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## FLORISTIC AND ECOLOGICAL SIGNIFICANCE OF COAL BALLS FROM LATE MIDDLE PENNSYLVANIAN STRATA OF WESTERN PENNSYLVANIA, U. S. A.

BY

Bing-cheng Feng

#### A DISSERTATION

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for the degree of

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Department of Botany and Plant Pathology

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#### ABSTRACT

FLORISTIC AND ECOLOGICAL SIGNIFICANCE OF COAL BALLS FROM LATE MIDDLE PENNSYLVANIAN STRATA OF WESTERN PENNSYLVANIA, U. S. A.

By

#### Bing-cheng Feng

342 coal balls or pieces of coal balls, representing a single concretionary mass occupying the full thickness of the original peat mass of a thin Allegheny Formation coal seam, were collected at the Derringer Corners locality, Lawrence County, western Pennsylvania, late Middle Pennsylvanian age.

In the study of systematics of pteridosperms, two stem species (<u>Schopfiastrum decussatum</u> and <u>Sutcliffia</u> <u>insignis</u>), two leaf species (<u>Alethopteris lesquereuxii</u> and <u>Alethopteris sullivantii</u>), and one seed species (<u>Pachytesta noei</u>) are described and illustrated; the concentric leaf traces of <u>Sutcliffia</u> has been proved; one new stem species (<u>Heterangium crossii</u>) is designated. Morphological and anatomical variance of medullosan roots are also discussed. The technique transferring the entire epidermal tissue and cuticle of alethopterid pinnules from coal ball specimens, macerated by using EDTA solution, has been illustrated. Such preparations provide threedimensional structure.

The coal ball flora was composed of four major

plant groups comprising about 30 genera common in the Pennsylvanian Euramerican coal swamps. By using a grid method of mapping, 13,203 cm<sup>2</sup> are quantitatively analysed from the middle peel of each of the coal balls or piece of coal balls. Lycopods were the dominant plants in this flora (66.5 %); pteridosperms were of secondary importance (22.9%), ferns and sphenopsids were 8.0% and 4.6% respectively; and cordaitean plants were absent. Root systems contributed the most abundant part (57.7% of the total identifiable plant material in the coal balls) of the flora; stems occupied 31.7% of the plant mass (volume), leaves constituted 9.5%, and fructifications contributed only 1.5%. The aerial parts ("shoot") of the flora preserved in the permineralized peat mass have a ratio of 0.73 to the root (shoot/root ratio).

The abundance of lycopods is generally recognized as an indicator of a wet environment or habitat. However, the low shoot/root ratio infers relatively dry conditions in the coal-forming peat swamps at the Derringer Corners. The discrepancy of these two environmental indicators is discussed, and it is suggested that the regional climate was relatively dry, compared to that of some earlier coalforming environment, but edaphic and perhaps geomorphic conditions resulted in local areas of wet habitat.

## TO MY DEAR MOTHERLAND

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#### INTRODUCTION

A fossil may be defined as any trace or remain of any former living organisms preserved in the rocks or sediments of the earth's crust.

James M. Schopf (1975b) recognized four distinct modes of fossilization. One is cellular permineralization resulting from infiltration and precipitation of soluble silicates, carbonates, iron compounds and other minerals into cells and the spaces between them, forming a rock matrix supporting the embedded plant tissues. Permineralization includes all specimens which have been called petrifactions in that internal cellular structures of plant tissues are preserved in an embedding and penetrating mineral matrix. The Devonian Rhynie chert, Precambrian Gunflint chert, Triassic wood from the Petrified Forest of Arizona, and the Tertiary Sequoia trunks in Yellowstone National Park are a few examples of silicic permineralization. Coal balls are examples of carbonate permineralization which may be calcareous or dolomitic and mixed with other minerals in various combinations (iron carbonates, iron pyrite, marcasite, and even silica).

The second mode of fossilization is coalification

including all compressions formed of coalified plant material (vitrinized, fusinized). The third is authigenic preservation or cementation to which molds (including impressions) and casts belong. The last is duripartic preservation of original or partially altered mineral matter, such as diatoms, charophytes, animal shells, skeletons or complex organic tissue, such as conodonts, chitinozoa, and acritarchs.

Because of the fragmentary nature of plant fossils, it is often desirable to apply a specific or generic name to a single plant fragment or organ, e.g., such as a stem, leaf, or reproductive structure, even including spores or pollen grains.

In assigning names to fossil plants, there are two major problems. One is the multiplication of names due to assigning new names to parts of plant or organs based only on a few specimens which show a little difference in size, shape, or structure. It is clear that living plants exhibit great variation in morphology and anatomy. The same organs of different individuals of the same species may show morphological and size differences as a result of differential growth in response to different environments, nature of exposure, or other factors. Similar variations in fossil plants have also been identified as due to such climatic and edaphic factors. In addition, normal morphological and anatomical changes occur during growth of some plants due to size increase or other factors.

For example, stelar character of lycopod stems changes from protostele at lower levels to siphonostele at higher levels (Walton, 1935; Eggert, 1961). Batenburg (1977) demonstrated that the leaf type of <u>Sphenophyllum</u> <u>emarginatum</u> ranges from simple leaves with a single unbranched vein to planated and webbed leaves where the veins dichotomize up to four times and that the tips of some leaves have pointed teeth while others are rounded. His study supports the previously postulated concept that leaf morphology, number of leaves per whorl and number of veins per unit area cannot be used alone to distinguish species of Sphenophyllum.

Early studies of <u>Medullosa</u> emphasized the number, size, and shape of vascular strands in a stem as important species characters (Stewart, 1951). It is now known that the number of vascular segments in stems of <u>Medullosa primaeva</u> may vary from 2 to 20 or more (Stewart and Delevoryas, 1952). In a comprehensive account of medullosan stems, Delevoryas (1955) was able to show that most of the variability of the vascular system represented developmental changes that occurred at a given level in a species of <u>Medullosa</u> as its stem grew older. He concluded that many of the previously described "species" appear to be only growth stages of a single species.

Consequently, assignment of names to fossil plant fragments should be based on as much data as possible from

external morphology, internal anatomy, epidermal structure, reproductive features, and so on, to reduce the multiplication of names as much as possible.

Another problem in assigning fossil plant names is simply identifying fossil plants with previously described fossil plants or with living plants without careful investigations in detail. One example is the history of discovery of the genus Metasequoia. The fossil specimens of Metasequoia had been assigned to Sequoia langsdorfii for nearly a century. Miki (1941), who investigated some specimens generally assigned to Sequoia langsdorfii, from Pliocene deposits of Japan, noticed that many specimens exhibited several distinctive characters, e.g., opposite leaves on deciduous branches and seed cones with deciduous scales and long slender stalks. Because these characters distinguish such plants from Sequoia, he established the new genus Metasequoia for these specimens. At about the same time, a large, unknown conifer was discovered in Sichuan Province of Southwest China. Hu and Cheng (1948) then determined this extant conifer was actually the same as the fossil Metasequoia described by Miki and assigned the name Metasequoia glyptostroboides to the "living fossil" plant.

The identification of angiosperm leaves is another example. There are about 300 families of angiosperms and nearly half of them have a fossil record. But for more than 100 years, angiosperm leaf identification (mostly Tertiary) has been largely based on

comparison of the gross morphology of impressions and compressions with modern taxa. It has been suggested that 60 per cent or more of the fossil angiosperm leaves identified in this way have been incorrectly identified. It is evident that many fossil leaf types represent extinct genera which cannot be assigned to any modern taxa. It is necessary to utilize cuticles exhibiting epidermal structure and fine venation patterns, and any other morphological and anatomical characters which can be discerned for a reinvestigation of most previously "identified" angiosperm leaf fossils (Dilcher, 1974; Doyle, 1973; Hickey and Doyle, 1977; Hickey and Wolfe, 1975).

Obviously, a better understanding of plant variation, as well as comprehensive studies of external morphology, epidermal structure, and internal anatomy, wherever possible, is needed to minimize problems involved in assignment of plant fossils to proper systematic position. On the basis of advances in knowledge resulting from new generations of paleobotanical research, paleobotany has reached a new epoch of "Structural Paleobotany" (Cross, 1984, personal communication).

A major goal for paleobotanists is reconstructing whole plants from their dissociated parts. There are generally three kinds of evidence for reconstruction.

Evidence from actual attachment is the most

reliable and desirable. An outstanding example for this was the discovery by Beck (1960a, 1960b) of the attachment of <u>Archaeopteris</u> leaves to the gymnospermic stem <u>Callixylon</u> which led to the establishment of the class Progymnospermopsida.

Evidence for attachment can be inferred by similarity of anatomical features. A classic example is the demonstration by Oliver and Scott (1904) of the organic connection of foliage-bearing stem Lyginopteris <u>oldhamia</u> with a cupulate structure bearing Lagenostoma <u>lomaxi</u> seeds, thus enabling the establishment of the Pteridospermae. Their establishment was based on the similarity of capitate glands; the actual attachment of the seeds to the stems was observed later by others.

Evidence for attachment based on frequent association is a tenuous approach. However, when the same association is found repeatedly, the probability of relationship between the dispersed organs is enhanced. One good example is the relationship between medullosan ovules and pollen grains. Stewart and others (Stewart, 1983, p.263) investigated the pollen chamber contents of 100 specimens of <u>Pachytesta illinoensis</u> and found that in 8 of these pollen chambers <u>Monoletes</u> was the most abundant pollen grain type. Three species of microsporangiate organs containing <u>Monoletes</u> type pollen have been described (Taylor, 1971; Ramanujam et al., 1974; Eggert and Rothwell, 1979) from the coal ball samples of the

Berryville locality, where many specimens of <u>P</u>. <u>illinoensis</u> have been found, and of these three species only <u>Dolerotheca formosa</u> is present in an abundance corresponding to the <u>P</u>. <u>illinoensis</u> ovules. These examples provide indirect evidence that the pollen organ <u>Dolerocheca formosa</u> and the ovule <u>Pachytesta illinoensis</u> are conspecific.

Coal balls (carbonate permineralization) provide valuable information of internal structure and cellular details with little distortion. In fact, most of our knowledge of internal structures of Carboniferous vascular plants has come from coal ball studies. On the basis of these studies, it is possible to deal with ontogeny of Carboniferous plants. Twigs with apical cells of Sphenopsida (Good,1971; Good and Taylor, 1972); pollen grains of a pteridosperm with a branched pollen tube (Rothwell, 1972); pollen grains of a seed fern showing stages in the development of the microgametophyte (Millay and Eggert, 1974; Millay and Taylor,1976); nuclear division (meiosis); and microgametophyte development of a lycopod cone (Brack-Hanes and Vaughn, 1978); are some examples of excellent preservation in coal balls.

As with everything with advantages, there are some disadvantages. Coal balls generally reveal little external morphology of plant organs. Identification of medullosan seeds of <u>Pachytesta</u> preserved in coal balls with casts, molds, and compressions of Trigonocarpus by

Hoskins and Cross (1946a, 1946b), and exposing the external morphology of coal ball plant organs, especially foliage, by using mechanical or chemical methods (Leisman, 1960; Baxter and Willhite, 1969; Ramanujam et al., 1974; Rothwell, 1980b), are examples of fortuitous discovery and special techniques used to correlate plants with structure preserved in coal balls with plants known from casts, impressions and compressions. However, these types of correlation are still rare.

The value of coal balls has been restricted by the techniques involved in coal ball study, and by the stratigraphic occurrence of coal balls, mostly restricted to Carboniferous in Europe, and North America.

The recent discovery of Chinese coal balls is an exciting event. So far as I know, the coal balls from Guizhou Province of China of the Upper Permian age are the youngest Paleozoic coal balls known. Valuable new information should be derived from the Chinese coal balls which have different occurrence both geographically and stratigraphically from those previously described. The discovery of Late Permian coal balls in China and Neogene silicified coal balls in Alaska (Knoll, 1985) make it reasonable to expect to find coal balls in different geological periods where the environments were favorable for their formation.

The coal balls for the present study were collected from Middle Pennsylvanian strata at the

Derringer Corners locality, Lawrence County, Western Pennsylvania. This locality is the easternmost locality yielding American coal balls.

The present study has three major objectives:

First is the systematics of some pteridosperms in this coal ball flora based on the internal structures, especially vasculature. The anatomical variations recognizable in the same species provide a more reliable basis for proper naming and classifying these plants.

The second is to demonstrate a technique to reveal plant organs or tissues in three-dimensional aspect, toward the goal of revealing intact coal ball plants.

The third objective is to make a quantitative analysis of proportions of the different plant groups in the coal ball flora to reveal some aspects of the paleoenvironments where the coal swamp plants grew in the past.

#### ORIGIN OF COAL BALLS

Coal balls are generally considered to be permineralized peats, in irregular or nodular masses, preserved in local areas within coal seams. Early permineralization of the plant matter of the peats resulted in cessation of decay and protection from further compaction or loss of volume or organization by embedding and permineralizing plant tissues.

According to the generally accepted definition of coal balls, other nodular masses, which may or may not contain organic tissues, occurring within other clastic mineral deposits (mudstone, siltstone, etc.) instead of in the peat swamps which formed the coal seams, are not coal balls.

Mamay and Yochelson (1953, 1962) distinguished four major types of coal balls: "normal" coal balls containing only plant tissues, "faunal" coal balls containing only marine animal fossils, "homogeneous mixed" coal balls containing intermixed faunal and floral remains, and "heterogeneous mixed" coal balls containing cores of marine fossil bearing carbonates mantled by "normal" plant-bearing carbonates. Here only the origin of the "normal" coal balls is discussed.

The origin of coal balls is a significant and unresolved question in which botanists and geologists have been interested for long time. Various hypotheses, such as the "<u>in situ</u>" theory and the "drift" theory, "marine origin" and "non-marine origin", have been offered.

Analyses of coal ball compounds indicate that the main constituents of Euramerican coal balls are calcium and magnesium carbonates, iron pyrites, as well as silica, which is the most important secondary compound (Stopes & Watson, 1909; Cross, 1969; Rao, 1985). A fundamental problem in the formation of coal balls is the source and the mode of such massive quantities of carbonates usually

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concentrated very locally in coals.

Based on the occurrence of marine shells in almost all of the shales or other sediments which lie immediately above the coal seams containing coal balls, and the significant amount of soluble calcium and magnesium sulphates in sea water, the most widely accepted hypothesis of coal ball origin is the marine in situ origin theory proposed by Stopes and Watson (1909). Zaritsky (1959), Zaritsky et al. (1971), Mamay & Yochelson (1962), Cross (1969), Tian (1979), and Rao (1985) support the concept that formation of coal balls is related to marine transgressions. Many coal swamps were at or near sea level and may have been episodically inundated during high stands of sea level. During such marine transgressions, sea water inundated coal swamps, and the calcium and magnesium ions that were dissolved in sea water reacted with elements of dead plants in the swamps and formed calcium and magnesium carbonates which in turn infiltrated and permineralized dead plant tissues to form coal balls.

Stopes & Watson (1909) carried out an interesting experiment. They prepared a solution of calcium sulphate with ferric hydrate in suspension in a closed bottle with fresh and decayed woods and fish. A year later, it was found that calcium carbonate had been formed leaving little or no calcium sulphate, and that the wood had been impregnated as though fossilized, though most other plant

tissues had entirely disappeared.

Generally heavier isotopes (such as  $^{13}$ C) are concentrated in more oxidized forms of matter, whereas lighter isotopes (such as  $^{12}$ C) are enriched in organisms where carbon of CO<sub>2</sub> has been reduced and incorporated into organic compounds by photosynthesis of green plants (Craig, 1953; Krauskopf, 1979, p. 211-212). The extreme deficiency of  $^{13}$ C of normal coal balls indicates that the carbon in normal coal balls came from decomposed plants instead of sea water (Weber & Keith, 1962; Anderson et al., 1980).

Taking a comprehensive view, the formation of "normal" coal balls is presumably described as follows: In local shallows or basins in coal swamps where coal-forming plant materials were deposited, water-logged plant debris would accumulate, be buried by further plant growth, and be shut off from the effects of the atmosphere. Preservative properties of the peaty acids would help to keep the plant remains from rapid decay (Stopes & Watson, 1909). During marine transgressions, sea water became mixed with fresh water in the swamps. Carbon dioxide formed by decomposition of plants would start reacting with calcium and magnesium sulphates dissolved in the mixed solution to form dissolved calcium and magnesium carbonates which in turn infiltrated the tissues and were deposited in cells and intercellular spaces of plant tissues, leading to the permineralization of the vegetable

matter. The permineralization was probably initiated by presence of salts of which microscopic crystals acted as nuclei for chemical deposition in the plant cells. The permineralization of the plant tissues escape the more normal diagenetic processes of coalification which proceeded to alter the main part of the plant matter in the peat swamps. and the permineralized peats were then preserved in the form of coal balls.

There have been some questions about the hypothesis. According to this hypothesis, for example, coal balls would have been massively formed; in fact, however, coal balls sometimes are just scattered without evident order or arrangement in coal seams.

Another outstanding question is the general absence of coal balls in coal beds later then Pennsylvanian. This question is only slightly mitigated by the discovery of the Chinese coal balls of Upper Permian age (Tian, 1979; Tian & Zhang, 1980; Hsu, 1981) and the reported coal balls in a single occurrence in Alaskan Cretaceous deposits.

The literature contains conflicting interpretations on the organic composition of coal balls.

The organic matter contained in the coal balls from the United States is light brown, the color of peat or brown coal, whereas the plant material in European coal balls is black like the surrounding coal (Lyons et al., 1983). The color and detailed morphological preservation

of plant tissues in American coal ball suggest a physical resemblance to modern peat. Consequently, this organic material has been commonly called "fossil peat" (Phillips et al., 1974). Baxter (1964) reported starch grains in coal balls from Kansas, though the result of chemical testing for starch is negative, and stated that lignin was probably preserved in American coal balls. Schopf (1966) Claimed that vitrinite was absent in both American and European coal balls and that cellulose and lignin, the common components of modern peat, were preserved in American coal balls.

However, Darrah (1941) showed, using sulfuric acid test, that there is no cellulose and lignin in the organic material in the coal balls from Iowa, and, therefore, that the organic matter was coalified. Teichmuller (1966) reported that she had observed vitrinite in coal balls from Europe, implying that the plant material preserved in those European coal balls were coalified.

Recently, Hatcher et al. (1982) and Lyons et al. (1983), using elemental, petrographic, and solid-state  $^{13}$ C nuclear magnetic resonance (NMR) technique, are able to show that there is absence of cellulose and lignin in medullosan plant tissues preserved in coal balls from the Illinois Basin, and that the percentage of the elements (C, H, N, O) in those plant tissues is very close to that of the coal surrounding the coal balls. Consequently, they

concluded that the plant tissues in those coal balls are about the same rank as the surrounding high-volatile C bituminous coal. If they are correct, the plant tissues preserved in coal balls from the Illinois Basin are not peat but coal.

#### DISTRIBUTION OF COAL BALLS

Since the first report of coal balls by Hooker and Binney (1855) from Lancashire, England, plants from coal balls have been widely described from over 10 countries including Europe, North America and Asia (Figs. 1, 2).

Cross (1969) reported a number of American coal ball occurrences in his summary stratigraphic chart of Euramerican coal ball stratigraphy, and Phillips (1980) in a more extensive and complete summary detailed the stratigraphic and geographic occurrence of coal balls in Europe and North America. According to Phillips, there are five major geographic regions of Euramerican coal balls: Donets Basin of the U.S.S.R., the Western European countries, the Appalachian Basin, the Eastern Interior Basins, and the Western Interior coal regions of the United States (Figs. 2, 3, 4).

The earliest recognition of coal balls in the Donets Basin of Ukraine, U.S.S.R. was made by Zalessky (1910). There are now at least 21 coal mines yielding coal balls in that basin (Zaritsky, 1959; Snigirevskaya, 1972).



Geographical distribution of coal ball deposits in Europe and Asia (modified from Phillips, 1980).



Fig. 2. Major coal ball deposits in the United States (from Phillips, 1980).

These coal balls are of the Middle Carboniferous age; no Russian coal balls of the Upper Carboniferous age have been reported.

The coal regions containing coal balls in European countries include The Netherlands, Belgium, France, Germany, Poland, Czechoslovakia and Yugoslovia and adjacent areas in Hungary with a questionable occurrence in Spain. Those include the earliest coal swamp floras known in detail especially those from the Union or Halifax Hard Bed of England, and continental equivalents, the Bouxharmont of Belgium and the Finefrau-Nebenbank of The Netherlands and Germany. Some of these coal balls are of Lower Carboniferous age.

It was not until 1923 that Noe' published the first report of the existence of coal balls in North America. The first North American coal ball specimen was obtained by the Illinois State Geological Survey from O'Hara Mine No.9 in Kentucky. Coal balls are now known to occur in three regions in the United States.

The Appalachian region of North America is the most recent area of coal ball discoveries. The early reports of Appalachian coal balls were given by Foster and Feicht (1946), Cross (1952, 1967), Schopf (1961). Later reports have been given by Good and Taylor (1974), McLaughlin and Reaugh (1976), Rothwell (1976), and McCullough (1977) from western Pennsylvania, eastern Ohio, eastern Kentucky, and northwestern West Virginia. Coal

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balls have been reported from New Brunswick, Canada (Baxter, 1960). There are nine coals containing coal balls in this region.

The occurrences of coal balls in the Eastern Interior or Illinois Basin (Illinois and adjacent portions of western Indiana and western Kentucky) are summarized by Phillips et al. (1973). There are more then 60 mines and a number of stream bank localities that have yielded coal balls. More than one-half of the localities are from the Springfield (No. 5) and Herrin Coal (No. 6) members, which form the upper part of a group of successive Carbondale coals containing coal balls, beginning with the Colchester Coal member. These permit some precise stratigraphic determination of swamp changes and related plant occurrences.

The stratigraphic positions and nomenclature of American coals containing coal balls largely follow the previous charts by Schopf (1941), Cross (1969). The use of the terms Lower, Middle, and Upper Pennsylvanian for stratigraphic occurrences of coal balls in the United \* States has been quite irregular in the literature. According to the United States Geological Survey policy (Bradley, 1956, p. 2285), almost all North American coal balls are of Middle and Upper Pennsylvanian age; so far there are no coal balls known from the Lower Pennsylvanian of the United States. Phillips (1980) reported that the youngest North American coal balls, some of which are

Permian age, occur in Young County area near Newcastle, Texas.

The discovery of Chinese coal balls extends the distribution of coal balls to the Asian Continent geographically and to the Uppermost Permian stratigraphically. The first Chinese coal ball specimens were collected from Wangjiazhai Coal Mine, Shui Cheng, Guizhou Province of Southwest China during the Middle 1970's (Tian, 1979; Tian & Zhang, 1980; Hsü, 1981). In this locality, there are at least 4 coal seams yielding coal balls of which the occurrences are so massive that in some places the coal seams are completely occupied by coal balls. These calcareous coal balls contain much preserved plant materials (Tian, 1979; Tian & Zhang, 1980; Li, 1983, 1986a,b).

The second locality of Chinese coal balls has been discovered at Ximing Coal Mine, Taiyuan City, Shanxi Province of the central China in 1980. The coal balls were found in an exposed section beside a road, and are of Upper Carboniferous age. Plant tissues are very-preserved in the coal balls. Lycopods, <u>Sphenophyllum</u>, <u>Calamites</u>, <u>Psaronius</u>, ferns, <u>Cordaites</u> and other plants have been identified (Feng, 1981).

Recently, another locality in China at which the coal seams contain siliceous coal balls was reported by Qiu et al. (1985) from Fengjiangxi Coal Field of Shaoyang, Hunan Province of south China, the Upper Permian age. The

primary mineral component of the coal balls is SiO<sub>2</sub> of which the percentage is 85.35% of the total mineral compounds of the coal balls. Some preserved fern roots have been identified.

### MATERIALS AND METHODS

The coal ball specimens reported in this study were collected by Dr. Aureal T. Cross and his students in 1965, 1966 and 1967 from the Derringer Corners, Lawrence County, Western Pennsylvania, near the boundary between Ohio and Pennsylvania. This was the second record of good, plant rich coal balls in the Appalachian region. The collection was made from the smaller of two, laterally contiguous, concretionary masses of coal balls (Fig.1, 2, Pl. 1) which was about 1.2 m high, and 1.8 m wide, occupying the whole thickness of a thin, local coal below the Washingtonville marine shale and above the Middle Kittanning coal. This Middle Alleghenian position correlates with upper Desmoinesian, near the top of the Carbondale group of the Eastern Interior Basin and is very close stratigraphically to the well-known coal ball rich seams, Herrin (No.6) and Harrisburg (No.5) coals of Illinois (Cross, 1967). These coal balls are of upper Middle Pennsylvanian age.

This was a very large, coherent mass of coal ball concretions. It was so big that it was impossible to

collect the whole mass. The projecting portion of the coal ball mass, which protruded Ø.6 m from the highwall (mineface) in this surface mine, was then broken down by sledges and hammers, and all the fragments of coal balls, over 300 pieces weighing several tons, were collected. The uppermost layers of the concretionary mass of coal balls contained some marine animal fossils, such as bryozoans and brachiopods, intermixed with plant detritus. The base of the concretion contained more lycopods, which may help in determining the positions of coal balls in the fragments which constituted the original concretionary mass.

Standard peels, slides, and photographic techniques were used. Coal balls and broken specimens were cut into thicknesses of about 5 cm. Cellulose acetate peels were made from each surface. The numbering system for locating the peels is as follows: A-B-C-a (or -b), where A is the number of one coal ball, B is the number of total slices of the coal ball, C is the slice from which the peel was made, "a" represents the top, and "b" indicates the bottom of the slice. 25-7-5a means, for example, that the number of the coal ball is 25, cut into 7 slices, and the peel was made from the top of the 5th slice. When desirable, peels of transverse sections and longitudinal (radial and/or tangential) sections of the same cells, tissues or organs were made simultaneously in order to correlate the transverse sections of plant organs

with those of longitudinal sections, thus obtaining threedimensional views of some of the coal ball plants.

For making permanent slides, the selected portions of peels were dried by air, and mounted on glass slides with Kleermount Resin.

EDTA (Ethylinediamine tetraacetic acid) solution was used to dissolve the embedding carbonate matrix from a few leaves to reveal whole alethopterid pinnules with complete cuticles and other pinnule tissues which could be studied in original form and structure. The technique of EDTA preparation of these fossils will be discussed in detail later.

Both light microscope and SEM photographs of peel sections and cuticles were prepared.

All specimens are housed in the Paleobotanical Collections, Department of Geological Sciences, Michigan State University.

# DESCRIPTION OF THE PTERIDOSPERMAE

The Pteridospermae, or seed ferns, may be tersely defined as plants with fern-like foliage on which seeds were borne. A new class, the Cycadofilices, that seemed to share vegetative characters of ferns and cycads was created for this group (Grand'Eury, 1877; Williamson, 1887; Schenk, 1889; Potonie, 1899). Oliver and Scott(1904) correlated the cupulate seed (Lagenostoma) with <u>Sphenopteris</u>-type leaves and stems (<u>Lyginopteris</u>) based on the similarity of the capitate glands borne upon all parts of the plant and established the new class Pteridospermae for "those Cycadofilices that bore seeds". Oliver and Scott's discovery was an epochal mark in the history of paleobotany. From that time on, the actual attachments of seeds to <u>Sphenopteris</u>, <u>Neuropteris</u>, <u>Pecopteris</u>, and <u>Alethopteris</u> leaf types have been demonstrated (Kidston, 1904; Halle, 1929, 1933).

The Pteridospermae include a large and diverse plant group, and has been classified differently. According to Taylor (1981), the Division Pteridospermophyta includes eight orders: Lyginopteridales, Medullosales, Callistophytales, Calamopityales, Caytoniales, Corystospermales, Peltaspermales, and Glossopteridales. Stewart (1983), however, classified pteridosperms as Pteridospermales, one of the orders of Cycadophytes; and he included four wellknown groups, given family ranking: Lyginopteridaceae, Medullosaceae, Callistophytaceae and Calamopityaceae in the Pteridospermales. In the present thesis, the latter classification is used.

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#### LYGINOPTERIDACEAE

Lyginopterid Stems:

Schopfiastrum decussatum Andrews

(PLATE 2)

- Andrews, 1945, p. 350, pl. 10, figs. 17-18; p. 352, pl. 11, figs. 20-21; p. 360, pl. 15, fig. 36.
- Rothwell and Taylor, 1972, p. 2650, fig. 1; pl. 1-4, figs. 2-24; p.2653, fig. 25.
- Stidd and Phillips, 1973, p. 465, figs. 1-11; p. 467, figs. 12-19; p.469, figs. 20-32; p. 471, figs. 33-46; p. 472, figs. 47-48.

Comments:

Besides the pteridospermous stem features (i.e., massive leaf traces, alternate rows of bordered pits on radial walls of secondary tracheids, and longitudinally oriented sclerenchyma bands in the outer cortex, the diagnostic features of this monostelic pteridosperm are the rectangular outline of the primary xylem of the stem in cross section, longitudinally oriented, amber colored ducts (resin canals) in inner cortex, and petioles with abaxial, toothed vascular bundle. Andrews' original description (1945) was limited to cauline anatomy and suggested that the leaf arrangement was, as the specific epithet indicated, subopposite and decussate, based on inference from the disposition of protoxylem groups. Rothwell and Taylor (1972) and Stidd and Phillips (1973) independently observed that the leaf arrangement is alternate and distichous, which is not known from other Upper Carboniferous seed ferns but is the characteristic of the Lower Carboniferous genus <u>Protopitys</u> (Solms-Laubach, 1893; Scott, 1923). Now several orders of branching of the rachis with W-, Y-, or V-shaped vascular bundles, exarch, protostelic, adventitious roots, and <u>Mariopteris</u> type pinnules have been described.

Description of the Derringer Corners Specimens:

The principal specimen consists of a crushed stem fragment 3 cm long bearing one petiole. The maximum and minimum diameters of the stem are 3.1 cm and Ø.9 cm respectively.

The protostelic, exarch primary xylem is rectangular in cross section (Pl. 2, Fig. 1) and composed of protoxylem strands and metaxylem. The protoxylem strands are very small so that in the crushed stem only 3-4 protoxylem strands can be recognized. Tracheids of the protoxylem are about 10-15 Jum in diameter and show spiral wall-thickening (Pl. 2, Fig. 5, 6). The main constituents of the primary xylem are the large metaxylem tracheids which are mostly pentagonal in cross section measuring about 50-60 Jum in diameter. They exhibit bordered pitting wall-thickening. Alternate, crowded, horizontal, elongated pits are present on both radial and tangential walls (Pl. 2, Figs. 5, 6). A few metaxylem tracheids adjacent to protoxylem have relatively small diameter (30-40 Jum) and are characterized by a scalariform thickening pattern (Pl. 2, Figs. 5, 6). In the metaxylem zone, there are a few scattered, parenchyma cell strands that are mostly one cell wide and 10-15 cells high in longitudinal section.

Secondary xylem is conspicuous and up to 3.0 cm thick. It is composed of tracheids and xylem rays. The xylem rays are interspersed to divide the xylem into radially aligned segments, the width of which varies from one to 4 cells (Pl. 2, Fig. 3). Tracheids of the onecell wide segments are pentangular in cross section, about 35-55 Jum in diameter. 4-7 rows of alternate, crowded, angular, bordered pits with crossed apertures are present on the radial walls similar to those of metaxylem.

The xylem rays are uniseriate or multiseriate. Vascular cambium and secondary phloem are rather poorly preserved. Between immature secondary tracheids and phloem there is a vascular cambium zone. There is a thin zone of phloem composed of sieve cells and phloem rays. Sieve cells are 20-25 Jum in diameter. Sieve area and sieve pores have been observed on both cross section (Pl. 2, Fig. 3) and longitudinal section (Pl. 2, Fig. 7). Phloem rays are opposite to xylem rays forming continuous rays from secondary xylem through secondary phloem (Pl. 2, Fig. 3). Cells of the phloem rays are roughly isodiametric measuring 20-25 Jum in diameter.

Conspicuous canals that contain amber-colored

material surround the secondary phloem and are scattered in the outer cortex (Pl. 2, Fig. 1). The canals are oval in cross sectional outline and up to 0.2 x 1.0 mm in cross section. They are elongated vertically measured to 9.0 mm without ends visible (Pl. 2, Fig. 4). The canals have been interpreted as resin canals (Rothwell and Taylor, 1972).

Primary cortex is about 2.0 mm thick. In the outer part of the cortex there are radially elongated sclerenchymatous strands. Neither fusing nor branching of the sclerenchyma strands has been observed in longitudinal section (Pl. 2, Fig. 2). No periderm is present.

An isolated petiole with an abaxial, toothed vascular bundle and an attached rachis with an Y-shaped vascular bundle has been observed (Pl. 2, Fig. 8).

## Heterangium crossii sp. nov.

(PLATES 3 - 6)

Pteridospermales Lyginopteridaceae <u>Heterangium</u> Heterangium crossii Feng

### Diagnosis:

Stems up to 1.1 cm in diameter with mixed protostele; 1-, 2-, or 3-celled groups of metaxylem tracheids are randomly arranged in ground parenchyma. Primary xylem is pentagonal in cross section and divided into 5 sections by longitudinal parenchyma plates that radiate from the stem center.

Protostele is exarch. The protoxylem strands are distinct at periphery of the primary xylem. Some protoxylem strands are in pairs, one strand on each side of a parenchyma plate; some are single. Total number of the protoxylem strands: as many as 18 counted.

Secondary xylem conspicuous, 2 mm thick with uni-, bi-, or triseriate rays. Sieve cells of secondary phloem with numerous sieve pores on walls without differentiation of sieve plate.

Prominent periderm layer on periphery of the secondary phloem consists of phelloderm and phellem. Peripheral cortex is composed of 6-7 cell layer of normal ground parenchyma and 2-3 cell layers of small, sclerotic cells at outermost cortex. Epidermis consists of one layer of small cells. The cuticle is about 10 um in thickness. The petiole contains a bilobed vascular bundle.

## Holotype:

Slides and peels of specimen of coal ball MSUCB S8 are deposited in the Paleobotanical Collections, Department of Geological Sciences, Michigan State University, East Lansing, MI 48824. All figures present on Plates 3-6.

Etymology:

The specific epithet "crossii" is in honour of Dr. Aureal T. Cross for his contributions to paleobotany and for his collection and study of the Derringer Corners coal balls studied in detail in this dissertation.

# Locality and Age:

A local coal below the Washingtonville marine shales and above the Middle Kittanning Coal at Derringer Corners, Lawrence County, western Pennsylvania; the age is the upper Middle Pennsylvanian, Allegheny Formation.

## Description:

The new species is based on 3 stem segments. The stems are up to 11 mm in diameter. The primary xylem is monostelic and the mixed protostele measured 3-4 mm in diameter. Metaxylem tracheids of the primary xylem are 1-, 2- or 3- celled in groups and surrounded by parenchyma cells. The metaxylem tracheids are roughly circular in cross section and range up to 260 Jum in diameter (Pl. 3, Figs. 1, 5). Longitudinal sections show metaxylem tracheids with tapered ends that exhibit scalariform thickening or multiseriate, crowded, bordered pits on the walls (Pl. 4, Figs. 3, 4). Parenchyma cells which form a one- or two- cell thick layer surrounding the metaxylem tracheid strands are small and elongated peripherally.

Parenchyma cells between the metaxylem tracheids are relatively larger and up to 80 µm in diameter.

The protostele of the primary xylem is divided into 5 sections by longitudinal parenchyma plates that radiate from the stele center (Pl. 3, Fig. 1). The parenchyma plates are 3-4 cells wide and connected with rays of the secondary xylem (Pl. 4, Fig. 1). The cells of the parenchyma plates are square or slightly elongated parallel with the length of the stem and exhibit scalariform thickening on the walls, while the cells of the rays of the secondary xylem are horizontally elongated and without sclerotic thickening (Pl. 3, Fig. 4). Among the parenchyma cells of the protostele, the same type of scalariform cells also can be observed on both cross- and longitudinal sections (Pl. 3, Fig. 2).

The primary xylem is exarch; protoxylem strands occur on the periphery. Some protoxylem strands are single, others are in pairs, one strand on each side of the parenchyma plate. The single protoxylem strands are larger and more distinct than the paired ones (Pl. 4, Figs. 1, 2). As many as 18 protoxylem strands have been identified in a single stem. The protoxylem strands protrude into the secondary xylem, resulting in an undulating inner margin of the secondary xylem in cross section (Pl. 4, Figs. 1, 2). The elements of protoxylem are 10-20 Jum in diameter and show spiral and/or scalariform wall thickenings (Pl. 4, Figs. 3, 4).

Secondary growth is conspicuous in two specimens. Secondary xylem is about 2 mm thick (Pl. 4, Fig. 1; Pl. 5, Fig. 7). The tracheids of the secondary xylem vary in size and shape. Generally, they are smaller than those of the metaxylem and are as much as 160 Jum in diameter. They are rectangular or polygonal in cross section with multiseriate, crowded, bordered pits present on the walls (Pl. 4, Fig. 4). Uni-, bi-, or triseriate rays are interspersed in the secondary xylem (Pl. 4, Figs. 1, 3). The rays that abut the protoxylem strands or the parenchyma plates of the primary xylem are usually, if not always, wider than others. No parenchyma cell with secondary thickening has been observed in the rays. Vascular cambium and secondary phloem are poorly preserved. However, in some places, sieve cells of the secondary phloem can be recognized in both cross section (Pl. 4, Fig. 5) and longitudinal section (Pl. 4, Figs. 6, 7; Pl. 5, Figs. 1-4).

Outside the secondary phloem zone there is a layer of cells most of which have very thick walls and small lumens. This is phellem. The cells are almost isodiametric (Pl. 5, Figs. 5, 6). Between the secondary phloem zone and the phellem area there is a layer of tangentially-elongated, thin-walled parenchyma cells. This layer may represent phelloderm.

Most outer cortex was destroyed due to the formation of periderm. In one cross section, a small

amount of outer cortex and epidermis are intact (P1. 5, Fig. 6). Outside of the phellem the cortex is composed of a 4-5 cell-wide zone of parenchyma cells and a 2 cell-wide sclerotic layer; no sclerotic strands have been identified. Epidermis is a layer of small compact cells with rather thick cuticle (about 10 um).

In serial cross sections, 3 leaf traces have been observed. The specimen is not long enough to determine the phyllotaxy. All three leaf traces occur adjacent to the parenchyma plates of the primary xylem and are bilobed; i. e., each of these leaf traces arises from a pair of the protoxylem strands located on each side of the parenchyma plate. However, it is observed that, in longitudinal section, a leaf trace arises from a single protoxylem strand not adjacent to parenchyma plate.

The leaf traces depart from the stem very slowly. In a distance of about 10 mm, the leaf trace is almost parallel to the stem axis (Pl. 6, Fig. 4). After passing through the secondary xylem, leaf traces are surrounded by phellem (Pl. 6, Fig. 1). The leaf trace is composed of spiral and scalariform protoxylem elements, metaxylem tracheids, possessing bordered pits with roughly horizontal elongated apertures, and primary phloem (Pl. 6, Figs. 2, 3).

At the base of petiole, leaf trace becomes alate in cross section near a dichotomy (Pl. 3, Fig. 5).

Another young stem specimen with little secondary

growth is 4 mm in diameter. In primary xylem, only 3, instead of 5, parenchyma plates are obviously present (Pl. 3, Fig. 5). It seems likely that the number of the parenchyma plates varies and increases with stem growth. Most extrastelar tissue have been destroyed so that the outer cortex and epidermis are not preserved.

### Discussion:

Heterangium is a well-known pteridosperm genus which mainly includes stem and petiole remains. The genus was founded by Corda in 1845, based on fragmentary stem specimens from the coal balls of Bohemia, of middle Coal Measures age. As the generic name indicates, originally Corda interpreted the wood to be composed of two kinds of vessels, large ones and small ones. The larger elements are the tracheids of primary wood; but the smaller ones were confused with the intermingled parenchyma cells. According to the comprehensive work of Scott (1917), the genus is characterized mainly by a mixed mesarch, protostelic stem with sclerenchyma bands in the outer cortex and horizontal sclerenchyma plates in the inner

Scott recognized two subgenera based mainly on leaf trace emission: 1) subgenus <u>Heterangium</u> (= <u>Euheterangium</u>; the prefix Eu- is not allowed according to Article 21 of the Botanical Code (ICBN)): leaf traces are simple when initiated, and the protoxylem area is poorly

defined ; 2) subgenus <u>Polyangium</u>: leaf traces are initially double; protoxylem strands are well defined and approach the exarch condition.

Most species of the genus have been reported from England. <u>Heterangium americanum</u>, the first species described from North America (Andrews, 1942), was distinguished by the small size of metaxylem tracheids groups (2- or 3-celled). The species is assigned to the subgenus Polyangium.

Shadle and Stidd (1975) reported four orders of branching of fronds of <u>Heterangium americanum</u> which is vascularized by 2-10 traces depending on the levels where the sections were cut. According to the authors, the fronds of <u>H</u>. <u>americanum</u> may be correlated with the compression fossil <u>Sphenopteris obtusiloba</u>. The assignment of the fronds to <u>H</u>. <u>americanum</u> is not based on organic connection but upon anatomical features common on both stem and frond, such as cortical sclerotic plates, outer fibrous cortex, epidermal features (including cuticle), and xylem pitting.

Another monostelic, monotypic genus <u>Microspermopteris</u> was initially described by Baxter (1949, 1952), and emended by Taylor and Stockey (1976). The mixed protostele of <u>M. aphyllum</u> is very close to that of <u>Heterangium</u>. The differences between the two genera are as follows: 1) the primary xylem of <u>Microspermopteris</u> is divided into 5 sections by longitudinal parenchyma plates

that extend radially from the stem center, whereas the parenchyma plates are absent in the primary xylem of <u>Heterangium</u>; 2) in <u>Heterangium</u>, the protoxylem strands are mesarch and occur singly on the periphery, whereas exarch protoxylem strands occur in pairs, one strand on each side of a parenchyma plate in <u>Microspermopteris</u>; 3) <u>Heterangium</u> fronds possess 2-10 vascular bundles, but only a single Cshaped trace is present in Microspermopteris.

Stidd (1979) has, however, described a new species, Heterangium lintonii, the second species of Heterangium reported from North America. The species appears to share more features with Microspermopteris aphyllum in exarch protoxylem and the radially aligned parenchyma in primary xylem, though, according to Stidd, the longitudinal continuity of the radially aligned parenchyma was not observed in H. lintonii. The principal difference between the two species is the position of protoxylem strands and leaf traces. In H. lintonii, a single trace becomes double in the petiole base, and protoxylem strands occur singly on the periphery; whereas the petiole has a C-shaped single trace and protoxylem strands occur in pairs in Mircospermopteris. Therefore, H. lintonii shows very close affinity to M. aphyllum.

Pigg at el. (1986) described a stem of <u>Microspermopteris</u> aphyllum with an axillary branch and petiole attached. According to these authors, the frond of

the stem consists of three orders of branching, and the pinnules are 2-, 3- or 4- lobed. This study adds differentiating features of branch and frond between the two genera, <u>Heterangium</u> and Microspermopteris.

Taylor and Stockey (1976) pointed out that until the reproductive organs are known from both <u>Microspermopteris</u> and <u>Heterangium</u>, petiole anatomy would continue to be the distinguishing character between these two genera.

It is of interest to note that the Derringer Corners specimen shows the features of both <u>H</u>. <u>lintonii</u> and <u>M</u>. <u>aphyllum</u>. It bears extremely close resemblance to <u>H</u>. <u>lintonii</u> in primary xylem structure, leaf trace emission and prominent periderm layers; but its radially aligned parenchyma forms longitudinally continuous plates dividing the protostele into 3 to 5 sections similar to the condition of <u>M</u>. <u>aphyllum</u>. The exarch protoxylem strands of the Derringer Corners specimen occurs on the periphery, some of which singly randomly distributed, as in <u>H</u>. <u>lintonii</u>, and some in pairs, one strand on each side of parenchyma plate as in M. aphyllum.

The sieve cells of secondary phloem of the Derringer Corners specimen are without definite sieve plates which differs from the presence of horizontal sieve plates in sieve cells of <u>H</u>. <u>americanum</u> (Hall, 1952).

Since the petiole anatomy is thought to be the distinguishing feature for the two genera, Heterangium and

<u>Microspermopteris</u>, the Derringer Corners specimens, with double traces at the petiole base, is assigned to <u>Heterangium</u>. Because some leaf traces are initiated singly, while some are initially double, it seems to be proper not to place the Derringer Corners specimens into any subgenus of <u>Heterangium</u>.

With the link of the Derringer Corners specimens, the new species <u>H</u>. <u>crossii</u>, the structures of stems, especially vasculature, <u>H</u>. <u>lintonii</u>, <u>H</u>. <u>crossii</u>, and <u>M</u>. <u>aphyllum</u> are so close to each other that it is possible that the three species may represent different portions or different developmental stages of the plants within the same species, or the same genus. The difference of frond and branch between these two genera may indicate only an interspecific difference. It is better, for the time being, to leave the relationship of the three species open to question until more information about fronds and reproductive organs are available.

## MEDULLOSACEAE

Medullosan Stems:

## Sutcliffia insignis (PLATES 7-10)

Scott, 1906, p. 69-72, pl. 7-10, figs. 1-22. de Fraine, 1912, p. 1032-1035, figs. 1-5; p. 1036, figs. 6-7; p.1038, fig. 8; p. 1040, fig. 9; p. 1043, fig. 10; p. 1044, fig. 11-13; p.1048-1053, figs. 14-19.

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C t 1 a C 18 We th to se en pro Par "Di con trac 8tra Comments:

<u>Sutcliffia insignis</u>, a medullosan stem genus, was originally described by Scott (1906). The specimen from the Lower Coal Measures of Lancashire, England, measuring 12 X 65 cm in diameter, and the detached petioles were of about the same size. The vascular system of the stem is composed of massive stelar segments of which one or two large ones occupied the central part of the stem, and were more or less surrounded by smaller stelar segments that departed from the central ones and in turn continued to divide to produce the leaf traces. The large stelar segments consist of a massive amount of primary xylem enveloped by weakly developed secondary xylem.

The exarch primary xylem is composed of protoxylem and large metaxylem tracheids with interspersed parenchyma so that the large stelar segments are exarch "mixed" protostele. The leaf traces were thought to be concentric (traces with phloem surrounding xylem) and each trace was surrounded by a ring of sclerenchymatous strands.

de Fraine (1912) described the same species also

from the Lower Coal Measures of Lancashire, England and prepared a restoration drawing of the cauline vascular system in which one or two large central segments divide and anastomose repeatedly, with some smaller vascular divisions departing as leaf traces.

It was not until 1963 that Phillips and Andrews reported the occurrence of <u>Sutcliffia</u> with the petiole attached from a middle Pennsylvanian coal ball from Illinois. The Illinois' specimens were not very well preserved anatomically and were regarded as being closely related to the English species with the exception of the presence of rather massive cortical emergences. Therefore, Phillips and Andrews named the Illinois specimens as a variety of <u>Sutcliffia insignis</u>, <u>Sutcliffia insignis</u> Scott var. <u>tuberculata</u>.

Stidd et al. (1975) described <u>Sutcliffia</u> foliage members from seven localities of the Illinois Basin ranging in age from the Middle to Upper Pennsylvanian. According to the authors, the fronds were large, probably 3-4 m long and 4-5 times pinnate. A diagrammatic drawing depicting a suggested relationships among isolated frond members of <u>Sutcliffia</u> was made. With the exception of the petiole attached to the stem, the attachment of these frond members to the stem was not known. The criteria used by Stidd et al. (1975) to identify isolated <u>Sutcliffia</u> frond fragments are as follows: 1) fewer and larger bundles; 2) concentric bundles enclosed by fiber rings or

embedded in outer sclerenchyma zone; 3) arrangement of vascular bundles; 4) the quite large emergences on the surface. In their report, no pinnule had been found attached to any branching order of the pinna.

Based only on the association of <u>Linopteris</u> pinnules with <u>Sutcliffia</u> in every coal ball used in their study, Stidd et al. (1975) suggested that <u>Linopteris</u> pinnules were borne on <u>Sutcliffia</u> fronds.

An anatomically preserved pteridosperm pollen organ was identified by Stidd (1978) with the compression fossil, <u>Potoniea</u>. Because the <u>Potoniea</u> specimens were associated with "net-veined (<u>Reticulopteris-Linopteris</u>), Stidd (1978) further suggested that <u>Potoniea</u> might have been borne on fronds of <u>Linopteris</u> which , in turn, was believed by Stidd et al. (1975) to have been borne on Sutcliffia stems (Stidd, 1978).

Description of the Derringer Corners Specimens:

Several specimens of <u>Sutcliffia</u> have been found from the Derringer Corners coal balls. But the description of <u>Sutcliffia</u> here is mainly based on one specimen (M.S.U. CB 342-9). It is about 16.5 cm long; the cortex is not completely preserved, but the stem is about  $6.0 \times 9.0$  cm in cross section. Some stelar segments and leaf traces are preserved very well. The central segment is the largest one, about 1.5 x 3.5 cm, and it is surrounded by a number of small stelar segments (Pl. 7, Fig. 1).

The stelar segments are exarch mixed protosteles (Pl. 7, Figs. 2, 4). The number of the protoxylem strands increases with increasing sizes of stelar segments. In the central segment, there are as many as 15 protoxylem strands. Elements of the protoxylem strands are rather small, 20-25 Jum in diameter exhibiting annular or spiral wall thickening (Pl. 7, Fig. 6; Pl. 8, Fig. 3). Conspicuous metaxylem tracheids, up to 300 um in diameter, are circular or polygonal shape in cross sectional outline. They are isolated or in groups of 2-5 cells interspersed with parenchyma cells (Pl. 7, Figs. 1, 2). On both tangential and radial walls of the metaxylem tracheids, there are multiseriate, crowded, circular bordered pits with elongated apertures (Pl. 7, Fig. 6) or scalariform thickenings (Pl. 8, Fig. 3). The parenchyma cells are slightly, horizontally elongated in both tangential and radial sections.

Most stelar segments have weak secondary growth (P1. 7, Figs. 1, 2). A layer of bifacial vascular cambium, 3-6 cells wide radially, produces secondary xylem centripetally and secondary phloem centrifugally. The fusiform initials are brick-like, elongated tangentially in cross section and vertically in longitudinal section (P1. 7, Figs. 5, 7).

The secondary xylem is composed of tracheids and xylem rays. The width of the secondary xylem is correlated with the sizes of the stelar segments, varying from 1 to

15 cells. Tracheids of the secondary xylem are much smaller than those of the metaxylem, and up to about 100 um in diameter. They are square or polygonal in cross section. Multiseriate, circular, bordered pits, similar to those of metaxylem tracheids, are present on both tangential and radial walls (Pl. 7, Figs, 6, 7).

Multiseriate rays of the secondary xylem are strongly developed, dissecting the secondary xylem into isolated radial rows. The rays are even wider than the secondary xylem tracheid zone, tangentially (Pl. 7, Fig. 4, 5).

Primary phloem of stem steles of <u>Sutcliffia</u> have not been previously described and it was not observed in the Derringer Corners specimens.

Some information about secondary phloem is available from previous authors. In the original description, Scott (1906) reported that near the wood some well-defined, small elements which were greatly elongated with tapered ends were present. He wrote "presumably they represent the sieve tubes". Scott illustrated the phloem with one sketch showing wall structure, but no photograph was presented. De Fraine (1912) presented a sketch showing some thick-walled elements of secondary phloem of <u>Sutcliffia</u> in cross section but no wall structure was illustrated. Phillips and Andrews (1963), Stidd et al. (1975) did not mention the phloem of <u>Sutcliffia</u> stems.

In the Derringer Corners specimens, secondary

phl is The abo ph] squ dia ini of cer sec dis ce] tar the Vit Po PO On le th 50 Of Per the phloem of the stem is well-preserved. The secondary phloem is composed of sieve elements, rays and parenchyma cells. The thick-walled sieve elements, of which the walls are about 10 Jum thick, are distinctively different from other phloem elements (Pl. 7, Fig.5). In cross section, they are square or polygonal in shape, measuring about 40 Jum in diameter, and disposed immediately outside of fusiform initials of vascular cambium (Pl. 7, Fig.7). Ray initials of the vascular cambium produce the secondary xylem rays centripetally and secondary phloem rays centrifugally. The secondary phloem rays connecting with secondary xylem rays dissect sieve elements into radial rows which are about 20 cells thick radially (Pl. 7, Fig. 5).

The sieve elements are greatly elongated with tapered ends. On both tangential and radial sections, most the sieve elements show smooth, light-brown colored walls without exhibiting sieve area structure. But several that possess dark-brown walls do show evenly distributed sieve pore structures on radial sections (Pl. 8, Figs. 3, 4). In one of the sieve elements, the sieve pores are more or less arranged horizontally (Pl. 8, Figs. 5, 6) similar to those of <u>Heterangium americanum</u> described by Hall (1952). No defined sieve area was observed on lateral walls.

Among phloem parenchyma cells there are a number of secretory cells containing dark material that exhibit perforations or holes somewhat similar to sieve pores of the sieve elements. These cells are almost isodiametric,

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and are therefore by no means sieve elements (Pl. 7, Fig. 5; Pl. 8, Fig. 3).

A sieve plate-like structure has been observed on a end of one sieve element. Because of its position it may represent a sieve plate. If this interpretation is correct, at least some of the sieve elements of <u>Sutcliffia</u> <u>insignis</u> stem are sieve tubes, instead of sieve cells which are typical in gymnosperms and lower vascular plants.

Stelar segments vary in size. Some give rise to several leaf traces. In cross section, some leaf traces near stelar segments are not surrounded by sclerenchyma strands and are difficult to distinguish from small stele segments. Each leaf trace possesses either paired protoxylem strands as described by Scott (1906) and de Fraine (1912) or two isolated protoxylem strands, or only one protoxylem strand (Pl. 9, Fig. 1).

One diagnosis of <u>Sutcliffia</u> distinguishing it from <u>Medullosa</u> is that the leaf traces are concentric (traces where phloem surrounds xylem), rather than collateral (traces where phloem is outside of xylem) as in <u>Medullosa</u>. In his original description, Scott (1906) observed that xylem of a leaf trace was surrounded by a ring of large elements which simply appeared to be long tubes in longitudinal section and which were usually separated from one another by small cells. These elongated tubes were different from both tracheids and secretory canals, and

suggested by Scott to be sieve tubes. However he wrote "I have not been able to detect any characteristic markings on their walls. ... We may hope that more perfect longitudinal sections may ultimately furnish decisive evidence." (Scott, 1906 p. 58-59).

Because no such a decisive evidence of such sieve tubes had been reported since Scott's original publication, Basinger et al. (1974), Taylor (1981), and others presumed that <u>Sutcliffia</u> might just be a species of Medullosa.

The well-preserved Derringer Corners specimens make it possible to provide sufficient evidence to determine the position of phloem elements in leaf traces. Over 200 peels showing serial cross sections and longitudinal sections of the leaf traces were prepared for the present study. The observations are as follows:

1) In longitudinal sections, greatly elongated elements measuring about 30 um in diameter, occur on both sides of xylem elements of leaf traces. Sieve pores similar to those of sieve elements in the stele segments have been observed on lateral walls of these elongated tubes. These tube-like cells are sieve elements with certainty. In cross sections, vascular cambium cells have already developed between the sieve elements and xylem strands (Pl. 9, Fig. 2). This indicates that these sieve elements are secondary.

In this case, there is no evidence to determine

the leaf trace is either concentric or collateral because the terms of both concentric and collateral are usually delimited to describe primary vascular systems.

2)Sieve elements of primary phloem occur on both sides of leaf traces with only primary growth (Pl. 9, Fig. 4). The sieve elements which have sieve pores on the walls are of the primary phloem (Pl. 9, Figs. 5, 7). They are about 30 Jum in diameter, and different from those of the secondary phloem in their shorter length and usually 3-5 times the width, similar to those described by Scott (1906) in the thin walls which are not easily distinguished from surrounding parenchyma cells in cross section.

In tangential section, at the periphery of the primary xylem of the trace, branch-like arrangement of sieve element strands of the primary phloem have been observed (Pl. 9, Fig. 8), which correlates with Scott's description (1906, fig. 20).

3) Serial cross and longitudinal sections have been made of a typical leaf trace. This is closely identified with that originally described by Scott (1906) in the way that it possesses only primary xylem surrounded by a ring of conspicuous large and greatly elongated tube like cells ("sieve tube" by Scott). The whole leaf trace in turn is surrounded by a ring of sclerenchyma strands (PL. 10, Fig. 1).

Longitudinal sections through the ring of the

tube-like cells demonstrated that these tube-like cells are indeed sieve elements (Pl. 10, Figs. 1-4). Although most of their wall structures are not preserved, these sieve elements are quite different from tracheids. On cross section, the sieve elements are thin-walled and small, and are separated by parenchyma cells from the xylem strands. Partially destroyed or poorly preserved tracheids usually, if not always, can be identified by the presence of complete pits, sectioned pits, or even by pit apertures remaining on tracheid walls (Pl. 10, Fig. 6). In contrast, the remnant walls of the sieve elements show numerous sieve pores. In spite of some slightly elongated sieve pores similar in shape to the apertures of the tracheid pits, the sieve pores are quite different from the tracheid apertures.

It is concluded, with confidence, that the leaf traces of <u>Sutcliffia insignis</u> are concentric. But the taxonomic significance of this feature remains in question.

Several detached petioles have been found. They are characterized by a peripheral ring of leaf traces embedded in sclerenchyma tissue of outer cortex, and by concentric leaf traces and a ring of sclerenchyma strands surrounding each leaf trace.

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### Medullosan Leaves

Comments:

The form genus <u>Alethopteris</u> was established by Sternberg (1825) for certain Upper Paleozoic fern likeleaf compressions which have since proven to be an abundant and widespread element of the world's Pennsylvanian floras (Baxter and Willhite, 1969). <u>Alethopteris</u> is characterized by broadly attached pinnules which possess a prominent midrib, open dichotomous venation, rachial (subsidiary) veins and decurrent base.

In his monograph of <u>Alethopteris</u>, Wagner (1968) studied the compression specimens of <u>Alethopteris</u> from Europe (Spain, British, Isles, France, Germany, Czechoslovakia), North America (the United States and Canada), and Asia Minor (Turkey) of the Upper Westphalian and Stephanian (=the Middle and Upper Pennsylvanian in North America). He listed 29 species and varieties. The classification of the genus is based on the external morphological features. Furthermore, since the foliage remains are often fragmentary, i.e. dispersed compound pinna or pinnules, species have frequently been defined based on external morphology of the pinnule.

Of the genus, only two species, <u>Alethopteris</u> <u>sullivantii</u> and <u>Alethopteris</u> <u>lesquereuxii</u>, have been described from the North American coal balls of Middle Pennsylvanian age (Leisman, 1960; Baxter and Willhite,
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1969; Reihman and Schabilion, 1976a,b, 1985; Oestry-Stidd and Stidd, 1976). Silicified pinnules of <u>Alethopteris</u> <u>aguilina</u> were reported from Stephanian or Autunian of France (Rothwell, 1980a). Foliage segments of <u>Alethopteris</u> have been described from the Upper Pennsylvanian deposits of Illinois and Ohio (Schopf,1948; Ramanujam et al., 1974; Mickle and Rothwell, 1982).

Because fertile pinnules have not been found (i.e. no fern sporangia have been identified on these pinnules) and because of the occasional discovery of foliage specimens with large seeds attached (Halle, 1927; Arnold, 1947, p. 221, fig. 106 B), the affinity of <u>Alethopteris</u> to pteridosperms has long been recognized. The frequent association of dispersed leaf compressions of <u>Alethopteris</u> with compressions of the medullosan pollen organ genus <u>Dolerotheca</u> and with the seed genus <u>Pachytesta</u> further suggests that <u>Alethopteris</u> constituted at least one of the leaf types borne by the medullosan stem genus <u>Medullosa</u>.

Halle (1927) reported a seed-like body borne on a pinna of <u>A. norinii</u>, but a few years later, he suggested that the seed-like body might be a microsporangium (Halle, 1933). Stidd (1981) pointed out that some ovules of <u>Trigonocarpus</u> (compression seed genus of <u>Medullosa</u> identified with <u>Pachytesta</u> in coal balls), such as the specimens described by Gastaldo and Matten (1978), were very large, about 10 cm long, so that, he wrote, "It is difficult to believe that ovules of this size were borne

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at pinnae tips or even on the abaxial surface of an ultimate pinna rachis"; and "if they were, I should think the weight of such an ovule would cause the frond to bend abruptly".

In spite of the uncertainty of the seeds borne on Alethopteris leaves, anatomical evidence found from coal balls further supports the affinity of Alethopteris with Medullosa. Similar mucilage canals, sclerotic strands, multicellular hairs, and numerous scattered collateral vascular bundles are found in both the medullosan petiole Myeloxylon and the rachis and the ribs of Alethopteris sullivantii (Leisman, 1960). Because of the structural similarity between the penultimate pinna of Alethopteris and the peduncle of Dolerotheca, such as the number and arrangement of the vascular bundles, presence of the secretory canals and multicellular hairs, the structure of the ground tissue, and the absence of groups of hypodermal sclerenchyma strands, Ramanujam et al. (1974) concluded that Dolerotheca replaces a pinna on the peduncle, and is homologous with a penultimate pinna of Alethopteris.

By splitting coal balls randomly or along internal bedding planes to expose foliage on the coal ball surface, Leisman (1960) was the first to correlate anatomically preserved foliage of <u>Alethopteris</u> in coal balls with compressions of the genus. His study of <u>Alethopteris sullivantii</u> was the first to document the anatomy of a species of Alethopteris, and he provided the

needed permin There generi (Crid1 introd he had and fo Weiss charac Aletho the th Pecopt reduce chose emphas with i from F genera Calli appear genera Consid (1947,) needed evidence for its medullosan relationship.

Originally, Leisman (1960) referred the permineralized specimen to <u>Callipteridium sullivantii</u>. There is a certain amount of confusion in using of the generic name <u>Callipteridium</u> in the United States (Cridland et al., 1963; Taylor, 1981). Weiss (1870) introduced <u>Callipteridium</u> as a generic name for the plant he had previously described as <u>Neuropteridium mirabile</u> and for the specimen of <u>Callipteris sullivantii</u>. Because Weiss used the presence of accessory veins as the generic character, there are numerous transitions to the genera <u>Alethopteris</u> and <u>Pecopteris</u>. Therefore the separation of the three genera, <u>Callipteridium</u>, <u>Alethopteris</u>, and Pecopteris, had become quite difficult.

In his revision of <u>Callipteridium</u>, Franke (1913) reduced <u>C. mirabile</u> to synonymy under <u>C. pteridium</u>, and chose <u>C. pteridium</u> as the type species of the genus. He emphasized that the genus should include only species with intercalated pinnules which distinguishes the genus from <u>Pecopteris</u> and <u>Alethopteris</u>, though the latter two genera share the character of accessory veins with <u>Callipteridium</u>. The presence of the intercalated pinnules appears to be the unique feature of Callipteridium.

Franke's conception of <u>Callipteridium</u> has been generally employed by European paleobotanists. Considering the definition of <u>Callipteridium</u>, Arnold (1947,P.160) wrote: "this form genus is similar to

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<u>Alethopteris</u> and is sometimes confused with it. The pinnules differ from those of <u>Alethopteris</u> in being more blunt and all or only slightly decurrent. It also bears small accessory pinnae on the rachis between the normal pinnae. Some of the small forms resemble <u>Pecopteris</u> except that some of the veins enter the pinnule directly from the rachis."

According to Cridland et al. (1963), Franke's work has been overlooked in the United States where <u>Callipteridium sullivantii</u> (Lesq.) Weiss has been taken as the type species of the genus (Andrews,1955; Leisman, 1960). Because of the absence of intercalated pinnules, Wagner (1968) and Baxter and Willhite (1969) transferred <u>C. sullivantii</u> studied by Leisman (1960) to <u>Alethopteris</u> sullivantii.

Using the same method as Leisman, Baxter and Willhite (1969) described the second species of <u>Alethopteris</u> found in coal balls of Middle Pennsylvanian age from southeast Kansas. Based on strong similarities in size, shape and revolute margin of the pinnules, the authors assigned the specimens to <u>A. lesquereuxii</u>. Photographs of the specimens exposed on the fractured surface of the coal balls were also sent to Wagner who independently arrived at an identification with <u>A</u>. <u>lesquereuxii</u>.

Baxter and Willhite (1969) summarized the anatomical features common to the genus as follows: 1) the pre sub dif lay she bun low sec str cov Ale are Var Can f0] (19 gro fea of Sch Mic Vit <u>1</u> 1 1 1 epi Pap hai presence of a thin, small-celled, upper epidermis subtended by a hypodermis of conspicuously large cells; 2) differentiation of the mesophyll into an upper palisade layer and a lower spongy layer; 3) parenchymatous bundle sheaths and sheath extensions; 4) numerous vascular bundles in rachis; 5) uniseriate multicellular hairs on lower surface; 6) papillae on the abaxial epidermis; 7) secretory canals in rachis and midribs; 8) stomatal structure with sunken guard cells; 9) hair bases which cover one, two, or three epidermal cells.

Wagner (1968) recognized that genera, such as Alethopteris, which were based only on pinnule morphology, are more artificial and may include species of quite varied natural affinities, and that epidermal characters can be extremely useful for classification of pteridosperm foliages. Dealing with cuticles of compressions, Barthel (1962) has found that Alethopteris encompassed several groups of species with distinctly different epidermal features. According to extensive studies of the cuticles of A. sullivantii and A. lesquereuxii (Reihman and Schabilion, 1976a, b, 1978; Oestry-Stidd and Stidd, 1976; Mickle and Rothwell, 1982), these two species were grouped with A davreuxii, A grandini, A aquilina, and A ambigua. This group is characterized by a papillate lower epidermis, sunken stomata surrounded by a ring of papillae, and by the scattered occurrence of multicellular hairs on both the upper and the lower epidermis (Reihman

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and Schabilion, 1976a).

As far as the pattern of the stomata present in <u>A sullivantii</u> pinnules is concerned, Oestry-Stidd and Stidd (1976) identified the pattern as paracytic (syndetocheilic) whereas Reihman and Schabilion (1976a, b; 1985) and Mickle and Rothwell (1982) considered it to be haplocheilic. This argument will be discussed in detail later.

Systematics:

## <u>Alethopteris lesquereuxii</u> Wagner 1968 (PLATES 11-14)

- Wagner, 1968, p.90, fig.23, p.92, fig.24, p.250-261, pl. 30-35, fig.85-100.
- Baxter and Willhite, 1969, p.768, fig.l, p.770, fig.2, p. 772,fig.3-4, p.774, figs.5-6, p.776, figs.7-8, p. 778, figs. 9-10, p.780, figs.11-12, p.782, figs.13-14.
- Reihman and Schabilion, 1976a, p.11, figs.4-6, p.16, figs. 32-38, p.18, figs.27-31.
- Reihman and Schabilion, 1976b, p.1041, figs.4-5, p.1043-1044, figs.17-24.

Alethopteris sullivantii(Lesq.) Schimper 1869

(PLATES 15-16)

Leisman, 1960,

- Cridland, Morris and Baxter, 1963, pl.7, fig.45, pl.8, fig.46-47.
- Reihman and Schabilion, 1976a, P.11, figs.1-2, p.13, figs.7-10, p.14, figs.11-17, p.17, figs.18-24.
- ---- and ----, 1976b, p.1041, figs.1-3, p.1042 -1043, figs. 6-17.

---- and ----, 1985, p.1393, figs.1-9, p.1349, figs.3-9. Oestry-Stidd and Stidd, 1976, p.156, figs. la,b,c.

A comprehensive review of the synonymy and classification of these two species is given by Wagner (1968) and need not repeated here.

## Methods:

Pinnules of the two species were observed in variable sections on peel thin sections. Three pinnules of <u>A. lesquereuxii</u> which show external morphology were discovered on coal ball surfaces. Several complete cuticles of pinnules of <u>A. lesquereuxii</u> have been revealed from coal balls by using EDTA solution. These cuticles show the three dimensional morphology of the pinnules.

The procedure revealing the cuticles from coal balls are as follows:

 Dissolve EDTA Na4 powder (Ethylenediamine tetraacetic acid, tetrasodium salt, FW 434.22) in distilled water, preparing a concentration of Ø.2 M (pH. 10-11); then add glacial acetic acid until pH is 4-5.

2) Select specimens of <u>Alethopteris</u> identified in cross sections of pinnules, and recut the specimens perpendicular to the cross section of the pinnule.

3) Grind to within approximately one or two mm of the pinnule surface (if the pinnule is near the coal ball surface, steps 2) and 3) may be omitted).

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4) The specimen is suspended in the EDTA solution with the recut surface downwards, submerging it in the solution.

5) Keep specimen submerged, usually a few days, until the whole cuticle of the pinnule is completely exposed on the recut surface of the coal ball; during this step the EDTA solution may be replaced a couple of times, if necessary.

6) Carefully lift off the cuticle from the specimen with fine spatulas or needles, and bleach it with commercial Clorox (5.25 % NaClO).

7) Rinse the cuticle several times in water and preserve in glycerine.

8) For making permanent slides, stain the cuticle with 1% Safranin, then dehydrate with 50%, 75%, and 100% alcohol gradually, and finally mount on slides with Kleermont resin.

By this method, cuticles of entire pinnules of  $\underline{A}$ . <u>lesquereuxii</u> have been obtained; only fragmentary pieces of <u>A</u> <u>sullivantii</u> pinnules have been revealed because these pinnules had been already broken by pyrite recrystallization in the selected specimen.

Description of Derringer Corners Specimens:

Both <u>A. lesquereuxii</u> and <u>A. sullivantii</u> pinnules are preserved in the Derringer Corners coal balls. The former are more abundant then the latter. Cor Bax The pro 11, pin the ma x and 13, of alı ler Fig nea the \$i( ra Ia 80 00 ep di đej đej

The pinnules of A. lesquereuxii in the Derringer Corners coal balls closely resemble those described by Baxter and Willhite (1969) in size and general morphology. The pinnules are 2.7-4 mm wide by 6.0-9.5 mm in length, or proportionally 2-3 times as long as they are broad (Pl. 11, Figs. 1, 3). The apices and lateral margins of the pinnules are strongly revolute (Pl. 11, Figs. 1, 6). In the lateral view, the middle part of the pinnule has the maximum thickness of 1.6 mm, tapering towards both the tip and the base where the thicknesses are about 1.0 mm (Pl. 13, Fig. 5). The midrib is deeply sunken on the upper side of the pinnule, and extends from the base of the pinnule almost to the tip, about seven-eighths of the pinnule length, and is only faint on the upper surface (Pl. 11. Fig. 1; Pl. 13, Fig. 8). The pinnules vary in shape from nearly parallel-sided pecopterid-form on lower portions of the pinnule to pinnules with strongly decurrent lower side. The base of the pinnule is broadly attached to rachis with subsidiary veins arising directly from the rachis (Pl. 13, Figs. 1, 2). The swollen pinnule base, the so-called "double bulge" by Baxter and Willhite (1968), is not distinct in the Derringer Corners specimens. From the epidermal view, the lateral vein pattern is open dichotomy; most of the lateral veins divide once and depart from the midrib at a slightly oblique angle with a density of about 40 per cm (Pl.11, Fig. 4).

The external morphology of A sullivantii could

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not be described from specimens prepared here because of the fragmented nature of the exposed specimens.

Cross sections of the pinnules of <u>A</u>. <u>lesquereuxii</u> exhibit somewhat M-shaped pattern due to the strongly revolute margins and the sunken, abaxially ridged midrib (Pl. 11, Figs. 5, 6).

The upper epidermis consists of small cells which are rectangular and about 60  $\mu$ m periclinally (i.e., the cell wall parallel to circumference or to nearest surface of the pinnule) and 20  $\mu$ m anticlinally (i.e., the cell wall perpendicular to the nearest surface of the pinnule, see Esau, 1977, P.502, 518) in cross and longitudinal sections of the pinnule (Pl. 12, Figs. 1, 2). The cells of the upper epidermis are polygonal in the surface view, measuring about 50 x 60  $\mu$ m. Three-dimensionally, the epidermal cells are disk shaped as illustrated by Esau (1977, P.85). The epidermal layer is inconspicuous and usually very poorly preserved (Pl. 11, Fig. 4).

Below the upper epidermis, there is a hypodermal layer of exceptionally large cells which are irregular or pentagonal in outline and about 145 Jum (anticlinal) by 55 Jum (periclinal) in peridermic section, and about 130 Jum (anticlinal) in cross and longitudinal sections (Pl. 11, Fig. 4; Pl. 12, Fig. 1).

The hypodermis of <u>A</u>. <u>lesquereuxii</u> from the Derringer Corners coal balls is similar to that reported by Baxter and Willhite (1969). They wrote: "This hypodermis

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seems identical to what Leisman (1960) called the inner layer of a double epidermis in <u>A. sullivantii</u>. However, since the determination of a double epidermis is dependent on knowledge of its ontogeny, it is obviously impossible to use the term here with certainty (p. 773)." The layer of the extremely large cells of the Derringer Corners specimen is also referred to the subepidermis or hypodermis. According to Baxter and Willhite (1969), the large hypodermis of <u>A. lesquereuxii</u> and <u>A. sullivantii</u> is a significant taxonomic character because such a conspicuous hypodermis has not been found in any other leaves preserved in coal balls.

Of the pinnules of <u>A</u>. <u>lesquereuxii</u>, the epidermis consists mostly of one layer of cells. However, the epidermis occasionally consists a layer of two cells thickness. Although multiple epidermis can be identified only by developmental studies, considering the periclinal walls common to the two epidermal cells, the continuity of the anticlinal walls, and the difference in thicknesses of the normal epidermal cells (about 20 Jum in radial thickness) to those which are about half that thickness radially (10 Jum), it seems very likely that the two cells are produced by one periclinal division of an epidermal cell. The two cells are interpreted as components of a double epidermis in some portion of the pinnules (P1. 12, Figs. 1, 2).

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composed of palisade and spongy tissue. Immediately below the hypodermis is the palisade tissue, consisting of one or two layers of vertically elongated cells which are about 40 x 20 Jum and contain some dark material. The spongy tissue consists of irregularly-shaped cells, loosely arranged with numerous air spaces (Pl. 12, Fig. 1).

The midrib contains one to three vascular bundles depending on the position in the pinnule (Mickle and Rothwell, 1982). In the vascular bundle, the smallest tracheids of the primary xylem have spiral wall thickenings, indicating they are protoxylem element. The protoxylem tracheids are adjacent to some small browncolored, tube-like cells with pores on the walls which probably represent the sieve elements of the primary phloem. Accordingly, the primary xylem of the midrib is exarch. The metaxylem is composed of tracheids with scalariform, or reticulate wall thickenings.

A conspicuous bundle sheath, tightly enclosing the vascular bundle, consists of tubular parenchyma cells which elongate parallel to the lateral veins. The bundle sheath extends both upwards and downwards. The extension cells of the bundle sheath contain some dark-brown contents (Pl. 12, Figs. 1, 4).

The anatomical structure of pinnules of  $\underline{A}$ . <u>sullivantii</u> is very similar to that of  $\underline{A}$ . <u>lesquereuxii</u> described above. Besides the undulated walls of upper

epi Ā cel dif lov dis are rid the of t of p epic sto typ se 14 1 V đ ľ 1/. but that epidermal cells of <u>A</u> <u>sullivantii</u> pinnules, differing from <u>A</u> <u>lesquereuxii</u> pinnules of which the upper epidermal cells possess straight walls, the main anatomical difference between the two species is the structure of the lower surface of the pinnules.

In pinnules of A. lesquereuxii, there are distinctive ridges below the lateral veins, and stomata are distributed along grooves between the lateral vein ridges. Those can be observed from both cross sections of the pinnules (Pl. 11, Fig.5; 1. 12, Fig. 1) and cuticles of the lower epidermis (Pl. 13, Figs. 7, 9). On the basis of photographs showing the surface view of the lower epidermal cuticle and longitudinal section of stomata, the stomata of A. lesquereuxii seems to be of haplocheilic type: a pair of guard cells surrounded by a ring of several papillate subsidiary cells (Pl. 12, Fig. 5; Pl. 14, Figs. 3-6). The stomata are randomly oriented. The lower epidermal cells over the midrib and the lateral veins are square or somewhat elongated parallel to the veins. The epidermal cells in the grooves are irregular or polygonal in shape. Numerous uniseriate multicellular hairs occur along the revolute pinnule margin, the midrib, and the lateral veins (Pl. 13, Fig. 8). The hair bases are rather large and cover 1-2 epidermal cells (Pl. 14, Fig. 1). The tips of these hairs were consistently broken off, but a few intact hairs show the capitate tips indicating that the hairs may have been glandular (Pl. 12, Fig. 3).

In contrast, the lower epidermis of A.

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<u>sullivantii</u> pinnules is flat (Pl. 15, Figs. 1, 2). Stomata occur between lateral veins. Based on both paradermal view and cross section of the pinnule, the stomata also seem to be haplocheilic (Pl. 15, Fig. 7; Pl. 16, Figs. 6, 7). The lower epidermal cells over the midrib and the lateral veins, and the hairs are similar to those of <u>A</u>. <u>lesquereuxii</u> pinnules. Another distinctive feature of the lower epidermis of <u>A</u>. <u>sullivantii</u> is that the entire lower epidermis is papillate with the exception of the position over the midrib and the lateral veins proximal to the midrib. Usually there is one papilla per epidermal cell (Pl. 16, Fig. 5). Occasionally, the hair base is surrounded by a ring of papillae.

## Discussion:

The revealing of surface features of permineralized <u>Alethopteris</u> foliage on weathered or randomly fractured surfaces of coal balls has made it possible to correlate plant fossils preserved in coal balls with impression-compression taxa (Leisman, 1960; Baxter and Willhite, 1969; Ramanujam et al., 1974). By this method, two species of <u>Alethopteris</u>, <u>A. sullivantii</u> and <u>A. lesquereuxii</u>, are now known from both external morphology and internal anatomy. This kind of correlation has generally been restricted to the chance of obtaining exposed plant organs. Specimens of <u>A. lesquereuxii</u> pinnules showing external morphology, studied by Baxter

an С 51 aı tł we or or ana a d cha pla in te fı H C ĝe, đcį and 1 and Willhite (1969), were selected from large numbers of coal balls accumulated over twenty years.

Rothwell (1980) also succeeded in revealing the surface features of foliage preserved in coal balls, using an engraving tool, acting as a microjackhammer, to shatter the crystalline matrix down to a plane of weakness. The weak plane may occur at the actual outer surface of plant organ or may separate within the epidermis of the plant organ. Because the plant organ has been identified anatomically before the shattering, the technique provides a direct correlation of cellular anatomy with surface characteristics. By this technique, surface features of plant organs in coal balls can be artificially exposed, instead of being passively restricted by chance. This technique has proved to be practical and helpful in further studies (Mickle and Rothwell, 1982; Beeler, 1983; Hamer and Rothwell, in print).

Studies of macerated leaf cuticles have also provided detailed information on the epidermal features of <u>Alethopteris</u> pinnules (Wills, 1914; Reihman and Schabilion, 1976a, b, 1985; Oestry-Stidd and Stidd, 1976). Those studies have helped in demonstrating that the form genus <u>Alethopteris</u> is not a natural group. Further cuticular studies may allow a more natural grouping of the genus. However, the pieces of cuticle usually macerated by acid destruction of the matrix are generally fragmentary and it is difficult to tell where the pieces of cuticles

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In the present study, entire epidermal tissue and cuticles of whole pinnules of <u>A. lesquereuxii</u> have been revealed by maceration using EDTA solution. The advantage of this technique may be summarized as follows:

1) Revealing of the cuticles and epidermis <u>in</u> <u>situ</u> from the plant organs in coal balls enhances the proper correlation of plants identified in coal balls with those preserved as impressions compressions.

2) Such a correlation of internal anatomy with external morphology of plant organs in coal balls makes possible the study of more specimens than is possible by being dependent on chance exposure.

3) The artificially exposed cuticles retain the three-dimensional pinnule shapes and appendages (such as hairs) and their distribution. Cuticle shapes may be quite close to the original living condition of the pinnules. These features are difficult to show in compressionimpressions, and are not easily revealed even from coal balls.

There has been some disagreement about the type of the stomata present in <u>A</u>. <u>sullivantii</u> pinnules. Before discussing this problem, it is desirable to briefly review the terminology involved in classification of stomatal types. Two fundamental terminologies have been proposed: one is based on arrangement of subsidiary or neighboring cells surrounding quard cells; the other is based on

ontogenetic development of stomata. In the former, five types of stomata have been recognized: 1) Paracytic (parallel-celled) stoma, a stomatal complex in which one or more subsidiary cells flank the stoma parallel with the long axes of the guard cells; 2) Anomocytic (irregularcelled) stoma, a stoma without subsidiary cells; 3) Anisocytic (unequal-celled) stoma, three subsidiary cells, one distinctly smaller than other two surrounding the quard cells; 4) Diacytic (cross-celled) stoma, two subsidiary cells with their common walls at right angle to the long axes of the guard cells surrounding the stoma; 5) Actinocytic (radiate-celled) stoma, a stoma surrounded by a ring of subsidiary cells. From the point of view of ontogeny, there are three types of stoma: 1) Mesogenous: guard cells and neighboring cells, which may or may not differentiate as subsidiary cells, have common origin; 2) Perigenous, neighboring cells or subsidiary cells do not have common origin with the guard cells; and 3) Mesoperigenous: at least one neighboring or subsidiary cells is distinctly related to the stoma, other are not (Esau, 1977, p. 93; Dilcher, 1974, p.73).

Certainly, the systematic usefulness of cuticle analysis is greatly enhanced by an understanding of development; however, in paleobotany or systematics based on herbarium material where development cannot be observed, little use can be made of developmental terminology. Therefore developmental sequences are

ទប le on an by (s ce ha gu re an ha CO on đe Ċi Of th Ca in of th gU Vej suggested for mature fossil leaves or mature extant leaves. One ontogenetic type may correspond to more than one mature stomatal type and vice versa (Fryns-Claessens and van Cotthem, 1973).

For paleobotanists, the terminology established by Florin (1933) is generally used, i.e., syndetocheilic (subsidiary cells are derived from the same protodermal cell as the mother cell of the guard cells) and haplocheilic (subsidiary cells are not related to the guard cells ontogenetically).

Accordingly, paracytic has been referred to as mesogenous or syndetocheilic; whereas anomocytic, diacytic and actinocytic are referred as perigenous or haplocheilic. It should be understood, however, that those correlations do not represent developmental sequences but only "an educated guess of possible patterns of development." (Dilcher, 1974)

Oestry-Stidd and Stidd (1976) reported the discovery of the paracytic-syndetocheilic type of stomata of the pinnules of <u>Alethopteris sullivantii</u>. They noted that this was the first report of paracytic stomata in Carboniferous plants and they suggested this might indicate that Carboniferous seed ferns might be ancestors of angiosperms because paracytic stomata are present in the Bennettitales (Mesozoic) and some primitive angiosperms. According to the authors, the guard cells were completely enclosed by two subsidiary cells; the

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common end walls of the subsidiary cells meet at the midline through the long axis of the stoma and at each pole. But others (Reihman and Schabilion, 1976a, b, 1985; Mickle and Rothwell, 1982) believed that the stomata of <u>A</u>. <u>sullivantii</u> pinnules are of the actino-haplocheilic type, possessing guard cells surrounded by a ring of radiating subsidiary cells, similar to those found in various modern cycads and conifers.

Mainly based on a median longitudinal section through a stomatal apparatus, Reihman and Schabilion (1985) were able to conclude that the paracyticsyndetocheilic interpretation of stomata of <u>A. sullivantii</u> pinnules resulted from misinterpretation of the thickened ridge of the guard cells which gives the guard cells the appearance of being divided longitudinally into two cells (i.e., a guard cell and an accompanying subsidiary cell). In other words, they contended that the ring of papillae surrounding the guard cells are subsidiary cells.

Based on the examination of both peridermal views and longitudinal sections of stomata, the stomata of <u>A</u>. <u>sullivantii</u> and <u>A</u>. <u>lesquereuxii</u> pinnules in the Derringer Corners coal balls exhibit actino-haplocheilic type agreeing with those of <u>A</u>. <u>sullivanti</u> described by Riehman and Schabilion (1985).

It is necessary to emphasize that it is probably better not to put too much weight on evolutionary relationships based on a single stomatal type. Even if

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the stomata of <u>Alethopteris</u> pinnules were paracyticsyndetocheilic type, it would be a very limited basis on which to propose a possible evolutionary link between alethopterid pteridosperms, Mesozoic cycadeoids, and some angiosperms. The reasons for this are: 1) The correlations of mature stomatal types with ontogenetic types is only a suggestion, as mentioned above; 2) Among modern plants, the same species may show more than one type of stomata and the stomatal patterns may change during leaf development (Esau, 1977, p.93-94). When many features of cuticle are considered together, with an understanding of their variability, they are usually extremely useful in sorting out the systematic relationships of leaves (Dilcher, 1974).

Baxter and Willhite (1969) summarized several morphologic features that <u>Alethopteris</u> pinnules found in coal balls have in common, as mentioned earlier. The Derringer Corners specimens of <u>A. lesquereuxii</u> and <u>A. sullivantii</u> fit these features very well. As far as compression species of <u>Alethopteris</u> are concerned, these features cannot be considered as common to the genus as suggested by Baxter and Willhite (1969). Considering that <u>A. aquilina</u> lacks hypodermis and has hairs on the adaxial surface (Franks, 1963), and that <u>A. schneideri</u>, <u>A.</u> <u>lonchitica</u>, and <u>A. subdevreuxii</u> are without hairs and papillae, and have with superficial stomata, Mickle and Rothwell (1982) restricted the features common to the

genus <u>Alethopteris</u> as follows: 1) at least once pinnate fronds; 2) pinnules possessing entire margins; 3) A more or less defined midrib; 4) subsidiary veins arising from the pinna rachis; 5) open dichotomous venation of the lateral veins of the pinnules; and 6) haplocheilic stomata.

Baxter and Willhite (1969) listed four anatomical features separating <u>A</u>. <u>lesquereuxii</u> from <u>A</u>. <u>sullivantii</u> two of which involved comparison of the cell sizes of epidermis and hypodermis, as well the thickness of pinnules. Because cell size and pinnule thickness may vary widely in the same species, even in the same plant, depending on developmental stages, position on the plant, and habitat (environment) differences of different plants, these two features may not be constant and therefore cannot be used as diagnostic features of species.

In fact, Mickle and Rothwell (1982) reported that at least two morphological forms of <u>Alethopteris</u> species from Ohio and Illinois showed the identical features, and that possible interpretations of these observations may be: 1)several unrelated morphological forms of <u>Alethopteris</u> have similar anatomical characters; 2) the similarity of anatomical features may indicate that morphological differences merely reflect natural variation within a single alethopterid type.

In addition to characteristics of the cuticle, the anatomical features separating these two species of

<u>Alethopteris</u> are revised here as follows: 1) the lower surface is flat in <u>A</u> <u>sullivantii</u> while the lower surface of <u>A</u> <u>lesquereuxii</u> is ridged below the lateral veins ; 2) <u>A</u> <u>sullivantii</u> pinnules are flat, in contrast to <u>A</u> <u>lesquereuxii</u> pinnules which have strongly revolute, and tapered margins; 3) the upper epidermal cells of <u>A</u>. <u>sullivantii</u> have undulating walls, whereas <u>A</u> <u>lesquereuxii</u> pinnules possess the upper epidermal cells with straight walls; 4) papillae are distributed over the entire lower epidermis of <u>A</u>. <u>sullivantii</u>, while in <u>A</u>. <u>lesquereuxii</u>, papillae of subsidiary cells of stomata, are confined to the areas surrounding immediately guard cells.

Paleoecological Consideration:

Features such as thick cuticles, leathery pinnules, revolute margins, sunken stomata concentrated in grooves, papillae and hairs are thought to reflect xeromorphic response in the growth of the pinnules. Several species of <u>Alethopteris</u>, including <u>A</u>. <u>lesquereuxii</u> and <u>A</u>. <u>sullivantii</u>, show some of these features. Environmental conditions inducing formation of xeromorphic features of leaves may include water deficit, high light intensity and nitrogen deficiency (Shields,1950). Reihman and Schabilion (1976b) noted that some characters of xeromorphic alethopterids are similar to those of plants described by Warming (1909) in bog habitats, where soils tend to be very rich in organic material, and have lower pH due to the presence of humic acids, and lower nitrogen content. Such a bog condition might be similar to that in coal swamps in which plants were growing that were eventually preserved in coal balls. So that in coal swamps, a xeromorphic condition might be expected (Warming, 1909; Shields, 1950; Barthel, 1962). Apparently, <u>A. lesquereuxii</u> pinnules are more xeromorphic than <u>A</u>. <u>sullivantii</u> pinnules. But both species are present in the Derringer Corners locality.

This phenomenon may be interpreted in different ways. Concerning plants themselves, xeromorphic, less xeromorphic and mesomorphic may be analogous to sun leaves and shade leaves respectively (Hanson, 1917). Xeromorphic leaves may reflect an open canopy while less xeromorphic and mesomorphic leaves may correspond to a closed canopy (Mickle and Rothwell, 1982). It is possible that when plants were young possessing relatively open canopy the leaves showed xeromorphic growth characters; with further growth, the canopy becomes more "closed" and the leaves may exhibit more mesomorphic characters, or that during the same developing period, leaves borne on the top of the plants may exhibit xeromorphic character, while those borne the shaded portion of the same plants may show mesomorphic.

Medullosan Roots (PLATES 17-19)

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Earlier Reports
Scott, 1899
Arber, 1903, p.433, pl.XX, figs. 1-6;
Hoskins, 1931, p.541-548, figs.1-9;
Schopf, 1939, p.202, fig.8;
Steidtmann, 1944, pl.II, fig.6, pl.V, fig.2;
Andrews, 1945,
Baxter, 1949,
Stewart, 1951, p.714, figs.13-14, p.716, figs.
15-16;
Delevoryas, 1955, pl.13, fig.14;
Rothwell and Whiteside, 1974, pls.1-2, figs.1-12.
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Comments:

Medullosan roots are adventitious and represent a common component of many permineralized Carboniferous plant accumulations. Most medullosan roots are described from isolated specimens. Few of them were reported to be attached to medullosan stems. Delevoryas (1955) suggested that medullosan roots were most likely confined to basal portions of stems to explain their absence on many stems. According to Delevoryas, some stems with a considerable length preserved, which have no root attached, may represent more nearly apical sections of stems.

Because of frequent association with medullosan stems and the similarity of structure and anatomy to

medullosan stems, such roots seem to leave no doubt as to their affinity with pteridosperms.

Roots of <u>Medullosa anglica</u> Scott (1899) have been effectively described by Scott (1899) and Arber (1903) from British specimens. The primary xylem of the root is an exarch, triarch actinostele. In roots, with secondary growth, large xylem rays occur opposite the protoxylem points and divide the secondary xylem zone into three separate segments. The stele is surrounded by endodermis, cortex and epidermis in less mature roots, or by endodermis and periderm in older ones.

Hoskins (1931) described isolated medullosan roots from the Upper Pennsylvanian deposits of North America in which the protoxylem points or arms vary from 3 to 5, instead of typically 3 as in British specimens. Subsequent reports of the Upper Pennsylvanian medullosan roots generally agree with Hoskins' description (1931) (Steidtmann, 1944; Andrews, 1945; Baxter, 1949; Stewart, 1951; Delevoryas, 1955).

A detailed description of isolated medullosan roots from the Middle Pennsylvanian of North America was made by Rothwell and Whiteside (1974). According to these authors, the Middle Pennsylvanian medullosan roots can be distinguished from those assigned to <u>M. anglica</u> by a variation in the number of the protoxylem points and by a multiseriate endodermis found in <u>M. anglica</u>; both the England roots and the Middle Pennsylvanian roots of North

America can be separated further from the Upper Pennsylvanian roots of North America by the absence of endodermis in immature specimens of the latter.

Neither specific nor generic name has been assigned to medullosan roots.

Description of the Derringer Corners Specimens:

Medullosan roots are common components of the Derringer Corners specimens. The roots vary in size, from 1 to 8 mm in diameter. Generally, the Derringer Corners specimens are similar to those described by Rothwell and Whiteside (1974) from the Middle Pennsylvanian of North America. The principal structural and anatomical features are: exarch actinostele of primary xylem, number of the protoxylem points varying from 3 to 5 (Pl.17, Figs. 1-5), protoxylem composed of tracheids with spiral wall thickening (Pl. 18, Fig. 1), metaxylem composed of tracheids with reticulate and bordered pits, fusiform initials of vascular cambium that produce secondary xylem centripetally and secondary phloem centrifugally (Pl. 18, Figs. 2, 6), continuity of secondary xylem rays with secondary phloem rays, and the presence of pericycle, endodermis and peridermis.

Since a comprehensive study of the structure and anatomy of the Middle Pennsylvanian medullosan roots of North America has been given by Rothwell and Whiteside (1974), the description here is brief, emphasizing to add

some new information about the structural variation within the same specimens.

The number of the protoxylem points, one of the main differences between British and North American specimens, is that in the former, the primary xylem is typically triarch, while the primary xylem of the latter may be diarch, triarch, tetrarch or pentarch.

As suggested by Rothwell and Whiteside (1974), the slight variations in structure (i.e., the number of protoxylem points, presence or absence of endodermis) among the medullosan roots may represent either taxonomic difference or merely difference due to varying environments or growth conditions. A pentarch root of a Derringer Corners specimen has been observed to produce a rootlet with triarch primary xylem (Pl. 18, Figs. 4, 5). This demonstrates that variation in number of the protoxylem points has dubious taxonomic significance.

Hoskins (1931) pointed out that size of the medullosan root is not a factor in determining whether or not periderm is present. A similar relationship is found between the secondary growth and the root size from the Derringer Corners specimens. For example, a rootlet of one mm diameter arising from a parent root and a small root measuring 1.5 mm in diameter have already developed conspicuous secondary vascular tissues, while a root of two mm diameter has little secondary tissue, though generally the larger the root diameter the more the

secondary vascular tissues have developed.

As far as secondary xylem is concerned, according to Rothwell and Whiteside (1974) and Taylor (1981, p.337), a distinctive feature of the Middle Pennsylvanian medullosan roots is that the primary body is surrounded by secondary xylem. This is different from some medullosan roots in which the secondary xylem is separated into units by broad rays occurring opposite the protoxylem points (Scott, 1899). In the Derringer Corners specimens, both these types of the secondary xylem have been observed. In a pentarch root (Pl. 17, Fig. 5) broad rays with few, scattered tracheids are developed opposite the protoxylem points and dissect the secondary xylem into 5 wedges, whereas secondary xylem of a triarch root almost completely surrounds the primary xylem (Pl 17, Fig. 1). Also, some specimens exhibit a transition between these two types. In some specimens, rays opposite protoxylem points are broader than rays opposite metaxylem and may contain few rows of tracheids of which the sizes are smaller than the secondary tracheids opposite the metaxylem.

It is interesting to note the extent of variation of secondary xylem structure present in several Derringer Corners specimens. For example, in a triarch root, the secondary xylem opposite one protoxylem point has the same structure as that opposite the metaxylem; the secondary xylem opposite the second protoxylem point is

composed of broad rays and smaller tracheids, whereas the portion of the secondary xylem opposite the third protoxylem point is completely occupied by parenchyma tissue (Pl. 17, Fig. 3). A similar variation is shown in another root of which the secondary xylem opposite the protoxylem point, where a rootlet is arising, is mainly composed of parenchyma tissue (Pl. 17. Fig. 7). This parenchyma tissue is apparently related to the production of the lateral root.

Because of frequent branching of the roots, the development of lateral roots may be an important factor modifying the structure of the secondary xylem of the medullosan roots. The structure of the secondary xylem of the medullosan roots in cross sections may differ from level to level depending upon the distance of the cut from the points where lateral roots arise. There may be other factors influencing the structure of the secondary xylem of the medullosan roots.

Vascular cambium can be clearly observed in many of the Derringer Corners specimens. This layer is several cells wide and the cells are tangentially elongated in transverse section lying between secondary xylem and secondary phloem (Pl. 18, Figs. 2, 6). Vascular cambium sometimes produces some very small tracheids on the periphery of the secondary xylem (Pl. 19, Fig. 1). The function or significance of such small tracheids is unknown.

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Primary phloem cannot be described here because all the specimens observed had already developed secondary tissues.

Secondary phloem is well developed. In contrast to medullosan stems, the secondary phloem of medullosan root is confined to the areas adjacent to the portion of the secondary xylem opposite the metaxylem, so that the secondary phloem often appears as an arch in outline (Pl. 17, Figs. 2, 3, 4; Pl. 18, Figs. 2, 6).

The secondary phloem consists of sieve elements, rays and parenchymatous cells. The phloem rays are comparable to the xylem rays with which they are continuous. Sieve elements are thick-walled, either arranged as uniseriate radial rows or scattered in the phloem region. Arber (1903) reported that sieve elements had lateral sieve plates with horizontally elongated sieve pores. But he did not show any photos of the sieve plates, and only illustrated these by a drawing. In the Derringer Corners specimens, sieve pores of the secondary phloem are rather evenly distributed on the sieve element walls. No definite sieve plates have been identified. Secretory canals are present in the secondary phloem region (Pl. 19, Fig. 5).

In tangential section, throughout the outer part of the secondary phloem, phloem parenchyma cells between the sieve elements are much elongated horizontally, 3-4 times as long as wide (Pl. 19, Fig. 3). Some of these

contain dark material and exhibit pores on the walls which are similar to these of sieve elements. They are distinguished from the sieve elements by their horizontal elongation. These phloem parenchyma cells become isodiametric in the inner part of the secondary phloem (P1. 19, Fig. 4).

A zone of pericycle and endodermis is distinctive from the phloem parenchyma and normal cortical cells in somewhat tangentially elongated cells in transverse section. It appears as a ring tightly surrounding the stele (Pl. 19, Fig. 1). The endodermis is the innermost layer of the cortex and is characterized by special wall thickenings called Casparian Strips. The endodermal cells can be identified in cross section by thicker radial walls (Pl. 19, Fig. 1). Casparian Strips have been observed in radial section (Pl. 19, Fig. 6). The endodermal layer or zone is 1-3 cells wide, similar to the multiseriate endodermis described by Rothwell and Whiteside (1974). Sometimes the endodermis is difficult to distinguish from pericycle. A broad zone of periderm is very conspicuous in most the specimens. It occurs close to the stele. In some cases, cortex and epidermis are sloughed off, and the periderm becomes the outermost part of the roots.

In young roots, cortex and epidermis are preserved. The cortex consists of isodiametric cells some of which contain dark material (Pl. 17, Fig. 3). Epidermis of most specimens is destroyed but, occasionally, epidermal cells can be identified as a one-cell-wide layer, the cells of which are usually elongated both tangentially, in transverse section, and longitudinally.

The medullosan roots of the Derringer Corners specimens are rather extensively branched. In one sample (0.5 cm long), six lateral roots are produced (Pl. 19, Fig. 17). Vascular systems of the lateral roots arise from the protoxylem of the parent roots, and the extravascular tissues of the rootlets from the pericycle of the parent root.

The two most conspicuous and common features of medullosan roots are exarch actinostele of primary xylem and a well-developed broad peridermal zone; all other features, such as the number of the protoxylem points, the structure of the secondary xylem, the endodermis, vary in different specimens, even in different levels of the same specimen.

Based on the observation of the Derringer Corners specimens, these variations of the features of the medullosan roots may represent intraspecific, instead of interspecific, differences caused by varying growth or environmental conditions, or growth position. It is not likely that the structure and anatomy of the Middle Pennsylvanian medullosan roots might provide a basis of potential taxonomic significance, as suggested by Taylor (1981, p.337).

It is frequently observed that medullosan roots

have penetrated the medullosan petiole <u>Myeloxylon</u>, as lycopod rootlets often penetrate lycopod stems and the rhizome <u>Stigmaria</u>. In some specimens, penetrating roots are clearly separated from <u>Myeloxylon</u>-type of organs as identified by the presence of epidermis. In some specimens, however, it is likely that the roots show cellular continuity with <u>Myeloxylon</u> organs. If that is correct, these specimens may represent rhizomes of medullosan plants, and the medullosan roots may not be adventitious, which may be the reason why most described medullosan stems appear to have no roots attached. The rhizomatous nature of these Derringer Corners specimens should, however, be open to question until further investigation has been completed.

Medullosan Seeds

Introduction:

Medullosan seeds attached to medullosan foliage have long been recognized from impressions-compressions. In spite of the difficulty identifying whether fructifications attached to medullosan type foliage are ovules or pollen organs (Stidd, 1981), <u>Trigonocarpus</u>-type of seeds attached to <u>Neuropteris</u> and <u>Alethopteris</u> are convincing (Kidston, 1904; Jongmans, 1931; Halle, 1933; Arnold, 1947, p. 221). The position of seed attachment may be variable in lateral or terminal position on the pinnules in different species.

This concept is further supported by studies of coal ball plants. Stewart (1983, p.260) suggested that detached permineralized medullosan ovules of <u>Pachytesta</u> <u>illinoensis</u> were born on <u>Alethopteris</u>-type fronds (based on their proximity and frequency of association), and that the ovules may replace a terminal pinnule of an <u>Alethopteris</u> frond because the vasculature in the base of <u>P. illinoensis</u> is a ring of five or six bundles closely similar to that of terminal position of a vegetative Alethopteris pinna rachis.

Hoskins and Cross (1946b) listed nine genera thought to represent medullosan seeds, and eight of them are still valid. In addition to <u>Pachytesta</u>, the other seven genera are <u>Stephanospermum</u>, <u>Aetheotesta</u>, <u>Hexapterospermum</u>, <u>Polypterospermum</u>, <u>Ptychotesta</u>, <u>Polylophospermum</u> and <u>Codonospermum</u>. These genera share the characters of medullosan ovules, i.e. radiospermic, simple pollen chamber, double vascular system (both nucellus and integument are vascularized by a branching single vascular bundle), and stalked or sessile nucellus being free from the integument except at its base.

Ovules of modern cycads also have double vascular system and nucellus free from the integument in the distal end. This has served as a evidence indicating possible phylogenetic relationship between medullosan plants and cycads.

## The Genus Pachytesta:

<u>Pachytesta</u> is an organ genus of permineralized seeds. These are usually identified as <u>Trigonocarpus</u> when the seeds are preserved as casts, impressions or compressions. A long time elapsed before such a clear conception was reached. Hoskins and Cross (1946b) have provided a detailed historical survey.

The genus <u>Trigonocarpus</u> was established by Brongniart (1828) for radially symmetrical seeds characterized by three major longitudinal ribs. He did not give description for the genus but referred to the figures first given by Parkinson (1804). The first seed of <u>Trigonocarpus</u> with internal structure preserved was described by Hooker and Binney (1855). This is perhaps the earliest description of any seed with preserved structure.

The genus <u>Pachytesta</u> was established by Brongniart (1874a, b, 1881) for large silicified seeds from St. Etienne beds, France, which he stated had been assigned to <u>Rhabdocarpus giganteus</u> by Grand'Eury. According to Brongniart, the silicified seeds showed little in common with those of <u>Rhabdocarpus</u>, and the seeds were then assigned to a new genus, <u>Pachytesta</u>.

After a review of several species of <u>Trigonocarpus</u> and <u>Pachytesta</u>, Hoskins and Cross (1946a, b) pointed out that these species showed an integrating series with some characters in common: 1) radiospermic; 2)

nucellus entirely free from the integument; 3) both nucellus and integument vascularized by a single vascular bundle; 4) single, usually 3-layered, integument; 5) general agreement in shape, more or less ovoid, being circular in cross section and oval in longitudinal section. They then proposed that all these seeds should be included within a single genus, <u>Pachytesta</u>. Their proposal has been widely adopted. This investigation is, in fact, an example of the recommended practice of improving the knowledge of fossil plants by correlating plant fossils of impressions and compressions with those of permineralizations.

In the monograph of the American species of <u>Pachytesta</u>, Taylor (1965) described 13 species. A new species was added by Taylor and Eggert (1969). The genus ranges from the Lower Coal Measures of British Isles to the Upper Carboniferous of France. Specimens range from slightly less than one cm to about 11.0 cm in length.

Generally, the integument consists of three parts, a parenchymatous outer layer (sarcotesta), a middle fibrous zone (sclerotesta), and a uniseriate innermost layer (endotesta). Mostly the sclerotesta is more or less divided longitudinally by three prominent ribs extending from the base to near the micropyle. Sometimes between the three primary ribs there are smaller secondary, or even tertiary, radial extensions of the sclerotesta that may extend varying distances from apex to base. Secretory canals identical with those of <u>Myeloxylon</u> and <u>Medullosa</u> are common in seed coats. In transverse section at the middle level of a seed, the seed coat consists of three valves marked by indentations on the inner side of the integument, or separation of edges of adjacent "valves".

Numerous saccate pollen grains of the <u>Florinites</u> type were found in pollen chambers of <u>P. vera</u> (Hoskins and Cross, 1946); However they and Taylor (1981) discussed the probability that these <u>Florinites</u>-type pollen grains found in pollen chambers of <u>Pachytesta vera</u>, <u>P. gigantea</u> and other species may be foreign, i.e., they represent anemophilous contamination, because Monoletes-type pollen grains have been found in most of the other species of the genus and <u>Florinites</u> pollen are often found <u>in situ</u> in Cordaianthus sporangia (Cordaitales).

Megagametophytes have been observed in three species and a clearly distinguishable archegonium was reported from only one species, <u>P. hexangulata</u>, of this genus (Taylor, 1965).

Based on the structure and elaboration of the testa and its vascularization, Taylor (1965) presented a tentative scheme depicting evolutionary trends within the genus.

Systematics of <u>Pachytesta</u> <u>noei</u> (PLATES 20-22)

# Pachytesta gigantea,

Reed, 1939, p.776-779, figs.ll-21;

## Pachytesta noei,

Hoskins and Cross, 1946a, p.348-352, figs.68-71; Taylor, 1965, p.12, figs.4,4A, pl.15, figs.89-93.

Comments:

The first occurrence of <u>Pachytesta</u> in North American coal balls was reported by Reed (1939) from two incompletely preserved specimens which were referred to <u>P.</u> <u>gigantea</u>. Hoskins and Cross (1946a) reexamined a portion of the Reed's specimens and concluded that these seeds are not of P. gigantea but represent a new species, P. noei.

Seeds assignable to <u>P. noei</u> are 5.5-7 cm long and 2.5-3.1 cm in diameter. Transversely, the seeds are circular; the radially extended ribs are not conspicuous on the exterior of the seeds. The base of the seed is rounded, and, apically, the integument is tapered and forms a blunt micropylar beak.

Description of the Derringer Corners Specimens:

The description of <u>P. noei</u> here is based on a well-preserved specimen. The seed, 6.8 cm long and 2.7 cm in maximum diameter, has a rounded base and blunt micropyle (P1. 20, Fig. 1).

Integument:

The seed is similar to all other species of the genus in the increase in thickness of the integument both toward the apex and the base. At the mid-level, the seed coat is about 2.0 mm thick; in the chalazal region and the pollen chamber level, the integument is about 4.0 mm thick (Pl. 20, Fig. 1).

The seed coat (integument) consists of an outer fleshy layer (sarcotesta), middle stony layer (sclerotesta), and inner fleshy layer (endotesta).

The exterior of the seed is covered by a parenchymatous layer. Because of the delicate nature of the cells, this layer is not well-preserved. The epidermis and its cuticle are not observed in this specimen. Some portions of the seed coat, however, show an outer layer of 2-3 cells in thickness. The cells of this layer are roughly isodiametric measuring 25-40 Jum (Pl. 21, Fig. 2).

Beneath the sarcotesta there is a two-parted sclerotesta, an outer part consisting of horizontally arranged fibers and an inner part consisting of fibers arranged parallel to the long axis of the seed (Pl. 21, Fig. 1). The outer zone of the sclerotesta, that is the main portion of the integument, is 35-40 cells thick, and is generally uniform except that the elements near the margin of this zone are smaller than those of the central part. Transversely, there are simple pits on the cell

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walls; the cells are elongated in different degrees and the direction of elongation varies. Some strands of vertically elongated fibers are scattered in this zone, especially near the locations of vascular bundles (Pl. 21, Fig. 4).

The inner part of the sclerotesta is composed of vertically arranged fibers, 8-10 cells in thickness. The size of the fibers is much smaller than those of the outer part of the sclerotesta. Simple pits are also present on the fiber walls (Pl. 21, Fig. 3). Throughout this zone the cell diameters decrease toward the inner margin of the zone. Distally, the individual cells gradually become oriented horizontally; at the level above the pollen chamber, most of these cells are horizontally arranged (Pl. 21, Fig. 6).

The transverse section of the seed at about midway between the apex and the base shows an almost circular configuration. Three primary ribs divide the seed coat into 3 roughly equal valves. These ribs are not pronounced on the exterior of the seed. The primary ribs are, however, identifiable by the radial extension or penetration of the inner part of the sclerotesta into or through the outer part of the sclerotasta. This dense inner layer thus forms a lining along both sides of each suture or rib. The position of the ribs is also marked by small indentations on the inner surface of the seed coat (P1. 20, Figs. 4, 5). At the level above the pollen

chamber, one secondary rib is present (Pl.20, Figs. 2, 3).

In the transverse section at the level above the pollen chamber, the outer margin of the seed is still circular, whereas the inner margin exhibits a triangular configuration (Pl. 20, Figs. 2, 3). At this level the fibers of the inner part of the sclerotesta are horizontally arranged; the penetration of the inner layer of the sclerotesta into the outer zone is very conspicuous.

In the Derringer Corners specimens, the inner part of the sclerotesta extends from the base of the seed only into the base of the micropylar region and that this layer is absent in the region of the micropylar opening where three valves of the seed are separated by 3 radially directed layers of isodiametric or slightly elongated, thin walled cells. Possibly this seed was immature and these radially directed zones of parenchymatous tissue might have broken down, after further maturation, allowing the complete splitting of the integument into 3-valves for the full length of the seed.

A thin, fleshy tissue lines the sclerotesta internally. In most cases this endotesta layer is more or less destroyed before permineralization and is usually represented only by the cuticle of its epidermis facing the nucellar cavity (Pl. 21, Fig. 3). Opposite the ribs the inner cuticle and some cells of the endotesta have been pushed inward forming a fold which, in cross section,

appears as a sac-like structure identical to those called "rib trabeculae" by Hoskins and Cross (1946a) (Pl. 20, Fig. 4). Because of the continuity of the cells and the cuticle of the rib-trabeculae with those of the endotesta, it is believed that the formation of such a feature is caused by shrinkage of the seed before or during the fossilization.

## Nucellus:

The nucellus is supported by a stalk extending from the integument into the seed cavity. This stalk is about 2.0 mm in height, most of the tissue of which is not preserved. The remnant of the nucellus near its base and periphery are identifiable (Pl.21, Fig. 7). Cells of the nucellus are irregular in shape (Pl. 22, Fig. 1).

The pollen chamber is poorly preserved, and no pollen grains have been observed within it (Pl. 20, Fig. 1)

## Vascularization:

The integumentary vascular system consists of a ring of vascular bundles peripherally disposed. There are 8 vascular bundles in each valve of the seed coat, and totalling is 24 for the three valves of the seed coat between levels B and C (Pl. 20, Figs. 3-4). At the middle level (level D) of the seed there are 10 vascular bundles per valve of the integument (Pl. 20, Figs. 1, 5). The vascular bundles are very poorly preserved, and their positions are indicated by equally spaced lacunae that traverse the outer layer of the sclerotesta. The number of the vascular bundles is uncertain at the base of the seed.

The number of the vascular bundles in the nucellus is unknown in this specimen due to the incomplete preservation. The vascular bundles in the nucellus consist of spirally thickened protoxylem tracheids measuring 7-10 Jum in diameter, and metaxylem tracheids with scalariform wall thickening, 40-45 Jum in diameter (Pl. 22, Fig. 3).

In the transverse section of the seed base, the dichotomy of the vascular system has been observed (Pl. 20, Fig. 8). The outer branches of the vascular system enter the integument and the inner ones enter the nucellus.

# Discussion:

The Derringer Corners specimen of <u>Pachytesta noei</u> is well preserved. All essential features are present, such as the trimerous nature of the seed coat, the nucellus being free from the integument except at the chalaza, the double vascular system, the size and the shape of the seed, assigning the Derringer Corners specimen to Pachytesta.

<u>P. gigantea</u> and <u>P. noei</u> are generally similar to each other in size. Transverse sections show similar circular seed coats , with three primary ribs that are not pronounced on the exterior of the seed and the positions of the ribs are marked by indentations on the inner surface of the seed coats. The sclerotestas of both are composed of an outer zone of horizontally arranged fibers and an inner zone of fibers elongated parallel to the long axis of the seeds. However, the morphology and anatomy of these two species are different from each other in several ways: 1) <u>P. gigantea</u>, 6-7.0 cm in length and 3.0-4.8 cm in diameter, is larger than <u>P. noei</u>; 2) <u>P. gigantea</u> has more vascular bundles in the integument (51 in cross section at the middle level between the apex and the base, 40 at the level above the pollen chamber) than that of <u>P. noei</u>; 3) the integument of <u>P. noei</u> is more differentiated into layers than that of P. gigantea.

These two species may not be easily distinguished from each other. In fact, the specimen on which Hoskins and Cross (1946a) established <u>P. noei</u> was initially assigned by Reed (1939) to <u>P. gigantea</u>. The number of vascular bundles in the seed coat is dependent partially upon the size of the seed and the latter, in turn, is partially related to developmental stage and environments. So that the slight difference in seed size may or may not reflect interspecific features.

In previous descriptions of <u>P. noei</u>, the apex was unknown. The apex of the seed of this species from the Derringer Corners is well-preserved. Comparing the apex structure with that of P. gigantea provides more characters distinguishing these two species from each other. These characters are: 1) 3 secondary ribs are present in apex of <u>P. gigantea</u> but only one in <u>P. noei</u>; 2) the inner, cross-sectional outline of the apex of <u>P. noei</u> is triangular, while that of <u>P. gigantea</u> is star shaped; 3) the number of vascular bundles of the integument of <u>P. gigantea</u> decreases from middle level (51) to apex (40) by lateral fusion of the vascular bundles, whereas the maximum number of the vascular bundles, at the midst level of integument, of <u>P. noei</u> is 30 and the number of the vascular bundles of the integument, from middle-upper level (level C) to the apex, is constant (24).

A remnant of the stalk of the seed of <u>P. noei</u> from the Derringer Corners collection was observed. The stalk is about 1.0 mm in diameter, and about 2.0 mm long. The character of the vascular bundle sheaths, secretory canals, and papillate stomata on the surface of the stalk (P1. 22, Figs. 5-8) suggests that the seeds of <u>P. noei</u> were born on alethopterid-type foliage. This is in accord with supporting the reconstructions made by Halle (1933) and Stewart (1983).

# PALEOECOLOGY OF THE DERRINGER CORNERS COAL SWAMPS

Ecology is the study of the relationships between organisms and their environments. Plant paleoecology, therefore, is the study of interactions between fossil plants and their environments of life in the past. Basically, what paleoecology deals with is proposing hypotheses inferring paleoenvironments such as paleoclimate, paleogeography, and so on, based on data derived from fossil faunas or floras, and in turn inferring establishment and changes of the faunas or floras under the control of the paleoenvironments. The definition of paleoecology given by Krasilov (1975, p. 6) as "the science of the reconstruction of ecosystems of the geological past and of their development in time" is generally acceptable.

Many investigations of plant paleoecology have been based on spore floras, and megafossils (impressions, compressions, coal balls, and other permineralizations). In the present study, an attempt has been made to reveal some aspects as to the nature of the paleoenvironment, especially paleoclimate, of the Appalachian Basin at the late Middle Pennsylvanian time based on quantitative analysis data of the composition of vegetation preserved in coal balls.

#### PREVIOUS INVESTIGATIONS

Quantitative Analysis of Botanical Constituents of Coal Balls:

It has long been known that differences in kinds of coals are, in part, the result of different plant associations that constituted coal swamp vegetation. A great deal of study has been made on the plant constitution of coals using thin sections or polished coal surfaces. During the various stages of alteration of the plant debris (coalification) which constituted the original peats, there is disproportionate degradation of the different plant tissues and organs by biological agents and geochemical conditions (diagenesis); physical and chemical alterations during compaction or accumulation as a result of elevated subsurface temperatures (catagenesis); and, for some coals, further alteration to higher ranks of semi-bituminous and anthracite by further heat and pressure (metamorphism). During these stages of coalification, some of the original plant material becomes difficult to recognize, identify or account for. Because of coalification, it is generally difficult to identify most plant remains of which coals are composed based on observations of coal sections or coal surfaces. Some have attempted to interpret the plant constitution of the coal seams from plant casts, impressions, compressions, and the lithology found in the roof or bottom rocks of coal seams.

In such interpretations, however, the identification of plant remains is relatively easy, but this method is not reliable because the plants constituting the pre- or postpeat-swamp vegetation, found in the roof or bottom rocks of the coal seams, are generally different or are complexed into different communities from those plants forming the peat swamp communities. The reasons for this are that the plants of the coal-forming swamps were constrained by differences in habitats, from those of the lowland sites or semi-aquatic habitats where roof or bottom rock sediments were accumulating, and also that some of the plant fossils found in the roof or bottom rocks were, or may have been, transported.

Coal balls formed <u>in situ</u> by the permineralization of coal swamp peats probably entirely during the peat stage of diagenesis. The plant remains preserved within coal balls represent a reasonable sample of the plant material, in various stages of preservation and degradation, which went into the formation of the surrounding coal. Therefore, quantitative analyses of the plant organs, tissues, and taxa preserved in these coal balls is significant for study of coal composition, and plant paleoecology of the coal-forming swamps of Pennsylvanian time.

Schopf (1938b) noted that coal balls could serve as an index to the constitution of coals and obtained for the first time quantitative data of the botanical contents

of coal balls from the Herrin Coal, Illinois. He selected 7 coal balls and made nitro-cellulose peels, then measured plant remains on the peels with a glass millimeter rule under a microscope. Plant entities of different classes were totaled and the percentages of each were then computed. The most striking result of his study was the demonstration of the predominance of root material preserved in the coal balls. Rootlets of the tree fern, <u>Psaronius</u>, and rhizomes and rootlets of lycopods formed 51% of the total plant remains (by volume) in the coal balls of his pioneer study.

Nearly forty years later, Phillips et al. (1977) obtained quantitative data on the taxa and organ composition of eight or more coal ball zones from four localities along 142 Km east-west traverse in the Herrin Coal Member, Carbondale Formation, Desmoinesian Series, in the southern part of the Illinois Basin. Ten pieces of coal balls were selected respectively from six different zones. These were cut on a rock saw into slices about 2.5 cm apart, perpendicular to the top-bottom axes of the coal balls, to expose maximum cross sectional area of stratified peats inside the coal balls. Cellulose acetate peels were made and were ruled with a grid system (26 x 20 cm<sup>2</sup>). The area of the peels occupied by plant material was treated as volume in percentages. The results and conclusions of the quantitative analysis are as follows:

1) Five major plant groups constituted the taxa

present in the coal swamps: lycopods, sphenopsids, ferns, pteridosperms (seed ferns), and cordaites (primitive Coniferophytes).

Lycopods dominated (72-75%), and were represented by Lepidophloios, Lepidodendron, and their rhizome, Stigmaria; ferns were usually the second in abundance (11-17%), and were dominated by the tree fern <u>Psaronius;</u> pteridosperms were the mostly variable with 6-14%, dominated by <u>Medullosa</u> and <u>Myeloxylon</u>; sphenopsids were 1-4.5% dominated by <u>Calamites</u>; and <u>Cordaites</u> were about Ø.5%.

2) Each group was mainly represented by tree forms, of which the percentage was greater than 97% of the total identifiable plant material in the coal balls; with the exception of <u>Psaronius</u>, the swamp trees were woody or semi-woody. Unlike conifers and modern flowering plants, however, the lycopod trees developed massive bark layers thicker than their wood. <u>Cordaites</u> and hollow-stemmed <u>Calamites</u> formed higher proportions of wood than lycopods. Pteridosperms primarily contributed foliage detritus (raches and pinnules) and cortical tissues.

3) Lycopod trees, some were more than 30 m in height, generally dominated during the Early and Middle Pennsylvanian coal swamps; then tree ferns were dominant in coal swamps during the Late Pennsylvanian forests. The result of this change in floristic dominance was that the principal plant constituents of coals derived from above ground tissues and organs shifted from lycopod periderm or bark to the adventitious root-supported tree ferns. These shifts of plant dominance probably reflected broad paleoclimatic changes.

4) The strongly cyclic alternation of root zones and aerial zones of plant parts illustrated in the lower half of the Shawneetown profile may be interpreted as a sequence of 4-5 successive forest stands. This indicates that when litter and root substrate of the swamp forests became peats, young forests grew on the top of these swamp peats in successive repetitious communities. If this suggestion is correct, there were probably some ten successive forests stands during the span of the Herrin Coal swamp accumulation in that area. Phillips et al. estimated that, about 50-100 years for each major forest cover. On this basis, the plant constituents of the coal may have been accumulated in less than 1,000 years.

Regional and Interregional Change in the Pennsylvanian Coal Swamp Vegetation:

World wide differentiation of floral provinces occurred during the Carboniferous and Permian as paleocontinents progressively approached the pole-to-pole pangaean configuration (the united single land mass) which was fully established in the Triassic. The temperate Angaran Province was dominated by gymnosperms (various cordaites); the temperate Gondwana Province was dominated by gymnosperms (<u>Glossopteris</u>); and the tropic and subtropic Euramerican Province was dominated by lower vascular plants, especially lycopods (Chaloner and Creber, 1973; Phillips and Peppers, 1984).

Woody trees of the temperate provinces were gymnosperms which uniquely combined reproductive and vegetative dormancy indicated by seasonal growth rings of their woods (Krausel, 1964; Lepekhina, 1972; Meyen, 1977; Gould and Delevoryas, 1977). These trees may have been deciduous. The establishment of the tropical Euramerican Province in the Pennsylvanian Period was generally based on paleomagnetism studies (Irving, 1964; Habicht, 1979) and paleobotanical characters including lack of growth rings in the woods (White and Thiessen, 1913; Krausel, 1964; Schopf, 1975a; Stach, et al., 1982).

With accumulation of data derived from quantitative analyses of coal swamp plants and palynological studies during the last decade, a series of pioneer investigations as to changing patterns of the Pennsylvanian coal swamp vegetation over North America and Europe (Phillips, 1976, 1979, 1980; Phillips and Chestnut, 1980; Phillips and DiMichele, 1981; Phillips et al., 1974; Peppers, 1979; Peppers and Popp, 1979; DiMichele and Phillips, 1979, 1980; DiMichele et al., 1985) extended several concepts of plant ecology to a geological time scale (the whole Pennsylvanian Period) and to a Euramerican-wide geographic scale.

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Correlating vegetation pattern changes, dependent on biological requirements, with geological changes, in the Euramerican coal swamps, these authors attempted to reconstruct paleoclimates of the Pennsylvanian Euramerican coal swamps and to infer the control of the paleoclimate on the coal swamp vegetation. It is obviously impossible to deal with all aspects of the relationship between the different coal swamp communities and paleoclimate because such relationships were too complex considering the many variable parameters to be dealt with. Many paleoecological and paleoclimatic factors are not clearly known.

Feasibility of Reconstructing Paleoclimates of the Pennsylvanian Euramerican Coal Swamps:

The feasibility of reconstructing paleoclimates of the Pennsylvanian Euramerican coal swamps is based on following suggestions and facts:

1) Pennsylvanian coal ball plants of both North America and Europe are well known. This knowledge, together with information on the plant constitution of coal swamps of this period provide a data base for quantitative analyses of some of the Euramerican coal balls.

2) Because of the highly specialized environment of coal swamps (low pH, low available mineral nutrients, flooded conditions, and low oxygen level of peat substrates, and so on), only a small number of highly specialized plant groups were able to grow in the coal swamps. The low diversity in taxa of the plant communities in the coal swamps makes it practicable to compare community constitutions of the coal swamp vegetation through much of the Euramerican Province.

3) Most of the major plant groups in the coal swamps had very long stratigraphic ranges and very wide geographic distribution through North America and Europe during the Pennsylvanian Period.

4) Quantitative analyses of coal ball plants provide the most direct evidence of the vegetation and of the botanical constituents of the coals; but, coal ball plants preserved in situ may have been mainly under the control of local paleoenvironments, rather than regional or interregional conditions. This means that the data from the composition of coal swamp vegetation may not always be a good indicator of the paleoclimate in a large area. In contrast, palynological analyses of channel samples of coal are a good means of estimating regional, interregional and stratigraphic patterns of coal swamp vegetation; but because of the nature and extent of dispersal spores from surrounding vegetation into coal swamps, estimates of the coal swamp vegetation may be biased. The control of comparative data from permineralized peat deposits (coal balls) is needed.

There are relative, predictable relationships (including biases) between the dominant constituents of

spore assemblages and those of coal ball plants. This indicates that, by combining data from coal ball plants and coal spore floras, a more reliable basis for reconstructing coal swamp vegetation and for inferring paleoclimates can be assembled.

5) It is suggested that the Euramerican coal belt remained in the paleotropics during the Pennsylvanian period. The proposed position of the paleoequator for North America is generally an arc diagonally across the United States through or near the Canadian Maritime Province to Europe (Dott and Batten, 1976; Bambach et al., 1980; Heckel, 1977, 1980). Paleogeographic mapping of the land mass during the Carboniferous and Permian illustrates that the paleolatitudinal disposition of Laurussia, including North America, Greenland, Scandinavia, and the Russian Platform west of the Urals, did not change significantly during the Pennsylvanian time (Habicht, 1979; Ziegler et al., 1981).

Thus the studies of paleoclimatic control on the Pennsylvanian Euramerican coal swamp vegetation have been simplified to deal with the relationship between regional and interregional pattern changes of five major plant groups in coal swamps and the freshwater regimes over all Euramerica through the Pennsylvanian period.

Phillips and Peppers (1984) and Phillips et al. (1985) reported the main results of the investigations as to stratigraphic and interregional vegetative changes in
the Pennsylvanian Euramerican coal swamps and their environmental inferences, based on comprehensive analysis of the data on coal swamp vegetation from peat deposits (coal balls) of more than 65 coals in the United States and Europe and of spore floras from more than 150 coals in

the eastern United States.

Stratigraphic Ranges of the Major Coal Swamp Plant Groups and Their Biological Adaptations to Coal Swamps:

## Lycopods:

Many lycopod tree genera were present in the earliest Westphalian (the earliest Lower Pennsylvanian) coal swamps of Europe and the United States; they were dominant in most coal swamps during the early Middle Pennsylvanian, but only <u>Sigillaria</u> and herbaceous lycopods survived into the Later Pennsylvanian in the United States.

Lycopod trees were semi-wood and grew rapidly. Their determinate growth produced rather small and open canopies leaving enough open space for reproductive organ development and spore dispersal. Boat-shaped megasporophylls infer that dispersal of megaspores was by both wind and water (Phillips, 1979). The roots were a rhizomatous stigmarian system with specially arranged lacunose rootlets. None of lycopods appear to have had the capability of vegetative propagation.

Heterosporous lycopods represented a spectrum of very wet to relative drier or seasonally wet-dry adaption for sexual reproduction in freshwater swamps (Phillips and Peppers, 1984). The evolution of the tree habit, even with limited wood and phloem; the development of nutrient rich, highly dispersible propagules; the ability to exploit low nutrient, floating or partially submerged peat substrates; and living, and perhaps photosynthetic, zones in the outer periderm and leaf cushions, which may have enabled the plants to withstand physiological water stress by dropping many of the leaves and even branches, were major factors allowing their successful habitation of the coal swamps (DiMichele et al., 1985).

#### Cordaiteans:

In paralic (coastal) coal basins, the rise and decline of cordaiteans was entirely within the Middle Pennsylvanian (Phillips et al., 1985). The two main kinds of assemblages are <u>Mesoxylon</u> with <u>Mitrospermum</u> and <u>Pennsylvanioxylon</u> with <u>Cardiocarpus</u> ovules (Costanza, 1983).

The large cordaitean roots usually exhibited eccentric growth rings which were not evident in the trunks and branches. Such "growth rings" may have been a response to seasonal or sporadic flooding for prolonged periods, a phenomenon somewhat similar to the formation of

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eccentric growth rings in modern cypress knees (Phillips et al., 1985). Cordaitean roots in coal swamps influenced by brackish water conditions developed aerenchyma tissue (Costanza, 1983).

Cridland (1964) suggested that one cordaitean root species Amyelon iowense, found in some Iowa coal balls, shared many morphological features with the roots of modern mangrove Rhizophora mangle and inferred a mangrove habitat (physiologically dry condition in saltwater swamp) for the cordaitean plants which produced Amyelon iowense. Raymond and Phillips (1983) analyzed the community paleoecology of these Iowa coal balls and found that the distribution of cordaitean plants in these deposits was consistent with the suggestion given by Cridland (1964). Phillips et al. (1985) also suggested that the mangrove-like habitat, inferred for one particular species, Pennsylvanioxylon birame, should not be applied to all Desmoinesian cordaitean plants. Cordaites co-occurred with abundant seed ferns and tree ferns in early Desmoinesian coal swamps and appear to have been influenced by brackish water. They also postulated that the cordaitean habitat was different from that of lycopods based on the observation that abundant Mesoxylon roots penetrated into peats dominated by Lepidophloios harcourtii.

In general, cordaiteans became abundant in coal swamps only where the conditions were physiologically

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drier or brackish, and where excessive evaporation occurred or perhaps where seasonally wet-dry climate (with emphasis on the drier season) existed (Phillips and Peppers, 1984).

### Tree Ferns:

The tree ferns were mainly represented by <u>Psaronius</u> in the Pennsylvanian coal swamps. They were rare in the Lower Pennsylvanian strata but these marattiaceous ferns spanned the entire Pennsylvanian Period.

The only modern analogs for the environmental tolerances of <u>Psaronius</u> are the living Marattiales, which hardly compare with the tree size of <u>Psaronius</u>. They occur in the moist tropics in the understory along the lower slopes of mountains up to 2,000 m in tropical and montane rainforests, especially in islands (Troll, 1970), with the exception of <u>Marattia fraxinea</u> that occurs in the temperate areas (Phillips et al., 1985). Other modern tree ferns of the Filicales overlap the Marattiales environmentally and are much more widespread. They occur in mild temperate lowlands and wet tropical mountains and seem to be more tolerant of cool temperate climate conditions than the Marattiales (Troll, 1970).

It is possible that <u>Psaronius</u> might have been tolerant of slightly cooler temperatures, as exhibited by modern filicinean tree ferns, and could have inhabited lower elevations of mountains in the tropical belt. This consideration is mainly based on the conflict between miospore data and peat compression records of lowlands (Phillips et al., 1985), which will be discussed later.

According to Phillips and Peppers (1984), the early evolutionary development of <u>Psaronius</u> occurred largely outside coal swamps and then expanded in lowlands or wetland habitats prior to becoming abundant in coal swamps.

## Pteridosperms:

This group was represented by Lyginopteris, a liana or small tree, and <u>Medullosa</u>, the largest pteridosperm tree in the coal swamps. Lyginopteris was common during the Early Pennsylvanian and became extinct at the beginning of the Middle Pennsylvanian in the United States and at about the Westphalian A-B boundary in Europe (Patteisky, 1957; Gillespie and Pfefferkorn, 1979). Medullosans were uncommon in the early Westphalian peat deposits, but existed through the whole Pennsylvanian period.

It is thought that medullosans were generally diverse and dominant in moist lowlands of the Pennsylvanian (Pfefferkorn and Thomson, 1982; Peppers, 1970), and that medullosans did not expand into coal swamp environments or habitats until the Middle Pennsylvanian. Abundance of medullosans may infer higher nutrient levels

in the coal-forming peat swamps because they are found near mineral rich beds within the coals (Phillips et al., 1985).

Sphenopsids:

This group is represented by <u>Calamites</u>, the only tree form of this group, and <u>Sphenophyllum</u>, a small herb or vine. Their range extends through the entire period of Pennsylvanian coal swamps. Calamitean trees exhibited vegetative propagation and were more abundant in clastic rich wetlands than in coal swamps (Phillips and Peppers, 1984).

Changing Patterns In Coal Swamp Vegetation In Relation To Wet-Dry Alternation of Paleoclimates:

The climatic trends of the Pennsylvanian Euramerican tropical belt are viewed as a series of alternating wetter to drier pulses with each drier interval becoming more severe than the previous. There were two major drier intervals during the Pennsylvanian time. The first drier interval developed during the early Middle Pennsylvanian; the second drier interval occurred in the early Late Pennsylvanian, and the onset of the Permian probably marks the beginning of the third one. It is suggested, therefore, that there were three wetter phases separated by two drier phases developed at the Lower-Middle and the Middle-Upper Pennsylvanian boundaries, respectively. Conspicuous, synchronous (or nearly so) vegetative changes in the Pennsylvanian Euramerican coal swamps coincided with the first and the second drier intervals.

The term dry or drier interval is relative and not meant to convey arid or semi-arid. The terms Early, Middle, and Late Pennsylvanian are used here in the concept of Bradley (1956), and as commonly used by the United States Geological Survey, the top of the New River Formation of West Virginia and equivalent strata mark the Lower-Middle Pennsylvanian boundary; the Allegheny-Virgilian boundary of the northern part of the Appalachian region is equivalent to the Middle-Upper Pennsylvanian boundary.

The First Drier Interval:

This drier interval occurred near the Early-Middle Pennsylvanian in the United States and is equivalent to the Westphalian A-B boundary in Europe. The principal coal swamp vegetative changes included: 1) the fluctuating decline in the high level of lycopod dominance; 2) increased cordaitean abundance; 3) a rise in occurrence of herbaceous lycopods to form intercalated marshlands and an overall increase in floral diversity; and 4) a sustained rise in abundance and diversity of tree fern spores.

These major changes in coal swamps inferred the

shift of the more evenly moist tropics to moderately drier or seasonally drier tropical climate.

Tree ferns do not dominate any of the compression floras formed prior to the upper Westphalian D (upper Desmoinesian equivalent to the upper Middle Pennsylvanian), near the time of the second drier interval. Therefore, abundance of tree fern spores, which started to rise during the first drier interval, may indicate "spore rain" of tree ferns from other regions outside coal swamps prior to actual expansion of the tree ferns across the paleotropical lowland belt (Phillips et al, 1985). This conflict between miospore data and data derived from coal ball plants and compression flora records of the lowlands seems to be consistent with the suggestion that <u>Psaronius</u> tree ferns were better adapted to relatively cool and drier condition in lowlands of the tropical belt.

The Second Drier Interval:

This interval, the drier of the two Pennsylvanian intervals postulated, occurs at the time of Middle-Late Pennsylvanian boundary in the United States or Westphalian-Stephanian boundary in Europe. Major vegetation changes in coal swamps were the massive reduction of the lycopods, with the exceptions of <u>Sigillaria</u> and herbaceous lycopods, and the dramatic increase in abundance of tree ferns that replaced lycopods

as the dominant group in coal swamps. No coal ball deposits are known at the position of the Middle-Late Pennsylvanian boundary. Coal ball deposits indicate strong dominance of lycopods below the boundary and strong dominance of tree ferns above the boundary.

All the Missourian (the early Upper Pennsylvanian) coal ball deposits were dominated by tree ferns, but some small, scattered deposits of coal balls in Virgilian (later Upper Pennsylvanian) indicate that pteridosperms, calamiteans or cordaiteans may have been very abundant, if not dominant, in some places. On the whole, tree ferns were dominant during the Later Pennsylvanian (Phillips and Peppers, 1984).

The detailed sequence of significant change in floras, probably due to major climatic change, is not known because of unconformities or disconformities which interrupted the continuity of the stratigraphic record. But studies of changes in dominance of coal swamp vegetation in a series of coal by coal analyses strongly indicates a mosaic transition rather than a major break in the stratigraphic succession (Phillips et al., 1985). Pfefferkorn and Thomson (1982) reported, for example, that in upper Westphalian D (the upper Middle Pennsylvanian) and younger strata, tree ferns were the first or second in abundance in 11 of 14 floras.

Evidences Supporting the Hypothesis of Alternating Wet-Dry Conditions of the Pennsylvanian Euramerican Tropical Belt:

Evidences from Paleobotany:

1) Conifers that were adapted to cooler, drier climate first appeared during the early Middle Pennsylvanian (Westphalian B) of Europe (Scott, 1974), and became more common during the Late Pennsylvanian (Stephanian) deposits of both the United States and Europe (Florin, 1945).

2) During the first drier interval, it is proposed that a <u>Megalopteris</u> flora, including cordaiteans, <u>Pecopteris</u> (foliage from tree ferns being considered a drier-type flora) migrated eastward to, but not beyond the Appalachians, which would be consistent with a reduction in moisture from the east (Read and Mamay, 1964; Leary, 1981; Leary and Pfefferkorn, 1977). But Cross (1977) provided another explanation of <u>Megalopteris</u> distribution which will be discussed later.

3) Vegetation changes during the Later Pennsylvanian were detected in earlier studies of coal and clastic sediments in the United States (White and Thiessen, 1913; Kosanke, 1947; Schemel, 1957; Winslow, 1959) and in Europe (Davies, 1929; Stschegolev, 1975). For instance, based on field observation of compression floras, long before extensive data from spore and coal

ball studies were available, White and Thiessen (1913) noted that during Conemaugh time (early Stephanian) several changes in floras occurred, such as a rapid decrease, approaching extinction, of the tree-size lycopods (Lepidodendrae) and the rapid development of the large tree ferns (such as <u>Psaronius</u>), and that these changes might be caused by the occurrence of short dry seasons.

4) The absence of lycopod rhizome <u>Stigmaria</u> in the Upper Pennsylvanian in the Unite States has been noted by numerous workers (Huddle and Patterson, 1961).

5) Several examples of Missourian (Upper Pennsylvanian) woods with growth rings, probably reflecting wet-dry seasonality, were reported by Baxter and Hartman (1954) and Jensen (1982). This character is in contrast to the apparent absence of growth rings in woods of Desmoinesian age (Middle Pennsylvanian) in the Midcontinent (Phillips et al., 1985).

6) There was a marked west to east migration of gymnosperm plants that were adapted to drier conditions in the late Desmoinesian (Read and Mamay, 1964) while cordaiteans and conifers appeared in the middle to late Missourian (Late Pennsylvanian) deposits of Kansas (Elias, 1936; Winston, 1983; Mapes, 1984). These subsequently migrated into the major coal regions of the United States. This floral migration in the late part of the second drier interval resemble some the Early Permian distributional patterns when the paleotropical belt underwent further drying (Phillips et al., 1985).

7)Based on compression floras, vegetative changes occurred in the Euramerican floristic province at the Westphalian-Stephanian boundary. This appears to coincide with differentiation of the paleotropical belt into western Euramerican and eastern Cathaysian floristic provinces (Li and Yao, 1982).

Evidences from Analyses of Coal Quality:

Ash and sulfur content are two important characteristics determining coal quality. Some aspects of deposition of the coal quality are dependent on the geochemical environment of coal beds (peat swamps). Holocene peat deposits tend to occur: 1) in wet, cold temperate climates; 2) in warm temperate and subtropical climates where annual rainfall is relatively high but unevenly distributed (seasonal); and 3) in tropical climates where annual rainfall is high and evenly distributed (even/wet).

According to the geochemical model for coal beds based on geochemical observations of modern peat forming environments, Cecil et al. (1985) proposed two generalized types of peat forming environments in the Pennsylvanian tropical and subtropical belt of the Appalachian basin and the relation of these to formation of commercial quality

coal.

Under the even/wet tropical climate, peat deposits were probably domed (raised-bogs); low concentrations of dissolved solids in the peat formation water resulted in low buffering capacity. Organic acids caused acidic (pH less than 4), antiseptic conditions that resulted in intense leaching of mineral matter, minimal degradation of organic matter, and low ash and low sulfur peat deposit; the resulting coal beds are also low in ash and sulfur.

Under a seasonal tropical climate, when evaporation periodically exceeded rainfall, both dissolved solids and pH in surface or near surface water of peat swamps increased because ground water containing higher concentrations of dissolved mineral matter flowed into the peat swamps. In such cases, the surfaces of peat deposit were probably planar (not domed); water in peatforming and other depositional environments became more nearly neutral (pH 4-7). The coal beds derived from these peats are high and variable in both ash and sulfur contents.

The extensive analytic data of coal quality derived from 634 samples in the central Appalachian basin (Cecil et al., 1985) clearly illustrates the stratigraphical variation in ash and sulfur contents. Coals from the strata older than Allegheny Formation (upper Middle Pennsylvanian) contain low ash (average less

than 10%) and low sulfur (average less than 1%) in sharp contrast to ash and sulfur content of coals from the strata younger than Allegheny Formation which are high in both ash (average more than 10%) and sulfur (average more than 1%). The results indicate that there was an even/wet tropical climate before the late Middle Pennsylvanian and that the climate shifted conspicuously to seasonal tropical environments after the late Middle Pennsylvanian in the central Appalachian area. This is consistent with the postulated second drier interval that occurred at about the Middle-Late Pennsylvanian boundary of the Euramerican tropical belt.

# Evidences from Sedimentation:

The abrupt decrease in mineable coals from Desmoinesian (the late Middle Pennsylvanian) to Missourian (the Late Pennsylvania) rocks in Midcontinent of North America has been related to the probability that Missourian climate became at least seasonally drier than the Desmoinesian climate, representing a transition from the equatorial Desmoinesian rainforest climate to a semiarid climate in the Permian as North America moved northward. This change is also reflected in the progression of evaporites from western Colorado in the Desmoinesian to Kansas in the Permian. Direct climatic evidence from soils in two Missourian shales deposited at low stands of sea level includes caliche horizons.

incompletely leached, mixed-layer clays in contrast to intensely leached Desmoinesian kaolinite, and soil profiles resembling the vertisols which are developed under semi-arid conditions (Schutter and Heckel, 1985).

### Evidences from Coal Petrography:

Macerals are units of organic materials that comprise recognizable constituents of coal. They consist of three groups: 1) vitrinite, an oxygen rich group which is characteristic of vitrain and is composed of humic material associated with peat formation; 2) exinite, a hydrogen-rich group including sporinite, cutinite, alginite, and resinite, derived from spores, cuticles, resins and waxes; 3) inertinite, a carbon rich group including micrinite (no plant cell structure preserved), fusinite containing carbonized wood material, and sclerotinite. The formation of inertinite may reflect drier environment and more subaerial oxidation of plant matter than other two groups during coalification, although a considerable amount of micrinite may have resulted from fires in the peat swamps.

Based on the petrographic analyses of maceral distribution of Illinois coals of 326 face channel and drill core samples from 24 coal beds (or seams) of the Pennsylvanian System, Harvey and Dillon (1985) reported that the inertinite contents of the coals from the Missourian and Virgilian (the upper Late Pennsylvanian) Series averages 16.1%, compared to 9.4% for stratigraphically older coals from the Desmoinesian and older Series. This is an indication that there was generally more extensive oxidation in the peat that formed the younger coals and that this condition was at least in large part a result of greater exposure of the later peat swamps to weathering as the climate became drier and the water tables lower than was the case for the earlier coals of the Pennsylvanian Period.

Evidences from Paleotectonics:

A number of changes in continental configuration contributed to the climatic changes in the Carboniferous.

Equally important to the changes in global temperature brought out by continental drift are the changes in atmospheric circulation expected from the formation of an uninterrupted north-south continental mass and northward drift of the super-continent, Pangaea. The resulting precipitation patterns are vital to understanding the distribution of coal beds. Two paleogeographic developments are of particular significance with regard to the distribution of rainfall in the eastern North America (Rowley et al., 1985).

1) The increasing symmetry of land around the equator favored formation of zonal global circulation. In the Early Carboniferous, 72% of the exposed land area was south of the equator; before the Triassic, the land area was symmetrically disposed around the equator forming a pole-to-pole single continent, Pangaea, by the northward drift of the continent (Parrish et al., in press).

Monsoonal circulation consists of a circulation pattern that alternates seasonally between high pressure and low pressure as a result of alternating temperature regime over the continent; low pressure forms during the summer when the land is hot relative to the surrounding regions and high pressure forms during the winter when the land is relatively cold (Rowley et al., 1985).

The zonal global circulation, comprising a part of normal monsoonal circulation and the circulation caused by the earth rotation, consists of low pressure at the equator, high pressure at low mid-latitudes, low pressure at high mid-latitudes, and high pressure at the poles. Unlike the equatorial and polar systems, the high and low pressures at mid-latitudes have relatively little to do with temperature, but rather are responding to the influence of the earth rotation. Because of the rotation of the earth, heated air rising at the equator cannot flow directly to the poles and, likewise, cooled air sinking at the poles cannot flow directly toward the equator. The heat exchange is effected through an intermediate circulation at mid-latitudes (Rowley et al., 1985).

2) The Allegheny orogeny occurred during the Pennsylvanian period. Gondwana rotated clockwise and collided with Laurussian, resulting in the formation of

mountain systems, one segment of which, the Appalachians, was on the equator (Ziegler et al., 1979).

Normal equatorial circulation consists of westward flowing and ascending air, so that rain falls most heavily on the eastern margin of an equatorial continent where the air first encounters land. In the absence of mountains on the east coast, the rain is distributed across the continent; mountains on the east coast would concentrate rainfall on the coast, leaving the region to the west in the rain shadow, relatively dry.

A strong low pressure area created by very high mountains on the equator would prevent the summer monsoonal circulation from forming north or south of the equator, and therefore would decrease the intensity of the winter monsoon by preventing the development of a strong cross-equatorial contrast. In addition, rainfall would maintain its normal equatorial distribution, rather than being deflected away from the equator by the cross equatorial flow. A sufficiently high plateau on the equator would alter the zonal equatorial rain pattern to the extent that air might be drawn from the west as well as from the east. If the air from the west was from an oceanic region instead of a large land mass, heavy rain would fall on both side of the mountains (Rowley at al., 1985).

Combining the two paleotectonic events (the formation of the symmetrical continent around the equator

and the raised mountain systems on the equator caused by Allegheny orogeny), the climatic changes related to the tectonics would be in this way: The monsoonal conditions tended to dry out the equatorial region, including the Appalachian Basin, by deflecting rainfall north and south of the equator into the low pressure area in the summer hemisphere. Drying conditions in the Appalachian Basin would have been increased further by the rain shadow effect of the rising mountains on the east, which would block any remnants of the westward flowing trade winds. However, as the mountain on the equator rose higher, enough to be a "high altitude heat source" (Rowley et al., 1985) like the Himalayas, the equatorial low pressure would have been intensified; the low pressure would have been, in turn, sufficiently intense to draw air not only from the east, the normal source of the equatorial air, but also from the west, producing wet conditions in the Appalachian Basin. Subsequently, with cessation of mountain building and erosion of the mountains resulting in reducing the effect of the "high altitude heat source", the equatorial region tended to be drier again. The result would be a wet-dry cycle (Rowley et al., 1985).

Summary of Evidence for Alternating Wet-Dry Conditions:

In summary, two major vegetation pattern changes in the Pennsylvanian Euramerican coal swamps occurred



Fig. 5. Generalized stratigraphic patterns of abundance of Pennsylvanian coal-swamp vegetation in the United States with a relative wetness curve indicating the alternation of the wet and drier intervals (from Phillips at el., 1985)

synchronously (or nearly so) near the Lower-Middle Pennsylvanian (Westphalian A-B) and the Middle-Upper Pennsylvanian (Westphalian D- Stephanian) boundaries, respectively. These vegetative changes were consistent with two drier intervals of the Euramerican tropical belt during the Pennsylvanian Period, which is supported by evidence from paleobotany, palynology, coal petrography, sedimentology, distributions of coal beds and evaporites, and paleotectonics. The massive reduction of arborescent lycopods except for Sigillaria, and the rising dominance of tree ferns in the coal swamps coincided with the secondary interval (Fig. 5).

However, it is evident, on the other hand, that the massive reduction of lycopod trees at the Middle-Late Pennsylvanian boundary is a complex process, and cannot be attributed only to wet-dry alternation of the paleoclimate. This will be discussed later.

SOME LIMITATIONS OF QUANTITATIVE ANALYSIS OF VEGETATION PATTERNS OF COAL SWAMPS

Identifying Some Dismembered Plant Remains:

There is great difficulty in identifying and classifying some dismembered plant parts preserved in coal balls for quantitative analyses (Phillips et al., 1985). Identification of coal ball plants is based on their anatomical features. Distinguishing a fossil plant to generic or specific level generally requires at least part of the vegetative (stem, leaf, and root) or the reproductive organs, and, in many instance, a combination of both vegetative and reproductive features. Generally, well-preserved coal ball plants can be identified by using serial sections, complete cross sections, mediumlongitudinal sections, or a combination of the cross sections with the longitudinal sections of plant parts or organs.

But, during a quantitative analysis procedure, it

is sometimes very difficult to identify some plant remains in coal balls because the identification is only based on one random section which may be a cross-, longitudinal-, or oblique-section. An example of the difficulty in making such identification is illustrated by the following examples. The main difference between two cordaitean stem genera Mesoxylon and Pennsylvanioxylon is, for instance, that the leaf traces of Mesoxylon appear to be double and the sympodia (separate protoxylem strands), from which the leaf traces arise, are mesarch (Traverse, 1950; Baxter, 1959; Cohen and Delevoryas, 1959), while the leaf traces of Pennsylvanioxylon rise singly from an endarch sympodial complex (Vogellehner, 1965; Taylor, 1981, p.425-426; Stewart, 1983, p. 328-329). Obviously, it is impossible to distinguish the two genera from each other without making serial longitudinal sections to show the structure of the sympodia and to follow the course of a leaf trace.

The same difficult situation exists in distinguishing genera of lycopod trees. For example, <u>Paralycopodites</u>, first described by Morey and Morey (1977), differs from <u>Lepidophloios</u> and most species of <u>Lepidodendron</u> in having persistent, short, scale-like leaves (DiMichele, 1980). This means that if random sections of lycopod stems, present on peels used for quantitative analysis, do not pass through attached leaves, there is no way to separate <u>Paralycopodites</u> from other lycopod genera. Also, the differentiation of

<u>Diaphorodendron</u>, a lycopod stem genus established by DiMichele (1985), from other lycopod stem genera requires the identification of a combination of several anatomical features of both vegetative and reproductive organs (DiMichele, 1985).

With these few examples, one can understand the difficulty in identifying some dissociated plant parts in coal balls, based on only a random section available on a peel, in making a quantitative analysis of the constituent plants, comprising the peat, which are preserved in a coal ball. When such difficulties do appear occasionally, it is better not make any further guess beyond that which the random sections can illustrate because correct identification is required for quantitative analysis and incorrect identification would significantly reduce the reliability of the quantitative data.

# Shoot/Root Ratio:

Another limiting factor is the shoot (stem and its appendanges)/root ratios of coal ball plants. The amount of aerial plant parts is crucial for community analysis. From living taxa, it is estimated that 20-30% of original biomass of lycopods was root system and 70-80% was aerial part, i.e., a shoot system (Phillips and Peppers, 1984). Therefore if a whole tree was preserved as peat, it would result in a shoot/root ratio of roughly 4/1. But the actual shoot/root ratios of peats are commonly close to 1/1 indicting extensive disproportionate loss of aerial plant parts. This greatly reduces the accuracy of reconstructing the relative amounts of plants which make up the community structure of the vegetation of peat deposits represented by coal balls (Phillips and Peppers, 1984).

THE PURPOSE OF THE PRESENT ANALYSIS:

Previous investigations of coal swamp vegetation have been concentrated on the Illinois basin and the central Appalachian Basin in the United States because of the well-known coal ball plants from the Illinois Basin and of the many studies of the coal geology of the Paleozoic in the central Appalachian Basin.

The Appalachian Basin presents an extensive geological record of the upper Paleozoic (Gillespie and Pfefferkorn, 1979). In southeastern West Virginia and southwestern Virginia, sedimentation was continuous across the Mississippian-Pennsylvanian boundary (Englund, 1969). In many other parts of the Appalachian Basin and in other basins of the United States there is an unconformity at the Mississippian-Pennsylvanian boundary; the central Appalachian basin contains the most complete biostratigraphic and lithostratigraphic record of the coal-bearing Pennsylvanian and the Lower Permian strata (Cecil et al., 1985).

A comparison of the changes in coal swamp

vegetation of the Appalachian and the Midcontinent regions between the first and the second drier intervals of the middle part of the Middle Pennsylvanian has been difficult because of the dearth of permineralized peat deposits in coal beds in the Appalachian Basin (Phillips et al., 1985).

The Derringer Corners coal balls studied here were collected from near the Pennsylvania-Ohio state line in the Northern Appalachian Basin, geographically the easternmost coal ball locality known to date in the United States. The stratigraphic position of the locality is in the Kittanning coals of the Allegheny Formation, near the Middle-Late Pennsylvanian boundary at the time of the second drier interval. It is very close stratigraphically to the well-known, coal ball-rich seams, Herrin (No. 6) or Harrisburg (No. 5) coals in Illinois. Phillips et al. (1985, p. 81) made a preliminary quantitative analysis of 35 pieces (1,937 cm<sup>2</sup>) of the Derringer Corners coal balls from our collections. The present quantitative analysis of the Derringer Corners coal balls, the only Allegheny coal ball collection that has been quantified, provides some significant data for study of coal swamp vegetation of the Appalachian Basin near the second drier interval, and for comparison of the vegetation pattern in coal swamps between the Appalachian Basin and Illinois Basin.

### **TECHNIQUES OF ANALYSIS:**

The techniques used in the present study are basically those given by Schopf (1938b), Phillips (1976), Phillips et al. (1977), Phillips and DiMichele (1981), and Raymond et al. (1984). Coal balls were cut with a rock saw, serially, into pieces about 2.0 cm apart. Cellulose acetic peels were made from each surface. Plant parts included on the peels were measured using a grid system under a dissecting microscope. The measured plant parts of different groups were classified and the percentages of each were then computed. Some aspects of the techniques in this study are described below in more detail.

1) In the analyses given by Phillips et al. (1977), coal ball samples were collected stratigraphically through the entire thickness of the coal seams (vertical profile sample); the results of the analyses of the vertical profile samples provide greater accuracy than that of random samples. According to Raymond (in press), an analysis of a random sample based on 2,000 cm<sup>2</sup> or more yields quantitative results closest to those of vertical profile samples collected from the same locality as the random samples.

Although the Derringer Corners coal balls were randomly collected, i.e., without recording their orientation or position in the vertical profile (stratigraphically), all coal balls or broken pieces of

coal balls, from bottom to top, of the large concretionary mass of coal ball concretions which occupied the full thickness of the coal seam were collected for analysis by Dr. A. T. Cross and his students during 1965-1967. There may be little difference in results of the quantitative analysis of the present collection from those of coal balls from vertical profile samples. The sample size analyzed here  $(13,203 \text{ cm}^2)$  of the Derringer Corners collection is much larger than  $2,000 \text{ cm}^2$  quantitative analysis of coal ball peels from a random collection of coal balls from Iowa reported by Raymond (in press).

2) Because of the rather large collection of the Derringer Corners coal balls, it was not reasonable to measure all peels made from the whole collection. Phillips et al. (1977) used 189 coal balls or pieces of coal balls to test a "middle-peel" approach (measurement of the peels from the middle slice of each coal ball only) to determine quantitatively and qualitatively the relative proportions of the plant materials. The results obtained from the "middle-peel" method was very close to that obtained by the quantitative analysis of all peels from every slice, including the middle one, of each coal ball measured. Accordingly, the Derringer Corners collection (342 coal balls or pieces of coal balls) is large enough to use the "middle-peel" method for analysis. In this study, 342 middle peels have been measured with two exceptions when two rare plant parts (a seed of Pachytesta and a piece of

<u>Dolerotheca</u>) were identified on the other peels rather than the middle ones. In these cases, the two selected peels were chosen to replace the middle peels for analysis.

3) The method of measuring is modified from those given by Phillips et al. (1977), Phillips and DiMichele (1981) and Raymond et al. (1984). Those authors placed a transparent plastic sheet marked in a one cm<sup>2</sup> coordinate system over a peel from coal ball surface to be quantitatively and qualitatively analyzed. Using this grid system, they recorded only the taxonomic affiliations of the largest piece of plant remains seen in each grid square (1  $cm^2$ ), and disregarded all other plant remains smaller than the largest one. This system was modified for reproductive organs. Phillips et al. (1977) assigned one grid square  $(1 \text{ cm}^2)$  to each of the reproductive organs identified within a grid square, regardless of its size, whereas Raymond et al. (1984) counted only the largest piece or whole reproductive organ within each grid square, and disregarded the presence of smaller reproductive organs.

In the present study, a mapping method was used. A selected peel was placed over a paper grid system measuring of  $\emptyset.259 \text{ cm}^2$  for each square (the area of 100squares is  $5.09 \times 5.09 \text{ cm}$ ), and a carbon paper was inserted between the peel and the grid paper. The outlines of all plant parts on the peel were sketched with a pencil under a dissecting microscope at a magnification of  $10 \times 10^{-10}$ 

The resulting sketch of the plant remains on the grid paper shows the exact positions and areas occupied by all plant parts exhibited on the peel. Then the area of the squares occupied by different plants were counted and recorded.

In some peels, certain areas were occupied by several different kinds of plant debris (mostly leaves and rootlets); these plant units were sometimes so small and were mixed with each other so evenly that it was impossible to map and count each of these pieces or units separately. In such cases, besides mapping rare plant organs, the areas occupied by each plant group were estimated and mapped so that the mapping of these areas were not exactly consistent with the actual distribution of these plant parts on the peels. Because these areas were rather small relative to the whole of the areas analysed, the bias caused by the imprecise mapping in these instances can be disregarded.

It is believed that this mapping method should be more precise, then those applied by Phillips et al. (1977, 1981) and by Raymond et al. (1984), though it is not necessarily as efficient.

4) Because of the difficulty of identification of dissociated plant parts mentioned above, most plant remains were identified only to generic or group level in this study.

5) For calculating shoot/root ratios, one-half of

all <u>Psaronius</u> outer zone roots were considered to be aerial debris (Phillips and DiMichele, 1981). This is in contrast to classifying all <u>Psaronius</u> outer zone roots, that appeared to intrude the peats, as root debris (Raymond, in press).

6) Root penetration events were also computed. Penetrated units of plant debris were regarded as substrates of the penetrating roots, as proposed by Raymond (in press). The root penetration may indicate a successional sequence of coal ball plants, i.e., the growth of later plants on earlier litter or peat surfaces.

### RESULTS

The quantitative analysis of 13,203 cm<sup>2</sup> of the middle peels from each of 342 coal balls or pieces of coal balls from the Derringer Corners, western Pennsylvanian of the later Middle Pennsylvanian age are presented below:

 The coal swamp vegetation is composed of four major plant groups comprising about 30 genera, common in the Pennsylvanian Euramerican coal swamps: lycopods, pteridosperms (seed ferns), ferns, and sphenopsids (Table 1).

2) Lycopods were the dominant plants in the Derringer Corners coal swamps, contributing 66.6% of all identifiable plant parts preserved in the coal balls; pteridosperms were of the second importance (20.8%); ferns TABLE 1

Peat Composition (% of All Material) Based on Coal Ball Peats of Upper Allegheny Formation at Derringer Corners, Lawrence County, Western Pennsylvania.

Lycopods	42.9
Lepidodendron	7.9
Lepidophloios	Ø.5
Sigillariophyllum	1.0
Lenidonhylloides	Ø 4
<u>Stigmaria</u>	7 /
Destlets	/•¶ 9E 3
ROOTLETS	25.3
Cones	6.4
Sphenopsids	2.9
Calamites	2.6
Sphenophyllum	Ø.2
Astromyelon	Ø.1
Ferns	5.16
Psaronius stems	Ø.8
Stipitopteris	Ø.5
Pecopteris	0.04
Scoleconteris	Ø.2
Psaronius roots	3.5
<u>Ibaronius</u> 1000s	<i>a</i> 1
Anachoropteris Det mient en i e	
Botryopteris	10.02
Pteridosperms	13.30
Heterangium	0.05
Sutcliffia	0.08
Schopfiastrum	1.30
Medullosa	Ø.35
Myeloxylon	5.90
Alethopteris	
lesquereuxii	2.80
Alethopteris	
sullivantii	1.60
Neuronteris	Ø. 29
Medullogan Poot	0.25 0.70
Dechutosta NOOL	a 20
Pachytesta	
Dolerotneca	0.01
Marine Animals	0.0024
Bryozoans	0.0003
Brachiopods	0.0009
Other Shells	
	0.0012
Coal Material	15.5
Mineral Material	1.5
Unidentifiable	
Dlant Dohrie	18.6
I LUNC DEDILD	10.0
Inidant i fi shl s	
Dient Missuer	<b>a A</b>
Flant Tissues	10 • <del>4</del>

TABLE 2 Summarized Peat Composition (% of Identifiable Plant Biomass) and Frequency of Occurrence, in All Derringer Corners Coal Balls.

	<pre>Frequency of occurrence   in All Coal Balls(%)</pre>	Composition(%)
Lycopods	Ø.96	66.6
Sphenopsids	Ø.44	4.6
Ferns	Ø.58	8.0
Pteridosperms	Ø.64	20.8

TABLE 3

Organ Composition (% Total Identifiable Plant Biomass) of the Derringer Corners Coal Balls.

	Stem	Leaf	Reproductive Organ	Root	
Lycopods	12.5	2.2	Ø.84	51.0	*
Ferns	4.3	Ø.1	Ø	Ø.2 5.3	**
Pteridosperms	12.0	7	ؕ45	1.1	

\* This root system consists of rhizomes (11.5%) and rootlets (39.5%).
\*\* This root system consists of the outer-zone (2.4%) and the inner-zone (2.9%); one-half of the outer-zone has been regarded as aerial part of adventitious roots.

TABLE 4 Organ Composition (% Identifiable Biomass of Each Plant Group) of Derringer Corners Coal Balls.

	Stem	Leaf	Reproductive	Root	Shoot/Root
Lycopods Sphenopsids	18.9 95.1	3.3	1.25	76.7	Ø.24 18.95
Ferns Pteridosperm	27.9 57.8	Ø.9 34.7	3.62 2.16	67.5 5.3	1.Ø3 * 18.2Ø

\* Considering one half of the outer-zone roots of ferns (Psaronius) to be aerial part, the shoot/root ratio is 1.03.

and sphenopsids were 8.0% and 4.6% respectively (Table 2).

3) Root systems contributed the most abundant part (up to 57.6%) of the plant material in the coal balls; stems were 31.5%, leaves were 9.6%, fructifications were only 1.5%. The shoot (aerial parts)/root ratio was Ø.74 (Table 3).

4) Composition of each plant group:

The organ composition of each plant group is summarized in Table 4. Lycopods consisted primarily of <u>Stigmaria</u> (rhizomes) and its root system. Their rootlets contributed 76.7% of the total identifiable biomass of lycopods preserved in the Derringer Corners coal balls. Lycopod stems were mainly composed of twigs and leaves of Lepidodendralean type; only one piece of the primary xylem of <u>Lepidophloios</u> was identified; the presence of <u>Sigillaria</u> is evidenced only by its leaves preserved in the Derringer Corners coal balls. The shoot/root ratio of lycopods was extremely low, only 0.24 (Table 3).

The main representatives of sphenopsids were <u>Calamites</u> stems and <u>Sphenophyllum</u> stems. Calamitean stems comprised 81% of the total biomass of this group; <u>Sphenophyllum</u> stems were common elements of this flora. These two plants were not important volumetrically in the flora because of their rather small sizes.

The tree fern <u>Psaronius</u>, comprising 97.1 of the total identifiable plant remains of the fern group, consists primarily of root mantle which was 67.6% of the

total remains of the ferns preserved in the coal balls. The inner zone roots were 37.5%, and the outer roots were 30.0% of the total fern debris. Stems and petioles contributed 25.0% of the total volume of the fern remnants. Coenopterid ferns, such as <u>Anachoropteris</u>, <u>Botryopteris</u> and <u>Ankyropteris</u> were not rare but very small so that they constituted only 2.1% of the total fern biomass. The shoot/root ratio of this group was increased to 1.03 by regarding one half of the outer zone roots of Psaronius as aerial parts.

Pteridosperms, the second most abundant group of the plants in the coal swamps, comprised 20.8 % of the total plant parts preserved in these coal balls. The pteridosperms were mainly represented by their aerial parts which contributed 94.3% of the total identifiable biomass of the whole group. This group of plants exhibited relatively high diversity (in taxa). The aerial parts were primarily stems (57.8%), and leaves constituted 34.8%. The stems are comprised of four genera, <u>Heterangium</u>, <u>Schopfiastrum</u> (Lyginopteridaceae), <u>Sutcliffia</u>, and <u>Medullosa</u> (Medullosaceae). 71.1% of the stems were petioles identified as <u>Myeloxylon</u>. The leaves were mainly two species of <u>Alethopteris</u>, <u>A. lesquereuxii</u> and <u>A.</u> <u>sullivantii</u>. <u>A. lesquereuxii</u> was more abundant than <u>A.</u> sullivantii, roughly 2/1 in percentages.

The reproductive organs of pteridosperms, represented by the medullosan seed Pachytesta and the pollen organ <u>Dolerotheca</u>, constituted only 2.1% of the total biomass of the group.

5) Cordaitean plants were not recognized and appear to be absent in the Derringer Corners coal swamps.

6) The root penetration into previously accumulated plant debris has been summarized in Table 5. These were 97 occurrences of roots penetrating into other plant parts observed on the analysis of the peels . 86 of these penetration events were lycopod root penetration; 7 were tree fern root penetration, and 4 were penetration by pteridosperm roots (Table 5).

Penetration of Lycopod roots into seed ferns occurred 54 times (37 times into <u>Myeloxylon</u>, 14 times into <u>Sutcliffia</u>, 3 times into <u>Pachytesta</u>); and 7 times into <u>Psaronius</u> (4 times into stems, 3 times into roots). Lycopod roots penetrated into the lycopod rhizome, <u>Stigmaria</u> 19 times. <u>Psaronius</u> roots penetrated pteridosperm petioles 5 times, and calamitean stems 2 times. Pteridosperm roots were observed to penetrate pteridosperm petioles 4 times. No pteridosperm root was observed to penetrate any plant parts of other groups. Penetration by sphenopsid roots was not observed in this study.

It is noteworthy that there was certainly some relationship between the growth of roots or rhizomes of lycopods and pteridosperms. Of the four plant groups, the total number of the root penetrations was 97; roots

TABLE 5 Summarized Root Penetrating Events (=PE) and % of the Total Times Roots Penetrate Other Plant Organs of Derringer Corners Coal balls.

	Lycopods		Psaronius		Pteridosperms	
Substrates	PE	8	PE	8	PE	8
Lycopods	25	25.7	Ø	Ø	Ø	Ø
Calamiteans	Ø	Ø	2	2.1	Ø	ø
Tree ferns	7	7.2	Ø	Ø	Ø	Ø
Pteridosperms	54	55.6	5	5.1	4	4.3

PE=penetration events

Total penetrating events identified=97; total %=100%

TABLE 6 Summarized Composition (% Identifiable Plant Biomass) of 6 Coal Balls or Pieces of Coal Balls From the Top of the Derringer Corners Deposit.\*

	Lycopods	Sphenopsids	Ferns	Pteridosperms
Composition	92.9	Ø.3	2.2	4.2
* The coal b inferred to	alls conta be from	ining marine the top of th	animal ne peat	fossils are deposit
(Explanation	in text).		le peut	acpette
penetrating into other organs of other groups of plants were noted 68 times. Lycopod roots penetrated organs of pteridosperms 54 times, contributing 79.4 % of the total roots penetrating into organs of other groups of plants. In sharp contrast, no pteridosperm root penetration into lycopods was observed (Table 5).

It seems likely that lycopod plants were growing on peat formed of the remnants of pteridosperms and lycopods in the Derringer Corners coal swamps. At least some pteridosperm debris was serving as a part of the substrate for lycopod growth.

7) Based on the observation that there were some marine animal fossils preserved in the upper 25 cm (approximately) of the big, single, four-foot, concretionary mass of coal balls, from which all coal balls or pieces of coal balls used in this study were collected, it is suggested that the pieces of coal balls containing marine animal fossils may indicate their location on the top or in the upper part of the original big concretion and, therefore, the upper part of the peat swamp accumulation. If that is correct, these coal balls were stratigraphically younger than the other coal balls collected from the mass.

To test the nature of vegetation change stratigraphically, i.e., the succession of the plant communities within the Derringer Corners coal swamp, a quantitative analysis of the middle peels of 6 pieces of coal balls containing marine animal fossils was made. The results, shown in Table 6, illustrate that, compared with the results of the quantitative analysis of all coal balls collected (Table 2), the order of community abundance changed slightly in response to changing edaphic conditions, i.e., the lycopods increased in abundance from 66.6% to 92.9%, seed ferns and ferns decreased in abundance from 20.9% to 4.2 and from 8.0% to 1.3% respectively (Table 6). The increased abundance of the lycopods at the top of the big concretionary mass of coal balls, coinciding with the marginal marine inundation that brought in the invertebrates to the coal swamp, is consistent with the suggestion that lycopods had the capability of withstanding physiological water stress by dropping many of their leaves and/or branches (Phillips and Peppers, 1984).

## DISCUSSION

Composition of the Derringer Corners Coal Swamp Vegetation:

The most significant features of the vegetative composition of the Derringer Corners coal swamps are the dominance of lycopods, the low shoot/root ratio of the total identifiable biomass, especially of lycopods, and the absence of cordaitean plants.

The high abundance of lycopods was indicated by:

1) Lycopods constituted 66.6% of the total identifiable plant biomass (Table 2).

2) Lycopods abundance increased up to 92.9% at the top of the original mass of coal balls, i.e., in the stratigraphically younger beds at the top of the original peat swamp.

3) The frequency of occurrence of lycopods was 96% (Table 2), i.e., lycopods occurred in almost every coal ball.

4) Of the total penetrating roots, 88.7 % were lycopod roots.

The low shoot/root ratio of the plant community at the Derringer Corners coal swamp is mainly the result of the preservation of a large amount of the lycopod rhizomes and their rootlets, which constituted 51.0% of the identifiable biomass of the total plant groups. This indicates severe loss of the aerial parts of the trees, especially lycopod trees, because the shoot/root ratio of the lycopods was extremely low (0.24).

Inferring Paleoenvironments of the Derringer Corners Coal Swamps:

The results of the quantitative analysis strongly infers that the climate of the Derringer Corners coal swamps was relatively dry or seasonally dry tropical climate. The evidences for this are as follows.

1) The low shoot/root ratio.

In coal swamps, since plant root systems were buried in the peat by natural growth in length and diameter, they were less subject to exposure or loss by degradation, whereas aerial portions of trees were more subject to decomposition except when burial or submergence was fairly rapid. Therefore, in general, if other factors remained the same, the higher the water level in the coal swamps, the less loss of fallen trees by biological degradation. Accordingly, the shoot/root ratio of peat deposits can serve as a general index to relative trends in wetness of the coal swamps, i.e., high shoot/root ratio may indicate high water level or wetter condition of the coal swamps, and vice versa. These trends are consistent with environmental inferences drawn from the presence of certain plants as dominants in the coal swamps.

The inference from shoot/root ratio has been supported by other facts. For example, at the beginning of the first drier interval (the early Middle Pennsylvanian), coal resources on the Appalachian Basin declined, and the shoot/root ratio in the coal swamps also declined to a minimum at the same time (Phillips et al., 1985).

2) Composition of pteridosperm leaves.

The major representatives of pteridosperm leaves in the Derringer Corners coal swamps were two species of <u>Alethopteris</u>, <u>A. lesquereuxii</u> and <u>A. sullivantii</u>. As discussed in the systematic portion of this study, <u>A</u>. <u>lesquereuxii</u> was more xeromorphic than A. sullivantii on

the basis of their morphological and anatomical characteristics. The percentage of <u>A</u>. <u>lesquereuxii</u> leaves is nearly as twice that of <u>A</u>. <u>sullivantii</u> in the coal balls. This probably indicates a condition of reduced moisture in the coal swamps.

3) The ash and sulfur contents of commercial coals apparently increased from Allegheny Formation (the late Middle Pennsylvanian) up to the Upper Pennsylvanian in the Appalachian Basin. This infers, according to Cecil et al. (1985), a drying tendency in the coal swamps during this time which includes the Derringer Corners coal balls (lower Middle Allegheny Formation).

Comparison of Vegetation of the Derringer Corners Coal Swamps With other Coal Swamps in the Appalachian Basin and the Illinois Basin:

The composition of the peat deposits of upper Pottsville coals (lower Middle Pennsylvanian) in northeastern Tennessee and eastern Kentucky of the central Appalachian Basin is consistent with that of the Derringer Corners coal balls in the dominance of lycopods (average 68.7%) and low shoot/root ratio (average Ø.84), but is different in the abundance of cordaiteans (average 21.4%), based on random samples of coal balls (Phillips et al., 1985, p.62, Table 3).

Furthermore, it is interesting to note that there is an inverse relationship between cordaitean abundance and shoot/root ratios in the Pottsville coals. During a period of time when the abundance of cordaiteans increased from 1.7% to 36.7%, the shoot/root ratios decreased from 1.3 to  $\emptyset.47$ , i.e., the greater the abundance of cordaitean plants, the lower the shoot/root ratio. In contrast, such a relationship is not observed on the plant community at the Derringer Corners coal swamp where cordaitean plants were not identified, and the shoot/root ratio of the total plants of the community is low ( $\emptyset.78$ ).

The position of the Derringer Corners coal swamps is stratigraphically very close, though not equivalent, to that of Herrin (No.6) Coal in the Illinois basin (Cross, 1967). The composition of peat deposits from four localities of the Herrin Coal exhibited a dominance of lycopods (average 73.8%), with ferns averaging 13.9%, pteridosperms averaging 8.8%, and with only rare cordaiteans (average less than Ø.2%). The Derringer Corners coal swamp was also dominated by lycopods, but had somewhat different amounts of ferns, sphenopsids, and pteridosperms (Table 2). However, the shoot/root ratios from these two regions were guite different from each other. The shoot/root ratios (average 1.64 for total plants, 1.54 for lycopod group) in the Herrin Coals are much higher than those of the Derringer Corners Coal swamps (0.78 for total plants, 0.24 for lycopod group). This difference in shoot/root ratios between these two regions at approximately the same geological time (late

Middle Pennsylvanian) supports the suggestion by Phillips et al. (1984), based on very limited data, that the Appalachian coal swamps were not as wet as the Midcontinent during most of the late Middle Pennsylvanian time.

Discrepancies in Interpretation of Moisture Conditions in Derringer Corners Coal Swamps Based on Abundance and Shoot/Root Ratio of Lycopods:

Previous investigations have indicated a direct relationship between abundance of lycopods and higher shoot/root ratio in coal swamps. This was thought to be reasonable because both lycopod abundance and high shoot/root ratios were interpreted to be indicative of higher moisture conditions in coal swamps. In other words, reduced abundance of lycopods usually correlated with lower shoot/root ratios indicating drier condition in coal swamps.

For instance, the record of low shoot/root ratio of a lycopod dominated coal swamp, the upper Path Fork coal of eastern Kentucky, is consistent with a drier interval inferred by Peppers (1979) based on data of a local spore flora. Also, all the shoot/root ratios in these coal swamps were as low as about 0.5 (range 0.42-0.6) during the Late Pennsylvanian, a time when the major lycopod trees except <u>Sigillaria</u> were unimportant and the second drier interval occurred (Phillips et al., 1985). Therefore, the high abundance of lycopods in contrast to the relatively dry conditions, mainly inferred from the lower shoot/root ratio, is an unusual, distinctive feature of the Derringer Corners coal swamps. This discrepancy causes one to question the application of the concept that lycopods were reliable moisture indicators and, further, that massive reduction of a major group of lycopod trees (Lepidodendrae) was caused by the drier conditions resulting from the second drier climatic interval which occurred at about the time of the Middle-Late Pennsylvanian boundary.

The possible explanations for the discrepancy between the lycopod abundance and a postulated drier condition in the Derringer Corners coal swamps may be that shoot/root ratios are controlled in some places by other factors than moisture; or that the abundance of lycopods was related to other factors than wetness; or that local wet swamp conditions provided the proper environment for the lycopods in spite of regional or climatic conditions of less moisture than in earlier Pennsylvanian time.

Before discussing these possible explanations, it is necessary to emphasize that the approach of applying the changing vegetative pattern in coal swamps to inferring paleoenvironmental conditions has been simplified to consider only the relationship between vegetation change and wetness. This is known to be only one of several paleoenvironmental factor affecting the vegetation.

Actually, plant paleoecology is much more complex than this simplified relationship. Even ignoring biotic factors (mainly competition among organisms, e.g., plants, animals and microorganisms), which may be sometimes more important then the abiotic factors influencing plant communities, abiotic factors which affect vegetation are very complex. Besides temperature and moisture, a number of factors may influence the composition of plant communities of the coal swamps. Local geology, topography, basinal geology, local edaphic conditions, significant disturbances, such as incursions of brackish water, fires, floods, clastic influx, and other agencies or events may overshadow the role of paleoclimate and may have resulted in different local environments in the coal swamps from region to region and different microenvironments in the same coal swamp.

Keeping in mind the complexity of paleoenvironment, it is not difficult to understand the data that were not consistent with the changing vegetation-wetness model. For example, during the Pennsylvanian Period, excluding the first and the second drier intervals, lycopods were generally the most abundant plant group overall in the Pennsylvanian Euramerican coal swamps. But in the Iowa coal swamps of the Western Interior Coal Region of the same time (Lower Pennsylvanian), cordaiteans exhibited a greater abundance

(up to 81.0%) and diversity than in other regions of the United States (Raymond et al., 1983,1984; Phillips et al., 1985).

Another interesting example is the distribution of the Megalopteris flora, as mentioned above. The occurrence of this flora in the Illinois Basin was concurrent with the beginning of the first drier interval and it has been suggested that it migrated eastward to the Appalachians due to a reduction of moisture from the east (Read and Mamay, 1964; Leary and Pfefferkorn, 1977; Leary, 1981). However, Cross (1977) presented a different explanation for the distribution of this flora. He found that Megalopteris was most abundant where the Pennsylvanian strata occurred above pre-Pennsylvanian karst surfaces in which calcareous or terra rosa type soils had been formed, and that this unusual distribution feature occurred in all the localities west of the Appalachians. Accordingly, it was suggested that the widespread occurrence of the Megalopteris flora in the Midcontinent and western part of the Appalachian Plateau would be consistent with the near synchrony of the initiation of the Pennsylvanian sedimentation in these regions (Cross, 1977). If this interpretation is correct, it would indicate that, in these particular regions, edaphic conditions were more crucial than climatic conditions in controlling the occurrence and distribution of some plant communities.

The possible interpretations of the discrepancy between the abundance of lycopods and the drier condition in the Derringer Corners coal swamps are discussed below.

One possibility is that the dominant lycopods in the Derringer Corners coal swamps were primarily represented by <u>Sigillaria</u> instead of species of the Lepidodendreae type. The fact that <u>Sigillaria</u> was the only arborescent lycopod which apparently survived into the Late Pennsylvanian after the second drier interval (the Middle-Late Pennsylvanian boundary) indicates that <u>Sigillaria</u> may have been more tolerant of drier climate. If <u>Sigillaria</u> was the major constituent of the lycopod group in the Derringer Corners coal swamps, the discrepancy between using the abundance of the lycopods to indicate wetness and the lower shoot/root ratio to indicate drier conditions is therefore minimized.

Both <u>Sigillaria</u> leaves and <u>Lepidodendron</u> leaves are identified in the Derringer Corners coal swamps. But, it is difficult to distinguish stems of <u>Sigillaria</u> from those of the lepidodendralean types. This difficulty is exacerbated in the Derringer Corners flora by the poor preservation of the lycopod aerial parts in these coal swamps. One of the few ways to separate these two types of lycopod trees is to identify their rhizomes. The lycopods have subterranean, horizontal rhizomes, i.e., <u>Stigmaria</u>, and rootlets as ordered appendages emanating from nodal positions ("leaf scar") along the axes of Stigmaria. This

is the root system. Stigmarian root systems are wellpreserved in the Derringer Corners coal swamps.

The differences of morphological and anatomical features among the rhizomes of different groups of lycopods are difficult to recognize. Some stigmarian rootlets, which differ slightly from those of common species, Stigmaria ficoides, were observed from the Berryville locality where only sigillarian-type of lycopod stems had been observed (Delevoryas, 1957). Eggert (1972) concluded that these rootlets are borne on sigillarian rhizomes, i.e., sigillarian stigmarians, based on the absence of other types of lepidodendreae in the Berryville locality, and the observation of the actual attachment of rhizophore to Sigillaria approximata preserved in the coal balls collected from the same locality. According to Eggert (1972), the difference between the rhizomes of the sigillarian-type and the lepidodendralean type are: 1) Different differentiation of the complex cortex. 2) The secondary xylem is a continuous zone in sigillarian rhizomes, whereas the secondary xylem of lepidodendralean rhizomes is highly dissected by the secondary rays into a ring of numerous wedge shaped areas when viewed in cross sections. 3) A consistent feature of the rootlets borne on the sigillarian rhizomes is the presence of a relatively narrow bridge of parenchymatous tissue, so-called "connective", connecting the outer cortex with the inner cortex of the rootlets; the "connective" is rarely

observed in lepidodendralean rootlets.

In the coal balls studied here, most lycopod rhizomes are decorticated, and their secondary xylem and rootlets do not exhibit these features of <u>Sigillaria</u> rhizomes and rootlets. This appears to indicate that <u>Stigmaria</u> in the Derringer Corners coal balls did not belong to <u>Sigillaria</u>, and if not, logically, the major lycopod-type in the Derringer Corners coal swamps were of lepidodendralean-type instead of Sigillaria.

A second possibility, previously discussed, is that the low shoot/root ratio is not controlled by the regionally drier climatic conditions in the Derringer Corners coal swamps but more effectively controlled by other conditions, such as local edaphic or habitat conditions. Such other factors must be considered. It is possible, for example, that fallen aerial parts (mainly stems) might be floated out of the coal swamps by local, occasional or seasonal flooding, or be burned out by local fires before they were permineralized, causing the low shoot/root ratio, though the climate might be quite wet in these areas at the same time.

A third possibility is that abundance of lepidodendraleae-type of lycopods is controlled to a greater extent by other factors than wetness. Several evidences strongly infer this postulation.

 It is evident that climatic drying of the second drier interval was not a sudden event because many

of the features found in the sedimentology and clay mineralogy of the Missourian (Upper Pennsylvanian) can be found in upper Desmoinesian (upper Middle Pennsylvanian) strata as well. Thus, climatic drying in itself was probably not the sole factor responsible for the geologically abrupt massive reduction of the aquatic arborescent lycopods (lepidodendreae-type) noted at the Desmoinesian-Missourian boundary (Schutter and Heckel, 1985).

2) Arborescent lycopods, except <u>Sigillaria</u>, mainly disappeared from the coal ball and leaf floras in the eastern United States at the Middle-Late Pennsylvanian boundary. However, palynological evidence indicates that some of these types of plants survived into the Late Pennsylvanian in Virgilian (upper Pennsylvanian) of the Illinois Basin (Peppers et al., 1985) and in the Appalachian Basin (Clendening, 1974; Schemel, 1957). They are also clearly represented in the Sarre-Lorraine (Alpern et al., 1967), in Donets Basin of U.S.S.R.(Inosova et al., 1975), and in France (Liabeuf et al., 1967).

3) Compression fossils of lepidodendreae-type trees have been reported from Stephanian (Upper Pennsylvanian) of Spain (Lorenzo, 1979), the Donets Basin (Stschegolev, 1975), and China ( Li et al., 1982).

4) Lepidodendreae-type lycopod trees were dominant in coal balls of north China during the Late Pennsylvanian (Feng, 1981; Phillips et al., 1985) and of the south China during the Late Permian (Tian, 1979; Tian et al., 1980; Phillips et al., 1985).

These evidences indicate that some lepidodendreae-type of lycopod trees were also able to grow in regionally drier climatic environments than others, but these do not establish that they grew in dry habitats. Locally wet habitats have existed everywhere that coal-forming peat swamps developed.

Although the first possibility can be excluded with some degree of certainty, the discrepancy between the abundance of the lepidodendreae-type lycopods and the drier condition of regional climate in the Derringer Corners coal swamps is still open to question.

## SUMMARY AND CONCLUSIONS

342 coal balls or pieces of coal balls, from a single concretionary mass occupying the full thickness of the original peat mass of a thin Allegheny Formation coal seam, were collected at the Derringer Corners locality, Lawrence County, western Pennsylvania, late Middle Pennsylvanian age.

The two main objectives of the study of these coal balls are the systematic and morphological analyses of several genera of pteridosperms in the coal ball flora, and the quantitative analysis of proportions of the different plant groups comprising the flora.

Two stem species (<u>Schopfiastrum decussatum</u>, <u>Sutcliffia insignis</u>), two leaf species (<u>Alethopteris</u> <u>lesquereuxii</u>, <u>Alethopteris sullivantii</u>), one seed species (<u>Pachytesta noei</u>) are described and illustrated, one new stem species (<u>Heterangium crossii</u>) is designated. Some aspects of the morphology and anatomy of medullosan roots are also discussed.

The descriptions of these plants are based on the internal structure, especially the vasculature. The anatomical variations recognizable in the same species provide a more reliable basis for proper naming and classifying these plants.

Scott's primary criterion for separating Sutcliffia from Medullosa is the occurrence of

concentric vascular bundle in leaf traces of <u>Sutcliffia</u>. Because no decisive evidence of phloem of this genus has been demonstrated, the structure of the leaf trace is uncertain. In the present study, a well-preserved specimen of <u>Sutcliffia insignis</u> provides sufficient evidence of the phloem. The secondary phloem of the stem is composed of sieve cells with tapered ends and parenchyma cells. The sieve pores are evenly distributed on both radial and tangential walls of the thick-walled sieve cells. Primary xylem of the leaf trace is surrounded by a ring of large sieve cells of primary phloem. Therefore, this study proves for the first time the concentric leaf trace occurring in this genus. The taxonomic significance of this structure remains in question.

With the link of the new species <u>Heterangium</u> <u>crossii</u>, the structure of the stems, especially the vasculature, of <u>H. lintonii</u>, <u>H. crossii</u>, and <u>Microspermopteris aphyllum</u> are so close to each other that it is possible that the three species may represent different portions or different developmental stages of the same plants; but, on the other hand, the difference of fronds and branches between these two genera may indicate an interspecific difference.

The anatomical variation of medullosan roots observed in this study illustrates that the number of the protoxylem points, the structure of the secondary xylem vary in different specimens, even in different

levels of the same specimen, and has little taxonomic significance.

The observation of some specimens which probably represent medullosan rhizomes are very interesting and there is no conclusion yet until further investigation has been made.

The entire epidermal tissue and cuticle of whole pinnules of <u>Alethopteris lesquereuxii</u> were transferred from the coal ball specimens by maceration using EDTA solution, and studied three-dimensionally. The epidermal tissues and cuticles of these specimens show feathers of the form of the living pinnules and fine epidermal structure. This technique enhances the correlation of plants identified in coal balls with those preserved as impressions or compressions.

The study of the Derringer Corners specimen of <u>Pachytesta noei</u> adds new information of the apical structure of the seeds to this species, and, therefore, provides more anatomical features to separate this species from <u>P. gigantea</u>.

The first sufficient quantitative analysis data of the vegetational composition of peat deposits in the coal swamps from the Derringer Corners, western Pennsylvanian of the later Middle Pennsylvanian age (the top of Allegheny Formation) provides a basis for comparing the Middle Pennsylvanian coal swamps between the Illinois and the Appalachian Basins. The vegetation of the

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Derringer Corners coal swamps is similar to that of stratigraphically close Herrin (NØ. 6) Coal of the Illinois Basin in abundance of lepidodendraleae-type lycopod trees and in a dearth or absence of cordaiteans. The lower shoot/root ratio of the Derringer Corners coal swamps than that of Herrin (No. 6) Coal supports the suggestion that the regional conditions in the Appalachian Basin may have been drier than the Illinois Basin during the middle part of Middle Pennsylvanian.

The data showing the discrepancy between the abundance of lepidodendralean-type lycopod trees and the drier condition, mainly inferred by the low shoot/root ratios of peat deposits from the Derringer Corners coal swamps, provides a direct evidence that the actual set of factors causing massive reduction of major arborescent lycopods would be much more complex than simply a "drier climate".

In spite of complexity of paleoclimate, the similar pattern of vegetation changes in coal swamps over all of North America and Europe synchronously with (or nearly synchronously with) the geologic periodicity coinciding with the wetter-drier climatic alternation during the Pennsylvanian Period, strongly indicates that climatic moisture ("wetness") was a major, but not the sole, factor in control of vegetation changes in coal swamps. Quantitative analyses of vegetation patterns of peat deposits in coal swamps is one of the approaches to infer the variability and time shifts of paleoclimate, especially the water availability, over the Euramerican tropical coal belt during the Pennsylvanian time. This approach may yield better results by combining the evidences from coal megafossils, palynology, paleomagnetism, coal petrology, sedimentology, and paleotectonics.

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Derringer Corners coal balls in place in highwall of strip mine, Lawrence County, Pennsylvania, U.S.A., June, 1967. The floor of the strip mine is the top of the thick Middle Kittanning coal (Allegheny Formation, Upper Pennsylvanian). The top of the larger of the two masses of coal balls (left arrow and top of tape, Figure 1; top of ladder, Figure, 2) is 3.3 m above top of Middle Kittanning coal. The larger coal ball mass is 1.25 m thick; smaller coal ball mass collected by study (to right of ladder, Figure 2) is Ø.82 m thick. To the left of the larger mass of coal balls the coal seam containing the coal balls is 0.31 m thick, but to the right of the smaller coal ball mass, this begins to thin and is zero thickness in 27 m. The picture (Figure 1) overlies a 2.75 m thick zone of gray, brackish/marine shale that contians decalcified invertebrate fossils indicading brachiopods and bryozoans. The upper 20 to 30 cm of each two masses of coal balls contains normally preserved invertebrates of same types.



- Figs. 1-8. Schopfiastrum deccussatum. All figures from M.S.U. CB 36-7 with the exception of Fig. 8 from M.S.U. CB 11-6-6.(CO=cortex, LT=leaf trace, MX=metaxylem, PH=secondary phloem, PX= protoxylem, RC=resin cannal, SC=sieve cell, X<sub>1</sub>=primary xylem, X<sub>2</sub>=secondary xylem)
  - Cross section of the stem showing rectangular outline of the primary xylem, a leaf trace with an abaxial, toothed vascular bundle, resin canal some of which are pointed at by arrows in the inner cortex, cortex and epidermis. x 20.
  - 2. Cross section (above) and tangential section of the outer cortex of the stem showing the vertically arranged fiber strands. x 62.
  - 3. Cross section of the stem showing the secondary xylem, secondary phloem, sieve cells, and resin canals. x 160.
  - 4. Longitudinal section of the stem showing the secondary xylem, resin canals, cortex, and fibers in the outer cortex. x 66.
  - 5-6. Tangential section of the stem showing metaxylem, protoxylem, and secondary xylem. x 200.
    - 7. Longitudinal section of the stem showing a sieve cell of the secondary phloem with a tapered end (at arrow) and sieve pores. x 968.
    - 8. Cross section of a petiole (below) with an abaxial, toothed vascular bundle and of an attached rachis (above) with an Y-shaped vascular bundle. x 65.

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- Figs. 1-6. <u>Heterangium crossii</u> sp. nov. Figs. 1-4 from <u>MSU CB S8-3-1</u>, Figs. 5-6 from M.S.U. CB 14-5-2B. (LT=Leaf trace, MT=metaxylem tracheid, MX=metaxylem, PD=periderm, PP=parenchymatous plates in primary xylem, RAY=rays of secondary xylem, X=secondary xylem)
  - Cross section of the stem of the type specimen showing the "mixed" primary xylem divided into 5 sections by 5 parenchymatous plates, and secondary xylem. x 34.
  - Cross section of the stem showing some sclerotic parenchyma cells among metaxylem tracheids.
     x 244.
  - 3. Cross section (above), radial section (left below) and oblique radial section (right below) of the stem. The radial section is through one of the parenchyma plates and rays of the secondary xylem, and the oblique radial section is through the tracheids of the metaxylem and the secondary xylem. x 33.
  - 4. Enlargement of the radial section of Fig. 3 showing longitudinal continuity of the parenchymatous plate and its connection with the rays of the secondary xylem with narrow peel of matching cross section at top of figure. x 117.
  - 5. Cross section of an young stem without secondary growth showing "mixed" primary xylem with 3 parenchymatous plates, and two leaf traces. x 85.
  - 6. Cross section (above) and radial section (right below) of the young stem. The radial section is cut through the position of one of the parenchymatous plates showing the longitudinal continuity of the plate. x 76.

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- Figs. 1-7. Heteranguim crossii sp. nov. (continued). All figures from M.S.U.CB S8-3-1. (CB=vascular cambium, MX=metaxylem, PD=periderm, PH=secondary phloem, PX=protoxylem, RAY=rays of secondary xylem, SC=sieve cell of the secondary phloem)
  - 1. Cross section of the stem showing protoxylem strands some of which are paired (one is located on each side of a parenchyma plate); some are randomly located. x 100.
  - 2. Enlargement of one of the randomly located protoxylem strands shown in Fig. 1. x 245.
  - 3. Radial section of the stem showing metaxylem, protoxylem, and rays of the secondary xylem. x 301.
  - 4. Tangential section of the stem showing the metaxylem, protoxylem and the secondary xylem. x 301.
  - 5. Cross section of the stem showing the secondary xylem, vascular cambium, the secondary phloem and sieve cells, and periderm. x 245.
  - Longitudinal section of the stem showing parenchyma cells, secretory cells and sieve cells of the secondary phloem. x 380.
  - 7. Enlargement of one of the sieve cells in Fig. 6 showing sieve pores. x 954.



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- Figs. 1-7. Heterangium crossii sp. nov. (continued). Figs. 1-4 from M.S.U. CB 24-4-2-3B-3, Figs. 5-7 from M.S.U.CB S8-3-1. (CO=cortex, EP=epidermis, LT=leaf trace, PD=periderm, PH=secondary phloem, PLD=phelloderm, PLM=phellem, SC=sieve cell of the secondary phloem)
  - Cross section (above) and tangential section of the stem. The tangential section is through the secondary phloem. x 107.
  - 2. Enlargement of the tangential section of Fig. 1 showing the secondary phloem and sieve cells. x 322.
  - 3. Enlargement of one of the sieve cells in Fig. 2 showing sieve pores (at arrows). x 973.
  - 4. Enlargement of another sieve cell in Fig. 1. x 973.
  - 5. Cross section of the stem showing phellem and phelloderm. x 322.
  - 6. Cross section of the stem showing periderm, the cortex and epidermis. x 245.
  - 7. Cross section of the stem showing two leaf traces arising from paired protoxylem strands, one strand on each side of the parenchymatous plate. x 27.

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Figs. 1-6. Heterangium crossii sp. nov. (continued). Figs. 1-3 from M.S.U. CB S8-3-1, fig. 4 from M.S.U. CB 14-5-2B-10-10, Figs. 5-6 from M.S.U. CB 24-4-2-3B-9. (LT=leaf trace, MX=metaxylem, PD=periderm, PH=primary phloem, PX=protoxylem )

- 1. Cross section of a leaf trace surrounded by periderm tissue. x 243.
- Longitudinal section of the leaf trace in Fig.1 showing metaxylem, protoxylem, and primary phloem. x 313.
- 3. Enlargement of one of the sieve cells in Fig. 2. x 989.
- 4. Cross section (above) and longitudinal section (below) of the young stem (see Pl. 3, Fig. 5) showing a leaf trace arising from a paired protoxylem strands. x 42.
- 5. Cross section (above) and tangential section (below) of the stem showing a leaf trace arising from a single protoxylem strand (at arrow). x 39.
- 6. Enlargement of the leaf trace in Fig. 5. x 98.

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- Figs. 1-7. <u>Sutcliffia</u> <u>insignis</u>. All Figures from M.S.U. CB 342-9. (CM=vascular cambium, LT=leaf trace, MX=metaxylem, PH=secondary phloem, SC=sieve cell, X<sub>1</sub>=primary xylem, X<sub>2</sub>=secondary xylem )
  - Cross section of the stem showing several steles. Thelower left stele is the central and largest one. x 16.
  - Enlargement of one of the steles in Fig.1 showing "mixed" primary xylem, slightly developed secondary xylem, and secondary phloem. x 29.
  - 3. Cross section of the stem showing cortex, a leaf trace and epidermis. x 94.
  - 4. Cross section of a stem stele showing metaxylem, protoxylem, secondary xylem, rays, and secondary phloem. x 72.
  - 5. Enlargement of the stem stele in Fig. 4 showing the secondary xylem, rays, vascular cambium, and sieve cells and rays of the of the secondary phloem. x 241.
  - 6. Radial section of the stem showing the metaxylem, protoxylem, and the secondary xylem. x 324.
  - 7. Radial section of the stem showing the secondary xylem, fusiform initials of the vascular cambium, and the secondary phloem. x 249.

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## Figs. 1-7. Sutcliffia insignis (continued). All figures from M.S.U.CB 342-9. (MX=metaxylem, PH=secondary phloem, PX=primary xylem, SC=sieve cell of the secondary phloem, X<sub>2</sub>=secondary xylem)

- 1. Cross section (above) and radial section (below) of a stem stele showing primary xylem, secondary xylem, and secondary phloem. x 55.
- Cross section (above) and tangential section through secondary phloem of the stem stele in Fig. 1 showing sieve cells and secretory cells. x 37.
- 3. Radial section of the same stem stele shown in Fig.1 showing metaxylem, protoxylem, secondary xylem and secondary phloem. x 238.
- 4. Enlargement of three sieve cells in Fig.3 showing sieve pores. x 995.
- 5. Radial section of a stem stele showing secondary xylem and secondary phloem. x 307.
- 6. Enlargement of one of the sieve cells in Fig. 5 showing somewhat horizontally elongated sieve pores. x 939.
- 7. Paradermal section of the epidermis of the stem showing the epidermal cells. x 96.

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- Figs. 1-8. <u>Sutcliffia</u> insignis (continued). All figures from M.S.U. CB 342-9. (MX=metaxylem, PH=phloem, PX=protoxylem, SC=sieve cell)
  - Cross section of two leaf traces. One possesses a pair of protoxylem strands while another has a single protoxylem strand. The protoxylem strands are pointed at by arrows. x 75.
  - 2. Cross section of a leaf trace with slight secondary growth (at arrow). x 141.
  - 3. Cross section (above) and longitudinal section (below) of a leaf trace with secondary growth showing xylem and sieve cells of secondary phloem. x 49.
  - 4. Cross section (above) and longitudinal section (below) of several leaf traces showing sieve cells of primary phloem occurring both sides of the primary xylem of the left leaf trace (concentric vascular bundle). x 31.
  - Longitudinal section of a leaf trace showing metaxylem, protoxylem, and primary phloem. x 234.
  - 6. Longitudinal section of a leaf trace showing tracheids of metaxylem, and sieve cells and secretory cells of primary phloem. x 235.
  - 7. Longitudinal section of a leaf trace showing a sieve cell and some wall remnant of sieve cells (at arrows) of primary phloem. x 1000.
  - 8. Longitudinal section of a leaf trace through the outer part of the primary phloem showing branchlike phloem elements. x 90.

PLATE 9



- Figs. 1-6. Sutcliffia insignis (continued). All figures from M.S.U.CB 342-9. (FS=fiber strands, X=primary xylem)
  - Cross section of a typical leaf trace. The leaf trace is surrounded by a ring of fiber strands, and the primary xylem of the leaf trace is surrounded by a ring of large sieve cells (at arrows) of the primary phloem (concentric vascular bundle). x 90.
  - 2. Cross section (above) and longitudinal section (below) of the leaf trace. The longitudinal section is through some of the large sieve cells (at arrows) surrounding the primary xylem. x 48.
  - 3-4. Longitudinal section of two sieve cells of the leaf trace in Fig. 2 showing remnant of cell walls with sieve pores (at arrows). Fig.3, x 1311, Fig.4. x 953.
    - 5. Longitudinal section of one of the large sieve cells of the leaf trace in Fig. 2 showing a number of dark ball-like material in the cavity of the sieve cell. x 234.
    - 6. Longitudinal section of a tracheid of the metaxylem of the leaf trace in Fig.2 showing remnant of the tracheid wall. x 234.

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### Figs. 1-7. <u>Alethopteris</u> <u>lesquereuxii</u>. (MB=midrib, PL=petiole, RC=rachis, RD=ridges below vascular bundle of lateral vein)

- Upper paradermal view of two pinnules exposed on weathered surface of a coal ball. These two pinnules attach to the rachis pointed at by arrows. M.S.U. CB 46-6-5. x 6.
- 2. Upper paradermal view (left) and cross section (right) of a pinnule. The paradermal surface is exposed on weathered surface of a coal ball, and the cross section is etched by 3 % HCL showing the revolute blade margin and the sunken midrib. M.S.U. CB 118-3-2. x 11.
- 3. Upper surface view of cuticles of two pinnules exposed on the etched coal ball surface by EDTA solution. M.S.U. CB 118-3-1. x 7.
- 4. Paradermal section of a pinnule showing thin epidermal layer, conspicuous hypoderm layer beneath the epidermis, midrib and dichotomous lateral veins. Because of curvature of the pinnule base, the midrib has been cut off at the base of the pinnule. M.S.U. CB 94-7-4A-37. x 60.
- 5. Cross section (right) and oblique cross section (left) of two pinnules attached to each other showing sunken midribs and revolute blade margins (compatible with the cross section in Fig. 2), and ridges below vascular bundles of the lateral veins. M.S.U. CB 73-8-2B-34. x 66.
- 6. Cross section of a pinnule (left) attached to the rachis (right). M.S.U. CB 106-5-1-35. x 90.
- 7. Longitudinal section of a medullosan petiole (<u>Myeloxylon</u>) bearing an alethopterid rachis (left middle, at arrow) in cross section. M.S.U. CB 14-5-3-49. x 39.



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- Figs. 1-8. <u>Alethopteris</u> <u>lesquereuxii</u> (continued). Figs.1-2 from M.S.U. CB <u>108-4-3-10-7-4</u>, Figs.3-8 from M.S.U. CB <u>118-3</u>. (BL=vascular bundle of lateral vein, CL=cuticle, ED=epidermis, HD=hypoderm, HR=hair, PE=cellulose acetate peel, PS=palisade, RC=rachis, RD=ridge below lateral vein, SG=sponge, SH=vascular bundle sheath, SW=stoma)
  - Longitudinal section of a pinnule showing double cell layer of the epidermis, hypodermis, palisade, and spongy mesophyll, vascular bundles of lateral veins, ridges below the lateral veins, and grooves between the ridges. One stoma in a groove is pointed at by arrow. x 248.
  - Enlargement of Fig. 1 showing the double cell layer of the upper epidermis, and cuticle cover -ing the upper epidermis. x 926.
  - 3. Longitudinal section of a pinnule showing multicellular and capitate hairs on a ridge on the lower surface, and a stoma in groove (at arrow). x 231.
  - 4. Longitudinal section through midrib of a pinnule showing the vascular bundle, canals, and bundle sheath. x 241.
  - 5. Cross section of a pinnule showing a stoma in longitudinal section in the groove of the lower surface of the pinnule. x 1269.
  - 6. Cross section of four pinnules A, B, C, D (arrows pointing at their midribs) of a pinna. x 6.
  - 7. Upper surface view of cuticles of the tops of the pinnule B, C, D in Fig.6 revealed by EDTA solution. x 7.
  - 8. Upper surface view of the cuticle of the main part of the pinnule A and B (arrows point to the midribs) attached to the pinna rachis. The cross section of the two pinnules exhibit on the cellulose acetate peel (left side) which covers the cut surface of the coal ball shown in Fig. 6. x 7.

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- Figs. 1-9. Alethopteris lesquereuxii (continued). All Figures are of surfaces of pinnules macerated by EDTA solution. (GV=grooves on the lower surface of pinnules, HR=hair, LC=cuticle of pinnule lower epidermis, MB=midrib, RC=rachis, RD=ridge below lateral vein, SM=stoma, UG=cuticle of pinnule upper epidermis)
  - Upper surface view of the same pinna shown in Pl.11, Fig.8 showing cuticles of four pinnules E, F, G, H on the other side of the pinna rachis exposed on the etched surface of the coal ball by EDTA solution. Arrows point to the blade margins of the pinnules. x 4.
  - 2. The bleached cuticle of one of the pinnules (above) and the rachis (below) in Fig.l showing the midrib, the upper and lower epidermis, and the attachment of the pinnule to the rachis. Some lateral veins (at arrow) arise directly from the rachis. x 39.
  - 3. Enlargement of the complete cuticle of one pinnule in Pl.11, Fig.3. x 10.
  - 4-7. The bleached cuticle of Fig. 3 as viewed here was floated in water to show the upper surface view (Fig. 4), lateral view (Fig. 5), oblique lateral view (Fig. 6) and the lower surface view (Fig.7). x 10.
    - 8. Enlargement of the lower surface view of the cuticle of the pinnule top of Fig. 7 showing the revolute blade margin, the tip of the midrib extending near the top of the pinnule, the lateral veins, and a number of multicellular hairs among the curved blade margin and at the tip of the midrib. x 27.
    - 9. Inner side of cuticle of a pinnule (lower epidermis) showing midrib, and the wave pinnule lower surface. Stomata concentrated in grooves. x 95.

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- Figs. 1-6. <u>Alethopteris</u> <u>lesquereuxii</u> (continued). All figures are cuticle of pinnules from M.S.U. CB 118-3. (AP=stoma aperture, GC=guard cells, GV=groove, HB=hair base, LV=lateral vein, MB=midrib, SB=subsidiary cells of stoma)
  - Inner side of lower epidermal cuticle of a pinnule over the midrib, lateral veins. Hair bases (at arrow) cover more than one epidermal cells. x 242.
  - 2. The upper epidermal cuticle of the pinnule in Fig.l showing epidermal cells with straight walls. x 367.
  - 3. Lower epidermal cuticle of a pinnule showing a haplocheilic stoma: a ring of papillate subsidiary cells surround the guard cells. x 1296.
  - 4. The same stoma as that in Fig.3 on different focus showing the pair of the guard cells and the aperture. x 1296.
  - 5. SEM photograph of a haplocheilic stoma taken from outer side of lower epidermal cuticle of a pinnule showing a ring of papillate subsidiary cells surrounding the guard cells.
  - 6. SEM photograph of a haplocheilic stoma taken from inner side of lower epidermal cuticle of a pinnule showing the aperture, the guard cells, and the bases of a ring of 8 subsidiary cells.



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- Figs. 1-7. <u>Alethopteris</u> <u>sullivantii</u>. Fig. 1 from M.S.U. CB 96-5-5, Figs. 2-7 from M.S.U. CB 109-6-2. (AP=aperture of stoma, BD=pinnule blade, BL=vascular bundle, CU=cuticle, EP=epidermis, GC=guard cells, HD=hypoderm, MB=midrib, MX=metaxylem, PA=papillate, PX=protoxylem, RC=rachis, SH=vascular bundle sheath)
  - Cross section of a pinnule showing a half of flat blade, and midrib attached to the rachis. x 79.
  - Cross section of a pinnule showing slightly curved blade margin, and the flat lower epidermal surface. x 37.
  - 3. Cross section of a pinnule showing the upper epidermal cuticle, the upper epidermis, hypoderm, palisade, sponge, and papillate surface of the lower epidermis. x 242.
  - 4. Longitudinal section of the same pinnule as that in Fig. 3 showing the hypoderm, palisade, two vascular bundles of the lateral veins, and the flat and papillate surface of the lower epidermis. x 242.
  - 5. Longitudinal section of a pinnule midrib showing protoxylem, metaxylem and bundle sheath. x 941.
  - Lower epidermal cuticle of a pinnule showing a haplocheilic stoma: the guard cells are surrounded by a ring of papillate subsidiary cells. x 1338.
  - 7. Cross section of a pinnule showing a stoma in longitudinal section of the lower epidermis. x 993.



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Figs. 1-7. <u>Alethopteris</u> <u>sullivantii</u> (continued). All Figures are surfaces of pinnules macerated by EDTA solution. (AP=aperture of stoma, GC=guard cells, HB=hair base, LV=lateral vein, MB=midrib, PL=poles of guard cells, SB=subsidiary cells of stoma)

- 1. A piece of lower epidermal cuticle of a pinnule over midrib and lateral veins. x 42.
- 2. Lower epidermal cuticle of a pinnule tip. Arrows point to the margin of the tip. x 89.
- 3. Lower epidermal cuticle of a pinnule showing the flat surface of the lower epidermis, dichotomous lateral veins (the white lines), stomata (dark dots) concentrated in the area between the lateral veins, and the lateral margin (at arrows) of the pinnule blade. x 54.
- Upper epidermal cuticle of a pinnule showing the undulate walls of the upper epidermal cells.
  x 306.
- 5. Lower epidermal cuticle of a pinnule showing the flat, papillate lower epidermal surface, and hair bases. x 244.
- 6-7. SEM photograph of a haplocheilic stoma on lower epidermal cuticle showing the guard cells, aperture, and a ring of 6 papillate subsidiary cells. Fig. 6 is taken from the inner side of the cuticle whereas Fig. 7 from the outer side of the cuticle.



- Figs. 1-7. Medullosan roots. All Figures are in cross sections. (CO=cortex, EP=epidermis, MX=metaxylem, PD=periderm, PH=secondary phloem, PL=pericycle, PX=protoxylem, RAY=rays of secondary xylem, RL=rootlet, X=secondary xylem)
  - A root with 3 protoxylem strands, and the secondary xylem almost completely surrounds the primary xylem. The cortex (outer part of the periderm) is not preserved. M.S.U. CB 1-3-2B-26. x 103.
  - 2. A root with 3 protoxylem strands. Amount of tracheids of the secondary xylem zone opposite different protoxylem strands are different from one protoxylem strand to another. The secondary xylem zone opposite the protoxylem strand (above) is mainly composed of tracheids, whereas that opposite the left protoxylem strand is composed of rays; the secondary xylem zone opposite the right protoxylem is composed of roughly equal amount of tracheids and rays. Secondary phloem zones locate between the proto-xylem strands. M.S.U. CB 116-6-4-2C-1-6. x 36.
  - 3. A root with 4 protoxylem strands (at arrows). The primary cortex and epidermis are well preserved. M.S.U.CB 116-6-4A. x 103.
  - 4. A root with 4 protoxylem strands. The composition of the secondary xylem zones opposite different protoxylem strands is different similar to that in Fig. 2. M.S.U.CB 112-4-1-33. x 64.
  - 5. A root with 5 protoxylem strands. The secondary xylem is divided into 5 discontinuous sections by rays opposite the protoxylem strands. M.S.U. CB 345-1-4-8B-41. x 49.
  - 6. A root with 3 protoxylem strands and a rootlet is arising from the left protoxylem strand. M.S.U.CB 116-6-4-2E-1-18. x 51.
  - 7. A root with 4 protoxylem strands. The composition of the secondary xylem zones opposite different protoxylem strands is different similar to that in Fig. 2. The secondary xylem zone opposite the lowest protoxylem strand, where a rootlet is produced, is mainly composed of rays. M.S.U.CB 345-4-2A. x 98.

PLATE 17





Figs. 1-6. Medullosan roots (continued).

(FI=fusiform initial of vascular cambium, MX=metaxylem, PD=periderm, PH=secondary phloem, PL=pericycle, PX=protoxylem, RAY=rays of secondary xylem, RI=ray initial of vascular cambium, X=secondary xylem)

- Radial section of a root showing metaxylem, protoxylem, and rays of secondary xylem. M.S.U. CB 116-6-4-15-9. x 1073.
- Cross section of a root showing secondary xylem, vascular cambium, pericycle, and periderm. M.S.U.CB 116-6-4-1-6. x 314.
- 3. Radial section of a root showing secondary xylem and secondary phloem. M.S.U.CB 354-9-2-3A-12-17. x 249.
- 4. Cross section (above and below) and longitudinal section (middle) of a root showing that the root with 5 protoxylem strands is producing a small root (at arrow) with 2 or 3 protoxylem strands. M.S.U.CB 254-9-2-3A-8. x 24.
- 5. Enlargement of the small root in Fig.4 showing the longitudinal section (left) and the cross section (right) of the small root of which the probable protoxylem strands are pointed at by arrows. x 97.
- 6. Cross section of a root showing some small tracheids (at arrows) at the periphery of the secondary xylem zone. M.S.U.CB 116-6-4-10-8. x 257.



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Figs. 1-7. Medullosan roots (continued). (CB=vascular cambium, CS=Casparian Strips on endodermal cells, ED=endoderm, MX=metaxylem, PD=periderm, PH=secondary phloem, PL=pericycle, X=secondary xylem)

- Cross section of a root showing protoxylem, metaxylem secondary xylem, vascular cambium, secondary phloem, pericycle, endoderm, and periderm. M.S.U.CB 1-3-2B-26. x 236.
- Cross section (above and left) and longitudinal section (below and right) of a root showing secondary xylem, secondary phloem, and periderm. M.S.U.CB 14-5-4-2A-11-12. x 72.
- 3. Longitudinal section of a root through the outer zone of the secondary phloem showing sieve cells and horizontally elongated parenchyma cells between the sieve cells. M.S.U.CB 14-5-4-2A-5-11. x 238.
- 4. Longitudinal section through the inner zone of the secondary phloem of the same root in Fig.3 showing the sieve cells and isodiametric parenchyma cells between them. x 238.
- 5. Longitudinal section of a root showing sieve cells and canal cells of the secondary phloem zone. M.S.U.CB 109-6-2-2-7-2. x 1014.
- 6. Tangential section of a root showing endoderm layer of which one cell exhibits Casparian Strips, and several endoderm cells illustrate the thick radial walls (at arrows). M.S.U.CB 109-6-2-2-13-4. x 317.
  - 7. Longitudinal section of a root showing frequent production of roots. M.S.U.CB 345-14-4B-25. x 24.



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- Figs. 1-8. Pachytesta noei. All Figures from M.S.U.CB 116-6-5B,-6. (BC=seed base, CUE=cuticle of endotesta, INT=integument, MP=micropyle, NU=nucellus, PC=pollen chamber, PR=primary rib, RT=rib-trabeculae, SK=nucellus stalk, SR=secondary rib, VB=vascular bundle)
  - Longitudinal section of the seed showing the integument, micropyle, pollen chamber, nucellus, nucellus stalk, and seed base. x 2.
  - 2-8. Cross section of the seed .Figs. 3-8 are turned over 90° clockwise from Fig. 2.
    - 2. Cross section of the seed at level A showing triangular outline of the inner margin of the integument, two primary ribs, one secondary rib, and 8 vascular bundles (indicated by holes among the outer margin of the integument) in each of 3 values of the integument. x 2.
    - 3. Cross section of the seed at level B showing the same as that of Fig.1. x 3.
    - 4. Cross section of the seed at level C showing two primary ribs without secondary ribs, cuticle of the endotesta, and the rib-trabeculae. x 2.
    - 5. Cross section of the seed at level D (near the mid-level) showing one primary rib; another primary rib is damaged. Because of the branching of two vascular bundles (at arrows), the total number of vascular bundles per valve of the integument is 10. x 3.
    - 6. Cross section of the seed at level E showing two primary ribs (at arrows) which are loss conspicuous than above, 8 vascular bundles per valve of the integument, cuticle of the endotesta, and remnant of the nucellus. x 7.
    - 7. Cross section of the seed at level F showing the integument, the cuticle of the endotesta, and the nucellus stalk. The ribs are difficult to identify so that the total number of vascular bundles of the integument at this level is uncertain. x 3.
    - 8. Cross section of the seed at level G showing double vascular system: the outer ring of the vascular bundles enter the integument, and the inner ring of vascular bundles enter the nucellus. x 3.





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- Figs. 1-7. Pachytesta noei (continued). All Figures from M.S.U.CB 116-6. (CUE=cuticle of the endotesta, ISC=inner part of the sclerotesta, OSC=outer part of the sclerotesta, MP=micropyle, MX=metaxylem, NU=nucellus, PX=protoxylem, SC=sieve cell of primary phloem, ST=sarcotesta)
  - Longitudinal section of the seed integument showing a narrow layer of the sarcotesta (right), and two-zoned sclerotesta. x 70.
  - 2. Enlargement of Fig.1 showing the parenchymatous sarcotesta (right), and the horizontally elongated fibers (with single pits on cross section of the cell walls, at arrow) of the outer zone of the sclerotesta. x 304.
  - 3. Enlargement of Fig.1 showing the outer zone of the sclerotesta, the vertically elongated fibers with single pits of the inner zone of the sclerotesta, and the cuticle of the endotesta (at arrow). x 259.
  - 4. Enlargement of Pl.20, Fig.4 showing the fibers of the outer zone of the sclerotesta, and a strand of vertically elongated fibers (at arrow). x 242.
  - 5. Longitudinal section of a vascular bundle in the integument showing protoxylem, metaxylem, and primary phloem. x 1035.
  - 6. Longitudinal section of the seed showing the micropyle, and the tips of the integument where the fibers of the inner zone of the sclerotesta have shifted to be horizontally elongated similar to that of the outer zone of the sclerotesta. x 26.
  - Longitudinal section of the seed near the base showing the nucellus remnant and nucellus stalk. x 48.



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- Figs. 1-8. Pachytesta noei (continued). All figures from M.S.U.CB 116-6. (CC=cannal cell, HR=hair, MX=metaxylem, SC=sieve cell, SH=vascular bundle sheath, SM=stoma, PX=protoxylem, VB=vascular bundle)
  - Longitudinal section of the seed showing irregular shaped cells of the nucellus remnant. x 242.
  - 2. Enlargement of Pl.20, Fig.8 showing the vascular bundle of the chalaza (the central hole). x 242.
  - 3. Longitudinal section of a vascular bundle in the nucellus. x 303.
  - 4. Cross section (above) and longitudinal section (below) of the seed base showing the remnant of the seed stalk (at arrow). x 70.
  - 5. Longitudinal section of the seed stalk remnant showing a vascular bundle and the bundle sheath. x 293.
  - 6.Enlargement of Fig.5 showing metaxylem, protoxylem, sieve cells of the primary phloem of the vascular bundle in the seed stalk. x 938.
  - 7. Longitudinal section of the seed stalk showing a stoma on the stalk surface with papillate subsidiary cells . x 968.
  - Longitudinal section of the seed stalk showing two multicellular hairs on the stalk surface. x 968.

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