Amer. J. Bot. 63(10): 1302–1310. 1976.

STUDIES OF PALEOZOIC SEED FERNS: ANATOMY AND MORPHOLOGY OF MICROSPERMOPTERIS APHYLLUM[1]

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ABSTRACT

The discovery of numerous specimens of the monostelic pteridosperm genus *Microspermopteris* in Pennsylvanian coal ball petrifactions from the Lewis Creek and What Cheer localities provides additional information about the anatomical and morphological variability within the genus. Specimens are now known up to 1.1 cm in diam that bear epidermal appendages in the form of variously-shaped trichomes. The external surface of the stem is further ornamented by longitudinal flaps of cortical tissue. Petioles exhibiting a single C-shaped vascular strand with abaxial protoxylem are produced in a 2/5 phyllotaxy. Large petiole bases that clasp the stem produce primary pinnae alternately. The presence of axillary branching appears similar to that reported in *Callistophyton* and *Lyginopteris.* Triarch to polyarch adventitious roots, some with secondary tissues, are produced at both nodal and internodal regions. Of the currently recognized monostelic seed fern genera, *Microspermopteris* is most similar to *Heterangium.* Information is presented that supports current ideas regarding the evolution of the gymnospermic eustele from protostelic Devonian ancestors.

THE GENUS *MICROSPERMOPTERIS* was initially described by Baxter (1949) from petrifaction material collected from the What Cheer locality of Iowa, with a subsequent variety added from material collected from the Fleming Coal of Kansas (Baxter, 1952). Recently, the taxon has been reported from several coals in Illinois (Mahaffy, 1975) and eastern Kentucky (Taylor and Stockey, 1975). In the initial description the genus was characterized as a leafless pteridosperm with an exarch, partially mixed protostele up to 5.0 mm in diam. Stems were described as being irregular in outline and lacking leaves. Multicellular emergences together with adventitious roots were described on some stem fragments. The genus was further characterized by the presence of secondary tissues, concentric branch traces, and distichous branching.

During the past several years we have accumulated a number of specimens of this plant from two petrifaction localities in North America, especially the Lewis Creek site in eastern Kentucky where it represents a common element of the flora. It is our intent in this paper to provide additional information about this taxon, offer a reinterpretation of several morphological features, and discuss the genus *Microspermopteris* in light of recent theories regarding the evolution of the gymnospermous habit.

The following description is based upon 36 axes representing numerous orders of branching. Specimens were collected from the What Cheer and Lewis Creek petrifaction localities which are designated Middle and Early Pennsylvanian, respectively (Good, 1975). Cellulose acetate peels were used to determine anatomical and morphological features. All specimens and slides are housed in the Paleobotanical Collections, Department of Botany, The Ohio State University, and include acquisition numbers 6,489–6,912, 12,177–12,420, 12,422–12,466.

DIAGNOSIS—*Microspermopteris aphyllum* (Baxter) Taylor et Stockey emend. Stems up to 1.1 cm in diam with mixed exarch protostele consisting of large metaxylem tracheids and up to 10 peripherally positioned protoxylem strands. Petioles arranged in 2/5 phyllotaxy, with single trace slightly C-shaped with abaxial protoxylem; petiole base large and clasping up to one half stem circumference, primary pinnae produced alternately; axillary branches with abundant secondary xylem. Cortex of thin-walled parenchyma with secretory cells in younger stems, and peripherally disposed longitudinal sclerenchyma; periderm of thick-walled radially aligned cells. Stem surface ornamented by longitudinal flaps of cortical tissue, and multicellular, typically flattened trichomes. Metaxylem tracheids elongate, with multiseriate bordered pits; protoxylem elements scalariform. Primary xylem pentagonal in cross section and divided into 5 sections by longitudinal parenchyma plates that radiate from stem center; protoxylem strands occur in pairs, one strand on each side of a parenchyma plate.

[1] Received for publication 17 December 1975.
The authors are indebted to Dr. John W. Hall for making several What Cheer specimens available for study, and to the National Science Foundation for partial support of this research (BMS74-21105).

Secondary vascular tissues well-developed, secondary xylem tracheids with uni- and multiseriate bordered pits. Xylem rays up to 2 cells wide. Triarch to polyarch adventitious roots, some with secondary tissues, arising at both nodal and internodal regions.

Type species—*Microspermopteris aphyllum* Baxter 1949, p. 297–298, pl. 2, Fig. 1–4; pl. 3, Fig. 5–7; pl. 4, Fig. 8–12.

Synonymy—1952. *Microspermopteris aphyllum* var. *kansensis* Baxter; Trans. Kansas Acad. Sci. 55: 101–103.

DESCRIPTION—*General features*—Stems range from 0.5–11.0 mm in diam, with the most complete specimen extending approximately 38.0 cm through the coal ball. Most stems exhibit a sinuous habit in the matrix making longitudinal stem sections difficult to obtain and possibly reflecting a liana or shrub-like growth habit. A pentagonal protostele containing longitudinal plates of parenchyma (Fig. 1, 4, 15) is surrounded by a well-developed zone of secondary xylem. To the outside of this tissue is a vascular cambium, a zone of secondary phloem, and a parenchymatous cortex containing patches of sclerenchyma and secretory cells (Fig. 1, 4, 7, 11, 16). Multicellular trichomes and longitudinal cortical flaps extend from the stem surface (Fig. 2, 5, 8, 9, 25).

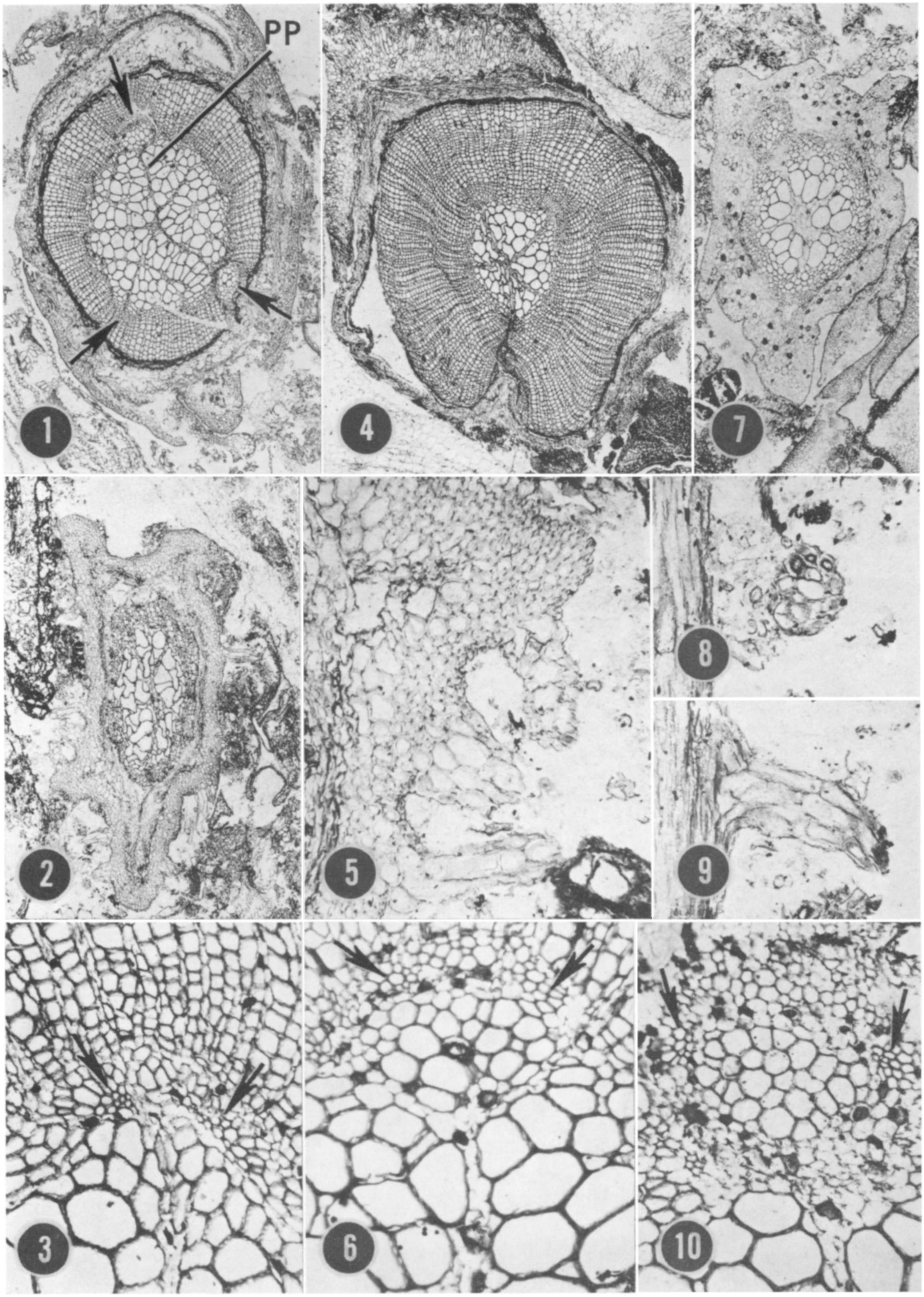
Primary tissues—In transverse section the primary xylem is typically pentagonal in outline as defined by radiating parenchyma plates (Fig. 1, 4). At the more distal levels of the stem this configuration is maintained by clusters of metaxylem tracheids separated by patches of parenchyma (Fig. 7). In the stem that contains the most secondary xylem (Fig. 4) (Lewis Creek) the primary xylem measures 1.1 mm in cross sectional diam, whereas the stem illustrated in Fig. 1 (What Cheer) has approximately one-third the secondary tissue development and the primary xylem is 1.7 mm in diam. The stem illustrated in Fig. 7 is represented almost entirely by primary tissues.

The protoxylem strands in *Microspermopteris*, as determined by cell diameter and presence of annular-scalariform wall thickenings, are situated on either side of the parenchyma plates that radiate from the stem center (Fig. 3). Figures 3, 6, and 10 illustrate successively higher levels through protoxylem strands in a region of trace emission. In Fig. 3 the arrows on either side of the metaxylem parenchyma indicate the small protoxylem strands. At a slightly higher level (Fig. 12) the 2 strands unite to form an abaxial C-shaped bundle containing a circular strand of large metaxylem tracheids. After the trace has been formed it remains within the stem cortex for some distance (approximately 6.0 mm) before passing outward into the petiole base.

The most conspicuous aspect of the cross sectional configuration of *Microspermopteris* is the presence of large, angular metaxylem tracheids (Fig. 1). In longitudinal section, metaxylem elements measure up to 1.0 mm and possess slightly tapered end walls, and multiseriate, simple-reticulate-bordered pits (Fig. 19). Parenchyma in the metaxylem is organized into longitudinal plates up to three cells wide that radiate from the center of the stem to form the characteristic pentagonal stem configuration (Fig. 4). We have observed a larger number of plates in some stems; however, in all instances this increase in number of plates appears to have resulted from additional divisions of the original five plates (Fig. 1).

Axillary branching—One of the newly interpreted features of *Microspermopteris* is the presence of axillary branching (Fig. 24). Figures 12–14, 17–18 illustrate progressive stages of stem and petiole separation, and axillary branch origin. The production of an axillary branch begins with a large amount of secondary xylem extending laterally from the stem stele (Fig. 13). At a slightly higher level (Fig. 12, 14) it becomes separated to form a terete axillary branch stele. Figure 17 represents the axillary branch, traced for a distance of approximately 5.3 mm. In this specimen the more distal organization of the axillary branch could not be determined because of faulty preservation. In tranverse section the axillary branch stele is circular with a central region of small crushed cells possibly representing protoxylem elements or parenchyma, surrounded by a zone of up to 12 rows of secondary xylem tracheids. At the point of axillary branch origin there is a distinct interruption in the secondary xylem of the stem stele (Fig. 17, 18, arrows). At higher levels a few files of secondary xylem tracheids are present.

Petiole—The petiole or rachis clasps the stem axis for approximately one half of the diameter of the stem at the level of axillary branch formation (Fig. 12, 24). At higher levels the cross sectional configuration of the petiole is V-shaped to almost flattened (Fig. 17, 21). In several specimens it has been possible to trace alternately arranged primary pinna axes (Fig. 20–22). The pinna trace consists of a single lateral xylary extension that shows the same anatomical organization as the petiole trace. Two longitudinal extensions of tissue ornament the adaxial surface of the petiole near the level of pinna trace formation (Fig. 21–22). It has not been possible to demonstrate conclusively more than a single order of petiole branching or the presence of laminar pinnules.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Secondary tissues—In almost all of the stems examined there is evidence of some secondary development. In older stems (Fig. 4) secondary xylem consists of radially aligned tracheids interspersed with vascular rays. Wood segments vary from 1–4 cells wide with the individual tracheids square to rectangular in outline. Tracheids in the secondary xylem are approximately one eighth the cross sectional diam of the metaxylem elements. Pitting is similar to that found on the metaxylem tracheids. Bordered pits are also present on the radial walls of secondary xylem tracheids, but typically lack a regular arrangement. Xylary rays are constructed of procumbent parenchyma that is organized in both uniseriate and biseriate files. A narrow, poorly preserved cambial zone is present to the outside of the secondary xylem (Fig. 1, 16).

Small, rectangular sieve cells up to 25 μm in diam and phloem parenchyma constitute the zone of secondary phloem (Fig. 11). The smaller phloem parenchyma cells are organized in tangential chains of 2–5 cells that alternate with larger cells, presumed to be sieve elements. This is similar to what has been described in *Callistophyton* (Rothwell, 1975). In the stem illustrated in Fig. 11 this region is approximately 0.3 mm thick. Preservation does not allow for the positive identification of sieve areas. Phloem rays show some increase in width toward the periphery of the stem (Fig. 11). Parenchyma of the phloem rays is identical to the parenchyma of the plates in the metaxylem.

Several stems show distinct differences in symmetry (Fig. 4). This feature is quite noticeable in relatively mature stems with extensively developed secondary xylem, and appears to be the result of gaps formed in the secondary xylem when branches are produced (Fig. 4, 17, 18).

Cortex—The cortex is irregular in outline and is constructed of thin-walled cells. Toward the periphery of the stem the cortical cells decrease in diameter and possess slightly thicker walls. We have not been able to distinguish with any degree of regularity the two-parted cortex reported by Baxter (1949) in the initial work on the genus, nor a zone of tangentially aligned sclerotic cells. Vertically aligned mucilage cells are scattered among the parenchyma of the cortex of some stems (Fig. 7). The presence of these cells, as well as the tangentially oriented sclerotic fibers, appears to depend upon the age of the stem, degree of preservation, and level of section. In some stems a well-developed periderm is present within the cortex. It consists of up to several rows of radially aligned cells that probably constitute the phelloderm, and an outer, thinner zone of thick-walled cells of the phellem (Fig. 16).

Longitudinal lateral extensions of the cortex give the more distal stems a wing-like appearance (Fig. 2, 7, 23). These lateral extensions lack a distinct morphology and reflect the irregular outline of the cortex. In addition to these cortical flaps, there are irregularly-shaped multicellular trichomes (Fig. 5, 8, 9). They may be sharply tapered (Fig. 9), or clustered into several finger-like projections that arise from a common, expanded base (Fig. 5). These structures are present at all levels of the stems (Fig. 25), but appear to be more common along the distal parts of axes, and at nodes. These structures do not appear to have been produced in any orderly arrangement.

Roots—Triarch to polyarch adventitious roots, some showing well developed secondary tissues are present at all levels along the stems except on distal axes (Fig. 25). Roots are present at both nodal and internodal levels. Many branch and display a sinuous course throughout the coal ball similar to that exhibited by small stems. Older roots may be distinguished from younger stems with small amounts of secondary xylem by the absence of radial parenchyma plates. Both exhibit prominent mucilage ducts in an irregularly shaped cortex.

DISCUSSION—There are a number of so-called monostelic seed ferns to which *Microspermopteris* may be compared. These include the genera *Stenomyelon*, *Lyginopteris*, *Callistophyton*, *Schop-*

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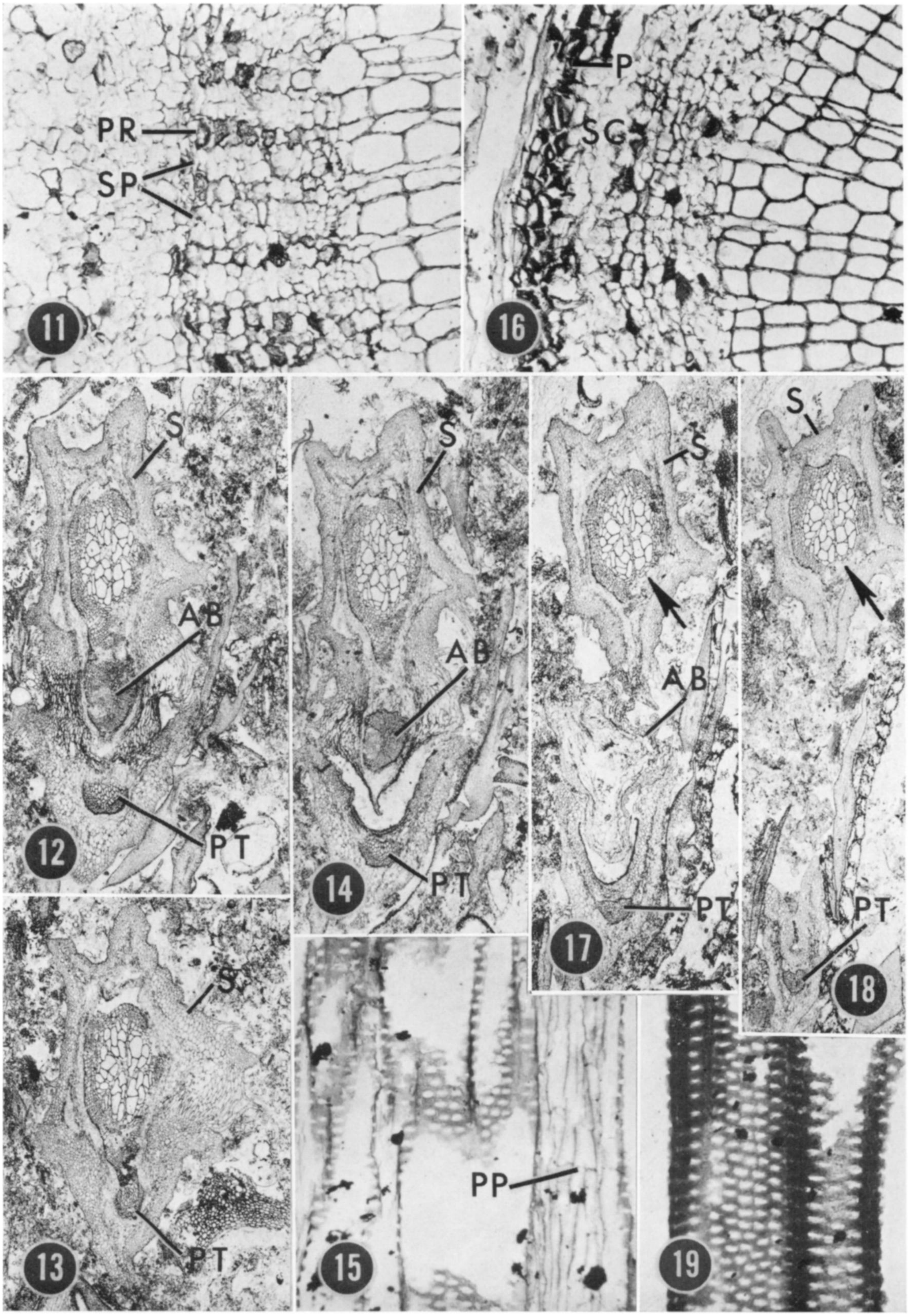
Fig. 1–10. *Microspermopteris aphyllum*. **1.** Transverse section of stem showing pentagonal primary body, well-developed secondary xylem, and extraxylary tissues. Arrows indicate positions of departing petiole traces. C.B. 1298 B (1)I(2) #10. × 16. **2.** Transverse section of stem showing irregular outline and numerous cortical projections. C.B. 198A, #106. × 25. **3.** Section showing formation of petiole trace. Arrows indicate position of protoxylem elements. Larger cells represent metaxylem tracheids. C.B. 6057 C top, #123 β. × 95. **4.** Transverse section of stem with well-developed secondary xylem. Note pentagonal configuration of primary body. C.B. 6057 C top, #123 β. × 16. **5.** Transverse section of stem showing cortical projections. C.B. 198A, #106. × 100. **6.** Formation of petiole trace at slightly higher level than that of Fig. 3. Arrows indicate position of protoxylem tracheids. C.B. 1298 B(1)I(2), #5. × 95. **7.** Transverse section of young axis showing secretory cavities in cortex and irregular stem outline. Note small amount of secondary xylem. C.B. 1061 B bot, #3. × 24. **8.** Transverse section of multicellular trichome. C.B. 198A side, #30. × 100. **9.** Longitudinal section of multicellular trichome. C.B. 198A side, #30. × 100. **10.** Transverse section of petiole trace at slightly higher level than Fig. 6. Arrows indicate the position of protoxylem elements. C.B. 1298 B(1)I(2), #5. × 95. pp, parenchyma plate.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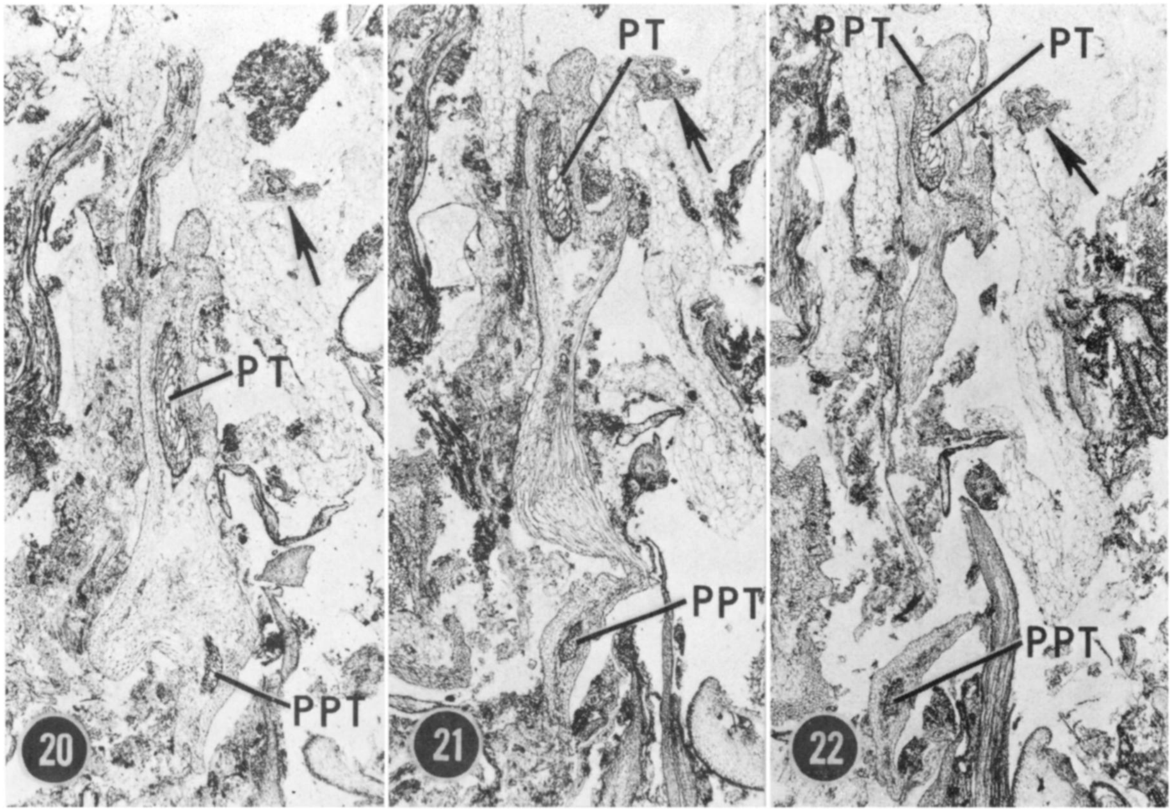

Fig. 20–22. *Microspermopteris aphyllum.* Successive series showing departure of primary pinnae. **20.** Departing pinna trace still within petiole cortex. C.B. 6057 C top, #91. × 17. **21.** Higher level than Fig. 20 showing primary pinna almost separated from petiole. Note the flattened configuration of the pinna axis. C.B. 6057 C top, #123 β. × 47. **22.** Still higher level showing pinna separated from petiole, and initiation of new trace from opposite side of petiole. C.B. 6057 C top. #146 β. × 17. Arrow in each figure depicts primary pinna axis from lower level. PT, petiole trace; PPT, primary pinna trace.

fiastrum, *Rhetinangium*, *Calamopitys*, and *Heterangium*. Of these the genus *Heterangium* shows the closest affinity to *Microspermopteris* when only features of the stele are considered.

Specimens of *Heterangium* are relatively rare in North American petrifaction material. Graham (1935), and Fisher and Noé (1938) reported the occurrence of the genus in coal balls from the Illinois Basin, while Andrews (1942) detailed the stelar anatomy of a new species, *H. americanum*. The recent study by Shadle and Stidd (1975) has expanded our knowledge of the rachial anatomy and pinnule organization of the *Heterangium* frond.

Stems of *Heterangium* extend up to 5.0 cm in diam and are characterized by irregular branch-

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Fig. 11–19. *Microspermopteris aphyllum.* **11.** Transverse section showing extraxylary tissues. C.B. 1298 B(1)I(1) bot, #2. × 100. **12.** Transverse section at level where stem, axillary branch, and petiole are attached. Note interruption produced in stem secondary xylem near point of branch departure. C.B. 198 B bot, #226. × 15. **13.** Section of stem below that of Fig. 12 just after petiole trace departure. C.B. 198 B bot, #313. × 15. **14.** Transverse section slightly higher than Fig. 12 in which petiole has separated from stem. Note clasping C-shaped configuration of petiole. C.B. 198 B bot, #205. × 15. **15.** Radial section of metaxylem showing longitudinal organiztion of parenchyma plate. C.B. 6000 I side, #214, × 110. **16.** Transverse section of stem showing periderm and sclerenchyma of cortex. C.B. 1298 B(1)I(2) #10. × 95. **17.** Transverse section at level higher than Fig. 14 with axillary branch almost separated from stem. Axillary branch stele is missing. C.B. 198 B bot, #157. × 15. **18.** Transverse section considerably higher than Fig. 17 showing relationship between stem and petiole. C.B. 198 B bot, #95. × 15. **19.** Circular bordered pits of metaxylem tracheid. C.B. 198 A side, #47. × 180. AB, axillary branch; P, periderm; PP, parenchyma plate; PR, phloem ray; PT, petiole trace; S, stem; SC, sclerenchymatous cortex; SP, secondary phloem.

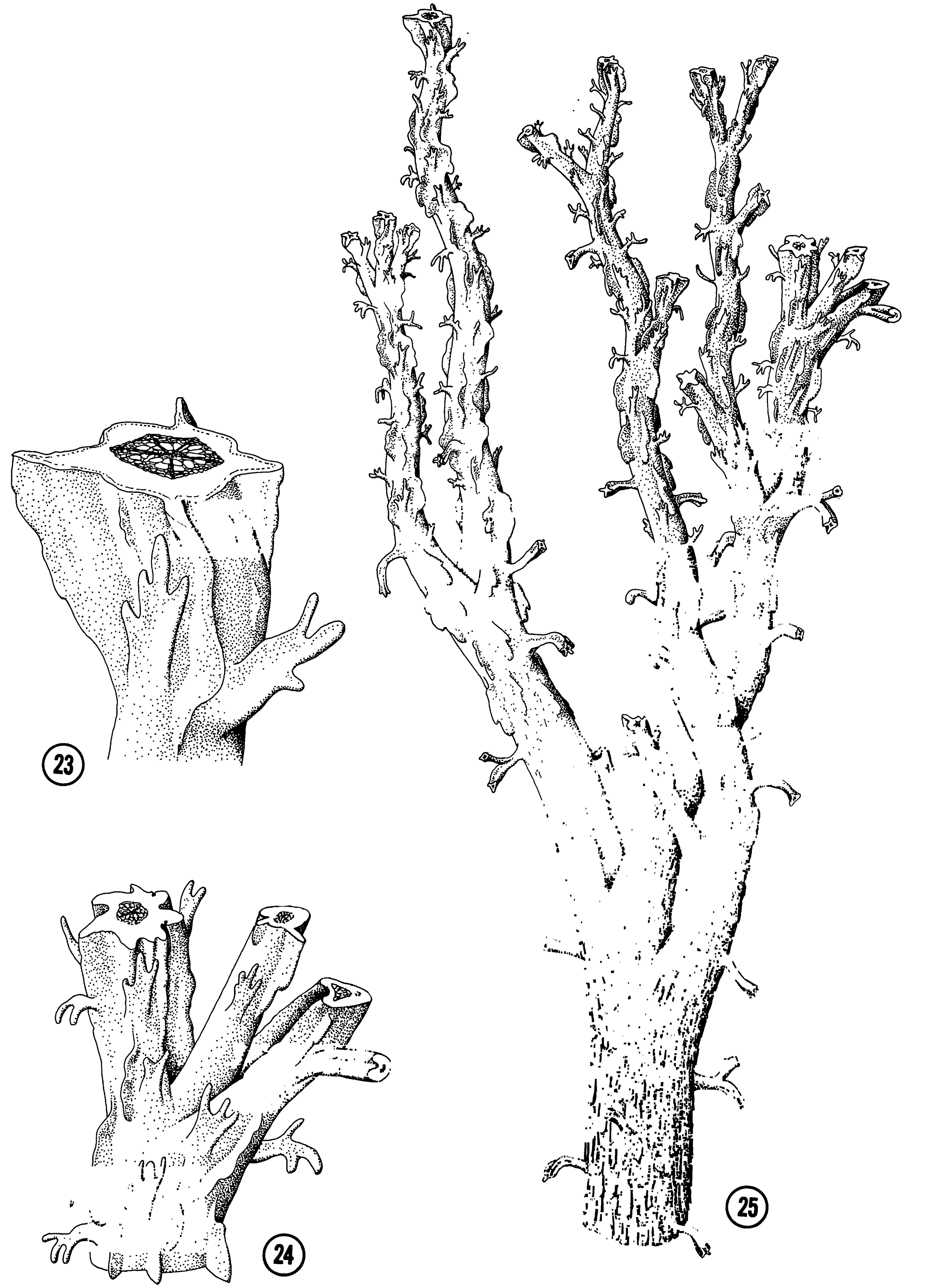

Fig. 23–25. *Microspermopteris aphyllum*. **23.** Stem segment showing irregular outline of cortex and flattened epidermal trichomes. **24.** Segment of stem at node showing origin of axillary branch. Note clasping petiole. **25.** Suggested reconstruction showing stem morphology.

ing. The primary body consists of a mixed, mesarch protostele in which the large tracheids occur in clusters surrounded by parenchyma. Secondary xylem is produced in varying amounts. Radially elongate bands of fibers are present in the outer cortex, while the inner cortex is delimited by horizontal plates of thick-walled cells. One of the principal differences between the two genera is the number of traces to the petiole. In *Microspermopteris* one trace is present, while the frond of *Heterangium* is vascularized by 2–10 strands depending upon the level of section (Shadle and Stidd, 1975).

Vascular rays of *Heterangium* broaden toward the outside of the stem and may appear wedge-shaped, while those of *Microspermopteris* remain relatively uniform throughout their extent. The mixed, mesarch protosteles of most *Heterangium* axes usually contain more parenchyma than do steles of *Microspermopteris*. The large metaxylem tracheids of *Heterangium* are more circular in transverse section than those of *Microspermopteris*. Throughout the course of this study we have noticed a small number of stems of *Heterangium* from the Lewis Creek and Derringer Corners localities that have primary bodies that resemble the condition seen in *Microspermopteris* axes; i.e., the presence of 5 prominent large wedges of metaxylem tracheids and radiating arms of parenchyma. A few of these *Heterangium* axes have uniseriate-biseriate rays with just a few wedge-shaped vascular rays, but exhibit the typical petiole anatomy of *Heterangium*. Until the reproductive organs are known for both *Microspermopteris* and *Heterangium*, petiole anatomy will continue to be the distinguishing character.

During recent years there has been an increased interest in the primary body of vascular plants. This has been brought about principally through the work of Beck and co-workers (Namboodiri and Beck, 1968 a, b, c) who have described in detail the primary vasculature in a number of coniferophytic gymnosperms. Beck (1970) has convincingly demonstrated that the eustelic form like that of *Lyginopteris* or *Callistophyton* has evolved by longitudinal dissection of a protostele followed by modification of columns of vascular tissue into discrete sympodial systems arranged in a cylinder. Beck has postulated a phylogenetic series beginning with a number of protostelic forms included within the Calamopityaceae beginning with species of *Stenomyelon* and *Calamopitys* and extending to *Lyginopteris*. *Stenomyelon tuedianum* (Kidston and Gwynne-Vaughan, 1912) is interesting in that it consists of a protostele divided into 3 longitudinal columns by radiating bands of parenchyma. Despite the three-angled appearance of this stem in transverse section, traces originate from 5 positions. This is similar to the organization in *Microspermopteris* where there are also 5 axial bundles. In *Microspermopteris*, however, the protoxylem strands occur on either side of the outer edges of the metaxylem parenchyma plates, with each member of a pair arising from a different axial bundle. In *S. tuedianum*, traces are not positioned near the parenchyma plates. In *Stenomyelon* the presence of a cylindrical system of 5 sympodia is identical to that described in *Callistophyton* (Rothwell, 1975) and *Lyginopteris*; however, in *Stenomyelon* the basic protostele is maintained. Whether or not the metaxylem wedges and associated protoxylem strands of *Microspermopteris* should be regarded as sympodia can not be stated with certainty at this time. We have been able to follow the parenchyma plates for up to 3 cm. Serial transverse sections indicate that they remain intact for a considerable extent throughout the stem; however, they do undergo some change in position.

In addition to the similarity of the sympodial system in *Microspermopteris* to that of some other monostelic seed ferns, the stelar organization may be regarded as occupying an intermediate position between some calamopityean axes of Devonian age and younger eustelic Carboniferous forms, with reference to the amount of parenchyma. In a few stems, especially those from the What Cheer site, we have observed a further dissection of the metaxylem wedges by secondary files of parenchyma (Fig. 1). These parenchyma plates, however, generally arise at right angles to the principal metaxylem plates. At some levels the number of these secondary plates increases to the extent that relatively small clusters of metaxylem tracheids become surrounded by parenchyma. This organization is quite similar to the primary xylem organization of *Heterangium*. Thus *Microspermopteris* may be added to a series that demonstrates a conversion from the protostele to the eustele by an increasing medullation of the primary xylem cylinder.

There are slight differences between *Microspermopteris* axes from different localities. For example, stems from What Cheer typically display larger primary xylem cylinders and lesser amounts of secondary xylem than those of equivalent size from Lewis Creek. The What Cheer stems show a further dissection of the 5 primary xylem segments by additional parenchyma plates that extend at right angles to the 5 main plates (Fig. 1, 4). Whether this feature is a phylogenetic trend, since Lewis Creek fossils are Early Pennsylvanian and What Cheer, Middle Pennsylvanian, or merely a geographical variation, is not certain.

Of additional interest is the presence of epidermal trichomes and cortical flaps of tissue arising from the stems of *Microspermopteris*. There are numerous Devonian genera that produced epidermal appendages varying from what have been described as spines to papillae (e.g., *Crenaticaulis* (Banks & Davis, 1969), *Kaulangiophyton* (Gensel, Kasper and Andrews, 1969), *Sawdonia* (Hueber, 1971), *Pertica* (Kasper and Andrews, 1972), *Psilophyton* (Banks, Leclercq and Hueber, 1975). Epidermal appendages have been described on the stems of *Callistophyton* (Rothwell, 1975) and *Lyginopteris* (Oliver and Scott, 1904) in the form of glandular trichome-like emergences. As far as can be determined from the literature no other supposed monostelic seed fern genera are known with epidermal trichomes or cortical flaps of tissue. It is of interest to note that the surface of *Stenomyelon tuedianum* is characterized by epidermal emergences that vary from short and blunt to elongate forms with swollen ends. The authors suggest that they may represent transverse sections of longitudinal ridges of the stem (Kidston and Gwynne-Vaughan, 1912).

Microspermopteris may now be included with *Callistophyton* and *Lyginopteris* as examples of monostelic seed ferns in which axillary branching is present. Rothwell (1975) has demonstrated the presence of axillary buds in *Callistophyton* consisting of a mound of parenchymatous tissue, in the smallest buds, with two associated cataphylls. In some cases the bud, which is clothed in a mass of multicellular hairs, becomes an axillary branch with abundant secondary tissue. Oliver and Scott (1904) reported the presence of "bud-like structures" in *Lyginopteris* (= *Lyginodendron*) which are borne in the axils of leaves, and are also clothed with long and often glandular "emergences." These buds also appear as young or arrested branches in the axils of leaves on larger stems. Associated with the axillary branch of *Microspermopteris* are groups of multicellular epidermal trichomes that also occur on younger stems. Additional specimens of larger stem fragments may yet determine whether the axillary branch gave rise to reproductive structures or was merely an axillary bud giving rise to vegetative foliage.

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