

STELASTELLARA BAXTER, AXES OF QUESTIONABLE GYMNOSPERM AFFINITY WITH UNUSUAL HABIT — MIDDLE PENNSYLVANIAN

WILLIAM A. DIMICHELE and TOM L. PHILLIPS

Botany Department, University of Illinois, Urbana, Ill. (U.S.A.)

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ABSTRACT

DiMichele, W.A. and Phillips, T.L., 1979. *Stelastellara* Baxter, axes of questionable gymnosperm affinity with unusual habit — Middle Pennsylvanian. *Rev. Palaeobot. Palynol.*, 27: 103–117.

Two specimens of *Stelastellara* are described from Middle Pennsylvanian age coal balls from mid-continent United States. The stellate main axis of both specimens has a solid, exarch, actinostele with elliptical to circular bordered pitting, secondary growth and a distinctive cortex with differential thickenings. One axis is assigned to *S. parvula*; it divides sympodially at one end into four typical *S. parvula* axes. A second specimen described as a new species, *S. baxteri*, is 6 mm in diameter, highly stellate with primary xylem ribs extended radially up to 1.25 mm and with radially elongate and thickened cortical cells. Along the 5 cm length, seven endogenous structures are produced, mostly from one face. The axes are largely root-like and the morphological alternatives are considered. A gymnosperm affinity is suggested. The peculiar anatomy of the root-like axes and lack of *in situ* evidence suggest the possibility of some kind of a perched habit.

INTRODUCTION

Relatively few swamp plants of doubtful or unknown general affinities have been discovered from coal balls in recent decades. With few exceptions, the swamp plants from Pennsylvanian age coal balls represent lycopods, ferns, sphenopsids, pteridosperms, or cordaites. Despite their antiquity, the plants are morphologically quite advanced, exhibiting well-defined stems, roots and leaves and ranging from simple to very complex anatomy. Anatomically there are some very simple ferns and pteridosperms, but it is relatively exceptional to study well-preserved axes from coal balls and lack firm interpretations of their morphology and affinities. Small roots are the most common exception, but usually these can be found related to other identifiable organs of the plants.

Stelastellara proves the exception, and the discovery of the attachments of the root-like axes of *S. parvula* to a larger axial system still affords a very limited means by which to determine its natural affinities. In our descriptions we have also recognized a second species of the genus which is larger and also protostelic. While this augments significantly what we know about

the genus, there is still a lack of clear-cut distinctions among specimens between root and stem anatomy. We suspect that *Stelastellara* exhibited some kind of unusual habit, perhaps as a small liana or epiphyte. From its peculiar anatomy one cannot safely assume that the plant was autotrophic.

Stelastellara is known only from the initial discovery of the genus by Baxter (1965). The parts of the plant are all similar root-like axes, less than 4 mm in diameter with lengths up to 10–14 cm, showing no nodes, leaves or branches; the only departing (endogenous) traces, in two of his twelve specimens were imperfectly preserved, and there was no indication of the type of structure supplied. The three unusual features of these axes are the peculiar stelar outline and its relationship to the non-vascular tissues, the frequent presence of some type of secondary growth, and the “collenchyma-like” cortex. These serve to distinguish *Stelastellara* from other polyarch, exarch actinostelic axes we have seen in coal balls. The axes described by Baxter (1965) had 5–10 separate primary strands of xylem (eustelic) with a pith region. The whole stelar system appears to be stellate (hence the name) in cross-section rather than circular as in most axes. Periderm was of endogenous origin, perhaps in the pericycle, as in roots and normally preceded the development of secondary xylem which lacked rays found in typical wood. The cortex is peculiar because of tangential wall thickenings. Baxter’s specimens were from the Middle Pennsylvanian of Iowa and Kansas; our specimens are also Middle Pennsylvanian in age from Iowa, Illinois, Indiana and Kentucky.

Within our collection of specimens are two actinostelic axial systems which include a sympodially divided system bearing *S. parvula* axes (Plates I–III) and a highly stellate, larger axis which frequently emits endogenous traces mostly along one face (Plate IV). The latter is described as a new species. A gymnosperm affinity is suggested by the combination of elliptical to circular bordered pitting of the metaxylem tracheids, the seriated, possibly secondary xylem tracheids, and the eustelic configuration of parts of the plant axis.

MATERIALS AND SOURCES

Specimens of *Stelastellara* were examined from 10 coal balls stratigraphically from as low as the coals in Iowa and Indiana, considered to be correlative to the Murphysboro Coal Member of Illinois, near the lowermost part of the Spoon Formation, up to the “Baker” coal member, Lisman Formation of Kentucky. All are Desmoinesian in age or middle Pennsylvanian. Coal-ball numbers, slides, their stratigraphic occurrences and locality sources are given below.

Specimen 18046, from A. Huyser’s Star Mine, SW of Oskaloosa, Iowa, Albia 15’ Quad (SW, NW Sec. 10, T74N, R17W). According to M.J. Avcin (personal communication), Iowa Geological Survey, the coal is correlative to the Murphysboro Coal Member of Illinois; specimens 9936, 10262, 10291, 10347, 12400, 12396, and 19188, slides I13739–13803, from the Maple

Grove Strip Mine, unnamed coal member (also considered equivalent to the Murphysboro Coal Member of Illinois according to R.A. Peppers (Illinois State Geological Survey) Staunton Formation, Raccoon Creek Group, Cayuga, Fountain Co., Indiana, Newport Quad. (Sec. 34, T18N, R9W); 12483, from the Sahara Coal Company Mine No. 6, Herrin (No. 6) Coal Member, Carbon-dale Formation, Kewanee Group, Saline Co. Illinois, Carrier Mills Quad. (Sec. 30, T9S, R5E); 7535, slides I13804—13910, from the "Baker" coal member, Lisman Formation Providence, Webster Co., Kentucky, Providence 7 1/2' Quad. (37°24'52 1/2"N, 87°46'9"W).

DESCRIPTION

All of the photographic illustrations (Plates I—III) of the *S. parvula* specimens have the same orientation with the same magnification ($\times 32$). The larger axis of the new species (Plate IV, 10, 11) is one half of that ($\times 16$).

STELASTELLARA PARVULA BAXTER

Branching

The main axis of the branched specimen of *S. parvula* is 7.0 mm long. It is 1.9 mm in diameter above the zone of branching. Four typical *S. parvula* axes emanate from the base of the main axis; they range in diameter from 0.89 mm to 1.54 mm and were preserved up to a maximum length of 1 cm (Fig.1). Orientation of the specimen is based partly on the sympodial branching pattern with the divisions presumably substrate-oriented and partly on the bipolar diminution of secondary growth upward on the main axis and downward in the branch divisions. The interpretive options seem to be either that of a specialized branched root system or a transition between a cauline axis and basal roots. This is discussed later.

The hexarch actinostelic main axis divides into six vascular strands, each with one protoxylem group, continuous with those of the main axis. These individual strands terminate basally and may bear root-like divisions which flare outward and extend downward as shown in Fig.1. There is one principal root-like division, hexarch as in the main axis, three diarch to tetarch divisions, and two poorly developed, minor vascular extensions which abruptly terminate near the main axis. The four major axes, however, are clumped together without indications of *in situ* growth.

Main axis

The main axis is exarch with a solid actinostele through most of its preserved length (Plate I, 1—4). It sympodially branches basally with each of the six xylary arms of the actinostele continuous with a division (Plate II, 6, 7; III, 8, 9). Upwardly it is progressively more poorly preserved, lacking secondary growth on one side and the integrity of the central xylem becomes indistinct (Plate I, 1).

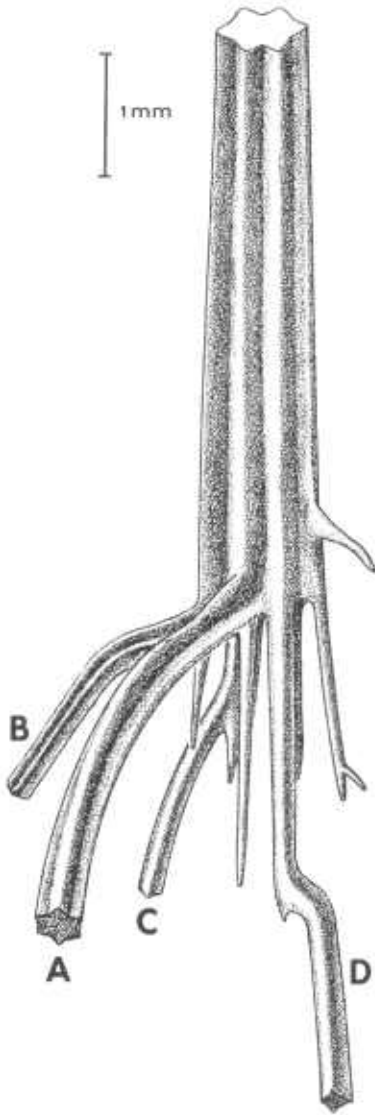


Fig. 1. Partial reconstruction of the primary xylary system of *Stelastellara parvula* showing the sympodial branching into axes labeled A–D; anatomical cross-sections representative of this sequence are shown in Plates I–III. Further explanation is given in the text.

PLATE I

- All plates of *Stelastellara parvula* (1–9) are of same magnification, $\times 32$, and orientation.
- 1–4. *Stelastellara parvula* main axis. Representative cross-sections downward (see Fig. 1) through main axis to beginning of branching; series continued in Plate II and III. Protoxylem poles (PX and arrow) are not covered by secondary xylem which is unevenly developed about the axis and increases in thickness basally. Slides I 13742, 13747, 13749, 13756.
 5. *Stelastellara parvula* axes derived from branching of main axis. A–D correspond to designations of axes in Plate III, 9 and Fig. 1. Slide I 13787.

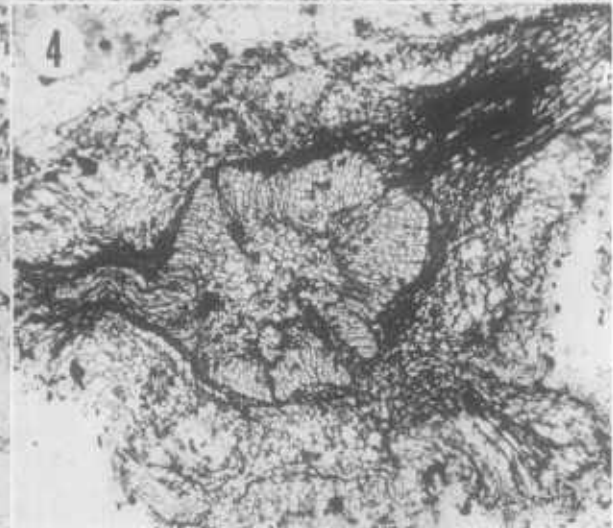
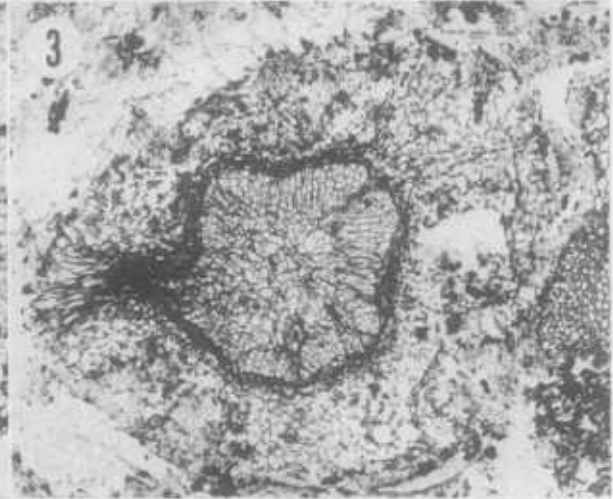
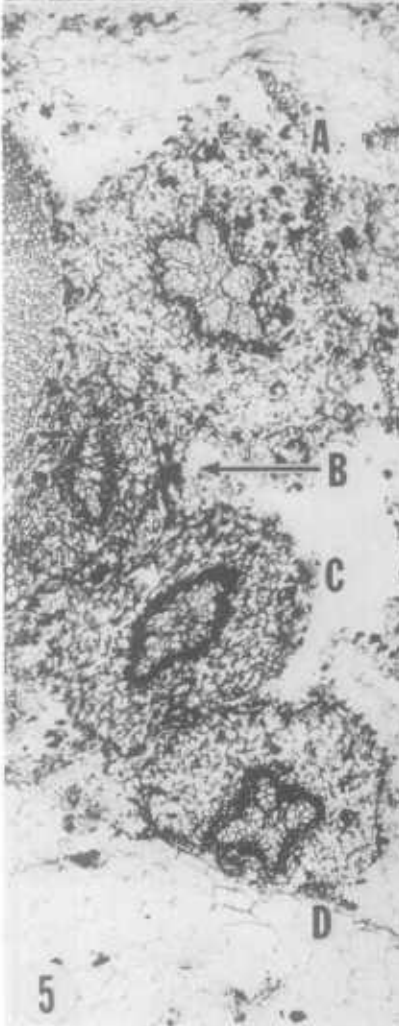
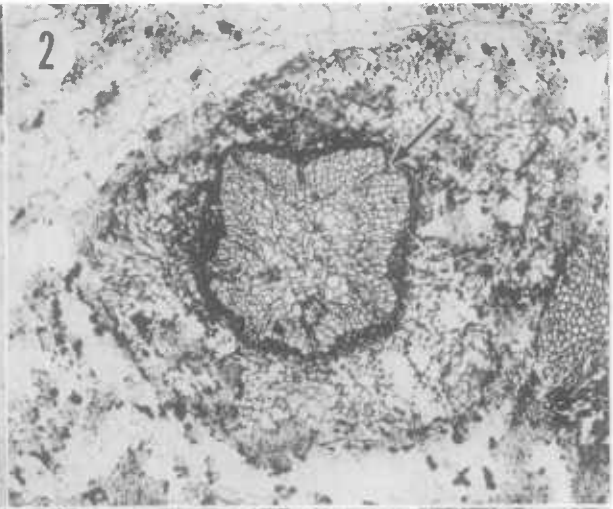
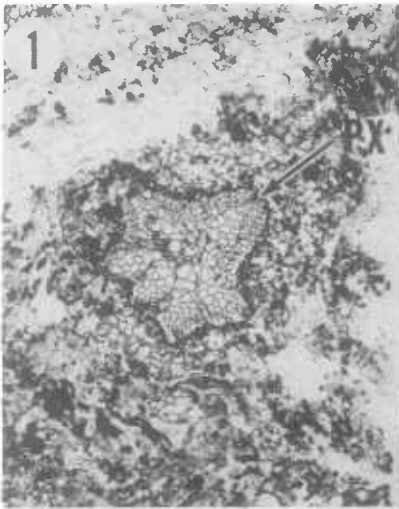
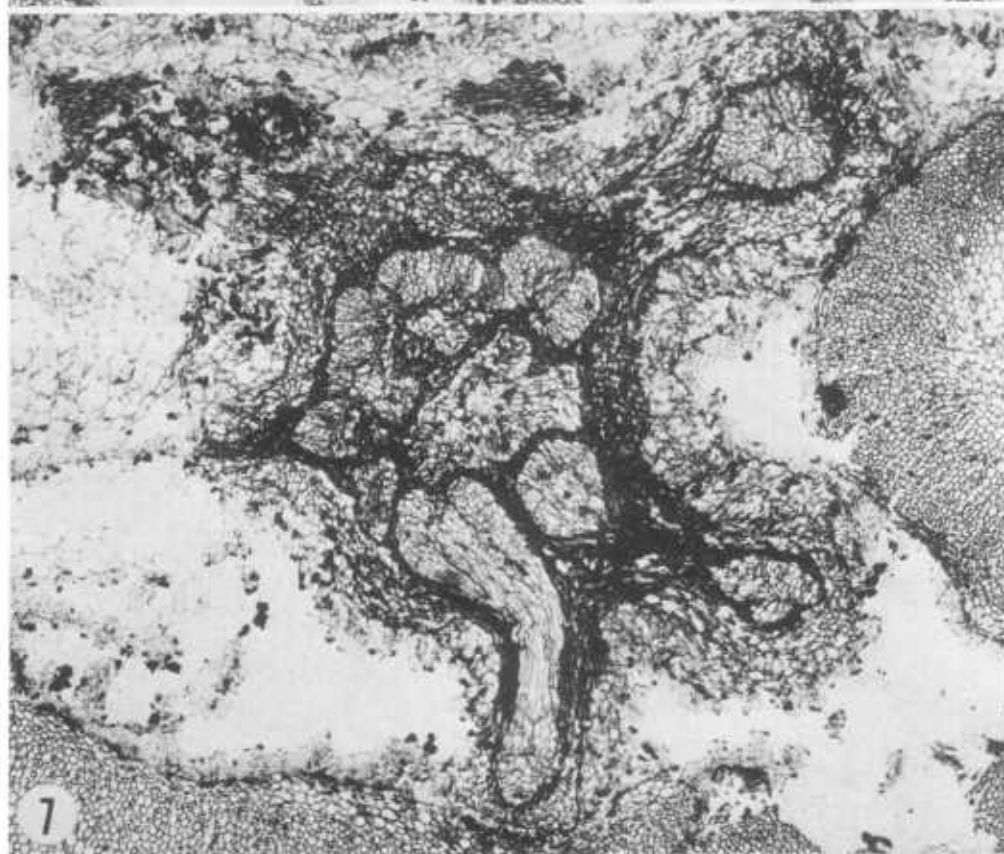
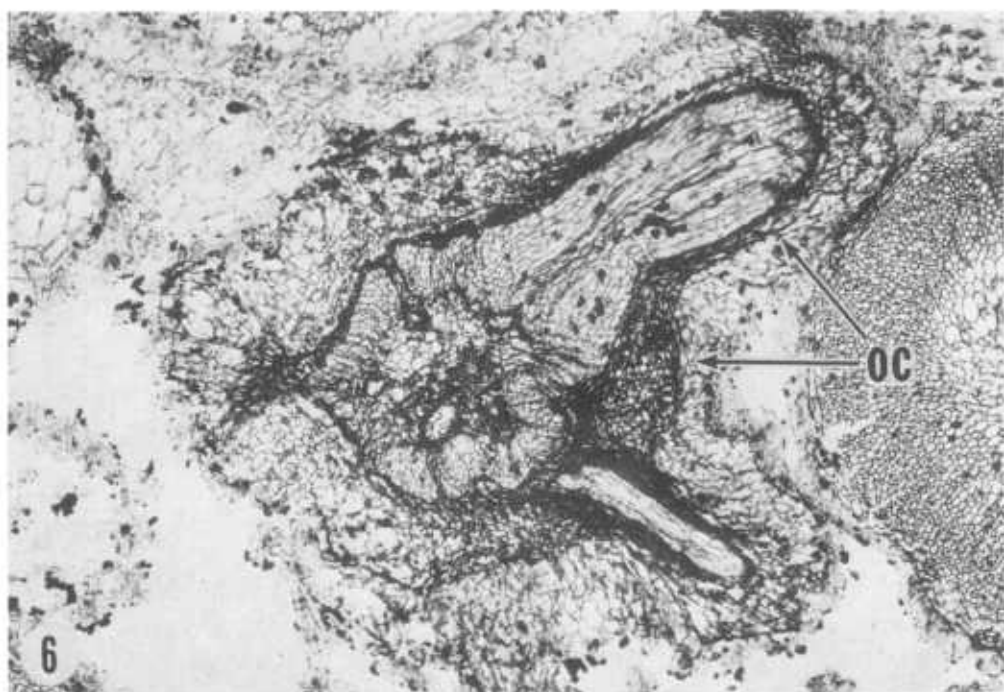


PLATE II



The xylary portion of the stele is 0.8 mm in diameter; metaxylem tracheids are up to 75 μm in diameter; secondary tracheids are up to 50 μm in diameter. The secondary xylem is asymmetrical. It decreases upward to none on one side and as few as four tracheids in radial file on the other (Plate I, 1). Basally the main axis has up to thirteen tracheids in file but secondary xylem never completely extends around the protoxylem poles (Plate I, 4). Wood is most abundant in the interfascicular areas, as noted by Baxter (1965). Contoured around the outermost xylem, primary or secondary, is a melasmatic "phloem zone" which does arch over the protoxylem poles (Plate I, 4).

The primary tissues conform to the stellate outline of the vascular system of the main axis; no periderm was present in any part of the branched specimen. The primary cortex is composed of two zones. The inner zone, 450 μm wide, consists of vertically elongate cells with conspicuous tangential wall thickenings; the cell dimensions are approximately 35 μm tangentially and up to 80 μm radially. Differential preservation results in clepsydroid wall outlines in section (Plate I, 2, 3). The outer cortex is 200 μm wide and composed of isodiametric parenchyma cells up to 80 μm in diameter. No epidermis was preserved.

Transitional anatomy

The primary xylem of the protostelic main axis separates basally into discrete inequally sized strands, each composed initially of one protoxylem group and metaxylem arm (Plate III, 8, at arrows). Within the interval of branching, the distribution of secondary xylem and phloem is progressively altered from abaxial to circumferential about each primary xylem bundle (Plate II, 6, 7). The primary bundles of the main axis have slightly spurred minor extensions downward (Fig.1). At a level where all the xylem systems are separate but contained within a common cortical envelope, the complex is pseudopolystelic (Plate II, 7; III, 8). The cortical tissues present are as those in the main axis but the outer cortex is wider (Plate II, 6). The inner cortex is up to 40 μm wide and the outer cortical parenchyma extends around all the axes; parenchyma also appears in the center of the cluster of axial steles. The pitting of tracheids of the primary and secondary xylem was observable in departing axes and agrees with that given by Baxter (1965).

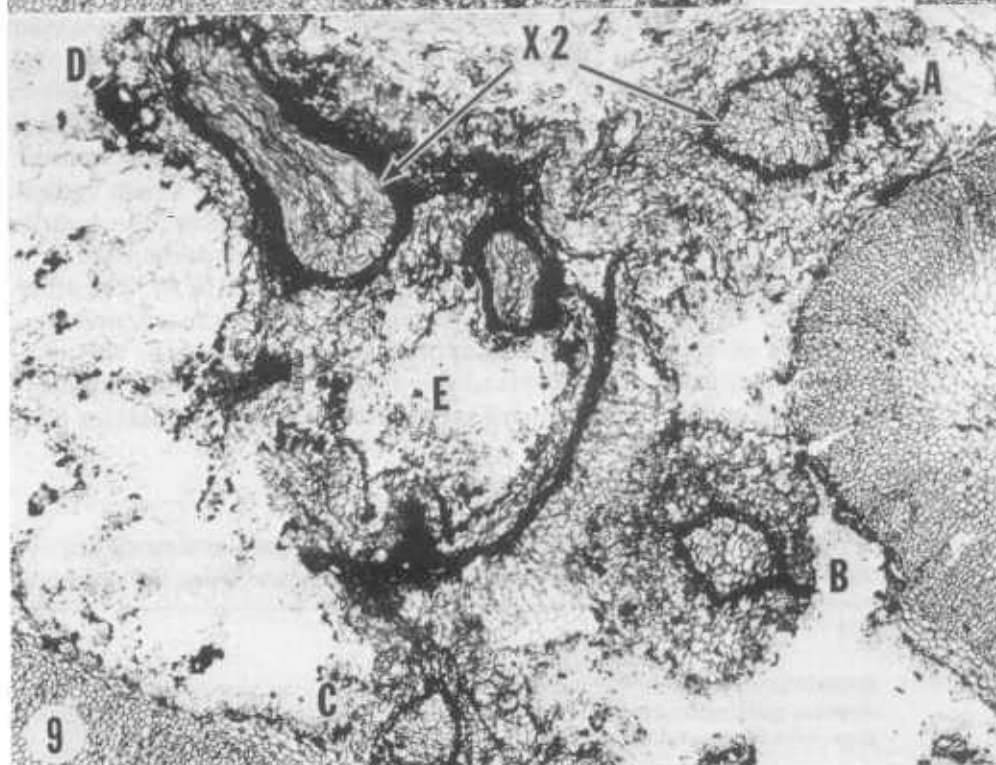
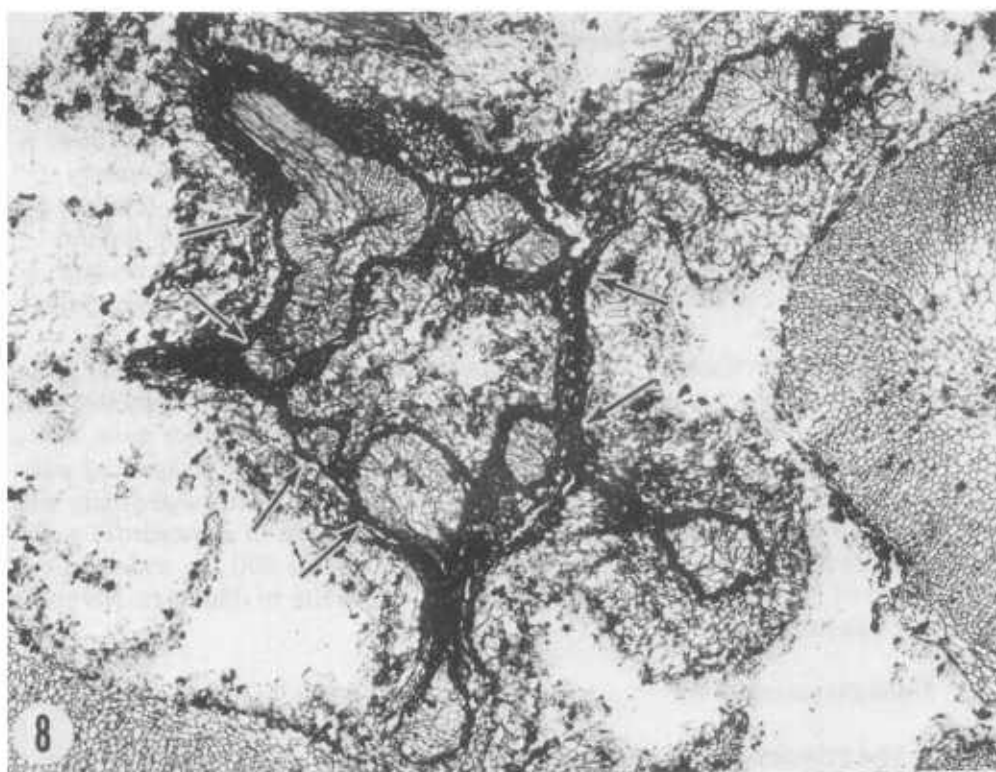
Branch axes

At a progressively lower level in the sections, six vascular strands are evident (Plate III, 8, at arrows) as axes begin to separate from the common

PLATE II

6—7. *Stelastellara parvula* branching — transition region. Upper part of transition region showing early separation of sympodial strands which connect with typical root-like axes; axes are bound by a common cortex (OC). Slides I 13759, 13766.

PLATE III



cortex. Two (Plate III, 9, A, D) of the four prominent axes have several files of tracheids but lack secondary growth of any kind a very short distance away from the point of branching (Plate I, 5, A, D). The largest derived axis (Plate I, 5, A) is 1.54 mm in diameter with a hexarch cluster of exarch primary xylem arms, 0.64 mm in diameter. The metaxylem is so appressed as to prohibit distinction between a solid protostele or discrete xylary strands. The axes of intermediate size are tetarch (Plate I, 5, C, D) and 1.0–1.15 mm in diameter. The smallest distinct axis is diarch with a fusiform xylem strand in cross-section, 0.51 mm by 0.18 mm, with a gross diameter of 0.89 mm. Distally none of the axes exhibits secondary growth and the distinct inner cortical layer is the outermost preserved tissue.

Stelastellara baxteri DiMichele et Phillips, sp. nov.

Axis up to 6 mm in diameter with solid exarch, polyarch actinostele composed of a central zone, up to 0.78 mm in diameter, extended peripherally into six flanges or flange-like ridges which appear in transverse section as attenuated tapering arms. The xylary ribs extend about 1.25 mm peripherally and attain a maximum width of about 150 μ m. Metaxylem tracheids up to 150 μ m diameter with multiseriate, elliptical bordered pitting with elongate apertures; primary xylem surrounded by secretory-phloem zone of elongate superposed cells with opaque contents, thicker in interfascicular areas; cortical zone conformable to stellate vascular system and composed of radially elongate cells with irregular, differential wall thickenings, primarily on radial walls; secondary cortex formed internal to primary cortex and composed of elongate tabular cells; endogenous lateral structures formed along radii of xylary ribs at frequent intervals.

Holotype: Specimen 7535 (Plate IV), slides I 13804–13910, Paleobotanical Collections (Morrill Hall), Botany Department, University of Illinois, Urbana, Ill., U.S.A.

Occurrence: “Baker” coal member, Lisman Formation, Desmoinesian equivalent in mid-continent terminology, Middle Pennsylvanian; Providence, Webster Co., KY.

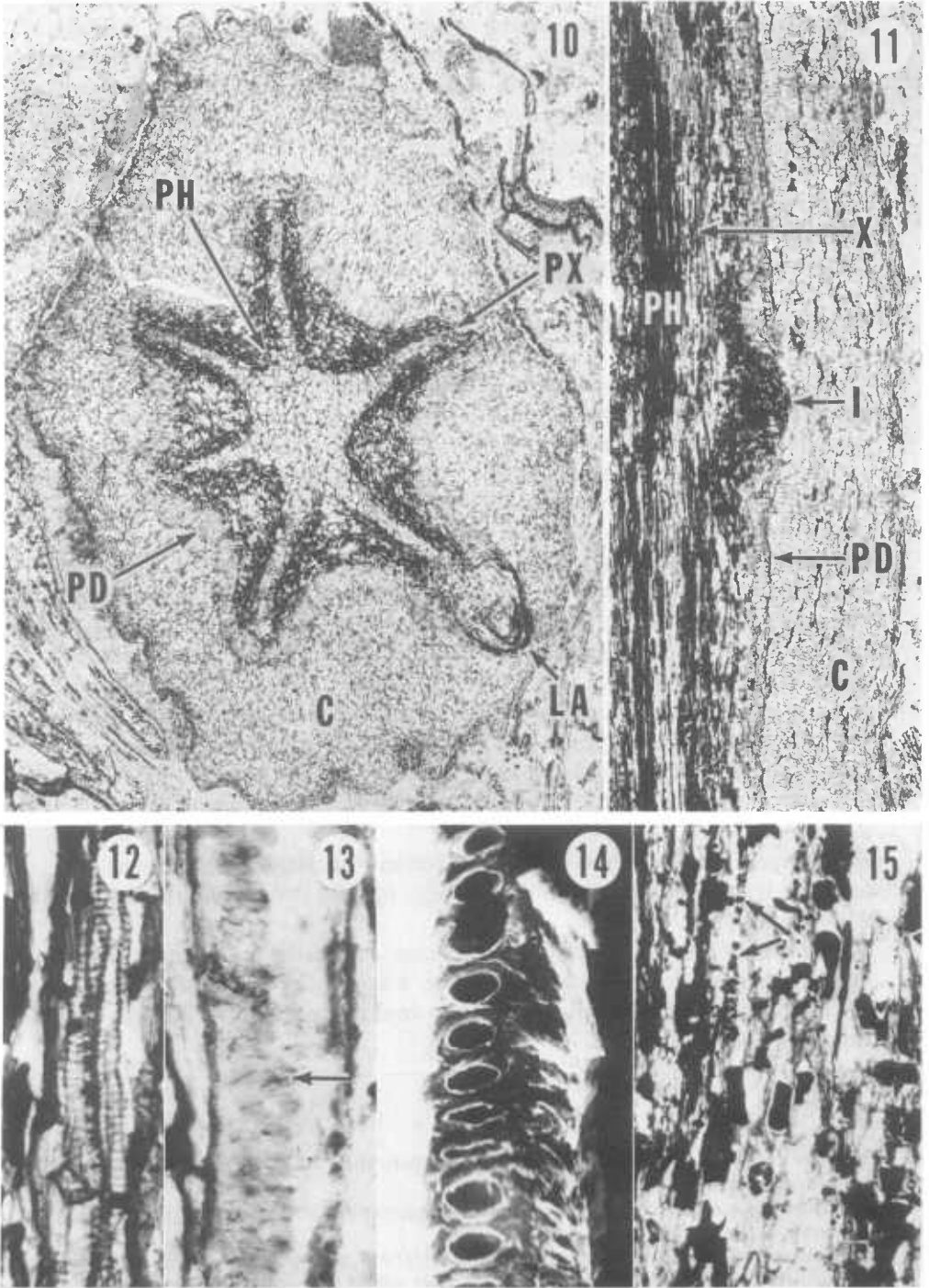
Derivation of specific epithet: The species is named for Professor Robert W. Baxter, University of Kansas, Lawrence, who first described *Stelastellara* and has made so many contributions to the coal swamp flora of Kansas and the American Pennsylvanian.

PLATE III

Stelastellara parvula branching — transition region, showing progressive separation of derived axes. Slides I 13769, 13774.

8. Near-basal section of branching region with six xylem strands (arrows); outer cortex shown in center of section.
9. Section at terminus of branching region. A–D = *S. parvula* axes as indicated in Plate I, 5 and Fig. 1; central area (E) is beyond outer cortex. Secondary xylem (X2) envelops adaxial side of two primary xylem strands (A, D).

PLATE IV



The new species of *Stelastellara* is based on one specimen which is 6 mm in diameter and 5 cm in length. The most characteristic feature of the axis is the solid actinostele (Plate IV, 10) which consists of a central cylindrical portion, 0.78 mm in diameter, with six radiating arms which are up to 1.25 mm in length and 150 μm wide along most of their length. This forms a highly stellate pattern around which all other tissues conform, including the periderm and primary cortex.

Vascular tissues

The metaxylem tracheids are up to 150 μm in diameter with the largest in the central cylindrical part of the stele. Metaxylem pitting is multiseriate, crowded elliptical to circular bordered with elongate apertures (Plate IV, 13). Tracheidal diameters diminish toward the attenuate arms which are composed largely of small diameter tracheids, the outermost of which can be designated protoxylem (Plate IV, 12). These are 14 μm in diameter. No secondary xylem is present in the specimen.

Surrounding the primary xylem is a very dark tissue which is up to 450 μm wide in interfascicular areas and diminishes in thickness to one to several cells around the protoxylem poles. This includes the "phloem zone" (Plate IV, 10, 11, PH; 15). The cells in this zone are up to 35 μm wide and 117-225 μm long; they are superposed in vertical columns. Most of the cells are filled with a brittle opaque substance. Other cells contain numerous dark globules (Plate IV, 15, at arrows). These secretory-like cells impart most of the blackness to the tissue. None of the intact cells exhibit sieve areas. Numerous portions of the tissue are degraded and it apparently included at least a second, less resistant type of cell. There was no cell parenchyma layer between the xylem and this zone of dark tissue.

Cortical tissues

The cortex (Plate IV, 10, 11, C) ranges in thickness from 1.9 mm between xylem arms to as little as 0.7 mm along the radius of the xylem ribs. The outer surface of the cortex is partly undulate and incomplete despite the rather good preservation of this kind of axis. The cortical cells show the

PLATE IV

Stelastellara baxteri sp. nov.

10. Cross-section of actinostelic axis with endogenous, lateral appendage (LA); PX = protoxylem; PH = phloem; PD = periderm; C = cortex. Slide I 13841. \times 16.
11. Radial longitudinal section of axis with incipient lateral appendage (I). X = xylem; PH = phloem; PD = periderm; C = cortex. Slide I 13880. \times 16.
12. Protoxylem with annular to spiral thickenings. Slide I 13878. \times 224.
13. Metaxylem tracheid with circular bordered pits with elongate apertures (arrow). Slide I 13877. \times 504.
14. Scanning electron micrograph of metaxylem tracheid with oval pitting. X 997.
15. "Phloem zone" with secretory cells containing opaque contents (arrows). Slide I 13878. \times 112.

unusual feature of being radially elongate and of approximately equal dimensions tangentially and vertically. In keeping with the radial elongation, the differential thickening of the cell walls is predominantly radial although the pattern is often irregular and occurs on adjacent portions of some tangential walls. The cells are up to about 90 μm radially and about 40 by 50 μm , tangentially and vertically.

Internal to the inner edge of the primary cortex is the fairly uniformly thick periderm or secondary cortex (Plate IV, 10, 11, *PD*), 187 μm wide and up to about ten cells thick. The cells are tabular, up to 100 μm vertically, 50 μm tangentially and 25 μm radially. There is no indication of a phellogen or bifacial differentiation.

Evidence of branching

Along the sectioned length of 5 cm at least seven lateral endogenous structures originated from the axis (Plate IV, 10, *LA*). None was preserved outside the cortex of the main axis. Five of the seven endogenous outgrowths emanated from one side of the axis from three adjacent lateral xylary arms; two originated from the other side. Four successive endogenous outgrowths developed from two adjacent arms. There were several minor protuberances observed at the periphery of the stele (Plate IV, 11), extending just into the cortex.

The best preserved endogenous structures exhibit their own cortex and vascular strand. While they lack positively identifiable organographic features, the array of tissue patterns present suggests that the lateral structures are endogenous roots.

DISCUSSION

The two specimens described agree with Baxter's circumscription of *Stelastellara* in the following anatomical features: exarch, polyarch, stellate axes with elliptical bordered pitting, secondary growth, and a distinctive cortex with differential thickenings. Both specimens differ from Baxter's diagnosis of the genus by having solid protosteles in the main axis. In the branching specimen which bore *S. parvula* axes, secondary xylem without rays developed without any periderm present. This is contrary to the normal developmental sequence observed in *S. parvula*; *S. baxteri* is consistent with that sequence having periderm but no secondary vascular tissue. *S. baxteri*, as a larger form of *Stelastellara* differs in two important respects; both are radially quantitative differences. The highly stellate construction is derived from xylary ribs which extend up to 1.25 mm away from the solid, central cylinder of xylem; the cortical cells are also radially elongate with predominantly radial wall thickenings. The thickenings, however, are less regular than in *S. parvula*.

Morphological interpretations

Based on our observations of typical *S. parvula* axes, we agree with Baxter's (1965, p. 1129) original and tentative conclusions that "... the interpretation as a root seems at present to have possibly a little more evidence in its favor than as a stem (rhizome)." The new specimens with solid protosteles and branching pose a similar dilemma as to interpretations of root or stem.

The branched specimen of *S. parvula* presents still another aspect of interpretation. One which anatomically involves a transition region between two axis systems, neither of which can be conclusively determined to be stem or root. Two alternatives of orientation of the specimen are considered. The axis designated the main axis may be a typical axis of *S. parvula* at levels above those observed and the growth of the axis may have resulted in a digitate type of apical branching producing the sympodium of smaller axes. The presence of secondary xylem or at least of seriated files of tracheids associated with the branching, diminishing away from the zone of branching, may simply reflect proliferation of tracheids in conjunction with such unusual apical branching. Somewhat similar tracheidal proliferation has been observed in outer roots of *Psaronius* (Ehret and Phillips, 1977) where many laterals are produced. *Psaronius* does not normally have such seriated tracheids or secondary growth elsewhere. The lack of wood rays continues to raise the question about the nature of the so-called secondary xylem. The interpretation just given did not argue for either stem or root interpretations, but it implies that there is essentially no organographic difference between the main axis and its derivatives. That kind of branching would be more likely from a root than a stem and its nearest analog would be in some of the roots of *Amyelon* (Cridland, 1964).

A second possible interpretation suggests that the transitional anatomy is indeed derived from a bipolar primary body which has developed roots in one direction and a stem in the other. The roots would apparently be primary in origin with a common cortex with the stem. There would be a multiplicity of roots which would form the primary root system. This collectively forms the transitional anatomy to the stem. The greatest thickness of secondary xylem at the top of the transition region (hypocotyl?) would be consistent with this interpretation, particularly if the specimen were a young seedling. Such an unusual primary vascular configuration may be closely tied to growth habit, perhaps a structurally modified root system. The possibility of an aborted primary root and subsequent development of a ring of lateral roots is unlikely in light of the common cortex shared by the stem and root axes. Neither of these alternatives seems to be entirely consistent with what is known about the specimen, nor do they help in determining the affinities of *Stelastellara* or the actual function of the radiating *S. parvula* axes.

Stelastellara baxteri presents a somewhat similar problem in interpretations. Its endogenous lateral structures are not well enough developed or

preserved to interpret, but their endogenous nature suggests root origins. Deeply seated periderm development in what may have been the pericycle of the main axis also suggests root structure but there are important exceptions as in *Sphenophyllum*. What seems to emerge from the morphology of the axis of *Stelastellara* is that there is no unequivocal evidence for any axis to be a stem since none bear exogenous foliar appendages. If *S. baxteri* is a rhizome, we have only found a root-producing portion of it.

From the observations reported by Baxter (1965) and our own of *Stelastellara*, the major actinostelic axes and their branches or laterals appear not to have been buried *in situ*. The plant parts known are relatively rare and it seems likely that the known peculiar features of their morphology might represent a perched habit of some kind. The sympodially branched specimen of *S. parvula* could have been dislodged from its anchorage, hence the severed and clumped axes which were not intergrown in the peat substrate. Similarly, the *S. baxteri* axis may have been removed from an original attachment along some aerial axis. The endogenous laterals were largely, but not exclusively, from one face of the axis. The peculiar vertical (*S. parvula*) or radial (*S. baxteri*) elongation of cortical cells with tangentially or radially thickened cell walls respectively, might not be so significant a taxonomic character if it were related to habit and perched position. Whether these plant parts, indeed, indicate climbing lianas, perched epiphytes or even semiautotrophs is entirely conjectural but not beyond the realm of possibility.

Natural affinities

The possible affinities of *Stelastellara* have been well considered by Baxter (1965) who tentatively suggested an alliance with the coenopterid ferns which he discussed in detail. The rarity of secondary growth in the Pennsylvanian ferns, particularly the development of a deeply seated periderm (Dennis, 1974; Phillips, 1974), does not lend further support to this suggestion. With the exception of the Marattialean ferns, the root systems are diarch in the Pennsylvanian ferns. There is also a very clear-cut distinction between stem, leaf and root in these true ferns of the Pennsylvanian.

The multiseriate elliptical bordered pitting, secondary growth and possible eustely are combined characters more commonly associated with gymnosperms than other plant groups of this period. Distinctions between cycadophyte and coniferophyte can not be suggested because there are no wood rays or other characters upon which a distinction can be made.

The root-like anatomy of *Stelastellara* has been discussed by Baxter (1965) and numerous comparisons can be made with gymnosperm roots. Medullosan roots, for example, are similar to *Stelastellara* prior to secondary growth. Some are known which lack secondary xylem over the protoxylem poles, but this has been interpreted as partially due to incomplete preservation (Rothwell and Whiteside, 1974). The transition region of branching in *S. parvula* is also superficially similar to that of *Medullosa* (Basinger et al., 1974) with secondary xylem found circumferentially around the primary strands of the sympodium.

The diminutive size of *Stelastellara* is paralleled by some small pteridosperms, such as *Microspermopteris*. The stem of *M. aphyllum*, 0.5–11.0 mm in diameter, has an exarch mixed protosteles divided into five sections by longitudinal parenchyma plates, simulating a eustelic construction. While pitting is also similar, there are differences in the wood, cortex and branching of these well-defined stems (Taylor and Stockey, 1976). The gross similarities are essentially those of size and possibly habit, a small liana or epiphyte.

Floral association of Stelastellara parvula

Stelastellara parvula is fairly rare in the coal swamps and the most numerous sources of specimens have been in the lower Middle Pennsylvanian. Numerous coal swamps between the Rock Island (No.1) and the Springfield (No.5) Coal Members of Illinois and their equivalents in the Western Interior Coal Province were composed of abundant cordaites, dominant or subdominant in relation to lycopod trees. *S. parvula* more commonly occurs in this type of swamp as does *Microspermopteris*. At the Star Mine locality in Iowa, cordaites dominate; at the Maple Grove Strip Mine in Indiana, cordaites are subdominant to lycopods.

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