MORPHOLOGY OF FERTILE *PECOPTERIS UNITA* FROM THE MIDDLE PENNSYLVANIAN OF ILLINOIS

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ABSTRACT. Ironstone nodules from the Francis Creek Shale (Middle Pennsylvanian) near Morris, Illinois, have yielded both fertile and sterile pinnae of *Pecopteris unita* Brongniart. Partly petrified pinnae bear decurrent pinnules at approximately 90° angles. Pinnules have entire downturned margins, taper slightly apically, measure 4–8 mm long, 2–3 mm wide, and have unbranched, apically curved lateral veins. Synangia are abaxial and composed of 5–7 radially arranged, laterally appressed sporangia that are free at their apices. Sporangia surround solid tissue basally, a central hollow area distally, and dehisce longitudinally along the midline of the inward-facing sporangial walls. Spores are monolete, reniform, measure 14–20 μm long, and possess a papillate sculpturing. These synangia compare favourably with the organ genera *Scolecopteris* Zenker and *Cyathotrachus* Watson, and are not similar to *Ptychocarpus* Weiss, a poorly understood genus with bilaterally symmetrical synangia.

IRONSTONE nodules containing sterile and fertile foliage that has affinities with marattialean ferns have been known from the Francis Creek Shale in the Mazon Creek area since the work of Lesquereux (1866, 1870). Although plants in these ironstone nodules are usually preserved as impressions or compressions, a significant minority of nodules include some structural preservation. Despite considerable attention to foliar impressions, the possibilities of this structurally preserved material have not been generally recognized or fully exploited. A small indication of the wealth of structural information obtainable from some nodular fossils is evident in studies of *Paracalamostachys* (Hibbert and Eggert 1965), *Mazostachys* (Kosanke 1955), and *Scolecopteris* (Jennings and Millay 1978).

One of the most common elements of the Mazon Creek flora is the fern foliage known as *Pecopteris unita* Brongniart (1836). Fertile material of this species has historically been incorrectly placed in the genus *Ptychocarpus* Weiss (e.g. in Noé 1925, Janssen 1940, Darrah 1970). In this study ironstone nodules containing well-preserved specimens of fertile *Pecopteris unita* were investigated with the primary emphasis directed toward elucidating synangial morphology, since the diagnostic features of the synangia have been insufficiently known. Our study shows that the three-dimensional morphology of these synangia conforms, at the generic level, to species that have been placed in the organ genera *Cyathotrachus* Watson (1906) and *Scolecopteris* Zenker (1837).

MATERIALS AND METHODS

The fossils utilized in this investigation were collected from the Francis Creek Shale member of the Carbondale Formation of Middle Pennsylvanian age (Willman *et al.* 1975). They were exposed on abandoned strip mine dumps in Sec. 26, 34, and 35, T. 34 N.; R. 7 E., Grundy County, Illinois (Morris 15′ Quadrangle), north-east of the town of Morris. Though plant fossils occur throughout the shale,

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particularly toward the base, structural preservation is found only in ironstone nodules which occur on the surface of the mine dumps as a lag deposit, that results as the shale weathers. The primary cementing minerals in these nodules are siderite, pyrite, and marcasite with secondary concentrations of calcite, sphalerite, and kaolinite. Petrifaction or permineralization, when it occurs, is the result of the introduction of either calcite and/or pyrite-marcasite as a preserving medium.

In fossil specimens with calcite as the primary medium of preservation, the nodular halves were glued back together, cut for various planes of section, and cellulose acetate peels were made. In most specimens, however, there is an admixture of pyrite or marcasite, which require a different etching technique. For this reason each polished surface was photographed and studied before a peel preparation was attempted. Spores were mechanically removed from the exposed surface of the nodule and treated with hydrofluoric acid (25%) to dissolve accompanying matrix. Spores were then prepared for light and scanning electron microscopy according to methods outlined in Millay and Taylor (1974). Illustrated specimens are deposited in the Paleobotany Collection; Department of Botany, The Ohio State University, S1. 7721–7731, Sp. 1–8.

DESCRIPTION

Specimens are once or twice pinnate and may be fertile, sterile, or a combination of these. In most cases the lamina of the pinnules is not preserved except for its impression. The pinna axis, pinnule midribs and synangia are present, but cellular preservation is generally poor (Pl. 123, fig. 9).

Pinnules are borne at nearly right angles to the pinna axis and are decurrent, showing varying amounts of lateral fusion with adjacent pinnules (Pl. 123, figs. 1–2). The pinna axis may appear quite broad relative to the size of the pinnules, and possesses fine longitudinal striations. Pinnules range from 4 to 8 mm long and 2 to 3 mm wide, with fertile pinnules often somewhat larger than sterile ones (Pl. 123, fig. 1). Pinnule margins are parallel or taper gradually distally, ending in a blunt-rounded apex (Pl. 123, figs. 1–2). Three-dimensional impressions show that the pinnule margins are smooth and slightly downturned. Pinnule midveins are strong and extend to the apex, generally forking near their distal extremity. A particularly distinctive feature of *P. unita* is the presence of arcuate lateral veins which have the concave side of the vein facing the pinnule apex (Pl. 123, fig. 2).

Synangia are borne in two rows, one on each side of the pinnule midrib, and are composed of 5–7 radially arranged, axially elongate, sporangia (Pl. 123, figs. 3, 4, 8, 9). Synangia may be 0·8–1·2 mm in diameter (Pl. 124, figs. 1–9) and are of approximately the same length. Synangia have a short pedicel that is continuous with the tissues present in the basal third of the synangium. The short axial extent of the central parenchymatous area is evident in serial sections through the synangial base (Pl. 124, figs. 1–3). Distal to this the sporangia surround a hollow area that progressively increases in diameter toward the apex of the synangium (Pl. 124, figs. 4–7).

Apically, the sporangia appear to be laterally free of one another for a relatively short distance, probably no more than one-third of their length (Pl. 124, figs. 7–8). Sporangia are up to 0·4 mm in diameter and have apices that are solidly cellular and taper gradually to an acute point (Pl. 124, fig. 9). Outward-facing sporangial walls are rather thin, consisting of three or fewer cell layers, while the inward-facing walls appear to be uniseriate. Dehiscence is longitudinal along the midline of the inward-facing sporangial walls (Pl. 123, fig. 9; Pl. 124, fig. 6 at arrow, 8).

The *P. unita* specimen that was most useful for structural information had undergone dehiscence and few spores were present. The specimen used for spore preparations is shown in Pl. 123, figs. 3, 4, and

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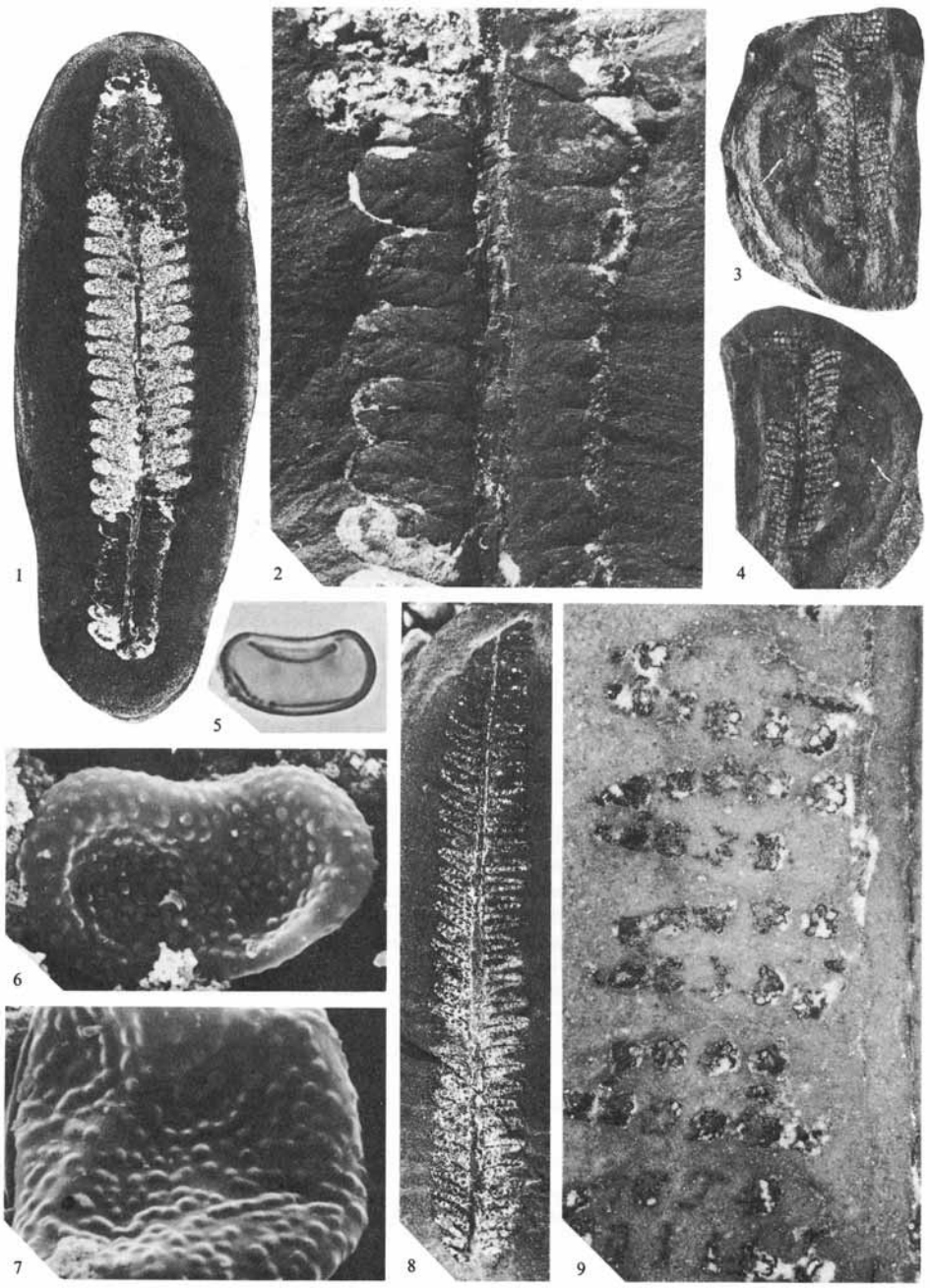
EXPLANATION OF PLATE 123

Figs. 1–9. *Pecopteris unita* Brongniart. 1. Fertile-sterile pinna, ×1. 2, detail of sterile foliage on combination fertile-sterile specimen, ×4. 3–4, fertile specimen from which spores were isolated, ×1. 5, lateral view of spore; monolete suture is to top of photograph, ×1460. 6, collapsed spore with papillate ornamentation, ×3400 SEM. 7, detail of spore with papillate ornamentation, ×7000 SEM. 8, fertile pinna with well-preserved synangia, ×1. 9, polished surface showing distribution of synangia on abaxial pinnule surface, ×7.



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contains the same type of spore as that observed in all our specimens. Spores appear reniform in lateral view with a concave proximal surface (Pl. 123, fig. 5) and appear oval in polar views. Spores range from 14 to 20 μm (av. 17 μm) long and 8 to 12 μm (av. 10 μm) wide. The monolete suture extends $\frac{1}{2}$–$\frac{2}{3}$ the length of the spore (Pl. 123, fig. 5) and has very thin labra. The spore exine is ornamented by papillae that are circular (0·5 μm diameter) in outline and have little relief (Pl. 123, figs. 6, 7). If found dispersed these spores would be called *Laevigatosporites minutus* (Ibrahim) Schopf, Wilson, and Bentall (1944).

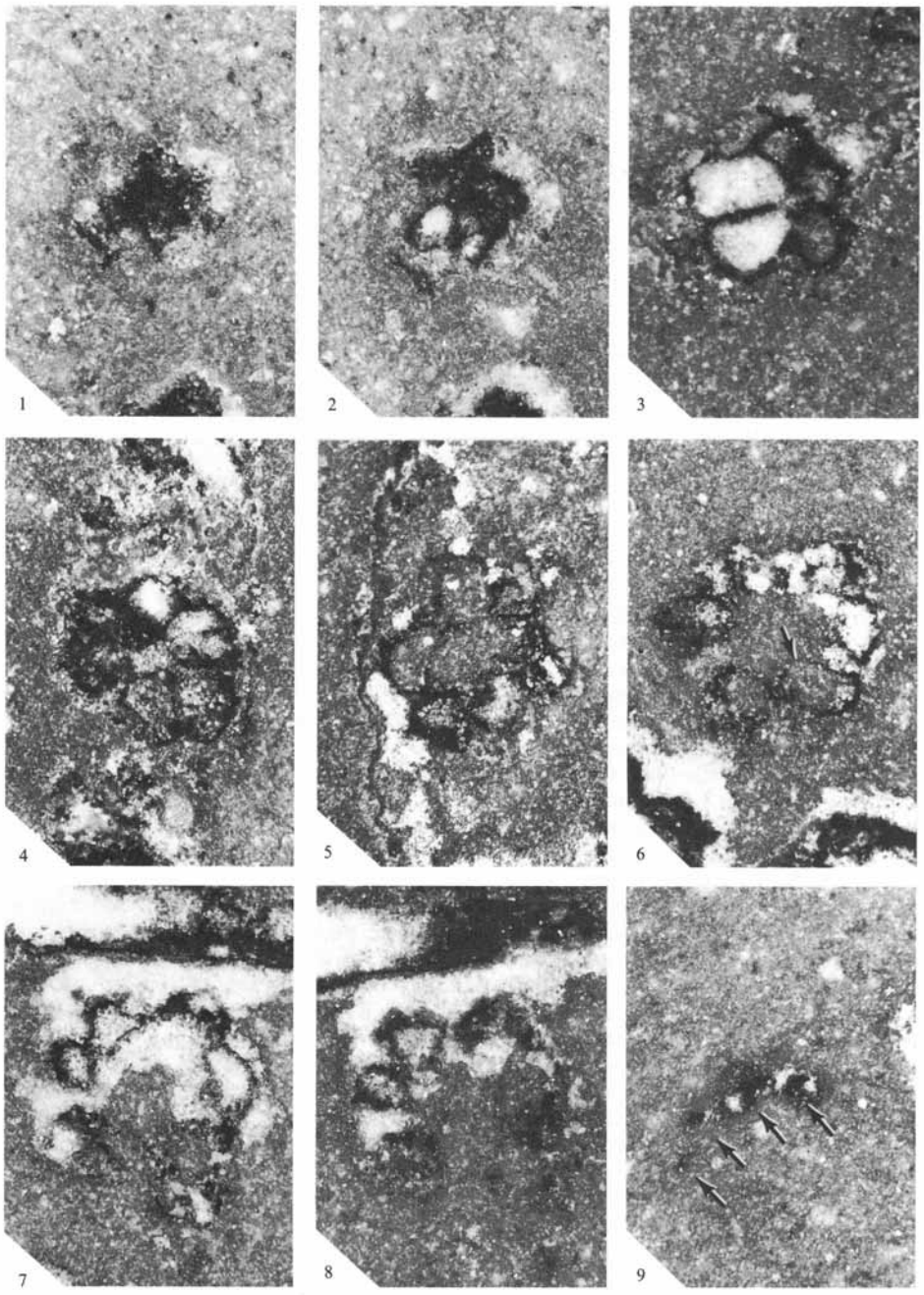
DISCUSSION

In both Europe and North America *Pecopteris unita* Brongniart (1836) is one of the most common and easily recognized pecopterid form species. In North America this species has been recognized in strata from the lower Allegheny to the upper Dunkard (Darrah 1970) and their stratigraphic equivalents. The pinnules of *P. unita* are characteristically united basally to varying degrees, have parallel margins, and have a decurrent midvein that produces simple, apically curved lateral veins, that extend to the pinnule margins. Our sterile foliage (Pl. 123, figs. 1–2) demonstrates this pinnule form and arrangement diagnostic of *P. unita*.

Only one previous study has described anatomically preserved fructifications of *P. unita* (Renault 1883). This foliage occurs in silicified blocks from Autun, France, and is either Stephanian or Lower Permian in age (Rothwell 1975). Unfortunately the synangia of *P. unita* were studied only from transverse sections, and no photographic illustrations of this material have been published. The line drawings provided by Renault indicate that the synangia are radial and composed of seven sporangia that surround a central parenchymatous area. Synangia measure 0·8 mm in diameter, but their length is unknown. Renault believed that the central cellular area extended to the synangial apex and that sporangial dehiscence had to take place through apical pores. In the North American material the sporangia surround a central hollow area apically, and dehiscence is longitudinal along the inner sporangial midline. This basic synangial organization is like that known for other anatomically preserved marattialeans such as *Acaulangium* Millay (1977), *Cyathotrachus* Watson (1906), *Eoangiopteris* Mamay (1950), and *Scolecopteris* Zenker (1837). The mode of synangial dehiscence indicated for *P. unita* by Renault is quite different from that known for other Paleozoic marattialeans. Renault (1883) makes it clear that he did not see the synangium of *P. unita* in longitudinal section, and that the central parenchymatous area was not observed to extend to the synangial apex. The idea that the centre of the synangium was solidly cellular distally, was presented as the most likely possibility based on the appearance of the synangia in compression specimens. It seems likely from our study of *P. unita* that the sections available to Renault were made through basal portions of the synangia, and that the sporangia surrounded a hollow area apically as in other anatomically preserved marattialeans.

EXPLANATION OF PLATE 124

Figs. 1–9. Synangia of *Pecopteris unita* Brongniart in transverse section, ×40. 1–3, basal one-third of synangium. 4–6, midlevels of synangium. Arrow indicates dehiscence slit. 7–9, distal extremities of synangium. Arrows in 9 indicate sporangial apices.



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In a later publication Renault (1896) referred material originally described as fertile *P. unita* (Renault 1883) to the genus *Ptychocarpus* Weiss (1869), and Renault's description has come to be regarded as definitive for the genus *Ptychocarpus*. The practice of referring fertile specimens of *Pecopteris unita* to *Ptychocarpus* has been followed by virtually all subsequent authors (Kidston 1925, Corsin 1951); however, these specimens are compression-impression fossils that have not been shown to possess the structural features reported by Renault. An examination of the original figures and description of *Ptychocarpus* in Weiss (1869, p. 94, pl. 11, fig. 2) indicates that Renault's specimens do not belong to this genus. Although *Ptychocarpus* is poorly known, several distinctive features can be noted. The fructification of *Ptychocarpus* is bipartite, bilaterally symmetrical, and appears to have an elliptical outline on fractured surfaces. In addition, the fructifications occur in three rows on units that apparently represent pinnules. It is therefore clear that fertile material of *Pecopteris unita* cannot be referred to the genus *Ptychocarpus* Weiss.

The question of the precise taxonomic status of Renault's fructifications of *Pecopteris unita* cannot be resolved at this time without additional anatomical information. In so far as it is known, the silicified *P. unita* from Europe compares most closely with *Cyathotrachus altissimus* Mamay (1950) in synangial organization and foliage type (Millay 1976). Our material of *P. unita* differs from that described by Renault in spore morphology and by the short extent of the central parenchymatous area in the synangium.

Synangia of the North American material of *P. unita* share basic synangial construction with *Cyathotrachus* and some species of *Scolecopteris*. In *Cyathotrachus* the synangia are cup-like with the sporangia surrounding an open central hollow area. Most species of *Scolecopteris* also have a central hollow area, but it is enclosed apically by the sporangia. The cup-like synangial organization of our *P. unita* specimens is present, however, in some species of *Scolecopteris* (e.g. *S. monothrix* Ewart 1961). In the opinion of Millay (1976), the genera *Scolecopteris* and *Cyathotrachus* may not be distinct. If this is correct, then our fertile material of *P. unita* conforms at the generic level to *Scolecopteris*. In the absence of certain critical cellular details of the synangia, it is not presently possible to correlate our fertile *P. unita* with any particular species of *Scolecopteris*.

Numerous investigators have isolated spores from fertile *P. unita*. Most have reported spores that are oval in contour, monolete, and range in diameter from 12 to 26 μm (Brush and Barghoorn 1964, Darrah 1952, Laveine 1970, Moore 1946 [pars], Remy and Remy 1957). Ornamentation has been described as smooth walled, infragranulate, or papillate. Laveine (1970) and Remy and Remy (1955) described specimens with spores measuring up to 48 μm in diameter and having monolete or trilete sutures. Among previous studies, only Pfefferkorn *et al.* (1971) obtained small, papillate, reniform spores from a specimen resembling fertile *P. unita*. It is interesting that these spores and those of *Cyathotrachus altissimus* described in detail in Millay (1976) are essentially identical to those of our fertile *P. unita*.

The variety of spore types isolated from fertile *P. unita* foliage suggests that a number of different biological species are represented by this foliage form. In addition, this study indicates that at least two synangial morphologies were borne on foliage of the *P. unita* type. It is therefore evident that accurate delimitation of

natural taxonomic entities within the Paleozoic Marattiales is possible only by employing a comprehensive approach that utilizes the full range of morphological characters obtainable from fructifications, spores, and sterile foliage.

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REFERENCES

BRONGNIART, A. 1836. *Histoire des Végétaux Fossiles.* **1,** 488 pp. Paris.

BRUSH, G. S. and BARGHOORN, E. S. 1964. The natural relationships of some Carboniferous microspores. *J. Paleont.* **38,** 325–330.

CORSIN, P. 1951. Bassin houiller de la Sarre et de la Lorraine. I. Flore fossile, quatrième fasc., Pécoptéridées. *Étud. Gîtes minér., France.* 177–370, Atlas, pls. cviii–cxcix.

DARRAH, W. C. 1952. The materials and methods of palaeobotany. *Palaeobotanist,* **1,** 145–153.

—— 1970. A critical review of the Upper Pennsylvanian flora of eastern United States with notes on the Mazon Creek flora of Illinois. W. C. Darrah (1969), 220 pp. *Gettysburg.*

EWART, R. B. 1961. Two new members of the genus *Scolecopteris. Ann. Mo. bot. gdn.* **48,** 275–289.

HIBBERT, F. A. and EGGERT, D. A. 1965. A new calamitalean cone from the Middle Pennsylvanian of southern Illinois. *Palaeontology,* **8,** 681–686.

JANSSEN, R. E. 1940. Some fossil plant types of Illinois. *Ill. St. Mus. Scient. Pap.* **1,** 1–124.

JENNINGS, J. R. and MILLAY, M. A. 1978. A new permineralized marattialean fern from the Pennsylvanian of Illinois. *Palaeontology,* **21,** 709–716.

KIDSTON, R. 1925. Fossil plants of the Carboniferous rocks of Great Britain. *Mem. geol. Surv. Gr. Br. Palaeont.* **2,** 523–670.

KOSANKE, R. M. 1955. *Mazostachys*—a new calamite fructification. *Rep. Invest. Ill. St. geol. Surv.* **180,** 1–37.

LAVEINE, J.-P. 1970. Quelques pécoptéridinées houillères à la lumière de la palynologie (II). Implications paléobotaniques et stratigraphiques. *Pollen Spores,* **12,** 235–297.

LESQUEREUX, L. 1866. Report on the fossil plants of Illinois. *Ill. St. geol. Surv. Palaeontology,* **2,** 425–470.

—— 1870. Report on the fossil plants of Illinois. Ibid. **4,** 377–508.

MAMAY, S. H. 1950. Some American Carboniferous fern fructifications. *Ann. Mo. bot. Gdn.* **37,** 409–477.

MILLAY, M. A. 1976. Synangia of North American Pennsylvanian petrified marattialeans. Ph.D. Dissertation, Univ. Illinois at Urbana-Champaign.

—— 1977. *Acaulangium* gen. n., a fertile marattialean from the Upper Pennsylvanian of Illinois. *Am. J. Bot.* **64,** 223–229.

MILLAY, M. A. and TAYLOR, T. N. 1974. Morphological studies of Paleozoic saccate pollen. *Palaeontographica,* **147B,** 75–99.

MOORE, L. R. 1946. On the spores of some Carboniferous plants; their development. *Q. Jl geol. Soc. Lond.* **102,** 251–298.

NOÉ, A. C. 1925. Pennsylvanian flora of northern Illinois. *Bull. Ill. St. geol. Surv.* **5,** 1–113.

PFEFFERKORN, H. W., PEPPERS, R. A. and PHILLIPS, T. L. 1971. Some fern-like fructifications and their spores from the Mazon Creek compression flora of Illinois (Pennsylvanian). *Circ. Ill. St. geol. Surv.* **463,** 1–56.

REMY, R. and REMY, W. 1955. Mitteilungen über Sporen, die aus inkohlten Fruktifikationen von echten Farnen des Karbon gewonnen wurden. *Abh. dt. Akad. Wiss. Berl.* **1,** 41–48.

REMY, W. and REMY, R. 1957. Durch Mazeration fertiler Farne des Paläozoikums gewonnene Sporen. *Paläont. Z.* **31,** 55–65.

RENAULT, B. 1883. Cours de Botanique Fossile. Trois. année, 242 pp., G. Masson, Paris.

—— 1896. Bassin houiller et Permien d'Autun et d'Épinac. Flore fossile, quat. fasc., deux. part. *Étud. Gîtes minér.,* 578 pp. France.

ROTHWELL, G. W. 1975. The Callistophytaceae (Pteridospermopsida): I. Vegetative structures. *Palaeontographica,* **151B,** 171–196.

SCHOPF, J. M., WILSON, L. R. and BENTALL, R. 1944. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. *Rep. Invest. Ill. St. geol. Surv.* **91,** 1–66.

WATSON, D. M. S. 1906. On a 'fern' synangium from the Lower Coal Measures of Shore, Lancashire. *Jl. R. microsc. Soc.* **1906,** 1–3.

WEISS, C. E. 1869. Fossile Flora der jüngsten Steinkohlenformation und des Rothliegenden im Saar-Rhein-Gebiete. pt. 1: 1–100, A. Henry, Bonn.

WILLMAN, H. B., ATHERTON, E., BUSCHBACH, T. C., COLLINSON, C., FRYE, J. C., HOPKINS, M. C., LINEBACK, J. A. and SIMON, J. A. 1975. Handbook of Illinois stratigraphy. *Bull. Ill. St. geol. Surv.* **95,** 1–261.

ZENKER, F. C. 1837. *Scolecopteris elegans* Zenk. Ein neues fossiles Farrngewächs mit Fructificationen. *Linnaea*, **11,** 509–512.

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