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PHLOEM ANATOMY AND PHYLOGENY OF SELECTED CARBONIFEROUS FERNS AND PTERIDOSPERMS

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PHLOEM ANATOMY AND PHYLOGENY OF SELECTED 
CARBONIFEROUS FERNS AND PTERIDOSPERMS

DISSERTATION

Presented in Partial Fulfillment of the Requirements for the 
Degree Doctor of Philosophy in the Graduate School of 
The Ohio State University

by
Edith L. Smoot, B.S., M.Sc.

***

The Ohio State University
1983

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CHAPTER 1 - INTRODUCTION

Our knowledge of the anatomy and histology of fossil phloem has lagged far behind many other areas of paleobotany. With just a few exceptions (e.g., Stewart, 1940; Hall, 1952), only within the last decade has an attempt been made to systematically describe the phloem of fossil plants (e.g., Eggert and Gaunt, 1973; Galtier and Hébant, 1973; Wilson and Eggert, 1974; Eggert and Kanemoto, 1977; Smoot and Taylor, 1978a; Smoot, 1979). Except for these few detailed studies, most of the information on fossil phloem has been presented as a part of contributions on specific plants or floras. For example, Renault's (1893; 1896) description of a late Carboniferous-early Permian flora from Autun and Épinac (France) included a number of examples of well-preserved phloem in several different taxa. Because the data on phloem anatomy in fossil plants are widely scattered or lacking in some groups, the work that has been completed will be discussed within the context of specific periods of geologic time. This approach will also facilitate comparison with related extant examples.

SILURIAN-DEVONIAN

It was during the late Silurian and early Devonian that vascular plants made their first appearance in the fossil record. Most of these early groups, such as the rhyniophytes, zosterophyllophytes and trimerophytes, are known primarily from compression fossils, although
some specimens do contain anatomically preserved tracheids. In order to
discern any details of phloem anatomy, therefore, it is necessary to
examine the few Siluro-Devonian floras that include petrified plants.
Perhaps the best known example is the middle Devonian plant assemblage
from the Rhynie chert of Aberdeenshire, Scotland. In their original
descriptions of these anatomically preserved plants, Kidston and Lang
(1917; 1920a; 1920b) noted a number of axes that contained
well-preserved cells surrounding the central xylem, although they were
never able to discern sieve areas or sieve pores in the material. In
Rhynia gwynne-vaughanii (Kidston and Lang, 1917), the extraxylary tissue
was composed of thin-walled cells with few intercellular spaces. In
longitudinal section, all the cells in this zone were elongate with
oblique end walls. Although no typical phloem parenchyma was present,
the authors noted that phloem cells in the upper regions of the stem
were slightly shorter than those in the basal region. The phloem in R.
major (Kidston and Lang, 1920a) was very similar to that in R.
gwynne-vaughanii. In Horneophyton (= Hornea of Kidston and Lang,
1920a), the phloem was less distinctive, being composed of cells only
slightly more elongate than the neighboring cortical cells. Near the
transition zone where the upright stem of Horneophyton met the bulbous
base (= rhizome of Kidston and Lang), the phloem was difficult to
distinguish.

In addition to these relatively simple plants from the Rhynie
chert, Kidston and Lang also described a plant that was structurally
more complex—Asteroxylon (Kidston and Lang, 1920b). Phloem was present
both in the stem and in the transition region between upright stem and
rhizome. The phloem zone in *Asteroxylon* was quite extensive, completely surrounding the metaxylem lobes, as well as filling the space between the lobes. As in *Rhynia* and *Horneophyton*, the phloem was composed entirely of elongate cells with either transverse or oblique end walls, and few intercellular spaces. Cells in the position of phloem could also be discerned in the departing leaf traces.

Phloem in the Rhynie chert plants has not been examined in any detail since the original descriptions of Kidston and Lang, with the exception of a report by Satterthwait and Schopf (1972). These authors examined the elongate cells from the phloem zone of *Rhynia major* and found thin, circular areas on the walls that were approximately 3–8 μm in diameter. These thin areas were composed of circular regions less than 1 μm in diameter. Two types of cells were present within the phloem zone: one type exhibited these thin, circular areas on the cell walls (perhaps equivalent to true sieve elements in geologically younger plants) and the other type, probably corresponding to phloem parenchyma cells, possessed smooth walls.

Phloem tissue has also been noted in other groups of Devonian plants. In the progymnosperms, for example, Arnold (1930), Beck (1957), and Scheckler and Banks (1971a; b) described primary and secondary phloem in several different genera (*Callixylon*, *Proteokalon*, *Tetraxylopteris*, *Triloboxylon*), based on specimens that were partially petrified. Although cells of the primary phloem were usually crushed, secondary phloem was preserved and consisted of phloem rays, fibers, tanniniferous cells, phloem parenchyma and thin-walled cells that probably represented sieve elements. Some localities that have yielded
anatomically preserved plants have great potential to provide more information on phloem anatomy in Devonian plants. Two that should be mentioned are the middle Devonian Millboro shale flora (Beck et al., 1979; Stein, 1982) and the late Devonian–early Carboniferous New Albany Shale flora (Scott and Jeffrey, 1914). The latter has already yielded a diverse and fairly well-preserved flora (e.g., Read, 1937; Beck, 1960; Beck and Bailey, 1967; Beck, 1978), with several examples of recognizable phloem tissue. *Stenokoleos simplex* has been described with cells in the position of phloem that resembled sieve elements, phloem parenchyma and fibers (Beck, 1960). *Chapelia* apparently included some secondary phloem tissue, composed of sieve elements and vascular rays, with a zone of fibers at the periphery (Beck and Bailey, 1967). For the most part, however, the quality of preservation in Silurian and Devonian plants is too poor to discern any histological details in the phloem, especially the occurrence of sieve areas and sieve pores. Nevertheless, the studies completed to date have provided information on the cellular composition and relative complexity of phloem tissue in these early vascular plants.

**CARBONIFEROUS–PERMIAN**

Our knowledge of phloem in early Carboniferous (Mississippian) plants is very similar to that in Siluro–Devonian taxa. Most of the floras are preserved as compressions with little anatomical detail, especially in the phloem zone. However, there are a few notable exceptions. For example, Galtier (1970) described a diverse, anatomically preserved flora from the Lower Carboniferous of Esnost and Montaigne Noire (France) that contained several taxa with evidence of
phloem cells. With a few exceptions, however, (e.g., Galtier and Hébant, 1973) the preservation was too poor to provide much histological detail. By far the greatest amount of data on fossil phloem has come from Upper Carboniferous plants. All of the studies that deal exclusively with phloem histology have utilized coal ball (calcium carbonate) permineralizations from the Pennsylvanian of North America (with the exception of Galtier and Hébant, 1973). This material is ideal for anatomical work, since a large number of specimens are available and the techniques are accessible (see, e.g., CHAPTER 2). Well-preserved phloem has also been noted in coal balls from the British coal fields, as well as silicified material from localities in Europe and elsewhere. Since these reports are numerous, they will be examined systematically, beginning with vascular cryptogams (lycopods, sphenophytes and ferns) and following with seed plants (pteridosperms and cordaites).

Vascular cryptogams - Perhaps the best-known vascular cryptogams from the Carboniferous are the arborescent lycopods. Their anatomy has been described from European and North American coal balls (see e.g., Williamson, 1887a; Eggert, 1961; Frankenberg and Eggert, 1969; DiMichele, 1979; 1981) and phloem tissue has been noted in both the underground (e.g., Stewart, 1940; 1947; Frankenberg and Eggert, 1969) and aerial organs. Yet, despite our rather complete knowledge of the structure and development of Carboniferous lycopods (see, e.g., Andrews and Murdy, 1958; Eggert, 1961), a great deal of controversy has existed over the phloem tissue in these plants. Some early workers described the presence of both secondary and primary phloem in Lepidodendron and
Lepidophloios (e.g., Scott, 1920; Weiss, 1901). However, the tissue that Weiss (1901) described as cambial was separated from the secondary xylem by several layers of cells and Seward later noted (1902) that typical sieve elements and sieve areas were not found in Weiss' material. Arnold later postulated (Arnold, 1960) that the "cambium" of Weiss probably represented a periderm-like tissue. Arnold was unable to find any tissue that was histologically comparable to phloem and concluded that the cambium in Carboniferous lycopods was unifacial, producing only secondary xylem cells (see also Lemoigne, 1964). One of the most important aspects of Arnold's contribution was his emphasis on demonstrating the presence of sieve elements with sieve areas in order to prove the existence of phloem tissue. He noted that some authors had previously distinguished this tissue system only on the basis of topographic position within the stem and not on histological details (e.g., Williamson, 1881; Weiss, 1901; Calder, 1933).

Lemoigne (1966) also examined phloem in the arborescent lycopods and concluded that all the phloem in Lepidodendron was primary, with one exception. In a single specimen, radial files of cells were present outside of the primary phloem, and Lemoigne suggested that these cells could be secondary phloem produced by irregular divisions in the outermost primary phloem elements. He went on to speculate on the evolutionary importance of the unusual position of this tissue and its meristematic zone. However, until sieve areas with pores are demonstrated in Lemoigne's material, this tissue should probably more correctly be considered periderm based on its position.
The most comprehensive examination of phloem in fossil lycopods to date is the paper by Eggert and Kanemoto (1977). They described a stem with a unifacial cambium and noted that all of the phloem cells were of primary origin, even in the oldest specimens. The phloem was present as scattered strands outside a region of thin-walled sheath parenchyma. In young stems, the sheath was narrow and situated adjacent to the primary xylem, but appeared wider in older stems due to the production of "secondary parenchyma" (terminology of Lemoigne, 1966). Eggert and Kanemoto suggested that this zone probably represented the cambium of earlier workers (e.g., Weiss, 1901).

The phloem of Carboniferous sphenophytes has been described from underground (Wilson and Eggert, 1974) and aerial axes (Renault, 1893; 1896; Agashe, 1964; Eggert and Gaunt, 1973; Hass, 1975). Renault found well-preserved phloem in several species of *Arthropitys*. In *A. bistriata*, he described well-preserved sieve elements with numerous, irregular sieve areas containing many pores (Renault, 1893; 1896). However, there was no indication as to whether these cells represented primary or secondary phloem. In *A. communis* (Renault, 1893; 1896), the phloem appeared in transverse section as semi-circular groups of cells located opposite the protoxylem poles and outside the vascular cambium. This tissue probably represented primary phloem, but the sieve elements were too poorly preserved to distinguish sieve areas in longitudinal section.

Agashe (1964) described extraxylary tissue in both stems and roots of calamites. Although some of the cells he described were elongate, others were unlike typical phloem elements. Since no sieve areas were
observed, and only one longitudinal section was illustrated, it is difficult to compare this work to later studies.

More recently, Wilson and Eggert (1974) described the phloem in the calamite root Astromyelon (see also Renault, 1893; 1896). In young roots, primary phloem strands alternated with the primary xylem, and consisted of peripheral protophloem and central metaphloem cells. In larger roots, secondary phloem was present in a continuous ring around the secondary xylem. Since there was no evidence of a vascular cambium, it was assumed that Astromyelon exhibited a determinate growth pattern (see also Eggert, 1962). The secondary phloem consisted of an axial system composed of relatively short, presumed sieve elements (190 um long) and phloem rays that were 1-3 cells wide. Although Wilson and Eggert's specimens appeared to be well-preserved, they were unable to discern any sieve areas on either primary or secondary phloem cells.

Hass (1975) detailed the anatomy of a new species of Arthroxylon with well-preserved cells. Adjacent to the cambium, he found thin-walled cells that appeared rectangular in longitudinal section. They were arranged in vertical series with horizontal end walls and graded into the cells of the so-called inner cortex, which were similarly shaped but slightly longer. Between the phloem and the inner cortex were a number of large diameter (30-130 um) cells that were very long (approximately 3.0 mm). The end walls were tapered and the side walls exhibited a kind of pitting which Hass described as reminiscent of sieve areas. The material was apparently too poorly preserved to exhibit sieve pores within these areas.
Although Williamson and Scott (1894) noted phloem cells in *Sphenophyllum*, another common Carboniferous sphenophyte, this tissue was only recently examined in detail (Eggert and Gaunt, 1973). Eggert and Gaunt divided the xylem and phloem into "fascicular" (opposite the protoxylem poles) and "interfascicular" (between the protoxylem poles) zones. Primary phloem was present only in the three interfascicular areas, and consisted of vertically superposed cells with horizontal to slightly oblique end walls. These authors proposed that the vascular cambium first arose as three arcs between the protoxylem points (i.e., in the interfascicular zones) and was bifacial. In older stems, the secondary phloem was separated from the wood by a zone of thin-walled cells termed the postmeristematic parenchyma sheath. The fascicular secondary phloem consisted of small (20-40 µm in diameter), elongate (280-370 µm long) sieve elements with horizontal end walls and phloem rays that were uni- or biseriate in the inner phloem, but expanded tangentially in the peripheral areas. In the interfascicular phloem, the sieve elements were much longer (500-900 µm in the inner phloem and 1250-1440 µm farther out) and wider (91-100 µm in diameter), and the rays varied from uniseriate in the inner portion to multiseriate at the periphery. Primary phloem was not visible in those axes with secondary growth, and no sieve areas or sieve pores were recognized. In addition, it is difficult to determine whether or not phloem parenchyma was present in these stems. Figures 21 and 22 in this work were cited as examples of progressively smaller "rays" (quotation marks Eggert and Gaunt) in the inner portion of the phloem. But these figures were later referenced as illustrating vertical strands of parenchyma (i.e., axial
parenchyma, not ray parenchyma). The authors stated that both the fascicular and interfascicular secondary phloem contained axial and ray systems, but these were difficult to distinguish from one another in cross section, and do not appear to be adequately illustrated in longitudinal section. As Eggert and Gaunt noted, part of the problem may be related to a lack of information on the development and structure of the cambium and its derivatives. Perhaps the recent work of Cichan and Taylor on cambial function and growth of the secondary xylem in *Sphenophyllum* (Cichan and Taylor, 1982) will also help to clarify phloem structure and ontogeny in this taxon. Although both of the detailed studies on Carboniferous sphenophyte phloem (i.e., Eggert and Gaunt, 1973; Wilson and Eggert, 1974) compared the anatomy of the fossils to extant *Equisetum*, our knowledge of phloem histology in these early representatives is still too incomplete (since sieve areas and sieve pores have not generally been observed) for a detailed comparison.

The ferns are another important group of Carboniferous vascular cryptogams that have been described with well-preserved phloem (e.g., Renault, 1893; 1896; Smoot and Taylor, 1978a; 1978b; 1981a; Smoot, 1979). Renault (1893; 1896) noted a *Zygopteris* petiole (= *Etapteris*) with well-preserved phloem, which he described as consisting of phloem parenchyma and darker-colored sieve elements. However, no longitudinal sections were illustrated, so the identification of these cells cannot be confirmed. The phloem of *Etapteris* and *Botryopteris* petioles was later described in detail (Smoot and Taylor, 1978a; Smoot, 1979). Both contained a primary phloem zone that consisted entirely of sieve elements and was separated from the xylem by a uni- or biseriate
parenchyma sheath. The conducting cells were relatively short (about 90-138 um in *Botryopteris* and 120-360 um in *Etapteris*) and narrow (21 um and 16 x 31 um, respectively), and were present in vertical series with irregular, elliptical sieve areas or scattered sieve pores on their walls. The phloem of these two ferns was comparable to that described for *Lepidodendron* (Eggert and Kanemoto, 1977) in the relatively unspecialized structure of the conducting cells (see also Hébant, 1968). In addition, the overall composition and structure of the phloem in Carboniferous lycopods and ferns is comparable to that described for extant members of these groups (see, e.g., Lamoureux, 1961; Hébant, 1969; Hébant et al, 1978; Smoot, 1979).

**Seed plants** - Among the Carboniferous and Permian seed plants, there have been more contributions on the phloem of seed ferns than any other group. As early as 1887, Williamson described phloem tissue in *Kaloxylon* and *Heterangium* (Williamson, 1887b). The secondary phloem in *Heterangium* consisted of long sieve elements (cross walls were not seen) and phloem rays, that he divided into so-called primary rays (uni- or biseriate in transverse section) and secondary rays, which underwent massive tangential expansion in the older phloem. In a subsequent contribution, Williamson and Scott (1896) illustrated elliptical sieve areas containing numerous dark masses. Although they were unable to distinguish phloem parenchyma in transverse section, it was visible in longitudinal section. In addition, these authors were able to discern tapered end walls in the secondary sieve elements and the presence of strands of primary phloem. They speculated as to why such delicate structures as sieve elements and sieve areas would be fossilized and
concluded that the dark masses within the sieve areas probably represented the "carbonized remains" of cell contents that had adhered to the sieve areas. These contents would probably be equivalent to the callose deposits of later studies (e.g., Eggert and Kanemoto, 1977). More recently, Hall examined the phloem of *H. americanum* and found that the North American species exhibited some important differences when compared with the British specimens (Hall, 1952). The secondary phloem of *H. americanum* consisted of alternating, tangential bands of sieve elements and phloem parenchyma, separated by vascular rays. The sieve elements were approximately 44 um in diameter and so long that the two ends of one cell were not observed in a single section. Well-preserved sieve areas were present on the radial walls and the sieve pores appeared to be open, i.e., they were not covered by callose deposits.

The oldest presumed pteridosperm that has been described with structurally preserved phloem is *Calamopitys* from the Lower Carboniferous of France (Galtier and Hébant, 1973). This stem exhibited phloem similar to that seen in *Heterangium*. Secondary phloem consisted of alternating, tangential bands of sieve elements and phloem parenchyma. The conducting cells were extremely long (more than 2.5 mm) with numerous, lenticular sieve areas on the lateral and oblique end walls. Axial parenchyma was present in vertical series and the rays were very high and multiseriate. Primary phloem strands were present opposite the protoxylem points and these consisted of small groups of sieve elements and parenchyma, often surrounded by cells with dark contents. Galtier and Hébant noted the structural similarities between the phloem of *Calamopitys* and other Carboniferous pteridosperms,
especially Heterangium and Callistophyton, and suggested that the phloem anatomy provided some additional evidence for the placement of the Calamopityales within the seed ferns.

The pteridosperm Callistophyton has been described several times with well-preserved phloem. Delevoryas and Morgan (1954b) illustrated secondary phloem composed of alternating, tangential bands of sieve elements and phloem parenchyma in their original description of the genus. In addition, they were able to discern clusters of brown masses on the radial walls of the sieve elements which they interpreted as callose plugs within sieve areas. In his extensive study on the vegetative anatomy and morphology of the Callistophytales, Rothwell (1975) also found well-preserved phloem similar to that described by Delevoryas and Morgan (1954b). More recently, Russin (1981) added an analysis of secondary phloem in both stems and roots of _C. boysetii_ from North American coal balls. He described sieve areas with varying amounts of callose deposition, and compared the phloem of Callistophyton with that of other gymnosperms, both fossil and extant.

One of the earliest and most detailed examinations of phloem structure in a Carboniferous seed fern was the study by Bertrand and Renault on _Poroxylon_ (1886). These authors described secondary phloem in _P. boysetii_ that was very similar to that seen in Callistophyton (the genus was placed in synonymy with Callistophyton by Rothwell [1975]). Sieve elements and phloem parenchyma were present in alternating, tangential bands separated by phloem rays. The material was well-preserved, and a number of sieve elements with sieve areas were illustrated. In addition, histological differences between the
first-formed phloem cells and the last-formed elements were detailed. Renault later re-examined *P. boyssetii* (1893; 1896) and noted that this species could be distinguished from *P. edwardsii* on the basis of phloem anatomy. *Poroxylon edwardsii* contained sieve elements and phloem parenchyma that were produced in irregular tangential bands, while in *P. boyssetii*, the cells generally exhibited a very regular pattern.

Other Carboniferous seed ferns that have been described with some phloem preserved include *Lyginopteris* (Williamson and Scott, 1896; Blanc-Louvel, 1966), *Rhetinangium* (Gordon, 1912), *Medullosa* stems (Smoot and Taylor, 1981b; Stewart, 1951) and roots (Rothwell and Whiteside, 1974), *Schopfiastrum* (Rothwell and Taylor, 1972; Stidd and Phillips, 1973) and *Microspermopteris* (Taylor and Stockey, 1976). However, in almost all of these contributions the phloem was too poorly preserved to observe critical histological details such as sieve areas or pores.

Another group of seed plants that was prominent in the Carboniferous and Permian is the Cordaitales. Renault (1893; 1896) made some of the earliest observations on phloem structure in this group. He described *Cordaites* phloem that consisted of sieve elements and axial parenchyma, with the older sieve elements often developing into "gum" cells. In some species, phloem fibers were present. In *Hapaloxyylon* (Renault, 1893; 1896), two cell types were observed in the phloem tissue—large sieve elements with well-preserved, elongate sieve areas and sieve pores; and phloem parenchyma cells in regular, concentric bands. Sieve areas were also illustrated in the phloem of *Cordaixylon* (Renault, 1893). In this same work, Renault described a new genus of cordaite stem, *Retinodendron*, that exhibited unusual secondary phloem,
consisting of four types of cells that were generally arranged in concentric bands. Included were elongate cells with dark contents that Renault termed "resin or tannin canals" (Renault, 1896), rectangular, sclerified cells that alternated regularly with the resinous cells, and thin-walled axial parenchyma that occurred in bands 3-4 cells wide between the other, darker colored cells. In addition, a few examples of sieve cells with sieve areas were also noted (Renault, 1896).

Maslen (1911) later described some phloem cells from Mesoxylon sutcliffii, as did Traverse (1950) from M. thompsonii, but Cridland (1964) has provided the most recent information on the phloem in cordaites. He examined specimens of the cordaite root Amyelon and divided the phloem into two regions. The tissue adjacent to the vascular cambium was termed the compact phloem and consisted of tangential layers of thick-walled phloem fibers, thin-walled axial parenchyma and sieve cells. Phloem rays were present that greatly enlarged in the peripheral portion of the compact phloem. Outside of this compact zone was a region of so-called aerenchymatous phloem. The phloem rays and fibers appeared to extend out into this zone, although the position of the cells was distorted. Since no sieve areas were found in either of these phloem zones, it is not possible to confirm the identification of all the cell types in this tissue.

MESOZOIC-TERTIARY

As was the case in the Silurian and Devonian, the amount of information on phloem structure in plants younger than the Permian is meager, due to the comparatively low number of anatomically preserved specimens from these time periods.
The Triassic Ischigualasto Formation in Argentina has yielded several examples of structurally preserved plants with phloem tissue, including the polystelic stem *Rhexoxylon* (Archangelsky and Brett, 1961) and a cycad axis, *Michelilloa* (Archangelsky and Brett, 1963). The internal phloem in *R. piatnitzky* (Archangelsky and Brett, 1961) was well-preserved and contained some fibers in the most recently formed phloem, as well as large parenchyma cells in the older phloem. The sieve cells exhibited large, uncrowded sieve areas on their lateral walls.

There have been a number of examples of Mesozoic and Tertiary fern stems and petioles described with structurally preserved phloem tissue, especially in the Osmundaceae (e.g., Kidston and Gwynne-Vaughan, 1907; 1908; 1909; Arnold, 1952; Archangelsky and de la Sota, 1963; Arnold and Daugherty, 1964; Miller, 1971; 1982; Gould, 1973). Kidston and Gwynne-Vaughan found that the phloem completely surrounded the xylem in *Osmundites* (Kidston and Gwynne-Vaughan, 1907), *Zalesskya* (Kidston and Gwynne-Vaughan, 1908) and *Thamnopteris* (Kidston and Gwynne-Vaughan, 1909). Of these genera, *Osmundites* provided the greatest amount of information on phloem histology. The sieve elements were separated from the xylem by a wide parenchyma sheath. Immediately outside of the sieve elements was a zone of tangentially elongated cells with pits or sieve areas on their walls. These probably correspond to the "porose cells" that are known to occur in extant Osmundaceae (see, e.g., Zenetti, 1895) and that are considered by some to be part of the protophloem (Esau, 1969). Arnold (1952) was also able to distinguish a porose layer in his specimens of *Osmundites chandleri*, as was Wang (1983) in *Osmundacaulis*. 
However, Miller (1971) has provided the most complete information to date on the phloem of the fossil Osmundaceae. He was able to distinguish three tissues within the phloem zone, all consisting entirely of sieve elements. The metaphloem was situated just outside the xylem sheath and contained elongate sieve cells with overlapping, rounded end walls. Protophloem was located internal to the pericycle, and between these two cell types was the porose layer. Miller (1971) noted that a controversy has existed over the exact identification of this tissue (see, e.g., Seward and Ford, 1903) and suggested that it be referred to as "transitional phloem," indicating that it arose ontogenetically between the proto- and metaphloem.

A few instances of well-preserved phloem tissue involve silicified bark specimens collected from localities that have yielded petrified wood (e.g., Shimakura, 1937; Wheeler and Matten, 1977). Ramanujam and Stewart (1969) described an example of anatomically preserved bark that was found attached to Taxodioxylon wood. A large portion of the bark was preserved, consisting of secondary phloem on the inside, and alternating zones of secondary phloem and periderm nearer the periphery. Like modern members of the same family (see, e.g., Isenberg, 1943; Chang, 1954), the phloem consisted of regularly repeating, tangential bands of phloem fibers, sieve cells, axial parenchyma, sieve cells, fibers, etc. Oval sieve areas were confined to the radial walls where they occurred in a single row, with each sieve area consisting of 3-6 groups of sieve pores. The authors compared this Cretaceous bark with extant taxodiaceous taxa, especially Sequoia, and noted that their material was very similar to a bark specimen Stopes had described from
the Lower Greensand of the Isle of Wight (Stopes, 1915). Stopes' material was named *Vectia* and consisted of vascular rays and alternating, tangential bands of fibers and thin-walled elements, the latter presumed to represent sieve cells. Longitudinal sections of this bark (Stopes, 1915) showed single rows of oval-round sieve areas on the radial walls, but no higher magnification was illustrated and it is impossible to determine whether or not sieve pores were present.

In a later paper, Ramanujam (1970) described another example of petrified bark (*Cupressinocortex albertaense*) from the Cretaceous of Alberta which was slightly older than the taxodiaceous specimen (Ramanujam and Stewart, 1969). As in the taxodiaceous bark, the cellular components of the secondary phloem in *Cupressinocortex* were arranged in a repeating, tangential pattern of fibers, sieve cells, parenchyma, sieve cells, fibers, etc. The sieve cells exhibited sieve areas on their radial and end walls with pores aggregated into groups. Vertical resin canals with multiseriate epithelia were also present. Successive layers of periderm were produced in the outer bark, and these had the effect of disrupting the tissues of the secondary phloem. Based on the structure of the bark, Ramanujam placed this new taxon within the Cupressaceae. Some of the characters that were used included the presence of vertical resin canals in the bark and the lack of expansion of phloem rays near the periphery of the tissue.

From the preceding discussion, it is apparent that our understanding of phloem anatomy and phylogeny in fossil plants is more extensive for Carboniferous plants than any other time period. However, there are a number of gaps in our knowledge even within this period.
The present study is intended to provide more data on phloem histology of Carboniferous ferns and seed ferns, and with this information, to speculate on possible evolutionary trends in phloem structure.
CHAPTER 2 - MATERIALS AND METHODS

All of the specimens were borrowed from seven collections of mid-continent and Appalachian coal balls. These are listed at the end of the Specimen Directory.

**SPECIMEN DIRECTORY**

<table>
<thead>
<tr>
<th>Coal Ball No.</th>
<th>Collection</th>
<th>Locality</th>
<th>Taxon</th>
</tr>
</thead>
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<tr>
<td>370</td>
<td>O.U.</td>
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**Anachoropteris** (Tubicaulis):

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<td>283</td>
<td>O.S.U.</td>
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<td>863</td>
<td>O.S.U.</td>
<td>Berryville, IL</td>
<td>T. stewartii</td>
</tr>
<tr>
<td>2114</td>
<td>O.S.U.</td>
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<tr>
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**Psaronius**:

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### Callistophyton:

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<td>C. boyssetii</td>
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<td>Mackie Clemens #23</td>
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<td>&quot; &quot; &quot;</td>
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<td>U.K.</td>
<td>Berryville, IL</td>
<td>M. endocentrica</td>
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</tbody>
</table>

E.S.U. = Paleobotanical Collection, Department of Biology, Emporia State University, Emporia, KN 66801 (Coll. of Dr. Gilbert M. Leisman)  
O.U. = Paleobotanical Herbarium, Department of Botany, Ohio University, Athens, OH 45701 (Coll. of Dr. Gar W. Rothwell)  
O.S.U. = Paleobotanical Collection, Department of Botany, The Ohio State University, Columbus, OH 43210 (Coll. of Dr. Thomas N. Taylor)  
O.S.U.-Lima = The Ohio State University, Lima Campus, 4240 Campus Drive, Lima, OH 45804 (Coll. of Dr. Charles W. Good) (filed with O.S.U. collection)  
U.I. = Paleobotanical Collections, Department of Botany, University of Iowa, Iowa City, IO 52242 (Coll. of Dr. Jeffry R. Schabilion)  
U.K. = Paleobotanical Collections, Department of Biology, University of Kansas, Lawrence, KN 66044 (Coll. of Dr. Robert W. Baxter)
LOCALITIES

Berryville, IL: Upper Pennsylvanian, Calhoun Coal, Mattoon Formation, McLeansboro Group, Summer 15' Quad. (Sec. 7, T2N, R13W), Lawrence Co., IL

Lewis Creek, KY: Lower-Middle Pennsylvanian, Hamlin Coal, Breathitt Formation, Cutchin 7.5' Quad., Leslie Co., KY

Mackie Clemens No. 23 mine, KN: Middle Pennsylvanian, Bevier Coal, Bevier Formation, Cherokee Group, Joplin Quad. (Sec. 21, T9S, R25E), Crawford Co., KN

New Calhoun, IL: Upper Pennsylvanian, Calhoun Coal, Mattoon Fm., McLeansboro Group, Summer 15' Quad. (Sec. 32, T 3 N, R 14 W), Richland Co., IL

Ottumwa, IA: Middle Pennsylvanian, Unnamed Coal, Cherokee Group, Wapello Co., IA

Palmer Mine, KN: Middle Pennsylvanian, Bevier Coal, Bevier Fm., Cherokee Group, Fort Scott Quad. (Sec. 28, T28S, R25E), Crawford Co., KN

Providence, KY: Middle Pennsylvanian, No. 11, 12 or 14 Kentucky Coal, Baker Coal Member, Lisman Formation, Allegheny Series, Providence 7.5' Quad. (37°24'52.5"N, 87°46'9"W), Webster Co., KY

Sahara, IL: Middle Pennsylvanian, Herrin (No. 6) Coal, Carbondale Formation, Kewanee Group, Harrisburg 15' Quad. (Sec. 30, T9S R4E), Williamson Co., IL
Steubenville, OH: Upper Pennsylvanian, Duquesne Coal, Duquesne Formation, Conemaugh Group, Wayne Twp. (Sec. 6, NE¼, SE¼, SE¼), Jefferson Co., OH

The stratigraphic position of most of the North American coal ball localities is fairly well-established (see, e.g., Darrah, 1941b; Cross, 1969; Phillips et al, 1973). Information on their relative positions and correlation with North American coal seams and European material has been discussed most recently by Phillips (1980; 1981). Recent mapping of the region around the Lewis Creek, KY site indicates that these coal balls occur within the Hamlin coal bed (Ping, 1977) and not the Copland (Taylor) coal as previously cited.

The specimens were prepared for light microscopy using the cellulose acetate peel technique (Joy et al., 1956; Stewart and Taylor, 1965). In order to increase the contrast of some of the cell walls, especially the fibers in *Medullosa*, the peels were stained with Malachite green, according to the technique of Bartholomew et al. (1970). Measurements were made either with an ocular micrometer or on a Zeiss Videoplan image analyzer. However, most sieve pores were either too indistinct to accurately measure utilizing transmitted light optics, or the pores were obscured with callose (e.g., *Medullosa*). In these cases a rough estimation of pore size was obtained from scanning electron micrographs. In addition, small pieces of the axes were mounted on stubs for scanning electron microscopy, and prepared according to the techniques of Smoot (1979), by etching for 5-10 minutes in dilute hydrochloric acid (2% of stock), followed by 10 minutes in saturated EDTA (ethylenediaminetetraacetic acid). The rock was
subsequently dried, coated with gold and viewed with a Hitachi S-500 instrument. Slides, peels, stubs and slabs of coal ball numbers 53, 66, 200, 228, 283, 418, 831, 861, 863, 929, 979, 1564, 1695, 1696, 1809, 1966, 2087, 2114, 2129, 2162, 2222, 2259, 2296, 2579, 2674, 2918, 4183, 6199, 6200, 6538, 6686, 7700, 8010, 8342 are deposited in the Paleobotanical Collections, Department of Botany, The Ohio State University. The materials borrowed from other sources are deposited in their respective collections.
Investigations of the phloem anatomy of fossil plants have the potential to contribute a great deal to our knowledge of the phylogenetic specialization of phloem tissue, not only at the level of tissue composition and organization, but also at the level of cellular features specialized for conduction. Phloem preserved in coal balls of Pennsylvanian age provides one of the best opportunities for study, due to the excellent preservation and cellular continuity that is often present. Examples of this remarkable detail of preservation include the description of well-preserved sieve areas in the phloem of such diverse genera as the seed ferns Heterangium (Hall, 1952) and Callistophyton (Delevoryas and Morgan, 1954b; Russin, 1981), and the vascular cryptogams Lepidodendron, Etapteris and Botryopteris (Eggert and Kanemoto, 1977; Smoot, 1979).

Continuing detailed investigation of phloem histology in vascular cryptogams, such as the work done on sphenophytes (Eggert and Gaunt, 1973; Wilson and Eggert, 1974), lycopods (Eggert and Kanemoto, 1977) and ferns (Smoot and Taylor, 1978a, 1981a; Smoot, 1979), is needed for several reasons. A great deal of work has been completed recently on the structure and development of phloem in extant cryptogams (see, e.g., Hébant, 1969; Evert and Eichhorn, 1974; Behnke, 1975; Dute and Evert, 1978; Nair and Shah, 1980; Warmbrodt, 1980 and references cited
therein). Information on fossil forms would permit comparison with the extant material and could thereby form the basis for a suggested phylogenetic scheme of phloem anatomy in these groups of plants. In addition, fossil cryptogams offer an excellent system in which to study the structure of primary phloem in specimens where the tissue has not been obliterated by secondary growth. The present study describes primary phloem anatomy in the petioles of two common Carboniferous ferns, *Anachoropteris* and *Ankyropteris*. Material consists of coal ball permineralizations collected from various localities in North America. Information regarding the collecting localities, stratigraphic position, specimen numbers and repositories is provided in CHAPTER 2.

*Anachoropteris* is a form genus that was instituted by Corda (1845) for isolated petioles exhibiting a C-shaped xylem strand. The "arms" of the C-shaped trace may or may not be rolled in toward the center of the trace, but in the majority of the North American specimens the trace is extremely involute, and the petioles are placed in the species *Anachoropteris involuta*. It was known for some time that these isolated petioles bore a resemblance to petioles that had been found attached to the fern stem *Tubicaulis*, but it was not until 1961 that Hall determined that petioles of *A. involuta* were borne by *Tubicaulis* stems (Hall, 1961). Although *Anachoropteris* petioles have not subsequently been found attached to any other genus of stem, isolated material continues to be designated by the form generic name *Anachoropteris* (see, e.g., Eggert, 1964; Phillips, 1974). From their attachment to stem material, and the position of protoxylem strands, it is clear that the open section of the "C" faces the abaxial side of the petiole. Early
workers, noting this unusual situation, placed these plants in the order Inversicatenales (e.g., Corsin, 1937). *Anachoropteris* specimens were later allied with the coenopterid ferns, an artificial group of plants characterized by unusual petiole traces in transverse section (Eggert, 1964; Phillips, 1974). Additional work based on fertile and sterile specimens suggests that many of these plants probably had filicalean affinities (see, e.g., Eggert and Delevoryas, 1967).

The *Anachoropteris* specimens in the present study are of three types. The first type, consisting of isolated petioles only, is the common species *A. involuta*, which exhibits the characteristic involute xylem arms in transverse section (Fig. 1, 4). The second type is found in close association or attached to stem material of *Tubicaulis stewartii* (Eggert, 1959a), and possesses a petiole trace that is less involute in transverse section (Fig. 2). Finally, specimens of *A. clavata* from the Berryville coal ball locality exhibit a simple C-shaped trace with expanded, club-shaped arms (Fig. 8) (Graham, 1935; Delevoryas and Morgan, 1954a).

*Ankyropteris* is also believed to have filicalean affinities, but was initially placed within the order Coenopteridales as well (e.g., Baxter, 1951; Eggert, 1959b). The genus was originally described from anatomically preserved specimens that consisted of a stem with a five-lobed protostele (Bertrand, 1907; Scott, 1912). The cortex of the stem also enclosed a terete axillary branch and petiole with a central, H-shaped xylem strand (Kidston, 1910). As in *Anachoropteris*, the petioles are commonly found detached. When the fertile parts of *Ankyropteris* were discovered, it was suggested that the genus had
affinities with the filicalean ferns (Eggert and Taylor, 1966; Mickle, 1980). Although both fertile and sterile specimens of Ankyropteris are fairly well-known in North American and British coal balls (Williamson, 1889; Holden, 1930; Darrah, 1941a; Andrews, 1956; Eggert, 1963; Mickle, 1980), as well as silicified specimens from France (e.g., Bertrand, 1909; Corsin, 1952), little information is available on the phloem in this taxon. The present material consists of petioles (both isolated and attached to stems) of A. brongniartii (Mickle, 1980).

DESCRIPTION

Anachoropteris-General anatomy - Anachoropteris petioles demonstrate a wide range of sizes, extending from 2.6 x 3.4 mm in cross-sectional diameter, with the central trace as small as 1.5 x 2.0 mm across in A. clavata. Anachoropteris involuta specimens are generally somewhat flattened and range from 1.9 x 2.1 mm up to 3.5 x 5.6 mm. Petioles of Tubicaulis stewartii are the largest examined, ranging from 5.3 x 6.2 mm near their attachment to the stem to 10.3 x 12.0 mm further out. The C-shaped traces undergo a similar enlargement from 1.3 x 2.9 mm to 2.4 x 3.5 mm. In all specimens, the xylem portion of the trace is 1-2 cells wide in the center of the "C" (e.g., Figs. 2, 4, 8). Secondary wall thickenings on metaxylem tracheids vary from multiseriate scalariform (Fig. 5) to circular bordered or unbordered pits. Protoxylem elements, which are scattered along the adaxial surface of the trace, usually possess helical secondary wall thickenings.

The central xylem trace is completely surrounded by a zone of thin-walled phloem cells, which, in turn, is bounded by a three-parted cortex. In some specimens, an epidermal layer with hairs is preserved.
The cortical structure is similar to that seen in several other Pennsylvanian fern petioles (e.g., Ankyropteris, Botryopteris, Etapteris). Cells of the innermost cortex are only rarely preserved and are about 65 μm in diameter and from 60 to 300 μm in length. The middle cortex consists of large diameter, somewhat elongate, thin-walled cells (Fig. 3). The outer cortex is made up of narrow (around 30 μm in diameter), thick-walled fibers, which range from 130 to 600 μm in length. Cells that appear histologically similar to cortical cells occur in the center of the space enclosed by the C-shaped trace (e.g., Figs. 2, 4, 6, 8).

Phloem anatomy -- The phloem in Anachoropteris is more complex than that described for other fossil ferns (see, e.g., Smoot, 1979), and consists of three different types of cells whose distribution varies according to position within the petiole. On the side of the xylem that faces the stem, i.e., the adaxial side (= zone external to the "C"), the phloem zone is narrow and generally somewhat crushed (Fig. 6, 7). It consists entirely of small diameter, elongate sieve elements (Fig. 3). In the region of the protoxylem elements, a parenchyma sheath separates the xylem from the phloem elements, but the external phloem is usually so poorly preserved that the full lateral extent of this sheath cannot be determined. Outside of the phloem, in the position of a pericycle and/or endodermis, is a zone of 1-2 layers of larger, rectangular cells (30 x 45 μm) (Figs. 3, 7). Although these cells form a continuous layer similar to an endodermis, no Casparian strips have been observed on the cell walls. Sieve elements in the adaxial phloem are narrow (mean diameter about 9.8 μm), elongate (78-375 μm) and arranged in vertical
series. Due to their generally poor preservation, it is often difficult to distinguish end walls, but most appear to be horizontal or only slightly oblique. Sieve areas are present (e.g., Figs. 9, 10), but are often somewhat degraded (Fig. 15). They occur on vertical walls as well as oblique end walls, and do not appear to be more specialized on end walls. Therefore, according to the terminology of Cheadle and Whitford (1941), these cells are sieve cells (see also Esau, 1969; APPENDIX). Some of the sieve areas contain evenly distributed dark spots, and these are interpreted as sieve pores with callose deposits (Figs. 9, 10). In addition, a few specimens contain what appear to be open pores, and these may be arranged singly (e.g., Fig. 16) or grouped into sieve areas (Fig. 10, arrowhead).

The phloem zone within the C-shaped xylem trace faces away from the axis and should be correctly termed the abaxial phloem. However, since most specimens represent isolated petioles, it is less confusing to refer to this tissue as internal phloem, i.e., within the "C" of the trace (Figs. 1, 2, 4, 6, 8). The internal phloem is more complex than the external phloem and is generally more completely preserved. Sieve elements are separated from the xylem cells by a parenchymatous sheath that is 1-2 cells wide and consists of rectangular cells approximately 30 x 72 um in size (Fig. 5). Internal to this are small sieve elements ranging from 8 to 27 um in diameter which exhibit horizontal or slightly oblique end walls (Figs. 5, 11); only rarely are very oblique end walls observed. These elements are relatively long (195-618 um) and are positioned immediately adjacent to the parenchyma sheath cells. They are continuous around the xylem trace with the sieve elements in the
external phloem. A second band of small sieve elements borders the cortical cells that occupy the center of the trace (Fig. 6). Large sieve elements are present in the center of the internal phloem tissue surrounded by the smaller cells with no intergradation in size (Figs. 1, 4, 5, 6, 11). They range from 48 to 120 um in diameter and possess end walls that are so oblique it is difficult to distinguish lateral walls from end walls (e.g., Fig. 5, arrow). This layer of large sieve elements is 1-2 cells wide and often discontinuous in A. involuta and A. clavata (e.g., Fig. 1, 4, 6), but usually quite conspicuous and continuous in T. stewartii (Fig. 2). The elements are extremely long and arranged in vertical series. Measured cells extend from 1.23-2.74 mm in length, but in many instances the cells extend up to 2.5 mm with no end wall visible in the section so that the mean length of these elements could not be accurately determined. Sieve areas are present wherever two cells share a common wall (Figs. 5, 11, 12, 13, 14). However, since the end walls are extremely oblique, it is difficult to determine whether these sieve areas occur exclusively on end walls or on side walls as well. In some instances, it is obvious from the narrow diameter of the cell (30 um or less) that the sieve areas in question are present on a tapered end wall (e.g., Figs. 13, 14). However, in other instances (Fig. 12), often due to the irregular nature of the preservation, it is impossible to tell the exact location of the perforated sections of the wall. Sieve areas range from approximately 5 to 8.5 um in diameter, and are aggregated into groups. In transmitted light, they appear as pale areas or as perforations (i.e., clear areas) in the wall (Figs. 12, 13, 14). Due to their large size, it was assumed
that these perforations in the sieve element walls represented sieve areas rather than pores. However, no pores could be clearly observed within these areas utilizing transmitted light, although there was some evidence of structures within the sieve areas (Fig. 14). Most of the sieve element walls in both the internal and the external phloem were so thin that they appeared almost translucent in peel preparations (e.g., Fig. 5). This lack of contrast coupled with the probable small size of the sieve pores necessitated the use of the scanning electron microscope to confirm the shape and occurrence of sieve pores and sieve areas in Anachoropteris.

Sieve areas in the internal phloem are clearly visible under the scanning electron microscope, although they generally exhibit low relief, even after extensive acid etching (Fig. 18, arrow). They appear as circular to oval areas and are often surrounded by a raised portion of the sieve element wall that gives the appearance of a border around the sieve area (Figs. 17, 19, 20, 22). In a few instances, this "border" is not present, and the sieve area appears flush with the sieve element wall. It is often difficult to discern specific cells when an etched surface is examined under the electron microscope, since the extensive etching generally causes delicate phloem cells to collapse. It is apparent that the cell walls are very brittle, since there is evidence of cracking and collapse (e.g., Fig. 17, right, 19). After etching, the surface layer generally contains the remains of many cell walls, some with sieve areas and some without, but the overall effect is a greater abundance of sieve cell walls than is apparent utilizing light microscopy. For this reason, it is very important to orient the
specimen prior to etching and examination. Although at first glance the sieve areas appear similar to bordered pits due to the raised edge around the perforations, they occur exclusively on phloem cells and these can easily be distinguished from metaxylem tracheids by their considerably smaller size (Fig. 18). In addition, although the diameter of some of the smaller sieve elements is comparable to that of protoxylem tracheids, the sieve elements examined occurred within the internal phloem (i.e., abaxial to the xylem), while the protoxylem cells are present on the adaxial side of the trace. Closer examination of the structure of these circular areas reveals that they are more similar to primary pit fields than to tracheal pitting. Each circular to oval region is covered by criss-crossed fibril-like material that fills the sieve area (Figs. 19, 20, 21, 22). Small openings are present between some of the fibrils that are a fraction of a micron in diameter (Figs. 21, 22). The overall appearance is similar to primary pit fields seen in extant plants that contain plasmodesmata-sized openings between the bundles of cellulose fibrils. It is not possible at this time to determined the chemical composition of these fibrils. However, since the material was heavily etched in HCl and then washed in saturated EDTA (see CHAPTER 2), it is likely that the remaining wall material is organic, at least in part.

Ankyropteris-General anatomy - The petioles of Ankyropteris can be distinguished in transverse section by their characteristic H-shaped xylem trace (Fig. 23). The axes in the present study exhibit a wide range of sizes (from 3.2 x 2.7 mm up to 6 x 10 mm) which may be related to position within the frond (Mickle, 1980). The xylem trace is about
1.0 mm in diameter and consists of a central bar (Fig. 27) (= apolar of Bertrand, 1909) of metaxylem tracheids with scalariform thickenings. Attached to either end of the bar are two antennae (Fig. 27) (terminology of Bertrand, 1909). Each antenna contains a parenchymatous peripheral loop that is bordered on the inside by metaxylem and on the outside by protoxylem cells. Generally the tracheids that make up the antennae are somewhat smaller in diameter (approximately 50 um) than those in the central bar (100 um) (Fig. 27). Traces to the primary pinnnae are given off from the antennae in two alternate ranks and form a two-dimensional, planated frond. As reconstructed by Eggert (1963), Ankyropteris fronds are bipinnate and bear aphlebiae at various points along the rachis (see also Mickle, 1980). The cortex of Ankyropteris petioles is similar to that in Anachoropteris and consists of an outer region of thick-walled, small diameter cells that grades into a central region of slightly larger cells (Fig. 23). Surrounding the phloem is an inner cortex of very thin-walled cells which is only rarely preserved.

Phloem anatomy - The phloem in Ankyropteris completely surrounds the central H-shaped trace and extends from three to five cells in thickness (Fig. 28). Separating the phloem from the xylem is a 1-2 cell thick parenchymatous sheath. The sheath cells in the vicinity of the central bar are slightly elongate, with a mean diameter of 27 um and length of 50 um. Around the antennae they are generally smaller in diameter (approximately 19-20 um) and longer (about 75-80 um), and are only present discontinuously (e.g., Fig. 25). It is not possible at this time to determine whether or not this distribution reflects preservational problems. Although the diameter of the sheath cells
overlaps that of sieve elements, these two cell types can easily be distinguished in longitudinal section (Figs. 24, 25). The size of the sieve elements in *Ankyropteris* also varies according to position within the trace. All of the elements are narrow (13.5 \( \mu m \)), but those around the antennae are generally a few microns smaller and may be as narrow as 7.5 \( \mu m \). The elements along the central bar are usually shorter (about 167 \( \mu m \)) than those near the antennae, where the cells can extend up to 460 \( \mu m \) in length (Fig. 24). Vertical strands of phloem parenchyma are occasionally present (Figs. 24, 31). The orientation of the end walls on the conducting elements varies from horizontal to oblique (Fig. 26, 29) and some of the elements along the central bar exhibit slightly rounded end walls. Sieve areas have been observed on both side and oblique end walls of the sieve elements. These appear as round to oval clear areas on the cell walls and measure approximately 4.3 x 5.4 \( \mu m \) in diameter (e.g., Figs. 26, 30, 33, 34). Although there is some indication of structures that appear as darker spots within a number of sieve areas, the preservation is too poor to definitely describe these as sieve pores. Scattered, individual pores have been observed on some cells, however (Fig. 32), and these measure around 0.9-1.8 \( \mu m \) in diameter. In a number of cells, the wall material is apparently somewhat degraded, and the longitudinal walls of the sieve elements present a pattern of horizontal clear areas separated by regions of more completely preserved, darker-colored wall material (Fig. 29, 33). These clear areas are various shapes ranging from oval to elongate and are here interpreted as the remains of one to several sieve areas that have
become confluent due to the loss of intervening wall material during fossilization.
Figs. 1, 3-5. Phloem of *Anachoropteris* involuta. Fig. 2. *Tubicaulis stewartii*. 1. Transverse section of half of an involute petiole trace, showing large and small sieve cells in internal phloem. 2777 A(5) top #4. X 20. 2. Transverse section through trace of *Tubicaulis* illustrating phloem zone completely surrounding the xylem cells' and continuous layer of large sieve cells in internal phloem. 863 C top #25 C. X 27. 3. Longitudinal section of external phloem. Note large, rectangular cells in the position of a pericycle or endodermis and poorly preserved inner cortex. 2918 G₁ side #55. X 110. 4. Transverse section illustrating distribution of large diameter sieve cells within involute arms (arrows). 2918 G top #507. X 27. 5. Longitudinal section through internal phloem, showing parenchyma sheath cells, small sieve cells adjacent to the sheath, large sieve cells and metaxylem tracheids. Arrow indicates oblique end walls of two large sieve cells. 2918 G₁ side #93. X 110. E = external (adaxial) phloem. I = internal (abaxial) phloem. IC = inner cortex. L = large sieve cells of internal phloem. MC = middle cortex. P = parenchymatous xylem sheath. S = small sieve cells. X = metaxylem tracheids.
Figs. 6-7, 9-10. Transverse sections of *Anachoropteris* phloem. Fig. 8. *Anachoropteris clavata*. 6. Section through part of involute arm illustrating extent of external and internal phloem zones. 2918 G top #507. X 65. 7. Overview of external phloem consisting of thin-walled sieve cells delimited by larger cells in the position of an endodermis. Cells in the position of the inner cortex are not preserved. 2918 G top #484. X 110. 8. Petiole of *A. clavata* showing typical club-shaped arms and tissue continuity from xylem to cortex. 2674 B #38. X 33. 9. External phloem with sieve areas in face view (arrow) and partial side view (arrowhead). 2918 G top #223. X 440. 10. Higher magnification of sieve areas in Fig. 9 using differential interference contrast microscopy. The sieve area in face view (arrow) contains dark areas interpreted as callose deposits, while the one in side view (arrowhead) has open pores. 2918 G top #223. X 1100. E = external (adaxial) phloem. I = internal (abaxial) phloem. IC = inner cortex. X = metaxylem tracheids.
PLATE III

Figs. 11-14, 16. *Anachoropteris involuta* phloem in longitudinal section. Fig. 15. *A. clavata* phloem. 11. Section through internal phloem showing xylem sheath, small and large sieve elements, and cortical cells. 2918 G₁ side #92. X 200. 12. Sieve areas on large sieve elements of internal phloem. 2918 G₁ side #90. X 275. 13. Internal sieve cell showing tapered end wall with crowded sieve areas. 2918 G₁ side #99. X 110. 14. Sieve areas on tapered end wall, some with possible contents (arrows). 2918 G₁ side #61. X 1100. 15. Partially degraded sieve areas in external phloem. 2674 B₁ (a) side #2. X 1500. 16. Individual sieve pores (arrows) on sieve cell in external phloem. 2918 G₁ side #79. X 1000. IC = inner cortex. L = large sieve cells of internal phloem. MC = middle cortex. P = parenchymatous xylem sheath. S = small sieve cells.
PLATE IV

Figs. 17-22. All figures represent large sieve cells in internal phloem of *Tubicaulis stewartii*. 863 C top. 17. Slightly tapered end wall of sieve cell with crowded sieve areas. Note cracked and collapsed cell at right. X 1000. 18. Overview of phloem (left) and xylem. Sieve cells with sieve areas at arrow. X 100. 19. Single sieve area showing fibrillar organization of wall. X 10,000. 20. Sieve areas with "borders" around them. X 5000. 21. Higher magnification of central sieve area in Fig. 20. Note fibrillar structure of wall and conspicuous pores between fibrils. X 20,000. 22. Sieve area seen at lower left of Fig. 20. Note pores and calcium carbonate adhering to sieve area. X 15,000. X = metaxylem tracheids.
Figs. 23-27. Phloem of Ankyropteris. 23. Transverse section of petiole showing central H-shaped trace. 2087 D top #6. X 25. 24. Longitudinal section through antenna, showing narrow sieve elements and strands of phloem parenchyma on the outside of the antenna (left) and parenchymatous xylem sheath on inside (right). 2222 C₂ (a) bot #43. X 140. 25. Longitudinal section through antenna with xylem sheath and poorly preserved sieve elements. 2222 C₂ (a) bot #48. X 500. 26. Sieve areas on oblique end wall of sieve cell. 2222 C₂ (b) top #112. X 1000. 27. Oblique transverse section through trace showing central apolar with larger diameter tracheids and peripheral antennae with smaller tracheids. 2222 C₂ (b) top #7. X 16. A = strands of phloem (axial) parenchyma. IC = inner cortex. MC = middle cortex. P = parenchymatous xylem sheath. S = sieve cells. X = metaxylem tracheids.
Figs. 28-34. Phloem of *Ankyropteris*. 28. Oblique transverse section through apolar, illustrating phloem zone delimited by layer of large, dark cells (arrows). 2222 C₂ (b) top #7. X 65. 29. Longitudinal section showing sieve cells with tapered end walls and degraded sieve areas. 2222 C₂ (a) bot #43. X 1000. 30. Partially degraded sieve cell with sieve areas (arrows). 1564 G₃ side #12. X 1000. 31. Longitudinal section of phloem with narrow sieve cells and strand of phloem parenchyma. 2222 C₂ (a) bot #48. X 500. 32. Sieve cells with individual pores (arrow). 2222 C₂ (a) bot #43. X 1350. 33. Elongate sieve cell with numerous sieve areas (clear regions). 1564 G₃ side #17. X 400. 34. Two poorly preserved sieve cells with circular sieve areas. 1564 G₃ side #24. X 640. IC = inner cortex. S = sieve cells. X = metaxylem tracheids.
CHAPTER 4 - PHLOEM OF *PSARONIUS*

The marattialean ferns are generally considered to be a natural order of synangiate ferns which were fairly widespread during the Carboniferous (Stidd, 1971; 1974; Millay, 1979). Today they are represented by 6-7 genera that, for the most part, are tropical in distribution (Tryon and Tryon, 1982). There have been a number of investigations on the anatomy and morphology of both fossil and extant marattialean ferns. Many of these have been concerned with the architecture of the cauline vascular system and the production and position of leaf traces (e.g., Blomquist, 1922; Brebner, 1902; Farmer and Hill, 1902; Gwynne-Vaughan, 1905; Mettenius, 1863; Morgan, 1959). The marattialean stele is a complex, polycyclic dictyostele with traces produced in either a helical, whorled or distichous pattern. Although the majority of investigations of this group have focused upon the stelar morphology, there are a few studies on extant marattialeans that have included histological details of the stem, roots or leaves as well (e.g., Kühn, 1889; Poirault, 1893; Shove, 1900; Brebner, 1902; Palm, 1937; Lamoureux, 1961).

The best-known fossil member of the Marattiales is the genus *Psaronius*, which is known primarily from Carboniferous and Permian deposits, although a few specimens have been reported from the Triassic (Hirmer, 1927). The genus has been reconstructed as a small tree (up to
about 25 feet; Morgan, 1959) with sterile foliage of the Pecopteris type, fertile foliage often placed in Asterotheca (see, e.g., Herbst, 1977; Brousmiche, 1979), and an extensive, adventitious root mantle covering the distal regions of the stem. The taxon was instituted by Cotta in 1832 for anatomically preserved trunks characterized by a polycyclic stele and attached rootlets. The adventitious roots generally are embedded in a parenchymatous tissue close to the stem (the "bound" root zone) and are free from one another towards the periphery of the stem (the "free" root zone) (Ehret and Phillips, 1977). Structurally preserved stems, petioles and fronds are known from both silicified specimens (Gillette, 1937; Baxter, 1953; Rothwell and Blickle, 1982) and coal ball material (Morgan and Delevoryas, 1952a; 1952b; Morgan, 1959; Stidd and Phillips, 1968; Stidd, 1971). In addition, the pattern formed by leaf scars on the surface of the stem has been given several generic names, e.g., Caulopteris and Megaphyton (Pfefferkorn, 1976), and fossils of these surface features are known from compression, mold/cast and petrified material.

Although phloem tissue has been observed in Carboniferous specimens of Psaronius (e.g., Scott, 1920; Gillette, 1937; Moon, 1939; Morgan, 1959; Rothwell and Blickle, 1982), the quality of preservation has not been good enough to characterize many histological features. Since it represents one of the few Carboniferous taxa that can be placed in an extant order (along with its related fertile parts such as Scoleoopteris, Eoangiopteris, etc.), a detailed examination of the phloem in Psaronius provides an excellent opportunity for direct phlogenetic comparison with living relatives. The material included in
the present study consists of coal ball specimens (calcium carbonate permineralizations) collected from Lower-Middle Pennsylvanian strata near Lewis Creek, Kentucky and from Upper Pennsylvanian rocks near Berryville, Illinois.

DESCRIPTION

General anatomy - In transverse section, *Psaronius* stems consist of a parenchymatous ground tissue containing a number of concentric meristelees that produce C-shaped leaf traces. When found isolated, structurally preserved petioles are placed in the form genera *Stipitopteris* (Morgan and Delevoryas, 1952a; Stidd, 1971) or *Stewartiopteris* (Morgan and Delevoryas, 1952b). In a typical transverse section of a *Psaronius* stem, persistent petiole bases are usually visible around the periphery, separated from the cauline system by a band of sclerenchyma. There are generally a number of large mucilage or secretory canals in the ground tissue and their arrangement has been used as a taxonomic character (see, e.g., Morgan, 1959). In the Lewis Creek specimens, these canals are filled with dark-colored material and delimited by an epithelial layer of small, thin-walled cells (Fig. 35).

Each meristele consists of a central band of xylem that is generally two to five cells wide (Figs. 35, 38). Protoxylem elements are scattered along the adaxial side of each meristele and exhibit helical secondary wall thickenings, while metaxylem tracheids possess scalariform thickenings (Fig. 37). The central xylem arm is separated from the surrounding phloem by a sheath of irregularly shaped parenchyma cells that varies from two to five cells in width (Figs. 36, 38, 39, 44). Although these cells are about the same size (approximately 50 um)
and shape in transverse section as the adjacent phloem cells, they can usually be distinguished by their slightly thinner walls (e.g., Figs. 36, 39). Since they are approximately isodiametric, they are readily visible in longitudinal sections (Fig. 44). Outside of the stelar tissue, no pericycle or endodermis is visible, and the phloem elements border directly on primary cortical cells. The cortex in *Psaronius* can be divided into three areas. The zone that borders on the phloem tissue consists of thin-walled cells that are slightly larger (90-120 μm in diameter) than the phloem elements; this zone often appears disrupted or otherwise poorly preserved (e.g., Figs. 35, 38). The middle zone of cortical cells contains slightly larger, more thick-walled parenchyma cells and scattered cells with dark contents (Fig. 35). These have been termed tannin-like cells (see, e.g., Morgan, 1959). This zone also contains the large (approximately 570 μm diameter) mucilage ducts. Some of these are scattered throughout the tissue, while others form rows on either side of each meristele (Fig. 35). The third cortical zone is a narrow band (0.3-1.0 mm) of sclerenchyma that marks the outer limit of the cauline system.

Preservation of the stem in the specimens of *Psaronius* sp. from Lewis Creek is very uneven, and usually only the xylem portion of the meristeles is preserved within any particular cross section. Although the sclerenchyma band that marks the outside of the stem is sometimes present, in many cases the tissues are too crushed to determine whether or not a particular vascular segment represented part of the cauline system or an attached petiole base. The specimens of *P. blicklei* and *P. chasei* from Berryville, however, are preserved relatively intact.
Although the phloem cells are only preserved in patches, the stems are generally not crushed or otherwise distorted. Axes of *Psaronius* sp. from Lewis Creek (without the root zone) measure approximately 2.7 x 11.2 cm and parts of the bound root zone are visible either attached to the outside of the stem segments or present within the same slab.

**Phloem anatomy** — When present, phloem completely surrounds each meristele and cellular continuity is present from the metaxylem to the cortex. Phloem cells are conspicuous in transverse section because their walls are slightly thicker than either the xylem sheath or the cortical parenchyma cells. This difference in wall thickness is especially apparent at very low magnifications where the phloem appears as two dark bands on either side of the central xylem trace (e.g., Figs. 35, 38). The phloem zone is generally about 0.2 mm wide on the adaxial side of the trace, but is more developed on the abaxial side and may extend up to 0.35 mm in that region. Although the cellular composition of both zones is the same, there are more cell layers present in the abaxial phloem. The central part of each band of phloem is occupied by a layer of large cells that range from 90 to 120 um in cross sectional diameter. In the abaxial phloem, the layer is a continuous arc (Figs. 37, 39, 42), but is more discontinuous adaxially (Figs. 36, 37, 42). These cells have an unusual appearance in longitudinal section. They are connected together in vertical series and have bluntly rounded or slightly oblique end walls (Fig. 37). Each elongate cell, however, contains cross walls at irregular intervals that serve to subdivide the large, tube-like cells (mean length = 595 um) into smaller units (mean length = 262 um). These cross walls are transverse or oblique (up to
45°) and appear to be thinner than the side walls (Fig. 40, 41). They can also be observed in transverse sections, since they appear almost translucent in peel preparations (Fig. 39). Lateral and end walls in a single series of these cells are differentially thickened, and this gives the cell wall a wavy appearance (Fig. 40, arrow). In addition, the lateral and end walls contain perforations that are comparable in size and shape to those present on the smaller sieve elements.

Surrounding these large cells are a number of narrower cells that are approximately 30 μm in diameter. In the adaxial phloem, these narrow cells form a single layer on either side of the central larger-diameter elements (Fig. 36). Abaxially, however, these layers are generally from three to four cells wide (Fig. 39). Whether these cells represent sieve elements or phloem parenchyma cannot be determined utilizing only transverse sections, since the range of diameters for these two cell types overlaps and their walls are of similar thickness. In longitudinal section, however, most of the larger cells (46 μm diameter) are relatively short (approximately 68 μm long) and possess smooth walls. These cells are arranged in vertical strands and no doubt represent phloem parenchyma (Figs. 43, 50). The sieve elements are generally smaller in diameter (approximately one-half the size of the parenchyma), and are more or less elongate with a mean length of 238 μm. Their end walls range from oblique (Fig. 43) to transverse or rounded (Fig. 51), although the majority are transverse (Figs. 45, 46, 47). The side and end walls of these cells exhibit a number of circular to oval sieve areas that are relatively crowded (e.g., Figs. 43, 45, 46, 47). Due to the large number of these cells and their relatively small
diameters, a single longitudinal section contains many sieve element walls (e.g., Fig. 43) and, therefore, these sieve areas appear to be very common. They are the same level of specialization on both side and end walls, indicating that these cells should appropriately be termed sieve cells. The sieve areas range from about $3 \times 7.5$ $\mu$m to $4.5 \times 9$ $\mu$m in diameter, and many are surrounded by an area of slightly darker wall material that resembles a border (Fig. 48). Some of the sieve areas show evidence of pores (Fig. 46, arrow), but the majority appear simply as clear areas in the sieve element wall (e.g., Figs. 45, 47). Due to the small size of the sieve areas and pores, electron microscopy was utilized to examine the structure of the sieve areas and confirm the presence of perforations. The sieve areas are abundant on the sieve element walls (Figs. 49, 51) and serve to distinguish these cells from phloem parenchyma cells, which are smooth-walled (Fig. 50). The sieve cell wall structure appears as a faint spiral pattern of fibrillar wall material (Figs. 48, 49, 51). The fibrils that border the sieve areas stand out somewhat from the remainder of the wall (Fig. 48), and this thicker band corresponds to the "border" observed with transmitted light. The wall of the sieve cells is generally degraded (e.g., Fig. 48), and there is little evidence of pores within the sieve areas (Fig. 48). The size of these pores and the sieve areas enclosing them is nearly identical to the size of primary pit fields (and plasmodesmata) in extant plants (Esau, 1969). In many vascular cryptogams, sieve areas and pores overlap primary pit fields in size (Lamoureux, 1961). In the absence of any cytological evidence, such as the presence or absence of certain organelles, or staining properties of the cytoplasm, it is
difficult to determine whether these cells represent sieve cells with sieve areas or parenchyma cells with primary pit fields. However, the absence of any other cells in the phloem tissue that are specialized for conduction indicates that these cells must have functioned as sieve elements, regardless of the size of perforations on their walls.

On the abaxial side of the xylem trace, there is a discontinuous arc of very small cells located between the xylem sheath and the metaphloem (Fig. 39). They are approximately 7.8 μm in diameter and are visible in longitudinal section (Fig. 40) as very narrow cells with evident sieve areas. These elements are distributed evenly along the abaxial xylem sheath and probably represent protophloem cells. Their position between the sheath parenchyma and the metaphloem elements, and their small size is consistent with the location and diameter of protophloem cells in extant marattialean ferns.
Figs. 35-39. Phloem of *Psaronius* sp. 35. Transverse section through part of a C-shaped trace. Note poorly preserved inner cortex and secretory canals in middle cortex. 7700 K top #7. X 9.5. 36. Transverse section of adaxial phloem zone illustrating discontinuous layer of large sieve cells surrounded by small sieve cells and phloem parenchyma. Parenchymatous sheath separates phloem zone from xylem. 7700 K top #7. X 70. 37. Longitudinal section through trace showing metaxylem tracheids, parenchymatous xylem sheath, adaxial and abaxial phloem. 7700 D*$_1$* side #58. X40. 38. Transverse section through trace. Tissues correspond to those in Fig. 37. 7700 K top #7. X 20. 39. Transverse section of abaxial phloem showing central layer of large sieve cells surrounded by small sieve cells and phloem parenchyma. Xylem sheath separates phloem and xylem. 7700 K top #7. X 70. Ab = abaxial phloem. Ad = adaxial phloem. IC = inner cortex. L = large sieve cells. MC = middle cortex. P = parenchymatous xylem sheath. X = metaxylem tracheids.
Figs. 40-44. Phloem of *Psaronius* sp. in longitudinal section. 40. Abaxial phloem showing vertical series of large sieve cells surrounded by smaller sieve cells. Arrows indicate wavy walls of sieve cells. 7700 D₁ side #75. X 70. 41. Same, adaxial phloem. 7700 D₁ side #75. X 70. 42. Oblique section through region of large sieve cells, illustrating arrangement in vertical series and greater numbers of these cells in abaxial phloem. 7700 D₁ side #20. X 27. 43. Small sieve cells with numerous sieve areas and smooth-walled phloem parenchyma. 7700 D₁ side #75. X 208. 44. Irregularly-shaped cells of the xylem sheath. 7700 D₁ side #20. X 150. A = phloem (axial) parenchyma. Ab = abaxial phloem. Ad = adaxial phloem. IC = inner cortex. L = large sieve cells. P = parenchymatous xylem sheath. X = metaxylem tracheids.
PLATE IX

Figs. 45-47. Phloem of Psaronius sp. 45. Sieve areas on sieve cell with both tapered and transverse end walls. 7700 D₁ side #75. X 520.
46. Detail of sieve areas with possible pores (dots within sieve area at arrow). 7700 D₁ side #75. X 1100. 47. Portion of a sieve cell with sieve areas that appear devoid of contents. 7700 D₁ side #75. X 520.
Figs. 48-51. Phloem of *Psaronius* sp. All 7700 A. 48. Detail of sieve areas with "borders" formed by prominent groups of fibrillar material. Lower sieve area shows some evidence of degraded pores. Stub #2. X 4000. 49. Transverse section of sieve cell showing spiral pattern of wall fibrils and intervening sieve areas. Stub #1. X 1500. 50. Smooth-walled phloem parenchyma cell. Stub #2. X 600. 51. Typical sieve cell with rounded end wall (below) and numerous sieve areas. Note also spiral pattern of wall fibrils. Stub #1. X 1500.
CHAPTER 5 - PHLOEM OF MEDULLOSA

The late Paleozoic seed fern Medullosa is well-known from coal ball localities in North America and Europe. The taxon was instituted by Cotta (1832) for structurally preserved stems of Permian age, and is characterized by a large number of vascular segments in transverse section ("steles" of earlier workers). Medullosa was originally thought to possess a polystelic vascular system, but the work of Basinger et al. (1974) on leaf trace production in these stems suggested rather that the cauline vasculature is fundamentally monostelic, as in other Carboniferous seed ferns.

Although phloem anatomy has not been used as extensively in systematic studies as wood anatomy, there are a few contributions that have applied anatomical (e.g., Chang, 1954; Zahur, 1959) and ultrastructural (e.g., Behnke, 1972; 1974; 1981) characteristics of phloem to systematic problems, both in angiosperms and gymnosperms. To date, this approach has not been used with fossil plants, perhaps because of the small number of fossil taxa with well-known phloem structure. The Carboniferous pteridosperms represent an excellent group in which to examine the phylogenetic and taxonomic importance of phloem anatomy for many reasons. Phloem in several different genera of seed ferns has already been examined and is sufficiently preserved to discern critical anatomical details. The secondary phloem of Heterangium
(Hall, 1952) and Callistophyton (Bertrand and Renault, 1886; Russin, 1981) has been described in detail from Upper Carboniferous specimens. In addition, phloem structure in Calamopitys, a stratigraphically older member of the seed ferns (Lower Visean), has been described from European material (Galtier and Hébant, 1973).

Stems of Medullosa were collected from various coal ball localities in North America ranging from Lower/Middle Pennsylvanian to Upper Pennsylvanian. These permineralizations contain well-preserved vascular tissues and provide an excellent opportunity to examine phloem anatomy in detail. Additionally, the quality of preservation is good enough to facilitate comparison with other Carboniferous pteridosperms as well as with extant gymnosperms.

**DESCRIPTION**

**General anatomy** — Phloem is present in stems of several species, including Medullosa anglica (from Lewis Creek, Kentucky), M. endocentrica (Berryville, Illinois), M. noei (Berryville and Sahara, Illinois) and Medullosa sp. (Steubenville, Ohio). Medullosa endocentrica represents the type material of this species, as described by Baxter (1949). The stems of M. noei are the largest specimens (up to 10 cm in diameter); M. anglica averages 4 x 14 cm in diameter; M. endocentrica specimens are approximately 1.0 cm in diameter, and the species of Medullosa from the Steubenville locality has the smallest stems (approximately 1.8 x 0.7 cm in diameter). The axes contain a variable number of vascular segments, each consisting of a central region containing primary xylem and parenchyma, surrounded by a broad zone of
secondary xylem. The wood is the manoxylic type, with rays present about every 2-4 rows of tracheids (e.g., Fig. 52). Secondary tracheids have scalariform pitting and their cross-sectional diameter decreases gradually from the first-formed cells next to the primary xylem (about 260 \( \mu \text{m} \times 210 \mu \text{m} \)) to the most recently formed ones near the cambium (200 \( \mu \text{m} \times 177 \mu \text{m} \)). The vascular segments are embedded in a parenchymatous ground tissue that contains scattered secretory cells (Fig. 52).

In some specimens, a vascular cambium of thin-walled cells is present (Fig. 53). This zone varies from one to three cells in thickness, but is more often two cells wide. A transverse section through the cambial region shows a rapid decrease in cell diameter from the large, presumably mature tracheids on one side to the first recognizable phloem fibers and sieve elements (approximately 65 \( \mu \text{m} \) in diameter) on the other (Fig. 53).

**Phloem anatomy-General** - Preservation of the phloem is variable, but it is generally more complete on the inner face of the vascular segments. Secondary phloem surrounds each of the individual vascular segments and consists of alternating, tangential bands of fibers, sieve elements and parenchyma, separated by phloem rays (Figs. 57, 61, 66). These bands are quite distinctive even at lower magnifications (e.g., Fig. 55), and the pattern they form can be followed from the vascular cambium to the periphery of the secondary tissue, a distance of up to 45 cell layers (Fig. 56).

The width of the zone of secondary phloem is variable and does not appear to be correlated with the size of the particular vascular segment. Additionally, there seems to be no relationship between the
number of xylem and phloem cells present within a single radial row. It is difficult to quantify this aspect of secondary development in Medullosa, since only those specimens in which the xylem and phloem are preserved in their entirety can be considered. As an example, however, development of secondary phloem as compared to xylem within the same radial row includes the following values:

<table>
<thead>
<tr>
<th>Phloem</th>
<th>Xylem</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Cells</td>
<td>Width of Zone</td>
</tr>
<tr>
<td>46</td>
<td>1.85 mm</td>
</tr>
<tr>
<td>47</td>
<td>2.55 mm</td>
</tr>
<tr>
<td>48</td>
<td>2.75 mm</td>
</tr>
<tr>
<td>50</td>
<td>2.10 mm</td>
</tr>
<tr>
<td>66</td>
<td>3.70 mm</td>
</tr>
</tbody>
</table>

All of these values are taken from a single stem. They show no clear relationship to one another, but are affected by such features as trace departure and differential growth rates. For example, the radial rows that contain 46 and 50 phloem cells (18 and 16 xylem cells, respectively) were in a region of the stem that had recently produced a leaf trace and the band of vascular tissue was considerably narrower than in other regions of the same section. The row with 66 phloem and 58 xylem cells included an area adjacent to the vascular cambium in which a number of small diameter derivatives were apparently produced within a relatively short distance (Fig. 54). Similar cambial activity in some extant plants has been described as a response to wounding or other kinds of trauma (see, e.g., Zimmermann and Brown, 1980). On the other hand, the rows with 47 and 48 phloem cells (34 and 48 xylem cells)
appeared normal in all respects. Based on specimens such as these, the differential production of xylem cells versus phloem cells does not appear to have taxonomic importance in Medullosa. By analogy with extant plants, the activity of the cambium may be more accurately related to such factors as environment, age of the plant, or position within the stem.

Axial parenchyma - The phloem parenchyma appears in transverse section as tangential rows of small-diametered cells bordering a band of fibers on the inside and sieve elements on the outside (Figs. 57, 61). Each row of parenchyma extends from one ray to the next and may include up to twelve cells tangentially, and one to two cells (occasionally three) radially (Fig. 66). Generally, the parenchyma bands are less distorted in the outer layers of the secondary phloem than the sieve elements (e.g., Fig. 65), and in the Steubenville stems, they are often the only cells preserved (Fig. 58). These cells are oblong, approximately 34 x 35 um in diameter and vary extensively in length, ranging from 96 um to 385 um (mean = 206 um) (Fig. 60). They are often present in vertical strands (Figs. 60, 68). A general increase in the diameter of the axial parenchyma cells is present from the cambium outward for approximately 10-12 cell layers (e.g., Fig. 65). Beyond this point, the mean diameter of the axial parenchyma cells decreases as they are gradually crushed (Fig. 55) (Table 1). As Table 1 illustrates, the greatest change in diameter of these cells is due to an increase in the radial dimension. Axial parenchyma cells are easily distinguished from the sieve elements in longitudinal section by their length (approximately ten times shorter than sieve elements), and by their
Table 1

Diameter of Axial Parenchyma Cells in Medullosa

<table>
<thead>
<tr>
<th>Location</th>
<th>Radial Diameter</th>
<th>Tangential Diameter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Next to cambium:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean (n=30)</td>
<td>33.85 μm</td>
<td>34.49 μm</td>
</tr>
<tr>
<td>Range</td>
<td>18.84-55.46</td>
<td>19.17-60.02</td>
</tr>
<tr>
<td>10-12 rows from cambium:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean (n=30)</td>
<td>56.23 μm</td>
<td>36.28 μm</td>
</tr>
<tr>
<td>Range</td>
<td>27.74-87-48</td>
<td>18.22-66.25</td>
</tr>
<tr>
<td>Outer edge of phloem:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean (n=21)</td>
<td>30.95 μm</td>
<td>34.48 μm</td>
</tr>
<tr>
<td>Range</td>
<td>16.25-52.23</td>
<td>19.79-47.80</td>
</tr>
</tbody>
</table>

nearly horizontal end walls (e.g., Fig. 60). However, it is often difficult to differentiate these two cell types in transverse section. The range of their diameters overlaps, although the size of the parenchyma cells partially depends upon the number of cells in each tangential band (i.e., how many anticlinal divisions have taken place in the initials), as well as upon their position in relation to the cambium (Table 1). In undistorted sections, axial parenchyma can be located by its position just outside a band of phloem fibers (Figs. 57, 61).

Phloem fibers - At lower magnifications, the thickened walls of the phloem fibers are conspicuous in peel preparations and can be discerned, even in partially crushed sections, out to the periphery of the secondary tissue (Figs. 55, 56), since they are generally the last cells to be crushed in the older phloem tissue. Histologically, the walls of most of the fibers appear poorly preserved (e.g., Figs. 57, 61), although the cells can still be identified by the presence of the distinctive, slit-like lumen (Fig. 57, at arrow). Each tangential band of fibers may be one to two cells wide radially and two to three cells tangentially, and is bordered on the inside by a band sieve elements and
on the outside by axial parenchyma cells (Figs. 61, 66). Fibers are generally rectangular in transverse section, measuring approximately 90 μm (tangential) x 35 μm. The range of tangential diameters is quite large (71-151 μm), depending upon whether there are two, three or four fibers present in each band, and this depends, as is the case in the parenchyma strands, on the number of anticlinal divisions in the initials or their derivatives. Fibers are extremely long and pass out of the plane of section in most specimens. The few cells that could be measured extend up to 4.2 mm.

From the cambium outward, there is an increase in the radial diameter of the fibers (from 33 to 55 μm) and a slight increase in tangential diameter (from 22 to 28 μm). These changes are accompanied by a large increase in the thickness of the cell wall (from 16 to 26 μm). A group of fibers is present at the outermost edge of the secondary phloem in continuity with the radial rows of conducting elements (Figs. 59, 72). The individual radial rows of fibers are often surrounded by a ring of meristematic cells (Figs. 59, 64), and continued division can eventually isolate the fibers from the rest of the secondary phloem (Fig. 64). The cells produced by this meristematic activity are histologically similar to those previously described in medullosan stems as an internal periderm (see, e.g., Delevoryas, 1955).

**Phloem rays** - Vascular rays are continuous from the secondary xylem into the secondary phloem, and are regular in composition and size from specimen to specimen. The majority are five cells wide, although they range from three to nine cells in width. In transverse section, each ray consists of three central rows of elongated cells (tangential
diameter 45 um) with a row of slightly larger cells (tangential diameter 67 um) forming a border on both sides (Figs. 62, 63). Many of the ray cells contain a dark brown material that may completely fill the lumen of the cell (Figs. 61, 63, 65). Farther away from the cambium, the tangential width of the rays may increase by as much as 100 um (Figs. 62, 63). Although some cell divisions have been observed, this increase is due, for the most part, to cell enlargement or stretching. Typical ray cells are approximately 88 (radial diameter) x 46 um close to the cambium and 85 x 136 um at the periphery of the phloem; while the tangential diameter increases considerably, the radial diameter actually decreases slightly. A few uniseriate rays are present that extend up to 10 cells in height, but the majority of the rays are multiseriate (usually 4-7 cells wide) and several hundred cells high (Fig. 67).

Sieve elements - In transverse section, the sieve elements of the secondary phloem are bordered by a band of parenchyma cells internally and fibers externally (Fig. 66). Each tangential band may contain from two to four sieve elements that are generally larger in diameter than the axial parenchyma (mean = 66 um) with slightly thinner walls. Sieve elements are elongate, ranging from 1.6-4.2 mm (mean = 3.1 mm). End walls taper gradually, and are difficult to distinguish from lateral walls. These oblique end walls can sometimes be observed in transverse section as thin, diagonal lines across the lumen of some cells. Crowded, oval sieve areas occur on the radial and end walls of the sieve elements (e.g., Figs. 69, 71, 75). The degree of specialization of the sieve areas is similar on both side and end walls, indicating that these cells represent sieve cells. Sieve areas measure approximately 27.3 um
by 7.8 um with numerous pores and are variably preserved. In stems from
the Steubenville locality, for example, sieve cells appear to be
partially degraded (e.g., Fig. 70) and sieve areas appear as
aggregations of dark brown spots on the cell walls (Fig. 71). In the
specimens from other localities, sieve areas generally appear as dark
ovals with darker spots on them (e.g., Figs. 73, 75), although a few
specimens exhibit groups of clear ovals on the sieve cell walls (Fig.
68). The dark spots are interpreted as the remains of callose plugs on
the sieve pores, while the clearer sieve areas are assumed to lack
callose. This identification is based on the position and shape of the
dark-colored material and not on any chemical tests for callose.

With the scanning electron microscope, sieve areas were readily
apparent on the sieve element walls as elongate ovals that appeared to
be slightly elevated above the remainder of the cell wall (Figs. 74, 78,
79). Evenly distributed within the oval sieve areas are a number of
"knob"-like structures that correspond in position to sieve pores.
These "knobs" are interpreted as callose plugs adhering to the cell wall
in the region of the individual sieve pores. Several of these plugs
possess a hollow center, thus forming a ring of callose that surrounds
the inside of the pore and projects out from the cell wall slightly
(Fig. 77). In a few instances, the plug material was dislodged during
the maceration process and the sieve pore is clearly visible beneath
(Fig. 76). These pores measure approximately 0.1-0.2 um in diameter and
there are usually approximately 40-50 pores per sieve area.

Changes in the outer phloem - The secondary phloem of Medullosoa
shows several histological changes from the region of the most recently
formed phloem cells next to the cambium out to the older elements at the periphery of the stele. In most specimens, the sieve elements, axial parenchyma cells and phloem fibers appear to be fully differentiated immediately outside of the narrow cambial zone (i.e., 1-2 cells from mature tracheids). These cells are assumed to be mature when they have attained their full diameter.

One of the first histological changes associated with the transition from inner to outer phloem is an increase in the thickness of the cell walls in the phloem fibers, which results in a 60% increase in the overall diameter of the cell (Figs. 59, 64). As the walls become thicker, they also appear less dense, probably indicating that the enlargement of the fiber walls is a process of passive hydration or swelling. At the same time, the cells within the bands of axial parenchyma undergo approximately a 60% increase in radial diameter (Table 1, 10-12 rows from cambium). Although many sieve cells in extant plants deposit definitive callose on the sieve areas as they become non-functional, this stage was not observed in Medullosa. The sieve cells are generally the first cells to collapse in the outer phloem and the tangential bands of parenchyma can be seen some distance beyond the area in which sieve cells are first crushed (Fig. 65). The early collapse of the sieve elements is no doubt related to the relatively thin walls of the sieve cells, the expansion of the other cells in the secondary phloem, and the dilation of the phloem rays toward the periphery of the stele. Eventually, the axial parenchyma cells are also crushed and the secondary phloem tissue is then delimited only by a row of fibers. Some specimens clearly show the presence of crushed wall
material between the fiber cells, while this cannot be resolved in other instances. Finally, a discontinuous phellogen (internal periderm of earlier authors [e.g., Delevoryas, 1955]) is often present in the vicinity of these outermost phloem fibers (e.g., Figs. 59, 64, 72).

To the outside of the peripheral rows of fibers are a few cells which are extremely crushed and do not appear to be arranged in radial rows (Figs. 64, 72). Some of these cells exhibit thickened walls and could represent the remains of primary phloem fibers or sieve cells. Although they are in the correct position for primary tissue, the cells are too poorly preserved for positive identification.
Figs. 52-56. Phloem of *Medullosa* in transverse section. 52. Section through part of a vascular segment, with secondary xylem, secondary phloem and cortex containing large secretory canals (arrows). Note tissue continuity from xylem to cortex. 831 $B_1$ bot #2$\gamma$. X 13. 53. Detail of vascular cambium. 831 $A_1$ #4$\beta$. X 130. 54. Section through region of proliferated cambial cells, illustrating presumed "wound" response, i.e., production of a large number of smaller cells. 831 $B_1$ bot #18$\beta$. X 42. 55. Secondary phloem with repeating tangential bands of phloem cells. Note conspicuous rows of phloem fibers, which appear as slightly darker cells. 831 $B_1$ bot #6$\beta$. X 36. 56. Specimen containing largest phloem zone (4.0-4.5 mm wide) with cells intact from vascular cambium out to peripheral phloem fibers. 831 A #4$\gamma$. X 14. C = cortex. F = phloem fibers. P = secondary phloem. V = vascular cambium. X = secondary xylem.
PLATE XII

Figs. 57-61. Phloem of Medullosa.  57. Transverse section of secondary phloem close to cambium, with rays above and below, phloem parenchyma, sieve cells and fibers center. Unstained peel preparation—compare with Fig. 66. 831 B₁ bot #87. X 110. 58. Transverse section through secondary phloem with xylem at far left. Phloem is poorly preserved, but tangential bands of axial parenchyma are intact. 1379 F bot #3. X 50. 59. Peripheral secondary phloem in transverse section. Note groups of fibers surrounded by meristematic tissue. See also Fig. 64. 831 B₁ bot #2β. X 40. 60. Longitudinal section through cambial zone, showing secondary tracheids with circular bordered pits (left) and secondary phloem (right). 831 B₁ side #24α. X 110. 61. Possible formation of ray initials from fusiform initials (arrow). Repeating tangential bands of sieve cells, fibers and parenchyma also evident. 861 D bot #6α. X 110.  A = axial parenchyma.  F = phloem fibers.  R = phloem rays.  S = sieve cells.  V = vascular cambium.
Figs. 62-66. Phloem of Medullosa in transverse section. 62. Poorly preserved specimen illustrating thin-walled ray cells and dilation of phloem rays. 861 D bot #31α. X 65. 63. Specimen with dilated phloem rays. Note dark contents of ray cells and absence of other phloem cells. 1379 F bot #3. X 55. 64. Detail of group of fibers in peripheral secondary phloem (see also Fig. 59) illustrating thin-walled, meristematic cells (so-called "internal periderm") surrounding fibers and possible primary phloem (arrow). 831 B₁ bot #2β. X 110. 65. Transition zone showing inner and outer phloem, enlarged parenchyma cells (arrows) and collapsed sieve cells. 831 B₁ bot #18α. X 70. 66. Secondary phloem stained with malachite green to highlight bands of fibers. Also note relatively large, thin-walled sieve cells (S). 831 B₁ bot #6β. X 176. A = axial parenchyma. F = phloem fibers. R = phloem rays. S = sieve cells.
Figs. 67-73. Phloem of Medullosa. 67. Tangential section of phloem rays (left and right) and sieve cells (center) with tapered end walls. Arrows mark ends of sieve cells. Sieve areas are visible in side view as thin areas in the sieve cell walls. 831 A₁ side #3. X 50. 68. Longitudinal section of elongate sieve cell with numerous sieve areas and strands of axial parenchyma. 831 B₁ side #16. X 140. 69. Radial wall of sieve cell with relatively uncrowded, oval sieve areas. 831 B₁ side #16. X 350. 70. Radial section showing two sieve cells and degraded aspect of sieve areas (center). Ray cells to right and left filled with dark contents. 1379 F₁ a side #26. X 176. 71. Sieve areas with sieve pores are visible as dark dots within the oval sieve areas (arrows). 1379 F₁ a side #16. X 440. 72. Transverse section through periphery of secondary phloem. Two groups of fibers visible at the left in continuity with crushed cells (dark line, arrow) representing possible primary phloem. 831 A #4⅓. X 50. 73. Several sieve areas that are interpreted as being covered by callose deposits. 831 A₁ side #3. X 240. A = axial parenchyma. F = phloem fibers. R = phloem rays.
Figs. 74-79. Phloem of *Medullosa*. 74. Radial section through secondary xylem (left) and phloem. Sieve cell with numerous, oval sieve areas visible in center. 831 B₁. X 200. 75. Detail of sieve areas in upper part of Fig. 69. 831 B₁ side #1a. X 800. 76. Possible callose plugs within sieve area. Pores are visible beneath some of the plugs that have been displaced (arrows). 831 B₁. X 10,000. 77. Sieve area with several probable callose masses that appear as rings surrounding a central cavity (arrows). 831 B₁. X 5000. 78-79. Stereo pair of sieve cell showing elongate sieve areas on radial wall. Sieve pores generally covered by callose, but arrow indicates some open pores. 831 B₁. X 850.
CHAPTER 6 - PHLOEM OF CALLISTOPHYTON

Callistophyton (Delevoryas and Morgan, 1954b) is probably the most completely known Paleozoic seed fern (see, e.g., Rothwell, 1975; 1980). Recently placed in their own order (Rothwell, 1981), the Callistophytales have many vegetative and reproductive features which set them apart from both the medullosan and lyginopterid pteridosperms. Phloem has been observed in a number of specimens of Callistophyton (e.g., Bertrand and Renault, 1886), including the type material examined by Delevoryas and Morgan (1954b). In Rothwell's detailed study of the vegetative anatomy and morphology of Callistophyton (Rothwell, 1975), certain features of the secondary phloem were noted, including cellular composition of the tissue and the presence of primary phloem in young stems. A number of authors, e.g., Bertrand and Renault (1886), Bertrand (1889), Delevoryas and Morgan (1954b), and Rothwell (1975) have illustrated sieve elements with well-preserved sieve areas on their radial walls.

To date, the most extensive investigation of secondary phloem anatomy in Callistophyton was the work of Russin (1981). He examined secondary phloem in both stems and roots and attempted to quantify some of the anatomical features, as well as making a comparison between the phloem of roots and stems. For example, Russin looked at the relative production of secondary xylem and phloem by the vascular cambium and
presented data to support a fairly equal production of these two tissue systems (in number of cells per radial row). He was able to explain the different appearances of sieve areas and sieve pores based on the extent of presumed callose deposition, and illustrated a sequence of proposed developmental changes in the ontogeny of sieve elements.

In this paper, Russin provided an excellent comparison of the anatomy of Callistophyton with other gymnosperms, both fossil and living. However, he was not able to make a detailed comparison with other Carboniferous pteridosperms, since data were only available for stems of Heterangium (Hall, 1952). Recent work by Rothwell suggests that the Callistophytales may represent a group with some features that are intermediate between the cordaite- or conifer-like plants on one hand, and the other Paleozoic seed ferns on the other. In light of this work, an examination of the structure, ontogeny and phylogenetic significance of Callistophyton phloem is needed at this time, especially from a systematic viewpoint. A detailed comparison of phloem anatomy in the Callistophytales and the Medullosales may provide some additional data that can be used in evaluating the systematic position of these Carboniferous plants.

DESCRIPTION

General anatomy - All specimens represent stems of Callistophyton boyssetii and are of Middle Pennsylvanian age. They range from about 6.0 cm. to 14.2 cm. in diameter, and exhibit the anatomical features typical of the genus, including a parenchymatous pith containing scattered cells with dark contents, abundant secondary xylem, and a
primary cortex with secretory cavities (Figs. 80, 81). In well-preserved specimens, phloem tissue is continuous with the vascular cambium on the inside and the cortex (or periderm) tissue on the outside. The cambial zone varies in width, but is generally three to four cells wide. Initials appear rectangular in cross section and can be distinguished from mature phloem by their relatively small diameter (approximately 49 um), especially radial diameter (26 um) and their thin walls (Fig. 83).

Phloem anatomy-General - The width of the secondary phloem zone, as measured in relatively uncrushed sections, ranges from 0.95 to 2.0 mm. The tissue consists of an axial system of alternating, tangential bands of sieve elements and phloem parenchyma with scattered secretory cells (Figs. 85, 94). Phloem rays are simple and continuous with the secondary xylem rays. In some younger stems, the tissue is bordered on the outside by primary cortical cells (e.g., Figs. 81, 82, 85). Groups of small diameter, slightly thick-walled cells are present at the outer edge of the secondary phloem in a few specimens (Figs. 82, 85) and these may represent primary phloem strands. Each strand consists of cells that are more thin-walled and larger (sieve elements?), mixed with smaller, thick-walled cells (phloem parenchyma?) (Fig. 82). Additionally, a few strands are closely associated with cells containing dark contents, i.e., so-called secretory cells (Fig. 82). These presumed primary phloem bundles are evenly distributed around the circumference of the axis (Fig. 85). In longitudinal section (e.g., Fig. 92), the cells are generally too crushed to discern sieve areas or pores.
In most of the older stems, a phellogen is present in the outer secondary phloem (e.g., Figs. 84, 95), and this serves to disrupt the outer phloem cells and prevent an accurate measurement of the total width of the secondary phloem zone. Although Russin (1981) found an approximately equal distribution of secondary xylem and phloem in his *Callistophyton* specimens, this relationship was not apparent in the present material. With just one exception (see Table 2), the phloem zone was always narrower than the secondary xylem, but generally contained many more cells per radial row than did the corresponding row of tracheids (Table 2). In each case, both the xylem and phloem derivatives of a single fusiform initial were measured. Assuming that some secondary phloem would be lost or badly disrupted during the development of the periderm, those specimens with no phellogen present in the phloem should provide an accurate estimate of the relative proportions of xylem and phloem. Even these specimens clearly indicate that the production of xylem and phloem by the vascular cambium is unequal, although a few specimens do show an approximate 1/2 ratio of xylem to phloem in number of cells produced (Table 2, 24:41, 24:40). Additionally, the width of the xylem and phloem zones does not appear to be directly correlated with the overall diameter of the axis, although generally the larger axes do possess slightly more secondary tissues than the smaller axes (Table 2). The relative proportions of secondary tissues produced may have been affected by age or environmental factors as they are in living plants (see, e.g., Artschwager, 1950), and therefore would vary from plant to plant. In addition, the distribution of the tissues may also vary depending upon
<table>
<thead>
<tr>
<th>Stem Diam. (mm)</th>
<th>C.B. #</th>
<th>Width in mm</th>
<th># Cells/Radial Row</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Xylem</td>
<td>Phloem</td>
</tr>
<tr>
<td>7.4 x 13.1</td>
<td>303 B top</td>
<td>2.0</td>
<td>1.25(1.5)</td>
</tr>
<tr>
<td>7.5 x 13.8</td>
<td>303 B top</td>
<td>2.0</td>
<td>1.30(1.7)</td>
</tr>
<tr>
<td>7.5 x 13.8</td>
<td>303 B top</td>
<td>1.8</td>
<td>1.05</td>
</tr>
<tr>
<td>7.0 x 9.5</td>
<td>979 F top</td>
<td>1.75</td>
<td>1.05(1.18)</td>
</tr>
<tr>
<td>7.2 x 13.8</td>
<td>303 A</td>
<td>2.01</td>
<td>1.25</td>
</tr>
<tr>
<td>7.2 x 13.8</td>
<td>303 A</td>
<td>2.01</td>
<td>1.25</td>
</tr>
<tr>
<td>7.0 x 12.0</td>
<td>979 D bot</td>
<td>1.95</td>
<td>1.25 a</td>
</tr>
<tr>
<td>7.0 x 10.0</td>
<td>979 E bot</td>
<td>1.75</td>
<td>0.95(1.25 b)</td>
</tr>
<tr>
<td>7.0 x 10.0</td>
<td>979 E bot</td>
<td>1.75</td>
<td>0.95</td>
</tr>
<tr>
<td>6.0 x 9.2</td>
<td>979 F bot</td>
<td>1.70</td>
<td>1.00(1.25 b)</td>
</tr>
<tr>
<td>6.0 x 9.2</td>
<td>979 F bot</td>
<td>1.70</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Numbers listed first represent inner phloem. Numbers in parentheses are the inner plus the outer phloem. Inner phloem includes all the cells from the cambium out to either the primary cortex or the area of extensive wall thickening and associated histological changes (the outer phloem). The width of the outer phloem zone is difficult to measure accurately due to these histological changes which disrupt the position of the cells within the secondary phloem. (See text for complete explanation)

a = no histological changes in the peripheral secondary phloem were present in this specimen (see Changes in outer phloem). The secondary phloem could be measured out to the primary cortex.

b = although changes in the peripheral secondary phloem cells were present, the cells were not totally disrupted, and the width of the zone of phloem could be measured out to the primary cortex.
position in the stem and proximity to leaf traces or branches. It is especially difficult to quantify this aspect of development in fossil plants, since the specimens may have been affected by crushing and distortion prior to fossilization. In *Callistophyton*, the shape and size of cells can be further distorted by histological changes in the older phloem and by the production of periderm tissues.

**Secretory cells** - In the present material, secretory or resinous cells were observed in the axial system of the stems, but not in the rays. Russin (1981) described secretory cavities in both the axial and ray systems, but noted that they were more numerous and conspicuous in the rays of *C. poroxyloides* than in *C. boysetii*. Some ray cells with dark contents were occasionally noted, but these were generally associated with the older phloem (e.g., Figs. 86, 90, 95) and were histologically different from the secretory cells present elsewhere in the phloem. The resinous cells in the inner portion of the phloem appear similar to those present in the pith and cortex. They are noticeable within a few cells of the cambial zone (Figs. 83, 85) and are generally randomly scattered throughout the secondary phloem, although in a few specimens (Fig. 85), they almost appear to be oriented in tangential bands. These cells may replace a single sieve cell, one or two phloem parenchyma cells, or an entire tangential band of parenchyma (up to four cells) (Rothwell, 1975). In transverse section, they may be rectangular, like the adjacent sieve cells, but in many specimens they have undergone some enlargement and are more spherical (Fig. 85). In longitudinal section, these resinous cells sometimes appear elongate (Figs. 93, 95), but in other cases, cross
walls are clearly evident (Figs. 96, 98), a feature that was also noted by Rothwell (1975). No epithelial layer is present.

**Axial parenchyma** - The bands of phloem parenchyma range from two to four cells wide tangentially, but are only rarely more than one cell thick radially. The alternating pattern of sieve cells and phloem parenchyma is very regular, and only occasionally is the pattern disrupted by the loss of a row of parenchyma cells. Immediately adjacent to the cambium, the phloem parenchyma cells are present in a relatively undistorted state, but within a distance of five or six cells from the cambium, the central cells in each band become flattened (e.g., Fig. 83). This crushing may be due to a slight increase in diameter of the adjacent sieve cells. Closer to the periphery of the secondary tissue, the axial parenchyma cells often become almost spherical in transverse section (Fig. 90) (see Changes in outer phloem). The mean diameter of parenchyma cells close to the cambium is 21 x 25 µm, while those at the periphery are about 19 x 24 µm in diameter. In longitudinal section, the cells are rectangular (Figs. 93, 98) and range from 104 to 215 µm in length (mean = 164 µm).

**Vascular rays** - Phloem rays are continuous with the xylem rays and generally two cells wide, although they may range up to three cells wide. From the cambium outward, the rays undergo considerable tangential expansion due almost entirely to cell enlargement (Russin, 1981). For example, the diameter of the xylem rays at the level of the vascular cambium is approximately 41 µm, while the phloem rays just a few cells away have already expanded to about 68 µm in width. Towards the periphery of the functional phloem, the rays expand considerably.
and can extend up to 353 \( \mu \text{m} \) wide. Although occasional cell divisions can be observed, the major part of this expansion is caused by tangential stretching of the ray cells (Figs. 82, 87). A typical ray cell changes from a mean tangential diameter of 26 \( \mu \text{m} \) near the cambium to about 82 \( \mu \text{m} \) at the periphery of the stem and at the same time, there is a decrease in the radial diameter of the cells. As Russin (1981) noted, there are some rays observed in transverse section that do not extend all the way to the cambium and he suggested that these may have been formed from declining fusiform initials. Occasional production of rays of this type would account for the broad range of ray sizes that can be seen in tangential sections (Russin, 1981). Small, uniseriate and biseriate rays are present that may be up to seven cells high along with biseriate and triseriate rays that are more than 200 cells in height (Fig. 89).

Sieve cells - The sieve elements in *Callistophyton* are elongate with very tapered end walls (Fig. 89). Sieve areas are similar on both end and side walls, indicating that these cells should be classified as sieve cells. In transverse section, they vary from slightly flattened tangentially to almost circular in outline, and range from 28 x 38 \( \mu \text{m} \) to 80 x 99 \( \mu \text{m} \) in diameter (Fig. 94). Although there is a change in cell diameter from the xylem across the vascular cambium to the phloem, the difference between the mean diameter of the tracheids next to the cambium (62 \( \mu \text{m} \)) and the sieve cells (53 x 73 \( \mu \text{m} \)) is not very large (see, e.g., Fig. 80). Sieve cells are extremely long and have been measured up to 1.7 mm with no evidence of an end wall. Russin (1981) found cells as long as 7.6 mm in his material. Numerous, crowded sieve
areas are present on radial and end walls. These are usually oval (e.g., Figs. 97, 100), but can be quite variable. In some cases, the individual sieve areas are truncated and appear almost rectangular (Figs. 101, 102), while in other instances, they are elongate and tapered (Figs. 97, 100). Russin (1981) correlated the various appearances of sieve areas in *Callistophyton* with different amounts of presumed callose deposition, and these stages are reflected in the present material. Compare Fig. 99 with relatively light colored sieve areas (= presumably little callose deposition) to those in Fig. 100 (= pores lined with callose). The very dark-colored sieve areas (e.g., Figs. 101, 102) have been interpreted as definitive callose deposits (Russin, 1981).

**Changes in the outer phloem** - Although Rothwell (1975) noted some histological changes toward the periphery of the zone of secondary phloem in his *Callistophyton* specimens, a detailed examination of these changes has not been completed. The present material clearly illustrates a number of histological differences between the inner and outer phloem. The inner phloem is considered to include those cells from the most recently formed phloem adjacent to the cambium out to the zone of thick-walled phloem elements (Figs. 80, 90, 91). The outer phloem consists of these more peripheral, thick-walled cells. The use of these two terms is purely arbitrary and does not relate to the terms "inner bark" and "outer bark" used in some studies dealing with anatomy of extant plants, since these designations apply not only to structural features, but often to functional changes as well.
One of the first changes that can be recognized in the older cells of the inner phloem is an enlargement in the tangential diameter of the ray cells (Fig. 87, 91). This increase does not result in much disruption of the sieve cells, however, probably due to a concomitant increase in the circumference of the stem. For the most part, the ray cells seem to be passively stretched, since their tangential diameter increases from the cambium outward, while the radial diameter decreases from 65 um near the cambium to 45 um at the periphery (both means, no. = 50). The ray cells often appear at this stage to have dark-colored cell contents (e.g., Fig. 87). At about the same distance from the cambium that the rays begin to increase in size, the phloem parenchyma cells also increase in diameter until they appear circular in transverse section (Figs. 81, 90). This expansion sometimes results in a slight flattening of the adjacent sieve cells which become more rectangular in transverse section. Within about 6-8 rows from the beginning of these changes in cell size, there is a rapid change (within two or three cell layers) from relatively normal-looking phloem to extremely altered, obviously non-functional phloem. The sieve cells undergo a change in wall thickness and expand somewhat in tangential diameter (from 73 um to 81 um), becoming rounder (Fig. 90). At about the same level, the axial parenchyma and ray cells also develop very thickened walls, so that they are generally not crushed by the enlarging sieve cells (Figs. 90, 91). All cells contain dark contents at this stage. The result of the general increase in wall thickness and diameter of the secondary phloem is that some cells are crushed (e.g., Fig. 88) and the radial rows of phloem cells become extremely
disrupted. In many instances, it is impossible to trace a single row of conducting cells or a phloem ray out to the cortical cells. These cells in the outer phloem with thick walls and dark contents were noted by Bertrand and Renault (1886) and interpreted by Rothwell (1975) as sclereids. In longitudinal section, the thickening of ray cell walls is especially conspicuous (Figs. 86, 95) and the presence of dark contents within the axial cells is also apparent (Fig. 88).

Periderm - A discontinuous cork cambium differentiates in the outer cortex and begins to produce phellem at a stage when the secondary vascular tissues are well-developed (e.g., Fig. 80). As the outer cortex and epidermis are sloughed off, successive phellogenens are formed, first in the primary cortex (e.g., Figs. 81, 92) and later at the outer edge of the secondary phloem (Fig. 95). As a result, in older stems (e.g., Fig. 84), the extraxylary tissues consist of inner, presumably functional phloem; outer, presumably non-functional phloem; and periderm.
PLATE XVI

Figs. 80-85. Phloem of *Callistophyton*. 80. Transverse section of a portion of the stem. Xylem below, phloem, cortex and periderm above. Note dark secretory cells (arrows) within secondary phloem. 979 F top #2. X 40. 81. Detail of peripheral phloem with primary cortical cells above. Although histological changes are present in the outer phloem, radial rows (arrows) can still be followed out to cortex. 979 E₁ bot #15. X 60. 82. Transverse section through peripheral secondary phloem. Arrow indicates presumed primary phloem bundle. 979 E₁ bot #15. X 130. 83. Transverse section through thin-walled cells of cambial zone. 303 A #22. X 160. 84. Transverse section illustrating disruption of secondary phloem by formation of periderm. Outer phloem left, phellum right. Arrows indicate approximate position of phellogen. 303 A #22. X 70. 85. Transverse section through stem showing continuity of tissue from secondary xylem to cortex. Arrows indicate presumed bundles of primary phloem. 979 D₁ bot #1. X 55. C = cortex. IP = inner phloem. OP = outer phloem. P = secondary phloem. R = phloem ray. S = sieve cell. V = vascular cambium. X = secondary xylem.
Figs. 86-90. Phloem of Callistophyton. 86. Radial section showing thickening of ray cells (center) and conducting elements (arrow) in transition from inner to outer phloem. 979 F₁ side #11. X 55. 87. Transverse section through periphery of outer phloem zone illustrating enlarged ray cells with dark-colored contents. 303 A #22. X 110. 88. Tangential section illustrating crushing of sieve cells (arrows) at periphery of secondary phloem. Arrow denotes sieve areas in intact sieve cell. 979 E₁ side #1. X 130. 89. Tangential section illustrating large and small rays. Note sieve areas on sieve cells (arrowheads). 979 E₁ side #6. X 140. 90. Transverse section illustrating histological changes during transition from inner to outer phloem. Thickening of cell walls in sieve cells and axial parenchyma usually precedes occlusion of cell lumen seen in the outermost phloem (center). 979 F top #2. X 140. A = axial parenchyma. C = cortex. IP = inner phloem. OP = outer phloem. R = phloem ray. S = sieve cell.
PLATE XVIII

Figs. 91-95. Phloem of Callistophyton. 91. Transverse section through outer phloem zone showing dark-colored contents in phloem cells and disruption of radial rows. 979 F top #2. X 140. 92. Longitudinal section through outermost secondary phloem, cortex and periderm. Arrow indicates possible primary phloem cells. 979 F₁ side #11. X 120. 93. Radial section showing phloem ray, secretory cells (dark cells, right), sieve cells and strand of axial parenchyma. 979 F₁ side #11. X 160. 94. Transverse section illustrating alternating pattern of sieve cells and axial parenchyma, separated by phloem rays. 979 F top #3. X 150. 95. Longitudinal section through outermost secondary phloem (left) and periderm (right). Note elongated ray cells and formation of periderm within ray (arrow). 979 E₁ side b #6. X 65. A = axial parenchyma. C = cortex. IP = inner phloem. OP = outer phloem. P = secondary phloem. R = phloem ray. S = sieve cell.
PLATE XIX

Figs. 96-102. Phloem of Callistophyton phloem in longitudinal section.
96. Radial section of secondary phloem, showing secretory cells with numerous primary pit fields. 979 E₁ side #9. X 120. 97. Degraded sieve areas on sieve cell wall. 979 F₁ side b #6. X 480. 98. Secondary phloem illustrating two secretory cells with primary pit fields on their walls and dark contents. 979 E₁ side #9. X 176. 99. Tapered end wall of sieve cell with sieve areas (arrowheads). 979 E₁ side #6. X 208. 100. Radial section showing irregularly shaped sieve areas. 979 E₁ side #6. X 350. 101. Sieve areas with numerous callose plugs. 979 E₁ side #1. X 400. 102. Detail of sieve areas with presumed callose covering sieve pores. 979 E₁ side #3. X 1600.
A = axial parenchyma.
CHAPTER 7 - DISCUSSION

In comparison to our extensive knowledge on xylem in fossil plants and xylem evolution in general (see, e.g., Carlquist, 1975), almost nothing is known about the phloem of fossil plants and comparatively little about the evolution of this tissue system (see, e.g., Esau et al., 1953; Cheadle & Whitford, 1941; Cheadle, 1948; Zahur, 1959). In her extensive review of phloem anatomy, development and function, Esau stated that, "paleobotany has provided no significant data that could be used in discussions of the evolutionary trends in the tissue." (Esau, 1969, p. 359). Many of the detailed contributions on fossil phloem have appeared since the publication of this work in 1969, but even today our knowledge of phloem phylogeny is relatively meager when compared with the data available on xylem evolution.

There are probably a number of reasons for this relative lack of data. The phloem in extant plants is difficult to fix and there has been a long standing controversy (see, e.g., Eschrich, 1975; Evert, 1977; 1982; Spanner, 1978) over which preparation procedures provide the most accurate representation of the living and functioning state of the tissue. The difficulties that are often encountered while examining extant phloem pose equal, and usually greater, problems in studying fossil material. First, there are a number of problems associated with the presence of relatively thin walls in phloem cells. Xylem elements
remain rigid long after they have ceased to function and their salient features can be easily examined even in dried material. The thickness and rigidity of the cell walls probably accounts, in part, for the relative abundance of xylem in the fossil record as well. Similarly, the fact that the phloem cell walls are delicate may partially explain the relatively rare occurrence of well-preserved phloem in fossils. Another consequence of the delicate nature of most phloem cell walls is that first-formed cells, such as protophloem or peripheral secondary phloem, are usually crushed as new cells are produced. In fossil material, phloem cells can also be compressed or distorted during the processes of deposition and compression prior to fossilization. For this reason, it has generally been assumed that rapid burial in sediments (to exclude most decomposition) and immediate infiltration by mineral-rich water account for the preservation of delicate features such as phloem cells, sieve areas, etc. (Schopf, 1975).

In addition to the difficulties associated with the presence of thin-walled phloem cells, functioning sieve elements in living plants are known to be under hydrostatic pressure (Eschrich, 1975), and any sudden change in this pressure (e.g., cutting the axis) can cause rapid chemical and structural changes in the conducting elements. These can vary from taxon to taxon, but often involve the deposition of callose (in many groups of plants) and/or P-protein (= "slime") (only in angiosperms, see e.g., Evert, 1977). Additionally, a sudden release of pressure often causes a surge of the cytoplasm and its contents, i.e., plastids and other organelles, strands of P-protein, etc. to one end of the cell. Although no evidence of organelles or P-protein has been
found in fossil phloem, a few examples of probable callose deposits have been described, either lining the sieve pores (as in \textit{Medullosa}), plugging individual pores (as in \textit{Callistophyton} [Delevoryas and Morgan, 1954b; Russin, 1981]), or completely covering the sieve areas (as in \textit{Lepidodendron} [Eggert and Kanemoto, 1977] or \textit{Callistophyton} [Russin, 1981]). In extant plants, callose deposits that cover the entire sieve area are termed definitive callose accumulations and are believed to be deposited after the cell has ceased functioning.

In addition to the problems of preservation of fossil phloem, there are also difficulties associated with identification of the tissue and examination of various cellular features. Many studies have identified phloem in fossil plants only on the basis of its position within the stem and not on the presence of diagnostic features of the sieve elements, such as number, location, and relative size of sieve areas and pores. Some workers have differentiated presumed sieve elements and phloem parenchyma utilizing only transverse sections. This approach may be adequate in some plants, such as certain angiosperms. In this group, sieve plates are often conspicuous in transverse section and companion cells can be identified by their location, size and affinity for certain stains, even in transverse section. However, in most plants, and especially in the vascular cryptogams, the diameter and often the length of the sieve elements and parenchyma overlap, and the cells are difficult to distinguish in transverse sections, even with cytoplasmic characters available (see e.g., Lamoureux, 1961). In fossil material, since cytoplasmic features are not generally present, the difficulty of accurate identification of phloem elements is compounded. The
identification of sieve elements in fossil phloem based purely on topography has caused a number of misinterpretations in the past. For example, many of the vascular cryptogams possess a parenchymatous sheath separating the xylem and phloem (see, e.g., Lamoureux, 1961; Eggert and Kanemoto, 1977). In Lepidodendron, this tissue has been variously described as secondary phloem or vascular cambium based partially on its position in the stem (see, e.g., Williamson, 1881; Weiss, 1901). Following a detailed examination of the phloem in this taxon, Eggert and Kanemoto (1977) were able to show that the origin of the sheath was primary and that the vascular cambium was unifacial.

Another factor that directly affects the amount of evolutionary information that can be obtained from fossil phloem is the size of the sieve areas and pores. Esau and Cheadle (1959) found that the pores in dicotyledonous sieve plates averaged approximately 2.01 μm in diameter, with a maximum pore size (with callose cylinder) of 5.36 μm. Lateral sieve areas attained a maximum pore size of 1.36 μm. In vascular cryptogams, however, pore size is rarely as large as 1.0 μm and averages 0.5 μm—close to the resolution limits of the light microscope (Lamoureux, 1961). Features of this size are difficult to resolve in preparations of extant plants, but resolution problems are increased in fossil material, since the cells are viewed either through thin slices of rock or cellulose acetate peels (see CHAPTER 2 for preparation techniques). All of these factors serve to limit the resolution available in fossil material and make it difficult to ascertain details such as pore size and distribution that are critical to understanding phloem phylogeny.
Any attempt to describe and classify fossil phloem is complicated by the fact that many of the characteristics used to identify phloem cells in extant plants are cytoplasmic features. For example, sieve elements can generally be distinguished from companion cells by the presence of clearer cytoplasm, a necrotic nucleus (or lack of a nucleus), peripheral position of the cytoplasm and organelles, presence of a sieve element reticulum (= peripheral, stacked endoplasmic reticulum) and, in the cryptogams, the presence of refractive spherules. None of these features have been observed in fossil phloem, although other fossil cells have been described with some sub-cellular structure preserved (e.g., Millay and Eggert, 1974; Taylor and Millay, 1977; Brack-Hanes and Vaughn, 1978; Niklas et al., 1978). Consequently, fossil phloem must be distinguished based on a combination of non-cytoplasmic characters, including size, shape, and location of the cells and features of the cell wall, i.e., presence of sieve areas and sieve pores.

While all of the above factors no doubt limit the amount of data on phloem structure and evolution that can be obtained from fossil material, perhaps the most crucial factor is preservation. For this reason, most of the detailed studies on fossil phloem have relied on specimens from Carboniferous coal balls. The preservation of most coal ball material is excellent, and a large number of specimens are available, especially from mid-continent and Appalachian coal fields. In addition, the refinement of the cellulose acetate peel technique (see, e.g., Joy, et al., 1956; Stewart and Taylor, 1965) has greatly simplified the preparation procedures involved. A combination of all of
these factors probably accounts for the relative abundance of information on phloem anatomy from plants of this time period.

ANKYROPTERIS AND ANACHOROPTERIS

Although Ankyropteris has been described from Permo-Carboniferous material many times since the genus was first proposed by Stenzel (as a sub-genus of Zygopteris) in 1889, very few specimens are known with well-preserved phloem. Bertrand (1909) noted the presence of phloem in the petioles of A. bibractensis and A. corrugata. He assumed that phloem completely surrounded the central xylem, but cells were only preserved along the central bar and on the inner face of the antennae. The tissue was composed of a single file of large sieve elements bordered by smaller cells. Scott (1912) found a single or double band of large sieve elements in the position of phloem in a lateral branch of Ankyropteris (Zygopteris) grayi, while Corsin (1952) described a tissue with two different cell sizes in A. bertrandii. The presumed sieve elements were approximately 80-100 μm in diameter and the smaller cells 10-20 μm. Apparently, none of these authors examined longitudinal sections of their material and consequently, the identification of cell types is somewhat tentative. The largest amount of information available on phloem in Ankyropteris to date comes from Holden's study of A. corrugata (Holden, 1930). He examined phloem in both stems and petioles, and was the only one to indicate the presence of sieve areas on the vertical walls of the conducting elements. Phloem was continuous around the xylem and consisted of a central zone of large sieve elements (sieve tubes of Holden) surrounded by small-celled parenchyma. In the stem of A. corrugata, he was able to confirm the identification of sieve
elements by the presence of numerous, crowded sieve areas. Phloem in the petioles was very similar to that observed in stems, with 2-3 rows of large sieve elements surrounded by parenchyma. No longitudinal sections of the petiole were illustrated and the identification of the conducting elements is presumably based only upon their position and shape in transverse section.

There are several differences between the published descriptions of *Ankyropteris* and the material investigated in this study. Most of these discrepancies can be related to the fact that very few earlier workers examined the phloem in longitudinal section. Cells were generally identified on the basis of their diameter in transverse section—larger cells were assumed to represent sieve elements and smaller ones phloem parenchyma. Holden (1930) found that the phloem in the stem of *A. corrugata* consisted of two different-sized cells that both exhibited sieve areas on their vertical walls and were structurally identical. However, he provided no higher magnification illustrations of these cells in transverse section, and no pictures of longitudinal sections. He did note that the phloem was separated from the xylem by a narrow layer of parenchyma (presumably a xylem sheath) and from the cortex by a similar parenchymatous layer bounded by a probable endodermis (Holden, 1930). Several other authors, notably Bertrand (1909), Scott (1912) and Corsin (1952) described phloem with large and small cells, but since no sieve areas were described, it is difficult to determine what kind of cells or even the type of tissue involved. Phloem in the Lewis Creek *Ankyropteris* primarily contains only one kind of cell—the sieve cell, although strands of phloem parenchyma are occasionally present.
However, at the periphery of the phloem zone is a layer of large, thick-walled cells that sometimes appears as a dark line (see, e.g., Fig. 28). This layer is conspicuous and consists of oblong cells that measure approximately 30-33 x 64 μm. These cells may correspond to the band of "sieve tubes" that earlier workers described. However, since Holden (1930) offers evidence that the "sieve tubes" of *A. corrugata* are true sieve elements, the anatomical differences between his material and the Lewis Creek *Ankyropteris* may either be regarded as developmental or systematic in origin.

The phloem of *Ankyropteris* compares favorably with that previously described for *Etapteris* and *Botryopteris* (Smoot and Taylor, 1978a; Smoot, 1979), and is also similar to descriptions of fossil lycopod phloem (e.g., Eggert and Kanemoto, 1977). The phloem in all of these taxa is simply organized, consisting of sieve cells and a few strands of phloem parenchyma. There are some extant cryptogams that possess phloem containing sieve cells with little parenchyma present (e.g., some osmundaceous ferns and *Psilotum nudum* [Lamoureux, 1961]). In addition, Lamoureux (1961) notes that there are some ferns, e.g., the Polypodiaceae, in which sieve cells and parenchyma are so similar in size and shape that they can only be distinguished using cytologic features, such as the presence of refractive spherules and absence of nuclei. The presence of a nacreous wall in the sieve cell further distinguishes it from phloem parenchyma in some taxa. In fossil material, these cytologic characters are not available and it is therefore necessary to demonstrate the presence of sieve areas or sieve pores to confirm identification of sieve cells. Considering the
problems of fidelity of preservation and overlap of size and shape, the possibility will always exist that sieve elements may be identified as phloem parenchyma and vice versa. This problem was previously discussed in relation to the phloem anatomy of *Etapteris* (Smoot, 1979).

Table 3

<table>
<thead>
<tr>
<th>Taxon:</th>
<th>Ankyropteris</th>
<th>Etapteris</th>
<th>Botryopteris</th>
<th>Anachoropteris</th>
</tr>
</thead>
<tbody>
<tr>
<td>Diam. (um):</td>
<td>13.5 (apolar)</td>
<td>16-31</td>
<td>21</td>
<td>9.8 (ext.)</td>
</tr>
<tr>
<td></td>
<td>7.5 (antennae)</td>
<td></td>
<td></td>
<td>7.8-27.3 (int.)</td>
</tr>
<tr>
<td>Length (um):</td>
<td>167 (apolar)</td>
<td>120-360</td>
<td>90-138</td>
<td>78-375 (ext.)</td>
</tr>
<tr>
<td></td>
<td>460 (antennae)</td>
<td></td>
<td></td>
<td>195-618 (int.)</td>
</tr>
<tr>
<td>End walls:</td>
<td>horizontal-</td>
<td>horizontal-</td>
<td>horizontal-</td>
<td>horizontal-</td>
</tr>
<tr>
<td></td>
<td>oblique</td>
<td>oblique</td>
<td>oblique</td>
<td>slightly obl.</td>
</tr>
<tr>
<td></td>
<td>rounded (apolar)</td>
<td></td>
<td></td>
<td>(ext. &amp; int.)</td>
</tr>
<tr>
<td>ext. = external phloem</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>int. = small, internal sieve elements</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>int. a = large, internal sieve elements</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The sieve cells in *Ankyropteris* are generally comparable to those described for other fossil cryptogams in size and shape (Table 3), although they are slightly smaller. Sieve cells on the outside of the antennae (i.e., closely associated with the protoxylem) are smaller, and the possibility that they represent protophloem should be considered. In the absence of developmental data, Lamoureux (1961) suggests that protophloem should be distinguished by the crushed appearance of the cells rather than by cell size alone. In fossil material, however, it is too difficult to distinguish cells that were crushed during development from those that were crushed during fossilization, so relative cell size and secondarily, location must be the deciding
factors. Sieve cells of *Ankyropteris* are short when compared to the sieve cells of fossil gymnosperms (e.g., 3.1 mm long in *Medullosa*), but they are well within the range of other fossil cryptogams. In addition, the size and location of the sieve areas in *Ankyropteris* are similar to those described in *Etapteris* and *Botryopteris* (Smoot and Taylor, 1978a; Smoot, 1979), as well as in *Lepidodendron* (Eggert and Kanemoto, 1977). Although dark material that was assumed to represent callose was found in *Lepidodendron* sieve elements (Eggert and Kanemoto, 1977), nothing similar has been observed in any of the fossil ferns.

As in *Ankyropteris*, *Anachoropteris* petioles have been described several times in the past with well-preserved phloem cells, but few of these contributions have included longitudinal sections or details of sieve areas. In his monograph on *Tubicaulis*, Stenzel (1889) mentioned the presence of some small, distorted cells outside of the xylem. Although he provided an illustration of *T. solenites* with well-preserved phloem, his description indicates that little information beyond the size and shape of the cells in transverse section could be discerned.

Stopes (1906) found a few cells preserved in the position of phloem in the stem of *T. sutcliffii*. She detected two different-sized cells, but the material was too poorly preserved to provide more information. In another early contribution, Bertrand and Bertrand (1911) also found phloem cells of two different sizes. Based on transverse sections, they described phloem in the stem and petiole of *T. berthieri* as consisting of a central band 1-2 cells wide of large diameter "sieve tubes" with smaller-celled "parenchyma" on either side. In his extensive monograph on the Inversicatenales, Corsin (1937) found phloem present in the
petioles of three species of *Anachoropteris*, and his descriptions of the tissue are similar to those in earlier studies. On the inside (i.e., abaxial side) of the C-shaped trace, a row of large "sieve tubes" was present, interrupted occasionally by smaller cells. These large cells were only present within the curve of the involute arms. Elsewhere in the petiole, phloem cells were smaller. There were no cells preserved on the external (i.e., adaxial) side of the trace and no examination of longitudinal sections for sieve areas or pores was completed.

In two more recent studies, Delevoryas and Morgan (1954a) and Eggert (1959a) noted the presence of phloem in *A. clavata* and *T. stewartii*, respectively. The *A. clavata* material exhibited a dark layer one cell wide just outside the phloem, which the authors suggested could represent an endodermis. Their material also showed an internal phloem zone of large and small cells.

With just one exception, the material examined in this study can easily be compared to earlier descriptions. In the petioles of *T. berthieri* (Bertrand and Bertrand, 1911), the central xylem is completely surrounded by both large and small phloem elements. All of the other published descriptions, as well as the present material, suggest that the larger diameter phloem cells are present only on the abaxial side of the trace (i.e., within the "C"). In the specimens of *T. stewartii*, this layer is continuous along the abaxial side of the xylem, but in *A. involuta*, the large cells are often not preserved in the central region between the involute arms. The distribution of larger phloem cells only within the involute arms is consistent with the observations of Corsin on *A. gigas* phloem (Corsin, 1937). The coal ball specimens utilized in
the present study compare favorably with other specimens of the genus and provide the first data on size and shape of sieve elements in *Anachoropteris*, as well as the only data available on the distribution and structure of sieve areas on these cells. In addition, the information on cellular composition of the external phloem, although more fragmentary than the data on internal phloem, is nevertheless the first report with cells preserved in this region of the petiole.

Except for the very large diameter cells in the internal phloem, the sieve elements in *Anachoropteris* are within the size ranges exhibited by other fossil cryptogams (Table 3). Because of the presence and distribution of these large cells, however, the cellular composition of the phloem tissue in *Anachoropteris* is much more complex than that described for other fossil ferns or cryptogams. The pattern of concentric bands of smaller cells on either side of a central band of large cells (the "sieve tubes" of earlier workers) that occurs in the internal phloem is similar to the arrangement of the phloem cells in *Psaronius* (see CHAPTER 4; Smoot and Taylor, 1981a). A similar configuration has also been described in the phloem of *Botryopteris* stems (Holmes and Galtier, 1983) and some fossil members of the Osmundaceae, such as *Osmundites* (Kidston and Gwynne-Vaughan, 1907), *Zalesskya* (Kidston and Gwynne-Vaughan, 1908) and *Thamnopteris* (Kidston and Gwynne-Vaughan, 1909). Several workers (e.g., Hick, 1896; Holden, 1960; Holmes, 1977; 1981) have described phloem from the stem of *Psalixochlaena* (*Rachiopteris*) that was similarly constructed. Holmes (1977) examined the tissue in longitudinal section and found elements up to 2.0 mm long, but was unable to see any sieve areas.
The vascular anatomy of Anachoropteris can be compared to extant vascular cryptogams on several levels. The overall shape of the bundle and the presence of phloem completely surrounding the xylem trace occurs in a number of extant ferns. According to Ogura's grouping of extant ferns based on petiole anatomy (Ogura, 1972), Anachoropteris most closely compares with the "Osmunda form" (see also Bertrand and Cornaille, 1902). This type is characterized by a C-shaped trace with distinct, adaxial protoxylem points. Although phloem is present on both sides of the trace, it is generally poorly developed on the adaxial surface. Ogura notes that this form is present in several families, including the Gleicheniaceae (see, e.g., Chrysler, 1944) and Matoniaceae. Although the gross morphology of the petiole trace in Anachoropteris can be compared to these extant ferns, there are several problems with this comparison. The C-shaped trace in the fossil genus is positioned with the "C" facing away from the stem, while the traces in living genera are positioned oppositely. Moreover, it is important to underscore that the phylogenetic relationships of ferns, both fossil and extant, are based primarily on the morphology and anatomy of fertile structures, and not on features of petiole anatomy.

As noted above, phloem tissue with two different cell sizes has been described from fossil members of the Osmundaceae (Kidston and Gwynne-Vaughan, 1907; 1908; 1909). In living members of this family, the phloem consists of a central band of metaphloem elements which are usually fairly large and have clear lumens (e.g., Hewitson, 1962). The metaphloem is separated from the xylem by parenchyma and is bordered on the outside by a zone of narrow cells. These cells are generally
oriented tangentially and display prominent sieve areas in transverse sections of the stem. This layer is assumed to consist of sieve elements (see, e.g., Zenetti, 1895; Faull, 1901; Lamoureux, 1961; Esau, 1969), and has been described from fossil specimens (e.g., Kidston and Gwynne-Vaughan, 1907; Arnold, 1952; Miller, 1971; Wang, 1983). However, there is disagreement as to whether the cells represent proto- or metaphloem (Hewitson, 1962; Miller, 1971). Although there are no cells that are aligned tangentially in the phloem of Anachoropteris, the tissue is similarly constructed of large and small cells, all of which exhibit prominent sieve areas.

If the sieve elements of Anachoropteris are compared with those known from living cryptogams, there is general agreement on the structure of the small sieve elements. Most extant cryptogams contain sieve elements that are elgonate (although not as long as those in seed plants), with horizontal to slightly oblique end walls and similar sieve areas on both side and end walls. The larger sieve elements that are found on the abaxial surface of the trace in Anachoropteris petioles are more difficult to interpret. As noted above, because the end walls taper so gradually it is difficult to determine whether the groups of sieve areas seen on these cells are positioned on the side walls or oblique end walls. It is apparent, however, that the sieve areas are not random in their distribution, but are only present on certain regions of the wall. Where the walls of large sieve elements contact one another, the small, round sieve areas are closely crowded together (e.g., Figs. 5, 12). It is evident, even in face views of the sieve elements, that sieve areas from neighboring cells are positioned
adjacent to one another (e.g., Fig. 12). Along the walls that border other cells in the phloem, however, these groups of sieve areas are not visible (see, e.g., Fig. 11). There are several possible explanations for this configuration. These large cells may represent sieve tube members rather than sieve cells. Sieve tube members are defined as sieve elements that have more specialized sieve areas (i.e., with larger pores) on end walls than on side walls (see APPENDIX). The sieve areas that occur on end walls are grouped together to form sieve plates, which may be simple (one sieve area/plate) or compound. Although true sieve tube elements are rare outside of the angiosperms, they have been reported in Equisetum (e.g., Lamoureux, 1961; Dute and Evert, 1978), Cyathea (Shah and Fotedar, 1974) and possibly in Pteridium. There has been some controversy over whether or not the sieve elements in Pteridium are sieve cells or sieve-tube elements. Lamoureux (1961) noted that although there is a wide range of pore sizes present, there is no consistent distribution of the pores, and larger pores are not aggregated into sieve plates or localized on the end walls. As a result, he concluded that these cells should be termed sieve cells (Lamoureux, 1961). A similar situation occurs in Anachoropteris. The sieve areas are grouped together within a specific area of the wall, but the pores are relatively small in diameter. In order to confirm the identification of the large sieve elements in Anachoropteris as sieve-tube members, it would be necessary to confirm the size of the pores (or the lack of pores) on the lateral walls, regardless of the pore sizes on end walls. Although no lateral pores have been observed on these cells, it is difficult to determine definitively whether sieve pores were
present during the life of the plant or simply not preserved in the fossil. The sieve element walls appear continuous and undistorted in transverse section, but they present a wavy appearance in longitudinal section that probably indicates some crushing of the cells prior to fossilization. Even without the problems of preservation, however, it seems unlikely that these cells represent sieve-tube members, since the diameter of their sieve pores is closer to that of plasmodesmata than to the typical pores of angiosperm sieve-tube members (see, e.g., Esau and Cheadle, 1959).

Since these large cells probably do not represent sieve-tube elements, they must be regarded as sieve cells. In this case, the localization of the sieve areas within a certain wall area may simply reflect the fact that the connections between two sieve cells (i.e., sieve areas with pores) are generally more developed than those between a sieve cell and a parenchyma cell (i.e., a sieve area on one side and primary pit field on the other) (see, e.g., Esau, 1969). The lack of visible sieve areas on the other parts of the cell could simply mean that these connections were so small as to be within the size range of plasmodesmata and therefore, too difficult to resolve in the fossil preparations.

PHYLOGENETIC TRENDS IN FILICALEAN PHLOEM

There are several levels on which phylogenetic trends in filicalean phloem, both fossil and extant, can be discussed:

Topography — A great deal of information is available on the location of phloem in the ferns (e.g., Ogura, 1972; Foster and Gifford, 1974). As noted earlier, Ogura (1972) discusses the location of
petiolar phloem in the ferns and describes a range of bundle types from collateral to concentric. Although Ogura (1972) and other authors (e.g., Bertrand and Cornaille, 1902; Lin and Devol, 1977; 1978; Lucansky and White, 1974) have found that petiolar anatomy can sometimes be used as a taxonomic character, there are too many inconsistencies in the distribution of different types to utilize this character alone in constructing phylogenies. The petiolar trace in several Carboniferous ferns (e.g., *Etapteris*, *Ankyropteris*) is radially symmetrical in transverse section, and thus cannot be compared to most extant filicaleans, which exhibit bilaterally symmetrical petiole traces. The fossil ferns examined to date all possess concentric petiolar bundles, a type that is very widespread among living taxa.

**Composition** - There are several evolutionary differences in the cellular composition of phloem tissue that can be recognized in the taxa examined thus far. The simplest phloem tissue would be that with only one type of cell present — sieve elements. This type of tissue is found in the coenopterid fern petiole, *Etapteris* (Smoot, 1979). The phloem consists of relatively unspecialized* sieve elements. Although no parenchyma is present within the phloem itself, there is a parenchymatous sheath separating the xylem and the phloem. The next level of specialization in tissue composition is illustrated by the

*Since most authors (see e.g., Esau, 1969) assume that sieve elements originated from parenchyma cells, unspecialized sieve elements would be those that most closely resemble parenchyma cells in both size, shape and cytological features.
phloem of another coenopterid fern petiole, Botryopteris, which contains both sieve elements and so-called mucilage canals (Smoot, 1979).

Phloem structure in the species of Ankyropteris examined here is only slightly more complex. Although the tissue is composed primarily of sieve elements, there are occasional strands of phloem parenchyma. In addition, the size and shape of the cells varies with position in the axis. Sieve elements along the antennae are smaller and more elongate than those adjacent to the apolar. The narrowest phloem cells adjacent to the antennae are considered to represent protophloem, but a definite size difference is also present in the presumed metaphloem cells.

Of all the fossil ferns examined, Anachoropteris has the most complex phloem. The compliment of cell types is more diverse and varies according to position within the axis. The external phloem is relatively simple, consisting of narrow sieve elements and a few parenchyma cells. The internal phloem, however, contains both large and small sieve elements, as well as phloem parenchyma, and the cells within this tissue are organized in a very distinctive pattern of concentric bands of cells. Although a general trend from simple to more complex phloem tissue can be recognized within the fossil ferns examined thus far, it should be emphasized that the pattern of these changes is not related to the taxonomic position of these plants. All four of these taxa are members of extinct families and were present contemporaneously in Carboniferous coal swamps. Although Anachoropteris and Ankyropteris are considered to belong to an order with extant representatives (Filicales), the other two taxa have no living counterparts.
Histology - The size and shape of sieve elements and the distribution and morphology of sieve areas are considered by most workers (e.g., Esau et al., 1953; Zahur, 1959; Esau, 1969 and references cited therein) to be the factors that are the most important taxonomically, and which have the greatest potential for contributing to our understanding of phylogenetic trends in phloem tissue. As noted earlier, the origin of sieve elements in the ferns is assumed to result from modifications of parenchyma cells for more efficient conduction. In living plants, these modifications include not only features of the wall (such as development of sieve areas and pores, formation of a nacreous layer, etc.), but also cytoplasmic features (e.g., degeneration of nucleus, formation of peripheral endoplasmic reticulum, breakdown of tonoplast, etc.). The size and shape of sieve elements in the fossil ferns that have been examined to date (Table 3) is fairly similar, although the mean length of the cells is slightly longer in Ankyropteris and Anachoropteris than in Etapteris and Botryopteris. The shortest cells in these four genera are only about four times as long as they are broad, i.e., within the range of parenchyma cells. The longest cells are the large cells in the internal phloem of Anachoropteris, which can be as much as 50 times longer than wide. These cells would be considered the most advanced phylogenetically since they have diverged the furthest from parenchyma cells, both in length and diameter. The orientation of end walls is believed to have evolutionary importance in angiosperm sieve-tube members (see, e.g., Hemenway, 1913; MacDaniels, 1918; Zahur, 1959; Esau, 1969), and it is interesting to note that the
longest cells in these fossil cryptogams (i.e., presumably the most advanced) also exhibit end walls that are very oblique.

As far as the shape, size and location of sieve areas are concerned, the fossil ferns appear to be similar to most extant ferns. Living ferns usually exhibit numerous, crowded, horizontally elongate sieve areas (see, e.g., Palm, 1937; Lamoureux, 1961; Hébant, 1969; Nair and Shah, 1980). They are often so crowded on the lateral walls of the sieve elements that the strands of intervening, thicker wall material form a kind of reticulum. The sieve areas are equally differentiated on the lateral and end walls, and the pores are very small, generally only a few tenths of a micron. This general type is very similar to the sieve elements in *Ankyropteris*, *Etapteris* and *Botryopteris* (Smoot, 1979). In the large, internal elements in *Anachoropteris*, however, the sieve areas are less crowded and appear circular-oval in outline. Coupled with the larger diameter of the cells and extremely tapered end walls, these cells resemble the sieve cells of gymnosperms more than the sieve cells of typical vascular cryptogams.

In summary, it is evident that the sieve elements of the Carboniferous filicalean ferns that have been examined to date show a number of features that may be indicative of evolutionary development beyond a simple parenchyma cell. These include elongation, increasing obliquity of end walls, and specialization of sieve areas. Presumably, the evolutionary development of sieve areas from primary pit fields would occur first on both side and end walls, and subsequently more on end walls than on side walls. In addition, the least specialized sieve elements generally exhibit very narrow diameters, while the more
advanced elements, such as those in *Anachropteris*, are considerably wider.

The basic premise behind these proposed evolutionary trends is that the precursor of the pteridophyte sieve element was a typical parenchyma cell. There is some evidence from early land plants to support this hypothesis. Kidston and Gwynne-Vaughan described cells preserved in the position of phloem in *Rhynia*, *Horneophyton* and *Asteroxylon* (Kidston and Gwynne-Vaughan, 1917; 1920a; 1920b). They found a tissue composed entirely of narrow, elongate elements with few intercellular spaces. The end walls were either horizontal or slightly oblique, very similar to those seen in the Carboniferous ferns. However, Sattterthwait and Schopf (1972) later examined the phloem tissue in *Rhynia major* and found both elongate cells and "narrow parenchymatous cells." From their illustrations, the elongate cells are evident and appear similar to those illustrated by Kidston and Gwynne-Vaughan, but the parenchymatous cells are somewhat indistinct and difficult to identify accurately.

**PSARONIUS**

There have been very few examples of *Psaronius* stems with structurally preserved phloem found in the fossil record. Scott (1920) was one of the first to figure part of a *Psaronius* stele with intact phloem. *Psaronius renaulti* (Williamson, 1876) possessed phloem containing a central band of large cells on either side of the xylem arc. This same specimen was later illustrated in Bower (1926) and in Hirmer (1927). Moon (1939) also figured some thin-walled cells that may represent phloem, but too little of the tissue is illustrated to positively identify it. Gillette (1937) described some tissue preserved
in the position of phloem in *P. septangulatus* as small cells with thin walls. No illustrations or longitudinal sections were provided.

In her monograph on the American species of *Psaronius*, Morgan (1959) observed well-preserved phloem in both *P. blicklei* and *P. chasei*. The phloem completely surrounded the xylem arc and appeared similar to that in the present study. In transverse section, the tissue contained a central row of larger diameter cells—the presumed sieve elements. Morgan noted that the phloem zone in all specimens with adequate preservation was constructed similarly. Although longitudinal sections were prepared, Morgan was unable to discern sieve areas.

When the present material is compared with previous studies on *Psaronius* phloem, the anatomy of all the species that have been examined to date is fairly uniform, with the possible exception of Moon's material. Her specimen was apparently not preserved in its entirety and it is difficult to interpret the anatomy based on the information provided. The remaining species that have been described exhibit phloem tissue that completely surrounds the xylem and consists of a central band of "sieve elements," surrounded by small-celled "parenchyma." Since none of the previous contributions (with the exception of Morgan, 1959) have examined these cells in longitudinal section, their identification as conducting cells or parenchyma can only be tentative.

*Psaronius* is placed within the Marattiales (see, e.g., Rudolph, 1906; Bower, 1926), an order that contains both fossil and living genera, thus allowing for a direct anatomical comparison within a single group. The information from extant specimens on the phloem anatomy of the Marattiales is scarce and widely scattered. As Esau (1969) noted,
the conducting cells in this group have never been studied "using modern methods." Although Warmbrodt and Evert (1979) included *Marattia* in their study of homosporous ferns, only the minor veins of the leaves were examined. The group is interesting developmentally because it is the only group of vascular plants that exhibits centrifugal maturation of the phloem. Shove (1900) first described the protophloem in *Angiopteris* as present in a discontinuous arc directly outside the metaxylem cells. Metaphloem differentiates external to these protophloem points, as well as around the inner side of the metaxylem arc. Shove described the metaphloem as a continuous ring of "sieve tubes" which were very conspicuous in young steles because the metaphloem matured prior to the metaxylem cells (Shove, 1900). The mature external phloem was more extensive than the internal phloem, no doubt partially due to the production of protophloem only on the external face. In addition, the external sieve elements were usually larger and more thick-walled than the internal ones (Shove, 1900). Shove's contribution appears to be the only description of sieve elements in a marattialean stem (*Angiopteris*), but Van Tieghem (1870) looked at phloem cells in root tissue and his work was later discussed by Poirault (1893). In *Angiopteris* roots, Van Tieghem found sieve elements which he described as large cells with grey, oval perforated areas on their walls. He also examined *Marattia* roots but was unable to demonstrate the presence of perforated cells. In Shove's material, the sieve elements were large with transverse walls, but since they were not examined in longitudinal sections, no information is available on the length of the cells or sieve area size and position.
Brebner (1902) examined the sieve elements in Danaea roots and was able to distinguish them by their relatively thick, glistening walls (presumably nacreous walls) and the presence of "proteid" granules on the pitted areas (probably refractive spherules of later workers). Palm (1937), in his detailed study on filicalean phloem, examined the vascular anatomy in the petiole of Marattia alata and found that the sieve elements and parenchyma cells could not be distinguished from one another, even in longitudinal section. The cells were all elongate with few or no inclined end walls. Palm also described large cells near the periphery of the phloem zone with dark contents which he regarded as secretory cells. He found that when the secretory cells were cleared of their contents, they appeared similar to sieve cells and exhibited circular sieve areas on their lateral walls. Since he was unable to distinguish specific conducting elements, Palm (1937) concluded that the entire phloem tissue in Marattia must function as a whole in place of specialized sieve tubes.

Psaronius can be compared to living members of the order on several different levels. The phloem in Psaronius occupies a position within the stele that is comparable to that seen in extant taxa — the phloem completely surrounds the central xylem. In both cases, the external phloem is more developed than the internal, probably due to the presence of protophloem in the external zone. The protophloem in extant marattiales occupies a position between the metaxylem and the external metaphloem, i.e., the phloem develops centrifugally. Scattered, small diameter cells occur in this same position in the fossil material, and on the basis of location and size, these are assumed to represent
protophloem elements. None of the specimens represented very young stems, so no developmental data are available for the fossil taxa.

The phloem of *Psaronius* consists of a central band of larger cells surrounded by smaller cells, both with walls that are slightly thicker than neighboring parenchyma cell walls. In some extant specimens, this same configuration is also apparent. For example, Brebner (1902) illustrated sections of *Marattia* and *Kaulfussia* that exhibited the same arrangement of cells. Sections of young stems of *Angiopteris* appear similar, but the phloem in older stems is more homogeneous (Shove, 1900). In Palm's material (1937), no difference in cell types is apparent in transverse section. Perhaps, as Shove suggests (1900), the size differences between metaphloem sieve elements and phloem parenchyma vary with the age of the plant. Additionally, comparisons of cellular composition are difficult because many of the cell determinations in living material are based upon cytologic features. As far as can be determined, no clear illustrations of longitudinal sections of the stem or petiole phloem of living marattialeans have been published. Material from this group was unavailable to Lamoureux (1961) for his comprehensive study on the phloem of vascular cryptogams. However, he suggested that the pitlike areas seen on sieve element walls by some of the earlier workers (e.g., Van Tieghem, 1870) should probably be regarded as sieve areas. The somewhat controversial statement by Palm (1937) that sieve elements could not be distinguished from parenchyma in longitudinal sections has apparently never been questioned. Russow (1882) examined petioles of *Angiopteris evecta* and was able to distinguish thin-walled cells at the periphery of the phloem zone that
exhibited large circular-oval areas on their walls. Although the cells stained positively for callose in certain spots, he was unable to observe sieve pores, but concluded nevertheless that the cells probably represented sieve elements.

The fossil specimens help to clarify the confusion over the exact structure of the sieve elements in the extant marattialean ferns. Longitudinal sections of the phloem tissue in _Psaronius_ clearly show that cells of two different sizes are present, both with circular-oval thin areas on their walls. Some of these cells are elongate, while others are shorter and overlap parenchyma cells in size. With no evidence of refractive spherules or other cytologic features, the identification of these cells as sieve elements is somewhat tentative. However, the presence of obvious phloem parenchyma cells within the same tissue indirectly provides support for the characterization of the pitted cells as sieve elements.

*Phylogeny of marattialean phloem* - As Stidd (1974) and Millay (1979) have noted, the marattialean ferns are a group whose origins continue to remain obscure. Members of the order first appear in the Upper Carboniferous and the morphology and anatomy of the various fossil organs are quite characteristic even at this early stage. The phloem anatomy provides additional support for the observations of these earlier workers. The location of the phloem (concentric bundles), the cellular composition (concentric bands of large and small elements, separated from the xylem by a parenchyma sheath) and the structure of the sieve elements in _Psaronius_ are all comparable, if not almost identical, to those seen in extant marattialeans. Compared to other
fossil ferns, however, the sieve elements in Psaronius must be considered to be somewhat primitive. They are not very elongated and possess sieve areas of similar size and shape on both their side and end walls. Additionally, the few pores that have been observed within these sieve areas are very small — well within the range of plasmodesmata. The phloem anatomy can be considered as additional evidence that the order has changed little since the Carboniferous (Stidd, 1974; Millay, 1979).

**CALLISTOPHYTON**

Callistophyton stems have been observed with well-preserved phloem more often than probably any other fossil plant. When the genus was originally described by Delevoryas and Morgan (1954b), information on phloem anatomy was included. These authors illustrated secondary phloem containing sieve cells that exhibited the remnants of sieve areas and possible callose plugs on their radial walls. Tangential bands of phloem parenchyma and phloem rays were also present. Unlike species of *Poroxylon* from France, *C. poroxyloides* contained no secretory cavities in the phloem (Delevoryas and Morgan, 1954b). In his detailed monograph on the vegetative anatomy of the Callistophytaceae, Rothwell (1975) not only found secondary phloem preserved, but occasional examples of primary phloem cells as well. Secretory or resinous cells were also present in the secondary phloem of *C. boysetii*. In the older secondary phloem of this taxon, Rothwell (1975) found thick-walled cells that he compared to the sclereids seen in some living plants (e.g., *Pseudotsuga* [Grillos and Smith, 1959]).
The earliest detailed studies on Callistophyton phloem were a series of papers by Bertrand and Renault on Poroxylon from the Permo-Carboniferous of Autun and Grand'Croix, France (Renault, 1879; 1880; Bertrand and Renault, 1886; Bertrand, 1889). Rothwell later placed P. edwardsii (Renault, 1880) and P. boysetii (Renault, 1879) in synonymy under the binomial C. boysetii (Rothwell, 1975). Bertrand and Renault (1886) described and figured beautifully preserved, silicified stems containing sieve cells with numerous sieve areas on their radial walls. They found three types of sieve areas: those that appeared to be degraded; small, rounded sieve areas with a low number of pores; and larger areas with numerous, closely spaced pores. These larger sieve areas were present in transverse bands that covered the entire width of the radial wall (Bertrand and Renault, 1886; Bertrand, 1889). The present material exhibits a similar diversity in shape and size of sieve areas (e.g., compare Figs. 97, 99, 100, 101, 102).

One of the most interesting aspects of Bertrand and Renault's work is their description of histological changes that occur towards the periphery of the secondary phloem zone in Poroxylon (Bertrand and Renault, 1886). They found that all the elements were somewhat flattened near the cambium. Further out, the axial parenchyma cells enlarged slightly, partially flattening the sieve cells between them. Toward the periphery of the secondary tissue, the sieve cells also began to enlarge, the walls of both the parenchyma and the conducting cells thickened, and the ray cells enlarged drastically. All of these changes were observed in the North American Callistophyton specimens, as well. However, the French material differs from the stems described here by
the presence of abundant divisions (both radial and tangential) in the ray cells near the periphery of the phloem. In the oldest stems, Bertrand and Renault found that the secondary phloem abutted on cells of the periderm, as is the case with the North American specimens.

Russin's description of *Callistophyton* phloem based on coal ball specimens of *C. poroxyloides* and *C. boysetii* is generally similar to the present material, with a few exceptions. Concerning the proportions of secondary xylem and phloem, Russin found that axes with little secondary development had secondary xylem present with little phloem. In older axes, he found relatively equal amounts of secondary xylem and phloem. These different proportions were not observed in the present material. There are several possible explanations for this discrepancy. Studies on extant plants have found that the relative amounts of xylem and phloem produced by the cambium can vary with the age of the plant, time of year and other environmental factors (see, e.g., Artschwager, 1950; Bannan, 1955; Grillos and Smith, 1959). In extant cycads, for example, Chamberlain reported the following proportions of secondary xylem and phloem: 3/2, 1/1, 1/1, 10/1.4 (Chamberlain, 1911). As noted earlier, the number of phloem cells that are visible in each radial row in *Callistophyton* is dependent upon the histological changes that take place in the older phloem, as well as upon the timing of periderm production. There is very little information available from the fossil record on the relative production of xylem and phloem by the cambium. In *Heterangium americanum*, Hall (1952) found that secondary phloem may equal or exceed secondary xylem, but this observation was based on only one specimen. In *H. grievii* (Williamson and Scott, 1896), the amount of
secondary xylem apparently exceeded the phloem, while in *H. tiliaeoides*,
the ratio varied from slightly more xylem than phloem (Williamson,
1887b; Williamson and Scott, 1896) to approximately equal amounts of the
two tissues (Williamson 1887b; Scott, 1923). In *Lyginopteris*, the
production of secondary xylem greatly exceeded that of secondary phloem
(Williamson and Scott, 1896), and Stidd and Phillips (1973) found a
similar situation in *Schopfiastrum* (xylem/phloem = 7/1) (see also
Rothwell and Taylor, 1972). These examples illustrate the difficulty in
assessing the relative contribution by the cambium to xylem and phloem
in fossil plants. The information available is generally based on one
or two specimens, and poor preservation is much more likely to affect
the amount of phloem tissue present that the amount of xylem, for
reasons already discussed. Perhaps the best conclusion at this time is
that the data available on the relative proportions of xylem and phloem
are too meager to place any taxonomic or phylogenetic importance on this
feature alone.

Some of the differences between Russin's figures and the present
data may represent merely an artifact introduced during the size
analyses. Russin measured a large number of radial rows but apparently
did not compare the number of phloem cells and xylem cells within a
single radial row. Generally, he measured about five times as many
xylem rows as phloem ones (Russin, 1981, Table 2). In the one instance
where the number of rows was close to equal (5 phloem rows, 7 xylem),
the data indicated that there were approximately twice as many xylem
cells (53) as phloem (28). In addition, according to Russin's data, the
cambium in *Callistophyton* would have to initially produce more xylem
than phloem (xylem present, but little phloem), then produce relatively more phloem so that the overall proportions of the two tissues became more equal with development. Presumably as the ratio approached one, the production of phloem would slow down and eventually equal the production of xylem.

In extant gymnosperms, the composition of the secondary phloem and the arrangement of the cells is known to have taxonomic and presumably evolutionary significance (see, e.g., Holdheide, 1951; Chang, 1954). This appears to be the case in the Paleozoic seed ferns that have been examined, as well. The pattern of alternating bands of sieve cells and phloem parenchyma has been observed almost universally in the secondary phloem of Carboniferous seed ferns (excluding the medullosan pteridosperms). In Callistophyton, this pattern was very regular and the uniseriate bands were only rarely interrupted by the loss of a band of axial parenchyma. The same situation apparently existed in Heterangium (Hall, 1952), Microspermopteris (Taylor and Stockey, 1976), Lyginopteris (Williamson and Scott, 1896) and Calamopitys (Galtier and Hébant, 1973). In Calamopitys, the bands of sieve cells may be 1-2 cells wide radially, but in all the other taxa they are limited to one cell layer. Since Calamopitys represents the oldest material that has been investigated (Lower Carboniferous as opposed to Upper Carboniferous for the North American and British material), perhaps the more regular arrangement of the bands of sieve cells represents a derived feature. Outer (1967) reached the same conclusion based on comparative anatomy of extant gymnosperms.
The arrangement of secondary phloem cells in Callistophyton and other Carboniferous seed ferns has no parallel in extant plants. Among the living gymnosperms, only members of the Pinaceae and the Gnetales have phloem that consists exclusively of sieve cells and parenchyma. In some cases, the secondary phloem consists primarily of sieve cells, with axial parenchyma strands scattered throughout or present in poorly organized, tangential bands (Outer, 1967; Esau, 1969). Examples of this type are Pseudotsuga (Grillos and Smith, 1959; Outer, 1967) and some species of Pinus (Srivastava, 1963a; Esau, 1969). In other taxa (e.g., Abies and some species of Pinus), the sieve cells and phloem parenchyma regularly alternate as they do in Callistophyton, but the bands of sieve cells vary from 5-15 cells wide (Chang, 1954; Alfieri and Evert, 1968; Esau, 1969). In the Gnetales, the axial parenchyma is either randomly scattered (e.g., Ephedra) or in radial files (Gnetum) (Esau, 1969). Sclereids often develop in the older phloem of this group, much as they do in Callistophyton. The great majority of gymnosperms, however, including most of the conifers, cycads and Ginkgo have fibers present in their secondary phloem (Chang, 1954; Srivastava, 1963b; Outer, 1967; Esau, 1969), and thus cannot be directly compared with Callistophyton, even at the broadest level of cellular composition. Numerous conifers do show a very regular pattern of alternating tangential bands, but the bands consist of sieve cells, axial parenchyma, sieve cells, fibers, etc. in that order (Chang, 1954; Outer, 1967; Esau, 1969).

The histological changes that take place in the outer phloem cells of Callistophyton have been observed in a number of extant plants, and are considered to represent changes from functional to non-functional
phloem (see, e.g., Srivastava, 1964; Esau, 1969). Most of the studies that have been completed on this subject were concerned with conifer phloem, and these have shown that deposition of definitive callose is one of the first stages in the process (e.g., Srivastava, 1963a; Alfieri and Evert, 1968). Subsequently, the phloem parenchyma and ray parenchyma enlarge and appear rounder in transverse section, usually crushing sieve cells and albuminous cells as they increase in size. Some parenchyma cells may divide as well (e.g., Isenberg, 1943; Grillos and Smith, 1959, Srivastava, 1963a). In certain taxa, sclereids develop from parenchyma cells (e.g., Abies [Chang, 1954]; Pseudotsuga [Grillos and Smith. 1959]). Some of these may grow intrusively and greatly disrupt the cell patterns that were present in the functional phloem. Srivastava (1963a) concluded that sclereids were restricted to the non-functional phloem, although in some taxa they differentiated fairly close to the cambium. The changes in the peripheral phloem of Callistophyton are unique when compared to extant taxa, because there is evidence that not only the parenchyma cells, but also the sieve elements differentiated into sclereids in the older phloem. In extant plants, although the sieve element is not considered to be dead at maturity, disintegration and disappearance of the nucleus is a well-known aspect of sieve element ontogeny in angiosperms. In gymnosperms, degeneration of the nucleus is pycnotic, i.e., nuclear material becomes condensed and remnants of it may persist within the sieve cell (see, e.g., Evert, 1977; Alfieri and Kemp, 1983). The evidence for further differentiation of the sieve elements in Callistophyton into sclereids is clear, and was noted by Bertrand and Renault (1886) as well. Because this situation
has not been observed in extant phloem, the possibility that the sieve elements in Callistophyton were structurally or functionally different in some way should not be overlooked. Perhaps the nucleus remained active enough to function during deposition of cellular contents and thickening of the wall that are seen in the peripheral sieve elements. On the other hand, perhaps the dark material present in the peripheral sieve cells does not represent wall thickening, but the deposition of substances such as tannins, etc. In this case, the sieve element could play a passive role in the histological changes. In an analogous situation, Scott (1899) observed what appeared to be thick-walled cells in Medullosa phloem (see below). Since these were the only cells preserved in the phloem, Scott described them as sieve cells and suggested that perhaps the cells had undergone hydration and swelling after deposition, resulting in cell walls that appeared to be thickened in the fossil state, but were thinner during the life of the plant. Another possibility that should be considered is that the rings of material seen within the peripheral sieve cells in Callistophyton may represent the plasma membrane and cytoplasm that collapsed following plasmolysis of the cells. The regular distribution of these thick-walled cells in the peripheral phloem, and their absence elsewhere in the stem, however, suggests that these cells are a normal part of development in the older phloem. A comparison of these cells with those described in other fossil plants illustrates that they are similar to cells previously described as sclereids.

Increase in diameter of the stem in Callistophyton is initially accommodated by tangential expansion of the ray cells, and later by an
increase in diameter of all the elements in the outer phloem during the phase of wall thickening. Occasional cell divisions have been seen in ray cells, but these are rare. In living conifers, the tangential increase of the stem is accommodated by cell division (see, e.g., Grillos and Smith, 1959; Srivastava, 1963a), tangential cell enlargement (i.e., stretching), including radial separation of cells, and occasional formation of a dilatation tissue (Esau, 1969).

Russin (1981) provided a comparison of phloem histology in Callistophyton (including such features as size of sieve cells and structure of sieve areas) with that described for other Paleozoic seed ferns, extant cycads and conifers. He concluded that sieve areas were found on radial walls in all three groups, but the appearance of the sieve areas and the length of sieve cells in Callistophyton were more similar to those in cycads than those in conifers (Russin, 1981). The work of Carlquist (1975) on wood anatomy in relation to environment, however, suggests that the length of fusiform initials is dependent upon such factors as water stress and mechanical strength in the tracheary elements. Carlquist (1975) believes that the length of sieve-tube members is passively influenced by selective pressures on the xylem cells. Some comparative work has been done on the significance of sieve element length in the angiosperms (e.g., Cheadle and Whitford, 1941; Zahur, 1959), but no comparable data are available for gymnosperm sieve cells. The shape of the sieve elements and the location, size and shape of sieve areas in all of the gymnosperms, living and fossil, are very similar. Some of the conifers, e.g., the Pinaceae, have sieve areas that appear rounder and less crowded together than those in Medullosa
and Callistophyton, but these characters have never been examined quantitatively and any comparison between fossil and extant gymnosperms must be subjective.

On the basis of phloem anatomy alone, the question of whether Callistophyton is more closely related to the conifers or the cycads is still uncertain. The occurrence of fibers in Medullosa phloem and their absence in Callistophyton supports a closer relationship with taxa that lack fibers, such as the cordaites or non-fibrous conifers, rather than with the extant cycads. In addition, the relative amount of parenchyma in the secondary phloem of Callistophyton is less than that in Medullosa and this may also indicate closer affinities with some conifers than with the cycads. Based on morphology and anatomy of both vegetative and reproductive organs, Rothwell (1981) has suggested that the Callistophytales include characteristics of both the pteridosperms and conifers, and the data on phloem anatomy appears to support this conclusion.

**MEDULLOSA**

Anatomically, Medullosa is one of the most complex plants known from Paleozoic strata. Since it was originally described from silicified specimens of Permian age, a number of species have been detailed (see, e.g., Göppert and Stenzel, 1882; Scott, 1899; Delevoryas, 1955), ranging in age from the Upper Carboniferous (Westphalian A) to the Permian (Phillips, 1981). Only a few of these reports have mentioned the presence of phloem tissue, and in all of these the tissue has been fragmentary. The earliest reports of Medullosa phloem were those of Göppert and Stenzel (1882), Solms-Laubach (1897) and Scott
(1899). Despite the fact that the first two contributions were based on Permian fossils and the last on Upper Carboniferous material, the phloem anatomy was remarkably similar. All three described secondary phloem that consisted of elongate thick-walled cells with narrow lumens and tapered ends. The cells were arranged in radial rows and separated by parenchymatous rays. Since no thin-walled cells were present, Solms-Laubach (1897) concluded that these fiber-like cells must represent conducting elements. Scott (1899) agreed with this interpretation and suggested that these cells could not be fibers because (1) the walls were light in color, (2) if the phloem of Medullosa was very fibrous, it would be preserved more often as a fossil, and (3) there were no other elements present that could be sieve cells. Scott suggested that perhaps the cell walls were thin during the life of the plant, but swelled prior to preservation. Baxter (1949) and Stewart (1951) described phloem in _M. endocentrica_ and _M. pandurata_, respectively, which consisted of groups of large, thin-walled cells, separated by ray parenchyma. Baxter illustrated a transverse wall with very small pores preserved, and Stewart found somewhat better preserved sieve areas on the lateral walls of the sieve cells. Neither of these reports described fiber cells in the secondary phloem. Well-preserved phloem has also been detailed in medullosan roots. Arber (1903) described secondary phloem in _M. anglica_ roots as consisting of radial groups of small "sieve tubes," accompanied by parenchyma cells and separated by vascular rays. He illustrated sieve areas (somewhat degraded) in both stems and roots (Arber, 1903). Rothwell and Whiteside (1974) also described well-preserved secondary phloem from medullosan
roots. The sieve cells were elongate and present in radial rows that were 1-3 cells wide. Although no sieve areas were seen, they did observe thick-walled elements in some older axes.

Phloem has also been noted in Sutcliffia, a stem genus that is structurally similar to Medullosa (see, e.g., Phillips and Andrews, 1963). Scott (1906) illustrated primary and secondary phloem in S. insignis and was able to distinguish sieve elements (elongate cells with tapered end walls) from phloem parenchyma (short cells with transverse walls) in longitudinal section. A number of scattered cells with dark contents were present in the primary phloem as well. Later, de Fraine (1912) described a new species of the genus and found the phloem to be more like that described by Solms-Laubach (1897) and Scott (1899) in Medullosa. The elements were thick-walled with a reduced lumen and appeared in longitudinal section as elongate with tapered ends.

On the basis of cellular composition, the present material compares most closely with the earlier descriptions of Medullosa phloem (i.e., Göppert and Stenzel, 1882; Solms-Laubach, 1897; Scott, 1899), as well as with de Fraine's data on Sutcliffia phloem (de Fraine, 1912). Although these studies found only fibers present in the secondary phloem, the Medullosa stems under investigation here provide evidence that these specimens may not have reflected the true conducting state of the tissue. In the stems of M. noei examined in this study, large groups of fibers are present only at the periphery of the secondary tissue, i.e., in the presumably non-functional phloem. There are several possible reasons as to why these fibers occur with no intervening sieve cells or axial parenchyma. The vascular cambium may have initially produced a
number of fibers and thin-walled elements were not formed until later in
development. Presumably, the primary phloem would function in
conduction until secondary sieve cells matured. This sequence of events
could account for the peripheral rows of fibers in the present
specimens, and also explain the descriptions of earlier workers (e.g.,
Göppert and Stenzel, 1882; Solms-Laubach, 1897; Scott, 1899).

Another explanation for the distribution of fibers in Medullosa
phloem is that the sieve cells and axial parenchyma were crushed as the
phloem cells became non-functional, while the thick-walled fibers
remained relatively unaffected by changes in the outer phloem.
Alternatively, only the sieve cells may have been crushed and some of
the axial parenchyma cells underwent extensive wall thickening and
differentiated into sclereids (or fibers). The result in both of these
cases would be a tissue that appeared to be composed almost exclusively
of fibers and vascular rays. These phenomena (crushing of sieve cells,
sclereid formation from parenchyma cells) are very common in the
secondary phloem of many extant plants, both angiosperms and gymnosperms
(see, e.g., Holdheide, 1951; Grillos and Smith, 1959; Esau, 1969). This
sequence of events is a reasonable explanation for the distribution of
fibers in Medullosa phloem, and is supported by the occurrence in some
specimens of proportionally more fibers in the older phloem (e.g.,
Rothwell and Whiteside, 1974, as well as the present specimens). Fibers
also appear to be more numerous in zones where the vascular cambium has
undergone proliferation (see, e.g., the location of fibers in M. anglica
phloem [Smoot and Taylor, 1981b]). These zones are common in stems of
Medullosa and bear a close resemblance to cambia and callose tissue
formed as a response to wounding or other trauma in living plants (e.g., Brown and Sax, 1962; Zimmermann and Brown, 1980). The presence of extra fibers associated with these zones may simply reflect adjustments of the tissue, either by the production of extra fibers or by the obliteration of thin-walled cells, during the wounding or recovery processes.

Another possibility that Scott (1899) and Solms-Laubach (1897) discussed is that the so-called fibers in Medullosa stems are not truly fibers, but thin-walled elements whose walls have undergone some degradation and/or hydration following deposition. Barghoorn (1949; 1952; Barghoorn and Scott, 1958) described the effects of degradation upon tracheid walls in extant plants. He cited a number of chemical and structural changes in the cell wall that are visible in fossil material and concluded that many plant remains must be fossilized prior to degradation since their cell walls remain relatively intact, especially in coal ball material. In the specimens examined here, the tangential bands of fibers in the functional phloem are produced so regularly that it is very unlikely that they could have resulted from changes following deposition as Solms-Laubach (1897) and Scott (1899) suggested. Based on their histology and position, they appear to be a normal part of phloem development in this taxon. As noted above, however, the cell walls of many of the peripheral fibers do appear to have undergone some hydration or swelling (see, e.g., Fig. 64), but whether this occurred prior to or following deposition is unclear.

The present material clearly illustrates that fibers were a normal part of the presumably functional phloem in Medullosa, but these were present as alternating, tangential bands of cells and not in large
groups as they are in the non-functional tissues. The reports by Baxter (1949) and Stewart (1951) of Medullosa phloem composed only of thin-walled elements are difficult to reconcile with the current specimens composed of both thin- and thick-walled elements. One possible explanation for this discrepancy is that the phloem tissue examined in both of these contributions was very close to the xylem, and may have consisted of immature phloem elements or cambial zone initials. Although Stewart (1951) illustrated sieve areas in his paper, the phloem overall is fairly crushed and distorted. Baxter's material (the type specimen of *M. endocentrica* [Baxter, 1949]) was re-examined and it clearly shows that mature phloem with sieve areas was present. Delevoryas (1955) suggested that *M. endocentrica* might represent a young stage in the development of *M. noei*. If so, then the production of fibers by the vascular cambium could be a phenomenon that develops later in the growth of the cambium. However, Delevoryas (1955) also placed *M. pandurata* (Stewart, 1951) in *M. noei*, but did not consider it to be a younger stage of stem growth. Much of the controversy over the presence or absence of fibers in Medullosa may be explained by the development of fibers from parenchyma cells in the older phloem, similar to the situation in *Callistophyton*. Thus, these cells would not be visible in developmentally younger material. The solution to this controversy must wait until a more detailed developmental study on phloem fibers in medullosan stems can be completed.

The vegetative anatomy of the medullosan pteridosperms has been compared many times to that of extant members of the Cycadales (e.g., Scott, 1899; Worsdell, 1906; de Fraine, 1912; Bancroft, 1914;
Delevoryas, 1955; Stewart and Delevoryas, 1956). Seward (1917), in particular, believed that the secondary xylem and phloem anatomy in these two groups was very similar, and Delevoryas (1955) noted that the stele in extant cycads could easily be derived from the typical stele of Permian medullosans by the loss of the "star rings." The phloem anatomy of Medullosa provides some support for the presumed relationship with extant cycads, especially at the level of tissue composition. The discovery of fibers in the secondary phloem of Medullosa is the first clear evidence that this cell type was produced as a normal part of the functional phloem in the Paleozoic seed ferns. Fibers are not known to occur in any of the other Carboniferous seed fern genera that have been examined (e.g., Callistophyton [Russin, 1981]; Lyginopteris [Williamson and Scott, 1896]; Heterangium [Hall, 1952]; Microspermopteris [Taylor and Stockey, 1976]; and Calamopitys [Galtier and Hébant, 1973]), and their presence in extant cycads has made comparison between these two groups difficult. The number of fiber cells in extant cycads may vary with development and position in the stem (Miller, 1919; Chrysler, 1926), and this may be the case in Medullosa, as well. Chrysler (1926), working with Microcycas, stated that fibers were scarce in the earliest-formed phloem becoming more abundant in later-formed layers. In Cycas media, Miller (1919) noted that fibers were generally more common than sieve cells. Cycad fibers sometimes appear to be in tangential bands, but these are much more irregular than those in Medullosa (Mettenius, 1861; Dippel, 1869; Chamberlain, 1911; Esau, 1969).
Below the level of cellular composition, the information on cycad phloem is limited. Several studies have concentrated on types and contents of parenchyma cells (i.e., albuminous vs. crystal-containing cells) (e.g., Chrysler, 1926). Sieve cells have been described as elongate with gradually tapering end walls. Oval-elongate sieve areas with numerous pores occur on both radial and end walls (Chrysler, 1926), and most sieve areas extend the full width of the radial walls (Dippel, 1869; Esau, 1969).

Since the phloem anatomy of the Carboniferous medullosans agrees in many respects with that of extant cycads, it would be interesting to examine phloem in some Mesozoic cycadophytes. There are few specimens with phloem preserved, since the majority of the fossil members of this group are known from leaf compressions (see, e.g., Mamay, 1976). Perhaps the best-known structurally preserved Mesozoic cycadophytes are the cycadeoids described by Wieland (1906; 1916). Chamberlain (1911) remarked that the phloem in Dioon appeared similar to that described by Wieland (1906) in Cycadeoidea wielandi. Both of these taxa contained a large number of phloem fibers and relatively few sieve elements in the secondary phloem, but the cells did not appear to be oriented in tangential bands. Details such as the length of sieve elements, location and size of sieve areas, etc. were not available.

One of the most complete descriptions of phloem in a Mesozoic cycadophyte was the contribution of Lignier (1901) on Cycadeoidea micromyela. Near the cambium, the secondary phloem consisted of alternating bands of thin-walled, elongate cells (presumably sieve cells) and crushed cells, which were identified as axial parenchyma.
Further away from the cambium, a few fibers were intercalated into the rows of parenchyma. As in extant cycads, the fibers became more numerous towards the periphery of the axis, and they seemed to replace sieve cells, which became rarer. Lignier's material was too poorly preserved to discern any details in longitudinal sections. Archangelsky and Brett (1963), and Gould (1971) noted the presence of phloem in the Triassic stems *Michelilloba* and *Lyssoxylon*, respectively, although in both cases the tissue was rather poorly preserved. Gould was able to discern fibers in radial or tangential rows and a few thin-walled cells, while Archangelsky and Brett identified fibers, sieve cells and phloem parenchyma, separated by parenchymatous rays.

The phloem in the few Mesozoic cycadophytes that have been described is similar to that seen in both the medullosan pteridosperms and the extant cycads, at least as far as the composition of the tissue is concerned. The arrangement of the cells is more irregular in both the Mesozoic and extant representatives than it is in the Carboniferous taxa. Below this level, however, there is not enough histological detail available on the sieve cells of Mesozoic cycadophytes to make a comparison either with Paleozoic seed ferns or with extant cycads and other gymnosperms.

The discovery of fibers within the functional secondary phloem in *Medullosa* strengthens the proposed phylogenetic relationship with the Cycadales. The occurrence of these cells in the medullosans and their absence in the other groups of Paleozoic pteridosperms is a character that has both taxonomic and phylogenetic importance.
PHYLOGENETIC TRENDS IN GYMNOSPERM PHLOEM

Most of the work on the phylogeny of phloem has been concerned primarily with angiosperms, and most often, with monocotyledons. Cheadle and Whitford (1941) examined sieve-tube members in a number of monocot taxa and proposed four evolutionary trends in the development of sieve tubes: 1) localization of more specialized sieve areas on end walls, 2) change from oblique to more horizontal end walls, 3) change from compound to simple sieve plates on end walls, and 4) change from well-developed to poorly-developed lateral sieve areas (Cheadle and Whitford, 1941). In a later contribution, Cheadle (1948) examined certain aspects of the structure of sieve-tube members quantitatively and was able to discern the following correlations: 1) transverse or slightly oblique end walls were correlated with simple sieve plates, 2) more oblique end walls were correlated with compound sieve plates, and 3) very oblique end walls contained only compound sieve plates. Cheadle also found that the least specialized sieve-tube members occurred in roots, and the most specialized in leaves and reproductive axes. Elements in the stem were generally intermediate between these two extremes. These contributions confirmed earlier studies which proposed that the primitive sieve-tube member would be most similar to the sieve cell of conifers, i.e., elongate with very oblique end walls and similar sieve areas on both side and end walls (e.g., MacDaniels, 1918; Hemenway, 1911; 1913). It is immediately obvious that the four evolutionary trends listed above parallel those described for xylem vessels (see, e.g., Bailey, 1953; Carlquist, 1975). However, shortening of vessel elements is generally considered to be a significant trend in the evolution of tracheary elements and this trend has been difficult to
examine in secondary phloem, due to the presence of further divisions of the phloem mother cells prior to maturation. Zahur (1959) tried to correlate septation of sieve-tube mother cells with the evolutionary advancement of particular taxa, but Carlquist (1975), based on some of the ecological constraints on xylem anatomy, felt that Zahur's phylogenetic hypotheses were too simplified to be totally accurate.

Most of the contributions on phloem evolution have assumed that the gymnospermous sieve cell represents the primitive type from which sieve tube members evolved, but little comparative work has been done on gymnosperms to confirm this hypothesis. Outer (1967) examined representatives of most of the families of living gymnosperms and placed them within a phylogenetic framework, based on cellular composition, arrangement of the cells within the tissue, and the type of the intercellular connections present. He distinguished three types:

1. **Pseudotsuga taxifolia type** — considered the least specialized form, with a simple, homogeneous axial system consisting primarily of sieve cells with a few scattered parenchyma cells and fewer albuminous cells. This type is found in many members of the Pinaceae.

2. **Ginkgo biloba type** — axial system consists of alternating, tangential bands of phloem parenchyma and sieve cells and fibers occur scattered within the parenchyma bands. This type is found in the cycads, Araucariaceae, and some of the Podocarpaceae and Taxaceae.

3. **Chamaecyparis pisifera type** — axial system of regularly repeating layers of phloem parenchyma, sieve cells, fibers, sieve cells, parenchyma, etc. Considered to be the most specialized type.

The author noted that, according to this phylogenetic grouping, the most primitive type of axial system (**Pseudotsuga**) occurs with the most advanced type of ray system (i.e., heterogeneous rays with marginal ray-tracheids). Similarly, the **Chamaecyparis** type contains relatively
simple homogeneous rays. Outer defined evolutionary trends in
gymnosperm phloem to consist of: 1) an increase in the amount of axial
parenchyma, 2) a decrease in the number of albuminous cells in the rays,
3) an increase in axial albuminous cells, 4) an increase in sclerenchyma
cells, i.e., fibers, and 5) an increasingly regular arrangement of cell
types in repeating, tangential bands. The basis for establishing the
direction of these trends appears to be the belief of earlier workers
that the conifers have generally undergone evolutionary reduction
(Outer, 1967). At the present time, our knowledge of the phloem anatomy
in fossil gymnosperms is too meager to offer a definitive statement on
the direction of evolutionary trends. However, the fossil record does
provide some idea of relative degrees of specialization in gymnospermous
sieve cells.

At the level of cellular composition, secondary phloem anatomy in
the seed ferns indicates that a complex arrangement of cell types was
present in gymnosperm taxa as early as the Lower Carboniferous (in
Calamopitys [Galtier and Hébant, 1973]). Although the majority of
pteridosperms contain only two cell types in their axial system (i.e.,
sieve cells and parenchyma), the regularity of their arrangement in
alternating bands provides some indirect evidence on the specialization
of the conducting cells. It has long been recognized that parenchyma
cells are associated with conducting elements in all vascular plants
(see e.g., Esau et al., 1953). This association can be relatively
nonspecific, as it is in the vascular cryptogams, or very specialized as
is the case for angiosperm sieve tube members and companion cells. Esau
et al. (1953) suggested that perhaps the increasing cytoplasmic
specialization of the sieve elements necessary for efficient conduction could be correlated with an increase in functional dependence between the sieve elements and neighboring parenchyma cells. This trend would reach its zenith in the angiosperms, but the association of gymnospermous sieve cells and albuminous cells can be very specific as well. A similar type of functional interdependence may have occurred in the Paleozoic pteridosperms and this hypothesis could be used to explain the regularity of the association between sieve cells and parenchyma bands in the secondary phloem of these plants. Certainly this aspect of phloem anatomy in the seed ferns illustrates a stage of evolutionary development that is far beyond that seen in the vascular cryptogams, either living or fossil. In addition, the existence of regularly repeating layers of cells and the presence of fibers in the phloem of Medullosa as early as the Carboniferous provide data that question the applicability of Outer's evolutionary classification of gymnosperm phloem.

The morphology of the conducting elements of these Carboniferous seed plants is similar to that seen in gymnosperms today. The sieve cells are elongate with very oblique end walls and numerous oval-circular sieve areas on their radial and end walls. Since length of the elements appears to be a variable character even in closely related taxa (see, e.g., Esau, 1969; Carlquist, 1975), the histological characters available for phylogenetic consideration are the location, size, and shape of sieve areas, the number of pores and the size of the pores. Unfortunately, these characters have not been analyzed in any quantitative detail in the extant gymnosperms, and the fossils generally
appear to be similar to living examples. The presence of discrete, well-defined sieve areas with regularly spaced pores and evidence of callose deposits in these Carboniferous specimens indicates that, as far as morphological features are concerned, the sieve cell in seed plants has changed little in 300 million years. The presence of callose cylinders in presumably functional phloem and the existence of definitive callose in older cell layers correlates well with the pattern seen in living plants, and indicates that these fossil sieve cells must have functioned similarly to their modern counterparts as well.

In summary, there appear to be two separate evolutionary trends in phloem anatomy that can be examined utilizing structurally preserved Carboniferous plants. Within the vascular cryptogams, evidence is provided that supports a change from typical parenchyma cells to the type of sieve cells present in the Carboniferous vascular cryptogams. In most cases, this cell type is intermediate between a parenchyma cell and typical gymnospermous sieve cells, i.e., it is somewhat elongate and narrow with horizontal to slightly oblique end walls. Sieve areas are scattered on the side and end walls, and individual pores are occasionally present. The second general evolutionary trend has been suggested from comparative studies on extant plants and involves the development of angiospermous sieve-tube members from typical gymnospermous sieve cells. This change would include a shortening of the cell; change in end wall configuration from very oblique to horizontal and increased specialization of the sieve areas. Although the fossil material examined here does not provide evidence for the advanced stages in this evolutionary scheme, the data do show that the
gymnospermous sieve cell was well-developed by the Carboniferous. The Paleozoic seed ferns all contain sieve cells that are closely comparable to living gymnosperms—they are very elongate and exhibit sieve areas that are specialized to the extent that they are confined to radial and end walls and are all of a similar size and shape.

CONCLUSIONS

The present study illustrates that an examination of phloem anatomy in fossil plants can contribute considerably to our understanding of the evolutionary history of this tissue system. Esau et al. (1953) suggest that the important factors in understanding trends of specialization in phloem tissue are, for the most part, cytophysiological, and therefore unavailable in fossil material. Based on comparative data from extant plants, these authors conclude that the most primitive type of sieve element should be little more than a modified parenchyma cell. The same conclusion can be reached, however, by examining the phloem anatomy of some of the fossil ferns and other cryptogams. Moreover, they suggest that the cytologic specialization of the sieve element has probably led to a functional interdependence between conducting cells and parenchyma cells. Comparisons between the phloem in vascular cryptogams and pteridosperms provides evidence of this same type of trend. In some of the less specialized Carboniferous ferns, phloem parenchyma is absent or only randomly arranged within the axis, whereas in the pteridosperms, the parenchyma is so regularly arranged as to imply a close functional relationship between these cells and the sieve cells. Additionally, progressive specialization of sieve areas and sieve pores can be observed in the fossil material. By analogy with extant phloem, the
trend from scattered single pores and poorly organized sieve areas to regularly-shaped sieve areas with evenly distributed pores and evidence of callose cylinders must reflect a physiological specialization for more efficient translocation of solutes.

Esau et al. (1953) cite the development of two types of phloem fibers within the secondary phloem of seed plants as possible indications of morphological specialization in secondary phloem. The first of these types differentiates close to the cambium as part of the functioning phloem, and the second occurs as fiber-sclereids within the non-functioning phloem tissue. Similar cell types have been observed in the fossil material, both types in *Medullosa*, and the second type only in *Callistophyton*. The development of fiber-sclereids in the presumably non-functional part of the phloem provides indirect evidence for a sequence of physiological and physical changes in the secondary phloem of seed ferns that parallels similar changes in extant taxa. Finally, these authors suggest that the type and arrangement of parenchyma cells in the phloem may also have phylogenetic significance. Although information on the distribution of phloem cells is available in the fossil specimens, the classification of cell types is limited to those that can be inferred from their location, shape, etc., (e.g., companion cells in the angiosperms and the so-called "erect" cells [= some albuminous cells] in some gymnosperms).

Finally, it is important to emphasize that the amount of information available on fossil phloem, especially in plants from other time periods outside of the Carboniferous, is quite limited. Although some phylogenetic trends have been suggested here, these trends will
probably be modified as further studies of phloem anatomy in fossil plants are completed.
Before the proposal of Cheadle and Whitford (1941) for a standardized terminology in phloem anatomy, the use of such terms as "sieve tube," "sieve field," "sieve plate," etc. in the literature was very haphazard. Most of the older contributions used the term "sieve tube" for all conducting cells in the phloem, regardless of their structural characteristics. Other terms were equally vague. As an example, the term "sieve field" was sometimes used to refer to an entire sieve area, and other times to a portion of a sieve area with closely spaced sieve pores. A list of the applicable terms proposed by Cheadle and Whitford (1941) and others (e.g., Eames and MacDaniels, 1947; Esau, 1950, 1969, etc.) is given here:

Sieve element — a generalized term to include all types of phloem conducting cells, i.e., sieve tube members and sieve cells. This term has been especially useful in studies on fossil phloem (see, e.g., Eggert and Kanemoto, 1977; Smoot, 1979) where preservation problems can affect the structure of the cell walls and thereby prevent a more detailed classification of cell types.

Sieve cell — a type of sieve element, most often exemplified by those in Pinus or other gymnosperms, in which the sieve areas are similar on both the side and end walls of the cell. Although the shape of the cell is not technically part of the definition of a
sieve cell, this type of element is commonly thought of as elongate with tapered end walls (compare to sieve tube members).

Sieve tube member=sieve tube element -- a type of sieve element in which the sieve areas are more specialized on end walls than on side walls. The shape of sieve tube members can vary from elongate with tapering end walls to short with transverse end walls.

Sieve tube -- series of sieve tube members aligned end-to-end
Sieve area -- variously shaped wall area containing clustered pores
Sieve plate -- highly specialized part of wall containing sieve areas.

Sieve plates usually occur on the end walls of sieve tube members and they may contain a single sieve area (=simple sieve plate) or numerous sieve areas (=compound sieve plate). Compound sieve areas are either scalariform (sieve areas in one row) or reticulate (sieve areas scattered).

In addition to these terms for conducting elements, there are a number of terms that refer to phloem parenchyma cells:

Companion cells -- These cells are generally considered to occur only in angiosperms. They are physiologically and ontogenetically related to the sieve tube members, i.e., both cells develop from the same initial.

Albuminous cells -- Although often closely associated spatially with sieve cells, these cells are not believed to arise from the same initial as the conducting element. They are characteristic of gymnosperms. They do appear to be physiologically related to the sieve cells and share many cytological similarities with
companion cells, i.e., dense cytoplasm, numerous plasmodesmata connecting them with sieve cells, no starch at maturity.

Other parenchyma cells present in the phloem do not appear to be as closely related to the conducting elements, either spatially or physiologically, and may store starch, tannins, crystals, etc. Phloem parenchyma cells are generally classified based on their contents, but this system obviously has limited applications in the anatomy of fossil phloem. Some authors (e.g., Chrysler, 1913; Barghoorn, 1940) have suggested that the albuminous cells in gymnosperms can be distinguished by their position at the margin of rays and by their greater height. However, Srivastava (1963a) found that shape and location of the cells was not an accurate method of distinguishing albuminous cells from other phloem parenchyma. He suggested that a combination of morphology, including interconnections with sieve cells, and physiology (i.e., the absence of starch at maturity) be used to define these cells.

In the fossil material examined here, phloem parenchyma cells have been classified as axial or ray parenchyma cells. Only in the secondary phloem of Medullosa is there any evidence of cells with slightly different shapes that occur at the margin of rays (see CHAPTER 6). Whether these cells represent true albuminous cells or not cannot be determined at this time.


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