THE PETRIFIED PTERIDOSPERM STEM *MEDULLOSA ANGLICA* FROM THE PENNSYLVANIAN OF NORTH AMERICA

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ABSTRACT. Several specimens of the pteridosperm *Medullosa anglica* Scott are described from coal balls of Lower Pennsylvanian age from eastern Kentucky, U.S.A. These stems are remarkably similar anatomically to those originally described by Scott from the Lower Coal Measures, and represent the first critically examined material of this taxon from North America.

WITHIN recent years there has been a renewed interest in the morphology and systematics of Palaeozoic pteridosperms focusing on both vegetative and reproductive organs. In part this is due to the discovery of several exceptionally well-preserved specimens that have not only expanded our knowledge about the anatomy and morphology of the organs, but also have filled in several important gaps in our understanding of the evolution of the group. One need only cite as an example the large number of new synangiate pollen organs in the Medullosales that have been described in recent years. Of equal importance has been a number of studies that have focused on the reinterpretation of the vegetative structures of the medullosan pteridosperms relative to the architecture of the primary vascular system. These studies are most significant in providing a basic understanding of seed plant vasculature that can be used to compare diverse taxa in order to more accurately interpret the phylogeny of the organisms.

Historically the Carboniferous pteridosperms have been divided into two large groups: monostelic types (e.g. *Heterangium*, *Lyginopteris*), and those forms which appear to have several vascular segments in transverse section, the so-called polystelic types (e.g. *Medullosa*, *Sutcliffia*). Recently, Basinger, Rothwell and Stewart (1974) have suggested that the anatomy of the medullosan stem should be reinterpreted as a dissected monostele rather than a polystele. This suggestion is based upon a detailed analysis of a number of specimens in which the architecture of the primary vasculature was traced throughout various lengths of stem segment. This has provided an opportunity to more accurately discuss several anatomical features including the pattern of leaf trace formation, production of secondary tissues, and organization of the primary xylem.

The genus *Medullosa* was instituted in 1832 by Cotta for silicified specimens of Permian age from Europe. The first report of a Carboniferous medullosan stem was Scott's description of *M. anglica* (1899) from coal balls collected at Hough Hill, Stalybridge. This species was described as consisting of 3–4 central vascular segments (steles) surrounded by large, clasping leaf bases of the *Myeloxylon*-type. It is interesting to note that this was the first report of *Myeloxylon* petioles in organic attachment to stems of *Medullosa*. In transverse section the stems were triangular in outline with the leaves produced in a 2/5 phyllotaxy. Surrounding the vascular segments was a narrow band of periderm which was traversed by numerous leaf traces. The periphery of the stem was bounded by several rows of sclerenchyma fibres which extended longitudinally for some distance. Based upon the histology of the petioles, Scott compared them with *M. landriotii* of Renault (1876). *Medullosa anglica* was significantly different from the previously described Permian species in the smaller number of vascular segments and the relatively simple organization of the stem.

To date there is only one known specimen of *M. anglica* reported from North America. This specimen was mentioned by Thiessen (1920), and subsequently described in greater detail by Schopf

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(1939). The stem segment, from the Upper Pennsylvanian of Nebraska, was approximately 14·0 cm long and 2·0 cm in diameter. In his later description, Schopf designated the specimen as a variety of Scott's taxon on the basis of the relative number of primary tracheids and the smaller, more compact shape of the steles. In his monograph on the Medullosae, Delevoryas (1955) notes that the preservation of this specimen is so poor that histologic details are obscured and features of leaf trace emission are lacking. One other variety of *M. anglica* (var. *iowensis*), described by Andrews and Kernen (1946), was placed in synonomy with *M. primaeva* (Delevoryas 1955).

The recent discovery of several exquisitely preserved specimens of *M. anglica* in coal balls collected from the Lewis Creek site in eastern Kentucky provides the first opportunity to compare a specimen from North America with that initially described by Scott. Unlike the previously described *M. anglica* var. *thiessenii* Schopf, histological details of the Kentucky specimens are sufficiently preserved so that the pattern of leaf traces can be ascertained. In addition, the age of these specimens (Lower Pennsylvanian) is comparable to Scott's material (Lower Coal Measures), but considerably older than the material described by Schopf in 1939 (Upper Pennsylvanian).

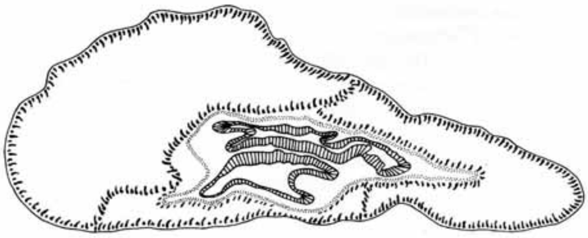
MATERIALS AND METHODS

This study is based upon seven specimens, two of which represent fairly complete medullosan stems with attached leaf bases. The material was examined by means of cellulose acetate peels. In addition, a small fragment of the coal ball was studied utilizing the scanning electron microscope in order to determine features of tracheid pitting.

The coal balls, nos. 1480, 1482, 1695, 1696, 1709, 1882, and 2068, and slides 7884–7886 and 11,198–11,251 are a part of the Paleobotanical Collection, Department of Botany, The Ohio State University, Columbus, Ohio, U.S.A.

DESCRIPTION

General features. The largest specimen measures 27·0 cm long and is only partially preserved in circumference. The second axis is 24·5 cm long and is roundly triangular in transverse section measuring 3·5 × 13·5 cm including the leaf bases (Pl. 94, fig. 1). In the central region of the stem are two tangentially elongated vascular segments that remain distinct throughout the length of the axis. In transverse section the vascular segments exhibit a sinuous outline with a somewhat endocentric development of the secondary xylem. The xylem strands are embedded in a thin-walled ground parenchyma that is bounded perpherally by a narrow band of internal periderm (text-fig. 1). To the outside of the periderm is a discontinuous cortex bounded by the decurrent leaf bases which are delimited by sclerenchyma strands. Although only petiole bases have been found in attachment to the stems, a few roots of the typical *Medullosa* type and a few foliage remains of the *Neuropteris* type have been found in the same coal balls.



TEXT-FIG. 1. Diagrammatic transverse section of *Medullosa anglica* specimen (from C.B. 1696 E, top). Hatched = secondary xylem; Stippled = periderm. Periphery of stem and leaf bases outlined with black.

Primary xylem. When viewed in transverse section, the primary xylem of *M. anglica* consists of two tangentially elongated and lobed groups of primary tracheids embedded in poorly preserved parenchyma (Pl. 94, figs. 4–7). In Scott's description of *M. anglica*, the protoxylem strands were observed in association with leaf traces and, in some instances, near the periphery of the primary body as well. However, neither the total number of strands nor their exact position was indicated. Basinger *et al.* (1974) recorded the number of protoxylem strands as 8? in the Kentucky specimens. Our observations are unable to confirm the consistent presence of this number of protoxylem strands due to the presence of anomalous secondary growth that has partially destroyed the configuration of the primary body. At other levels the primary strands are discontinuous due to the presence of numerous stigmarian lateral appendages. Protoxylem strands in the Kentucky specimens of *M. anglica* are present around the periphery of the primary body, and have also been observed in association with the production of leaf traces. The protoxylem tracheids are usually about 6–15 μm in diameter, and pitting ranges from spiral to scalariform.

Secondary xylem. Secondary development in *M. anglica* consists of the production of radial rows of muriform tracheids that are generally up to thirty-nine rows of cells toward the inside of the vascular segment, and only up to fifteen rows toward the outside. This endocentric development of secondary xylem is a relatively common feature in *Medullosa* stems, and appears to be variable throughout the different species. Although the amount of secondary xylem is dependent upon position within the stem (Delevoryas 1955), it is not known whether the endocentricity is also a consistent ontogenetic feature.

Extra-xylary tissues. Although phloem is not generally preserved in these *M. anglica* specimens, in a few instances, cells that resemble phloem fibres have been observed external to a cambium-like zone (Pl. 94, fig. 3). These fibres are separated by parenchymatous phloem rays, which are continuous with the secondary xylem rays.

The ground tissue of *M. anglica* is bounded by a zone of periderm that is uniformly developed throughout the circumference of the stem (Pl. 94, figs. 4, 5). This zone consists of rectangular cells and may be up to seventeen cells in thickness. The remaining portion of the ground tissue is made up of thin-walled parenchyma with scattered resin canals and is delimited externally by a thin band of sclerenchyma.

Several examples of anomalous tissue development are present at various levels of the stems. These may take the form of accessory cambia which arise around resin canals or groups of parenchyma cells in the cortex and produce rows of radially aligned cells (Pl. 94, fig. 8). In addition, anomalous cambia are present that extend from the cortex into the stele (Pl. 94, fig. 9). In this latter instance the cells are indistinguishable from the cells of the periderm. The continued occurrence of anomalous tissue development in many specimens of *Medullosa* may be the result of some external factors such as wound reactions, or may merely reflect structural changes occurring during the evolution of the medullosan stele. The presence of numerous tylosids in the secondary xylem tracheids adjacent to the anomalous growth (Pl. 94, fig. 9) may provide some indirect evidence of tissue damage.

Leaves. The leaves of *M. anglica* were produced in a 2/5 phyllotaxy and are decurrent along the stem. These leaf bases are bounded externally by a layer of sclerenchyma strands. Occasionally some well-preserved palisade and epidermal tissues are present outside of the sclerenchyma (Pl. 94, fig. 10). The remaining portion of the leaf base includes vascular bundles (Pl. 94, fig. 2) and resin canals scattered throughout the parenchymatous cortex. In general the histology of the leaf base is similar to that described for other species of *Medullosa* (Delevoryas 1955).

The production of leaf traces is initiated by the division of a protoxylem strand with one-half supplying the leaf trace and the other half remaining as a cauline strand. As the trace separates from the xylem cylinder it includes a central cluster of tracheids and parenchyma flanked by two crescent-shaped zones of secondary xylem (Pl. 94, fig. 4). As the trace moves into the cortex, it becomes more rounded and is surrounded by secondary xylem (Pl. 94, fig. 5). Near the periderm the secondary xylem diminishes and the trace undergoes a series of closely spaced dichotomies (Pl. 94, fig. 6). At this level the configuration of the trace changes from concentric to collateral. This sequence of trace formation in *M. anglica* appears to parallel that reported in other species of *Medullosa*.

Roots. A few adventitious roots were observed arising from the stem stele. These root traces can be recognized in cross-section by the presence of a small bulge that develops on the outer surface of the xylem cylinder (Pl. 94, fig. 7). This is associated with a loss of secondary xylem in that region of the stele, and the presence of scattered, radially aligned tracheids. No large typical *Medullosa* roots containing abundant secondary xylem were observed in attachment to the stem.

DISCUSSION

In the initial descriptions of *Medullosa* species, the primary criterion upon which taxa were delimited appears to have been based upon the number of vascular segments in the stem. This includes a large number of both European and North American studies prior to 1955. At that time the North American species were characterized, with a large number of the earlier species placed in synonomy (Delevoryas 1955). This reduced the number of North American taxa from approximately thirteen to six. The primary criterion upon which this taxonomic change was made involved an attempt to understand, for the first time, the development of the medullosan stem, including tissue histology and disposition, as well as changes in the number of steles from level to level. More recently (Basinger *et al.*, 1974), the genus *Medullosa* has been used in an attempt to better understand and integrate the vasculature of this plant in relationship to the evolution of the stele in other seed plants. This particular study was anatomical in nature and not concerned with the systematics of the species involved.

In his monographic treatment of the American medullosans, Delevoryas (1955) utilized a number of taxonomic criteria including: number and configuration of steles, ratio of tracheids to parenchyma in the primary body, relative extent of secondary xylem and periderm, the configuration of the leaf traces at their origin, and the number of traces within each leaf base. These features, together with the geographic and stratigraphic distribution of the fossils, represent those characters upon which species of *Medullosa* are distinguished today.

There are numerous features with which the Kentucky specimens may be directly compared with Scott's original description of *M. anglica*. Among the general features, these include the size and triangular configuration of the stem in transverse section, the arrangement of the secondary phloem, the 2/5 phyllotaxy, the absence of star rings, and the elongate and irregularly lobed shape of the vascular segments. In addition, the production of leaf traces as described by Scott is comparable, including the initial presence of a crescent of secondary tracheids flanking the leaf trace at the point of separation from the stele, which then appears more circular in transverse section at higher levels. Scott also notes the presence of some parenchyma in the centre of the trace and the gradual change to a collateral bundle configuration while the trace is still within the cortex of the stem.

The taxonomic value of several of these characters is somewhat questionable in the light of current information regarding the ontogeny of *Medullosa*. For example, the triangular outline of the stem may be a consistent taxonomic character since it occurs in both the specimens described here and in the original British material, or the stem configuration may simply be a result of the 2/5 phyllotaxy. Although the phyllotaxy is consistent in all specimens studied, the production of leaves is known to be variable depending upon the age of the plant as well as other factors. The elongate shape of the vascular segments in transverse section appears to be a consistent feature of this taxon and not the

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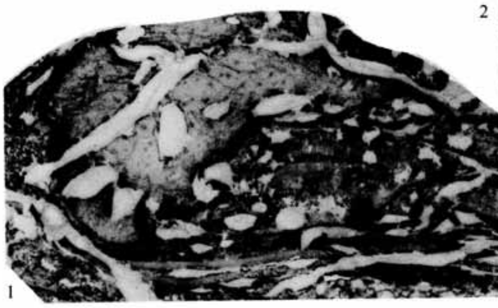
EXPLANATION OF PLATE 94

Figs. 1–10. *Medullosa anglica*. (P = periderm; *R* = root trace). 1, representative transverse section of stem. See text-fig. 1 for line-drawing of the same specimen with tissues indicated. C.B. 1696 E (top), no. 33, ×0·7. 2, transverse section of vascular bundle in leaf base showing collateral arrangement of tissues. C.B. 1695 F (top), no. 32, ×24. 3, section of portion of stele showing radial rows of phloem fibres (arrow). C.B. 1695 E (top), no. 16, ×25. 4–7, representative transverse sections showing departure of leaf trace (arrows) at successively higher levels. Also note root trace, 4, C.B. 1696 E (top), no. 37. 5, C.B. 1696 E (top), no. 180. 6, C.B. 1696 E (bottom), no. 129. 7, C.B. 1696 G(1) (top), no. 31. All ×9·5. 8, example of anomalous cortical growth C.B. 1696 G(1) (top), no. 125, ×25. 9, continuous zone of anomalous cambial-like development which extends from the cortex into the vascular tissue. C.B. 1696 F (top), no. 6. ×14·5. 10, periphery of leaf base showing well-preserved palisade tissue and epidermis external to the sclerenchyma strands. C.B. 1696 G(1) (top), no. 240, ×14.

PLATE 94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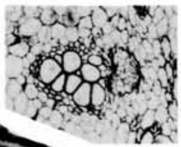
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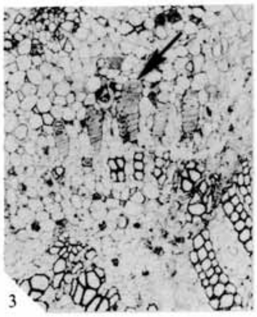
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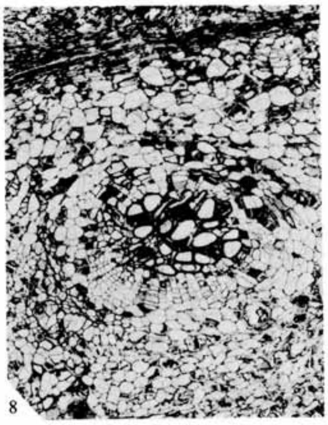
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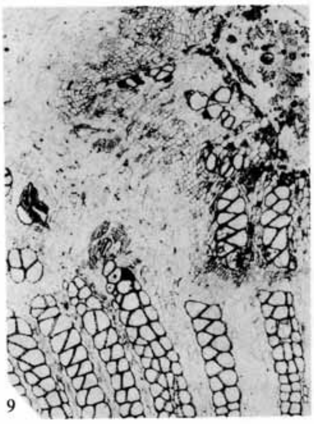
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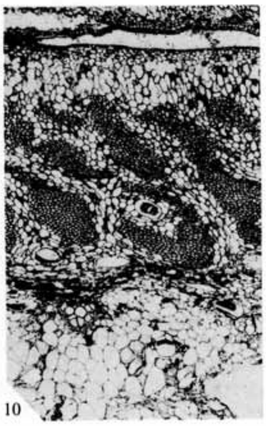
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SMOOT and TAYLOR, *Medullosa anglica*

result of differential compression after deposition since the primary xylem, ground parenchyma, and leaf bases are relatively undisturbed.

There are several features in both the British and Kentucky material that suggest the stem segments may have occurred in the distal portion of the plant and therefore constitute relatively immature specimens. These include the presence of a small amount of secondary xylem, relatively narrow periderm, and attached leaf bases. The absence of star rings may also be indicative of the immaturity of the stems. In the Kentucky specimens no large attached roots were identified, further attesting to the probable apical region of the plant.

One of the obvious difficulties in working with fossil plants with complex growth patterns like that in *Medullosa*, is the rarity of having extensive specimens in attachment that would illustrate changes in ontogeny. As a result, many species of *Medullosa* have been described that may represent growth stages of the same plant. Delevoryas (1955) has illustrated this problem with the North American species, but to date the same approach has not been used on the European taxa. In the case of *M. anglica* so few specimens have ever been described that the range of variability within the taxon is incompletely known. Future studies could indicate that *M. anglica* represents the distal portion of another taxon, and thus exhibits a broad range of variability compared to that known for several North American species (e.g. *M. noei*). If this is the case, *M. anglica* further underscores the problem in attempting to define species of *Medullosa* based on histologic features of isolated stem segments. Another possibility that must be considered is that *M. anglica* represents not the distal portion of another plant, but a *Medullosa* species that was small in stature with relatively little morphological and anatomical variability. This latter idea is supported by the fact that Scott's specimen *M. anglica* represents one of the largest species of *Medullosa* described from European sediments. Others, such as *M. pusilla* (2·2 × 1·3 cm) (Scott 1914), *M. centrofilis* (5·0 × 1·5 cm) (de Fraine 1914), and *M. geriensis* (3·0 × 2·0 cm) (Boureau 1951) are considerably smaller than *M. anglica*. In addition, the absence of any larger medullosan stems at the Kentucky site may be used as additional evidence of the over-all size of the plant.

If *M. anglica* does in fact represent a valid taxonomic species, it appears that the two most important characters that may be used to identify the taxon at this time are the configuration of the vascular segments and features associated with the production of leaves. Although these two features may at some later time be demonstrated as ontogenetic in nature, the consistent presence of these characters in *M. anglica* and their absence in other *Medullosa* species known in greater detail suggests these characters may be taxonomically useful.

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