a thin shell of scalariform tracheids surrounding a comparatively large pith. According to figures and descriptions, the corona teeth of *L. Harcourtii* are more prominent than in most other species, but in *L. Johnsonii* the proximity of the secondary wood, combined with frequent poor preservation along the contact zone in the xylem, often renders the corona somewhat obscure. In *L. Johnsonii*, however, the corona is present, and the surface of the primary xylem is not the featureless type such as exists in *L. brevifolium* or *L. vasculare*. It has not been possible to ascertain whether the traces of *L. Johnsonii* depart from the primary cylinder in exactly the manner described by Bertrand (2) for *L. Harcourtii*, but there is reason to believe that they arise from forks of the protoxylem ridges and that from the point of division two ridges continue upward.

The presence or the absence of secondary wood is not a dependable specific character, but if this tissue did form in *L. Harcourtii* it has never been observed in stems as large as 8 or 9 cm. and in which the central cylinder is 1 cm. The smallest known primary cylinder in *L. Johnsonii* is less than 1 cm., but is surrounded by 3.5 cm. of secondary wood.

The outstanding difference so far observed between the two species under consideration is the structure of the periderm. *L. Harcourtii* lacks, so far as is known, the regularly arranged tangential bands of glands. There is a row of glands just inside

the secondary cortical cylinder, but in the latter the tissue appears nearly homogeneous except for the outward-going leaf traces.

Whether or not the trunks of *L. Harcourtii* ever became as large as those of *L. Johnsonii* is conjectural, but there is no very good reason to doubt that both species grew to be large trees. It is only under exceptional circumstances that the largest trunks of any of the Paleozoic genera were preserved.

ASSOCIATED STIGMARIAN ROOTS

The tissues of the trunks of *L. Johnsonii* are everywhere invaded by the small rootlets of *Stigmaria*. These intruders, however, do not necessarily belong to the same kinds of plants as the trunks, but are in all probability the roots of various arborescent lycopods which grew in the swamps among the accumulating vegetable débris.

In addition to the small rootlets inside the trunks several portions of large silicified rootstocks have been found. Although somewhat crushed, and in general not so well preserved as the trunks, these organs are large, being at least 15 or 20 cm. in diameter. The thick extrastelar tissues consist of an outer layer, probably of secondary origin, and an inner layer, which was not preserved. The central cylinder (Pl. XI, Fig. 6), which is sometimes partly crushed, attained a diameter of 5 cm. or more.

A large pith from which all structure has disappeared occupies the center of the central cylinder. The surrounding wood is entirely secondary in origin, and is made up of inwardly directed wedge-shaped portions separated by "rays" of parenchyma, through which the lateral rootlets pass. The wood contains rather large scalariform tracheids

A critical study of the internal organization of the rootstocks is impossible because of poor preservation, but they agree in essential structural features with the well-known *Stigmaria verrucosa*,[1] the common form present in almost all plant-bearing Upper Carboniferous deposits. The features in common with *S. verrucosa* are the large pith, the apparent lack of distinct pri-

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[1] Equivalent to *S. ficoides*, over which the name *S. verrucosa* has priority.

mary xylem, the division of the secondary wood into segments, and the thick cortex with an outer periderm.

The small rootlets also agree with those assigned to *S. verrucosa* (Pl. XI, Fig. 7). The xylem strand consists of a small compact tracheid mass with a single protoxylem point. The tracheids are nearly surrounded by an empty zone representing the position of the phloem, and around this is the rather well preserved inner cortex. This inner cortical cylinder containing the vascular strand is usually somewhat misplaced within the large cavity formed by the breaking down of the middle cortex. Enclosing this inner space is the outer cortex, which is well preserved. The delicate tracheid strand which connects the vascular portion with the transfusion tissue in the outer cortex in stigmarian rootlets may be seen in part in favorably cut sections.

ASSOCIATED STEM-SURFACE IMPRESSIONS

Some of the black shale fragments scattered over the terrain among the silicified trunks bear the imprints of lepidodendroid foliar cushions (Pl. XI, Figs. 1–5). All the specimens are small, however, and very little of the delicate sculpturing which is necessary for exact identification is preserved.

The most common of the impression types has small transversely elongated cushions which bear a general resemblance to those of *Lepidophloios laricinus* (Pl. XI, Figs. 1–4). A few others with vertically elongated cushions having scars in the upper angle are more typical of *Lepidodendron*. No specific assignments can be made, but such forms as *Lepidodendron simile* and *Lepidodendron scutatum* are suggested (Pl. XI, Fig. 5).

Although the structure of the trunks is indicative of only a single species, the presence of more than one form of leaf cushion in the same formation offers proof of the existence during Pennsylvanian times of several types of arborescent lycopods in central Colorado. The *Lepidophloios* form of leaf is more abundantly represented than the *Lepidodendron* type, and since there is no very satisfactory anatomical basis for separation of the two genera, the possibility of the silicified trunks belonging to *Lepidophloios* must be admitted. This point cannot be determined with finality,

however, until a preserved trunk showing diagnostic surface features is discovered. Most of the imprints containing leaf cushions represent small twigs.

CONCLUSION

The *Lepidodendron* remains in the lower part of the Weber (?) formation indicate a westward extension of the typical Carboniferous coal-swamp flora into central Colorado. That members of the coal flora existed there during the earlier Pennsylvanian is probable (as is suggested by the flora of the Glen Eyrie shale at Colorado Springs), although in Colorado the interval constituting the late Mississippian and early Pennsylvanian was mostly one of erosion, during which no fossil records of the flora are known to have been preserved. Throughout this lost interval the dominant plant types probably were upland forms not associated with a neritic environment, and the well-drained and eroded terrain may have supported members of the primitive gymnosperm complex, forerunners of such genera as *Walchia* and *Lecrosia*, which in turn appear in formations succeeding the Weber (?) and Coffman in central Colorado. That there may have been an eastward migration of these early gymnosperms during the Pennsylvanian is suggested by the fact that recent investigations in central Colorado indicate an age as early as Des Moines for some of the *Walchia*-bearing beds, and also by the presence of a flora of typical Permian aspect in the Missouri series of Kansas. Future discoveries of *Walchia* and related types in successively lower horizons in the western states may lend support to this hypothesis.

The establishment of a typical Pennsylvanian swamp flora in central Colorado was probably on a comparatively small scale, and resulted from an environment which was temporarily different from that of the succeeding and, possibly, also the preceding stages. That this flora contained diversified types is indicated by the small flora described by Read (13) from the lower Weber (?) near Leadville. Among the species enumerated are one of *Lepidostrobus* and several of *Neuropteris* and *Sphenopteris*. The short duration of this swamp environment is probably the reason for the lack of an appreciable amount of coal in the lower Weber (?).

Although there seems to be ample justification for awarding the Weber (?) *Lepidodendron* specific status, it should be noted that from the structural standpoint the plant shows no great departures from other well-known species of the genus. It is quite like the Calciferous Sandstone species, *L. Wünschianus*, and were it not for the age difference and the great geographic separation, it might be difficult to present a convincing case for considering them specifically distinct. Because of poor preservation of many of the specimens some of the important anatomical features cannot be compared, as, for example, the trace structure in the inner cortex and certain details of the periderm. The periderm of *L. Johnsonii* is probably the thickest of all known species. On the other hand, similarities are just as important as differences when one is considering specific relations in their broader aspects, and probably the fact that should be most emphasized is that during early Pennsylvanian times there flourished in that part of North America now occupied by the Rocky Mountains a form of arborescent lycopod which was similar in all major structural features and environmental adaptations to certain well-known contemporaneous or preceding European species. This is another fragment of evidence for the widespread uniformity of the middle Carboniferous floras.

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PLATES I–XI

1

2

FIG. 1. Portions of silicified *Lepidodendron* trunks weathered from the black
   shales in the lower part of the Weber (?) formation. Southwest of Trout
   Creek Pass, Chaffee County, Colorado
FIG. 2. Data as for Figure 1

1

2
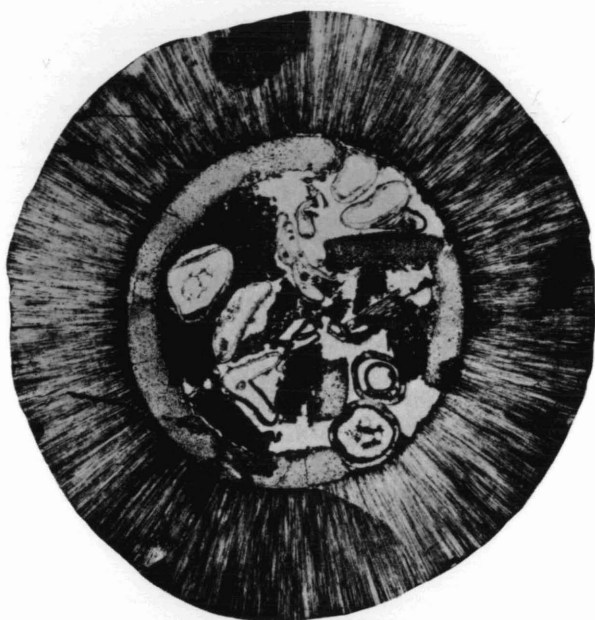
L. Johnsonii Arnold, sp. nov.

Fig. 1. Transverse section of central cylinder, showing the debris-filled pith region, the broken primary xylem cylinder, and the secondary xylem. × 1

Fig. 2. Transverse section, showing enlarged view of the primary xylem and the adjacent secondary xylem. × 3

1

2
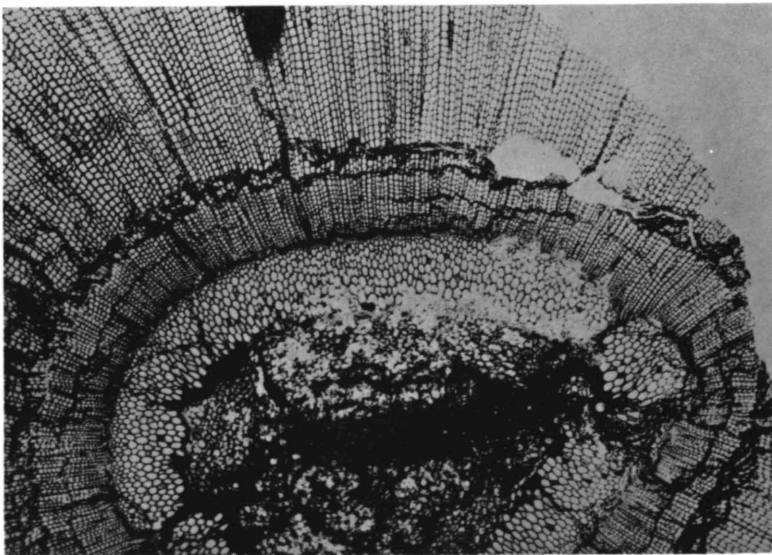
L. Johnsonii Arnold, sp. nov.

FIG. 1. Small central cylinder surrounded by a considerable thickness of secondary xylem.   × 3¼

FIG. 2. Enlarged view of central cylinder of the specimen shown in Figure 1, but from a different section.   × 8

1

2
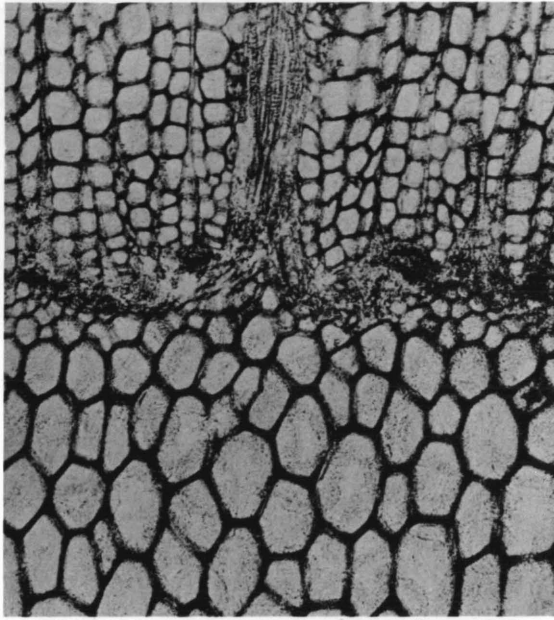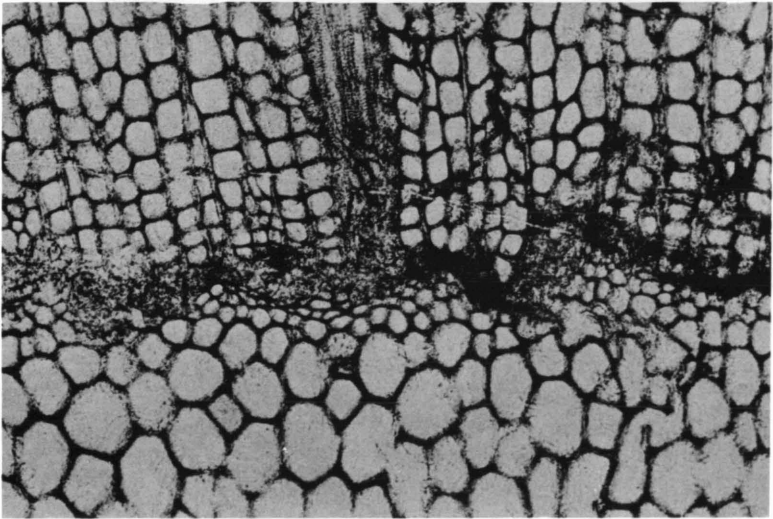
L. Johnsonii Arnold, sp. nov.

FIG. 1. Transverse section, showing departure of a leaf trace from the corona point. From specimen shown in Plate III.   × 80

FIG. 2. Transverse section, showing a leaf trace in a slightly more advanced stage of departure. From specimen shown in Plate III.   × 80

1

2

L. Johnsonii Arnold, sp. nov.

FIG. 1. Radial section, showing the two zones in the pith and the adja-
cent tracheids of the primary xylem. From specimen shown in Plate III.
× 26

FIG. 2. Radial section, showing primary xylem (left), the small tracheids
of the inner secondary xylem, and the larger tracheids of the outer
secondary xylem (right). From specimen shown in Plate III.   × 26

1

2
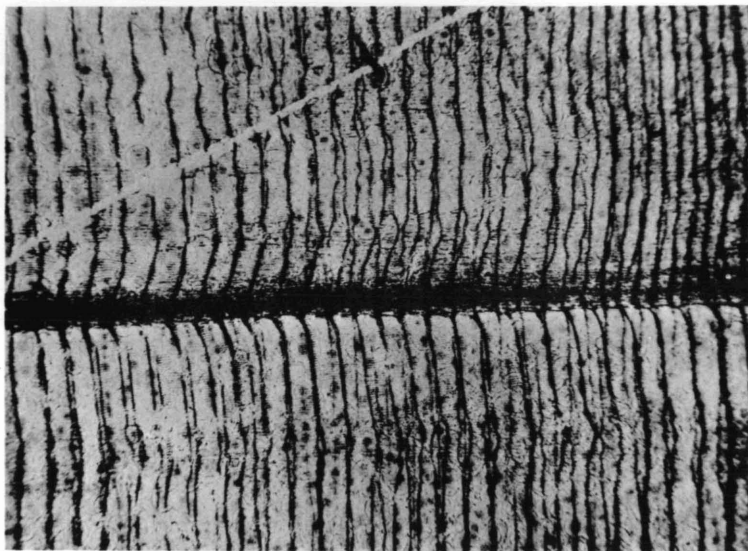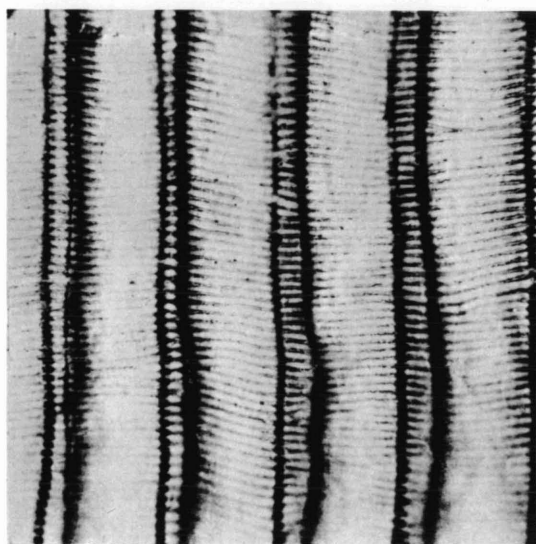
L. Johnsonii Arnold, sp. nov.

FIG. 1. Radial section of secondary xylem, showing a leaf trace pass-
ing horizontally through it. From specimen shown in Plate III.
× 36

FIG. 2. Longitudinal section of secondary xylem, showing detail of scalari-
form tracheids. × 110

1

2

3

4
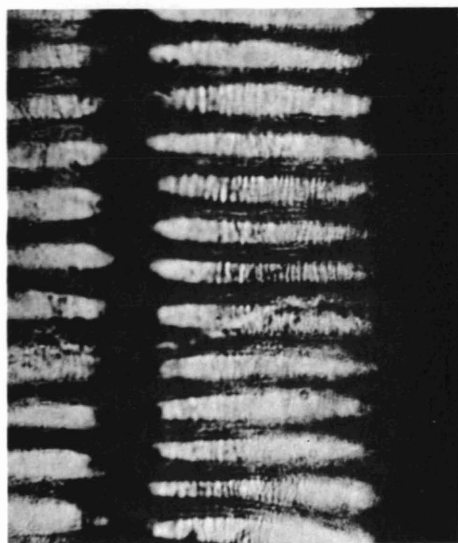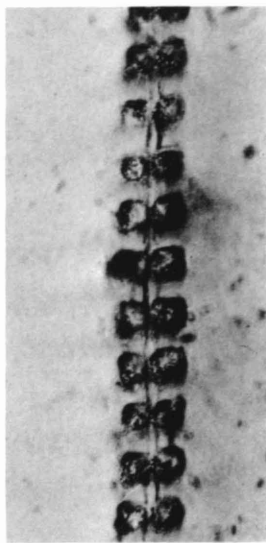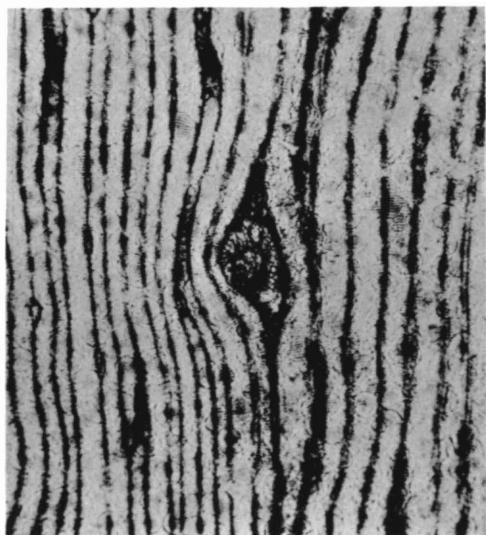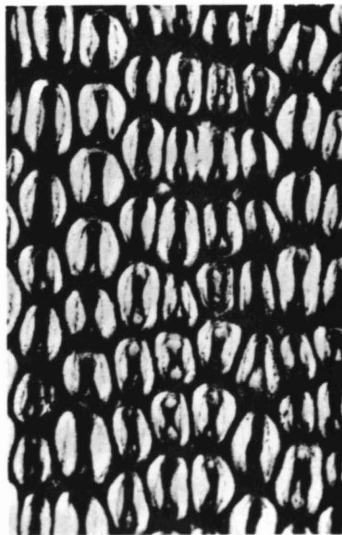
L. Johnsonii Arnold, sp. nov.

FIG. 1. Enlarged view of scalariform tracheid in longitudinal section, showing delicate vertical threads traversing the space between the scalariform secondary thickenings.   × 475

FIG. 2. Longitudinal section cut across the scalariform thickenings of the tracheid walls and showing the connecting vertical threads.   × 475

FIG. 3. Tangential section through the secondary xylem, showing an outgoing trace.   × 31

FIG. 4. Transverse section of the periderm, showing the fiber-like cells in which the innermost wall layers become detached along the radial surfaces.   × 120

1

2
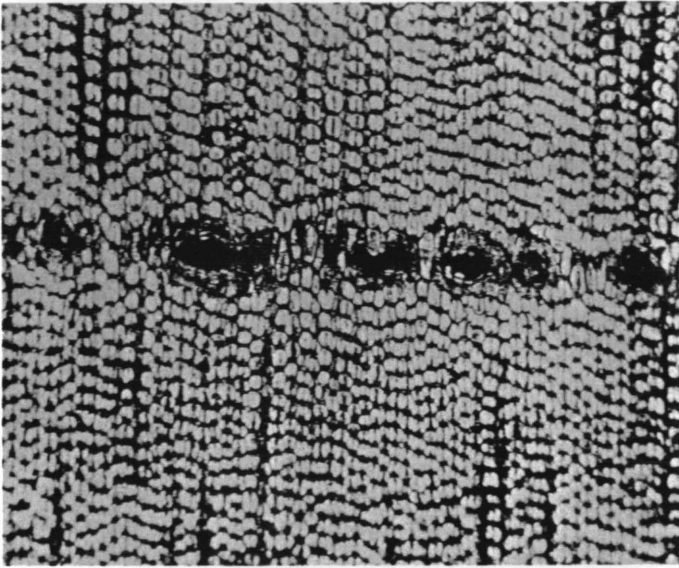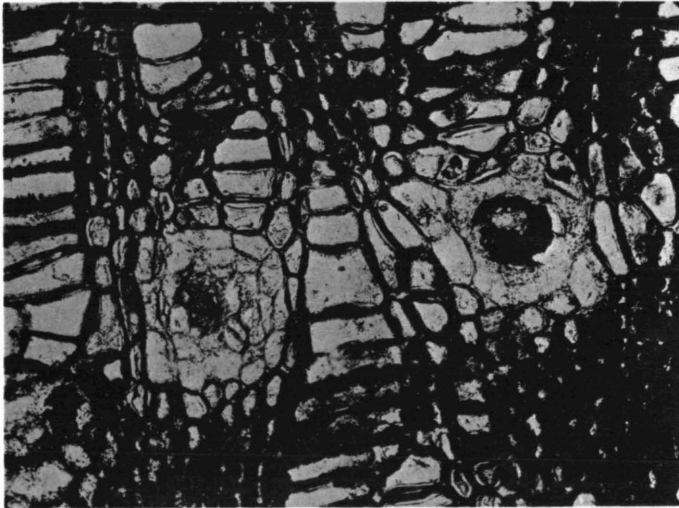
L. Johnsonii Arnold, sp. nov.

FIG. 1. Transverse section of secondary periderm, showing a band of glands. × 37

FIG. 2. Enlarged view of two glands in transverse section. × 65
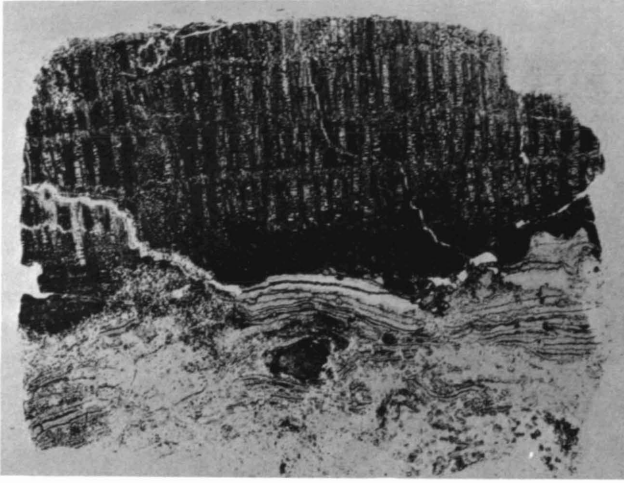
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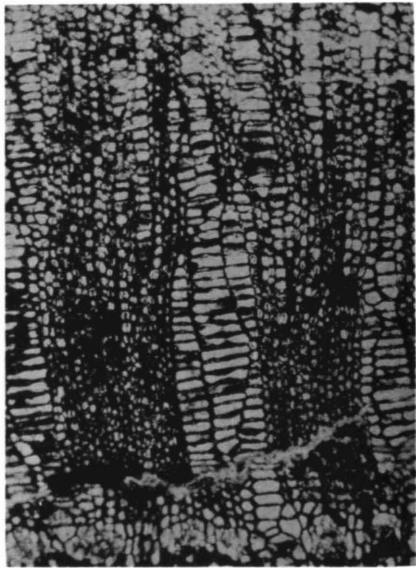
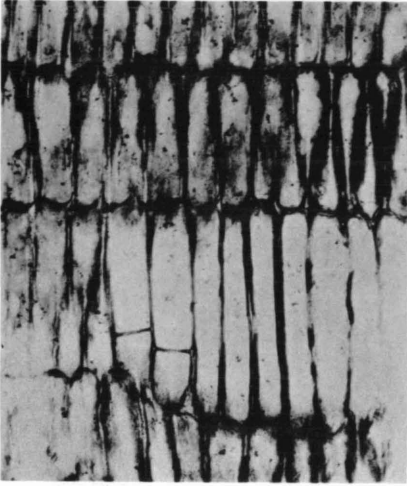2   3

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FIG. 1. Transverse section of innermost periderm. $\times\ 2\frac{3}{4}$

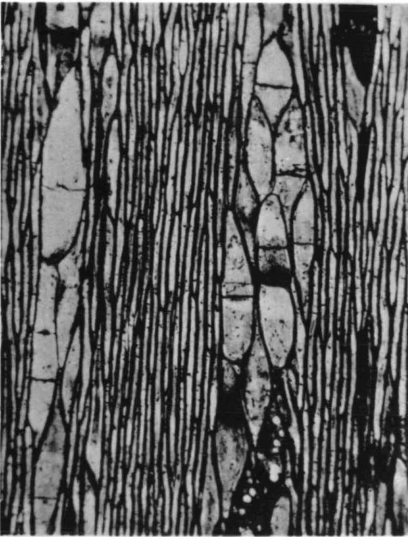FIG. 2. Transverse section of outer part of periderm, showing tangential bands of glands. $\times\ 2\frac{3}{4}$

FIG. 3. Transverse section of periderm, showing radially aligned bands of tangentially broadened "chambered" cells. $\times\ 25$
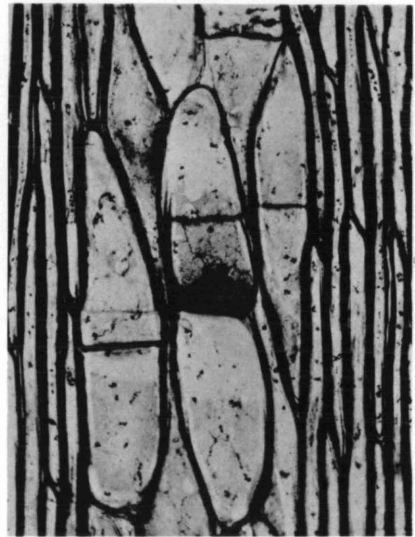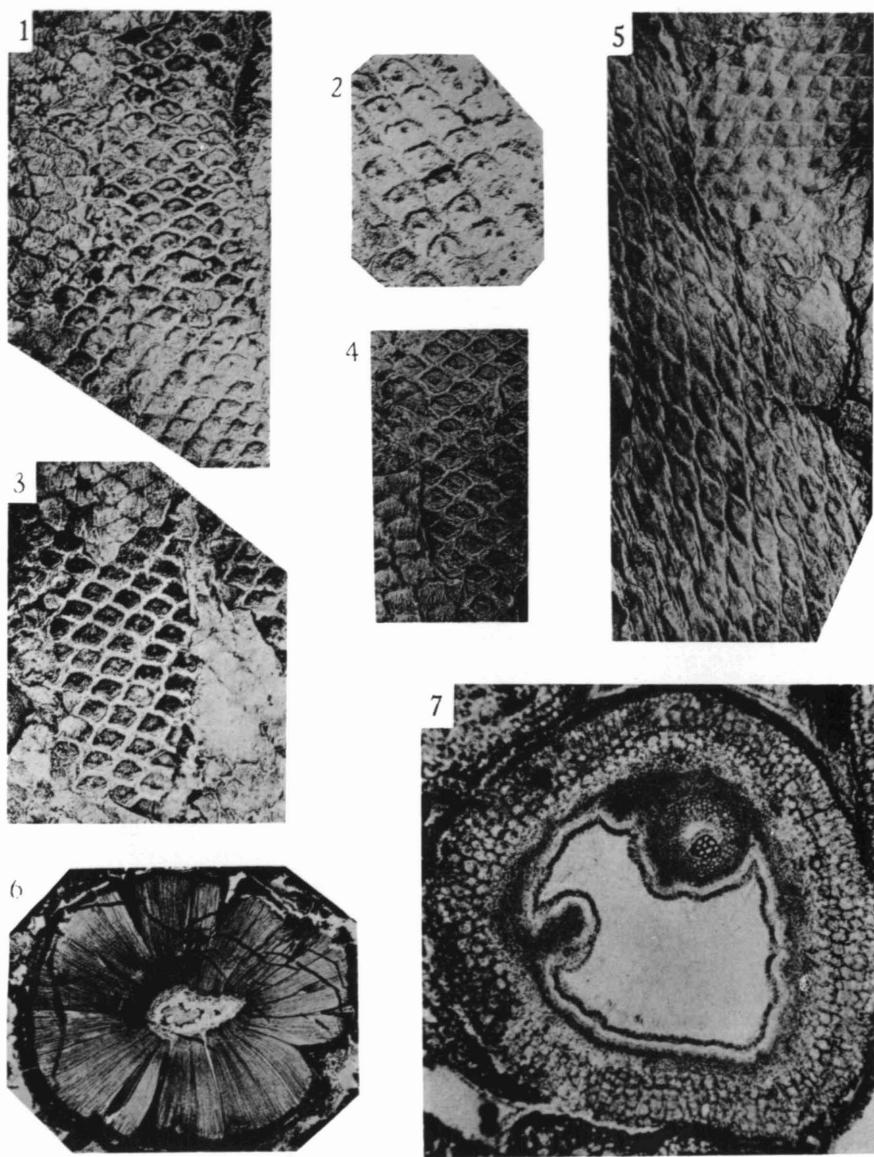
1

2

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4

L. Johnsonii Arnold, sp. nov.

FIG. 1. Periderm in radial section, showing the evenly aligned fibers and the "chambered" cells.   × 55

FIG. 2. Inner part of the periderm in tangential section, showing the shape and arrangement of "chambered" cells and the intervening fibers.   × 25

FIG. 3. Data as for Figure 2.   × 25

FIG. 4. Enlarged view of portion of Figure 3.   × 65

FIGS. 1-4. *Lepidophloios sp.* (cf. *L. laricinus* Sternb.). Surface imprints associated with *L. Johnsonii* Arnold. × 1

FIG. 5. *Lepidodendron sp.* Surface imprints associated with *L. Johnsonii* Arnold. × 1

FIG. 6. *Stigmaria verrucosa* (Martin) Miller. Central cylinder of large rootstock. × 1½

FIG. 7. *S. verrucosa* (Martin) Miller. Transverse section of lateral rootlet. × 12