

Lycopods of Pennsylvanian age coals: *Polysporia*

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Permineralized specimens of *Polysporia* are described from coal balls of three Middle Pennsylvanian age coals of the Illinois Basin. Identification is based on the presence of *Endosporites* microspores and *Valvisporites* megaspores along with sporangial fragments in the axils of leaves interpreted as sporophylls. The shoots exhibit alternating fertile and vegetative zones. Vegetative leaves are larger than sporophylls which are often desiccated and folded back against the stem surface; a short zone of transitional sterile leaves is found between vegetative and spore-bearing zones. Ligule pits are present on the adaxial surface of vegetative leaves. The stems are essentially herbaceous but robust and 4-6 cm in diameter. Small amounts of periderm and wood were produced but primary tissues were not disrupted. *Polysporia* is the first herbaceous lycopod with an alternation of fertile and vegetative areas found in Pennsylvanian peats and is compared with *Spencerites*, *Sporangiostrobus*, and *Lepidodendron dacydoides* (proposed vegetative stem of *Sporangiostrobus*) which are suspected to have similar structure. The rarity of *Polysporia* in coal balls and its frequent associations with *Sphenophyllum*, combined with low numbers of arborescent lycopods, *Psaronius* or *Medullosa*, suggest an environment of growth not frequently encountered in coal-ball studies of the swamps. *Polysporia* may have grown in marginal wetland environments where herbaceous and low shrubby plants predominated; this suggests that some *Endosporites*-rich coals of the Upper Pennsylvanian are derived in large part from marshland peats.

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Des spécimens minéralisés du *Polysporia* sont décrits à partir de trois dépôts de charbon provenant du Pennsylvanien moyen du bassin de l'Illinois. L'identification est basée sur la présence de microspores d'*Endosporites* et de mégaspores de *Valvisporites* liées à des fragments de sporanges à l'aisselle de feuilles identifiées à des sporophylls. Les parties aériennes présentent des zones végétatives alternant avec des zones fertiles. Les feuilles végétatives sont plus larges que les sporophylls, lesquelles sont souvent desséchées et rabattues contre la surface de la tige; une petite zone de feuilles stériles intermédiaires se trouve entre les zones végétatives et les zones productrices de spores. Les cicatrices des ligules sont présentes à la surface adaxiale des feuilles végétatives. Les tiges sont essentiellement herbacées mais robustes et de 4-6 cm de diamètre. De faibles quantités de périderme et de bois sont produites mais les tissus primaires ne sont pas séparés. *Polysporia* est la première lycopode herbacée trouvée dans les tourbières Pennsylvaniennes présentant en alternance sur la tige des aires fertiles et végétatives. Elle est comparée à *Spencerites*, *Sporangiostrobus* et *Lepidodendron dacydoides* (la partie végétative présumée du *Sporangiostrobus*) qui présenteraient une structure semblable. La rareté du *Polysporia* dans les dépôts de charbon et son association fréquente à *Sphenophyllum*, ainsi que la rareté des lycopodes arborescents, *Psaronius* ou *Medullosa*, indiquent un milieu de croissance rarement rencontré dans les études des charbons des marécages. *Polysporia* a dû croître dans un environnement marginal de terres humides où des plantes herbacées et buissonnantes prédominaient; ceci indique que les charbons riches en *Endosporites* du Pennsylvanien supérieur proviennent en grande partie de tourbes de marécages.

[Traduit par le journal]

Introduction

Herbaceous lycopods were a small component of the coal swamps often dominated by their arborescent relatives. Recognition of true small, herbaceous forms relies largely on the ability to distinguish them from terminal twigs of arborescent lycopods. This is primarily based on negative evidence: the lack of association with any large branches assignable to the same plants as the putative herbaceous

shoots. Small, probably herbaceous plants found as permineralized components of coal-swamp floras include the following: the eligulate *Spencerites* (Scott 1898; Berridge 1905; Leisman 1962; Leisman and Stidd 1967); the ligulate, heterosporous *Selaginella* (Fry 1954; Phillips and Leisman 1966; Schlanker and Leisman 1969); *Sporangiostrobus* (Leisman 1970; Leisman and Stidd 1977); *Lepidodendron serratum* (Felix 1952; Baxter 1965;

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Leisman and Rivers 1974); and a plant of possible lycopod affinities, *Natalina sinuata* (Baxter 1978). *Polysporia*, which Chaloner (1958) found to be a heterosporous "cone" compression, can be added to this list. Microsporangia containing *Endosporites* microspores, referable at least in part to *Polysporia*, have been reported from coal balls of eastern Kentucky (Brack and Taylor 1972; Taylor 1973). However, until the present report the vegetative morphology and the relationship of fertile and vegetative zones of *Polysporia* had not been established.

Permineralized specimens of *Polysporia* from three Middle Pennsylvanian coals of the Illinois Basin demonstrate a ligulate, probably herbaceous lycopod with alternating zones of sporophylls and vegetative leaves. This condition was suggested but not documented for both *Spencerites* (Leisman 1962) and *Sporangiostrobus* (Leisman 1970; Leisman and Stidd 1977); it occurs today in some species of *Lycopodium* (Selago type). *Polysporia* was relatively robust, up to at least 4 cm in diameter excluding the leaves. Leaf bases but not leaf cushions are present; vegetative leaves appear to have been broken from the main stem rather than abscised. Sporophylls were thinner and narrower than the vegetative leaves and were often desiccated and folded back against the stem. There are anatomical similarities between *Polysporia* and *Lepidodendron dacyriodioides* Leisman (1970), which Leisman and Stidd (1977) have suggested as the vegetative portion of *Sporangiostrobus*. *Polysporia* is also similar to *Spencerites* in form and some aspects of anatomy; however, there are important differences in some anatomical features and in their spores.

The stratigraphic range of *Polysporia*, based on *Endosporites*, encompasses coal swamps of the Middle and Upper Pennsylvanian (Phillips 1979), if *Endosporites* is a reliable indicator of *Polysporia* in the Upper Pennsylvanian. There is a marked change in swamp vegetation at the end of the Middle Pennsylvanian as a result of the extinction of *Lepidodendron* and *Lepidophloios* (Phillips et al. 1974). The persistence and inferred flourishing of *Polysporia* may have resulted in part from the development of environmental conditions that favored a smaller herbaceous growth habit and plants with repeated reproductive capacity. The late Pennsylvanian swamps were much more restricted areally and temporally. Plants most commonly found in association with *Polysporia* from the Herrin (No. 6) Coal Member and the Baker Coal Member are abundant *Sphenophyllum*, occasional

Lepidodendron dicentricum; associations with the common trees, *Lepidophloios*, *Psaronius*, or *Medullosa* are rare. The rarity of *Polysporia* in these coal swamps and the nature of the associated plants suggest a marsh-like association, perhaps in marginal wetland areas which are less likely to be sampled in the vast tree-dominated swamps of the Middle Pennsylvanian.

Materials and Methods

The morphology of 15 specimens of *Polysporia* preserved in coal balls was studied with serial cellulose acetate peels. Microspores and megaspores were macerated from coal balls with dilute HCl and examined with light and scanning electron microscopy. All slides and specimens are housed in the Paleobotanical Collections (Morrill Hall), Department of Botany, University of Illinois, Urbana, IL, U.S.A.

Specimens were examined from the following coals and locations: Coal balls Nos. 8491, 10257, 10897, 14166, 15390, 15417, 15447, 15470, and 15475 from the Baker Coal Member, Lisman Formation, Middle Pennsylvanian; Providence, Webster Co., KY, Providence 7½' Quadrangle (37°24'52.05" N, 87°46'9" W). Coal ball No. 17848 from the Herrin (No. 6) Coal Member, Carbondale Formation, Keweenaw Group, Middle Pennsylvanian; Sahara Coal Company No. 6 Mine, Saline Co., IL, Harrisburg Quadrangle (Sec. 30, T9S, R5E). Coal balls Nos. 17805, 18999, 19174, 21555, and 21562 from an unnamed coal equivalent to the Murphysboro Coal Member of Illinois in the Staunton Formation, Raccoon Creek Group, Middle Pennsylvanian; Cayuga, Fountain Co., IN, Newport Quadrangle (Sec. 34, T18N, R9W).

Results: Anatomy and Morphology

Identity of Specimens

Specimens described herein are included in *Polysporia mirabilis* which Newberry (1873) originally described from compressed fertile stems with subsequent additional descriptions and an emendation by Chaloner (1953, 1958). Identification of specimens which include fertile and vegetative parts in organic connection is based on the associated sporangia with spores. Microspores of the *Endosporites globiformis*-type have been found in detached sporangia in the axils of modified leaves interpreted as sporophylls. Megaspores of the *Vulvisporites auritus* (*Triletes auritus*) type occur mixed with sporangial fragments closely associated with and in the axils of sporophylls. The consistent occurrence of these spores in very large numbers in and associated with sporangia in the axils of sporophylls supports the identification of specimens as *Polysporia*. The same kinds of spores have been described from compression specimens (Chaloner 1958). *Polysporia mirabilis* is the only species known (Chaloner 1958), and there are some aspects which cannot be critically compared between compression and anatomically preserved fertile areas. From our material we cannot deter-

mine exact sporangial arrangements, sporangium size, or megasporangium number per sporangium.

Structural Morphology

All 15 specimens consist of alternating areas of vegetative leaves and sporophylls (Fig. 1). The maximum length of a fertile area is 8 cm; in most cases the shoot was broken within the fertile zone so that a vegetative portion occurred at either the basal or at the apical end only (Figs. 4–7). This frequent breakage provides a plausible explanation for the compressed *Polysporia* "cones" which lacked a peduncle or an apex. There are no marked changes in internal anatomy or in arrangement and density of the leaves between fertile and vegetative areas. However, sporophyll morphology differs considerably from that of the vegetative leaves. Stem specimens were usually flattened and fragmentary. Specimens with complete diameters measured 70 mm × 5 mm to 80 mm × 4 mm in transverse section (Figs. 2 and 3) and still larger incomplete ones had a greater development of periderm. The longest shoot specimen is 15 cm.

Stele

The stele of *Polysporia* stems is an exarch, polyarch siphonostele. Protoxylem groups of the corona are irregularly distributed, closely spaced, and separated by parenchyma (or cavities) that extends into irregular depressions partly or entirely through the tracheidal zone (Fig. 9). This parenchyma renders a dissected appearance to the outer margin of the stele. The contact between pith parenchyma and the scalariform-thickened metaxylem is irregular but sharp. The pith is entirely simple parenchyma; it contains no scattered tracheids, cells with secondary wall thickenings, or secretory cells. No tissue identifiable as phloem was observed in any of the stem sections. Stele dimensions were relatively constant from 6 mm × 1 mm to 8 mm × 1.5 mm in transverse section.

Cortex

The preserved cortex is a thick-walled parenchymatous tissue (Fig. 8). A lacuna occurs between the stele and cortical zone; degradation of a thin-walled primary parenchyma, part of a multiple-zoned cortex, may have given rise to the lacuna. The cortical cells are elongate and blunt-ended with differentially thickened radial walls. Irregular radial files of cells are recognizable even within the primary cortex. Cell diameters in transverse section were consistently 50–75 µm, although the thickness of the cortex varies among specimens from 2 to 5 mm. In specimens with periderm de-

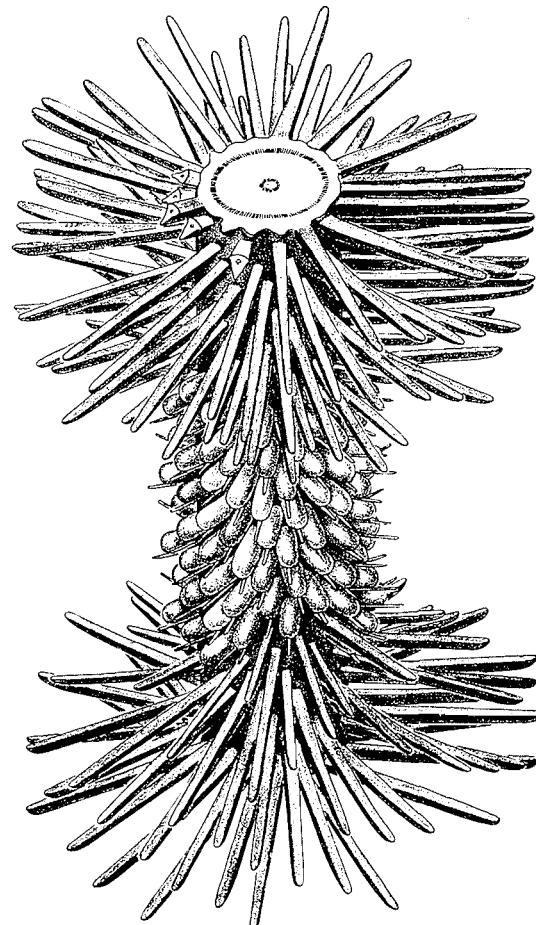


FIG. 1. Restoration of a portion of the *Polysporia* shoot with successive vegetative, fertile, and vegetative zones. Distal portions of leaves are largely hypothetical; some leaf bases without distal portion ends are shown at the top, the typical condition of specimens. Sporangia are shown attached throughout the fertile zone without distinctions between megasporangia and microsporangia. Some microsporangia were found unattached in the axils of sporophylls in the top of the fertile zone and megasporangia probably occurred below them. For further explanation see text. $\times 0.5$.

velopment of 15 to 20 cell layers, the primary cortical cells show distinct evidence of tangential expansion and secondary subdivision, especially between the leaf bases.

The preserved cortex is very homogeneous in both transverse and longitudinal section. *Polysporia* leaf traces lack the zone of thin-walled cells that surround the leaf traces of many arborescent lycopods and there is no evidence of a parichnos strand abaxial to the leaf trace in the cortex. A zone of cylindrical cells immediately subjacent to the xylem of the trace is interpreted as probably phloem rather than parichnos; parichnos in ar-

borescent lycopods is generally separated from the trace by one or more layers of parenchyma continuous with the phloem or inner cortex. Cells spatially and histologically similar to the cylindrical cells subjacent to the leaf trace in *Polysporia* originate immediately external to the stelar xylem in arborescent lycopods, the phloem of Eggert and Kanemoto (1977).

Secondary Tissues

At the inner margin of the preserved cortex is a periderm layer of radially aligned cell files, up to 20 cells long in the largest specimens (Fig. 8). The radially elongate cells are 50–60 μm tangentially and 50–100 μm radially. Radial walls are distinctly thicker than tangential ones. There is no distinction between phellem and phelloiderm-type tissues or any evidence of a phellogen. The similarity of these periderm cells in size and wall thickenings to those of the primary cortical parenchyma, as well as the secondary expansion and subdivision of primary cortical cells external to the periderm, imply that the periderm cells were living at maturity and were not cork-like.

Secondary xylem has been observed in three specimens. It was 14 tracheid layers and 500–600 μm in maximum thickness and was eccentrically developed. Wood was initiated opposite the protoxylem poles (Fig. 9) with gradual expansion of the number of cell files so that along some of its circumference the stele is bordered by a continuous arc of wood; in other parts of the stelar circumference isolated wedges of secondary xylem project along the radius of the protoxylem groups. The tracheids of the wood have a distinctly squarish cross-sectional outline. The rare occurrence and limited development of secondary xylem suggest that it was probably limited to the older parts of the stem.

Leaves

Shoots consist of alternating fertile and vegetative zones with considerable morphological differentiation between the sporophylls and vegetative leaves; there is a short transition zone between the two areas (Fig. 1). No abscission layer or evidence of abscission was found in either fertile or vegetative leaves. The leaves of the vegetative areas of the stem are not preserved beyond 1.5–4.0 mm from the stem surface (Figs. 5 and 6); however, robust, irregularly broken leaf bases with low abaxial keels (Figs. 4 and 7) indicate that sporophylls are borne in the same ontogenetic spirals as the vegetative leaves. Sporophylls are much thinner and often deformed but rarely removed. Apparently desiccated distal portions of the sporophylls

are often folded back against the stem surface (Fig. 13).

The vegetative leaf bases, up to 6 mm high and 4 mm wide, consist almost entirely of radially elongate cells with the same transverse diameter as cortical cells, 50–75 μm , but up to 150 μm radially. Epidermal cells have smaller diameters, 25–38 μm , and are isodiametric to tabular (Fig. 10). The interleaf areas of the stem and abaxial surfaces of the sterile leaves have abundant randomly distributed shallow crypts, 75–125 μm deep, as indicated by transverse and paradermal sections. These are most probably stomatal crypts, although guard cells have not been identified. On these same surfaces trichomes are abundant. The ligule pit occurs on the adaxial surface of the leaf, about 1.2–2.0 mm from the stem proper. The pit is a globose cavity that opens almost vertically to the surface via a small aperture (Fig. 11). The ligule pit is lined with columnar parenchyma cells, distinct from adjacent ones. No histologically preserved ligules were observed although a degraded layer of tissue is commonly appressed to the floor of the pit. Leaf breakage most often occurred between ligule pit and stem resulting in the lack of ligule pit preservation. The leaf trace, located in the upper one-third to one-fourth of the leaf base is distinctly V-shaped with protoxylem at the base of the "V" (Fig. 12); the two arms of the trace are often separated at the base resulting in two strands of xylem. Transfusion tissue is present above the trace at the base of the ligule pit. There is no parichnos.

Sporophylls were not found with organically attached sporangia; however, complete and partially preserved sporangia were found in some of the axils of sporophylls. In such cases a zone of disrupted cells on the upper surface of the sporophyll corresponded closely with the broad base of the detached sporangium (Fig. 14). The fertile leaves are elongate, approximately 1.5–2.0 mm thick near their attachment to the stem and 0.75 mm thick in cross section and 2.5 mm wide in the area of probable sporangial attachment. Sporophylls are often desiccated distally where they are about 1.2 mm wide (Fig. 16). Maximum preserved lengths measured were about 12 mm. No ligule pit was established in sporophylls and preservation distal to presumed sporangial attachment was very poor. At the base of the sporophyll the trace is V-shaped, as in vegetative leaves; it becomes terete distally and increases somewhat in diameter. Toward the distal end there is an enlargement composed of a knot-like grouping of irregularly oriented tracheids. This may constitute the point of attachment of the distal lamina which Chaloner (1958) reported for com-

pression sporophylls of *Polysporia*. The cells of the sporophylls are isodiametric to radially elongate parenchyma.

Transitional leaves are sterile. Their bases are smaller than those of vegetative leaves and have a flattened shape much like sporophylls. However, there is a low abaxial keel and the laminae are broken off, not folded back against the stem as are many sporophylls. They may have been stiffer than sporophylls. Unicellular epidermal hairs are common on the leaf bases and the narrow interleaf areas of the stem (Fig. 17). Where well preserved, the hairs were thinly spread over the stem surface and especially on the abaxial base of the vegetative leaves.

Sporangia and Spores

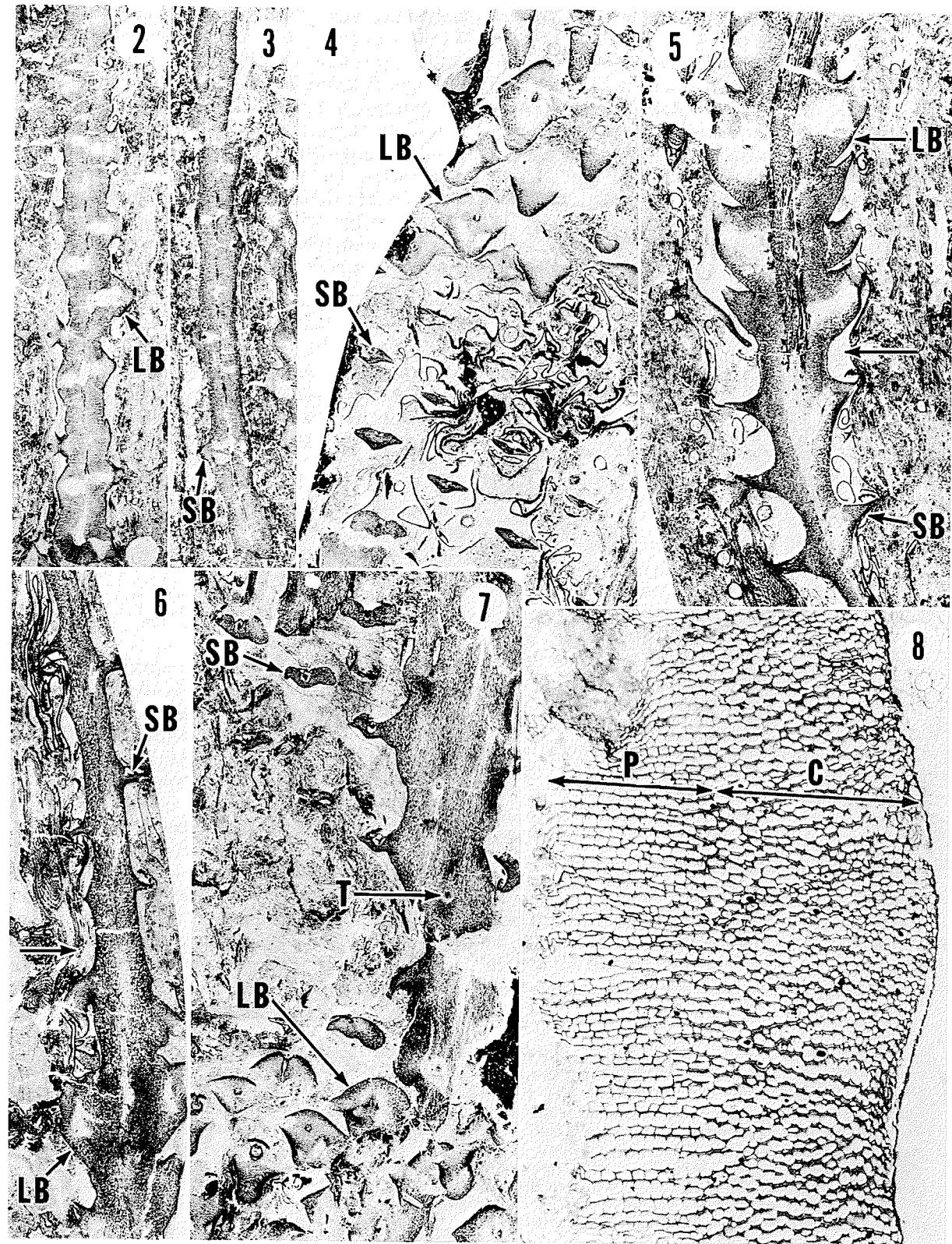
Sporangia are somewhat rectangular in tangential section and broadly stalked at their base. The sporangium has a wall two layers thick (Fig. 15) and a small amount of transfusion tissue extends adaxial to the sporophyll tissue. The outer layer of the sporangium consists of thick-walled rectangular cells. The inner layer consists of thin-walled, somewhat shriveled cells that may represent a tapetum, as suggested by Brack and Taylor (1972). Intact sporangia are rarely found. Most often, remains of broken sporangia are found mixed with spores in the axils of sporophylls (Figs. 4 and 6). The close association of *Endosporites* microspores and *Valvisporites* megaspores within and around fertile areas suggests that microsporangia and megasporangia were borne in the same fertile zones. However, the lack of attached megasporangia leaves some doubt about the physical relationship between microsporangia and megasporangia.

Microspores from the coal balls with *Polysporia* are assignable to the genus *Endosporites*. The circular to slightly triangular spores are trilete with a pseudosaccus attached only at the proximal end

(Figs. 19 and 20). A limbus is present at the equator and most spores display three interradial papillae (Fig. 18). The ratio of the spore saccus width to radius of the spore body, measured along the triradiate suture, was determined for 50 spores; 25 spores were measured from each of two coal balls from the Baker Coal. The spores were oriented in a polar view. The margin width of the saccus is 0.9 to 1.9 times the spore body radius with a mean ratio of 1.42 ± 0.23 SD. Spores of these dimensions fall within the species *E. globiformis* which is defined by Potonié and Kremp (1956) as having a spore body radius at the equator less than the width of the pseudosaccus. The size range (maximum diameter) for 50 spores is $67\text{--}140\,\mu\text{m}$ with a mean of $106\,\mu\text{m}$, ± 11.59 SD. The range given by Potonié and Kremp (1956) is $110\text{--}160\,\mu\text{m}$ and that by Smith and Butterworth (1967), $62\text{--}161\,\mu\text{m}$. A good Gaussian distribution was indicated for both spore body : saccus ratio and spore diameter, with no indication of bimodality even though some spores fell within the limits of *Endosporites ornatus* (*sensu* Potonié and Kremp) in both characters. This further supports the contention of Smith and Butterworth (1967) that the type species, *E. ornatus*, represents only one end of the range of variability attributed to *E. globiformis*.

Megaspores associated with *Polysporia* (Figs. 21 and 22) are assignable to the genus *Valvisporites* (Potonié and Kremp 1956) which is equivalent to the section *Auriculatae* of the genus *Triletes* (Schopf 1938). Megaspores were isolated from a compact mass of spores in close association with *Polysporia* as well as *Endosporites* (Fig. 25). In 21 spores, the maximum diameter ranged from 900 to $1560\,\mu\text{m}$ with a mean of $1284\,\mu\text{m}$, ± 199 SD. The auriculae, which are the most distinguishing characteristic of *Valvisporites*, range from well-developed radial or slightly bulbous extensions of the arcuate ridges at the end of the triradiate mark

FIGS. 2-8. *Polysporia*. Fig. 2. Transverse section of flattened stem through vegetative area with protruding leaf bases (LB). Specimen 15745C top, slide I14682. $\times 1.5$. Fig. 3. Transverse section of flattened stem through fertile zone; sporophyll bases (SB) protrude only slightly and anatomy is identical to vegetative zones. Specimen 15745E bot, slide I14682. $\times 1.5$. Fig. 4. Tangential section of fertile (below) and vegetative (above) zones; vegetative leaf bases (LB) are much larger than those of sporophylls (SB). Fragments of sporangial walls are present in the fertile region. Specimen 15417H₃, slide I14746. $\times 3$. Fig. 5. Radial section of junction between basal fertile and apical vegetative zones; unlabeled arrow marks upper limit of fertile zone. Shoot section corresponds in orientation to that in Fig. 4. Sporophyll bases (SB) are much thinner than the robust vegetative leaf bases (LB) which are irregularly broken. Specimen 15417H₃, slide I14739. $\times 3$. Fig. 6. Radial section of junction between upper fertile and lower vegetative zones; unlabeled arrow marks approximate lower limit of fertile region. Vegetative leaf bases (LB) are irregularly broken. Fragmented sporangial walls are present around sporophyll bases (SB). Specimen 15417H₂, slide I14733. $\times 3$. Fig. 7. Oblique tangential section of shoot across junction between upper fertile and lower vegetative zones; shoot section corresponds to radial section in Fig. 6. Leaf trace (T) is not surrounded by extensive areas of thin-walled parenchyma. SB, sporophyll base; LB, vegetative leaf base. Specimen 15417H₂, slide I14734. $\times 3$. Fig. 8. Transverse section of stem through cortex (C) and periderm (P). Cells of both tissues have differentially thickened radial walls; cells of periderm are in radial rows without evidence of a phellogen. Cortical cells are in irregular, short radial files. Specimen 15470C, slide I14714. $\times 40$.



(Fig. 23) to pointed extremities or no distinguishable auriculae. Trilete ridges are generally present but are not extremely pronounced and do not increase in size to form an apical peak. The arcuate ridges are generally well developed at the equator of the spore (Fig. 24). Ridges may be less accentuated in our specimens when compared with those isolated from compressions due to the uncomressed nature of our megaspores. At least one specimen shows pustulate ornamentation (Fig. 23) similar to that described by Bhardwaj (1957) for *V. sculptis*. Internally a thin membrane is present but lacks the papillae described by Winslow (1959).

The megaspores are clearly assignable to *Valvisporites* and they closely resemble several species which have been described in different treatments of the genus. Using the broad species concepts of Zerndt (1930, 1937), Dijkstra (1955), and Dijkstra and van Vierssen Trip (1946) the spores can be assigned to *Valvisporites auritus* var. *grandis* which Dijkstra (1955) realized encompassed more than one natural species. The megaspores Dijkstra (1955) described from Spain as *Triletes auritus* var. *grandis* agree well with the morphology and size range, 725–1546 μm , of our spores. Potonié and Kremp (1956) recognized numerous species of *Valvisporites* and our specimens are similar to those figured by them (Potonié and Kremp 1955, 1956) for *V. nigrozonalis*, *V. augustae*, and especially in size to *V. flavus*. Two dispersed species of *Valvisporites* (*Triletes*) have been described from the Illinois Basin (Winslow 1959); specimens of both *V. auritus* and *V. augustae* are similar to our megaspores but they have smaller maximum size ranges. The size range and morphological variability of our megaspores are within those known for *Polysporia mirabilis* compressions (Chaloner 1958) which also include several described taxa of *sporae dispersae*.

Taxonomy

The diagnosis of *Polysporia mirabilis* Newberry was emended by Chaloner (1958) based on fertile compression material. Our specimens fall within the limits of the emended generic diagnosis and

contribute new information regarding the morphology of *Polysporia*. There are differences in dimensions between our specimens and those of the compression *P. mirabilis* and incomplete preservation of sporophyll laminae. The similarity of spore types, general morphological features, and stratigraphic-geographic occurrences of *P. mirabilis* suggest that our specimens most likely belong to *Polysporia mirabilis* rather than a separate species. In view of the additional information provided by these permineralized specimens an addendum is given for the generic diagnosis of *Polysporia*.

Polysporia Newberry emend. Chaloner

EMENDED DIAGNOSIS: Chaloner, W. G. J. Paleontol. 32:201. 1958.

ADDENDUM: Herbaceous, ligulate lycopod shoots with exarch coronate siphonosteles consisting of alternating fertile and vegetative areas. Vegetative leaves and sporophylls in same ontogenetic spirals. Vegetative leaves considerably larger and apparently more rigid than sporophylls. Some periderm and wood may be present; wood initiated opposite protoxylem groups. Abscission layer and parichnos lacking in leaf bases, hence, no leaf cushions.

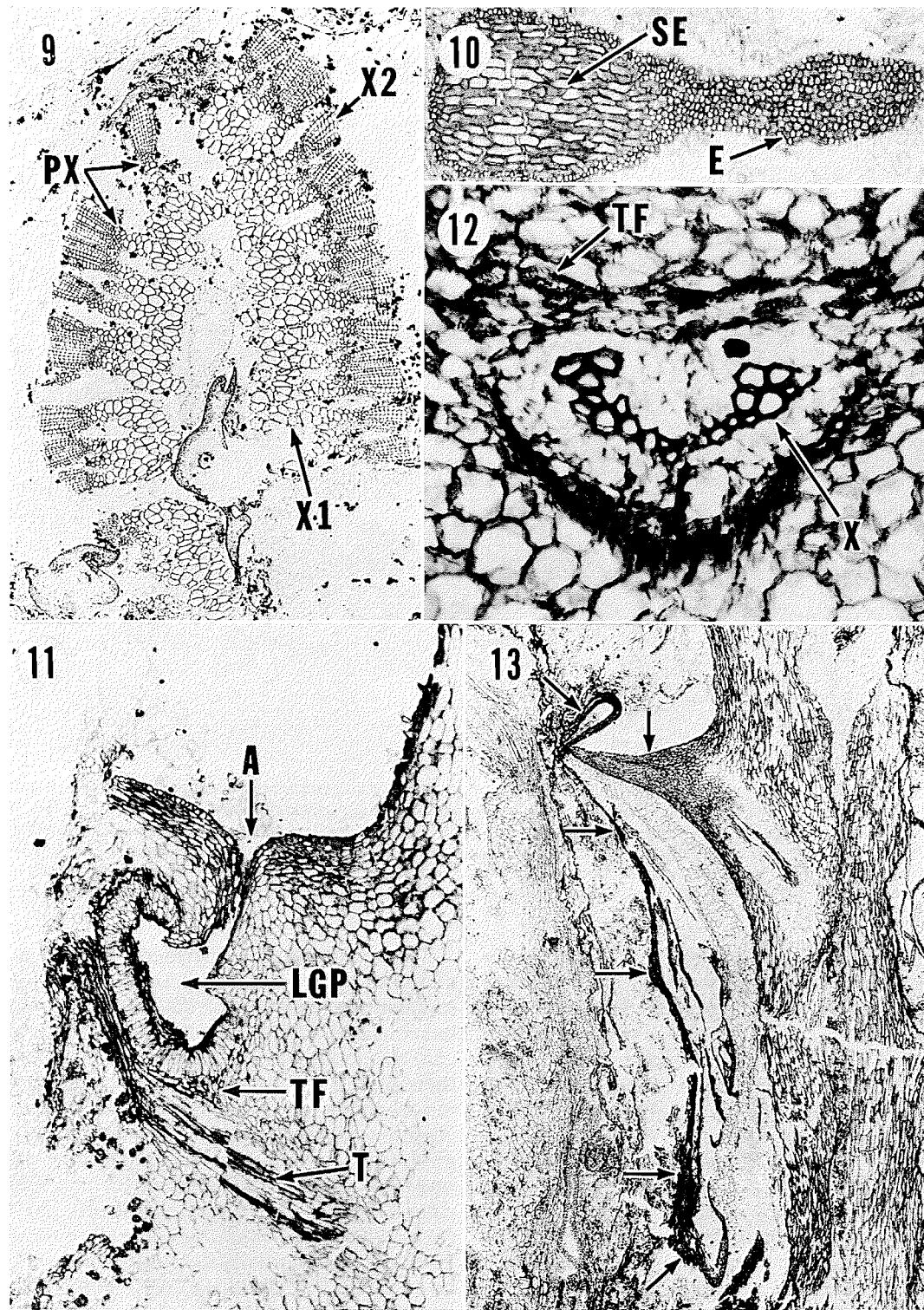
Discussion

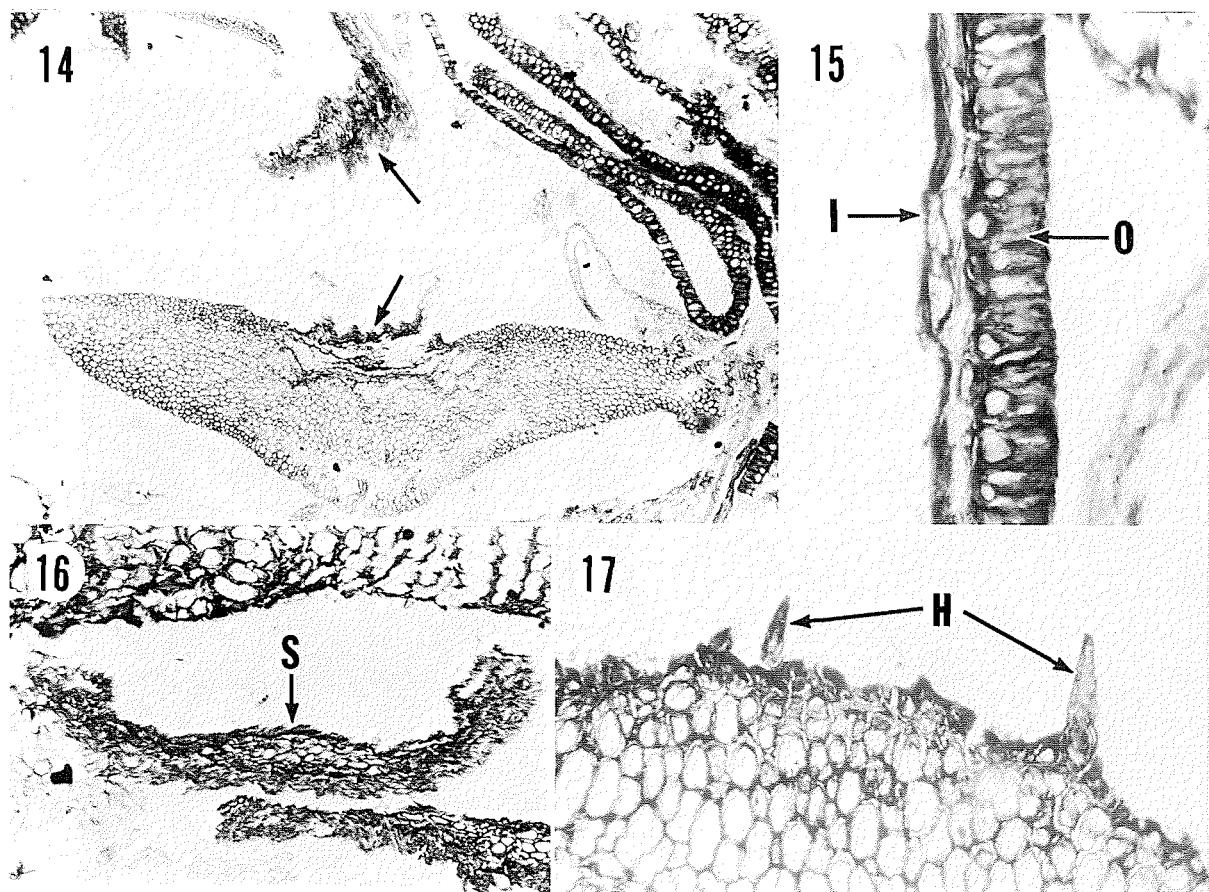
Morphology

Polysporia was an herbaceous plant with apparently an upright habit; support was derived from thick-walled outer cortical tissue and a small amount of periderm. The dimorphism of sporophylls and vegetative leaves sets *Polysporia* apart from the typical "selago" type exemplified by some eligulate homosporous lycopods from the Devonian to the Holocene. There is no evidence of parichnos in the simple leaf bases and the apparently delicate nature of the leaves results in our lack of details about their distal portions. No branched specimens were encountered.

Pennsylvanian age, ligulate, heterosporous lycopods exhibit considerable diversity in the forms of their leaf cushions or their leaf bases.

Figs. 9–13. *Polysporia*. Fig. 9. Transverse section of stele with secondary xylem (X2) wedges opposite protoxylem (PX) groups. Primary xylem (X1) is exarch; protoxylem groups are separated by irregular partings. Specimen 21555, slide I14753. $\times 15$. Fig. 10. Paradermal section of leaf base. Epidermal cells (E) are nearly isodiametric and much smaller than radially elongate subepidermal parenchyma (SE). Specimen 15417H₃, slide I14742. $\times 40$. Fig. 11. Radial (to stem) section of ligule pit (LGP). Pit is surrounded by rectangular cells, except along the pit aperture (A). Transfusion tissue (TF) is present above the leaf trace (T) up to the base of the ligule pit. Degraded tissue at base of the pit may be remains of ligule. Specimen 15417H₃, slide I14736. $\times 40$. Fig. 12. Transverse section of leaf trace with V-shaped xylem (X), smallest tracheids at the base and transfusion tissue (TF) (parenchyma with secondary wall thickenings) irregularly scattered above the trace. Specimen 15417H₂, slide I14734. $\times 195$. Fig. 13. Radial (to stem) section of downward folded sporophyll (unlabeled arrows) with distal portion desiccated. Specimen 10257, slide I14747. $\times 12$.

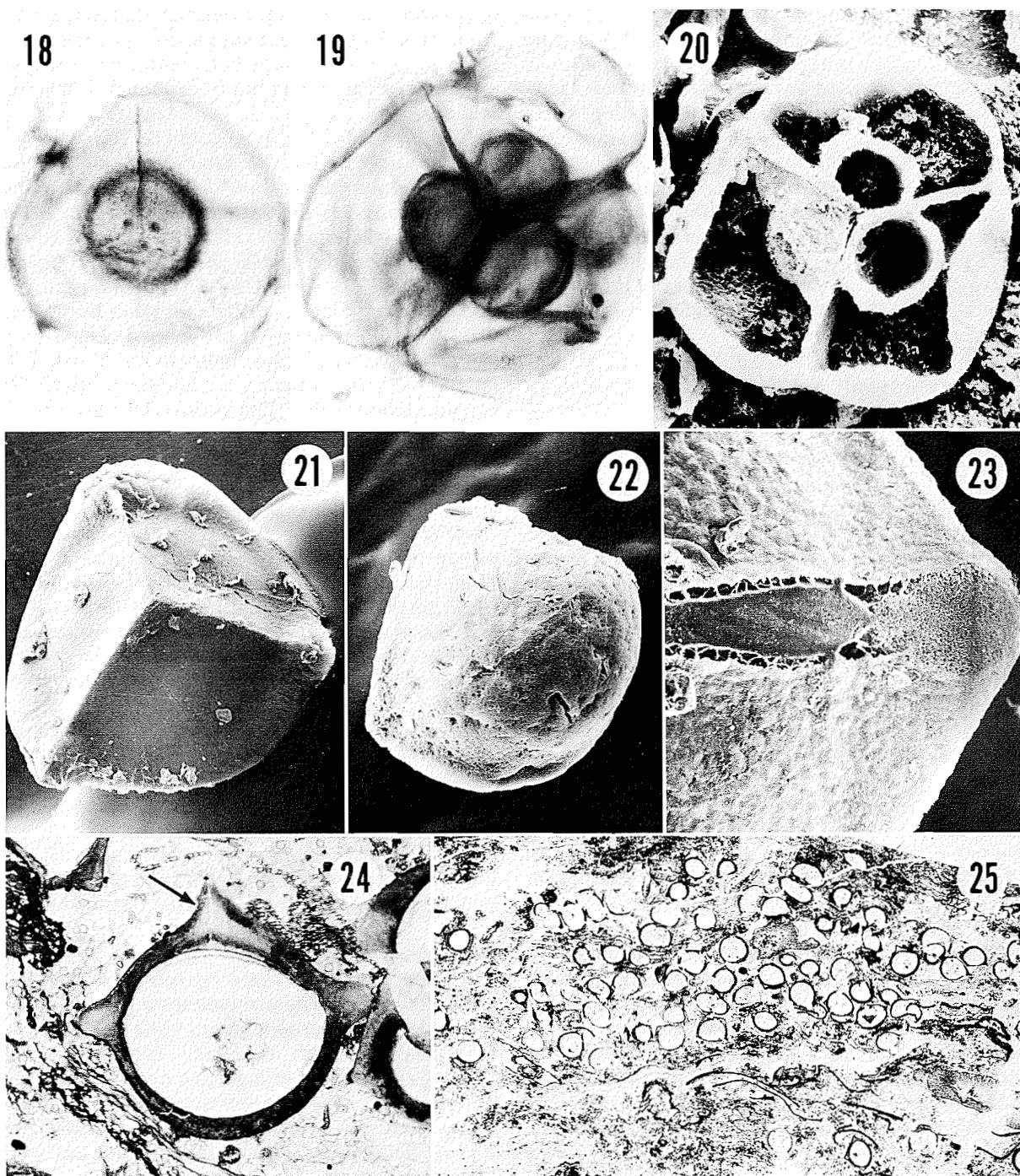




FIGS. 14–17. *Polysporia*. Fig. 14. Transverse section of sporophyll in region of presumed sporangial attachment; unlabeled arrows mark disrupted adaxial surface of sporophyll and corresponding sporangial base. Specimen 15417H₃, slide 114742, $\times 40$. Fig. 15. Cross section of two-layered sporangial wall; outer layer (O) is composed of thick-walled rectangular cells; inner layer (I) is composed of thin-walled poorly preserved cells, possibly representing a tapetum. Specimen 15470B, slide 114738, $\times 195$. Fig. 16. Transverse section of desiccated, distal portion of sporophyll (S). Specimen 15470, slide 114715, $\times 65$. Fig. 17. Section through abaxial portion of leaf base showing unicellular trichomes (H). Specimens 15470, slide 114699, $\times 100$.

These range from simple leaf bases as in *Polysporia* to complex large leaf cushions as in *Lepidophloios*. Some of the herbaceous forms such as *Lepidodendron serratum* exhibit leaf cushions with parichnos; others, such as *Bodeodendron*, have leaf cushions but lack parichnos (Wagner and Spinner 1976). The Carboniferous age *Selaginella* has neither leaf cushions nor prominent leaf bases. One arborescent species assigned to *Lepidodendron*, *L. brevifolium*, has simple leaf bases that apparently do contain small parichnos strands but there does not appear to have been leaf abscission. Although all these combinations of basal foliar morphology exist in the Pennsylvanian, the major arborescent genera, *Lepidodendron sensu stricto*, *Lepidophloios*, and *Sigillaria* (see Chaloner and Collinson 1975, pp. 92–94), have distinct variations in leaf cushion form with parichnos and leaf abscission.

The small amount of periderm-like development and rarer occurrences of wood in *Polysporia* serve to raise the question of distinction between herbaceous and arborescent lycopods. While arborescent lycopods are usually considered "woody," their high periderm to wood ratio and long-term maintenance of outer cortical tissues and leaf cushions are well-known. The spectrum of morphologies among the Carboniferous lycopods ranges from delicate (*Lepidodendron serratum*) to robust (*Polysporia*) "herbs or shrubs" to "trees" (*Lepidodendron*, *Sigillaria*), but all of these forms manifest an essentially herbaceous type of growth as expressed by Phillips (1979). Thus, the crux of the distinction between herbaceous and woody is not simply one of semantics, it is one of functional morphology uniquely expanded to arborescent size in lycopods. The arborescent forms exhibit mas-



Figs. 18–25. *Polysporia* spores. Fig. 18. Proximal view of *Endosporites* microspore with three interradial papillae. From specimen 15417, slide 114683. $\times 340$. Fig. 19. Tetrad of *Endosporites* in transmitted light. From specimen 15417, slide 114683. $\times 340$. Fig. 20. Section of triad of *Endosporites* with SEM showing proximal attachment of saccus to spore body. From specimen 15417. $\times 340$. Fig. 21. Proximal view of *Valvisporites* megaspore with SEM showing closed triradiate ridges, auriculae, and distinctive arcuate ridge. From specimen 15417. $\times 43$. Fig. 22. Distal view of *Valvisporites* with SEM. From specimen 15417. $\times 30$. Fig. 23. Partial proximal view (SEM) of auricula of *Valvisporites* with suture open (at left, filled with calcite) and well-developed auricula; proximal surface with pustulate ornamentation. From specimen 15417. $\times 120$. Fig. 24. Oblique longitudinal section of *Valvisporites* showing raised suture (arrow) and arcuate ridge (protrusions at equator). *Endosporites* microspores are scattered in the matrix. From specimen 15417, slide 114738. $\times 40$. Fig. 25. Mass of *Valvisporites* megaspores and sporangial wall fragments. Specimen 15417, slide 114738. $\times 5$.

sive primary bodies usually augmented by comparatively small amounts of wood and abundant living secondary cortex, usually in only the lower part or main trunk of most types. This seems indicative of quite rapid uninterrupted growth possible in semitropical to tropical coal swamps and characteristic of an herbaceous strategy. The other unique features of such lycopods seem to be consistent with such an interpretation. The inference of rapid herbaceous-like growth of many small and large lycopods of the coal swamps had an important bearing on their dominance in so many Pennsylvanian wetlands and the massive peat accumulations that resulted.

Comparison with *Spencerites* and *Sporangiostrobus*

Polysporia differs a great deal from both the diminutive *Selaginella* and the arborescent lycopods; pertinent comparisons are with *Spencerites* and *Sporangiostrobus*. Although *Spencerites* is elgulate and apparently homosporous, i.e., from a different evolutionary group, it shares with *Polysporia* several similarities in anatomy, gross morphology, and frequency of occurrences which may reflect convergence related to habitats. *Spencerites* appears to be herbaceous and may have consisted of alternating fertile and vegetative zones (Leisman 1962). In *S. majusculus* and *S. insignis* the stele is also a coronate siphonostele and major stem support is derived from the outer cortex. The outer cortex of *Spencerites* is two zoned and the middle cortical tissues are sometimes preserved (Scott 1898; Berridge 1905). These cortical features have not been observed in *Polysporia*. The sporophylls of *Spencerites* are verticillate; those of *Polysporia* are in a spiral phyllotaxy. *Spencerites* is a rare genus in Westphalian coal swamps and apparently did not survive the transition to the Stephanian.

Both *Sporangiostrobus* and *Polysporia* are heterosporous and ligulate with spirally arranged leaves and an outer cortex of homogenous thick-walled cells. *Sporangiostrobus* may represent a fertile segment of a shoot rather than a cone (Leisman and Stidd 1977; Wagner and Spinner 1976), but this has not been conclusively demonstrated. The stele of *Sporangiostrobus* is not well enough known to compare with *Polysporia*.

The leaf cushions of *Sporangiostrobus* have provided a basis for possibly determining the vegetative specimens of the plant but there are some uncertainties about interpretations. The probable vegetative stem of *Sporangiostrobus* was described as the compression *Bodeodendron* (Wagner and Spinner 1976) with which *Sporan-*

giostrobus "cones" were associated. The leaves of *Bodeodendron* are similar to the sporophylls of *Sporangiostrobus*. As in *Polysporia*, there was no evidence of parichnos; but *Bodeodendron* has true leaf cushions.

In Leisman's (1970) account of *Sporangiostrobus*, a stem from the same coal ball was described as *Lepidodendron dacrydioides* and suggested as possibly the vegetative stem of the plant. Leisman and Stidd (1977) later described a specimen of *Sporangiostrobus* with sporophyll "pseudocushions" similar to those of *L. dacrydioides* and suggested that *L. dacrydioides* and *Bodeodendron* were the same kind of lycopod. *Lepidodendron dacrydioides* is also similar to *Polysporia* with its homogeneous outer cortex and the partially dissected siphonostele. The protoxylem groups are not as prominent in *L. dacrydioides* and its stele is larger in diameter than known specimens of *Polysporia*. The leaf cushions of *L. dacrydioides* differ from the leaf bases of *Polysporia*; they have a teardrop shape with a patch of small-diameter cells above the leaf trace, interpreted as a ligule scar (Leisman 1970). Examination of the holotype of *L. dacrydioides* suggests that this tissue is actually a parichnos strand. It is present in all serial sections of a given leaf cushion. Parichnos strands in lycopods extend outward from the middle cortical region and characteristically are present on the abaxial side of the leaf trace. Using this for orientation of the leaf cushion, it is suggested that perhaps Leisman's illustration (1970, Fig. 47) is inverted. The leaf cushion would then be club shaped, a typical form for lycopods, rather than teardrop shaped. If *Lepidodendron dacrydioides* is the vegetative portion of *Sporangiostrobus*, the plant may well be related to *Polysporia* at the familial level.

Reproduction

The exact positions of megasporangia in *Polysporia* could not be determined from the specimens available, but microsporangia were intact in the uppermost portions of fertile zones. Chaloner (1958) found megasporangia and microsporangia at opposite ends of a compression "cone" of *Polysporia*. Because neither apex nor base were preserved, he assumed the megasporangiate end to be the lower portion. This is consistent with our observations. The sporophylls of *Polysporia* appear to have been ephemeral and the sporangial or spore packets have been dispersed or dislodged in most specimens. Stomatal crypts and trichomes were not observed on sporophylls.

The microspores were produced in large numbers per sporangium and masses of *Endosporites*

several centimetres in diameter are common in coal balls with *Polysporia*. The spores are usually found in tetrads. The dispersed megaspores are abundant in the same peat matrix but do not remain in tetrads.

So far as we know none of the swamp lycopods of the Carboniferous had adventitious root systems which would have facilitated vegetative propagation; most other groups did have but only the small ferns are known to have frequently reproduced vegetatively. Thus, the survival of lycopods depended on sexual reproduction. The cyclic development of vegetative and fertile shoot zones of *Polysporia* provided a means of repetitive sexual reproduction, advantageous in fluctuating marshlands and areas marginal to swamps. Only free-sporing lycopods with small granular-walled megaspores survived the transition into the late Pennsylvanian. The ultimate persistence of *Polysporia*, *Selaginella*, *Sporangiostrobus*, and *Sigillaria* (see Schopf 1941) was dependent, in part, on the ability of plants to repeatedly reproduce sexually.

Stratigraphic Occurrences

The occurrences of *Polysporia* in Middle Pennsylvanian peat deposits in coal balls appear to be rare in the Illinois Basin except at the western Kentucky site in the Baker Coal Member. However, according to Chaloner (1958) *Polysporia* extended geographically across Euramerica from Great Britain to Oklahoma. The other reports of *Endosporites* from peats come from the Copland coal bed of the Kanawhan of eastern Kentucky (Brack and Taylor 1972; Taylor 1973) and from either the Pittsburgh Coal or Redstone Coal in the Monongahelian of Ohio (Good and Taylor 1974). In European terminology, these Appalachian occurrences would be equivalent to Westphalian B and uppermost Stephanian.

While *Polysporia* has not yet been described from the Upper Pennsylvanian peats of coal balls, there is a clear inference from the abundance of *Endosporites globiformis* found in coals of the Illinois Basin (Peppers 1964; Phillips et al. 1974) that this herbaceous lycopod was a major element in numerous wetlands where *Psaronius* trees did not dominate. The relative abundance of auriculate megaspores of *Valvisporites* (*Triletes* in Winslow (1959)) is consistent with this late Pennsylvanian expansion of *Polysporia*. Both the studies of Peppers (1964) and of Winslow (1959) noted the earlier abundance of the microspores and megaspores attributed to *Polysporia* in several successive coals in the lower part of the Spoon Formation. In referring specifically to the Murphysboro Coal of Illinois,

Peppers (1964, p. 28) stated that there was "an unusually high frequency of *Endosporites* (9%) for this part of the Pennsylvanian."

The inferences from palynological data on stratigraphic occurrences of abundant *Polysporia* have presented somewhat of an enigma as to why the plant had not been previously found in peats. The rather delicate nature of the ground tissues, lack of any substantial amount of wood or periderm, and the loss of sporangia may account for our previous lack of recognition of *Polysporia* in some peats. Those of the Murphysboro equivalent contained beautifully preserved *Lepidodendron*-*Cordaites* vegetation but the *Polysporia* specimens were consistently of low preservational quality and the number of specimens recovered was very small for the sample size. In contrast, many of the delicate tissues were preserved in coal balls from the Herrin and Baker Coal Members. Only in the latter is *Polysporia* relatively abundant. This may be significant because of the stratigraphic position of the Baker Coal, very high in the Carbondale Formation. At present the Baker Coal is as high stratigraphically as we can abundantly sample *in situ* peats prior to the Middle-Upper Pennsylvanian transition in vegetation from arborescent lycopod-dominated swamps to those of tree ferns with pteridosperms and calamites.

Paleoecology

What can be deduced about the paleoecology of *Polysporia* is limited but it has a significant bearing on the nature of *Polysporia* wetlands in the late Pennsylvanian. A random sample of the peat from the Baker Coal, analyzed according to the quantitative methods of Phillips et al. (1977), indicates that lycopods constituted 82% of the volume, ferns and pteridosperms 8% each, and sphenopsids 2%. Despite the small percentage of sphenopsids, *Sphenophyllum* is more abundant than at any other site we have collected. *Polysporia* most often occurs with *Sphenophyllum* and with parts of *Lepidodendron dicentricum* (*L. schizostelicum*). Other common genera in the peats, *Lepidophloios*, *Psaronius*, and *Medullosa*, are poorly represented in the *Polysporia*-*Sphenophyllum* association. The coal ball from the Herrin Coal exhibits the same association; two of three additional coal balls with *Polysporia* recently found in this coal do also. Hence, we interpret the *Polysporia*-*Sphenophyllum* phase as an herbaceous to shrubby vegetation type.

The existence of such a low vegetation type in the late Des Moinesian suggests that late Pennsylvanian wetlands from which *Endosporites*-rich

coals were derived may have been largely marshes, in contrast to tree fern forests which generally characterize the Missourian of the Illinois Basin. The plant assemblages of the Baker Coal are somewhat transitional with taxa known previously from only the Middle or the Upper Pennsylvanian; but the seam as a whole was clearly dominated by arborescent lycopods. The fabric of the peat is quite open; there is an exceptional mixture of rotten logs and exquisite gametophyte and embryo stages of *Lepidocarpon* and *Achlamydocarpon* which are frequently fusinized, as are the sphenophylla. The coincidences noted between *Polysporia* occurrences in the Baker Coal and Murphysboro equivalent coal are not in plant associations (the latter was largely a *Lepidodendron-Cordaites* swamp) but in the peat fabric and high incidences of fusinized plants of the *Polysporia* phase. According to Stach et al. (1975, p. 311) such fusain may indicate low rates of subsidence, under shallow water cover with frequent access to air, i.e., drier conditions of peat accumulation. A marsh environment marginal to more typical arborescent lycopod swamps could be consistent with such observations.

The local abundance of *Polysporia* in the Baker Coal somewhat portends a vegetational type which expanded during the transition to the late Pennsylvanian and thereafter; similarly, the less prevalent communities of *Psaronius* and *Medullosa* found in Middle Pennsylvanian age peat profiles (Phillips et al. 1977) expanded with the loss of the giant lycopods in the Middle–Upper Pennsylvanian transition. The stature of the most abundant late Pennsylvanian swamp trees (ferns, pteridosperms) was markedly less than the surplanted lycopod trees, and *Polysporia* marshlands constituted a much smaller vegetational type resulting in less peat accumulation and ultimately thinner coals.

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