THE ANATOMY AND AFFINITIES OF *MEDULLOSA NOEI* STEIDTMANN, AND ASSOCIATED FOLIAGE, ROOTS, AND SEEDS

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INTRODUCTION

THE genus *Medullosa* was described by Cotta (1832) from the Rothliegende (Lower Permian) near Chemnitz, Germany. Later Scott (1899) described *Medullosa anglica* from the Lanar-

kian (Lower Coal Measures) of England, and fifteen years after that date Scott (1914) and de Fraine (1914) described additional species from the same source. In 1898 Potonié (1898) proposed the group name "Cycadofilicales" for *Medullosa* and any other plants having structural characteristics of both ferns and cycads. Subsequently, when one of the Cycadofilicales was found to be a seed plant, the term "Pteridospermae" was introduced to designate the Cycadofilicales that bore seeds.

The first account of petrified medullosan material from North America was Penhallow's description (1897) of *Myelopteris topekensis* from the Carboniferous of Kansas. No further mention of any members of this group appeared in American literature until Hoskins (1923) described similar material from coal balls that had just been discovered in Illinois. In 1931 Hoskins described a number of roots from the same source. In 1937 the present author gave a preliminary account of *Medullosa Noei* from coal balls from the McLeansboro formation of Illinois, and two years later Schopf (1939) described *M. distelica* from Herrin Coal No. 6 of the same formation.

The reason why paleobotanists have so long failed to recognize the remains of *Medullosa* in the Carboniferous of North America is probably to be found in the structural peculiarities of the genus. The stems contained so much parenchyma tissue that they disintegrated even under conditions under which other stems might have been well preserved. Consequently, a partially preserved medullosan stem would readily lose its identity, and so might easily be overlooked. Another plausible explanation for the tardy discovery of this genus is that the flora of North American coal balls, in which the remains of *Medullosa* are doubtless best preserved, is still inadequately known, since its study has only recently begun.

The presence of *Medullosa* in the McLeansboro group, near the top of the Pennsylvanian system in Illinois, supplies a new link in the geological history of the genus. The species here described is undoubtedly transitional between those from the Permian of Europe and those from the Lower Coal Measures of England.

The species of *Medullosa* described here was named in honor

of the late Professor A. C. Noé, of the University of Chicago, who discovered and first studied the coal balls of Illinois and who, under the auspices of the Illinois State Geological Survey, collected the material.

ACKNOWLEDGMENTS

THE GENUS *MEDULLOSA*

Cotta founded the genus *Medullosa* (see his description below) on a series of Carboniferous and Permian stems that culminate and disappear in the Permian period. These stems were variable in size and unbranched, and apparently were always surrounded by sheathing leaf bases that supported large petioles.

Internally the stem exhibits abundant parenchymatous tissue, in which are commonly imbedded two or more irregular steles. These steles consist of primary xylem mixed with parenchyma surrounded by secondary wood. In fact, each stele closely resembles the single stele of the genus *Heterangium*.

The combination of polystely and secondary wood is one of the outstanding features of *Medullosa* and distinguishes it from all known living plants.

The original description of *Medullosa* follows:

Geschlechts-Character.

Der horizontale Durchschnitt des Stammes ist am Umfange radial gestreift; die Streifen stehen rechtwinklich auf beiden Seiten einer der Peripherie parallelen Linie; die Mitte des Stammes besteht aus verschiedenartigen parallelen Gefässbündeln, welche entweder dicht beisammen oder entfernt von einander stehen.

Abstammung.

Wie die ganze Familie, so ist auch dieses Geschlecht noch von Niemand beschrieben worden, und nur in Wlch. findet man P. III. ξ Fig. 1 die Abbildung eines ähnlichen versteinerten Holzes, welches der Verfasser jenes Werkes für einen Buchenast hielt, dessen Kern ausgefault sey (vergl. Wlch. p. 47). Die radialen Streifen am Umfange und der dunkle Raum in der Mitte lassen mich glauben, dass das abgebildete Exemplar zu diesem Geschlecht gehört habe. Die in dieses Geschlecht gehörigen Versteinerungen stammen weder von Buchenholz noch von irgend einer andern bei uns gewöhnlichen Holzart ab, so viel ist gewiss; was es jedoch für Pflanzen gewesen seyn, die uns diese sonderbaren fossilen Reste hinterlassen haben, darüber habe ich weder in botanischen Werken, noch auch von den darüber befragten Botanikern Auskunft erhalten können.

Mikroskopische Untersuchungen zeigen, dass jene radialen Streifen durch Markstrahlen hervorgebracht werden, die den Spiegelfasern der gemeinen Holzarten fast ganz entsprechen; ihre Stellung zum Ganzen aber ist oft eine durchaus verschiedene von der in allen bekannten Holzarten, so ist z. B. die Kreislinie, auf welcher sie zu beiden Seiten rechtwinklich stehen, zuweilen unterbrochen, und dann stehen sie radial um ihre Endpunkte herum, so dass die einzelnen Theile dieser Linie, welche der Peripherie parallel im Stamme liegen, einzelne strahlige Körper bilden.

MEDULLOSA NOEI STEIDTMANN, 1937

Stem large, 20 cm. or more in diameter; vascular system generally composed of three separate protosteles measuring as much as 2 by 3.5. cm., with the secondary wood of each stele most abundantly developed toward the center of the stem; central primary region of each stele consisting of parenchyma, tracheids, and numerous tracheid bundles; a broad internal periderm zone separating the outer from the inner cortical region; other peridermlike strands present in the central fundamental parenchyma areas of the stem, and in anomalous situations within the steles themselves; large decurrent leaf bases present on the stem about 2 cm. thick at their greatest development, containing numerous centripetal collateral leaf-trace bundles with heavy sclerotic caps at the xylem end as seen in cross section; leaf-trace bundles at the junction of the cortex and leaf base generally oriented in opposite directions; a zone of sclerenchyma also separating these two areas from each other.

Locality. — Calhoun Mine, Richland County, Illinois.

Horizon. — Calhoun Coal, upper part of the McLeansboro group of the Pennsylvanian of Illinois.

Type number. — 1653, Museum of Paleontology, University of Michigan, Ann Arbor, Michigan.

GENERAL DESCRIPTION

The stem of *Medullosa Noei* that is considered here was found partially exposed and parallel to the long diameter of a somewhat oval coal ball measuring about 10 by 25 cm. A section of the ball (Pl. I, Fig. 1) shows more than one third of the moderately compressed transverse section of the stem, which is enough to reveal its salient features. In the thickest portion almost 15 cm. of the length can be followed through the calcified matrix. The stem is subtended by a particularly large leaf base (Pl. I, Fig. 1), which has lost most of the epidermal tissue as well as portions of the hypodermis. A longitudinal fracture (Pl. I, Figs. 2–3) shows the attachment of this leaf base to the stem. To judge from the arc subtended by this leaf base, the stem was probably not less than 20 cm. in diameter.

Somewhat apart from but almost parallel to the stem is a large petiole of the *Myeloxylon* type (Pl. I, Fig. 3). There are several smaller petioles of the same type intimately associated with the larger one, and they may possibly be branches of it. The close association of and the resemblance between the structures of the leaf base and the large petiole, as well as the evidence of the English forms, leave no question of generic relationship. Since these petioles have never been found actually attached to the parent stem, taxonomic precision requires that they be classified under the organ genus *Myeloxylon*.

The arrangement of leaf bases on the stem of the holotype is indeterminable. A later study of new material indicates a spiral phyllotaxy, as in other medullosan species.

Although the holotype specimen is a mere fragment of the complete trunk, the tissue preservation is good, and anatomical studies can be carried on without difficulty. Three original tissue systems are present: (1) the cortex, including the leaf bases; (2) the common ground parenchyma enclosing the steles;

and (3) the steles themselves. The periderm, which in this species is ubiquitous and irregular, has developed secondarily throughout all three of the original tissue systems.

The leaf bases are considered the outer boundary of the stem and are delimited from the cortical tissue by decurrent sclerenchyma zones (Pl. I, Fig. 1). Although present, the inner periderm is not conspicuous on the inner side of the cortex (Pl. III, Fig. 1). The inner cortical tissue, which merges with the common ground tissue, fills up the remainder of the stem that confines the steles. This ground tissue is poorly preserved, as is commonly true of parenchymatous tissues. It has been badly crushed and disorganized, and a few fragments of foreign material seem to have been pressed into it. The steles, of which apparently there are three, consist of phloem, secondary xylem, and primary xylem zones. That the number of steles is not necessarily constant throughout the length of the stem is shown by the fact that at one point in the stem there are two steles which either have just fused or else have just separated (Pl. II, Figs. 1–3).

The large leaf bases with their heavy petioles must have supported enormous leaves. Plants with such an abundance of ground tissue and a relatively small amount of mechanical tissue could not have grown to any appreciable height and supported leaves of the size indicated by the petiolar remains. It would be more logical to believe that they resembled plants like our living cycads.

<div align="center">ANATOMICAL FEATURES</div>

<div align="center">*Vascular System*</div>

The description of the steles is based primarily on the structure of one complete stele (Pl. I, Fig. 1) and of fragments of two others in the original type specimen. Additional information has been gained from the study of other material found more recently. The size of the steles varies, and there may be variations at different levels of a single stele (Pl. II, Figs. 1–3). At one plane a complete stele measures 2 by 3.5 cm.; at another, 1.8 by 6 cm. It is tangentially elongated with respect to the stem as a whole, and is somewhat reminiscent of the "snake rings" of *Medullosa*

Leuckarti (Pl. I, Fig. 1). The greater thickness of the wood is oriented toward the center of the stem. The shape of the stele, as shown in the holotype specimen, may not be quite natural, but may be slightly altered by compression. This is suggested by the crushed and faulted areas of secondary wood, a characteristic that would be expected in a manoxylic stele. Some of the irregularities are due to the formation of periderm within the secondary xylem when the plant was still alive (Pl. IV, Fig. 1). Such development might be the cause of considerable distortion.

A single stele, in cross section, consists of a central elongated area of primary xylem surrounded by secondary wood, which is enclosed by a narrow layer of phloem (Pl. III, Fig. 1). The primary xylem is complex in appearance and consists of tracheids, tracheid bundles such as those described by Rudolph (1922) for *Medullosa Leuckarti*, and conjunctive parenchyma. The parenchyma tissue is poorly preserved, but the character of the individual cells is still discernible in many places (Pl. III, Fig. 1). The position of the protoxylem has not been determined in the holotype or in any other specimen definitely assigned to *Medullosa Noei*. Schopf's statement (1939) that the protoxylem of *M. Noei* is mesarch is based upon a different species (No. 114 of the Illinois State Geological Survey collection) and not on any direct evidence secured from the material described here. It is probable that the protoxylem is mesarch, but its position cannot be demonstrated. The difficulty of locating spiral thickenings has prevented the author from making a definite analysis here just as it has hindered other workers from arriving at positive conclusions in regard to some of the other species of *Medullosa*. The tracheids of the primary xylem are multiseriately pitted and highly variable in size, ranging from 20 to 130 microns in diameter (Pl. IX, Fig. 3). Longitudinally these elements are irregular in form as well as in course, some apparently following a slightly oblique direction across the primary zone of the stele.

Tracheid bundles similar to those described by Rudolph (1922) in the primary xylem of *M. stellata* and *M. Leuckarti* are common and numerous in the primary xylem of *M. Noei* (Pl. IV, Fig. 2). Bundles of this type are somewhat concentric groups of tracheids,

and in this specimen are frequently surrounded by a zone of parenchymatous tissue that in every respect resembles periderm. Rudolph found tracheid bundles running horizontally, as well as vertically, throughout the primary xylem in most of the Permian medullosan species, but in *M. Noei* they do not do so. There is apparently no phloem associated with these structures. With few exceptions the conjunctive parenchyma of the primary wood is crushed in the holotype. The character of this tissue is best illustrated by another specimen in the Illinois State Geological Survey collection. Here the cells exhibit a rather regular rounded shape, and many of them contain secretions. Occasionally there are small secretory canals like those in the cortical region of the stem and leaf bases, but they are not numerous.

Another feature of considerable interest in the primary xylem of the steles of this stem is the presence of well-preserved highly developed tetrarch roots (Pl. V, Fig. 2). Roots of a similar type, but triarch, have been described for *Medullosa anglica,* but no reference is made to their intrastelar origin. Other isolated roots of the tetrarch type have been found in the coal ball containing *M. Noei,* and the structural details of this organ are considered at another point in this paper (p. 146).

The width of the secondary wood of the steles is quite variable. Some of the variation is due to changes during the process of preservation, but most of it is a natural endocentric variation. At its broadest point the complete stele of the original specimen measures more than one centimeter in radial extent (Pl. II, Fig. 3). It is composed of large radially arranged tracheids that measure from 60 to 250 microns in radial diameter and from 35 to 115 microns tangentially. Interspersed between groups consisting of from two to five rows of tracheids are multiseriate rays ranging from two to eight cells wide. In longitudinal section these rays have the appearance of deep layers of parenchyma (Pl. IX, Fig. 2). Andrews (1940) states, in referring to *M. Noei,* "that the rays for the most part are very narrow." This may be true for some of the rays as they approach the phloem, but as these rays extend toward the primary body they become broad. It is not uncommon to find rays twelve or more cells wide. The tracheids of

secondary wood are multiseriately pitted, with as many as twelve rows of bordered pits on the radial walls (Pl. VII, Fig. 2). Seriation of pits is apparently dependent upon the diameter of the elements in which they occur. The pitting is of the araucarian type.

The arrangement of the steles of *Medullosa Noei* is less complex than that of the Permian forms. Most of the latter contain practically solid concentric rings of steles, surrounded by the common ground tissue of the stem, in which there may be numerous small concentric steles or vascular bundles known as "star rings." *Medullosa Leuckarti* Goeppert and Stenzel (1882) is the simplest of these forms (Fig. 3), but even it sometimes manifests an anomalous series of concentric flattened "snake rings."

Medullosa Noei has no star rings. There are patches of tissue in the groundwork of the stem that were originally interpreted as possible forerunners of the star rings (Pl. II, Fig. 1), but further investigation has shown them to be large concentric strands of the ever-present periderm that have invaded the central ground tissue and formed loops around clusters of parenchyma cells. In some transverse sections loops appear to have become isolated from the original periderm zone. Although the strands superficially resemble star rings, they probably bear no relation to them.

In the arrangement of steles the North American species described here resembles *Medullosa anglica* Scott (1899), *M. pusilla* Scott (1914), and *M. centrofilis* de Fraine (1914). The fact that the stems of the English species are smaller in diameter than that of *M. Noei* may or may not be significant. If the stem branches profusely, size variations would not be significant; if, however, these medullosan stems were short and unbranched, and not especially woody — it is known that they are not — size relationships of the constituent tissues might be considered important criteria. So far as size relations are concerned, *M. Noei* is quite distinct from the English species.

Although *M. Noei* and *M. anglica* are similar in being tristelar, *M. anglica* differs in having small cortical accessory vascular strands, each of which is enclosed in a periderm sheath of its own. This feature has not been observed in *M. Noei*. Rudolph (1922)

found no tracheid bundles in Scott's species, but, as has been pointed out, they are characteristic of the primary wood of *M. Noei.*

Medullosa centrofilis has been distinguished from *M. anglica* on the basis of size and the difference in phyllotaxy, and by the presence of a single small concentric strand, called "star rings" by de Fraine (1912), running longitudinally through the center of the stem. These characteristics also serve to distinguish it from *M. Noei.* An apparently continuous band of periderm in the English *Medullosae,* represented somewhat differently in *M. Noei* and *M. Leuckarti,* may indicate a closer relationship than they are now thought to possess.

Periderm and Ground Tissue

The outstanding characteristic of this stem is the periderm tissue that pervades all tissues and apparently is without bounds. Most conspicuous is the ring of internal periderm that occurs in the inner cortical zone (Pl. I, Fig. 1). It is a wide variable, discontinuous band, often as much as 9 mm. broad; and it is generally uncrushed and well preserved. The cells are essentially isodiametric and are arranged in radial rows that may branch or converge (Pl. VIII, Fig. 2). Apparently the phellogen is external, and hence all the tissues formed from it are equivalent to the phelloderm of modern plants.

In the ground tissue in the center of the stem between the steles and in the inner cortical zone there are often groups of cells that have been completely surrounded by periderm (Pl. II, Fig. 3). There appears to be evidence that in some the ring of periderm from the inner cortex has invaded this central region, surrounding patches of cells in the ground tissue that later become free and separate strands. The same thing happens to the bast fibers; small clusters of these cells have become completely enclosed in a sheath of periderm (Pl. III, Fig. 2).

The leaf traces arise from the primary xylem and at first appear as simple groups of cells, in which tracheids are especially conspicuous (Pl. VII, Fig. 4). However, as soon as they have penetrated the inner cortex on their way to the outside, they in-

variably become surrounded by a thick sheath of periderm-like cells (Pl. X, Fig. 6).

One of the salient features of this stem, as pointed out above, is the presence of tracheid bundles in the primary xylem. Not only are they simple groups of tracheids, but in many of these each group is surrounded by a conspicuous sheath of periderm (Pl. IV, Fig. 2). The periderm forms in the secondary xylem as well as in the primary xylem. Medullary rays in some seem to have become active and to have formed periderm that is intercalated along the rays to stretch the stele in a tangential direction (Pl. IV, Fig. 1): Whenever the cells of portions of the medullary rays have divided they have formed large areas of periderm that have crowded the tracheids of the secondary wood out of their normal position.

There are still other periderm areas in the secondary wood (Pl. V, Fig. 1). They are slightly different from the ray periderm in that all the cells are disposed radially rather than tangentially. The cells are commonly somewhat smaller than the neighboring tracheids, and it appears that the periderm formation had briefly interrupted the growth of the secondary xylem.

Just how much of the periderm development was normal growth for a stem of this type is difficult to determine. The stem was probably an old one, and part of the abundant periderm formation is perhaps a characteristic of its old age. Some of it may be considered callus tissue that developed from parenchymatous cells for the protection of injured areas. The latter supposition may explain its presence in some of the outer regions of the stem, but it would not account for its general abundance in the internal areas.

Morphologically the periderm-like tissue of *Medullosa* is different from the periderm of living plants. In living plants it is the limiting tissue that forms the corky outer bark of woody plants, and suberization prevents the formation of living tissue external to it. It is initiated by a phellogen, the activity of which is mostly confined to the formation of phellem toward the outside of the stem and very little phelloderm toward the inside. The activity of the phellogen is apparently reversed in *Medullosa;* phelloderm

is chiefly produced.   The fact that a large amount of living cortical tissue existed outside the periderm zone of these plants is evidence that no extensive suberization could have occurred.   Arnold (1940), in his description of *Lepidodendron Johnsonii* from the Pennsylvanian of Colorado, mentions an analogous situation for the periderm of that plant.   There is not only an internal periderm, as there is in *Medullosa*, but also an extremely thick periderm, much thicker than in *Medullosa*.

There arises the question of what shall be included under the designation "periderm."   Von Mohl (1845) introduced the term in 1836 as a name for the brownish layer beneath the epidermis of woody plants.   Since then a broader interpretation has been given it.   According to Eames and MacDaniels (1925), the periderm consists of the cork or phellem, the cork cambium or phellogen, and the secondary cortex or phelloderm.   Kisch (1913) discussed the structure of periderm of fossil lycopods in considerable detail and, to judge from the historical portion of her paper, the question remains an open one.   It is evident, however, that the word "periderm," as it is now defined, does not necessarily require tissues to be suberized.   Consequently there should be no objection to its use in connection with *Medullosa*, even though the main body of the tissue remains unsuberized and consists morphologically of secondary cortex or phelloderm.

Although most of the cells of the periderm are comparatively thin-walled, it is probably better preserved and less distorted than any other tissues.   A possible explanation for its preservation may be that it was one of the last tissues formed just before petrifaction.   If that is so, the process of growth of the periderm itself caused distortion of other tissues.   Another explanation for the excellent preservation that is often evident in tissues composed of thin-walled cells is the greater permeability of such cells to petrifying solutions.   The lumina of the thin-walled cells became filled more quickly and as a result did not crush so badly as the less permeable thick-walled cells.   There is no positive evidence that the preservation of the tissue was brought about in this manner, but it is possible that it was, at least in part.

The function of periderm is unknown.   Because of its abun-

dance it might be thought to have contributed to the mechanical support of the plant, but this is doubtful. Another possibility is that it may have been used for the purpose of food storage. Since it can be considered a secondary cortical tissue and since such tissues have the rôle of storage, it is possible that the phelloderm acted in that capacity. However, most of the cells of this tissue are transparent and devoid of any contents such as are present in some other types of parenchymatous tissue. It surely did not materially interfere with the radial conduction of food and food materials because most of the living cortical tissues were external to it.

The cortical tissue outside the periderm is parenchymatous and contains secretory canals, patches of sclerotic cells, and many collateral leaf traces (Pl. I, Fig. 1). The inner boundary of the leaf base can be recognized by the internal band of sclerenchyma, the absence of leaf-trace bundles in the sclerenchyma zones, and the presence of numerous secretory canals. Another characteristic by which this boundary may be recognized is the orientation of the leaf-trace bundles in the adjacent areas (Pl. X, Fig. 6). In the cortex, just outside the band of periderm, the phloem of the traces is oriented toward the outside of the stem, but in the region of the adjacent leaf base the position is just reversed. The latter condition is only natural, for in the vascular bundles of the leaf base, as well as in those of *Myeloxylon* petioles, the phloem generally is toward the outside, particularly in the bundles of the periphery.

The vascular bundles of the cortex resemble those of *Myeloxylon* (Fig. 1; Pls. VI–VII) and are described in greater detail in connection with that genus (p. 154). An outstanding difference in these bundles is, however, the presence of pronounced sclerenchyma caps around the xylem. They must have contributed considerably to the mechanical support of the plant.

In addition to the outer cortex, there is another cortical layer just inside the periderm zone (Pl. III, Fig. 1), which is like the outer cortex but it is less well preserved; the cells are usually crushed, although occasional secretory canals and patches of sclerotic cells can be distinguished. In places there is evidence
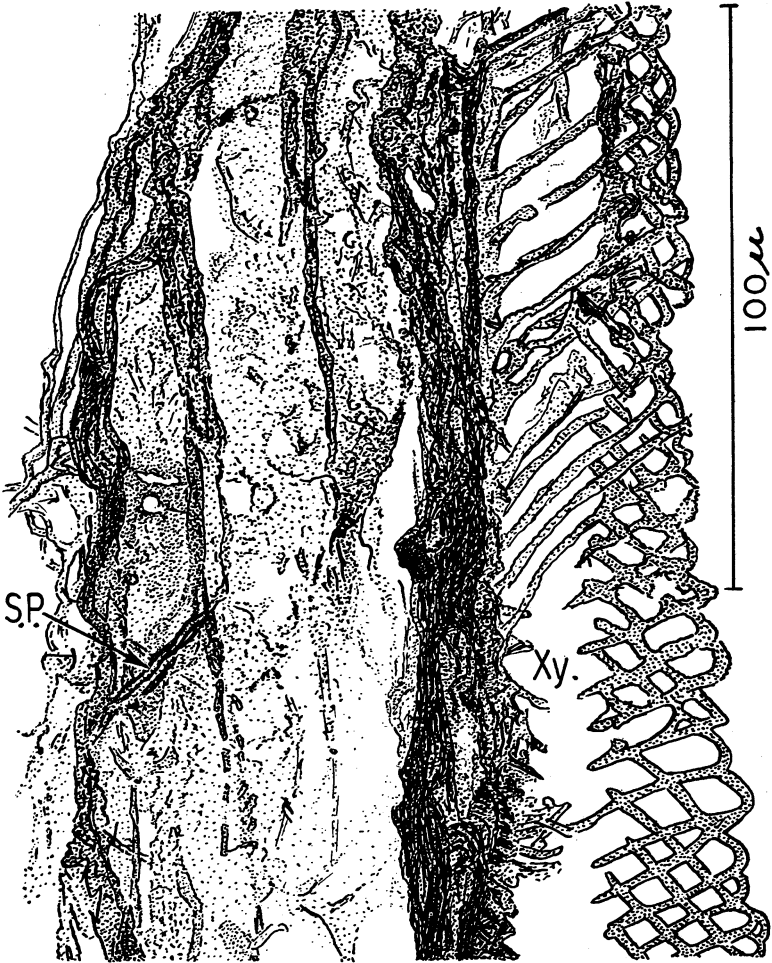
FIG. 1.   *Myeloxylon zonatum* (the petiole associated with *Medullosa Noei*). Longitudinal section through the phloem, showing sieve plates? Some of the longitudinal walls appear more or less perforated.   × 760

Abbreviations: S.P., sieve plates; Xy., xylem

of secondary cortical activity, and the cells that have been formed in this manner resemble periderm and are unusually well preserved.

The common ground tissue of the stem, as has been pointed out, is often poorly preserved. In some areas it is obliterated, and foreign materials have been pressed into its place. The occasionally well-preserved cells are rounded, and the walls are slightly heavier than those of typical parenchyma. Throughout the ground parenchyma may be found remains of secretory canals of the kind that are abundant in other parts of the plant (Pl. VIII, Fig. 3). The "resin rodlets" contained in these canals are smaller and more numerous than the characteristic large ones in the cortex and the leaf base. The periderm bundles in the ground tissue are evidently loops cut from the outer band of periderm that invaded this area. These have been described and need no further discussion.

Leaf Bases

An extremely large leaf base is present on the holotype of *Medullosa Noei* (Pl. I, Fig. 1). It measures 20 cm. in width and varies in thickness from 1 to 2 cm. This broad leaf base probably represents the lower extremity of a decurrent petiole which higher up becomes abruptly smaller. No isolated *Myeloxyla* have been found that are so large. Although the outer surface of this leaf base is mostly absent, it is evident from occasional remnants that there were an epidermal layer and a hypodermal layer of the sparganum type. The latter, in some respects, resembles collenchyma tissue. In it are patches of sclerotic cells such as often occur with secretory elements (Pl. VIII, Fig. 1). The remainder of the tissue of the leaf base is composed of parenchyma cells that are quite compactly arranged. The secretory elements are scattered abundantly throughout.

The vascular bundles of the leaf base are also of the collateral type and resemble those of the cortex, with the exception that they lack the conspicuous sclerotic caps and consequently are much less prominent (Pl. X, Fig. 6).

The secretory ducts, or mucilage canals, as they have been called, are numerous and are characteristic of the leaf base and

the associated petioles (Pl. VII, Fig. 3). They are generally sur-
rounded by one or more rows of epithelial cells and contain the
dark opaque contents known as "resin rodlets." These contents
are undoubtedly the carbonized remains of the organic substances
originally secreted (Pl. II, Fig. 7).

Whether the arrangement of the leaves on the stem was spiral
or whorled can only be conjectured. In *Medullosa Leuckarti*,
which most closely approaches *M. Noei* in size, the leaf bases are
generally not preserved. However, the relation of the stelar
complex of the stem (including the individual steles and the
ground tissue) to this leaf base is somewhat similar to the relation
of the steles and leaf bases in other species in which this part of
the plant is known, and the phyllotaxy is probably a simple
spiral one, as it is in *M. anglica*.

Roots

The roots of *Medullosa Noei* are tetrarch (Pl. II, Fig. 6), with
occasional triarch and pentarch forms. These differences in form
are probably only casual irregularities and of no taxonomic sig-
nificance. The roots that have been found range from less than
1 mm. to 8 mm. in diameter, with the smallest ones exhibiting
only primary structure. In transverse section the tetrarch ar-
rangement shows four definite protoxylem points forming the
corners of a four-angled primary xylem mass. In longitudinal sec-
tion the spiral protoxylem elements and the usual bordered pitting
of the metaxylem are distinguishable.

The secondary xylem developed opposite the metaxylem, and
consequently the four "arms" of the secondary xylem are sep-
arated from one another by broad wedge-shaped medullary rays
that extend outward from the protoxylem points (Pl. II, Fig. 6).
The nature of the tissue in the rays cannot be determined, since
it has not been well preserved and other materials have replaced
it. The secondary xylem elements are arranged in radial rows,
usually separated from each other by uniseriate rays. The tra-
cheids are rather regularly aligned tangentially. These elements
are similar to those of the stem in both size and pitting, but the
walls are not so heavy in the cells of the root wood as in the stem

wood. The thickness in cell wall structure, according to Eames and MacDaniels (1925), is one of the principal differences between root wood and stem wood of the same plant.

The cells of the cambium and phloem are decayed beyond recognition. Occasionally, at the ends of the secondary xylem arms remains of crushed phloem can be identified. In such remains there can also be recognized remnants of secretory canals, or their contents, which are characteristic of other portions of this plant.

The periderm of the roots is very prominent (Pl. II, Fig. 6), just as it is in the stem. Evidently it appeared at an early stage of development, for some of the extremely small roots have a definite sheath of this tissue. Apparently the development of periderm may have become arrested because in some of the larger roots it is no more extensive than it is in some of the smaller ones. Where it is present it is well preserved, except in small areas in which it seems to have been obliterated, probably by decay, around a broad poorly preserved cortical region. From all appearances the phellogen is endogenous in origin, and the periderm is formed centrifugally, in contrast to the centripetally formed periderm of the stem.

The most unusual feature of these roots is their connection with the stem. As stated previously, the central portion of each stele consists of primary xylem, conjunctive parenchyma, and tracheid bundles. In addition, root sections may be found in the central portion of each stele (Pl. II, Figs. 3, 5). In some of the material a fairly definite connection may be observed between the primary xylem of the stem and that of the root (Pl. II, Fig. 4). Furthermore, from evidence found in other sections it appears that the roots grew longitudinally through the primary stelar region for some distance and developed considerable secondary wood before emerging through the xylem of the stele along a diagonal course (Pl. V, Fig. 2).

In explaining the presence of roots within the steles the possibility must be considered of their having penetrated from the outside, just as *Stigmaria* roots are often found which have behaved in this way. In *Medullosa Noei* this seems improbable because in

two of the steles (one shown in Pl. II, Fig. 3) the roots in the primary portion of the stem can be seen passing outward through the wide rays of the wood without any disruption of the tissues. The relation of the root and stem tissue appears perfectly normal. Moreover, the periderm of the root is less well developed within the primary wood than on the outside.

The path taken by the roots of *Medullosa Noei* does not seem particularly anomalous when compared to what is known about the course of roots in other fossils or in some modern lycopods. A possible analogy is found in *Heterangium Grievii*, in which Benson (1933) found diarch roots following a course parallel to the stele through the cortex of the stem.   Adventitious roots take a similar path in *Psaronius* if the outer tissues through which the roots grow can be considered cortical.   In our modern lycopods, such as *Lycopodium*, adventitious roots follow a similar longitudinal path through the cortex before emerging.   The very fact that some of the roots of *M. Noei* originated in the stem, and consequently are adventitious, should be cause for believing them to have grown downward through some tissues of the stem, at least for short distances.

Associated Alethopteroid Leaves

Sections of alethopteroid pinnules associated with the medullosan material are abundant.   Naturally, since there are no visible connections their relationship must remain an open question. It is possible that the pinnules are merely the remains of other sterile fronds, but on the basis of general morphology and structural characteristics it seems fairly well established that they are the leaves of a medullosan type.   In fact, Grand'Eury (1877) pointed out the structural similarity between *Myeloxylon* and the petioles of *Alethopteris*, *Neuropteris*, and *Odenopteris*.

In most respects the structure of the pinnules resembles the medullosan foliage figured by Scott (1923).   The median nerve is large and prominent on the lower surface, and the margin of the pinnule is somewhat revolute (Pl. IX, Fig. 1).   The internal structure of the pinnule is comparatively simple and is like that of *Medullosa distelica* Schopf (1939).   The top of the leaf is de-

void of stomatal openings, but the lower surface appears to be well equipped with them, a condition not unlike that of our meso-phytic plants. The upper epidermis consists of cells that are flattened in the plane of the leaf and cover a layer of somewhat larger hypodermal cells, which are well preserved. The palisade parenchyma consists of compact vertically elongated cells to which is attached a second row of similar but more loosely ar-ranged cells. The spongy parenchyma is also of the usual type, that is, irregular cells separated by large intercellular spaces. Even though the tissues are well preserved there is no evidence of the preservation of chloroplasts within the cells.

The midrib of the pinnules contains a vascular bundle that is usually divided into two or three strands. It is difficult to find any real line of demarcation between the xylem and the phloem, but from all appearances the arrangement is no different from that in most living plants. The supporting tissue of the vein is also of the usual type, but, in addition, there are generally one or more secretory canals, similar to those found in the leaf bases of *Medullosa Noei* and *Myeloxylon zonatum*. When the midrib of a pinnule is cut transversely the secondary veins are cut longi-tudinally, or strongly on a bias. In *Alethopteris* leaves this is to be expected because the secondary veins leave the midrib at a steep angle, but they traverse the lamina at a wide angle.

A conspicuous external feature of the lower surface of the pinnules is the presence of comparatively large multicellular hairs (Pl. X, Fig. 2) on the veins of the leaves. They are usually badly fragmented owing to their size, but the general structure is still quite evident. Each hair is large at the base and tapers gradually toward its distal end, where it appears to be terminated by a bulbous tip. This tip is commonly detached, but can usually be located somewhere near the fragmented hair. The trichomes are about six cells long and one cell in diameter; they originate super-ficially from the epidermis over the veins. Although their struc-ture might be considered glandular, no secreted contents have been observed. The hairs somewhat resemble the glandular spines of *Lyginopteris*, but the spines are multicellular in diameter and subepidermal in their origin.

DISCUSSION

Classification of Medullosan Stems

Weber and Sterzel (1896) grouped the various species of *Medullosa* then known into *Formkreise* ("form cycles"). Such a form cycle consisted of a single species and its variations, which were closely related in their general and histological structure. They recognized four groups, of which the types were as follows: (1) *Medullosa stellata* Cotta; (2) *M. porosa* Cotta; (3) *M. Solmsii* Schenck; and (4) *M. Leuckarti* Goepp. and Stenzel (Solms-Laubach, 1897).

In *Medullosa stellata* (Fig. 2) the outer steles form a more or less continuous ring of wood. The star rings are variable in number but uniform in structure. The *M. porosa* type (Fig. 5) does not differ greatly in the general structure of the stelar zone, but the star rings are often completely surrounded by secondary xylem, especially those farthest from the center. Cotta's original specimen is the only one of this type known. In *M. Solmsii* (Fig. 4) the steles are numerous, usually being in the form of plates and arranged in two concentric circles. *M. Leuckarti* (Fig. 3) differs considerably from the others. The steles are numerous, large, sinuous, and so irregular in cross section that they have been referred to as "snake rings." The star rings may be present, but are usually few.

De Fraine (1914) added a fifth form cycle, using *Medullosa anglica* (Fig. 6) as the type specimen, which Scott described after Weber and Sterzel had made their groupings. In this cycle she placed *M. pusilla* Scott (1914) and her own *M. centrofilis*, all of which are characterized by their comparative simplicity of structure, absence of star rings (except for a single one in the center of *M. centrofilis*), and the presence of secretory canals. In many respects *M. Noei* resembles the members of the form cycle created by de Fraine, but its immediate relationship is still a little uncertain. The rather irregular steles are somewhat reminiscent of *M. Leuckarti*, as is the general size of the stem. They are similar in that they are very large stems as compared with those of the *anglica* group. If these are the remains of simple unbranched
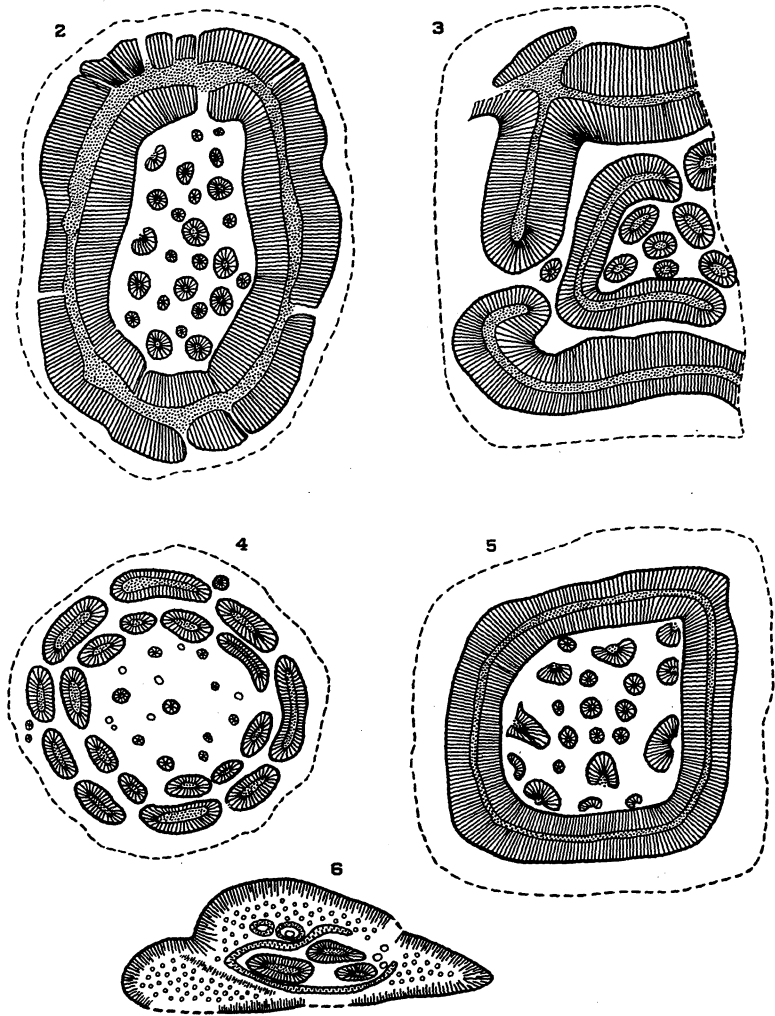
FIG. 2. *Medullosa stellata* Cotta   FIG. 3. *M. Leuckarti* Goepp. and Stenzel
FIG. 4. *M. Solmsii* Schenck   FIG. 5. *M. Porosa* Cotta
FIG. 6. *M. anglica* Scott

(These figures were used by Weber and Sterzel and by de Fraine as repre-
sentative of the various "form cycles.")

stems, their size is probably an important characteristic. No large stems have ever been described from the English Coal Measures, which may indicate that the Medullosae of the Lanarkian age were of a more slender type.

The horizons at which *M. Noei* and *M. Leuckarti* occur are near each other in age. It may be, then, that other specimens which have been found in the Calhoun horizon and which resemble *M. Noei* should be placed in the same group with *M. Leuckarti*.

In a recent paper Schopf (1939) suggested that *M. distelica* and the English species be given a formal taxonomic status and be assigned the subgenus name *Anglorota*. If this is accepted, as it should be for good taxonomic procedure, it might be well to introduce subgeneric names, rather than specific ones, for the other form cycles. Whatever procedure is followed, it should establish taxonomic regularity for the entire group.

As to the exact position of *M. Noei*, little more can be said. That it belongs between the English Coal Measure forms and the Permian forms is evident. De Fraine (1914) considers the presence of a single star ring in *M. centrofilis* important enough to foreshadow the Permian forms. In that event *M. Noei*, without star rings, would be looked upon as lower in the line of descent, even though it is actually considerably younger. Until more evidence is uncovered on the significance of star rings it may be necessary to place less emphasis on them.

In spite of the knowledge that has been accumulated here and abroad since Cotta first described *Medullosa* in 1832, his statement that "Das Geschlecht *Medullosa* wird mir immer das rätselhafteste unter allen bleiben" is still most significant.

Medullosan Roots

The only roots of *Medullosa* of which there are any records are those of *M. anglica* described by Scott (1899) and similar material described by Arber (1903). Both authors found the roots attached to the stem, and thus their true identity was established. They are usually triarch, and as they increased in size they formed more secondary wood, which was interrupted by three large medullary rays originating from the points of the protoxylem.

An outstanding feature of these roots is the development of a broad layer of periderm, endogenous in origin, which sooner or later decorticated the entire root.

More recently Hoskins (1931) described a number of roots from the McLeansboro group of Illinois. Some of them are similar in structure to those described by Arber and Scott; consequently he assigned them to *Medullosa*. Associated with this material were other unattached tetrarch roots resembling those of *Medullosa* in many respects. He referred to them as "cycado-filicinean" and suggested that they might belong to *Medullosa*.

The only other roots to which those of *Medullosa* bear any resemblance are the ones correlated with *Lyginopteris oldhamium*, known as *Kaloxylon Hookeri* (Williamson, 1876; Scott and Williamson, 1896). Here some of the roots are diarch and some are tetrach. This likeness may be insignificant when one takes into consideration the fact that no roots have been observed here that are more than pentarch; in *Kaloxylon* more highly polyarch roots are known. If any significance is to be attached to the slight similarity manifested by the roots of *Medullosa*, *Lyginopteris*, and *Heterangium*, it must be in an indication of an ancient phylogenetic relationship. The similarity certainly does emphasize the uniformity of root structure in the plant kingdom in both living and extinct plants. To judge from the conservative nature of its root structure, coupled with features of stem structure, leaf-trace bundles, and secretory elements, *Medullosa* may have developed through forms similar to *Heterangium* and *Lyginopteris* before it approached the cycads. This is theoretically substantiated by de Fraine's (1912) description and interpretation of the mono-stelic medullosan stem *Sutcliffia*, which is much like *Heterangium*, which she believed to be basic in the evolution of our living cycads. Her theory brings together to some extent the more divergent theories of Scott (1923) and Worsdell (1906).

Because of the observed connection and close association of these tetrach roots with the steles of *Medullosa Noei* they may be interpreted as the adventitious roots of this plant. Hoskin's supposition (1931) that the material was cycadofilicinean, and probably medullosan, seems well supported by the roots considered

here.   The fact that they are present helps to establish an earlier observation that the piece of stem of *Medullosa Noei* may have been the base of the stem of an old plant.

Alethopteroid Leaves

Alethopteroid foliage occurs abundantly wherever the medullosan stems and petioles are present.   Although none of it has been found attached, for a long time there has been a suspicion that it may be the foliage of the *Medullosaceae*.   It has been suggested that the genera *Neuropteris* and *Alethopteris* be excluded from the ferns on the ground that in spite of much research filicinean fructifications have never been found.   Because of this Scott (1923) placed these genera, with others, in the Neuropterideae.   The general external features of the leaflets agree closely with those of certain pinnules described as belonging to *Myeloxylon Landriotii*, which is taken to represent the leaf stalk of *Medullosa Leuckarti*. Scott had little doubt that *Alethopteris* constituted the foliage of the English *Medullosaceae*.

THE GENUS MYELOXYLON

The organ genus *Myeloxylon* was established for the reception of petioles believed to belong to the *Medullosaceae*.   These petioles are often found isolated and consequently can seldom be assigned to any of the specific stem types.

One petiole of this sort extends throughout the length of the coal ball that also contained the holotype of *Medullosa Noei* (Pl. I, Figs. 1, 3).   Because of the angle at which it rests in respect to the stem it may not have been connected to it.   Structurally it resembles the leaf base of *M. Noei*, but since there are other species in the Calhoun flora to which it might also belong, it is described under a separate name.

The history of our knowledge of *Myeloxylon* petioles is rather interesting, and there has been a great deal of speculation concerning the probable affinities of this organ ever since Cotta (1832) described it.   Among his stems from the Permian of Chemnitz was one specimen, *Medullosa elegans*, that was distinctly different

from the others. Only after many years was it suggested that it might actually be a petiole of a stem of the same genus. In the meantime a great deal of controversy had taken place in regard to the assumed relationships of this peculiar "stem." This led to the proposal of a number of generic names. Corda (1867), in his *Flora der Vorwelt*, described some similar Carboniferous plant remains that he considered palmaceous and introduced the name *Palmacites*. Brongniart (1849) examined Cotta's material and found what he considered doubtful monocotyledonous characteristics and named it *Myeloxylon*, which has been rather generally accepted. Goeppert (1864) reviewed the same material and made the rather significant observation that treelike characters of ferns, gymnosperms, and monocots were present and suggested that the name be changed to *Stenzelia*. Renault (1876) and other prominent workers of that time also studied the material and considered its structure fernlike, especially marattiaceous, and referred it to the ferns under the generic name *Myelopteris*. Schenck (1882) worked over much of the material upon which the various conclusions had been based and stated that there was no reason for discarding the name *Myeloxylon;* but added that, if the name was to be changed, Goeppert's *Stenzelia* would need to be given priority. Somewhat later Solms-Laubach (1891) suggested that *Myeloxylon* might be the petiole of *Medullosa*.

The first North American petiole of this type was described by Penhallow (1897) under the name *Myelopteris topekensis*. This specimen, which was obtained from the Pennsylvanian of Kansas, was so poorly preserved that much of the detail had been lost. Although Penhallow admitted that the vascular bundles, with their exarch protoxylem, were cycad-like, on the evidence of the secretory canals he preferred to believe that this petiole was closely related to the ferns, probably to something like the marattiaceous species *Angiopteris evecta*.

Since the discovery of coal balls in this country many petioles of this type have been found. Evidently the fragments of petioles were easily preserved in the calcareous nodules, in which they are abundant. Because of their excellent preservation precisely defined species of *Myeloxylon* may later prove to be of some value

to stratigraphic paleontologists. In the coal ball that contained *Medullosa Noei* and in associated coal balls there were many smaller petioles. In some the structure varies from that described here, possibly because of differences in size and the position on the plant. Some are certainly species that are different from *Myeloxylon zonatum* described below and represent other members of the *Medullosaceae*.

MYELOXYLON ZONATUM, SP. NOV.

DIAGNOSIS

Petiole large, with a single row of epidermal cells under which there is a region of small hypodermal cells with equally thickened walls; extending into this region is a zone of numerous irregular tangentially elongated patches of sclerotic cells often turned somewhat obliquely; a definite ring of vascular bundles bounds the inner surface of the sclerotic layer, and immediately within this is a row of large secretory canals, each of which is subtended by one or more patches of sclerotic cells; ground tissue composed of compactly arranged parenchyma cells in which are scattered the closed collateral vascular bundles and more secretory canals without sclerotic patches. Locality, horizon, and type number are the same as those of *Medullosa Noei* since both species occur in the same coal ball.

The largest petiole assigned to *Myeloxylon zonatum* measures 2.1 by 5.2 cm. in diameter and extends the entire length of the coal ball (a distance of 25 cm.). Since it lies in a plane slightly different from that of the stem and is unattached, the identity of the two organs cannot be demonstrated, but the close proximity and the similarity in structure with the attached leaf bases constitute strong evidence that the two belong together. The tissues of this large specimen are well preserved, as are those of several smaller associated petioles.

The epidermis, most of which has been sloughed off on the side where it was not surrounded by the matrix of the coal ball (Pl. X, Fig. 1), consists of a single row of rectangular cells. The outer wall of each cell is convex, and each cell is about three times the

size of the adjacent hypodermal cells. This hypodermal tissue is composed of small cells with heavy walls. On its inner side there are numerous irregularly shaped tangentially elongated patches of sclerotic cells (Pl. X, Fig. 3). They are rather asymmetrical groups and often assume a somewhat oblique position. The more irregular outline of these patches tends to distinguish them from the strands of *Myeloxylon Landriotii* and *M. radiatum*.

A rather definite ring of vascular bundles bounds the inner surface of the hypodermal layer of sclerotic strands, and immediately within it is a ring of secretory canals (Pl. X, Fig. 3), each subtended by sclerotic tissue. (This arrangement of structures in the periphery of the petiole suggested the specific name.) In longitudinal section these strands show as long thick-walled fibers. Throughout the central portion of the petiole they are lacking, except where the xylem of the vascular bundles is reinforced by bundle sheaths of similar cells. To reiterate a statement made earlier, the sclerotic accompaniment of bundles of the petiole is considerably thinner than are the caps that accompany the marginal ducts or the vascular bundles in the stem cortex. The sclerotic strands near the periphery of the petiole undoubtedly furnished the chief support for an enormous leaf and a leaf stalk.

The secretory structures are most characteristic of the petioles (Pl. X, Figs. 3–5). It has been mentioned before that they are present throughout the entire leaf base and petiole, in the ground tissue as well as in the subepidermal supporting tissues, although in the latter they are more numerous and of smaller diameter. Each duct is surrounded by one or more definite rows of epithelial cells that are elongated radially in the duct, or by simple cells differentiated from the surrounding ground tissue cells. The canals may range from 60 to 210 microns in diameter, the majority of them approaching the larger size. They may or may not have a resinous content; often they contain nothing but a clear mineral infiltration. Other canals are filled with a black carbonaceous substance. Frequently the content may take on the reddish-brown appearance of resin. Longitudinally the ducts are quite straight, but their length is undetermined (Pl. II, Fig. 7).

No evidence of branching has been observed.   Occasional structures that resemble septations are undoubtedly due to shrinkage and to the crystallization of the mineral contents.

In addition to the secretory ducts there are scattered individual cells in the ground tissue that are filled with dark homogeneous matter or contain globular inclusions.   Whether these are artifacts or stored food bodies has not been determined.

The ground tissue of the petiole is composed of parenchyma cells more or less compactly arranged and with rather inconspicuous intercellular spaces (Pl. X, Fig. 3).   Throughout the groundwork the compression of the cells produces the appearance of a network.   This condition may be due to pressure before and during fossilization and, according to Seward (1893; 1917), is characteristic of *Myeloxylon* (Pl. X, Fig. 5).   Cotta (1832) misinterpreted this peculiar appearance of cell compression as definite vascular structure and described it as "Gefässbündeln, welche 2 bis 5 kleinere enthalten."

The closed collateral bundles, similar to those that have been mentioned in the description of the cortex and the leaf base, are scattered about the center of the petiole with no apparent regularity.   This lack of arrangement of the bundles and their structure are suggestive of the monocotyledons and explain why material of this type has been misinterpreted at various times.   The preservation of some of the bundles in this material is excellent. Even the phloem, which ordinarily has disintegrated, is found intact (Pl. VI, Fig. 1).   The arrangement of the bundles is such that the phloem is commonly oriented toward the periphery of the petiole and the xylem in the opposite direction.   Petiolar bundle sheaths are always present, but are quite thin and consequently did not contribute much toward strengthening the petiole. In the leaf base and the cortex of *Medullosa Noei* the sclerous caps are much more conspicuous than in *Myeloxylon zonatum* and are developed in the same way as those accompanying the marginal ducts of the petiole.   The sheath does not completely surround the bundles, but is found chiefly as a layer one or two cells thick around the xylem end of the bundle.   The cells of the ground tissue next to the vascular bundles are small and constitute

a parenchymatous addition to the sheath, which is more strongly developed in the vicinity of the phloem.

The xylem portion of the vascular bundles is usually somewhat larger than the phloem. Since the bundles are collateral and exarch the protoxylem is between the phloem and the metaxylem. The position of the protophloem is more doubtful, but there is an area of crushed cells near the outer edge of the phloem, which resembles that tissue (Pl. VI, Fig. 1). The phloem consists of elongated cells, which may be sieve tubes, and interspersed small adjacent cells, which may be companion cells. The sieve tubes and companion cells are well preserved, but sieve plates cannot be observed with any degree of certainty. There are oblique cross walls that appear to have "sieve-plate" markings in them (Fig. 1, p. 144). These may simply be artifacts produced during the process of petrifaction.

Longitudinally the xylem elements show spiral scalariform and reticulately pitted sculpturing (Pl. VI, Fig. 2; Pl. VII, Fig. 1). The spiral elements are adjacent to the phloem which indicates the pattern of the protoxylem. Adjacent to these are the reticulately pitted tracheids; the scalariform elements occur farthest from the phloem. The scalariform elements usually have the larger diameter and the spiral ones the smaller.

<div align="center">DISCUSSION</div>

A comparison of *Myeloxylon zonatum* with *Myelopteris topekensis* on the basis of Penhallow's description indicates that the two species may have been somewhat similar in structure. Our present ignorance of the structural details of *M. topekensis* is due entirely to the limitations of Penhallow's material. Because of this perhaps it should never have been specifically identified.

Another North American petiole, *Myeloxylon missouriensis*, described by Arnold and Steidtmann (1937), also agrees in general with *M. zonatum*, but the structural details are decidedly different. In the former the sclerenchyma strands are smaller and more numerous, and often form a double row. Frequently there are gum canals present in these sclerenchyma strands. It does not contain the definite zone of vascular bundles and canals

inside the sclerenchyma zone, as does *M. zonatum*, a lack which is probably one of the outstanding differences between them.

Myeloxylon zonatum is also distinct from other species so far described. *M. Landriotii* Renault (1876) is considered the petiole of *Medullosa Leuckarti*, but how close a correlation exists between the two is quite unknown. *Myeloxylon Landriottii* is characterized by peripheral sclerotic patches in two or three concentric rows, the patches being reniform or circular. *M. zonatum* differs considerably from it.

Scott (1923) states that the petioles of *Medullosa anglica* are also of the *Myeloxylon Landriotii* type, which may indicate that *M. Landriotii* is correlative with at least two very distinct species of *Medullosa*. He did not give, however, specific descriptions of isolated petioles found in the Lanarkian coal balls, and if such a study were undertaken the petioles of the two species would probably prove to be quite distinct. This belief is based upon the difference in the age of the material and not upon anatomical details.

Myeloxylon radiatum Ren., which is the original *Medullosa elegans* of Cotta, is characterized by a peripheral layer of radially elongated sclerotic strands. Originally the species was described as having two concentric rows of these strands, and Zeiller (1890) contended that it should be regarded as specifically different. Weber and Sterzel (1896) however, pointed out that what Cotta had thought were two concentric rows of radiating strands were in reality only displaced pieces of the peripheral tissue. There are no definitely radiating sclerotic strands in *M. zonatum* comparable to those described above.

The only species, then, to which *Myeloxylon zonatum* bears any resemblance is *Myelopteris topekensis*. The specimen of *M. topekensis* is so poorly preserved that it cannot be adequately characterized, and hence its relationship to *M. zonatum* is problematical. The fact that *M. zonatum* is closely associated with *Medullosa Noei* and that there are many points of resemblance in structural details with the leaf bases of this medullosan stem indicates the probable correlation of *Myeloxylon zonatum* and *Medullosa Noei* at the Calhoun horizon.

ROTODONTIOSPERMUM ILLINOENSE

A few seeds of *Rotodontiospermum illinoense* recently described by Arnold and Steidtmann (1937) are associated with *Medullosa Noei*. They are 3.5 cm. in length and 2 cm. in diameter and are
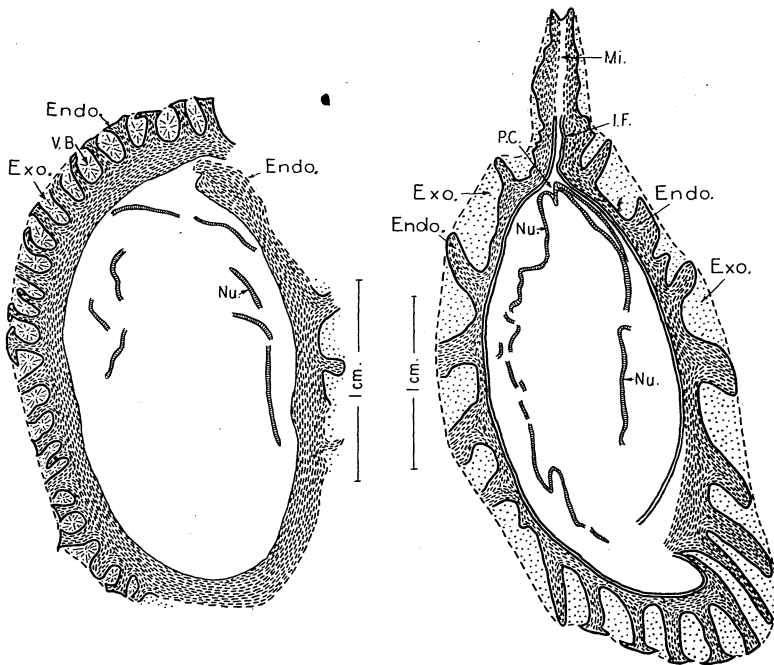

FIG. 7.   Seed of *Rotodontiospermum illinoense*

A. Transverse section. $\times 2\frac{3}{5}$ B. Longitudinal section. $\times 2\frac{1}{5}$

Abbreviations: Endo., endotesta; Exo., exotesta; I.F., inner flesh; Mi., micropyle; Nu., nucellus; P.C., pollen chamber; V.B., vascular bundle

well preserved, at least in part.   They are more or less oval and are constricted into an elongated beak at the micropylar end (Fig. 7).   The seed coat is differentiated into two layers, an outer exotesta that was probably spongy, and an inner endotesta, that, from all appearances, had a leathery, fibrous texture.   The endotesta is deeply cut by longitudinal furrows of equal depth.   The

ridges radiate outward and broaden at the apex to form anchor-like figures as they merge with the exotesta, which covers the entire seed. In the exotesta are vascular strands that alternate with the endotestal ridges as they pass from the base to the apex of the seed.

Inside the endotesta is the "inner flesh" of the seed composed of vertically elongated cells with dark contents. Bordering on this are the remnants of a nucellus. The amount of nucellus still present in different parts of the seed is variable. Along the sides it may only be a few cells thick, but in the region of the micropyle and near the base there are considerable areas of well-preserved nucellus. This may be due to the nature of the preservation or it may be that at the time of preservation the gametophyte of the plant had developed to such an extent that much of the nucellus had naturally been used up. In the nucellus at the base of the seed are well-preserved tracheids of the nucellar vascular strands.

The beak at the micropylar end of the seed, which was absent on the seeds described originally, was found intact on some material discovered more recently. It is 11 mm. long. A portion of the inner flesh is present and extends up the beak for 4 mm.; the remainder shows only the endotesta and the opening through it into which have been pressed the remnants of other plants. At the point where the micropyle opens into the seed there is an indentation into the nucellus that forms a definite pollen chamber. There is no trace of pollen grains or spores in this chamber that might be used as evidence in establishing other affinities.

Except for the comparatively well preserved nucellus, the inner flesh, and a small remnant of the gametophyte, the inner tissue of the seed has disappeared, and the remaining space is filled with mineral material where the entire female gametophyte must once have existed.

In close association with at least one of the seeds are numerous spores of the *Dolerotheca* type. Schopf (1938) found some very fine fructifications of *Dolerotheca* at the Calhoun horizon. There is a possibility that they may be the pollen grains of *Medullosa Noei*, and since they are so abundant in the coal balls a more detailed study may indicate their relationship.

Rotodontiospermum illinoense, which has a double vascular system, is supposedly a member of the Trignocarpales, a group of Paleozoic seeds, North American species of which have been described by Miss Krick (1932). The only genus to which they bear any resemblance is *Trignocarpus,* which has three primary and nine secondary ridges. The fact that *Alethopteris* pinnules are commonly found in association with the seeds is circumstantial evidence that there may be a close relationship between the two genera.

SUMMARY

Medullosa Noei (a stem), leaves, roots, and seeds are described from well-preserved petrifactions obtained from coal balls found in the Calhoun horizon of the Pennsylvanian of Illinois. The stem has three large irregular steles composed of primary and secondary xylem. It is subtended by an enormous decurrent leaf base, which is delimited from the cortical region by a layer of sclerotic strands. Both the leaf base and the cortex contain numerous closed collateral fibrovascular bundles, which are characteristic of the associated petioles named *Myeloxylon zonatum.* A broad inner periderm separates the outer cortex of the stem from an inner cortex. In it, as almost everywhere in the stem, is an abundance of periderm tissue, which is probably the most conspicuous feature of the entire stem.

Well-preserved roots exhibiting a tetrarch structure are attached to and associated with the stem.

Abundant associated leaf remains suggest that foliage of the *Alethopteris* type is correlated with this North American *Medullosa.*

Seed remains of *Rotodontiospermum illinoense* are found in close association with *Medullosa Noei* and may likewise be correlative.

Because of its anatomical structure, size, and stratigraphic position *Medullosa Noei* may be most nearly related to *Medullosa Leuckarti.*

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DESCRIPTIONS OF PLATES

The illustrations are from a single coal ball, No. 16563 in the Museum of Paleontology of the University of Michigan, except where otherwise noted in the plate descriptions. Duplicate sections of many are in the collection of the Illinois State Geological Survey at Urbana, Illinois.

EXPLANATION OF PLATE I

FIG. 1. Coal ball (blocks *a* and *b*) containing holotype of *Medullosa Noei.* Associated petiole (Pet.) of *Myeloxylon zonatum;* Leaf base (L.B.) of *M. Noei;* periderm (Pd.); stele (St.). $\times \frac{5}{8}$

FIG. 2. Portion of block *a* of Figure 1, tilted at an angle to show the relation of the transverse surface (X.) to the longitudinal fracture surface (Long.). $\times \frac{5}{8}$

FIG. 3. Longitudinal fracture of block *a* shown in Figure 1. The petiole at the left is a surface imprint only; the petiole itself is in block *b.* The arrow points to a plane corresponding to that shown in Figure 1. $\times \frac{5}{8}$

PLATE I
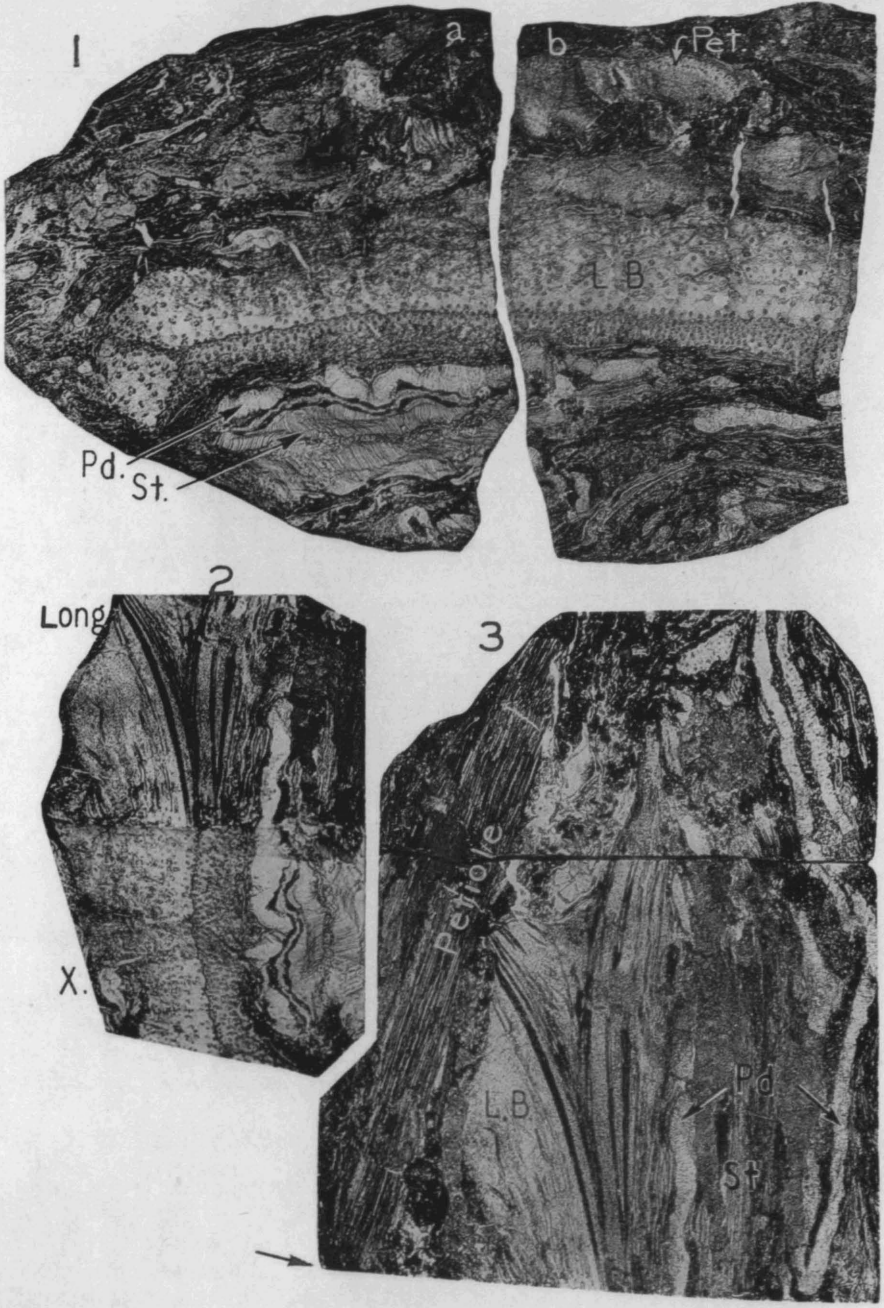
EXPLANATION OF PLATE II

FIG. 1. Transverse section of a large stele of *Medullosa Noei*, with constriction in the middle. $\times$ 1½

FIG. 2. Section similar to that of Figure 1, but about 8 cm. above or below it. The construction of the original stele has become complete, and apparently two steles are present. $\times$ 1

FIG. 3. Section similar to Figure 1, but taken at still another level. A root with considerable secondary wood (Rt.) is emerging from the smaller stele (St.); a similar root can be seen in the primary area of the larger stele (St. 2). $\times$ 1½

FIG. 4. Root in stele 1, Figure 3, at another level, where it is passing out of the stele through one of the rays. A thin band of periderm (Pd.) has already been formed. $\times$ 6

FIG. 5. Root in the primary area of stele 2, Figure 3, at another level. It also shows secondary xylem and a thin periderm band. $\times$ 7½

FIG. 6. Free root outside stem of *M. Noei*. Protoxylem (Px.) point of primary wood; secondary wood (X²); phloem, (Ph.); periderm band (Pd.). $\times$ 4½

FIG. 7. Longitudinal section of secretory canal with opaque resin rodlet (R.R.) from *Myeloxylon zonatum* petiole, similar to those in the leaf base of *M. Noei.* $\times$ 18¾
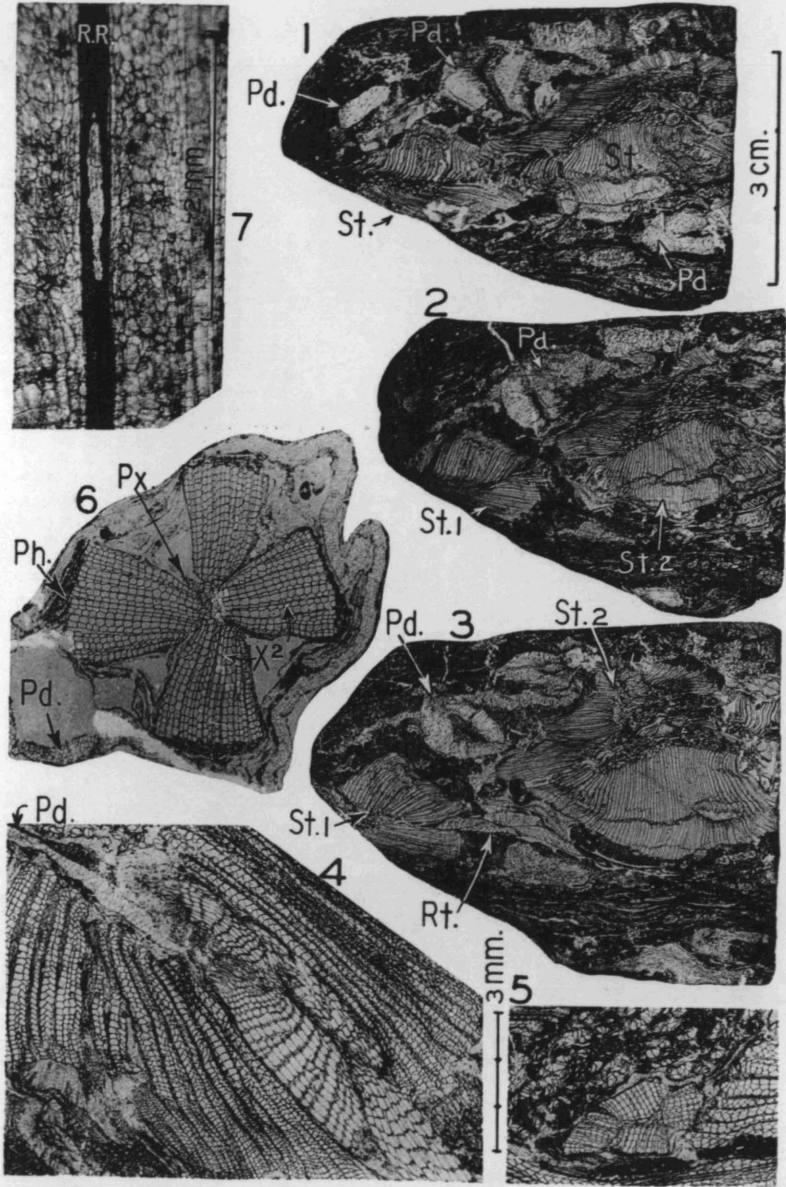
PLATE II

EXPLANATION OF PLATE III

FIG. 1. Transverse section of portion of large stele of *Medullosa Noei* illustrated in Plate I, Figure 1, showing double band of external periderm (Pd.), with crushed tissue between them and the stele; secondary wood (X²); primary xylem (X'). Many of the individual primary tracheid groups are surrounded by periderm, especially those at the left of the figure. × 6

FIG. 2. A group of bast fibers surrounded by periderm (see Pl. IV, Fig. 1). Photograph by Schopf. × 52

PLATE III

1

2
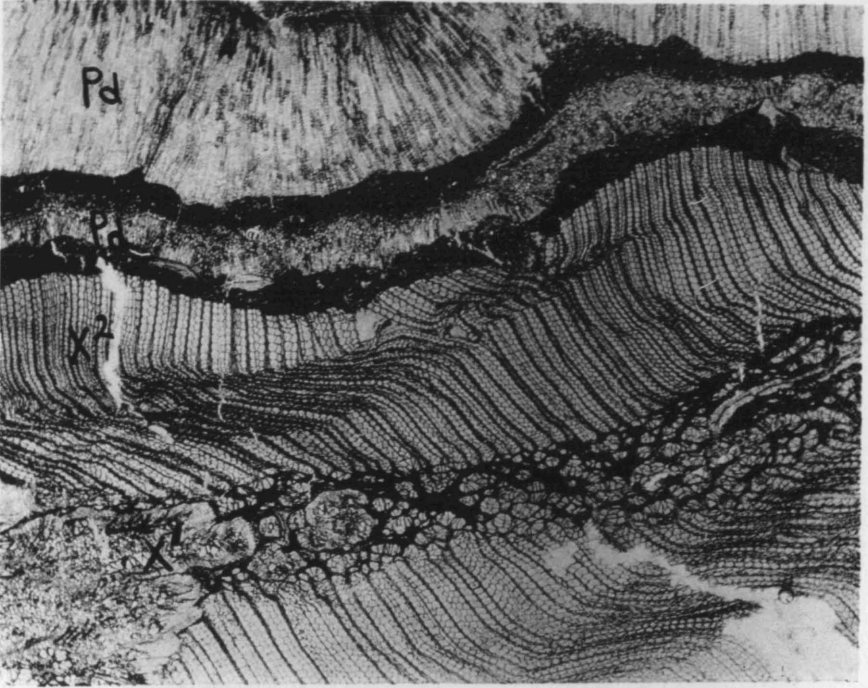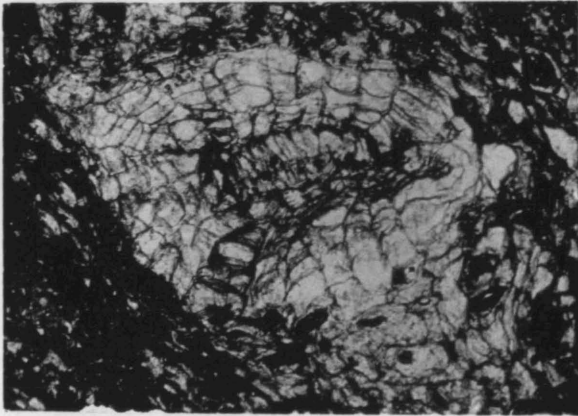
EXPLANATION OF PLATE IV

FIG. 1. Transverse section of portion of stele of *Medullosa Noei*, showing an "island" of periderm interrupting the rows of secondary xylem. At the lower right outside the dark zone of crushed phloem are three groups of bast fibers, each surrounded by a periderm sheath. Photograph by Schopf. $\times$ 17½

FIG. 2. Transverse section of a portion of a stele, showing groups of primary tracheid bundles, some with and others without a zone of periderm. Photograph by Schopf. $\times$ 17½

PLATE IV

1

2
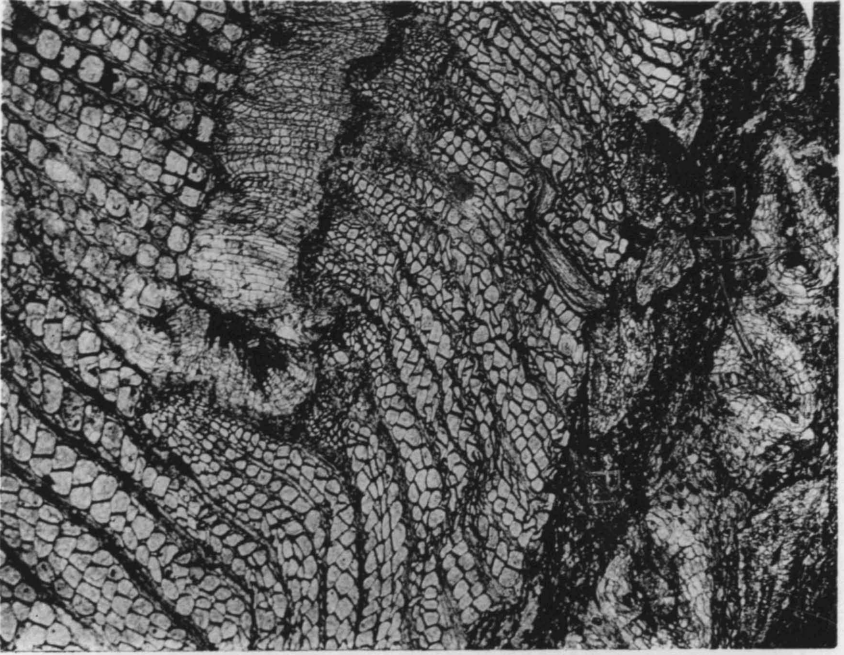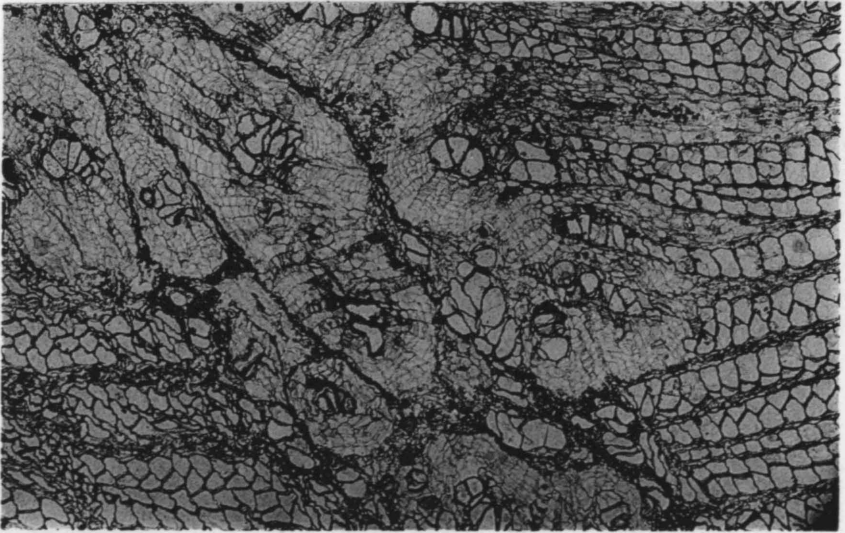
EXPLANATION OF PLATE V

Fɪɢ. 1. Periderm island in secondary wood of *Medullosa Noei*. The direction of secondary growth is indicated by an arrow. The small size of secondary tracheids upon resumption of growth is noteworthy. × 52

Fɪɢ. 2. Tetrarch root in stele of *M. Noei*, showing the general relationship to the stele. The root will pass out through the broad ray at the right of the figure. × 10

PLATE V

1

2
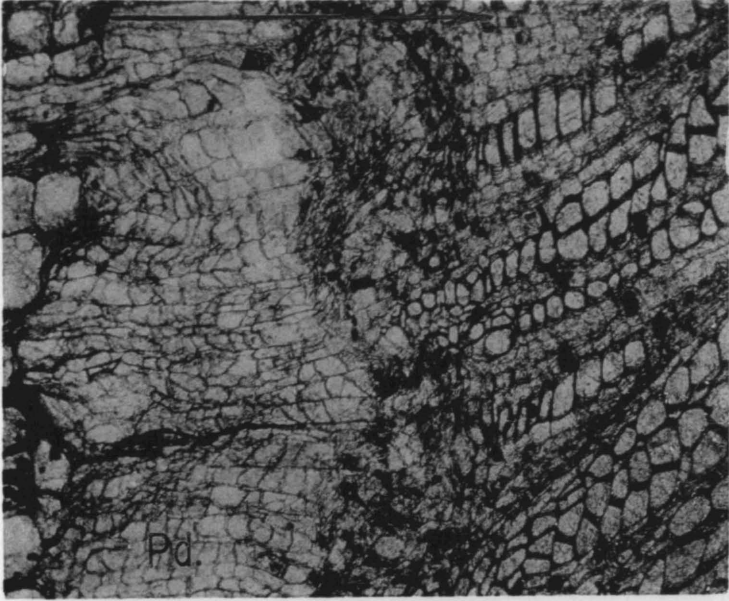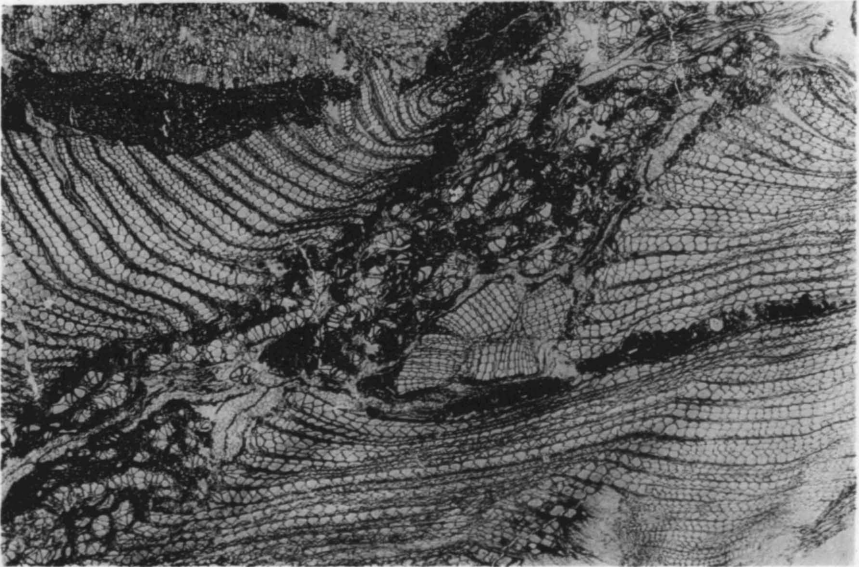
EXPLANATION OF PLATE VI

FIG. 1. Collateral bundle of *Myeloxylon zonatum* petiole associated with *Medullosa Noei;* transverse section showing phloem (Ph.), protoxylem (Px.), metaxylem (Mx.), and sclerenchyma sheath (Scl.). × 100

FIG. 2. Longitudinal section of bundle similar to that of Figure 1. The phloem, however, has disintegrated. Abbreviations as in Figure 1. × 100

PLATE VI

1

2
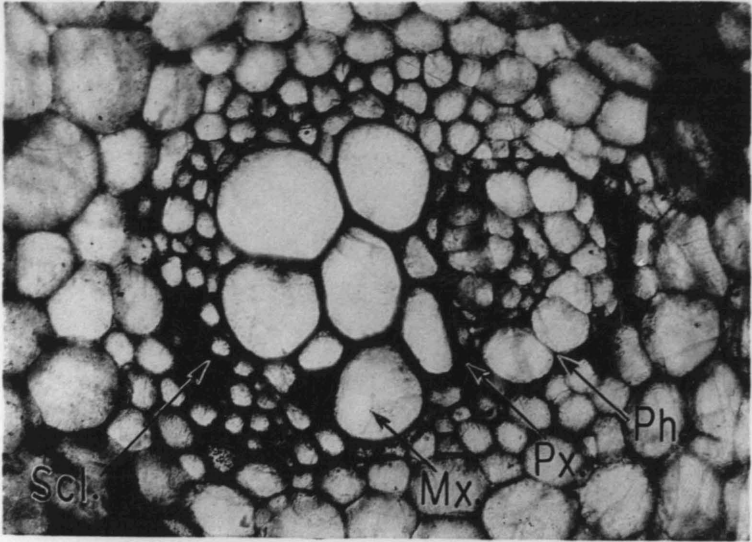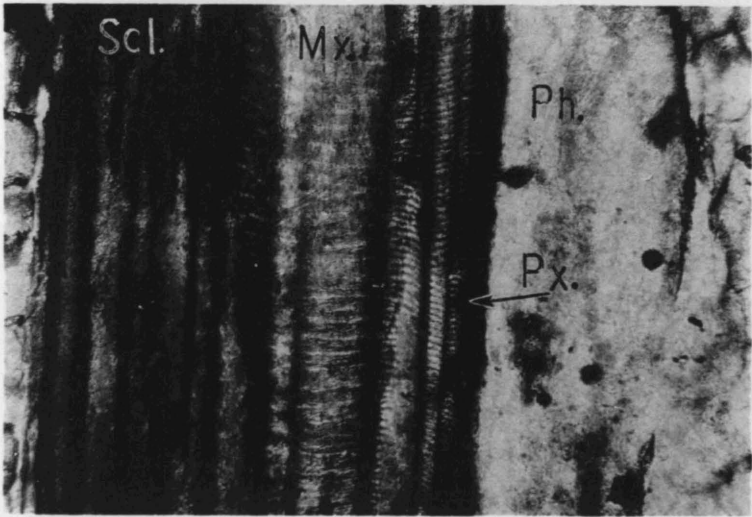
EXPLANATION OF PLATE VII

FIG. 1. Longitudinal section of a bundle similar to that of Figure 2, Plate VI, showing spiral thickenings on what appears to be metaxylem. × 100

FIG. 2. Radial wall of a secondary tracheid from *Medullosa Noei* holotype, showing dense multiseriate pitting. × 125

FIG. 3. Secretory canal from *Myeloxylon zonatum*, with a single row of epithelial cells. The resin rodlet incompletely fills the canal. × 100

FIG. 4. Proximal leaf trace of *M. Noei* included in periderm. The original phloem seems to have contributed to or has been engulfed in periderm, and the peridermal growth has filled the tracheids with tyloses. The bundle is larger in the proximal region than out in the petiole and has a concentric rather than a collateral structure. Photograph by Schopf. × 52

PLATE VII
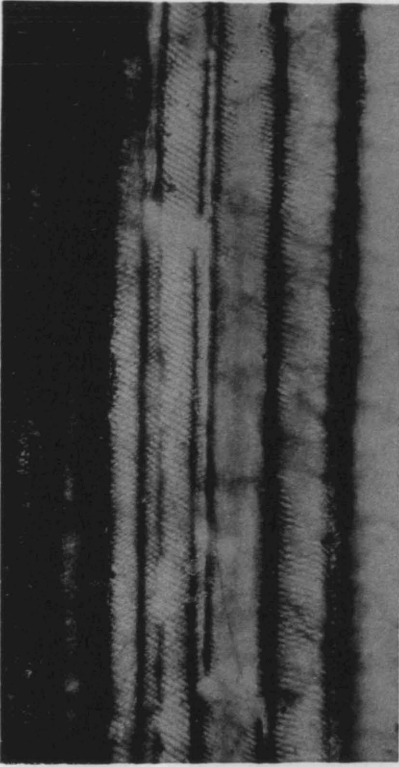
1
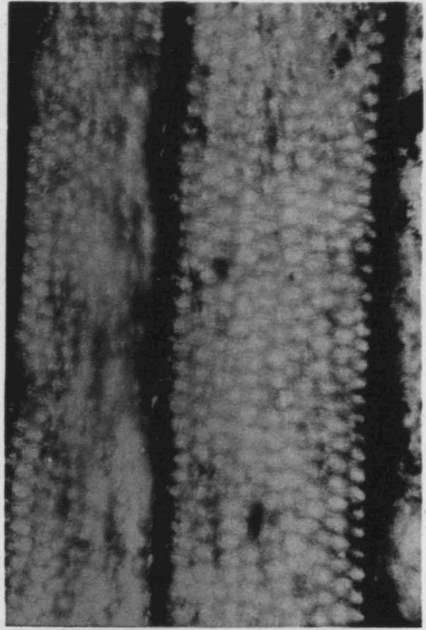
2
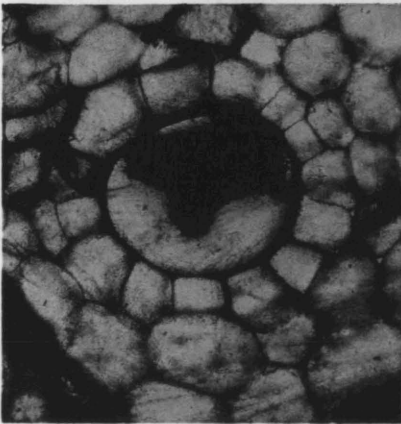
3
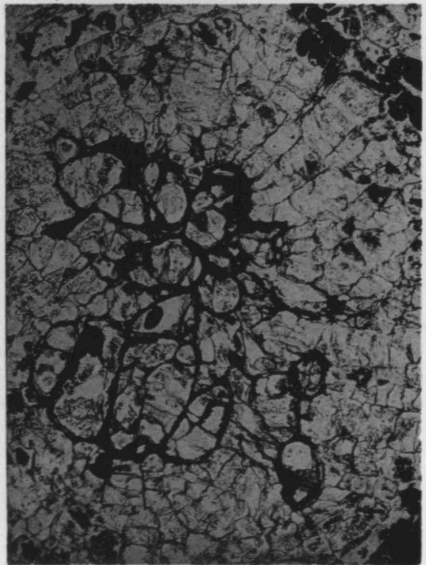
4

EXPLANATION OF PLATE VIII

FIG. 1. Secretory canal from the petiole of *Myeloxylon zonatum*, associated with *Medullosa Noei*. The resin rodlet is hollow, and the canal is surrounded by a sclerenchyma sheath. ×100

FIG. 2. Part of thick periderm of *M. Noei* holotype, showing the character of the cells and what apparently is a phellogen region (Phellog.) on the outer side. ×20

FIG. 3. Periderm around secretory ducts in the common ground tissue at the center of the stem of *M. Noei*. Photograph by Schopf. ×17½

PLATE VIII

1

Phellog.

2

3
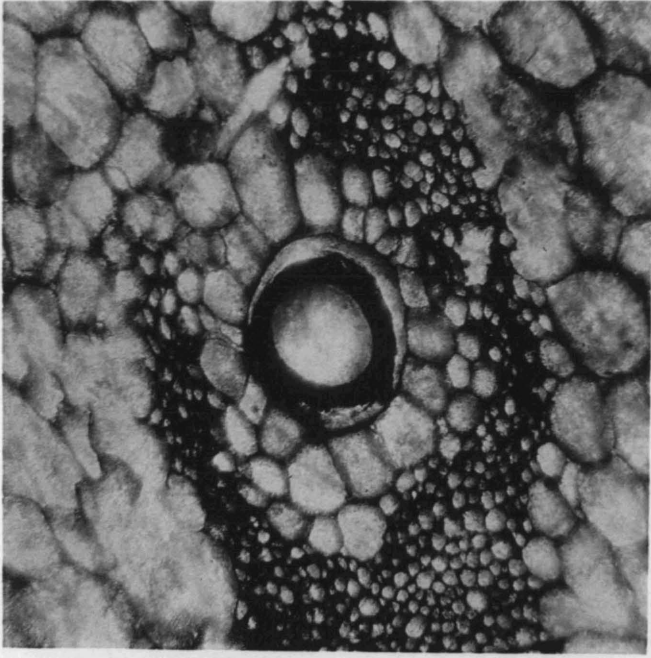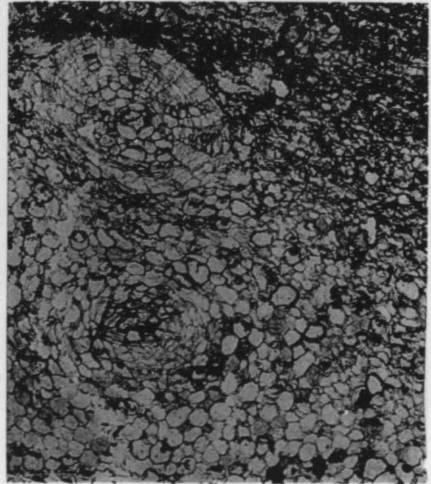
EXPLANATION OF PLATE IX

FIG. 1. Cross section of two alethopteroid pinnules of the type commonly found associated with *Medullosa Noei* and *Myeloxylon zonatum*. Hair bases on the lower surface are shown, and secretory canals are located in the midrib. × 17½

FIG. 2. *M. Noei*, tangential section in secondary wood close to the primary area, showing a part of a broad fusiform ray and the tangential wall of a tracheid with typical multiseriate bordered pits. The tapering end of a ray is illustrated at the lower right. Photograph by Schopf. From coal ball No. 292, B2 (S2), Illinois State Geological Survey collection. × 110

FIG. 3. *M. Noei*, longitudinal section showing tracheids and parenchyma (Par.) of primary area. Numerous parenchyma cells on the left have secretory contents. The primary tracheids have undulating longitudinal walls and rather blunt end walls. All tracheid walls have the typical multiseriate pitting. Photograph by Schopf. From coal ball No. 292, B2 (S2), Illinois State Geological Survey collection. × 110
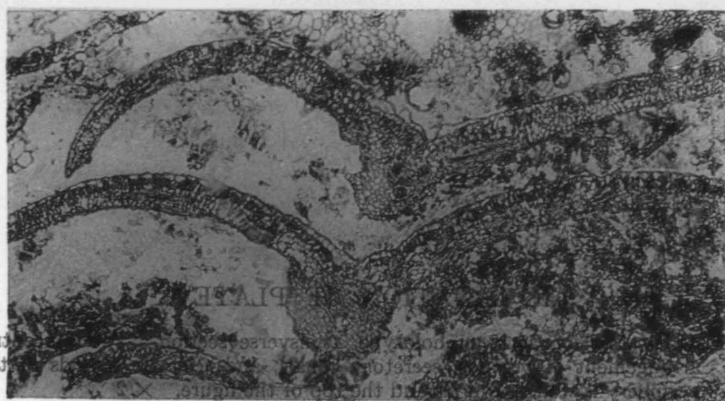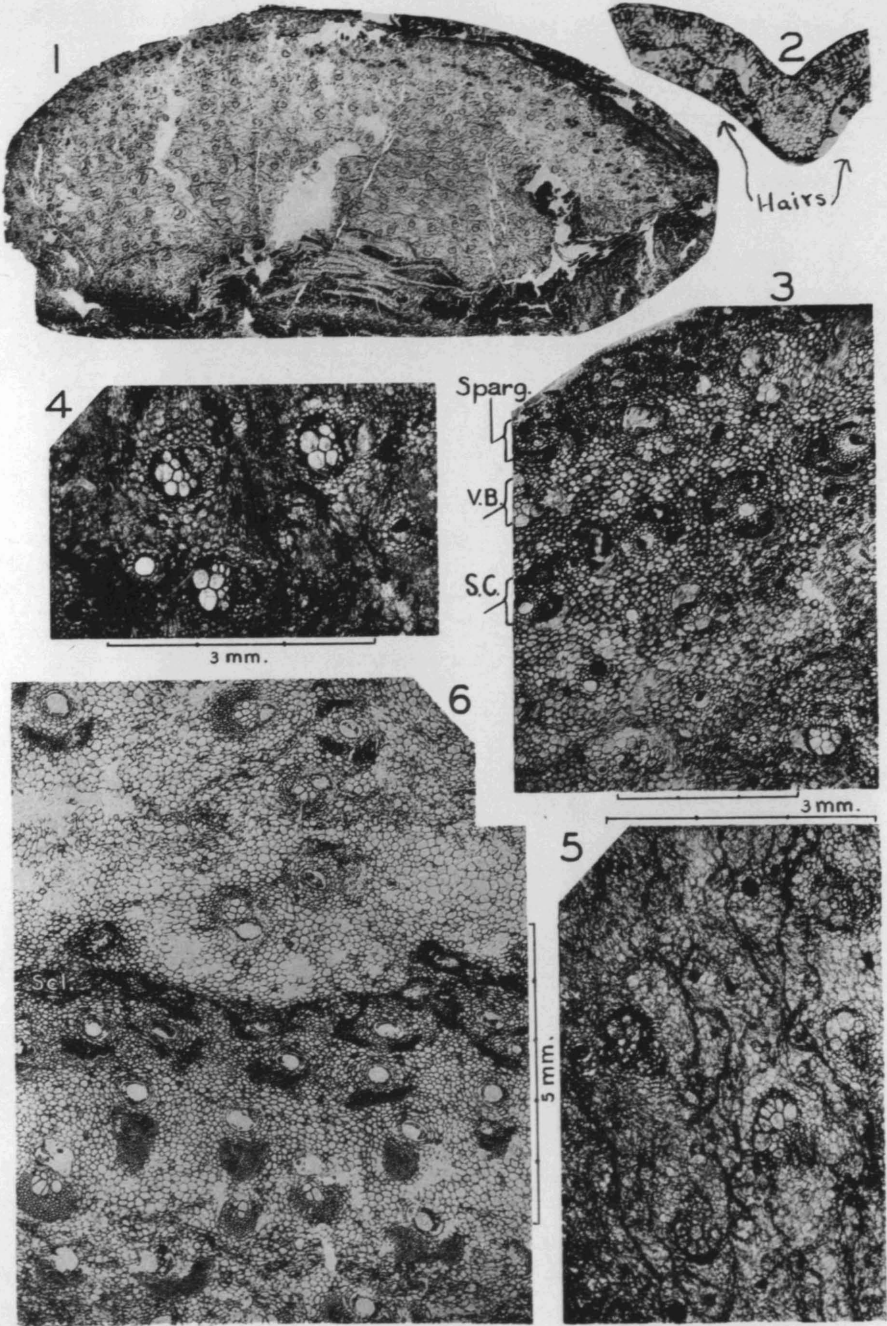
PLATE IX

2

3

EXPLANATION OF PLATE X

FIG. 1. *Myeloxylon zonatum* holotype, transverse section. The concentric arrangement of bundles, secretory canals, and sclerotic strands of the periphery is well shown around the top of the figure. × 2

FIG. 2. Portion of alethopteroid pinnule, showing attachment of epidermal hairs. × 13
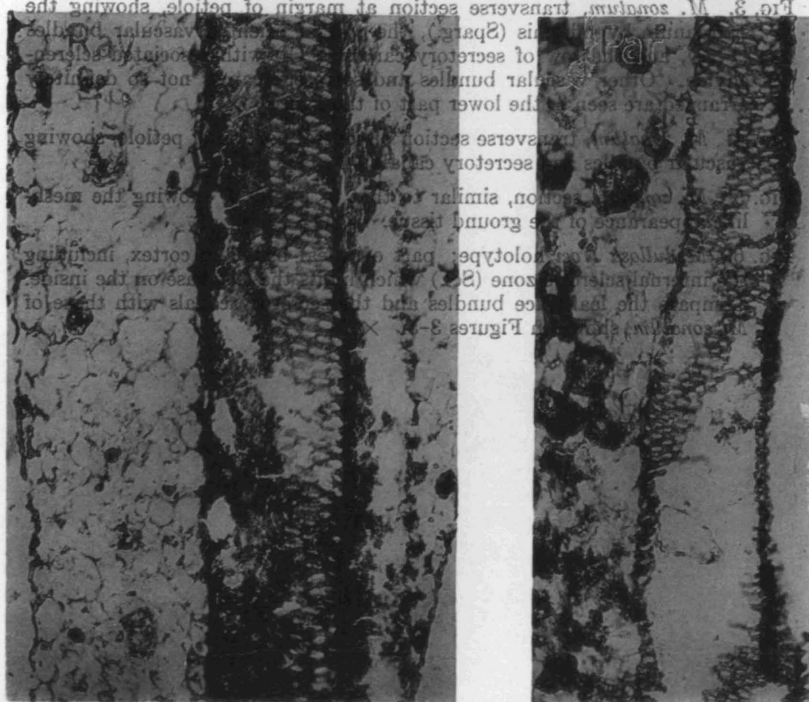
FIG. 3. *M. zonatum*, transverse section at margin of petiole, showing the sparganum hypodermis (Sparg.), the row of oriented vascular bundles (V.B.), and the row of secretory canals (S.C.) with associated sclerenchyma. Other vascular bundles and secretory canals not so definitely arranged are seen in the lower part of the figure. × 7½

FIG. 4. *M. zonatum*, transverse section of central portion of petiole, showing vascular bundles and secretory canals. × 11¼

FIG. 5. *M. zonatum* section, similar to that of Figure 4, showing the mesh-like appearance of the ground tissue. × 11¼

FIG. 6. *Medullosa Noei* holotype; part of a leaf base and cortex, including the internal sclerotic zone (Scl.) which limits the leaf base on the inside. Compare the leaf-trace bundles and the secretory canals with those of *M. zonatum*, shown in Figures 3-5. × 7½

PLATE X

1

2

Hairs

3

Sparg.

V.B.

S.C.

4

3 mm.

6

Scl.

5

5 mm.

3 mm.