Journal of
PALEONTOLOGY
A JOURNAL OF THE PALEONTOLOGICAL SOCIETY

A Middle Pennsylvanian macrofloral assemblage from wetland deposits in Indiana (Illinois Basin): a taxonomic contribution with biostratigraphic, paleobiogeographic, and paleoecologic implications

Arden R. Bashforth,[1*] William A. DiMichele,[1] Cortland F. Eble,[2] and W. John Nelson[3]

[1]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA ⟨bashfortha@si.edu⟩; ⟨dimichel@si.edu⟩
[2]Kentucky Geological Survey, University of Kentucky, Lexington, KY 40560, USA ⟨eble@uky.edu⟩
[3]Illinois State Geological Survey, University of Illinois at Urbana-Champaign, Champaign, IL 61820, USA ⟨jnnelson@illinois.edu⟩

Abstract.—Taxonomic analysis is provided for a Middle Pennsylvanian macrofloral assemblage collected from clastic wetland deposits in Clay County, Indiana, on the eastern margin of the Illinois Basin. Adpressed plant fossils were recovered from four distinct beds in the lowermost Staunton Formation, positioned above the Minshall Coal (uppermost Brazil Formation), part of a succession deposited near the Atokan-Desmoinesian boundary. The assemblage of 22 fossil-taxa is dominated by pteridosperms (including *Neuropteris flexuosa*, *Macroneuropteris scheuchzeri*, *Alethopteris densinervosa*, *Neuropteris ovata*, *Eusphenopteris neuropteroides*, and *Neuropteris missouriensis*) with lesser cordaitaleans (*Cordaites* spp. indet.) and sphenopsids (particularly *Sphenophyllum cuneifolium*). Lycopsids are uncommon, and ferns are rare. In contrast, the microfloral assemblage from the Minshall Coal and overlying clastic units is dominated by lycopsid and tree fern spores. Comparisons with established biozonation schemes yield different ages depending on the regional biostratigraphic framework used: (1) latest Bolsovian (*Radiizonates difformis* Biozone, American microfloras); (2) latest Bolsovian or earliest Asturian (*'Neuropteris' rarinervis* Biozone, Appalachian Basin macrofloras); or (3) earliest Asturian (*Linopteris obliqua* Biozone, European macrofloras). The placement and correlation of the Bolsovian-Asturian and Atokan-Desmoinesian boundaries, which have traditionally been equated by palynology, are evaluated in the context of this discordance. Several revised stratigraphic scenarios are proposed for this interval in the Illinois Basin, which is being increasingly recognized as a time of significant environmental change throughout Euramerica. Homotaxial comparisons with European macrofloral assemblages indicate that, of the 18 biological taxa recorded, between 14 and 17 (78–94%) also are common in coeval wetland deposits in Europe. The similarities exemplify the spatial conservatism and low diversity of wetland plant communities over vast areas of tropical Euramerica, a manifestation of the intrinsically stressful conditions that characterize such habitats, and indicates that neither the Laurentian Shield nor the Appalachian-Variscan Mountains were an insurmountable barrier to plant dispersal during the Middle Pennsylvanian.

Introduction

American paleobotanists have long been criticized by their European contemporaries for a perceived negligence in documenting Pennsylvanian-aged macrofloral assemblages preserved as adpressions (i.e., compression-impression floras). For example, after a reconnaissance fieldtrip to the USA in 1933, W.J. Jongmans summarized the status of Carboniferous paleobotany in America in an unflattering quote (Jongmans and Gothan, 1934, p. 17, translated from German), "If one considers then how poor most of the American illustrations are, how relatively few works are supplied with illustrations—most papers only contain lists with many names, which provide us no clue on which to base a judgment,—how confused the nomenclature is, because of parallel efforts by rather than collaboration between the American and European paleobotanists—, then it becomes clear to anyone that any attempt [of comparison] without one's own consideration [of the evidence] will be very difficult if not impossible." Thereafter, Jongmans (1937a, p. 364–366) and Bode (1958, p. 217, 218) expressed discontent about correlating between American and European successions, and pointed to the large size of (and distance between) Pennsylvanian basins in the USA, the use of parochial stratigraphic nomenclature in different states, the reliance of American paleobotanists on outdated literature that did not take European taxa into account, and the scarcity of publications with well-illustrated macrofloras. In particular, it was felt that the lack of consultation with the European literature had caused the introduction of many 'new species', creating the illusion that Pennsylvanian vegetation preserved on either side of the Atlantic Ocean differed more than expected.

* Current Address: Geological Museum, Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5-7, 1350 Copenhagen K, Denmark. Email: bashforth@snm.ku.dk

Since the mid-20th century, the breakdown of language barriers, better international access to publications, and collaboration between American and European paleobotanists has seen the resolution of many taxonomic issues, as W.C. Darrah foretold in a footnote in Jongmans (1937b, p. 394): "The number of [P]aleozoic plants with wide distributions in both Europe and America will increase rather than diminish with careful study." Furthermore, publications that involve North American adpression assemblages grew substantially after the 1920s (Pfefferkorn and Gillespie, 1980a). Nonetheless, the idea persists that Pennsylvanian macrofloral assemblages lack documentation in the USA (e.g., Cleal et al., 2009, p. 184), thus hindering comparisons and biostratigraphic correlations of strata across the Euramerican paleocontinent. A task of this paper is to demonstrate that such claims are exaggerated.

This contribution focuses on the description and illustration of a Middle Pennsylvanian (middle Moscovian) macrofloral assemblage collected from wetland deposits above the Minshall Coal (lowermost Staunton Formation) of Indiana, situated on the eastern margin of the Illinois Basin. Plant remains were collected at a single locality from four distinct beds, each containing a compositionally unique suite of fossil-taxa (sensu Cleal and Thomas, 2010), although all specimens are treated as belonging to one macrofloral assemblage to simplify biostratigraphic comparisons. The strata accumulated close to the Atokan-Desmoinesian Stage boundary, which has been correlated with the Bolsovian-Asturian Substage boundary of Western Europe (Peppers, 1996; Blake et al., 2002). The microfloral assemblage from the clastic beds and underlying Minshall Coal (uppermost Brazil Formation) also is tabulated, but only touched on in biostratigraphic context. Comprehensive synonymy lists are compiled for fossil-taxa in the macrofloral assemblage based on comparison with a suite of North American literature, which were singled out because they contain well-illustrated records of Middle Pennsylvanian plant remains, with a focus on the Illinois Basin. Homotaxial biostratigraphic comparisons with American and European biozonation schemes are presented, and uncertainties about the placement and correlation of

the Atokan-Desmoinesian and Bolsovian-Asturian boundaries are discussed. Evaluating the congruence of these boundaries is timely because they involve an interval that is being increasingly recognized as one of significant environmental change throughout Euramerica (cf., Cecil et al., 1985; Bertier et al., 2008; Van Hoof et al., 2013). Furthermore, nearly all macrofloral taxa identified also are present in contemporaneous deposits of Europe, and the paleobiogeographic and paleoecologic ramifications of this finding are considered in the context of Pennsylvanian wetland ecosystems in tropical Euramerica.

Geologic setting

Illinois Basin.—The Illinois Basin (also called the Eastern Interior Basin) is an interior cratonic basin (Leighton et al., 1991), one of several large depocenters in the USA that contain coal-bearing strata of predominantly Pennsylvanian age (Fig. 1.1). In its present configuration, the basin underlies much of Illinois and parts of western Indiana and western Kentucky, with small outliers in Iowa and Missouri (Fig. 1.2). The Illinois Basin contains a largely siliciclastic succession of Morrowan to Virgilian (Bashkirian to Gzhelian, upper Namurian to upper Stephanian) strata (Nelson et al., 1991, 2013), which accumulated on a low-gradient slope that dipped toward a shallow epeiric sea (Watney et al., 1989; Greb et al., 2003). Glacioeustatic fluctuations from the west resulted in cyclic marine transgressions across the continental platform (Wanless and Shepard, 1935, 1936; Heckel, 1986; Langenheim and Nelson, 1992; Algeo and Heckel, 2008), and in accord with its paleogeographic position, depositional environments in the Illinois Basin tend to be intermediate between the marine-dominated rocks of the Western Interior (Midcontinent) Basin and mainly deltaic to terrestrial strata of the Appalachian Basin to the east (Fig. 1.1; Heckel, 1977, 1980; Nelson et al., 2013). These basins developed in a paleoequatorial setting in the west-central part of Euramerica (Witzke, 1990), and were separated from eastern parts of the paleocontinent (present-day Europe)
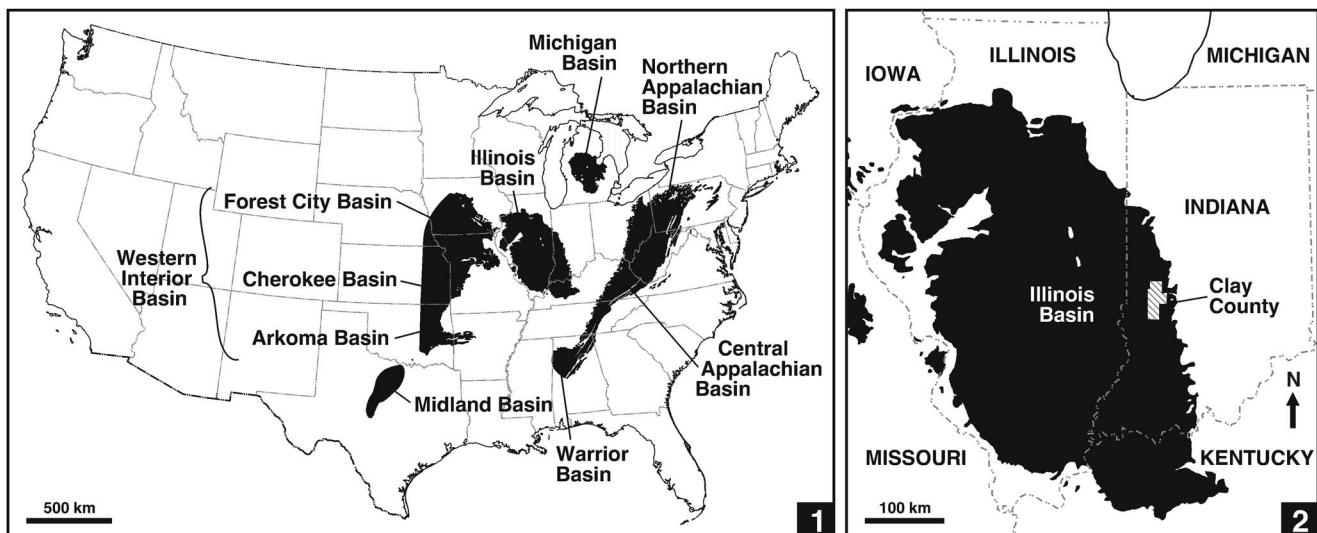

Figure 1. Basins in contiguous USA that contain coal-bearing strata of Pennsylvanian age. (**1**) Western Interior, Illinois, Appalachian, and Michigan basins, and their components. (**2**) Illinois Basin, and position of Clay County, Indiana on eastern margin of basin.

by uplands of the Laurentian Shield and, in part, by the Appalachian-Variscan Mountains (Blakey, 2013).

Study locality.—The study area is situated in Clay Country, west-central Indiana, on the eastern margin of the Illinois Basin (Fig. 1.1), where the thin and laterally discontinuous Lower Block, Upper Block, and Minshall coals of the upper Atokan Brazil Formation (Fig. 2) have been exploited due to their low to medium sulfur and ash content (Mastalerz et al., 2000, 2003; Kvale et al., 2004). The Brazil Formation, defined as being from the base of the Lower Block Coal to the top of the Minshall Coal (Hutchison, 1976), is equivalent to the middle part of the Tradewater Formation of Illinois and Kentucky (The Tri-State Committee on Correlation of the Pennsylvanian System in the Illinois Basin, 2001). In Indiana, strata above the Minshall Coal are assigned to the Staunton Formation, which includes the

Perth Limestone, the top of which defines the Atokan-Desmoinesian Stage boundary based on palynology (Peppers, 1996). The Minshall Coal and overlying Perth Limestone correlate with the Rock Island (No. 1) Coal and Seville Limestone of northwestern Illinois and the Empire Coal and Curlew Limestone of southwestern Kentucky (Fig. 2; Tri-State Committee, 2001; Nelson et al., 2013).

The macrofloral assemblage was collected from an open-pit mine north of Indiana Route 46, the now inaccessible Ashboro Pit (SW 1/4, SE 1/4, Section 17, Township 11N, Range 6W) operated by Log Cabin Coal Company. Plant fossils were collected during a reconnaissance in 1980, when the Lower Block and Upper Block coals were being mined, but the pit was idle and partly filled with water during a 1982 visit, leaving the upper highwall inaccessible. The west- and north-facing highwalls of the L-shaped pit are reproduced schematically in Figure 3. About 15 m of the Brazil and overlying Staunton formations were exposed, the lithostratigraphic boundary being the top of the Minshall Coal.

Correlation of limestone and coal members of the Brazil and Staunton formations is challenging due to their lenticular nature and variable lithology, but marker beds in the Ashboro Pit are identified with confidence (Fig. 3). The Lower and Upper Block coals are distinctive in this area, consisting of hard, dull-banded or 'splint' coal that separates into large cubic blocks along widely spaced joint planes. The type area of these coals is 15 km north of the locality, whereas the Minshall Coal and Perth Limestone have type sections five to 15 km farther north. No other marine unit in the Brazil or lower Staunton formations in this part of Indiana is likely to be confused with the Perth Limestone.

Most macrofloral remains were collected from an ~35 cm-thick package of 'roof-shales' immediately above the Minshall Coal on the west-facing highwall (Units 1 to 3; Fig. 3), whereas some adpressions presumably are from a bed (Unit 4) on the north-facing highwall at a stratigraphic position above the Perth Limestone. All sampled beds belong to USNM Locality 38354. Although the strata belong to the lowermost Staunton Formation, as currently understood and depicted in Figure 2, Units 1 to 3 are assigned to the uppermost Atokan and Unit 4 to the lowermost Desmoinesian. Based on new data presented here, the age of the fossiliferous strata and position of the Atokan-Desmoinesian and Bolsovian-Asturian boundaries will be discussed in the Biostratigraphy and age section.

Fossiliferous units

A light-gray, rooted paleosol ('underclay') underlies the 15 cm-thick Minshall Coal (Fig. 3), which is relatively uniform in thickness, but undulatory due to irregularities on the paleosol surface. Following the 'low-stand coal' model (cf., Cecil, 1990; Cecil et al., 2003, 2014; DiMichele, 2014), the Minshall Coal is interpreted to record peat buildup due to paludification and base-level rise under the (per)humid (everwet) conditions that attended a sea-level lowstand at maximum glaciation.

The ~35 cm-thick package of fossiliferous roof-shales above the Minshall Coal is divided into three distinct beds based on lithology and plant-fossil content (Units 1 to 3; Fig. 3). Gradational with the underlying coal, Unit 1 (~10 cm thick) is a
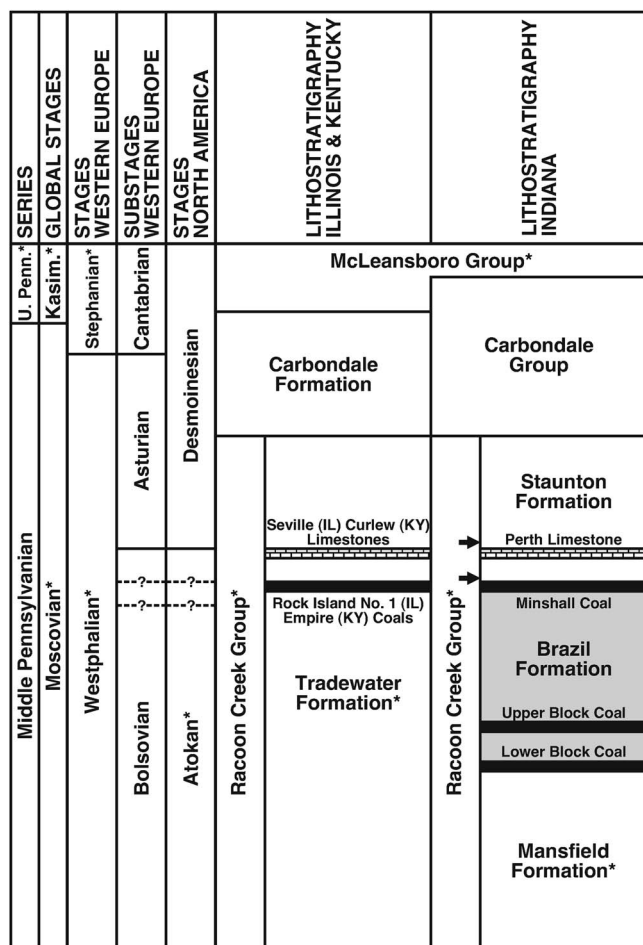

Figure 2. Stratigraphy of Middle Pennsylvanian of Illinois Basin (as currently understood), showing correlation between chronostratigraphic and lithostratigraphic units (* indicates incomplete unit); compiled from Davydov et al. (2010, fig. 2), Falcon-Lang et al. (2011, fig. 1), and Nelson et al. (2013, fig. 2). Brazil Formation (shaded) incorporates strata from base of Lower Block Coal to top of Minshall Coal. Macrofloral assemblage collected from lowermost Staunton Formation (arrows). Atokan-Desmoinesian Stage boundary and Bolsovian-Asturian Substage boundary shown as coeval and equivalent to top of Perth, Seville, and Curlew limestones, after Peppers (1996). Dashed lines denote possible positions of one or both boundaries based on biostratigraphic data presented herein (see Fig. 7; Biostratigraphy and age section).
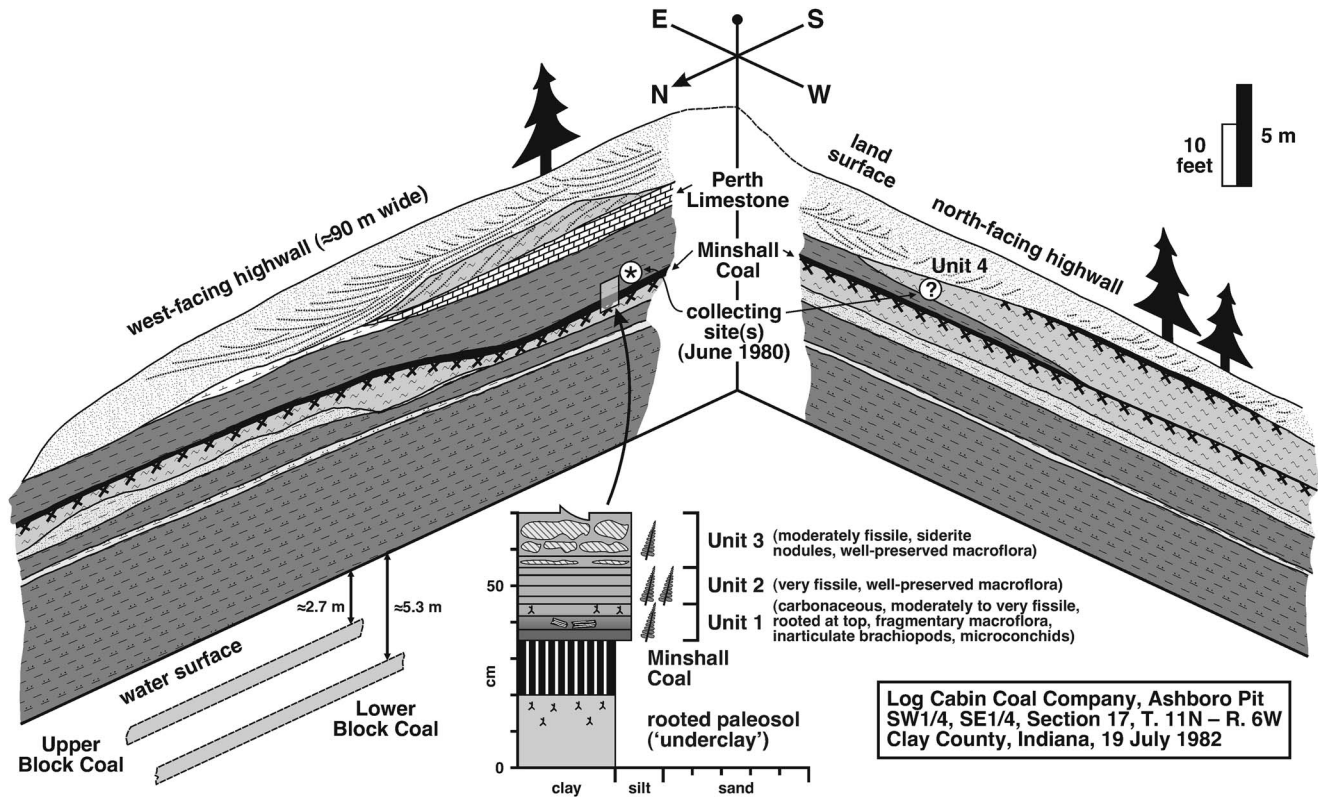
Figure 3. Schematic drawing of succession exposed in Ashboro Pit (now inaccessible open-pit mine of Log Cabin Coal Company; SW 1/4, SE 1/4, Section 17, Township 11N, Range 6W), north of Indiana Route 46, Clay County, Indiana, during visits in June 1980 and July 1982. Brazil Formation incorporates strata from base of Lower Block Coal (under water) to top of Minshall Coal, and overlying strata belong to Staunton Formation. Top of Perth Limestone corresponds to Atokan-Desmoinesian boundary (Peppers, 1996). Macrofloral assemblage collected from roof-shales above Minshall Coal (Units 1 to 3, marked with *) on west-facing highwall, and presumably from claystone-filled hollow (Unit 4, marked with ?) on north-facing highwall. Note that Unit 4 is at stratigraphic position above the Perth Limestone. All sampled beds belong to USNM locality 38354.

medium- to dark-gray, fissile, highly carbonaceous shale that contains abundant but fragmentary and poorly preserved plant remains. Spirorbiform worm-tubes (microconchids) are affixed to some fossil leaves, and inarticulate brachiopods occur sporadically. Fine root structures are present at the top of the bed. Unit 1 is interpreted to record deposition in the shallow, dysaerobic, and at least hyposaline waters of a tidally influenced mudflat or estuary, which developed above the precursor Minshall Coal during initial stages of transgression as deglaciation commenced (cf., Archer et al., 1994, 2016; Mastalerz et al., 1997). Accordingly, plant remains mainly represent the remnants of drowned peat-forming vegetation. Roots at the top of the unit indicate upward shallowing, emergence, and development of a 'clastic swamp' (sensu Gastaldo, 1987; Demko and Gastaldo, 1992). The time required for establishment and colonization of the clastic swamp implies a temporary lull in sea level rise, possibly even a minor regressive event. Elsewhere in Clay County, the Minshall Coal consists of two distinct 'benches' separated by a clastic unit (up to 2.7 m thick) with roots at the top. A similar pattern occurs farther south in Daviess County, where a persistent claystone (~5 cm thick) exists near the middle of the Minshall Coal (incorrectly called the Buffaloville Coal by mine operators). As such, clastic swamp deposits at the top of Unit 1 may coincide with, and/or are a lateral equivalent of, the upper bench (Clay County) or upper part (Daviess County) of the Minshall Coal.

Unit 2 (~10 cm thick) is gradational with Unit 1, and comprises medium-gray, fissile, and well-indurated shale. Adpressed plant fossils are abundant and well preserved. Unit 2 is interpreted to record renewed transgression and further accumulation of tidally influenced mudflat or estuarine deposits. Macrofloral remains in this bed are thought to represent litter shed from clastic swamp vegetation on the periphery of the mudflat or estuary.

Unit 3 (~15 cm thick) is gradational with Unit 2, and consists of maroon, very well-indurated mudstone that contains siderite nodules. Macrofloral remains are well preserved but only moderately abundant. Unit 3 presumably resulted from additional base level rise due to transgression, with the presence of siderite nodules reflecting a change in depositional and/or diagenetic conditions on the mudflat or estuary. Adpressed plant fossils probably were derived from wetland vegetation in local clastic swamp habitats.

Unit 4 (10s of cm thick) consists of pinkish light-gray, well-laminated claystone that contains sparse but well-preserved plant adpressions. The most probable provenance is the fill of a hollow (Fig. 3) that was eroded down to the level of the Minshall Coal during the onset of regression, a consequence of polar ice buildup. If this stratigraphic level is correct, Unit 4 may record the rapid filling of an abandoned channel, either in a fluvial or tidally influenced deltaic setting. Plant debris probably was shed from clastic wetland plant communities alongside the abandoned channel.

Quantification and general characteristics of floral assemblages

Macrofloral assemblage.—Most plant remains are preserved as coalified compressions or impressions (i.e., adpressions; Shute and Cleal, 1987), although a small number of specimens are 'naturally macerated' (cf., Zodrow and Mastalerz, 2009). Proximate analysis of a sample of the underlying Minshall Coal yields a vitrinite reflectance (%R_{omax}) of 0.57, a coal rank of high-volatile C bituminous (Teichmüller and Teichmüller, 1982). Such a low rank indicates that phytoleims (coalified compressions) probably contain epidermal cuticles, although no attempt was made to procure cuticles.

Table 1 presents a quantitative breakdown of the rock slabs and fossil-taxa in Units 1 to 4, and for the macrofloral assemblage as a whole. Of the 191 slabs collected, 326 slab faces bear macrofloral remains (excluding barren faces and counterparts). The quantification technique used is a variant of that described by Pfefferkorn et al. (1975): each slab face was treated as a quadrat, and a fossil-taxon was recorded as 'present' regardless of the number of specimens on the face. Through this process, 688 macrofloral occurrences were recorded on the 326 fossiliferous slab faces. Excluding seeds and some axes, which could not be tied to a particular fossil-plant taxon with confidence (termed 'unidentifiable' macrofloral occurrences in Table 1), there were 449 'identifiable' macrofloral occurrences.

Of the 22 fossil-taxa identified (Table 1), 18 can be considered 'biological' taxa (i.e., a reassembled conceptualization of a whole and once-living fossil plant; sensu Cleal and Thomas, 2010), whereas only four 'non-biological' taxa were recorded (*Cyperites bicarinatus* Lindley and Hutton, 1832, *Lepidostrobophyllum* Hirmer, 1927 [sp. indet.], *Calamites* Brongniart, 1828a [spp. indet.], and a putative conifer cone scale). It is noted, however, that each fossiliferous bed contains a low-diversity assemblage, ranging from six to 12 fossil-taxa and four to nine biological taxa. When relative abundances for the entire macrofloral assemblage are considered, pteridosperms are the predominant (60.8%) and most diverse plant group (nine biological fossil-species). The sphenopsids (11.8%) are relatively diverse (five biological species), whereas all cordaitalean remains (16.7%) are included in *Cordaites* Unger, 1850 (spp. indet). The lycopsids (9.4%) are represented by two biological species, and fern and putative conifer remains are very rare.

Microfloral assemblage.—Samples of the Minshall Coal and four fossiliferous clastic units (~150 g of rock/coal crushed and sieved through −20 mesh) were oxidized using Schulze's Solution (nitric acid saturated with potassium chlorate) to liberate spores and pollen, followed by digestion in 5% potassium hydroxide. The organic fraction was concentrated with zinc chloride solution, and treated with ethylene glycol monoethyl ether (2-ethoxyethanol) and ultrasonic vibration to remove fine particulate matter from the spore/pollen fraction. Slides were prepared by strew-mounting a small amount of spore/pollen residue with polyvinyl alcohol on cover glasses, which were fixed with a synthetic piccolyte resin. Line counts (250 palynomorphs per sample) were performed at 640X magnification to establish relative abundances, and additional slides were scanned at 250X to document forms of potential biostratigraphic significance that were not encountered in statistical counts. All slides, maceration residues, and unused portions of samples are stored at the Kentucky Geological Survey (KGS), University of Kentucky, Lexington, KY under KGS sample numbers 3264–3268.

Table 2 gives a quantitative breakdown of the plant groups and fossil-taxa found in the Minshall Coal and Units 1 to 4. Forty-nine miospore species were identified, seven of unknown affinity. The beds are dominated by spores of arborescent or sub-arborescent lycopsids (Minshall Coal, Units 1 to 3) or by tree ferns (Unit 4). Non-arborescent fern and calamitalean spores are rare, as is cordaitalean pollen. Although pteridosperm foliage dominates the macrofloral assemblage, it is emphasized that no samples contain pteridosperm pollen, despite targeted searches, even in maceration residues of the ≤250 μm size fraction. Thus, although pteridosperm pollen typically is very large (100–600 μm; Taylor, 1978) and may be excluded by traditional preparation techniques (Peppers and Pfefferkorn, 1970), some grains should have been found if present. Because this paper focuses on the macrofloral assemblage, the microfloral data are only used to provide complementary biostratigraphic control.

Biostratigraphy and age

The Minshall Coal and overlying Perth Limestone of western Indiana (Fig. 2), along with their correlates in southern Indiana ('Buffaloville' Coal [see below], Curlew Limestone), western Kentucky (Empire Coal, Curlew Limestone), and western Illinois (Rock Island [No. 1] Coal, Seville Limestone), have figured prominently in the discussion surrounding placement of the contentious Atokan-Desmoinesian Stage boundary in the Illinois Basin (e.g., Shaver, 1984; Peppers, 1996; Heckel, 2013; Nelson et al., 2013). Because a precisely defined Atokan stratotype has yet to be realized (Sutherland and Manger, 1984), in large part because the poorly fossiliferous Atoka Formation (defined in the Arkoma Basin, Oklahoma; Fig. 1.1) is depositionally and tectonically complex, the position of the Atokan-Desmoinesian boundary in the Illinois Basin has shifted depending on the fossil group used for biostratigraphic control. For example, marine faunas in the limestones have indicated either an early Desmoinesian age (ostracodes and fusulinids: Shaver and Smith, 1974, Shaver, 1984; conodonts: Rexroad et al., 1998; fusulinids: Wahlman, 2013) or a late Atokan age (fusulinid foraminifera: Douglass, 1987; conodonts: Barrick et al., 2013). Likewise, the Atokan-Desmoinesian boundary was placed at the top of the Seville, Perth, and Curlew limestones based on the correlation of microfloral assemblages from coal seams (Peppers, 1996; Fig. 2). By extension of these uncertainties, the position of the Minshall and equivalent coals remains uncertain in chronostratigraphic terms, although the seams usually are placed in the uppermost Atokan (Nelson et al., 2013).

Conodonts from the limestone directly overlying the Buffaloville Coal in its type area (southern Indiana) indicate that it is younger than the Perth, Curlew, and Seville limestones (personal communication, P.H. Heckel, 2014; Fig. 2). This result corroborates the palynological study of Peppers (1993),

Table 1. Fossil-taxa in macrofloral assemblage, from Units 1 to 4 above Minshall Coal (Fig. 3), segregated into plant groupings. Right-hand column indicates if fossil-taxon present in Europe. Symbols: (a) total slabs from unit; (b) slab faces with macrofloral remains (i.e., excludes barren faces and counterparts); (c) identifiable macrofloral occurrences + 'unidentifiable' macrofloral occurrences (e.g., axes and seeds); (d) occurrence indicates presence (in any quantity) on slab face; (e) 'biological' fossil-taxa + 'non-biological' fossil-taxa (*Cyperites bicarinatus* Lindley and Hutton, 1832, *Lepidostrobophyllum* Hirmer, 1927 [sp. indet.], *Calamites* Brongniart, 1828a [spp. indet.], and putative conifer cone scale); (f) reassembled conceptualization of once-living, whole fossil plant. See text for details.

Plant group	Fossil-taxon	Unit 1 (*n* [%])	Unit 2 (*n* [%])	Unit 3 (*n* [%])	Unit 4 (*n* [%])	Totals (*N* [%])	In Europe?
LYCOPSIDS		34 [37.36]	6 [3.06]	absent	2 [7.41]	42 [9.35]	
	cf. *Asolanus camptotaenia*	1 [1.10]	absent	absent	1 [3.70]	2 [0.44]	yes
	Synchysidendron sp. cf. *S. andrewsii*	1 [1.10]	absent	absent	absent	1 [0.22]	yes
	Cyperites bicarinatus	30 [32.97]	4 [2.04]	absent	absent	34 [7.57]	yes
	Lepidostrobophyllum sp. indet.	2 [2.20]	2 [1.02]	absent	1 [3.70]	5 [1.11]	yes
SPHENOPSIDS		2 [2.20]	12 [6.12]	32 [23.70]	7 [25.93]	53 [11.80]	
	Annularia sp. cf. *A. radiata*	absent	absent	absent	2 [7.41]	2 [0.44]	yes
	Annularia sphenophylloides	absent	absent	absent	2 [7.41]	2 [0.44]	yes
	Annularia sp. indet.	absent	absent	absent	1 [3.70]	1 [0.22]	yes
	Sphenophyllum cuneifolium	absent	12 [6.12]	32 [23.70]	absent	44 [9.80]	yes
	Sphenophyllum emarginatum	absent	absent	absent	1 [3.70]	1 [0.22]	yes
	Calamites spp. indet.	2 [2.20]	absent	absent	1 [3.70]	3 [0.67]	yes
FERNS	*Sphenopteris* sp. indet	1 [1.10]	4 [2.04]	absent	absent	5 [1.11]	(?)
PTERIDOSPERMS		absent	152 [77.55]	103 [76.30]	18 [66.67]	273 [60.80]	
	Alethopteris densinervosa	absent	3 [1.53]	25 [18.52]	absent	28 [6.24]	yes
	Macroneuropteris scheuchzeri	absent	51 [26.02]	25 [18.52]	absent	76 [16.93]	yes
	Neuropteris flexuosa	absent	69 [35.20]	25 [18.52]	absent	94 [20.94]	yes
	Neuropteris missouriensis	absent	absent	absent	14 [51.85]	14 [3.12]	*Laveineopteris dussartii*(?)
	Neuropteris ovata	absent	20 [10.2]	5 [3.70]	1 [3.70]	26 [5.79]	yes
	Neuropteris semireticulata	absent	absent	absent	2 [7.41]	2 [0.44]	yes
	"*Mariopteris*" *anthrapolis*	absent	6 [3.06]	absent	absent	6 [1.34]	no
	Eusphenopteris neuropteroides	absent	3 [1.53]	23 [17.04]	absent	26 [5.79]	yes
	Eusphenopteris sp. indet.	absent	absent	absent	1 [3.70]	1 [0.22]	(?)
CORDAITALEANS	*Cordaites* spp. indet.	54 [59.34]	21 [10.71]	absent	absent	75 [16.70]	yes
CONIFERS	conifer cone scale	absent	1 [0.51]	absent	absent	1 [0.22]	(?)
Slabs (*n*)[a]		62	64	43	22	191	
Fossiliferous faces (*n*)[b]		116	106	70	34	326	
Macrofloral occurrences (*n*)[c]		200	257	179	52	688	
Identifiable macrofloral occurrences (*n*)[d]		91	196	135	27	449	
Fossil-taxa (*n*)[e]		7	12	6	11	22	
'Biological' fossil-taxa (*n*)[f]		4	9	6	9	18	

Table 2. Fossil-taxa in microfloral assemblage, from Minshall Coal and Units 1 to 4 above coal (Fig. 3), segregated into plant groupings/growth forms.

Plant group	Fossil-taxon	Minshall Coal (%)	Unit 1 (%)	Unit 2 (%)	Unit 3 (%)	Unit 4 (%)
ARBORESCENT LYCOPSIDS		6.4	24.0	50.8	75.6	27.6
	Crassispora kosankei	0.0	0.0	0.4	0.0	0.4
	Granasporites medius	0.0	0.4	0.4	1.6	0.0
	Lycospora granulata	5.2	9.2	33.2	36.8	12.8
	Lycospora micropapillata	0.0	0.4	4.8	13.6	2.0
	Lycospora orbicula	0.0	1.6	8.0	15.6	0.8
	Lycospora pellucida	0.0	10.8	1.2	4.4	4.4
	Lycospora pusilla	1.2	1.6	2.8	3.6	7.2
SUB-ARBORESCENT LYCOPSIDS		51.6	28.8	2.4	2.0	0.0
	Anacanthotriletes spinosus	0.8	1.6	0.0	0.0	0.0
	Densosporites lobatus	5.2	1.2	0.0	0.8	0.0
	Densosporites sphaerotriangularis	0.8	0.4	0.0	0.0	0.0
	Endosporites globiformis	0.0	10.0	0.8	0.0	0.0
	Radiizonates difformis	44.8	15.6	1.6	1.2	0.0
	Radiizonates rotatus					
TREE FERNS		26.0	26.0	35.6	7.6	63.6
	Apiculatisporites saetiger	0.4	1.6	2.0	0.4	0.0
	Laevigatosporites globosus	3.6	1.6	0.0	1.2	3.2
	Laevigatosporites minimus	0.0	0.4	0.8	0.0	2.0
	Punctatisporites minutus	21.2	17.2	30.8	4.8	50.0
	Punctatosporites granifer	0.0	3.2	0.0	0.0	0.0
	Punctatosporites minutus	0.8	1.6	2.0	1.2	6.4
	Punctatosporites rotundus	0.0	0.0	0.0	0.0	2.0
	Torispora securis	0.0	0.4	0.0	0.0	0.0
NON-ARBORESCENT FERNS		6.4	4.8	4.0	4.8	2.8
	Acanthotriletes aculeolatus	0.0	0.8	0.0	0.4	0.0
	Acanthotriletes triquetrus	0.4	0.0	0.4	0.0	0.0
	Convolutispora florida	0.0	0.4	0.0	0.0	0.0
	Cyclogranisporites minutus	0.0	0.8	0.0	0.0	0.0
	Granulatisporites adnatoides	0.0	0.8	0.0	0.0	0.8
	Granulatisporites granulatus	0.8	0.0	0.4	0.0	0.0
	Granulatisporites parvus	3.2	0.4	0.4	0.8	0.0
	Granulatisporites pircformis	0.4	0.0	1.6	0.4	0.0
	Leiotriletes priddyi	0.0	0.0	0.4	0.0	0.0
	Leiotriletes subadnatoides	0.0	0.4	0.4	1.6	0.0
	Lophotriletes commissuralis	0.0	0.4	0.0	0.0	0.0
	Lophotriletes granoornatus	0.0	0.4	0.4	1.6	1.2
	Lophotriletes microsaetosus	1.2	0.0	0.0	0.0	0.0
	Punctatisporites pseudolevatus	0.0	0.4	0.0	0.0	0.8
	Raistrickia saetosa	0.4	0.0	0.0	0.0	0.0
CALAMITALEANS		4.8	4.4	3.6	1.2	2.4
	Calamospora breviradiata	0.0	2.0	2.8	0.4	0.8
	Calamospora microrugosa	0.0	0.4	0.0	0.0	0.0
	Calamospora pedata	0.0	0.0	0.4	0.0	0.0
	Laevigatosporites minor	4.8	2.0	0.4	0.8	1.6
CORDAITALEANS		4.8	4.8	2.0	8.4	1.6
	Florinites florini	4.0	2.0	1.6	6.8	1.2
	Florinites mediapudens	0.8	2.8	0.4	1.6	0.4
UNKNOWN AFFINITY		0.0	7.2	1.6	0.4	2.0
	Adelisporites multiplicatus	0.0	0.4	0.0	0.0	0.0
	Echnatispora knoxiae	0.0	0.0	0.0	0.0	0.8
	Spackmanites sp. indet.	0.0	0.8	0.0	0.0	0.0
	Tantillus triquetrus	0.0	0.4	0.0	0.0	0.0
	Triquitrites bransonii	0.0	0.4	0.0	0.0	0.0
	Triquitrites minutus	0.0	0.8	0.0	0.0	0.0
	Triquitrites sculptilis	0.0	4.4	1.6	0.4	1.2

who concluded that the true Buffaloville Coal is younger than the Minshall Coal.

According to Peppers (1996), the Atokan-Desmoinesian Stage boundary of North America coincides with the Bolsovian-Asturian Substage boundary of Western Europe (Figs. 2, 4). If placement of this coupled boundary at the top of the Perth Limestone (and correlates) is accepted, the implication is that the underlying Minshall Coal (and correlates) are late Bolsovian in age. In the following section, the taxonomic composition of the microfloral and macrofloral assemblages from the Minshall Coal and overlying roof-shales (Units 1 to 3) are compared with established biozonation schemes to determine whether or not this assumption holds. Unit 4, which is presumed to have been at a stratigraphic position above the Perth Limestone (Fig. 3), can be assigned an earliest Asturian age by default because it lies just above the Atokan-Desmoinesian boundary (Fig. 2).

Comparison with American microfloral biozonation.—Peppers (1984, 1996) constructed a microfloral biozonation scheme to facilitate regional correlation between the Illinois Basin and other parts of Euramerica. According to this framework (Fig. 4), the Brazil Formation is in the upper (but not uppermost)

SERIES	GLOBAL STAGES	STAGES WESTERN EUROPE	SUBSTAGES WESTERN EUROPE	STAGES NORTH AMERICA	LITHOSTRATIGRAPHY ILLINOIS & KENTUCKY	LITHOSTRATIGRAPHY INDIANA	MICROFLORAL BIOZONATION (PEPPERS 1984, 1996)
Middle Pennsylvanian	Moscovian*	Westphalian*	Asturian	Desmoinesian	McLeans. Gp.*		**[GM]** *Lycospora granulata Granasporites medius*
					Carbondale Formation	Carbondale Group	**[CP]** *Schopfites colchesterensis Thymospora pseudothiessenii*
			Bolsovian		Tradewater Formation*	Staunton Formation	**[MI]** *Cadiospora magna Mooreisporites inusitatus*
				Atokan		Brazil Fm.	**[RD]** *Radiizonates difformis*
					Mansfield Formation*		**[SF]** *Torispora securis Vestispora fenestrata*
Lower Penn.*	Bashkirian*		Duckmantian				**[NG]** *Microreticulatisporites nobilis Endosporites globiformis*

Figure 4. Microfloral biozonation scheme of Peppers (1984, 1996) correlated with chronostratigraphic and lithostratigraphic units (* indicates incomplete unit). Modified from Peppers (1996, pl. 1). Microfloral assemblage corresponds to upper *Radiizonates difformis* (RD) Biozone.

Bolsovian part of the *Radiizonates difformis* (RD) Biozone, with the top of the Minshall Coal corresponding to the top of the biozone (Peppers, 1996).

The composition of the microfloral assemblage (Table 2) supports assignment of the Minshall Coal and overlying roof-shales to the *Radiizonates difformis* (RD) Biozone. Of particular importance is the presence of the diagnostic densospores *Radiizonates difformis* (Kosanke, 1950) Staplin and Jansonius, 1964 and *Radiizonates rotatus* (Kosanke, 1950) Staplin and Jansonius, 1964, which are most abundant in the coal and Unit 1. Further, none of the beds (including Unit 4) contain the namesake taxa of the succeeding *Cadiospora magna-Mooreisporites inusitatus* (MI) Biozone (Fig. 4). *Cadiospora magna* Kosanke, 1950 first appeared at the Bolsovian-Asturian boundary, whereas *Mooreisporites inusitatus* (Kosanke, 1950) Neves, 1958 arose in the latest Bolsovian (Peppers, 1996). These factors collectively point to a late Bolsovian age for the Minshall Coal and overlying clastic beds.

Nonetheless, a microfloral assemblage from a clastic unit directly beneath the paleosol of the Minshall Coal adds uncertainty to this late Bolsovian assignment (these data, incorporated into another publication, are introduced here because they have important ramifications on the age of overlying strata). Most noteworthy is the statistically significant abundance of *Thymospora pseudothiessenii* (Kosanke, 1950) Wilson and Venkatachala, 1963. The spore is considered a reference for basal Asturian, although it first appears in uppermost Bolsovian strata (Peppers, 1996; Lesnikowska and Willard, 1997) and reaches its epibole in the middle Asturian *Schopfites colchesterensis-Thymospora pseudothiessenii* (CP) Biozone (Fig. 4). Equally intriguing is the fact that *Savitrisporites nux* (Butterworth and Williams, 1958) Smith and Butterworth, 1967 occurs (albeit very rarely) beneath the Minshall Coal, but not in the coal itself. Because this spore disappears just below the Bolsovian-Asturian boundary (Peppers, 1996), its absence in the coal does not in itself imply an Asturian age for the Minshall, but it does signify peat accumulation very close to the substage boundary. It is crucial to note that the scheme of Peppers (1984, 1996) is almost exclusively based on palynomorphs from coal, and many taxon ranges would be extended if clastic lithologies had been incorporated. These additional microfloral data signify that an earliest Asturian age for the Minshall Coal cannot be ruled out.

Comparison with American macrofloral biozonation.—Moore et al. (1944) and Read and Mamay (1964) segregated upper Paleozoic strata of the USA into fifteen macrofloral zones defined by the co-occurrence of common or diagnostic taxa. Unfortunately, the absence of range charts and ambiguity of zone boundaries make this biostratigraphic framework difficult to apply. Gillespie and Pfefferkorn (1979) discussed the temporal distribution of key taxa and charted their ranges in the Appalachian Basin. Extending this work, Blake et al. (2002) produced an updated chart that correlates between lithostratigraphic units of the Appalachian Basin, chronostratigraphic units of midcontinent USA and Western Europe, and macrofloral zones of the USA (Read and Mamay, 1964) and paleoequatorial Europe (Wagner, 1984). According to Blake et al. (2002, fig. 1, with updates from B.M. Blake, personal communication, 2014), the Atokan-Desmoinesian boundary, which they equated to the Bolsovian-Asturian boundary following Peppers (1996), is at the Upper Block (No. 5) Coal near the contact between the Kanawha and Allegheny formations (Fig. 5). This level correlates to the middle of Zone 9 ('*Neuropteris*' *rarinervis*) of Read and Mamay (1964).

Blake et al. (2002, fig. 2) also provided a biostratigraphic range chart that shows the distribution of important fossil-taxa in the Appalachian Basin. A pragmatic approach to determining the age of the macrofloral assemblage above the Minshall Coal has been to compile the ranges of key fossil-species in the Appalachian Basin (e.g., Read and Mamay, 1964; Darrah, 1969; Gillespie and Pfefferkorn, 1979; Blake et al., 2002; personal communication, B.M. Blake, 2014). The results of this exercise (Fig. 5) are somewhat ambiguous, in part because the first appearance datum (FAD) and last appearance datum (LAD) of *Neuropteris semireticulata* Josten, 1962, *Neuropteris ovata* Hoffmann, 1826a, 1826b, and *Neuropteris flexuosa* Sternberg, 1825 are poorly constrained. Additionally, a short hiatus may exist between the Kanawha and Allegheny formations (personal communication, B.M. Blake, 2014), further confounding age determination. Nonetheless, the compilation indicates that the macrofloral assemblage contains several species that first appear in the middle Bolsovian but extend into and are more typical of the

SERIES	Lower Pennsylvanian*	Middle Pennsylvanian*		
GLOBAL STAGES	Bashkirian*	Moscovian*		
STAGES WESTERN EUROPE	Westphalian*			
SUBSTAGES WESTERN EUROPE	Duckmantian	Bolsovian	Asturian	
STAGES NORTH AMERICA	Atokan	Desmoinesian*		
LITHOSTRATIGRAPHY APPALACHIAN BASIN	Kanawha Formation*	Allegheny Formation		Con.
FLORAL ZONES (READ & MAMAY, 1964)	Zone 7 *Megalopteris* spp.	Zone 8 *'Neuropteris' tenuifolia*	Zone 9 *'Neuropteris' rarinervis*	Zone 10 – *Neuropteris flexuosa* & *Pecopteris* spp.

Sphenophyllum cuneifolium
Eusphenopteris neuropteroides
Macroneuropteris scheuchzeri
Annularia sphenophylloides
Sphenophyllum emarginatum
Neuropteris semireticulata
Asolanus camptotaenia
Neuropteris ovata
Neuropteris flexuosa

Figure 5. Biostratigraphic ranges of key fossil-species in macrofloral assemblage correlated with chronostratigraphic units, lithostratigraphic units of Central Appalachian Basin, and American macrofloral biozonation scheme of Read and Mamay (1964) (* indicates incomplete unit); compiled from Darrah (1969), Gillespie and Pfefferkorn (1979), Blake et al. (2002), and B.M. Blake (personal communication, 2014). Maximum range overlap occurs in upper Kanawha to lower Allegheny formations (late Atokan to early Desmoinesian, late Bolsovian to early Asturian), equivalent to most of Zone 9 (*'Neuropteris' rarinervis*).

Asturian. Maximum range overlap occurs in a late Bolsovian to earliest Asturian interval, equivalent to much of Zone 9 (*'Neuropteris' rarinervis*) and in accord with the age suggested by the microfloral assemblage.

In contrast to Europe and Atlantic Canada (see below), in the USA *Neuropteris ovata* occurs sparingly in middle Bolsovian assemblages (Zone 8—*'Neuropteris' tenuifolia*), is abundant in (but not characteristic of) late Bolsovian to early Asturian assemblages (Zone 9—*'Neuropteris' rarinervis*), and only becomes more common in younger strata (Jongmans, 1937c; Read and Mamay, 1964; Darrah, 1969; Gillespie and Pfefferkorn, 1979; Blake et al., 2002). Likewise, Read and Mamay (1964) noted rare occurrences of *Neuropteris flexuosa* in Zone 8, but indicated that the species only became abundant in the middle to late Asturian (Zone 10—*Neuropteris flexuosa* and *Pecopteris* spp.); Darrah (1969) placed the FAD in the lower Allegheny Formation (lower Asturian).

That *Neuropteris ovata* and *Neuropteris flexuosa* first appear in middle to upper Bolsovian strata in the USA is supported by re-examination of specimens illustrated by Wood (1963), who documented assemblages from above the middle(?) Bolsovian Lower Block Coal in western Indiana (Fig. 2). Although poorly preserved and fragmentary, both species seem to be present: *N. ovata* was misidentified under *Neuropteris obliqua*? (pl. 9, fig. 10) and *Odontopteris subcuneata* (pl. 10, fig. 5), whereas *N. flexuosa* may have been both correctly identified (pl. 9, fig. 5) and referred to *Neuropteris heterophylla*? (pl. 9, fig. 6). However, all of these taxa are listed as being "not common" (Wood, 1963, p. 32), indicating that they were not characteristic of the assemblages.

This analysis indicates that roof-shales above the Minshall Coal are either late Bolsovian or early Asturian in age. However, the fact that *Neuropteris flexuosa* is the most abundant pteridosperm in Units 2 and 3 (Table 1), and that *Neuropteris ovata* also is a common element in these beds, indicates that an early Asturian age is most probable.

Comparison with European macrofloral biozonation.—Building on previous biostratigraphic schemes (e.g., Dix, 1934; Bell, 1938; Gothan and Remy, 1957; Corsin and Corsin, 1971; Laveine, 1977), a comprehensive framework for Carboniferous plant fossils was assembled by Wagner (1984), who compared the ranges of key taxa and incorporated preexisting floral zones to establish sixteen distinct biozones. The biozonation has been refined to improve its resolution, with several subbiozones now recognized (Cleal, 1991; Cleal and Thomas, 1994). Although primarily based on range data from western and central Europe, Wagner (1984) intended that the scheme would aid biostratigraphic correlations throughout the Euramerican paleoequatorial belt.

Comparison with the European biozonation (Fig. 6) is based on the compilation of taxon ranges as known in Western Europe (e.g., Laveine, 1987; Wagner, 1984; Cleal and Thomas, 1994). Although some taxa are long ranging, there is minimal overlap between the LAD of *Neuropteris semireticulata* and *Alethopteris densinervosa* Wagner, 1968 and the FAD of *Neuropteris flexuosa* and members of the *Neuropteris ovata* complex, the latter group being considered a guide to the basal Asturian (Van Leckwijck, 1964; Laveine, 1977; Wagner, 1984). Accordingly, the age of the macrofloral assemblage can be tightly constrained to the early Asturian, assignable to the *Linopteris obliqua* Biozone. The anomalous presence of *Sphenophyllum cuneifolium* (Sternberg, 1821) Zeiller, 1878-79a, more typical of lower Westphalian assemblages, does not override this outcome.

Stratigraphic ramifications.—These homotaxial comparisons yield slightly different age results for the Minshall Coal and overlying roof-shales depending on the fossil group or biostratigraphic framework used: (1) probably latest Bolsovian (American microfloras; Fig. 4); (2) latest Bolsovian or earliest Asturian (Appalachian Basin macrofloras; Fig. 5); or (3) earliest Asturian (European macrofloras; Fig. 6). Although all analyses clearly convey that both peat and clastic sediment accumulation

SERIES	Middle Pennsylvanian						U. Penn*
GLOBAL STAGES	Moscovian*						Kasimovian*
STAGES NORTH AMERICA	Atokan*			Desmoinesian			
STAGES WESTERN EUROPE	Westphalian*						Stephanian*
SUBSTAGES WESTERN EUROPE	Bolsovian			Asturian			Cantabrian
BIOZONES	Paripteris linguaefolia*			Linopteris obliqua	Crenulopteris acadica		Odontopteris cantabrica
SUBBIOZONES	Neuropteris semireticulata*	Laveineopteris rarinervis	Alethopteris serlii	Linopteris obliqua	Crenulop. micro-miltoni	Dick. plukenetii	Odontopteris cantabrica

Species ranges (biostratigraphic ranges shown as bars):
- Sphenophyllum cuneifolium
- Eusphenopteris neuropteroides
- Macroneuropteris scheuchzeri
- Neuropteris semireticulata
- Alethopteris densinervosa
- Sphenophyllum emarginatum
- Annularia sphenophylloides
- Laveineopteris dussartii
- Neuropteris flexuosa
- Neuropteris ovata

Figure 6. Biostratigraphic ranges of key fossil-species in macrofloral assemblage correlated with chronostratigraphic units and European macrofloral biozonation scheme. Compiled from Wagner (1984), Laveine (1987), Cleal (1991), and Cleal and Thomas (1994). Range of *Laveineopteris dussartii* (Laveine, 1967) Laveine, 2005 included because may be synonymous with *Neuropteris missouriensis* Lesquereux, 1879-80. Maximum range overlap occurs in lower *Linopteris obliqua* Biozone (early Asturian, early Desmoinesian).

occurred close to the Bolsovian-Asturian boundary, three crucial points need to be addressed before attempting to refine the stratigraphic resolution. First, the Minshall Coal and overlying roof-shales need not be the same age; the boundary may have been crossed in the interim between the final phases of peat accumulation and the drowning and burial of the mire during transgression. Second, significant (and perhaps undue) weight has been placed on coincidence of the Bolsovian-Asturian and Atokan-Desmoinesian boundaries, especially since they were defined in widely separated areas based on different parameters. Third, there must have been a temporal lag between the evolution of a new plant taxon and its dispersal to other parts of paleoequatorial Euramerica (cf., Laveine et al., 2000; Blake et al., 2002). These factors are taken into account as four stratigraphic scenarios are explored for the study section, each of which attempts to rectify the slightly disparate ages recorded in the microfloral and macrofloral assemblages.

Figure 7.1 shows the currently accepted correlation scheme in the Indiana portion of the Illinois Basin (with a focus on the Brazil and Staunton formations) and displays the relationships among chronostratigraphic, lithostratigraphic, and biostratigraphic units, at least as they have been understood prior to this analysis. The Bolsovian-Asturian Substage and Atokan-Desmoinesian Stage boundaries are equivalent and occur at the top of the Perth Limestone; the Minshall Coal belongs to the *Radiizonates difformis* (RD) Biozone and, by implication, the Minshall Coal and its roof-shales (Units 1 to 3) are upper Bolsovian. However, this scenario only is valid if *Neuropteris ovata* and *Neuropteris flexuosa* can occur in abundance in late Bolsovian assemblages. As noted above, both taxa make scattered appearances in middle to upper Bolsovian strata in the USA, but do not become common until the Asturian (Fig. 5; *N. ovata* in Zone 9, *N. flexuosa* in Zone 10 of Read and Mamay, 1964).

Introduction of the European macrofloral biozonation framework indicates that the roof-shales (Units 1 to 3) above the Minshall Coal (but not necessarily the coal itself) are no older than earliest Asturian (Fig. 6). At least four scenarios are possible (Fig. 7.2–7.5); all include the Minshall Coal in the *Radiizonates difformis* (RD) Biozone and its roof-shales in the *Linopteris obliqua* Biozone.

Scenario one.—The Bolsovian-Asturian and Atokan-Desmoinesian boundaries could remain coupled and lowered to the top of the Minshall Coal (Fig. 7.2). The implications are that the precursor mire existed during the latest Bolsovian (latest Atokan), and that a chronostratigraphic boundary was crossed before transgression and deposition of the roof-shales in the earliest Asturian (earliest Desmoinesian). As a consequence, the contact between the *R. difformis* (RD) and *Cadiospora magna-Mooreisporites inusitatus* (MI) microfloral biozones would be slightly younger than the late Bolsovian (late Atokan) age proposed by Peppers (1996; Fig. 7.1), and the basalmost Staunton Formation would correspond to the lower Asturian (lower Desmoinesian).

Scenario two.—The coupled Bolsovian-Asturian and Atokan-Desmoinesian boundary could be situated somewhere below the Minshall Coal (Fig. 7. 3), meaning that both the peat and overlying clastics accumulated during the earliest Asturian (earliest Desmoinesian). Consequently, the upper part of the *R. difformis* (RD) Biozone and uppermost Brazil Formation would be younger than currently understood (Fig. 7.1).

Scenario three.—The Bolsovian-Asturian and Atokan-Desmoinesian boundaries could be decoupled, with the former lowered to the top of the Minshall Coal and the latter remaining at the top of the Perth Limestone (Fig. 7.4). The ramifications mostly mirror those for point 1, except that the uppermost Brazil Formation, lowermost Staunton Formation, and lower part of the *C. magna-M. inusitatus* (MI) Biozone would be retained in the uppermost Atokan (although now correlative to the lowermost Asturian).

Scenario four.—The decoupled Bolsovian-Asturian boundary could be placed at an even lower position below the Minshall Coal (Fig. 7.5). As in point 3, the upper Brazil, lower Staunton, and lower *C. magna-M. inusitatus* (MI) Biozone
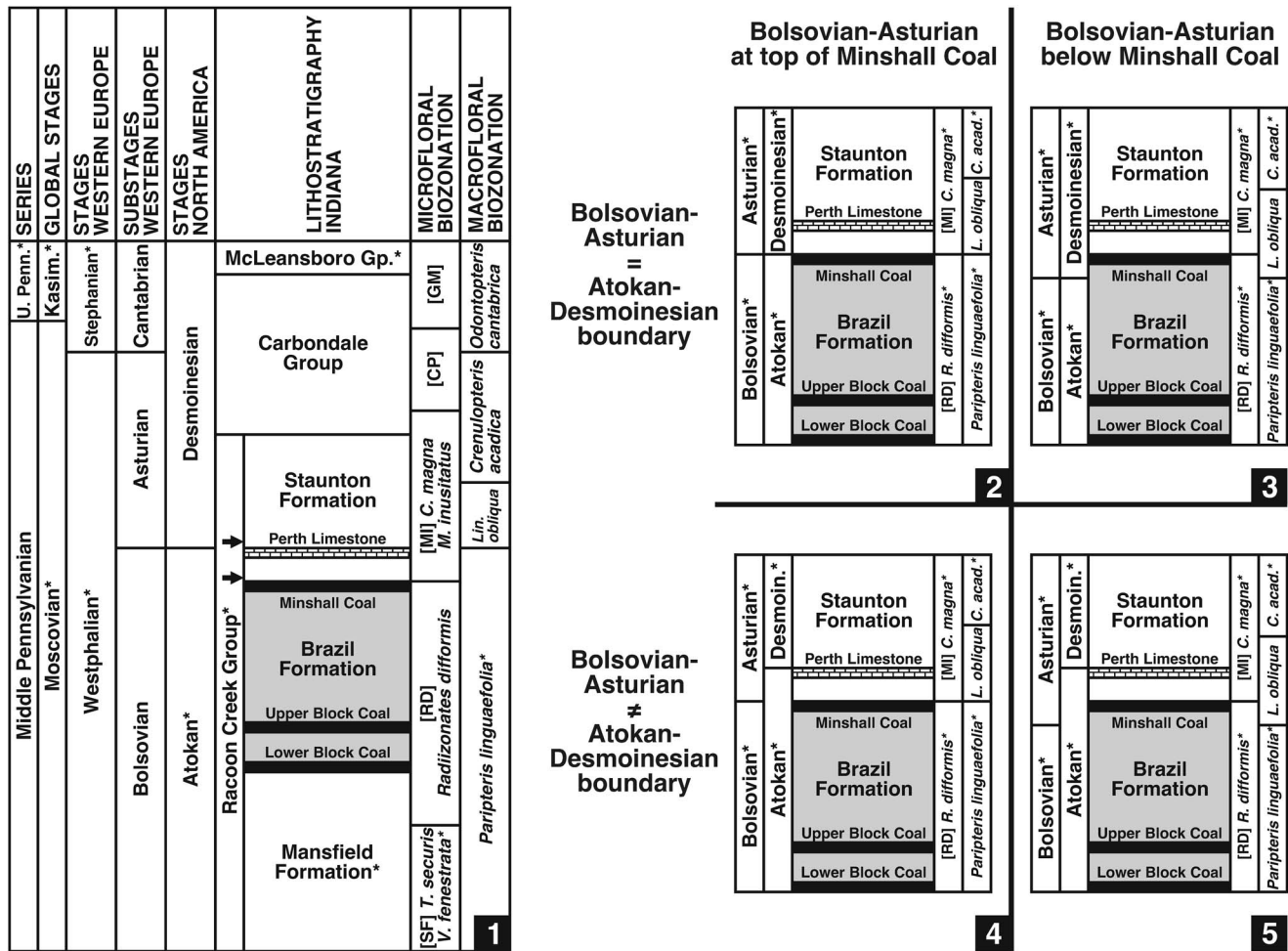
Figure 7. Options for placement of Atokan-Desmoinesian Stage boundary and Bolsovian-Asturian Substage boundary based on biostratigraphic data presented herein. (**1**) Stratigraphy of Middle Pennsylvanian of Indiana part of Illinois Basin (as currently understood), showing correlation between chronostratigraphic and lithostratigraphic units, and American microfloral and European macrofloral biozonation schemes (* indicates incomplete unit). Compiled from Figures 2, 4, and 6. Macrofloral assemblage collected from lowermost Staunton Formation (arrows). For all four scenarios presented in **7.2–7.5**, Minshall Coal retained in *Radiizonates difformis* (RD) Biozone and clastic units bearing macrofloral assemblage (arrows) in *Linopteris obliqua* Biozone. (**2**) Atokan-Desmoinesian and Bolsovian-Asturian boundaries remain coupled and lowered to top of Minshall Coal. (**3**) Atokan-Desmoinesian and Bolsovian-Asturian boundaries remain coupled and lowered to below Minshall Coal. (**4**) Atokan-Desmoinesian and Bolsovian-Asturian boundaries decoupled, with Atokan-Desmoinesian boundary retained at top of Perth Limestone and Bolsovian-Asturian boundary lowered to top of Minshall Coal. (**5**) Atokan-Desmoinesian and Bolsovian-Asturian boundaries decoupled, with Atokan-Desmoinesian boundary retained at top of Perth Limestone and Bolsovian-Asturian boundary lowered to below Minshall Coal. See discussion in text for stratigraphic ramifications of each scenario.

would remain in the upper Atokan, but would correspond to an even younger Asturian age.

All four scenarios have validity, but because this study deals with plant-fossil assemblages from one locality, no further attempt is made to recommend one over another. However, decoupling the Bolsovian-Asturian and Atokan-Desmoinesian boundaries, and lowering the former to the top of (or below) the Minshall Coal (points 3 and 4) is considered the least disruptive to the established stratigraphic framework. Similar studies at other sites in the Illinois Basin and elsewhere are necessary to rectify the position of the Bolsovian-Asturian Substage boundary of western Europe and its relationship to the Atokan-Desmoinesian Stage boundary in the USA.

Paleobiogeographic and paleoecologic implications

The temporal persistence of peat-inhabiting wetland vegetation in Pennsylvanian mires is well established, with evidence pointing to long periods of ecological stability through recurring glacioeustatic cycles, and the repeated reassembly of communities drawn from a small pool of edaphic specialists when climatic conditions were favorable (DiMichele and Phillips, 1996a, 1996b; DiMichele et al., 1996, 2002; Willard et al., 2007; Falcon-Lang and DiMichele, 2010). Comparable patterns of persistence and compositional recurrence also existed in vegetation from associated clastic wetland habitats (Scott, 1978; Pfefferkorn and Thomson, 1982; DiMichele et al., 1996; Cleal et al., 2012; Tabor et al., 2013). These low-diversity ecosystems were the product of prolonged evolution under the intrinsically stressful conditions that typify wetland settings, which are effectively closed systems with low rates of speciation and turnover, and that experience little taxonomic exchange with terra-firma habitats (Knoll, 1985; DiMichele et al., 1987; Wing and DiMichele, 1995; DiMichele and Phillips, 1996a; Cleal et al., 2012).

Pennsylvanian wetland communities also retained compositional conservatism at a variety of spatial scales. Over tens of

meters to a few kilometers, mire vegetation was markedly heterogeneous yet encompassed a limited species pool (Pfefferkorn, 1979; DiMichele and Nelson, 1989; Pryor and Gastaldo, 2000; Gastaldo et al., 2004, DiMichele et al., 2007, Opluštil et al., 2009a, 2009b), and clastic wetland floras displayed a comparable mosaic of low-diversity patches (Wing and DiMichele, 1995; Bashforth et al., 2010, 2011; Cleal et al., 2012). However, local-scale variability was masked at the landscape or regional scale, and disappeared into the background of the restricted wetland species pool. An expression of this homogeneity is discussed by Moore et al. (2014), who demonstrated that two contemporaneous clastic wetland floras, separated by 1100 km on the American craton, showed convergent dominance-diversity structures and a remarkable degree of compositional similarity.

A key result of this study is confirmation that Pennsylvanian communities from clastic wetland habitats showed spatial conservatism over vast areas of tropical Euramerica. Despite promulgations about the lack of similarity between American and European adpressed macrofloral assemblages, this notion can be tempered, at least for the Middle Pennsylvanian time interval studied. Of the 18 biological fossil-taxa documented (Table 1), at least 14 species (78%; including *Cordaites* spp. indet.) are common in contemporaneous European assemblages. Assuming that *Eusphenopteris* Gothan, 1913 ex Simson-Scharold, 1934 (sp. indet.) and *Sphenopteris* (Brongniart, 1822) Sternberg, 1825 (sp. indet.) also occur in Europe, which they almost certainly do, and considering that the American form *Neuropteris missouriensis* Lesquereux, 1879-80 may be conspecific with the European form *Laveineopteris dussartii* (Laveine, 1967) Laveine, 2005, the number of shared species could be as high as 17 (94%). Only the taxon identified as "*Mariopteris*" *anthrapolis* Langford, 1958 seems to be unequivocally unique to American floras of this age (Table 1). Hence, it is not hyperbole to state that the macrofloral assemblage could have been collected from a lower Asturian roof-shale in Europe. It is clear, yet unsurprising, that the intrinsic stress inherent to wetland settings existed wherever such environments developed in tropical Euramerica, resulting in low-diversity communities that showed a high degree of taxonomic mutuality over the paleocontinent.

The discovery of *Alethopteris densinervosa* in the macrofloral assemblage, and the realization that it had previously been misidentified as *Alethopteris serlii* (Brongniart, 1833-34) Göppert, 1836 in other American floras (e.g., Basson, 1968; Oleksyshyn, 1982; Moore et al., 2014), provides additional evidence for the spatial congruity in Pennsylvanian clastic wetland vegetation. Formerly only known from the Northern France Coalfield (Wagner, 1968; Laveine, 1987), and perhaps the Sydney Coalfield (Zodrow, 1986; Zodrow and Cleal, 1998), the presence of a relatively obscure fossil-species such as *A. densinervosa* in widely separated areas from strata of similar age (early Bolsovian to middle Asturian) highlights the commonality of Middle Pennsylvanian floras in wetland deposits of Euramerica.

From a paleobiogeographic perspective, these observations are important because west-central and eastern Euramerica were separated by the expansive uplands of the Laurentian Shield to the north and, in part, by the Appalachian-Variscan Mountains (Blakey, 2013). The similarity of wetland communities on either side of the paleocontinent confirms that, at least during the Middle Pennsylvanian, these elevated areas did not present an insurmountable barrier to dispersal for most wetland plants (cf., White, 1909; Pfefferkorn and Gillespie, 1980b; Blake et al., 2002). In fact, the mountain belt probably comprised a spatially and temporally discontinuous chain of tectonically active centers (Roscher and Schneider, 2006), which rose (and eroded down) earlier in the east than in the west in zipper-like fashion (Hatcher, 2002, 2010), rather than a continuous belt of high-elevation that spanned the entire equatorial region of Pangea. Of course, compositional differences and endemic taxa certainly existed in various parts of Euramerica (e.g., Bell, 1944; Pfefferkorn and Gillespie, 1980b; Gastaldo and Boersma, 1983a, 1983b; Cleal, 2002, 2008a, 2008b; Cleal et al., 2009, 2012; Šimůnek and Cleal, 2011), presumably a product of regional landscape partitioning due to elevational, latitudinal, and climatic factors (Blake et al., 2002; Falcon-Lang et al., 2011). Such variables would have determined when and where speciation occurred, and must have impeded the dispersibility of wetland vegetation to some degree. For example, *Neuropteris ovata* and *Neuropteris flexuosa* make scattered appearances in middle to upper Bolsovian strata in the USA (Jongmans, 1937c; Wood, 1963; Read and Mamay, 1964; Darrah, 1969; Blake et al., 2002), even though these species are key indicators to identifying the base of the Asturian in Europe and Atlantic Canada (Laveine, 1977; Wagner, 1984; Zodrow and Cleal, 1985; Cleal and Thomas, 1994; Cleal, 2007). The paleobiogeographic ramification of these precocious appearances in the USA is that *N. ovata* and *N. flexuosa* originated in the western part of the paleocontinent before synchronously arriving in Europe. Although such paleobiogeographic vagaries may hinder the precision of homotaxial biostratigraphic comparisons between American and European macrofloral assemblages, on the whole, correlations within Euramerica should be possible so long as regional peculiarities are taken into account.

The marked lithological and biological changes that led to the recognition of the Atokan-Desmoinesian Stage boundary in the USA and the Bolsovian-Asturian Substage boundary in Western Europe may record a common climatic shift that occurred throughout equatorial regions of Euramerica (cf., Cecil et al., 1985; Bertier et al., 2008; Van Hoof et al., 2012). At the core of this environmental change was a shift to increasing seasonality of equatorial precipitation at all phases of glacioeustatic cycles (Cecil et al., 1985; Roscher and Schneider, 2006), which corresponded to a progressive decrease in grounded ice in the Southern Hemisphere (Fielding et al., 2008) and the onset of a rise in global sea level (Rygel et al., 2008). Because the change may have begun (or at least initially was most strongly manifest) in western Pangea before rapidly spreading eastward, and given the vast equatorial area over which the modification occurred, the boundaries show a degree of temporal and spatial disjunction. As such, the expression of this major climatic shift in the rock record may present a more realistic model for the timing and effects of large-scale environmental changes than do short-term, globally contemporaneous catastrophes.

Tectonic activity also played a prominent role during this time interval in North America. In fact, the type Atokan Stage resides in the heart of the Ouachita orogenic belt (southern part of the greater Appalachian-Variscan chain), and the Ouachita

orogeny culminated near the end of the Atokan (Houseknecht, 1983). Assuredly, elevation of this new mountain range also affected regional climate.

Materials and methods

A selection of North American publications that provide detailed descriptive and illustrated records of Middle Pennsylvanian adpressions was the main source used for comparison with the macrofloral assemblage (Table 3). The list focuses on the Illinois Basin, and Indiana in particular, but includes records from the Western Interior, Appalachian, and Michigan basins of the USA, and the Maritimes Basin of Atlantic Canada. Almost all fossil-taxa in the macrofloral assemblages (Table 1) are described; the only exceptions are *Calamites* spp. indet. and the putative conifer cone scale. Likewise, most taxa are illustrated in Figures 8–11 (including the conifer cone scale, Fig. 11.7).

Repositories and institutional abbreviations.—Plant fossils are stored at the National Museum of Natural History (NMNH), Smithsonian Institution, Washington, DC, and illustrated

Table 3. Main literature sources used for comparison with macrofloral assemblage, and to compile synonymy lists. All publications provide detailed descriptive and/or illustrated records of Middle Pennsylvanian plant-fossil adpressions in North America, with focus on Illinois Basin (* indicates record from Indiana).

ILLINOIS BASIN
Lesquereux (1866)
Lesquereux (1870)
Jackson (1916)*
Noé (1925)
Janssen (1940)
Langford (1958)
Canright (1959)*
Langford (1963)
Wood (1963)*
Darrah (1969)
Boneham (1974)*
Gastaldo (1977)
Janssen (1979)
Pheifer (1979)*
Jennings (1990)
Wittry (2006)

WESTERN INTERIOR BASIN
White (1893)
White (1899)
Sellards (1908)
Basson (1968)
Moore et al. (2014)

APPALACHIAN BASIN
Lesquereux (1868)
Lesquereux (1879–84)
Gillespie et al. (1978)
Oleksyshyn (1982)
Blake et al. (2002)

MICHIGAN BASIN
Arnold (1934)
Arnold (1949)

MARITIMES BASIN
Bunbury (1847)
Bell (1938)
Bell (1940)
Bell (1962)
Zodrow and McCandlish (1980)
Zodrow (1989)
Zodrow and Cleal (1998)
Bashforth (2005)

---

specimens are reposited in the Plant Type and Illustrated Collection under USNM numbers 558409, 559867–559875, and 594359–594391. Components of the assemblage were the subject of a dissertation (Comer, 1992) that included specimens from several stratigraphic levels and depositional facies not included in this study.

Systematic paleontology

Division Tracheophyta
Class Lycopsida
Order Isoëtales Bartling, 1830
Family Diaphorodendraceae DiMichele and Bateman, 1992
Genus *Synchysidendron* DiMichele and Bateman, 1993
Synchysidendron sp. cf. *S. andrewsii* (Lesquereux, 1879-80)
Moore, Wittry, and DiMichele, 2014
Figure 8.1

1879-80	*Lepidodendron Andrewsii* Lesquereux, p. 389, pl. 64, fig. 6.
1938	*Lepidodendron dichotomum* Arber var. *bretonense* Bell, p. 92, pl. 95, figs. 5–9, pl. 96, fig. 1, pl. 97, fig. 4.
1940	*Lepidodendron dichotomum*; Bell, p. 122, pl. 7, fig. 4.
1944	*Lepidodendron dichotomum* var. *bretonense*; Bell, p. 89, pl. 45, fig. 3.
1962	*Lepidodendron bretonense* Bell, p. 53, pl. 47, figs. 5, 6(?), pl. 48, figs. 4, 6(?).
(?)1963	*Lepidodendron* Sternberg sp.; Langford, p. 153, figs. 712, 713.
1980	*Lepidodendron bretonense*; Zodrow and McCandlish, p. 80, pl. 116, fig. 1, pl. 118, figs. 1(?), 2.
1985	*Lepidodendron bretonense*; Wnuk, p. 169, pl. 2, figs. 7, 8.
2005	*Diaphorodendron bretonense* (Bell) Bashforth, p. 36, pl. 2, figs. 1–4, 7, 8.
2006	*Lepidodendron andrewsii*; Wittry, p. 106, figs. 1–3 [holotype: figs. 1, 2].
2014	*Synchysidendron andrewsii* (Lesquereux) Moore, Wittry and DiMichele, p. 28, pl. 1, figs. 1–13.

Holotype.—USNM 15430 (part) and USNM 15431 (counterpart), Plant Type and Illustrated Collection, National Museum of Natural History, Smithsonian Institution, Washington, from Francis Creek Shale, Carbondale Formation (middle Desmoinesian), Illinois Basin, Mazon Creek, Illinois.

Occurrence.—USA and Canada: common throughout Middle Pennsylvanian (Bell, 1938, 1962; Bashforth, 2005; DiMichele et al., 2013a; Moore et al., 2014).

Material examined.—One specimen from Unit 1.

Description.—The axis fragment is 42 mm long and 23 mm wide. Leaf cushions are contiguous, crowded, asymmetrical, 7–9 mm long and 6–7 mm wide (L:W ratio ~ 1.3), and quadrilateral to napiform with curved to obtusely rounded lateral margins. Upper angles appear obtusely to acutely pointed, whereas lower angles appear acutely pointed (but are
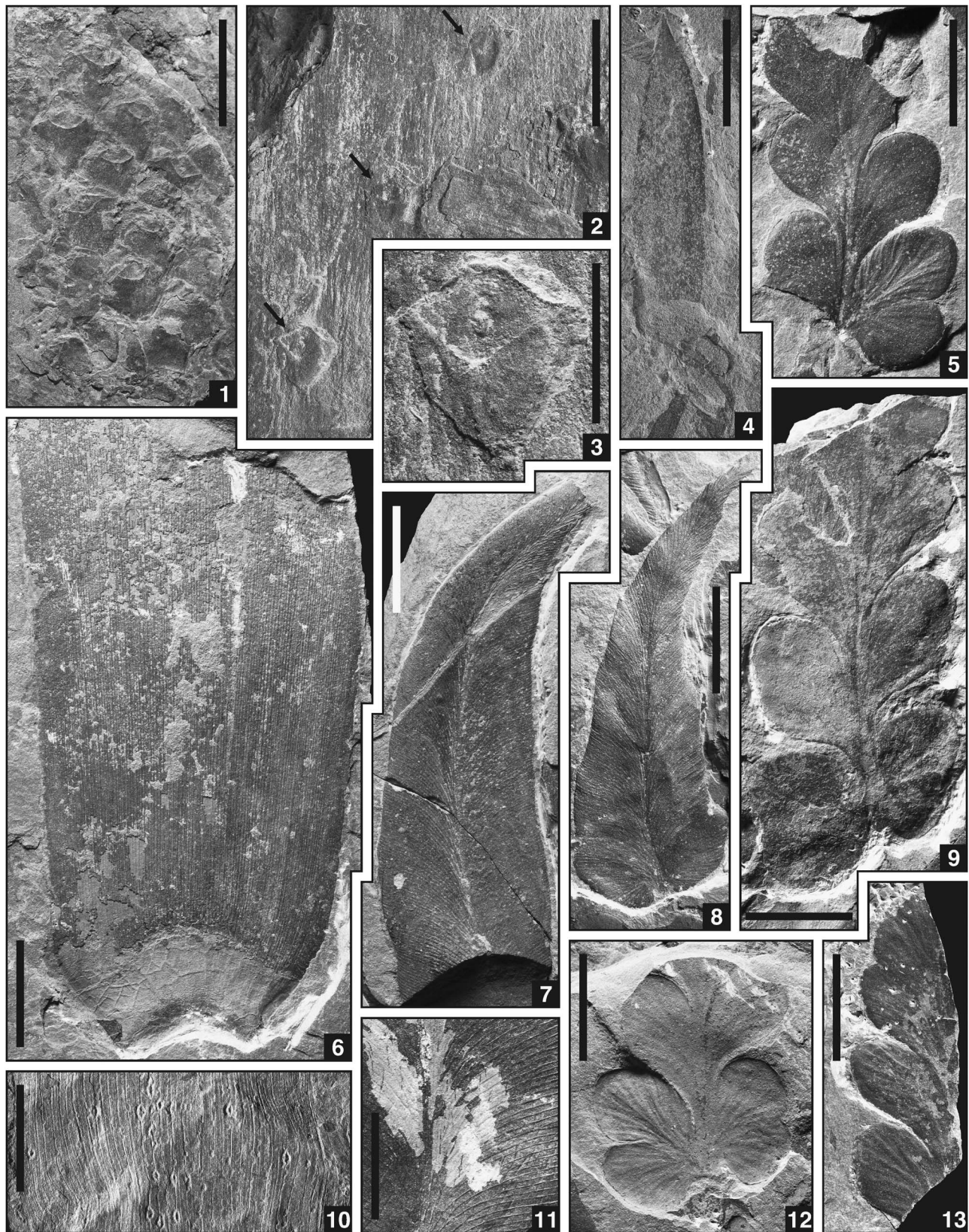
overlapped by the top of the subjacent cushion). Leaf scars are situated in the upper half of a cushion, slightly elevated, 1.2–1.8 mm long, 2.3–4.0 mm wide (L:W ratio ~ 0.5), with a broadly convex lower margin, a triangular upper margin with straight sides that converge to an obtusely pointed top, and acutely pointed lateral angles. Cicatricules are not preserved and their

position and dimensions are unknown. A gently arched ridge runs from each lateral angle of the leaf scar to the lateral margin of the leaf cushion, separating the cushion into upper and lower fields that lack obvious ornamentation.

Remarks.—In an adpressed state, the absence of infrafoliar parichnos scars beneath the leaf scar is the overriding character that confers assignment to *Synchysidendron* or *Diaphorodendron* DiMichele, 1985 of the Diaphorodendraceae (DiMichele, 1985; DiMichele and Bateman, 1992), and distinguishes it from true *Lepidodendron* Sternberg, 1820 (sensu DiMichele, 1983) of the Lepidodendraceae. Other features, such as the fleshiness of leaf cushions, the presence on large axes of flat interareas between leaf cushions, and the degree of ornamentation on the lower keel of the leaf cushion contribute to generic identification. Segregation of the Diaphorodendraceae from the Lepidodendraceae is more apparent in anatomically preserved examples, as the vegetative anatomy and reproductive organs are conspicuously different (DiMichele, 1979a, 1979b, 1983, 1985; DiMichele and Bateman, 1992). Furthermore, the two families can be differentiated by their growth habits (Wnuk, 1985, DiMichele et al., 2013a). Trunks of *Synchysidendron* and *Diaphorodendron* bear two opposite rows of large deciduous lateral branches (or branch scars) that extend into a dichotomously branched crown, whereas *Lepidodendron* only has a terminal dichotomous crown.

Leaf cushions of the study specimen approach equilateral dimensions (L:W ratio ~ 1.3), are contiguous to slightly overlapping, and markedly protrude from the stem surface, supporting assignment to *Synchysidendron* rather than *Diaphorodendron*, which tends to have relatively flat and non-protruding leaf cushions with a higher L:W ratio (Wnuk, 1985; DiMichele and Bateman, 1992; DiMichele et al., 2013a; Moore et al., 2014). The axis fragment probably was derived from a deciduous lateral branch, the most common litter elements of the Diaphorodendraceae (DiMichele et al., 2013a).

The specimen resembles adpressed examples of *Synchysidendron andrewsii*, a fossil-species that was documented by Moore et al. (2014) and is the most common form of *Synchysidendron* in the Middle Pennsylvanian of the USA (DiMichele et al., 2013a). The taxon has been recorded in Atlantic Canada under *Lepidodendron dichotomum* var. *bretonense* (Bell, 1938, 1944), *Lepidodendron bretonense* (Bell, 1962; Zodrow and McCandlish, 1980), and incorrectly assigned to *Diaphorodendron bretonense* by Bashforth (2005). Anatomically preserved axes of comparable morphology have been referred to *Synchysidendron*

dicentricum (Felix, 1952) DiMichele and Bateman, 1993 (DiMichele, 1979b; DiMichele and Bateman, 1992, 1993; DiMichele et al., 2013a). Similar to examples of *S. andrewsii* in Moore et al. (2014, pl. 1, figs. 1–13), the specimen has protuberant, napiform to quadrilateral leaf cushions, leaf scars wider than long that are situated in the upper half of the cushion, a gently arched ridge that runs between the scar and cushion margins, and the faint impression of a notch in the upper field just below the upper angle; such notches are exemplified in DiMichele et al. (2013a, fig. 5b). However, *S. andrewsii* tends to have weakly developed upper and lower keels and plications on the lower keel; absence of these features in the specimen makes referral uncertain.

Family Sigillariaceae(?) Unger (in Endlicher), 1842
Genus *Asolanus* Wood, 1860
cf. *Asolanus camptotaenia* Wood, 1860
Figure 8.2, 8.3

1860   *Asolanus camptotænia* Wood, p. 238, pl. 4, fig. 1.
1866   *Sigillaria monostigma* Lesquereux, p. 449, pl. 42, figs. 1–5.
1869   *Sigillaria camptotænia* (Wood) Wood, p. 342, pl. 9, fig. 3.
1870   *Sigillaria (Knorria) monostigma*; Lesquereux, p. 446, pl. 26, fig. 5.
1879-80   *Sigillaria monostigma*; Lesquereux, p. 468, pl. 73, figs. 3–6.
1899a   *Sigillaria (Asolanus) camptotænia*; White, p. 230, pl. 69, pl. 70, figs. 1, 3(?), 4.
1925   *Sigillaria camptotaenia*; Noé, pl. 11, figs. 1, 3.
1938   *Asolanus camptotaenia*; Bell, p. 102, pl. 104, figs. 1–3.
1940   *Asolanus camptotaenia*; Janssen, p. 22, pl. 5, figs. 1, 2, 3(?), pl. 6(?).
1949   *Asolanus camptotaena* [sic]; Arnold, p. 179, pl. 11, fig. 3.
1958   *Asolanus camptotaenia*; Langford, p. 108, text-figs. 200–202.
1962   *Asolanus camptotaenia*; Bell, p. 56, pl. 48, figs. 1–3.
1968   *Asolanus camptotaenia*; Basson, p. 40, pl. 1, figs. 1, 2.
1969   *Asolanus camptotaenia*; Darrah, p. 182, pl. 34, fig. 1.
1977   *Asolanus campotaenia* [sic]; Gastaldo, text-fig. 21.
1978   *Asolanus camptotaenia*; Gillespie et al., p. 50, pl. 20, figs. 1, 3.
2006   *Asolanus camptotaenia*; Wittry, p. 111, fig. 1.

Figure 8. Specimens from Units 1 and 2 (Fig. 3) above Minshall Coal, Clay County, Indiana; scale bars = 10 mm (**1**, **2**, **4–10**, **12**, **13**) or 5 mm (**3**, **11**). (**1**) *Synchysidendron* sp. cf. *S. andrewsii* (Lesquereux, 1879-80) Moore, Wittry, and DiMichele, 2014, lycopsid bark, Unit 1, USNM 559868. (**2**, **3**) cf. *Asolanus camptotaenia* Wood, 1860, lycopsid bark, with arrows (**2**) indicating position of leaf cushions and details of lowermost leaf cushion (**3**), Unit 1, USNM 559867. (**4**) *Lepidostrobophyllum* sp. indet., lycopsid cone scale, Unit 1, USNM 559870. (**5**) "*Mariopteris*" *anthrapolis* Langford, 1958, lyginopteridalean pteridosperm foliage, ultimate pinna with proximal quadrate pinnules that exhibit strongly incised acroscopic margin and division into rounded lobes, passing apically into strongly decurrent and spatulate to obovate pinnules, part of **12**, Unit 2, USNM 559873. (**6**) *Cordaites* sp. indet., cordaitalean leaf, with well-preserved leaf base, Unit 2, USNM 594360. (**7**) *Macroneuropteris scheuchzeri* (Hoffmann, 1826a) Cleal, Shute, and Zodrow, 1990, medullosalean pteridosperm foliage, subfalcate pinnule, Unit 2, USNM 594361. (**8**) *Macroneuropteris scheuchzeri*, subfalcate pinnule exhibiting initial stages of differentiation of pinnule base into two symmetrical lobes, eventually becoming small orbicular pinnules at base of trifoliate pinnule form, Unit 2, USNM 559875. (**9**) "*Mariopteris*" *anthrapolis*, Unit 2, ultimate pinna with large quadrate pinnules near base and spatulate to obovate pinnules near top, USNM 559871. (**10**) *Cordaites* sp. indet., with spirorbiform worm-tubes (microconchids) affixed to surface, Unit 1, USNM 559869. (**11**) *Macroneuropteris scheuchzeri*, exhibiting hair-like structures characteristic of taxon, Unit 2, USNM 594362. (**12**) "*Mariopteris*" *anthrapolis*, counterpart of **5**, Unit 2, USNM 559873. (**13**) "*Mariopteris*" *anthrapolis*, distal end of ultimate pinna with strongly decurrent and spatulate to obovate pinnules that meld into large lobate terminal pinnule with subtly crenulate margin, Unit 2, USNM 559874.

Holotype.—ASNP 695, Paleobotany Collection, Academy of Natural Sciences of Drexel University, Philadelphia, from "Anthracite Region of Pennsylvania" (Darrah, 1969, p. 183).

Occurrence.—USA: middle(?) Atokan to middle Virgilian, most common in upper Atokan to upper Desmoinesian (Darrah, 1969; Gillespie and Pfefferkorn, 1979; Oleksyshyn, 1982; Blake et al., 2002). UK: lower Duckmantian to lower Cantabrian (Cleal, 2007). Atlantic Canada: middle Asturian (Bell, 1938).

Material examined.—Two specimens from Units 1 and 4.

Description.—The illustrated axis fragment is 130 mm long and 105 mm wide, and involves three preservation states that represent degrees of decortification. All preservation modes exhibit longitudinally corrugated interfoliar areas, expressed as subparallel to slightly flexuous and discontinuous ridges and furrows; corrugations are coarser on the outermost layer, and finer on the innermost layer. Leaf cushions (Fig. 8.3) are spirally arranged and widely spaced, ranging from 14–23 mm apart (measured center to center in the helix), and their morphology is only preserved in the two outermost layers. Cushions protrude slightly from the axis surface, 6–8 mm long, 5–7 mm wide (L:W ratio ~ 1.1), with rhomboidal to subtriangular outlines (widest at the top). Upper angles are broadly convex, lower angles are obtusely rounded, and lateral angles are obtusely rounded to pointed. Leaf scars are situated at the very top of a cushion, slightly elevated, 2.0–3.3 mm long, 3.5–5.0 mm wide (L:W ratio ~ 0.6), with broadly curved upper and lower margins that converge laterally into acutely rounded to pointed lateral angles. Situated in the center of a leaf scar is a single prominent cicatricule, which is circular, ~1 mm in diameter, and consists of a raised rim around a central hollow; other equivocal pits may occur above and/or below the main cicatricule. Leaf cushions appear smooth and lack obvious ornamentation, although some exhibit a faint and finely pustular texture.

Remarks.—Specimens belong to one of a number of lycopsid genera characterized by widely spaced leaf scars, but identification is ambiguous because they exhibit a blend of features typical of multiple taxa. The relatively coarse longitudinal interfoliar corrugations resemble some fossil-species of *Bothrodendron* Lindley and Hutton, 1833 (particularly *Bothrodendron punctatum* Lindley and Hutton, 1833) and *Cyclostigma* Haughton, 1860, the latter synonymous with *Pinakodendron* Weiss (in Weiss and Sterzel), 1893 according to Cambier and Renier (1912) and Crookall (1964). However, neither of these fossil-genera have leaf cushions, leaf scars are oval to almost circular with rounded and inconspicuous lateral angles, leaf scars contain three foliar cicatricules, and a prominent ligule pit occurs above the leaf scar in *Bothrodendron* (absent in *Cyclostigma*). Because all of these morphological traits are incongruent with the material at hand, identity is unlikely.

The specimens most strongly resemble *Asolanus* (usually reported as *Asolanus camptotaenia*), which has affinities with *Sigillaria* Brongniart, 1822 (Wood, 1869; White, 1899a). Like the study examples, this taxon has leaf cushions with a convex upper angle and subtriangular lower angle, leaf scars that are rhomboidal to lenticular with sharp lateral angles, and a centrally positioned cicatricule that is circular and ring-like (Crookall, 1964). *Asolanus camptotaenia* exhibits a wide range of morphologies depending on preservation state and position on the original plant. However, in its most recognizable form, the species has unique interfoliar ornamentation that consists of straight to slightly flexuous, parallel striations that extend perpendicular from the four edges of the leaf scar, resulting in a rhomboidal pattern on the stem surface. This is inconsistent with the longitudinally corrugated surface on the specimen, so confident assignment to *A. camptotaenia* is not possible.

*Incertae sedis*
Genus *Cyperites* Lindley and Hutton, 1832
Cyperites bicarinatus Lindley and Hutton, 1832 emend.
Rex, 1983
Figure 9.9

1832   *Cyperites bicarinata* Lindley and Hutton, p. 123, pl. 43, figs. 1, 2.
1944   *Lepidophyllum* Brongniart sp.; Bell, p. 96, pl. 59, fig. 2.
(?)1959   *Lepidophyllum longifolium* Brongniart; Canright, pl. 1, fig. 9.
1963   *Lepidophyllum bicarinatum* (Lindley and Hutton) Langford, p. 159, text-fig. 726.
1963   *Lepidophyllum longifolium*; Langford, p. 159, text-fig. 728.
1963   *Lepidophyllum* sp.; Langford, p. 159, text-fig. 729.
1963   *Lepidophyllum* sp.; Wood, p. 37, pl. 2, fig. 2.
1967   *Lepidophyllum longifolium*; Tidwell, p. 22, pl. 1, fig. 3.
1974   *Lepidophyllum longifolium*; Boneham, p. 97, pl. 1, fig. 6.
1977   *Lepidophylloides* Snigirevakaya sp.; Gastaldo, text-fig. 18.
1978   *Lepidophylloides* sp.; Gillespie et al., p. 45, pl. 12, fig. 1, pl. 13, fig. 2.
1979   *Lepidophyllum longifolium*; Janssen, p. 62, text-fig. 44.

Figure 9. Specimens from Unit 2 (Fig. 3) above Minshall Coal, Clay County, Indiana; all scale bars = 10 mm. (**1**) *Neuropteris flexuosa* Sternberg, 1825, medullosalean pteridosperm foliage, pinna with large rhomboid to deltoid terminal pinnule, USNM 594364. (**2**) *Neuropteris ovata* Hoffmann, 1826a, 1826b, medullosalean pteridosperm foliage, pinna with small elongate terminal pinnule and 'mixoneurid' habit in distal lateral pinnules, USNM 594366. (**3**) *Neuropteris ovata*, pinna with small elongate terminal pinnule and 'mixoneurid' habit in distal lateral pinnules, USNM 594365. (**4**) *Neuropteris ovata*, pinna with lateral pinnules having a strongly incised acroscopic base and a pronounced basiscopic auricle, USNM 594363. (**5**) *Neuropteris flexuosa*, showing rounded acroscopic base of lateral pinnules, USNM 559872. (**6**) *Neuropteris flexuosa*, pinna with large rhomboid to deltoid terminal pinnule, USNM 594367. (**7**) *Sphenopteris* sp. indet., fern foliage of unknown affinity, USNM 594368. (**8**) *Neuropteris ovata*, pinna with lateral pinnules having a strongly incised acroscopic base and a pronounced basiscopic auricle, USNM 594359. (**9**) *Cyperites bicarinatus* Lindley and Hutton, 1832, lycopsid leaf, USNM 594369. (**10**) *Macroneuropteris scheuchzeri* (Hoffmann, 1826a) Cleal, Shute, and Zodrow, 1990, medullosalean pteridosperm foliage, subtriangular pinnule with asymmetrical base, USNM 594370. (**11**) *Neuropteris flexuosa*, pinna with large rhomboid to deltoid terminal pinnule, and lateral pinnules with pronounced basiscopic auricle, USNM 594371.
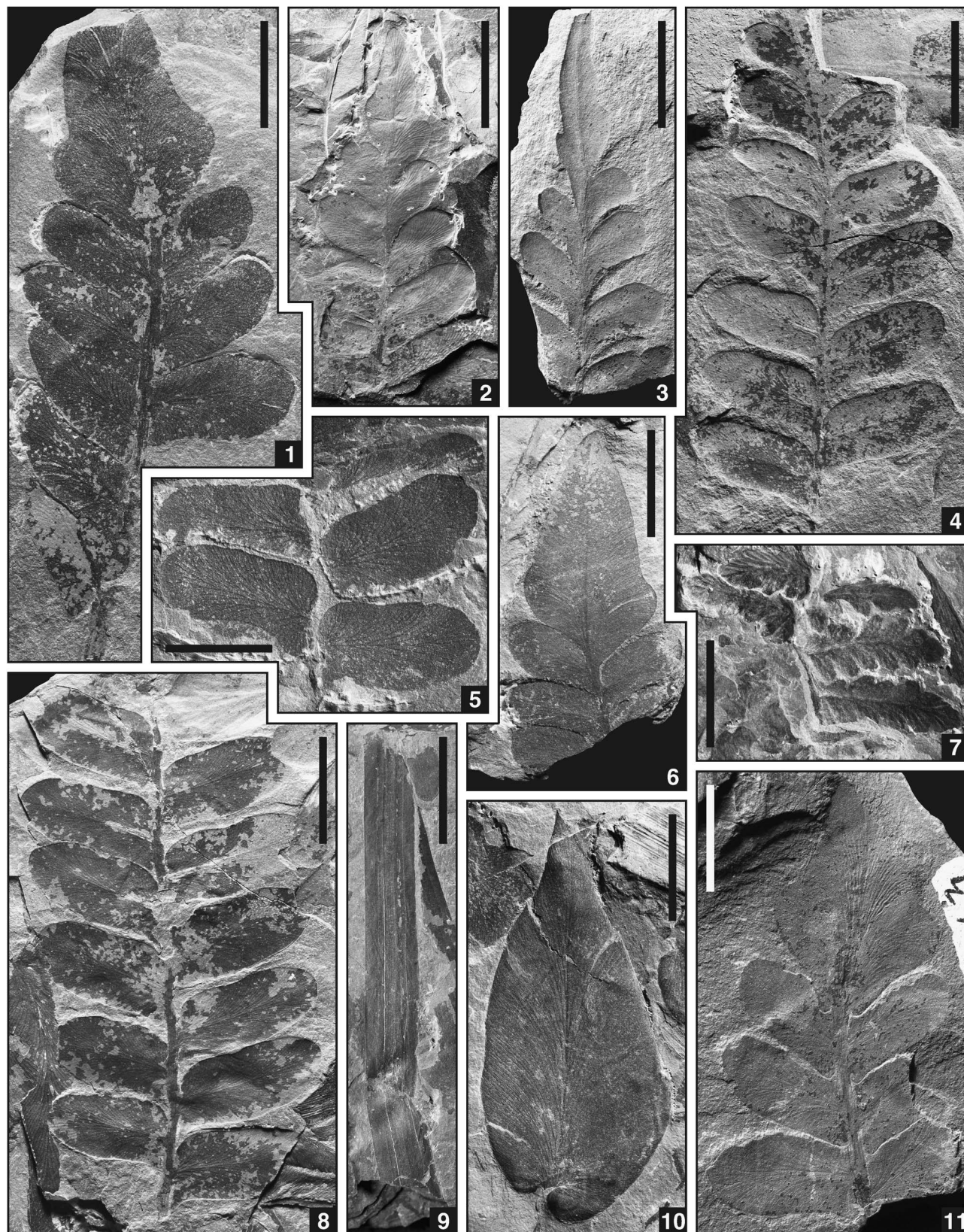
1979   *Cyperites bicarinatus*; Pheifer, pl. 1, figs. 29, 30.

(?)1980 *Sigillariophyllum* sp. Grand'Eury; Zodrow and McCandlish, p. 89, pl. 144.

1982   *Cyperites bicarinatus*; Oleksyshyn, p. 29, text-fig. 9b.

1983   *Cyperites bicarinatus* Lindley and Hutton emend. Rex, p. 81, pl. 1, pl. 4 [neotype: pl. 4, fig. 1].

1992   *Cyperites* sp.; Tidwell et al., p. 1018, text-fig. 4.4.
2005   *Cyperites bicarinatus*; Bashforth, p. 36, pl. 1, figs. 1, 2.
2006   *Cyperites* sp.; Wittry, p. 103, figs. 1, 3–5.

Type material.—Syntypes (lost?) from Leebotwood Coal Pit, Halesowen Formation (upper Asturian or lower Cantabrian), Shropshire, UK. Neotype (V.61563), Natural History Museum, London, from roof-shale of No. 10 Coal Seam, Kilmersdon Tip, Farrington Formation (upper Asturian), Radstock Coalfield, Somerset, UK.

Occurrence.—Euramerica: common throughout Carboniferous.

Material examined.—Thirty-four specimens from Units 1 and 2.

Description.—Leaves are linear and taper slightly distally, have entire lateral margins, and are up to 63 mm long (neither bases nor apices preserved) and 2–7 mm wide. A number of ridges and furrows exist on the leaf surface; an elevated or depressed belt (1–2 mm wide) runs along the center of the leaf, and a thin medial furrow (midvein?) may be present.

Remarks.—Isolated, linear lycopsid leaves are assigned to the fossil-genus *Cyperites*. The leaves had a complex 'butterfly' shape in transverse section, and the presence or absence (and number) of ridges and furrows on the exposed leaf surface depends on the path of the fracture plane across the fossil (Rex, 1983). Wider examples of *Cyperites* tend to belong to sigillarians and narrower leaves to lepidodendroids (Bashforth, 2005). Both size fractions exist in the assemblage, suggesting that both groups may be present, although no other macrofloral elements of *Sigillaria* were identified.

Genus *Lepidostrobophyllum* Hirmer, 1927, emend. Allen, 1961
Lepidostrobophyllum sp. indet.
Figure 8.4

Occurrence.—Euramerica: fossil-genus common throughout Carboniferous.

Material examined.—Five specimens from Units 1, 2, and 4.

Description.—Sporophyll laminae are 7–11 mm wide, broadest about 1/3 the way up the blade, ~20–45 mm long, and linear-lanceolate with convex, entire lateral margins that converge to an acuminate tip. Lateral angles at the base of sporophyll laminae do not project outwards, but appear flush with the pedicel top. Midveins (a rib on the adaxial surface) are 0.5–1.0 mm wide and faintly longitudinally striated. Pedicels are ~10 mm long and 5 mm wide, widest at the contact with the sporophyll lamina, have straight to slightly convex margins, and may terminate in a sharp base. An oval, thickened rim may be superimposed on the pedicel surface.

Remarks.—The description is imprecise due to poor preservation. Based on size and shape, the isolated sporophylls disaggregated from a lepidodendroid cone, and thus are assigned to the fossil-genus *Lepidostrobophyllum*. More than one fossil-species may be involved, but the closest comparison is with *Lepidostrobophyllum lanceolatum* (Lindley and Hutton, 1831) Bell, 1938 (e.g., Bell, 1938, pl. 98, figs. 7–11; Crookall, 1966, pl. 99, figs. 4, 5, under *Lepidostrobus lanceolatus*), which Lesquereux (1870, 1879-80) described under the junior synonym *Lepidostrobus oblongifolius*.

Class Sphenopsida
Order Sphenophyllales Seward, 1898
Family Bowmanitaceae Meyen, 1978
Genus *Sphenophyllum* Brongniart, 1822
Sphenophyllum cuneifolium (Sternberg, 1821) Zeiller, 1878-79a
Figure 10.1–10.3

1821   *Rotularia asplenioides* Sternberg, p. 30, pl. 26, figs. 4a, 4b (alternate name).
1821   *Rotularia cuneifolia* Sternberg, p. 33, pl. 26, figs. 4a, 4b.
1825   *Rotularia saxifragaefolia* Sternberg, p. 45, p. XXXII, pl. 55, fig. 4.
1831   *Sphenophyllum erosum* Lindley and Hutton, p. 41, pl. 13.
1847   *Sphenophyllum erosum*; Bunbury, p. 430, pl. 23, figs. 3a, 3b.
1848   *Sphenophyllum saxifragaefolium* (Sternberg) Göppert (in Bronn), p. 1166.
1868   *Sphenophyllum trifoliatum* Lesquereux, p. 853, pl. 1, fig. 7.
1878-79a *Sphenophyllum cuneifolium* (Sternberg) Zeiller, p. 30, 31, pl. 161, figs, 1, 2.
(?)1884   *Sphenophyllum saxifragæfolium*; Lesquereux, p. 726, pl. 93, figs. 9, 9a.
1891   *Sphenophyllum erosum*; Newberry, p. 215, pl. 19, fig. 1.
(?)1916   *Sphenophyllum cuneifolium*; Jackson, p. 411, pl. 1, fig. 6.

Figure 10. Specimens from Unit 3 (Fig. 3) above Minshall Coal, Clay County, Indiana; scale bars = 10 mm (**1**, **4–7**, **9**) or 5 mm (**2**, **3**, **8**). (**1**) *Sphenophyllum cuneifolium* (Sternberg, 1821) Zeiller, 1879, sphenophyll foliage, with whorls of several leaf forms, including (C) cuneate 'normal' leaves (forma *typica*), (S) cuneate 'divided' leaves (forma *saxifragaefolium*), and (L) 'deeply divided' to 'linear' leaves, USNM 594376. (**2**) *Sphenophyllum cuneifolium*, whorl with cuneate 'divided' leaves (forma *saxifragaefolium*), USNM 594379. (**3**) *Sphenophyllum cuneifolium*, whorl with cuneate 'normal' leaves (forma *typica*), USNM 594377. (**4**) *Eusphenopteris neuropteroides* (Boulay, 1876) Novik, 1947, lyginopteridalean pteridosperm foliage, ultimate pinna with trilobate to bilobate pinnules near base, passing upwards to quadrate or ovate pinnules and topped by small lobate terminal pinnule, USNM 594380. (**5**) *Eusphenopteris neuropteroides*, penultimate pinna, from which arises ultimate pinna with trilobate to bilobate pinnules near base and quadrate to ovate pinnules near top, USNM 594378. (**6**) *Alethopteris densinervosa* Wagner, 1968, medullosalean pteridosperm foliage, biconvex pinnule form, USNM 594372. (**7**) *Alethopteris densinervosa*, subtriangular pinnule form on pinnae topped by a small allantoid terminal pinnule, USNM 594375. (**8**) *Eusphenopteris neuropteroides*, strongly decurrent rounded pinnules and small terminal pinnule at distal end of ultimate pinna, USNM 594374. (**9**) *Alethopteris densinervosa*, exhibiting transition from biconvex pinnule form at top of pinna to elongate form at base, USNM 594373.
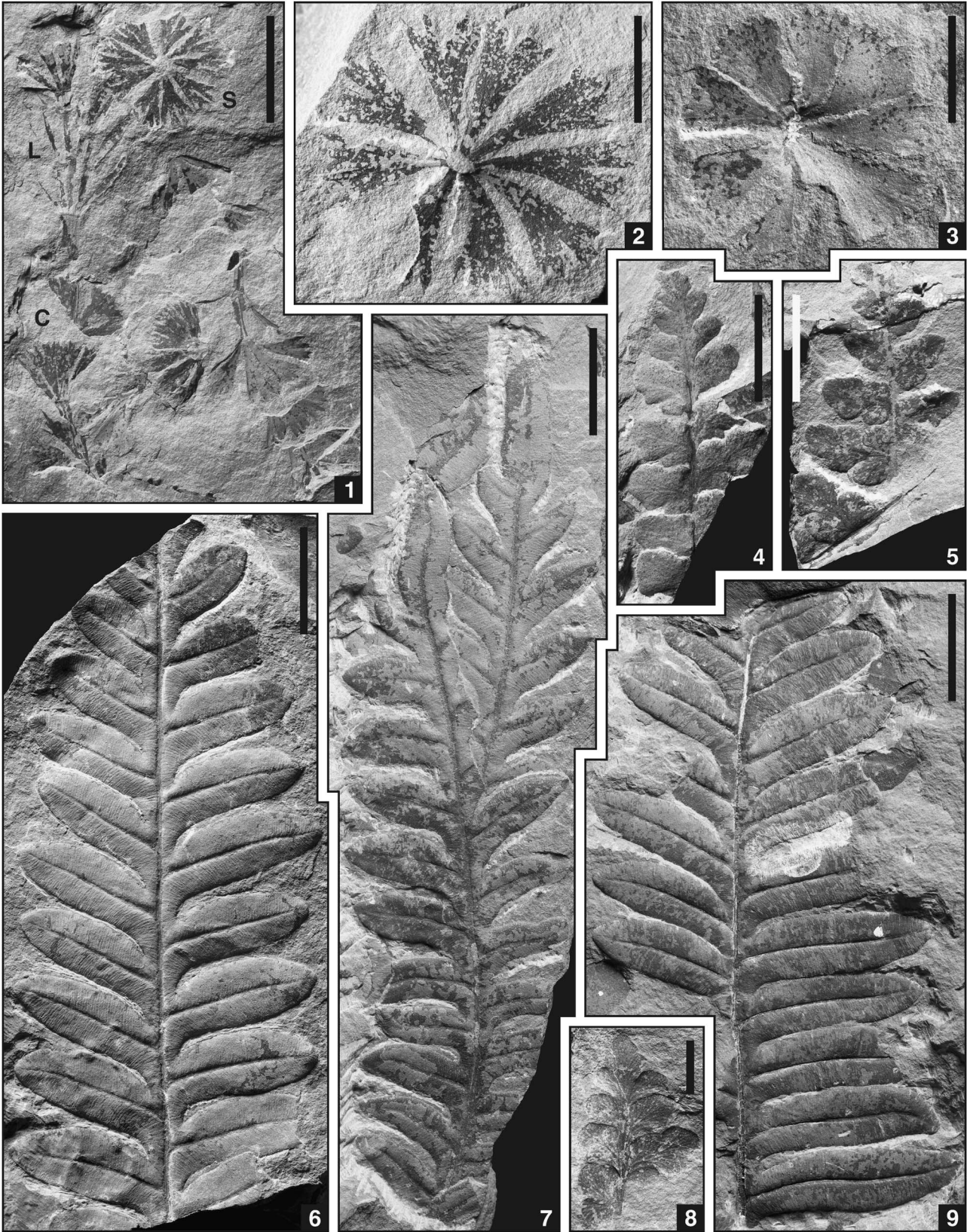
1934   *Sphenophyllum cuneifolium*; Arnold, p. 184, pl. 2, fig. 4, pl. 4, fig. 6.

1934   *Sphenophyllum saxifragaefolium*; Arnold, p. 184, pl. 2, fig. 2, pl. 3, fig. 6, pl. 4, fig. 3.

1938   *Sphenophyllum cuneifolium*; Bell, p. 89, pl. 92, figs. 6–8.

1944   *Sphenophyllum cuneifolium*; Bell, p. 105, pl. 75, fig. 6.

1944   *Sphenophyllum cuneifolium* forma *saxifragaefolium*; Bell, p. 105, pl. 75, fig. 5, pl. 76, fig. 10.

1949   *Sphenophyllum cuneifolium*; Arnold, p. 185, pl. 18, figs. 1, 3, 6, 9.

1949   *Sphenophyllum saxifragaefolium*; Arnold, p. 185, pl. 18, figs. 5, 8.

1959   *Sphenophyllum saxifragaefolium*; Canright, pl. 3, fig. 6.

1963   *Sphenophyllum cuneifolium*; Wood, p. 46, pl. 5, fig. 6.

1969   *Sphenophyllum cuneifolium*; Darrah, p. 178, pl. 44, fig. 2.

1978   *Sphenophyllum cuneifolium*; Gillespie et al., p. 72, pl. 28, fig. 4.

1980   *Sphenophyllum cuneifolium*; Zodrow and McCandlish, p. 75, pl. 107, fig. 1(?), pl. 109.

(?)1982   *Sphenophyllum cuneifolium*; Oleksyshyn, p. 43, text-figs. 10h, i, 11a, b.

1997   *Rotularia cuneifolia*; Kvaček and Straková, p. 58, pl. 16, fig. 3 [holotype]

2002   *Sphenophyllum cuneifolium*; Blake et al., pl. 18, figs. 7, 8.

Holotype.—E40a and E40b, National Museum, Prague, from Radnice Member (Bolsovian), Kladno Formation, Central and Western Bohemian Basin, Vranovice, Czech Republic.

Occurrence.—USA: lowermost Morrowan to upper Desmoinesian, most common from Atokan to lower Desmoinesian (Abbott, 1958; Darrah, 1969; Gillespie et al., 1978; Gillespie and Pfefferkorn, 1979; Blake et al. 2002). Europe: upper Namurian to upper Bolsovian (Wagner, 1984; Cleal and Thomas, 1994; Cleal, 2007). Atlantic Canada: lower Langsettian to upper Asturian (Bell, 1938, 1944; Zodrow, 1989; Calder, 1998).

Material examined.—Forty-four specimens from Units 2 and 3.

Description.—Whorls comprise leaves of numerous morphologies, depending on the axis order and position on the axis. Axes are 1–5 mm wide, expanded at the nodes, comprise longitudinal ridges and furrows, and may exhibit tiny pits that represent trichome bases. Nodes are 2–13 mm long (longest on the widest axes), shortening abruptly near the distal end of an axis (apoxogenesis) and less abruptly near the proximal end (epidogenesis), and each gives rise to a whorl of six to nine leaves. 'Normal' leaves (forma *typica*; Fig. 10.1, 10.3) are closely spaced, cuneate with straight lateral margins, 5–7 mm long, and 3–4 mm wide at the distal margin, which is slightly convex and comprises seven to nine triangular teeth with acute tips. 'Divided' leaves (forma *saxifragaefolium*; Fig. 10.1, 10.2) are less closely spaced, cuneate with concave lateral margins, 5–8 mm long, and 2–4 mm wide at the convex distal margin. In less-divided forms, two lobes (with two or three acutely pointed teeth) occur on either side of a central sinus ~ 1 mm deep; in more-divided forms, four lobes (with one or two teeth) are separated by a 2–3 mm deep central sinus and two shallower secondary sinuses. The most-divided forms (generally situated near the base or top of an axis; Fig. 10.1) comprise two linear lobes that are 7–8 mm long, less than 1 mm wide, and have acuminate tips; solitary linear leaves have the same dimensions. In cuneate leaves, a single vein enters each leaf, branching two to four times before terminating at the end of a tooth or lobe; linear leaves are centered by a single vein.

Remarks.—Much of the assemblage comprises divided leaflets that belong to *Sphenophyllum saxifragaefolium*, a morphological variant of *Sphenophyllum cuneifolium*; the designations 'forma *typica'* and 'forma *saxifragaefolium'* have sometimes been used (e.g., Bell, 1944; Crookall, 1969; Zodrow, 1989). *Sphenophyllum erosum* of Lindley and Hutton (1831) and *Sphenophyllum trifoliatum* of Lesquereux (1868) are junior synonyms of *S. cuneifolium*. The triangular and acutely pointed teeth on cuneate leaves (forma *typica*) of *S. cuneifolium* permit ready distinction from *Sphenophyllum emarginatum* (Brongniart, 1822) Brongniart, 1828b, which has semicircular to obtusely rounded teeth. Many sphenophylls possessed leaves tipped by stiffened, recurved hooks, and although known for *S. cuneifolium* (Barthel, 1997, pl. 1, fig. 4), no leaves with 'climber hooks' were observed.

Sphenophyllum emarginatum (Brongniart, 1822) Brongniart,
1828b emend. Batenburg, 1977
Figure 11.1

1822   *Sphenophyllites emarginatus* Brongniart, p. 234, pl. 2, figs. 8a, 8b.

1828b   *Sphenophyllum emarginatum* (Brongniart) Brongniart, p. 68.

(?)1870   *Sphenophyllum cornutum* Lesquereux, p. 421, pl. 19, figs. 1–5.

Figure 11. Specimens from Units 2 and 4 (Fig. 3) above Minshall Coal, Clay County, Indiana; scale bars = 10 mm (**2–6**, **11**, **12**) or 5 mm (**1**, **7–10**). (**1**) *Sphenophyllum emarginatum* (Brongniart, 1822) Brongniart, 1828b, sphenophyll foliage, with whorls displaying cuneate leaves, Unit 4, USNM 594381. (**2**) *Neuropteris missouriensis* Lesquereux, 1879-80, medullosalean pteridosperm foliage, pinna with large obtusely rounded terminal pinnule, Unit 4, USNM 594388. (**3**) *Neuropteris missouriensis*, pinna with large obtusely rounded terminal pinnule, Unit 4, USNM 594387. (**4**) *Neuropteris missouriensis*, pinna with large obtusely rounded terminal pinnule and small ovate lateral pinnules, Unit 4, USNM 594390. (**5**) *Eusphenopteris* sp. indet., lyginopteridalean pteridosperm foliage, Unit 4, USNM 594385. (**6**, **9**) *Neuropteris semireticulata* Josten, 1962, medullosalean pteridosperm foliage, with details of flexuous to pseudoreticulate venation characteristic of taxon in **11.9**, Unit 4, USNM 594382. (**7**) Possible cone scale of primitive conifer, Unit 2, USNM 558409. (**8**) *Annularia sphenophylloides* (Zenker, 1833) Gutbier, 1837, calamitalean foliage, Unit 4, USNM 594383. (**10**) *Annularia* sp. cf. *A. radiata* (Brongniart, 1822) Sternberg, 1825, calamitalean foliage, Unit 4, USNM 594384. (**11**) *Neuropteris missouriensis*, top of pinna with small terminal and elongate lateral pinnules, somewhat atypical of taxon, and prominent compression margin on some pinnules, Unit 4, USNM 594386. (**12**) *Neuropteris missouriensis*, large pinna with smaller, less obtusely rounded terminal pinnule and lateral pinnules that display prominent compression margin, Unit 4, USNM 594389.
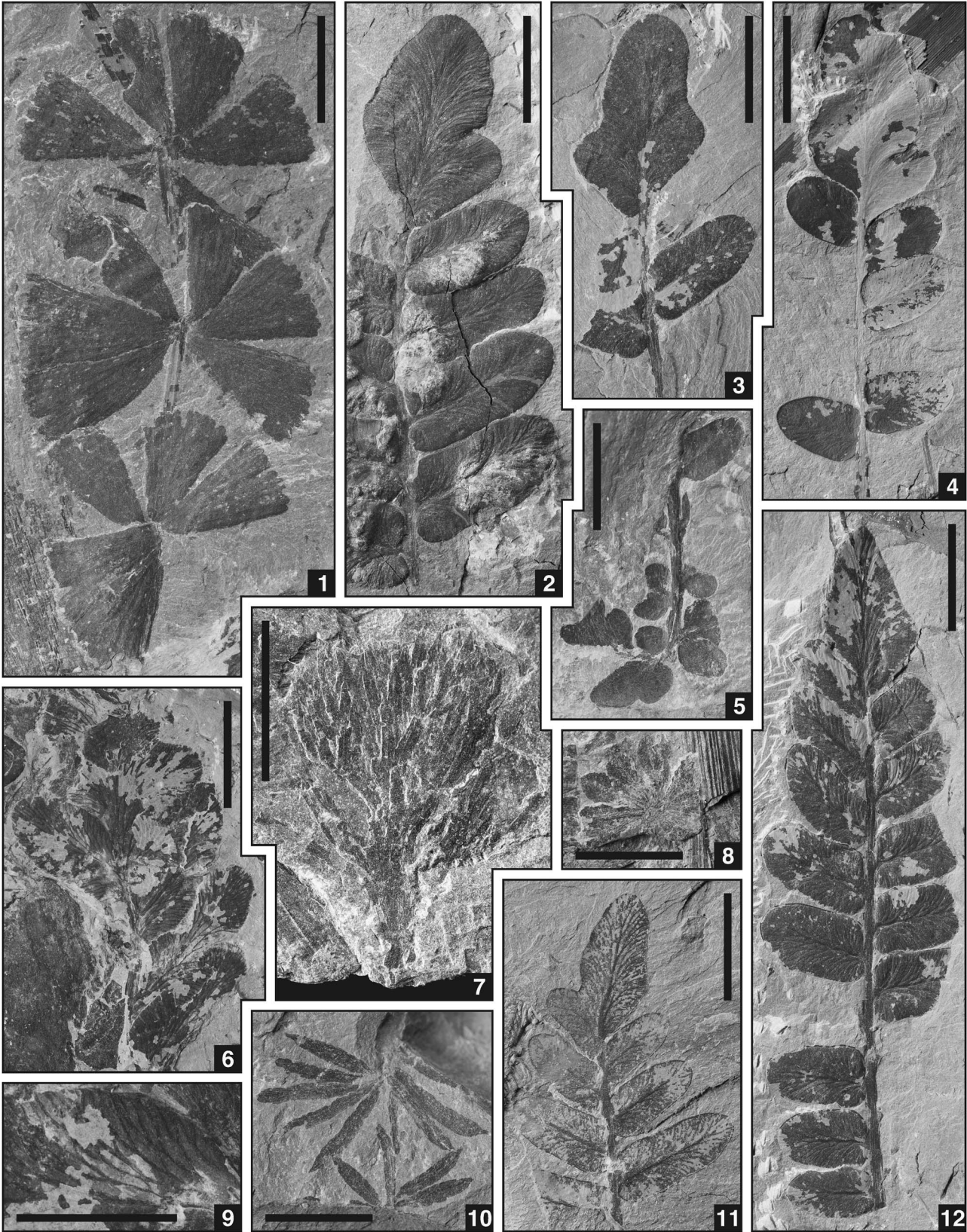
(?)1879-80 *Sphenophyllum cornutum*; Lesquereux, p. 56, pl. 56, figs. 5, 5a, 5b.

(?)1879-80 *Sphenophyllum schlotheimii* Brongniart; Lesquereux, p. 52, pl. 2, figs. 6, 7.

1899a *Sphenophyllum emarginatum*; White, p. 177, pl. 59, fig. 1d.

1925 *Sphenophyllum emarginatum*; Noé, pl. 6, figs. 3, 4, 5(?), 6(?).

1938 *Sphenophyllum emarginatum*; Bell, p. 89, pl. 93, figs. 1, 2, 3(?).

(?)1940 *Sphenophyllum cornutum*; Janssen, p. 12, pl. 1, fig. 2b.

1949 *Sphenophyllum emarginatum*; Arnold, p. 185, pl. 18, fig. 4.

1958 *Sphenophyllum emarginatum*; Abbott, p. 339, pl. 44, fig. 66a, pl. 45, fig. 72.

1958 *Sphenophyllum cornutum*; Abbott, p. 334, pl. 44, figs. 66b, 68(?).

1958 *Sphenophyllum emarginatum*; Langford, p. 55, text-fig. 78.

1959 *Sphenophyllum emarginatum*; Canright, pl. 3, fig. 5.

1962 *Sphenophyllum emarginatum*; Bell, p. 46, pl. 44, figs. 1–4, pl. 56, fig. 1.

1963 *Sphenophyllum emarginatum*; Wood, p. 47, pl. 5, fig. 7.

1968 *Sphenophyllum emarginatum*; Basson, p. 64, pl. 6, fig. 4.

1969 *Sphenophyllum emarginatum*; Darrah, p. 177, pl. 55, fig. 1.

1974 *Sphenophyllum emarginatum*; Boneham, p. 101, pl. 3, fig. 2.

1977 *Sphenophyllum emarginatum* (Brongniart) Brongniart emend. Batenburg, p. 81, pl. 2, figs. 3–6, pls. 3–6.

(?)1977 *Sphenophyllum* cf. *emarginatum*; Gastaldo, text-fig. 31.

1977 *Sphenophyllum emarginatum*; Remy and Remy, p. 386, text-fig. 237a, b [holotype].

1978 *Sphenophyllum emarginatum*; Gillespie et al., p. 72, pl. 28, fig. 8, pl. 29, fig. 1.

1979 *Sphenophyllum emarginatum*; Janssen, p. 92, text-fig. 80.

1979 *Sphenophyllum emarginatum*; Pheifer, pl. 4, fig. 52.

1980 *Sphenophyllum emarginatum*; Storch, p. 172, pl. 1, fig. 1 [holotype].

1980 *Sphenophyllum emarginatum*; Zodrow and McCandlish, p. 75, pl. 110.

1982 *Sphenophyllum emarginatum*; Oleksyshyn, p. 45, fig. 11c–f.

1989 *Sphenophyllum emarginatum*; Zodrow, p. 323, pl. 3, fig. 2, pl. 6.

1997 *Sphenophyllum emarginatum*; Wagner and Lyons, pl. 1, fig. 6.

2002 *Sphenophyllum emarginatum*; Blake et al., pl. 18, figs. 9, 10.

2005 *Sphenophyllum emarginatum*; Bashforth, p. 41, pl. 3, pl. 4, figs. 1, 2, 5, 8, 9.

2006 *Sphenophyllum emarginatum*; Wittry, p. 96, fig. 1.

Holotype.—No. 3519, Muséum national d'Histoire naturelle, Paris, from upper Westphalian (Asturian?), Saar Basin, Germany.

Occurrence.—USA: upper Atokan to lower Virgilian, most common in Desmoinesian (Abbott, 1958; Darrah, 1969; Gillespie and Pfefferkorn, 1979; Oleksyshyn, 1982; Blake et al., 2002). Europe: uppermost Duckmantian to middle Barruelian (Storch, 1980; Wagner, 1984; Laveine 1987). UK: lowermost Bolsovian to lower Cantabrian (Crookall, 1969; Cleal and Thomas, 1994). Atlantic Canada: lowermost Asturian to lower Cantabrian (Bell, 1938; Zodrow, 1989).

Material examined.—One specimen from Unit 4.

Description.—Axes are ~1 mm wide, expanded at the nodes, and comprise pronounced longitudinal ridges and furrows. Nodes are 9–10 mm long and give rise to a whorl of six leaves. Leaves are closely spaced, cuneate with straight lateral margins, 6–8 mm long, and 4–5 mm wide at the distal margin, which is straight to convex, comprises 10 to 12 obtusely rounded teeth, and contains a shallow (0.5–1 mm deep) central sinus. A single vein enters each leaf and branches two to four times before terminating in a tooth.

Remarks.—*Sphenophyllum emarginatum* can be readily distinguished from undivided cuneate forms of *Sphenophyllum cuneifolium* (i.e., forma *typica*), which has smaller leaves with triangular to acutely pointed teeth. Like most sphenophylls, *S. emarginatum* is remarkably heterophyllous (Batenburg, 1977); the example represents undivided cuneate leaves from last-order branches. Isolated, linear leaves in the assemblage (not described) may record disaggregated whorls from first-order branches. Not present are deeply laciniate leaves that Lesquereux (1870) erected as *Sphenophyllum cornutum*, a probable morphological variant of *S. emarginatum* (Batenburg, 1977). Abbott (1958, pl. 44, fig. 66b) figured *S. cornutum*-type leaves arising from a plant bearing typical *S. emarginatum* whorls, but many sphenophyll species produced deeply divided leaves with acuminate lobes that conform to the *S. cornutum* concept. According to White (1899a), much of what Lesquereux included in *Sphenophyllum schlotheimii* Brongniart, 1828b probably belongs to *S. emarginatum*.

Order Equisetales Du Mortier, 1829
Family Calamitaceae Unger, 1840
Genus *Annularia* Sternberg, 1821
Annularia sp. cf. *A. radiata* (Brongniart, 1822) Sternberg, 1825
Figure 11.10

1822 *Asterophyllites radiatus* Brongniart, p. 239, pl. 2, figs. 7a, 7b.

1825 *Annularia radiata* (Brongniart) Sternberg, p. XXXI.

1925 *Annularia radiata*; Noé, pl. 4, fig. 2, pl. 5, fig. 1.

1938 *Annularia radiata*; Bell, p. 85, pl. 88, fig. 2.

1949 *Annularia radiata*; Arnold, p. 183, pl. 17, fig. 3.

1958   *Annularia radiata*; Abbott, p. 317, pl. 41, fig. 56.
1958   *Annularia radiata*; Langford, p. 40, text-fig. 41.
1959   *Annularia radiata*; Canright, pl. 3, fig. 1.
(?)1962 *Annularia pseudostellata* Potonié; Bell, p. 50, pl. 45, figs. 2, 5.
1963   *Annularia radiata*; Wood, p. 40, pl. 3, fig. 8.
1974   *Annularia radiata*; Boneham, p. 99, pl. 2, fig. 6.
(?)1977 *Annularia radiata*; Gastaldo, text-fig. 29.
1978   *Annularia radiata*; Gillespie et al., p. 70, pl. 26, fig. 8, pl. 27, figs. 1, 2(?), 6(?).
(?)1979 *Annularia radiata*; Pheifer, pl. 3, fig. 42.
(?)1980 *Annularia radiata*; Zodrow and McCandlish, p. 68, pl. 91.
2006   *Annularia radiata*; Wittry, p. 90, figs. 1–3.

Holotype.—Repository and locality details not known.

Occurrence.—USA: upper Morrowan to Missourian, rare above uppermost Atokan (Abbott, 1958; Darrah 1969; Gillespie et al., 1978; Gillespie and Pfefferkorn, 1979; Blake et al., 2002). UK: upper Namurian to upper Duckmantian (Cleal and Thomas, 1994). Atlantic Canada: upper Bolsovian to upper Asturian (Bell, 1938).

Material examined.—Two specimens from Unit 4.

Description.—Axes are ~0.4 mm wide and longitudinally striated, with internodes ~5 mm apart. Whorls are probably symmetrical, slightly overlap the subjacent whorl, and comprise at least eight loosely spaced leaves of similar length. Leaves are linear to linear-lanceolate with acuminate tips, 3.5–11.0 mm long and 0.5–1.0 mm wide (L:W ratio ~7), and broadest near the midpoint but have parallel lateral margins through most of their length. Midveins are 0.1–0.2 mm wide, longitudinally striated, and protrude beyond the distal margin to form a blunt mucro.

Remarks.—The taxonomy of *Annularia* (calamitalean foliage) remains in disarray despite efforts to stabilize the nomenclature (Walton, 1936; Abbott, 1958; Crookall, 1969; Barthel, 2004). The morphological plasticity of the foliage is particularly troublesome because several fossil-species of *Annularia* may occur on one plant. None of the specimens examined in this study comprises a complete whorl, therefore the degree of symmetry and number of leaves in a whorl are equivocal; such features are important for specific determination. However, the examples compare best with what Abbott (1958) included in *Annularia radiata*, although at the low end of the size range. A transfer preparation of a specimen that Walton (1936, pl. 31, figs. 16, 17) determined as *A. radiata* is remarkably similar, showing leaves that end in a blunt mucro. According to Abbott (1958), specimens referred to *Annularia ramosa* Weiss, 1881 by White (1893, 1899a) belong to *A. radiata*.

Annularia sphenophylloides (Zenker, 1833) Gutbier, 1837
Figure 11.8

1833   *Galium sphenophylloides* Zenker, p. 398, pl. 5, figs. 6–9.
1837   *Annularia sphenophylloides* (Zenker) Gutbier, p. 436.

1868   *Annularia sphenophylloides*; Lesquereux, p. 852, pl. 1, figs. 5, 5a.
1879-80 *Annularia sphenophylloides*; Lesquereux, p. 48, pl. 2, figs. 8, 9.
(?)1908 *Annularia sphenophylloides*; Sellards, p. 425, pl. 53, fig. 5.
1925   *Annularia sphenophylloides*; Noé, pl. 5, figs. 2, 3.
1938   *Annularia sphenophylloides*; Bell, p. 84, pl. 85, fig. 3, pl. 87, fig. 1.
1958   *Annularia sphenophylloides*; Abbott, p. 319, pl. 41, fig. 55.
1958   *Annularia sphenophylloides*; Langford, p. 40, text-fig. 44.
1962   *Annularia sphenophylloides*; Bell, p. 51, pl. 44, fig. 7.
1963   *Annularia sphenophylloides*; Wood, p. 41, pl. 3, figs. 7(?), 9.
1968   *Annularia sphenophylloides*; Basson, p. 57, pl. 4, fig. 3.
1969   *Annularia sphenophylloides*; Darrah, p. 172, pl. 33, figs. 1, 2, pl. 43, fig. 7.
1978   *Annularia sphenophylloides*; Gillespie et al., p. 71, pl. 26, figs. 3(?), 6, 7.
1979   *Annularia sphenophylloides*; Janssen, p. 86, text-fig. 69.
1980   *Annularia sphenophylloides*; Zodrow and McCandlish, p. 69, pls. 92, 93.
1992   *Annularia sphenophylloides*; Mamay and Mapes, text-fig. 2g.
2005   *Annularia sphenophylloides*; Bashforth, p. 43, pl. 5, figs. 2, 4–7, 10.
2006   *Annularia sphenophylloides*; Wittry, p. 91, figs. 1, 2.
2011   *Annularia sphenophylloides*; Blake and Gillespie, pl. 5, fig. 3.
2013b   *Annularia sphenophylloides*; DiMichele et al., p. 291, text-fig. 4.4.
2014   *Annularia sphenophylloides*; Moore et al., p. 34, pl. 3, figs. 6, 7.

Holotype.—Private collection of Dr. Schüler of Jena, Thüringen, Germany, from Carboniferous of Zittau, Sachsen, Germany (Crookall, 1969, p. 736).

Occurrence.—USA: upper Atokan to upper Virgilian, most common above Atokan (Abbott, 1958; Darrah, 1969; Gillespie and Pfefferkorn, 1979; Blake et al., 2002). UK and Atlantic Canada: lower Bolsovian to lower Cantabrian (Bell, 1938; Cleal and Thomas, 1994; Cleal, 1997). Europe: extends to top of Stephanian (Wagner, 1984).

Material examined.—Two specimens from Unit 4.

Description.—Whorls are symmetrical and comprise ~12 crowded or partly overlapping leaves of similar length. Leaves are markedly spatulate with obtusely rounded tips (because the mucronate tips are embedded in the matrix), 3–7 mm long and 1–2 mm wide (L:W ratio ~ 3), and broadest close to the distal margin. Midveins are ~0.2 mm wide, longitudinally striated, and

flare at the distal margin (terminal expansion) before protruding as an acuminate mucro (not observed).

Remarks.—*Annularia sphenophylloides* is a common and easily recognized species in Middle to Upper Pennsylvanian strata of Euramerica. The small spatulate leaves are especially characteristic, and the embedding of the mucronate tip in the matrix is common for the taxon.

<p style="text-align:center">*Annularia* sp. indet.</p>

Material examined.—One specimen from Unit 4.

Description.—Leaves are at least 18 mm long (but presumably much longer) and ~2 mm wide, parallel-sided for most of their length but tapering towards the base and top, and centered by a midvein ~0.2 mm wide. Leaf surfaces are villous, with short trichomes oriented obliquely to the lateral margins.

Remarks.—The specimen is not illustrated given its incompleteness, and identification of these leaves is equivocal. However, the dimensions, presumed shape, and densely villous nature of the leaves point either to *Annularia carinata* Gutbier, 1849, an earlier synonym of *Annularia mucronata* Schenk, 1883 (cf., Barthel, 1976; Kerp, 1984), or *Annularia spinulosa* Sternberg, 1821, the proper name for what is commonly called *Annularia stellata* (Schlotheim ex Sternberg, 1825) Wood, 1860 (cf., Barthel, 2000). Assignment to *A. spinulosa* is most tenable given that complete leaves probably were oblanceolate (cf., Abbott, 1958). *Annularia stellata* auct. has commonly been recorded in North America under *Annularia longifolia* Brongniart, 1828b and *Annularia inflata* Lesquereux, 1870 (cf., Janssen, 1940; Abbott, 1958; Darrah, 1969).

<p style="text-align:center">Class Filicopsida
Incerti ordinis
Incertae familiae
Genus *Sphenopteris* (Brongniart, 1822) Sternberg, 1825
Sphenopteris sp. indet.
Figure 9.7</p>

Occurrence.—Euramerica: fossil-genus common throughout Carboniferous.

Material examined.—Five specimens from Units 1 and 2.

Description.—Foliar elements are polymorphic. Penultimate pinnae have a thin (~0.5 mm wide), winged rachis, and give rise to alternate and obliquely inserted ultimate pinnae centered by a weakly to moderately decurrent and somewhat flexuous rachis. Ultimate pinnae are linear, taper to an obtusely rounded tip, and range from 13–30 mm long and 5–12 mm wide. In distal positions, ultimate pinnae grade into pinnatifid pinnules that are linguaeform to subtriangular with an obtusely rounded apex, may overlap their neighbor, and are 8–11 mm long and 4–6 mm wide. Entire pinnules are obliquely inserted (more so distally), confluent, linguaeform to subtriangular, and 3–6 mm long and 1.5–3.0 mm wide. Pinnule midveins are thin and strongly decurrent, and give rise to thin, sparse lateral veins that branch

once (twice in largest pinnules) as they arch slightly to reach the lateral margin at a very oblique angle. Sporangia appear to be situated near the end of larger pinnules, but their dimensions, morphology and arrangement are equivocal.

Remarks.—The rarity and fragmentary nature of specimens, and ambiguity about sporangial organization, precludes taxonomic assignment. Although the fully developed, entire pinnules are linguaeform and thus resemble *Pecopteris* (Brongniart, 1822) Sternberg, 1825, more distal pinnae and pinnatifid pinnules can be subtriangular and appear more 'sphenopteroid.' Thus, inclusion in the fossil-genus *Sphenopteris* is tentative.

<p style="text-align:center">Class Spermatopsida
Order Medullosales Corsin, 1960
Family Alethopteridaceae Corsin, 1960 emend.
Cleal and Shute, 2003
Genus *Alethopteris* Sternberg, 1825 emend. Wagner, 1968
Alethopteris densinervosa Wagner, 1968
Figures 10.6, 10.7, 10.9, 13.1</p>

1932	*Alethopteris Serli* (Brongniart) Göppert; Corsin, pl. 29, figs. 1, 1a, 1b [holotype].
1961	*Alethopteris Serli*; Buisine, p. 74, pl. 6, figs. 1, 1a [holotype]
1968	*Alethopteris densinervosa* Wagner, p. 59, pl. 15, figs. 43–44a. [holotype: fig. 43]
1968	*Alethopteris serlii*; Basson, p. 71, pl. 11, fig. 1.
(?)1980	"*Alethopteris serli* morphogroups 1, 2, 3"; Scheihing and Pfefferkorn, pl. 1, figs. 1–6.
1982	*Alethopteris serlii*; Oleksyshyn, p. 99, text-fig. 20d.
2014	*Alethopteris serlii*; Moore et al., p. 40, pl. 7, figs. 5, 6.

Holotype.—USTL 349, Collection Paléobotanique, Université des Sciences et Technologies de Lille, Lille, from lower Faisceau d'Ernestine (middle Bolsovian), Northern France Coalfield, France.

Occurrence.—USA: rare in lower to middle Desmoinesian (Basson, 1968; Oleksyshyn, 1982; Moore et al., 2014). Northern France Coalfield: base of Bolsovian to lower Asturian (Buisine, 1961; Wagner, 1968; Laveine, 1987). Atlantic Canada (?): Asturian (Zodrow, 1986; Zodrow and Cleal, 1998).

Material examined.—Twenty-eight specimens from Units 2 and 3.

Description.—Ultimate pinnae are linear, but narrow slightly near the base and taper rapidly to an acutely rounded apex topped by a small, allantoid, individualized terminal pinnule (Fig. 10.7). Lateral pinnules are extremely variable in habit and size (Table 4; Fig. 12). Most pinnules are inserted obliquely (more so distally, perpendicular in larger forms), closely spaced and occasionally overlapping, moderately vaulted, and distinctly confluent with a marked acroscopic incision and a strongly decurrent basiscopic side, resulting in an asymmetrical shape and a 'wing' of lamina about the rachis. Average pinnules (Fig. 10.6, 10.9) have biconvex lateral margins and obtusely to acutely rounded tips, are widest in the middle, 12–15 mm long and 5–6 mm wide (L:W ratio ~2.4), and squatter in distal positions. Fully developed (elongate) pinnules (Figs. 10.9, 13.1)

Table 4. Morphometric data (length, width, L:W ratio, and venation density) from specimens identified as *Alethopteris densinervosa* Wagner, 1968. To facilitate comparison and validate identification (see Fig. 14), venation density data also are presented from type specimens and other previously illustrated examples of *A. densinervosa*, *Alethopteris missouriensis* (White, 1899a) Wagner, 1968, and *Alethopteris serlii* (Brongniart, 1833-34) Göppert, 1836. Data sources (measurements from actual specimens denoted by *): *A. densinervosa* (holotype)–Buisine (1961, pl. 6, fig. 1a); *A. densinervosa* (North American examples)–Basson (1968, pl. 11, fig. 1), Oleksyshyn (1982, text-fig. 20d), and Moore et al. (2014, pl. 7, fig. 6); *A. missouriensis* (syntypes)–White (1899a, pl. 37, fig. 2*, USNM E3594b; pl. 42, fig. 5, USNM E3591b); *A. missouriensis* (other North American examples)–unillustrated pinnules on syntype slab of White (1899a, pl. 37, fig. 2*, USNM E3594b) and Wittry (2006, p. 71, fig. 1a); *A. serlii* (syntypes)–Wagner (1968, pl. 56, figs. 162 [lectotype], 163); *A. serlii* (North American examples)–Lesquereux (1879-80, pl. 29, figs. 2–4*, USNM 12098–12100), Noé (1925, pl. 38, fig. 1), Langford (1958, text-fig. 436), Bell (1962, pl. 41, fig. 4), Wagner (1968, pl. 57, fig. 167a), Darrah (1969, pl. 50, fig. 1), Scheihing and Pfefferkorn (1980, pl. 1, figs. 1–6), Oleksyshyn (1982, text-fig. 20c), and Blake et al. (2002, pl. 8, fig. 1; pl. 28, fig. 4).

Pinnule shape	Parameter	Range	Percentiles	Mean	N
Alethopteris densinervosa (STUDY SPECIMENS)					
Biconvex	Length	8.4–17.3	12.3–14.9	13.6	44
	Width	4.1–7.2	5.2–6.2	5.7	44
	Length:Width	1.7–2.8	2.2–2.5	2.4	44
	Venation density	38–56	45–52	48	49
Elongate	Length	12.8–30.0	14.6–22.0	18.9	12
	Width	5.1–8.0	5.4–7.0	6.2	15
	Length:Width	2.4–4.3	2.6–3.3	3.0	12
	Venation density	37–50	41–46	44	18
Subtriangular	Length	4.3–12.1	8.2–10.0	9.0	30
	Width	2.5–5.0	2.9–4.0	3.6	30
	Length:Width	1.4–3.4	2.2–2.9	2.5	30
	Venation density	39–55	44–50	47	21
Terminal	Length	13.7–14.3	n/a	14.0	2
	Width	4.5–4.7	n/a	4.6	2
	Length:Width	3.0	n/a	3.0	2
	Venation density	45–53	47–50	49	4
All pinnules	Length	4.3–30.0	9.5–14.9	12.8	88
	Width	2.5–8.0	4.0–6.0	5.0	91
	Length:Width	1.4–4.3	2.3–2.8	2.5	88
	Venation density	37–56	44–50	47	92
Alethopteris densinervosa (HOLOTYPE)					
Biconvex	Venation density	42–54	47–53	49	11
Alethopteris densinervosa (NORTH AMERICAN EXAMPLES)					
Variable	Venation density	42–53	44–48	46	12
ALL *Alethopteris densinervosa* COMBINED					
Variable	Venation density	37–56	44–50	47	115
Alethopteris missouriensis (SYNTYPES)					
Elongate	Length	22.3–29.0	25.0–28.2	26.3	15
	Width	4.2–7.0	5.0–6.0	5.4	17
	Length:Width	4.1–6.3	4.6–5.0	5.0	14
	Venation density	32–48	35–42	39	28
Alethopteris missouriensis (OTHER NORTH AMERICAN EXAMPLES)					
Variable	Venation density	32–46	36–41	38	24
ALL *Alethopteris missouriensis* COMBINED					
Variable	Venation density	32–48	36–41	39	52
Alethopteris serlii (SYNTYPES)					
Biconvex	Venation density	29–38	32–35	33	19
Alethopteris serlii (NORTH AMERICAN EXAMPLES)					
Variable	Venation density	26–41	29–35	32	82
ALL *Alethopteris serlii* COMBINED					
Variable	Venation density	26–41	30–35	32	101

reach 30 mm long and 8 mm wide (L:W ratio ~ 3.0), are parallel-sided but narrower near the base, and symmetrical due to reduction of the acroscopic incision and basiscopic wing. Less typical are widely spaced, subtriangular pinnules (Fig. 10.7) ~ 8–10 mm long and 3–4 mm wide (L:W ratio ~ 2.5) with a more acute top. Midveins are non-decurrent, depressed in a distinct furrow, moderately strong, straight to slightly down-curved, and extend to just below the pinnule apex. Lateral veins are thin and dense (typically 44–50 veins per cm, mean 47; Table 4; Figs. 13.1, 14), and originate obliquely but immediately curve and travel straight to reach the lateral margin at ~ 90°. Most veins branch close to the midvein and some bifurcate again on approach to the margin; unbranched veins are rare. Subsidiary veins extend from the rachis into the pinnule base on the basiscopic and acroscopic sides.

Remarks.—Specimens belong to a group of Middle Pennsylvanian alethopterids that Wagner (1968) segregated into five distinct species based on subtle differences in pinnule shape, size, and venation density: *Alethopteris serlii*, *Alethopteris missouriensis* (White, 1899a) Wagner, 1968, *Alethopteris lonchitifolia* Bertrand, 1932, *Alethopteris densinervosa*, and *Alethopteris westphalensis* Wagner, 1968. With the exception of *A. serlii*, excluded from the complex based on its somewhat flexuous venation, Cleal (1978) observed that examples of the other four taxa are present in large assemblages and represent morphological variants of one species (the earliest legitimate synonym being *A. missouriensis*). Scheihing and Pfefferkorn (1980) corroborated the opinion that these taxa (but including *A. serlii*) formed a morphological continuum, which they termed the

"*Alethopteris serli* group." Again excluding *A. serlii*, Zodrow and Cleal (1998) synonymized the other four taxa under *Alethopteris lonchitica* Schlotheim ex Sternberg, 1825. Wagner and Álvarez-Vázquez (2008) rejected identification with *A. lonchitica* (and we agree with their opinion), and maintained that *A. missouriensis*,

A. lonchitifolia, *A. densinervosa*, and *A. westphalensis* are different species with partly overlapping characters. Resolving how many biological species are in this complex will require a detailed morphometric and cuticular analysis of the types and associated specimens, and although some morphometric data are presented here, a full study is outside the scope of this contribution.

Given the morphological similarities among taxa in the aforementioned alethopterid complex, Wagner (1968) considered venation density as a key distinguishing criterion. The venation density in various pinnule forms (biconvex, subtriangular, elongate, and terminal) in the assemblage is provided in Figure 14 and Table 4. The range of all pinnule types is 37–56 veins per cm on the lateral margin, with most pinnules having 44–50 (mean 47) veins per cm. Based on the descriptions of Wagner (1968), only two species in the complex—*Alethopteris missouriensis* and *Alethopteris densinervosa*—have a similarly dense venation, both ranging from 40–50 veins per cm. Of the two, the material compares most closely with *A. densinervosa*. The full range of pinnule morphologies can be accommodated in the species, which was best illustrated by Buisine (1961, pls. 1–7; pl. 8, figs. 1, 1a; pl. 10, figs. 1, 1a, 3, 4) under *Alethopteris Serli*. Despite the likeness, however, referral of the study specimens to *A. densinervosa* initially presented a conundrum. In North America, Middle Pennsylvanian alethopterids with this morphology are almost invariably included in *A. serlii* (rarely in *A. missouriensis*), and given that *A. densinervosa* has to date never been confirmed outside of the Northern France Coalfield, identity with the latter would make this the first record from North America.
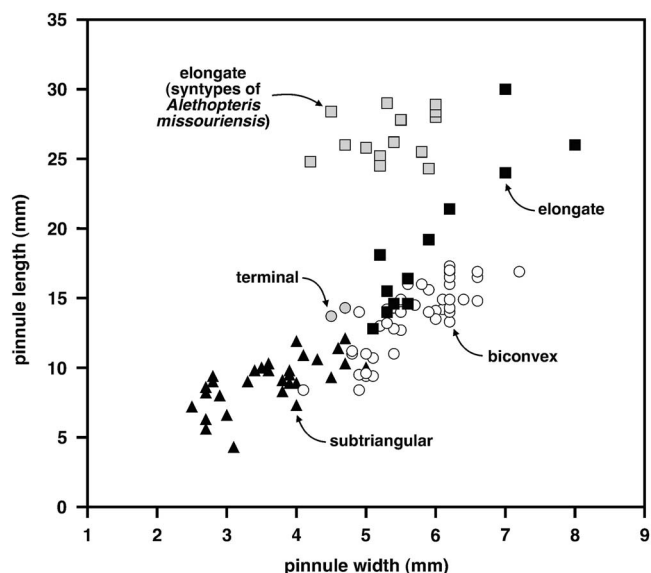

Figure 12. Bivariate (length, width) plot of several pinnule types of *Alethopteris densinervosa* Wagner, 1968 in the macrofloral assemblage ('study specimens' in Table 4), and comparison with elongate pinnules of syntypes of *Alethopteris missouriensis* (White, 1899a) Wagner, 1968 from White (1899a, pl. 37, fig. 2, USNM E3594b; pl. 42, fig. 5, USNM E3591b).
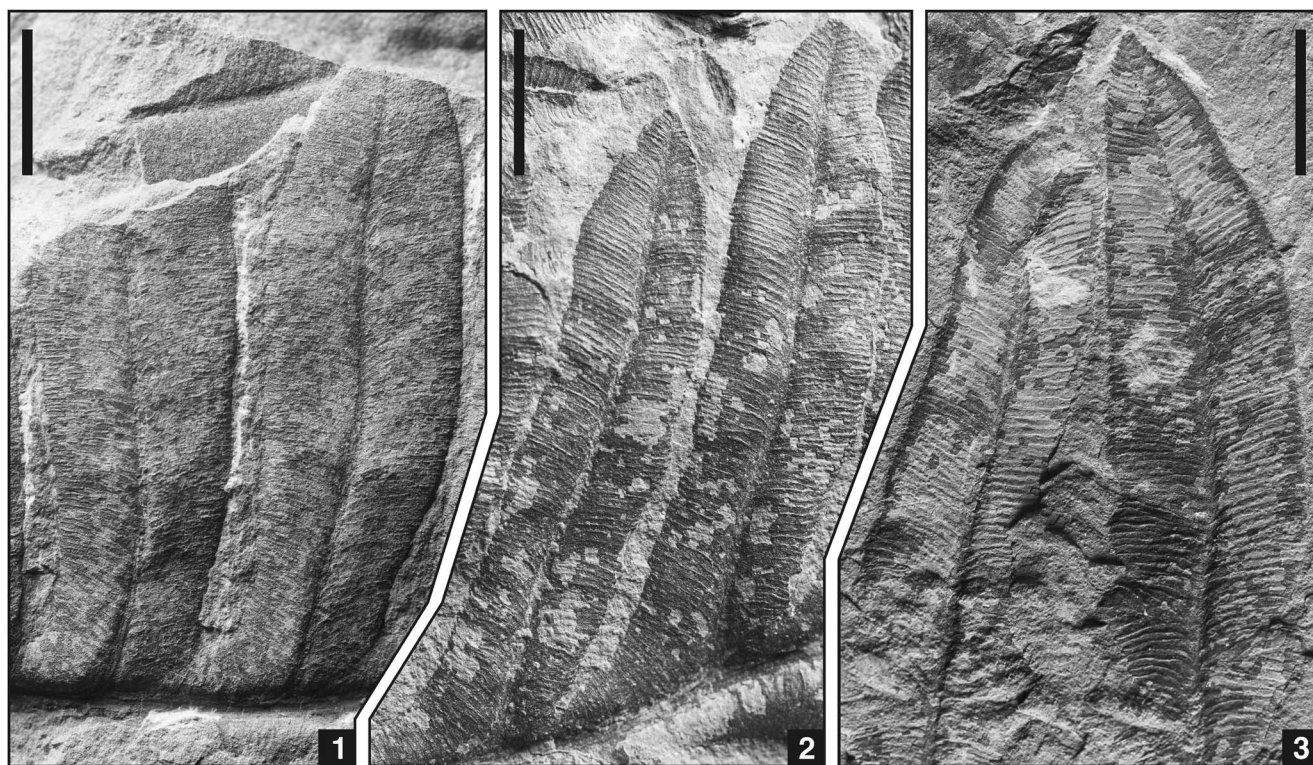

Figure 13. Comparison of elongate pinnule types of *Alethopteris* Sternberg, 1825, showing differences in venation density measured directly from illustrated pinnules; scale bars = 5 mm. (**1**) *Alethopteris densinervosa* Wagner, 1968, Unit 3, USNM 594391 (43–50 veins per cm). (**2**) Syntype of *Alethopteris missouriensis* (White, 1899a) Wagner, 1968, illustrated by White (1899a, pl. 37, fig. 2), USNM E3594b (40–44 veins per cm). (**3**) Specimen of *Alethopteris serlii* (Brongniart, 1833-34) Göppert, 1836, illustrated by Lesquereux (1879, pl. 29, fig. 4), USNM 12100 (32–36 veins per cm).
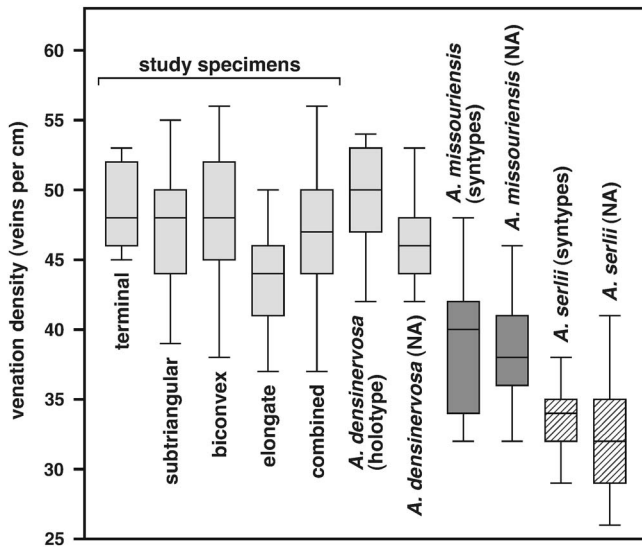
Figure 14. Box and whisker plots showing range, 25th and 75th percentiles, and median of venation densities of several pinnule types from specimens identified herein as *Alethopteris densinervosa* Wagner, 1968. Comparison with venation density data from type specimens and other previously illustrated examples of *A. densinervosa*, *Alethopteris missouriensis* (White, 1899a) Wagner, 1968, and *Alethopteris serlii* (Brongniart, 1833-34) Göppert, 1836 confirm identification of study specimens as *A. densinervosa*. See Table 4 for data sources.

To facilitate identification, venation density data were gathered from illustrations of North American material referred to *Alethopteris serlii* or *Alethopteris missouriensis* (see Table 4 for list of sources), augmented by measurement of actual specimens where possible (e.g., a syntype of *A. missouriensis* [White, 1899a], reillustrated here [Fig. 13.2] and three specimens of *A. serlii* recorded by Lesquereux [1879-80], one reillustrated here [Fig. 13.3]). Venation densities also were measured from photographs of the syntypes of *A. serlii* (Wagner, 1968), a syntype of *A. missouriensis* (White, 1899a), and the holotype of *A. densinervosa* (Buisine, 1961).

These venation density data (Fig. 14; Table 4) reveal that at least three distinct fossil-species (*Alethopteris serlii*, *Alethopteris missouriensis*, and *Alethopteris densinervosa*), united in similarity of pinnule morphology but differentiated by venation density, are present in Middle Pennsylvanian strata of North America. The lateral veins of *A. densinervosa* are extremely dense (most 44–50, mean 47 veins per cm; Fig. 13.1), comparable to the diagnosis of 40–50 veins per cm (Wagner, 1968), whereas those of *A. serlii* are more widely spaced (most 30–35, mean 32 veins per cm; Fig. 13.3), faithful to the emended diagnosis of 30–35 veins per cm (Wagner, 1968). The foliar elements of these species are otherwise nearly indistinguishable. The venation density of *A. missouriensis* is intermediate (most 36–41, mean 39 veins per cm; Fig. 13.2), equivalent to the 35–40 veins per cm claimed by Wittry (2006), but somewhat lower than the 28–42 veins per cm given in the diagnosis (White, 1899a), although Wagner (1968, p. 108) noted that the lower part of this range only applies to what White (1899a, p. 117, pl. 37, figs. 1, 1a) considered the non-varietal form of *A. serlii*. *Alethopteris missouriensis* is characterized by more elongate pinnules (Figs. 12, 13.2), and Figure 14 and Table 4 demonstrate that specimens in the assemblage have L:W

ratios that largely range from ~2.5 (subtriangular and biconvex forms) to ~3.0 (elongate forms), whereas elongate pinnules of the syntypes of *A. missouriensis* are narrower (L:W ratio ~ 5.0). To verify the separation of *A. serlii*, *A. missouriensis*, and *A. densinervosa* based on venation density, 'post-hoc' pairwise comparisons after a Kruskal-Wallis test ($H = 253.1$, p[same] <0.0001) confirm that there are statistically significant differences among the three species groupings (p[same] $\leq$ 0.003), and that there are no statistically significant differences between the type material of each species and other measured specimens identified as such. These results support the assertion that the three taxa are separate species (Wagner, 1968; Wagner and Álvarez-Vázquez, 2008).

This exercise also demonstrates that *Alethopteris densinervosa* is not only present in the study population in the Illinois Basin, but has previously been documented in the Western Interior and Appalachian basins under *Alethopteris serlii* (see synonymy list) by Basson (1968), Oleksyshyn (1982), and Moore et al. (2014), the latter noting comparison with *A. densinervosa*. Venation density data provided by Zodrow and Cleal (1998, table 1, fig. 7) for specimens included in their concepts of *Alethopteris lonchitica* and *A. serlii* suggest that some examples in the Sydney Coalfield probably also belong to *A. densinervosa*, as Zodrow (1986) initially proposed. In contrast, venation densities recorded for the "*Alethopteris serli* group" (morphogroups 1 to 3) of Scheihing and Pfefferkorn (1980, table 3, means of 42–43 veins per cm) imply that *A. densinervosa* was represented, but such high-density values could not be duplicated based on measurements of their illustrated specimens; thus, the material documented by Scheihing and Pfefferkorn (1980) probably belongs to *A. serlii*.

Family Neurodontopteridaceae Cleal and Shute, 2003
Genus *Macroneuropteris* Cleal, Shute, and Zodrow, 1990
Macroneuropteris scheuchzeri (Hoffmann, 1826a) Cleal, Shute, and Zodrow, 1990
Figures 8.7, 8.8, 8.11, 9.10

1826a	*Neuropteris Scheuchzeri* Hoffmann, p. 157, pl. 1b, figs. 1–4.
1847	*Neuropteris cordata* Brongniart; Bunbury, p. 423, pl. 21, figs. 1a, c–f.
1847	*Neuropteris cordata* Brongniart var. *angustifolia* Bunbury, p. 424, pl. 21, fig. 1b.
1847	*Odontopteris subcuneata* Bunbury, p. 427, pl. 23, figs. 1a, 1b.
1854	*Neuropteris hirsuta* Lesquereux, p. 417.
1866	*Odontopteris Wortheni* Lesquereux, p. 432, pl. 36, figs. 1, 1b.
1866	*Odontopteris heterophylla* Lesquereux, p. 433, pl. 38, figs. 2–5.
1868	*Neuropteris hirsuta*; Lesquereux, p. 857, pl. 3, fig. 6, pl. 4, figs. 1–16.
1870	*Neuropteris fasciculata* Lesquereux, p. 381, pl. 5, figs. 1–4.
1870	*Odontopteris subcuneata*; Lesquereux, p. 390, pl. 8, fig. 10, 10b.
1879-80	*Neuropteris hirsuta*; Lesquereux, p. 88, pl. 8, figs. 1, 4, 5, 7, 9.

1879-80 *Neuropteris angustifolia* Brongniart; Lesquereux, p. 89, pl. 8, figs. 2, 3, 6, 8, 10, 11.

1879-80 *Neuropteris fasciculata*; Lesquereux, p. 93, pl. 24, figs. 5, 6.

(?)1879-80 *Odontopteris cornuta* Lesquereux, p. 128, pl. 22, figs. 7–9.

1879-80 *Odontopteris heterophylla*; Lesquereux, p. 129, pl. 22, fig. 6.

1879-80 *Odontopteris worthenii*; Lesquereux, p. 130, pl. 22, fig. 1.

(?)1879-80 *Odontopteris subcuneata*; Lesquereux, p. 134, pl. 22, figs. 4, 5.

1880 *Neuropteris decipiens* Lesquereux, p. 93.

1884 *Neuropteris decipiens*; Lesquereux, p. 733, pl. 94, figs. 1, 2.

1899a *Odontopteris? bradleyi* Lesquereux; White, p. 125, pl. 42, fig. 2, 2a.

1899a *Neuropteris scheuchzeri*; White, p. 132, pl. 37, fig. 4, pl. 42, figs. 3, 3a, pl. 64, fig. d.

1908 *Neuropteris gilmani* Sellards, p. 403, pl. 58, fig. 4.

1925 *Neuropteris decipiens*; Noé, pl. 24, figs. 2–4, pls. 25, 26, pl. 27, figs. 1, 2.

1925 *Odontopteris subcuneata*; Noé, pl. 37, fig. 1.

1925 *Odontopteris worthenii*; Noé, pl. 37, fig. 4.

1938 *Neuropteris scheuchzeri*; Bell, p. 57, pl. 51, figs. 1–4, pl. 52, figs. 1, 2(?).

1938 *Neuropteris scheuchzeri* Hoffmann forma *angustifolia* Bell, p. 57, pl. 50, figs. 3, 4, pl. 51, fig. 5.

1938 *Odontopteris subcuneata*; Bell, p. 62, pl. 57, figs. 1–8, pl. 58, figs. 1–3.

1940 *Neuropteris scheuchzeri*; Janssen, p. 45, pl. 13, figs. 2, 3.

1940 *Odontopteris subcuneata*; Janssen, p. 50, pl. 12, figs. 1(?), 2, 4, 5.

1949 *Neuropteris scheuchzeri*; Arnold, p. 189, pl. 20.

1958 *Neuropteris scheuchzeri*; Langford, p. 189, text-figs. 327, 328.

1958 *Odontopteris subcuneata*; Langford, p. 238, text-figs. 428–432.

1959 *Neuropteris scheuchzeri*; Canright, pl. 4, figs. 8, 9.

1962 *Neuropteris scheuchzeri* forma *angustifolia*; Bell, p. 44, pl. 37, figs. 1, 2, 5.

1963 *Neuropteris scheuchzeri*; Langford, p. 222, text-fig. 845.

1963 *Neuropteris scheuchzeri*; Wood, p. 60, pl. 10, fig. 1.

1968 *Neuropteris scheuchzeri*; Basson, 100, pl. 24, fig. 1.

1969 *Neuropteris decipiens*; Darrah, p. 94, pl. 1, figs. 1–4, pl. 2, fig. 3, pl. 5, figs. 1, 2, pl. 6, fig. 2, pl. 8, figs. 1–3, pl. 46, fig. 3, pl. 76, fig. 1.

1974 *Neuropteris scheuchzeri*; Boneham, p. 109, pl. 5, fig. 5.

1977 *Neuropteris scheuchzeri* Hoffman [sic] forma *scheuchzeri* Gastaldo, p. 138, text-fig. 50.

1977 *Neuropteris scheuchzeri* Hoffman [sic] forma *decipiens* Gastaldo, p. 138, text-fig. 51.

1978 *Neuropteris scheuchzeri*; Gillespie et al., p. 104, pl. 42, figs. 1–3, 5–9, pl. 46, fig. 8.

1979 *Neuropteris scheuchzeri*; Janssen, p. 149, text-figs. 8, 137.

1979 *Odontopteris worthenii*; Janssen, p. 161, text-fig. 154.

1979 *Neuropteris scheuchzeri*; Pfeiffer, pl. 6, figs. 65, 66.

1980 *Neuropteris scheuchzeri*; Zodrow and McCandlish, p. 47, pl. 37, figs. 2, 3, pls. 38–42, pl. 43, fig. 1.

1980 *Odontopteris subcuneata*; Zodrow and McCandlish, p. 53, pl. 53, figs. 1, 2, pl. 54.

1982 *Neuropteris decipiens*; Oleksyshyn, p. 105, text-fig. 24a.

1982 *Neuropteris scheuchzeri*; Oleksyshyn, p. 119, text-figs. 24b–f, 25a, b.

1990 *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute, and Zodrow, p. 488.

1999 *Macroneuropteris scheuchzeri*; Tidwell et al., p. 301, text-fig. 2d.

2002 *Macroneuropteris scheuchzeri*; Blake et al., pl. 24, figs. 1–6.

2003 *Macroneuropteris scheuchzeri*; Zodrow, figs. 2, 3, 6–13.

2005 *Macroneuropteris scheuchzeri*; Bashforth, p. 61, pl. 13, figs. 6, 7.

2005 *Macroneuropteris scheuchzeri*; DiMichele and Chaney, text-fig. 3.3.

2005 *Macroneuropteris scheuchzeri*; DiMichele et al., text-fig. 4.

2006 *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute, and Zodrow forma *decipens* [sic] Wittry, p. 57, figs. 2–4.

2006 *Odontopteris subcuneata*; Wittry, p. 64, fig. 1.

2006 *Odontopteris worthenii*; Wittry, p. 65, figs. 1–3.

2011 *Macroneuropteris scheuchzeri*; Blake and Gillespie, p. 110, pl. 6, figs. 1–6.

2012 *Macroneuropteris scheuchzeri*; Stull et al., text-figs. 2, 3, 5.

2013 *Macroneuropteris scheuchzeri*; Stull et al., text-figs. 2.3, 2.4.

2013b *Macroneuropteris scheuchzeri*; DiMichele et al., p. 298, text-figs. 10.1, 10.2.

2014 *Macroneuropteris scheuchzeri*; Moore et al., p. 38, pl. 6, pl. 7, figs. 1, 2.

Holotype.—Geologisch-Paläontologische Sammlungen, Martin-Luther-Universität Halle-Wittenberg, Halle, from Osnabrück(?) Formation (basal Asturian), Piesberg Coalfield (Osnabrück Highlands), Germany.

Occurrence.—USA (assuming synonymy with *Neuropteris decipiens*): lower Atokan to middle Wolfcampian, common above Atokan (Darrah, 1969; Gillespie and Pfefferkorn, 1979; Oleksyshyn, 1982; Wagner, 1984; Blake et al., 2002; Stull et al., 2012). Europe: Langsettian to uppermost Cantabrian, common from upper Duckmantian to middle Cantabrian

(Wagner, 1984; Cleal and Shute, 1995; Laveine and Belhis, 2007). Atlantic Canada: Bolsovian to lower Cantabrian (Bell, 1938, 1962; Zodrow, 2003).

Material examined.—Seventy-six specimens from Units 2 and 3.

Description.—Pinnules exhibit a wide range of size and morphology. Typical pinnules are conspicuously large, with complete specimens 27–74 mm long and 9–23 mm wide (Table 5), linear-lanceolate to subtriangular (and frequently subfalcate; Fig. 8.7, 8.8) with an acutely rounded or acuminate tip, and pedicellate with a cordate to oblique (asymmetric) base (Fig. 9.10). Pinnules are rarely trifoliate (Fig. 8.8), with the pinnule base first differentiating into two symmetric lobes that, as development proceeds, become small orbicular to subtriangular pinnules that are 12–19 mm long and 7–8 mm wide (Table 5); such orbicular pinnules frequently are isolated from the main pinnule. Rare subulate pinnules are >95 mm long and ~17 mm wide and taper to an acuminate tip, whereas laciniate pinnules with deeply divided lateral margins only are represented by small fragments. Midveins are set in a furrow, are initially robust but narrow distally, and extend close to the pinnule apex. Lateral veins are thin, arise at an acute angle, branch twice close to the midvein, and then abruptly curve before extending nearly straight to reach the lateral margin at ~65–80°, branching once or twice more along their course; veins may curve upwards at the margin. Lateral veins are dense, with the venation density typically 29–37 veins per cm (range: 24–46, mean: 33; Table 5). Venation density broadly correlates with pinnule size, although lateral veins are more widely spaced and reach the lateral margin more obliquely in apical parts of large pinnules. Pinnule surfaces may display sparsely and randomly distributed hair-like structures (Fig. 8.11) that are ~1 mm long, bristle-like, straight to slightly curved, and generally oriented apically such that they cross-cut lateral veins, imparting a conspicuous yet falsely reticulate venation pattern.

Remarks.—*Macroneuropteris* is typified by large pinnules (generally over 2 cm long) with a narrow basal attachment to the rachis, a non-decurrent midvein that extends for much of the pinnule length, and unique epidermal characteristics (Cleal and Zodrow, 1989; Cleal et al., 1990; Cleal and Shute, 1995, 2012). The frond architecture of *Macroneuropteris* is less divided than in most neuropteroids (e.g., *Neuropteris* [Brongniart, 1822] Sternberg, 1825 or *Laveineopteris* Cleal, Shute, and Zodrow, 1990), resulting in comparatively large pinnules that are homologous to ultimate pinnae of other genera (Laveine, 1967; Cleal et al., 1996, 1998; Laveine and Belhis, 2007).

Macroneuropteris scheuchzeri is characterized by conspicuously large pinnules that often are isolated, trifoliate, and exhibit prominent hair-like features on the lower surface, and by laciniate pinnules of myriad morphologies (Laveine, 1967; Zodrow, 2003; Laveine and Belhis, 2007). The stiff and bristle-like structures on the abaxial surface of most pinnules support assignment to *M. scheuchzeri*. Zodrow et al. (2014) reinterpreted the hair-like structures as self-organizing epicuticular chemical deposits, but Laveine and Oudoire (2015) determined that they represent subepidermal resin-filled canals. The frequent occurrence of isolated pinnules points to a caducous plant, an

Table 5. Morphometric data (length, width, L:W ratio, and venation density) from specimens identified as *Neuropteris flexuosa* Sternberg, 1825, *Neuropteris ovata* Hoffmann, 1826a, *Neuropteris missouriensis* Lesquereux, 1879-80, *Neuropteris semireticulata* Josten, 1962, and *Macroneuropteris scheuchzeri* (Hoffmann, 1826a) Cleal, Shute, and Zodrow, 1990. To facilitate comparison between *N. flexuosa* in the assemblage and elsewhere (see Fig. 16), venation density data also are presented from the holotype and other previously illustrated specimens. Data sources: holotype—Stockmans (1933, pl. 4, fig. 3); American examples—Noé (1925, pl. 20, fig. 1, pl. 23, fig. 3) and Jongmans (1937c, pl. 40, figs. 18, 19, pl. 41, fig. 25); Canadian examples—Bell (1938, pl. 46, figs. 6, 7, pl. 47, figs. 1, 2, 4, pl. 48, fig. 1) and Cleal and Zodrow (1989, text-figs. 13a, 13c); UK examples—Crookall (1959, pl. 37, figs. 1, 3, pl. 38, figs. 1–3, pl. 50, fig. 4).

Pinnule type	Parameter	Range	Percentiles	Mean	N
Neuropteris flexuosa (STUDY SPECIMENS)					
Lateral	Length	7.0–35.0	10.0–15.0	12.7	163
	Width	4.0–14.0	5.4–7.4	6.6	163
	Length:Width	1.4–2.5	1.7–2.1	1.9	163
	Venation density	21–40	26–31	28	73
Terminal	Length	19.3–46.0	22.0–24.0	25.5	13
	Width	10.4–18.5	11.3–15.7	13.4	18
Neuropteris flexuosa (HOLOTYPE)					
Lateral	Venation density	20–32	24–28	26	12
Neuropteris flexuosa (AMERICAN EXAMPLES)					
Lateral	Venation density	21–37	24–31	27	27
Neuropteris flexuosa (CANADIAN EXAMPLES)					
Lateral	Venation density	18–43	23–32	28	36
Neuropteris flexuosa (UK EXAMPLES)					
Lateral	Venation density	24–50	28–36	33	44
Neuropteris ovata (STUDY SPECIMENS)					
Lateral	Length	5.0–14.2	7.5–12.6	9.8	50
	Width	3.0–7.0	4.8–6.2	5.4	50
	Length:Width	1.2–2.3	1.6–2.0	1.8	50
	Venation density	29–44	35–40	37	31
Terminal	Length	13.0–23.0	na	19.0	3
	Width	5.0–6.2	na	5.6	3
	Length:Width	2.6–3.8	na	3.4	3
Neuropteris missouriensis (STUDY SPECIMENS)					
Lateral	Length	7.7–23.7	8.6–13.9	11.6	29
	Width	3.8–10.0	5.2–6.9	6.0	29
	Length:Width	1.4–2.6	1.6–2.1	1.9	29
	Venation density	20–32	23–26	25	34
Terminal	Length	16.0–20.0	16.2–20.0	18.4	5
	Width	9.2–13.6	9.4–12.7	11.5	5
	Length:Width	1.5–1.7	1.5–1.7	1.6	5
Neuropteris semireticulata (STUDY SPECIMENS)					
Lateral	Length	12.7–17.0	14.0–15.9	14.9	6
	Width	5.3–8.1	6.5–7.0	6.7	7
	Length:Width	1.7–3.2	1.9–2.3	2.2	6
	Venation density	28–36	30–33	32.0	9
Terminal	Length	>13.0	na	na	1
	Width	14.9	na	na	1
Macroneuropteris scheuchzeri (STUDY SPECIMENS)					
Elongate	Length	~27–95	na	na	22
	Width	9.0–23.0	13.5–17.9	15.6	22
	Length:Width	~2.2–5.6	na	na	22
	Venation density	24–46	29–37	33.0	20
Orbicular/subtriangular	Length	11.5–19.0	11.8–15.5	14.2	3
	Width	6.8–8.0	7.3–7.6	7.4	4
	Length:Width	1.5–2.4	1.6–2.1	1.9	3
	Venation density	28–34	28–30	30.0	4

established trait of the species. Although trifoliate pinnules are rare in the assemblage, the scattered presence of small orbicular pinnules, originally situated at the base of trifoliate forms, attests to pinnule disaggregation. Laciniate pinnules are equally rare and fragmentary; well-preserved examples from elsewhere are divided into spatulate or cuneate lobes with an 'odontopteroid' attachment to the rachis. Such forms were borne near the main frond bifurcation (Laveine, 1967; Laveine and Belhis, 2007), and have been assigned a variety of names, including *Odontopteris lindleyana* Sternberg, 1833 in the UK (Crookall, 1959),

Odontopteris subcuneata in Atlantic Canada (Bell, 1938; Zodrow, 2003), and *O. subcuneata*, *Odontopteris heterophylla*, *Odontopteris worthenii*, and *Odontopteris cornuta* in the USA (Lesquereux, 1866, 1879-80; White, 1899a). All of the aforementioned features help differentiate *M. scheuchzeri* from *Macroneuropteris macrophylla* (Brongniart, 1831) Cleal, Shute, and Zodrow, 1990, the pinnules of which are smaller, lack obvious hair-like structures, have an asymmetric cordate base with a prominent basiscopic auricle but no lobate pinnules, and which usually are affixed to the rachis (Bell, 1938; Crookall, 1959; Cleal et al., 1996, 1998). The American species *Neuropteris clarksonii* Lesquereux, 1854 is a junior synonym of *M. macrophylla* (Kidston, 1888; Bell, 1938; Crookall, 1959; Cleal et al., 1996; Wittry, 2006).

Previous authors seem unanimous in the opinion that the American species *Neuropteris hirsuta* is identical to *Macroneuropteris scheuchzeri* (White, 1899a; Crookall, 1959; Laveine, 1967; Darrah, 1969; Gastaldo, 1977). In contrast, there has been longstanding debate about the relationship between *M. scheuchzeri* and *Neuropteris decipiens* (cf., Laveine and Belhis, 2007), the latter found almost exclusively in the Mazon Creek Flora (Carbondale Formation) of Illinois, where the former is rare (Wittry, 2006). Some authors considered *N. decipiens* to be a junior synonym or variety/form of *M. scheuchzeri* (Crookall, 1959; Laveine, 1967; Gastaldo, 1977; Schabilion and Reihman, 1985; Wittry, 2006; Stull et al., 2012), whereas others maintained the taxa as different species (Lesquereux, 1880, 1884; White, 1899a; Darrah, 1969; Oleksyshyn, 1982), in part because of the highly restricted distribution of *N. decipiens*. As summarized by Gastaldo (1977), pinnules of both taxa share many morphological features (large size, abaxial hair-like structures, trifoliate and laciniate forms, an extended midvein, and similarly arching lateral veins), although *N. decipiens* generally has larger, more linguaeform pinnules with an obtusely rounded apex and somewhat sparser lateral veins. All study specimens have acutely rounded to acuminate tips, and fall within the limits of *M. scheuchzeri* sensu stricto. However, illustrated examples that conform to *N. decipiens* have been included in the synonymy list because the issue of identity will not be resolved without a detailed morphometric and cuticular analysis. Given the extremely long stratigraphic range and wide paleobiogeographic distribution of *M. scheuchzeri* sensu lato, as well as morphological changes through time (White, 1899a; Bell, 1938; Darrah, 1969; Gillespie et al., 1978), it is probable that more than one species is involved (Laveine and Belhis, 2007).

Genus *Neuropteris* (Brongniart, 1822) Sternberg, 1825 emend. Cleal, Shute, and Zodrow, 1990
Neuropteris flexuosa Sternberg, 1825
Figure 9.1, 9.5, 9.6, 9.11

1823 *Osmunda gigantea* var. β Sternberg, p. 36, pl. 32, fig. 2.
1825 *Neuropteris flexuosa* Sternberg, p. XVI.
1925 *Neuropteris flexuosa*; Noé, pl. 20, fig. 1, pl. 23, fig. 3.
1933 *Neuropteris tenuifolia* Schlotheim; Stockmans, p. 14, pl. 4, fig. 3 [holotype].
1937c *Neuropteris ovata* sensu ampl.; Jongmans, p. 418, pl. 40, figs. 17–19, 21, pl. 41, figs. 24, 25.

1938 *Neuropteris* (*Mixoneura*) *flexuosa*; Bell, p. 55, pl. 46, figs. 6, 7, pl. 47, figs. 1–3.
1938 *Neuropteris flexuosa* forma *magna* Bell, p. 55, pl. 47, fig. 4, pl. 48, figs. 1, 2.
1959 *Neuropteris ovata* Hoffmann forma *flexuosa* Sternberg; Crookall, p. 158, text-fig. 52 [holotype].
(?)1958 *Neuropteris gigantea* Sternberg; Langford, p. 201, text-figs. 357, 359.
(?)1959 *Mixoneura* Weiss sp.; Canright, pl. 4, fig. 12.
1962 *Neuropteris* (*Mixoneura*) *flexuosa*; Bell, p. 42, pl. 34, fig. 2, pl. 37, fig. 3(?)
(?)1963 *Neuropteris flexuosa*; Wood, p. 57, pl. 9, fig. 5.
1963 *Neuropteris heterophylla*? (Brongniart) Sternberg; Wood, p. 57, pl. 9, figs. 6, 7(?)
(?)1969 *Neuropteris ovata* forma *typica*; Darrah, p. 105, pl. 10, fig. 2.
(?)1969 *Neuropteris ovata* forma *flexuosa*; Darrah, p. 106, pl. 73, fig. 1.
(?)1977 *Neuropteris ovata* forma *flexuosa*; Gastaldo, text-fig. 48.
(?)1978 *Neuropteris ovata*; Gillespie et al., p. 104, pl. 43, figs. 1, 2.
(?)1979 *Neuropteris flexuosa*; Janssen, p. 150, text-fig. 139.
1979 *Neuropteris plicata* Sternberg; Janssen, p. 150, text-fig. 140.
1980 *Neuropteris* (*Mixoneura*) *flexuosa*; Zodrow and McCandlish, p. 40, pl. 22, fig. 2(?), pls. 23, 24.
(?)1980 *Neuropteris flexuosa* forma *magna*; Zodrow and McCandlish, p. 42, pl. 25.
1989 *Neuropteris flexuosa*; Cleal and Zodrow, p. 856, text-fig. 13.
1997 *Neuropteris flexuosa*; Wagner and Lyons, pl. 1, figs. 1, 2.
(?)1997 *Neuropteris* cf. *ovata*; Wagner and Lyons, pl. 4, fig. 1, pl. 5, fig. 3.
(?)2005 *Neuropteris ovata*; DiMichele et al., text-fig. 6b.

Holotype.—V.9405, Natural History Museum, London, from Radstock Formation (upper Asturian), Bristol-Somerset Coalfield, UK.

Occurrence.—USA: upper Atokan to upper Virgilian, rare below lower Desmoinesian, common in upper Desmoinesian to middle Virgilian (Wood, 1963; Read and Mamay, 1964; Darrah, 1969). UK: basal Asturian to lower Cantabrian (Cleal and Thomas, 1994; Cleal and Shute, 1995; Cleal, 2007). Atlantic Canada: upper Bolsovian to lower Cantabrian, very rare below Asturian (Bell, 1938, 1962; Zodrow and Cleal, 1985; Zodrow, 1986).

Material examined.—Ninety-four specimens from Units 2 and 3.

Description.—Ultimate pinnae are linear and taper to an obtusely rounded apex. Terminal pinnules (Fig. 9.1, 9.6, 9.11) are large, typically 22–24 mm (but up to 46 mm) long and 11–16 mm wide (L:W ratio ~ 1.9; Table 5; Fig. 15), rhomboid to deltoid and asymmetric with a basal lobe on one or both sides,
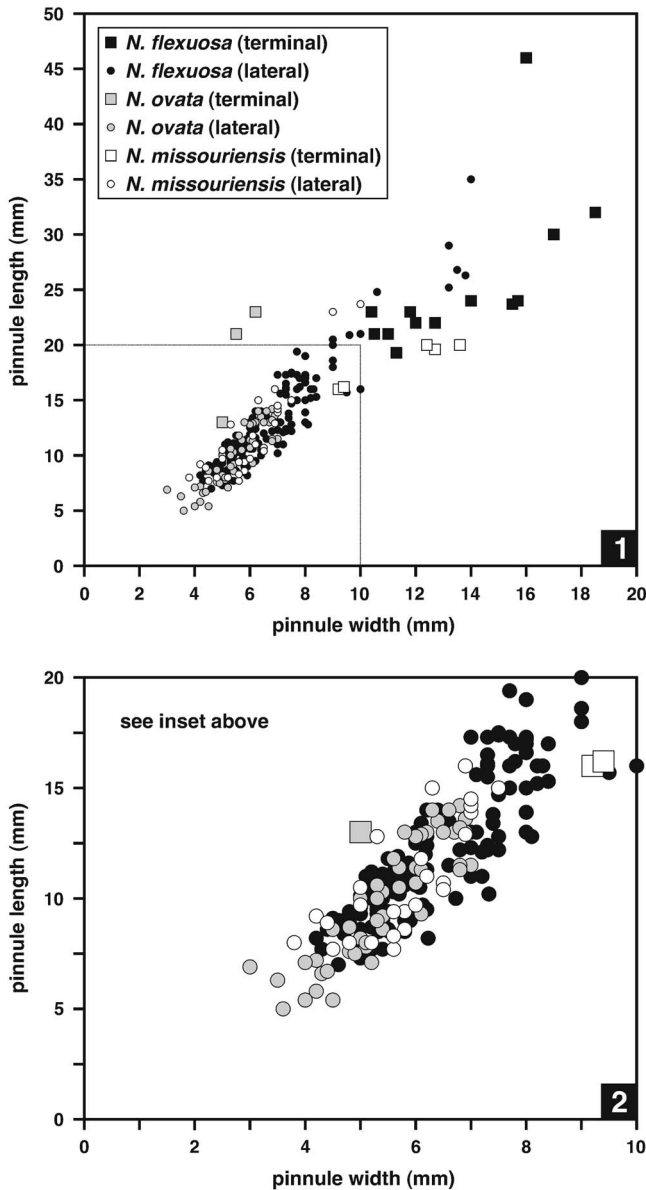
Figure 15. Bivariate (length, width) plot of terminal and lateral pinnules of *Neuropteris flexuosa* Sternberg, 1825, *Neuropteris ovata* Hoffmann, 1826a, 1826b, and *Neuropteris missouriensis* Lesquereux, 1879-80, in the macrofloral assemblage (study specimens in Table 5). (**1**) Complete dataset. (**2**) Inset magnifying lower left corner of plot.

and have an obtusely to acutely rounded apex. Lateral pinnules are variable in size, with most 10–15 mm long and 5–7 mm wide (L:W ratio ~ 1.9), and large forms reaching 35 mm long and 14 mm wide (Table 5; Fig. 15). Pinnules are inserted slightly obliquely, generally crowded and often overlapping, mainly linguaeform to rectangular with an obtusely rounded apex (becoming more elongate to slightly falcate in the largest forms), and are characterized by a pronounced basiscopic auricle (Fig. 9.11) and a rounded acroscopic base (Fig. 9.5) that may overlap the pinna rachis. Lateral pinnules are almost exclusively pedicellate (only the most distal pinnules have a broadly attached, 'mixoneurid' base), although the point of attachment is relatively wide because the midvein may be accompanied above and below by subsidiary veins derived from the rachis. Midveins are slightly decurrent, more so apically, depressed in a
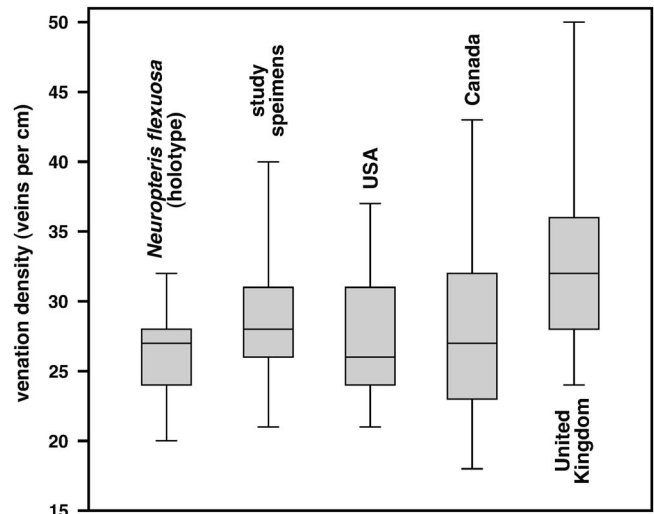

Figure 16. Box and whisker plots showing range, 25th and 75th percentiles, and median of venation densities of lateral pinnules of *Neuropteris flexuosa* Sternberg, 1825, showing comparison between study specimens, holotype, and examples from USA, Canada, and UK. See Table 5 for data sources.

shallow furrow, somewhat flexuous, thin, and extend to the pinnule midpoint before dissipating. Lateral veins are thin, arise at an acute angle, branch close to the midvein and two to three more times on approach to the margin, which they reach at ~60–80°. Veins extend straight between successive forks, imparting a subtly flexuous appearance, and are sparse, with the venation density typically 26–31 veins per cm (range: 21–40, mean: 28; Table 5; Fig. 16). In the largest pinnules, midveins extend farther, and lateral veins reach the margin at ~90° and may be more dense due to an additional dichotomy.

Remarks.—Specimens are assigned to *Neuropteris flexuosa*, one of a group of neuropterids closely allied to *Neuropteris ovata* that are typified by epidermal characters, lateral pinnules that can be partially fused to the rachis in distal parts of pinnae ('mixoneurid' habit), and thin decurrent midveins that extend no more than two-thirds the pinnule length (Wagner, 1963; Cleal and Zodrow, 1989; Cleal et al., 1990; Cleal and Shute, 1995, 2012). Distinguishing features of *N. flexuosa* include the combination of a large, asymmetric, deltoid terminal pinnule, and relatively large lateral pinnules with a rounded acroscopic base, auriculate basiscopic side, and a relatively coarse and slightly flexuous venation; broadly attached pinnules only occur at the extreme top of ultimate pinnae. The degree of uncertainty expressed in the synonymy list reflects the challenge of separating species in this neuropterid complex, particularly when relying on photographs.

We initially were reluctant to assign specimens to *Neuropteris flexuosa* because the average venation density has previously been reported as ~ 30–45 veins per cm (e.g., Bell, 1938; Crookall, 1959; Wagner, 1963; Darrah, 1969; Cleal and Zodrow, 1989). Although the study specimens range from 21–40 veins per cm, most have a sparser venation (26–31 veins per cm, mean 28; Table 5). To investigate this disparity, veins were counted on illustrated specimens of *N. flexuosa* from elsewhere in the USA, Canada, and the UK, including the British holotype (see Table 5 for list of sources). Comparison

indicates that venation densities of the holotype and examples from the USA and Canada are similar to those measured in the study specimens (and perhaps more importantly, lower than reported), whereas British specimens tend to have a denser venation (Fig. 16). 'Post-hoc' pairwise comparisons after a Kruskal-Wallis test ($H = 32.26$, p[same] <0.0001) confirm that the venation density in the British specimens (excluding the holotype) is significantly different from *N. flexuosa* in the assemblage and from the broader suite of North American specimens (p[same] ≤0.0004). One explanation for the inconsistency between reported and actual venation density in some publications may be a tendency to overemphasize larger pinnules, which have a denser venation. It also is possible that differences reflect an actual species distinction, as suspected for the *Macroneuropteris scheuchzeri-Neuropteris decipiens* complex.

Due to their morphological similarities, some authors considered *Neuropteris flexuosa* to be synonymous with, or a form of, *Neuropteris ovata* (Jongmans, 1937c; Crookall, 1959; Darrah, 1969). However, in addition to epidermal differences (Cleal and Zodrow, 1989), comparisons based on specimens in the assemblage (Table 5; Figs. 9, 15) reveal consistent differences that permit segregation of these two species. In particular, *N. flexuosa* can be distinguished from *N. ovata* by having overall larger lateral pinnules, a large deltoid terminal pinnule, lower venation density, and by the fact that broadly attached lateral pinnules only occur (if at all) at the extreme top of an ultimate pinna.

A closely related American fossil-species is *Neuropteris vermicularis* Lesquereux, 1861, which Crookall (1959) and Jongmans (1937c) considered identical to (or a form of) *Neuropteris ovata*. However, Lesquereux (1861, 1879-80), Darrah (1969), and Wittry (2006) maintained that *N. vermicularis* was a distinct taxon characterized by larger and more symmetrical terminal pinnules (sometimes with a lobate margin), a coarser venation, and lateral pinnules with a more constricted or cordate base. Examination of *N. vermicularis* specimens in the Lacoe Collection (NMNH), most of which were determined by Lesquereux or White, adds to the ambiguity. Large pinnules with a dense venation are virtually indistinguishable from equally large forms of *Neuropteris flexuosa*, although with a less prominent basiscopic auricle (Lesquereux, 1861). In contrast, smaller and/or more distal pinnules of *N. vermicularis* have a coarser venation and are markedly elongate-linguaeform (L:W ratio ~2–3, compared with ~1.5–2.0 in equivalent pinnules of *N. flexuosa*). As such, *N. vermicularis* may be a unique species, and has been excluded from the synonymy list. Representative examples believed to conform to Lesquereux' concept of *N. vermicularis* were illustrated (under a variety of names, including *N. flexuosa*) by Noé (1925, pl. 20, fig. 3, pl. 24, fig. 1), Jongmans (1937c, pl. 41, figs. 22, 23), Janssen (1940, pl. 25, fig. 2; 1979, text-fig. 142), Darrah (1969, pl. 2, figs. 1, 2), Boneham (1974, pl. 5, fig. 4), and Wittry (2006, p. 59, 60, figs. 1, 2, 4, 5).

According to White (1899a), *Neuropteris missouriensis* also resembles *N. flexuosa*, but differs in having very large, oblong-ovate to oblong-deltoid terminal pinnules in the smallest pinnae, and oblong to ovate lateral pinnules typified by an equally rounded (i.e., cordate or non-auriculate) base and a more distinct midvein.

Neuropteris missouriensis Lesquereux, 1879-80
Figures 11.2–11.4, 12

1879-80   *Neuropteris Missouriensis* Lesquereux, p. 104, pl. 7, figs. 5, 6, 6a.

(?)1893   *Neuropteris flexuosa* Sternberg; White, p. 91, pl. 5, figs. 1, 2.

1899a   *Neuropteris missouriensis*; White, p. 130, pl. 41, figs. 4, 5, pl. 42, figs. 4, 4a, pl. 45, fig. 3.

(?)1963   *Neuropteris flexuosa*; Wood, p. 57, pl. 9, fig. 5.

(?)1967   *Neuropteris dussarti* Laveine, p. 191, pl. 48.

1968   *Neuropteris missouriensis*; Basson, p. 97, pl. 22.

(?)1991   *Neuropteris dussarti*; Josten, p. 322, pls. 186, 187.

(?)2005   *Laveineopteris dussartii* (Laveine) Laveine, p. 464.

Type material.—One syntype (USNM 30861; Lesquereux, 1879-80, pl. 7, fig. 6, 6a) in Plant Type and Illustrated Collection, National Museum of Natural History, Smithsonian Institution, Washington, from Drywood(?) Formation (lower Desmoinesian), Western Interior Basin, Clinton, Missouri.

Occurrence.—USA: upper Atokan to lower Desmoinesian (White, 1899a; Sellards, 1908; Darrah, 1969). *Laveineopteris dussartii* (possible synonym), in UK: upper Bolsovian to upper Asturian (Cleal, 1978; Cleal and Shute, 1995); in northern France and northwestern Germany: middle(?) Asturian (Laveine, 1967, 1987; Josten and Laveine, 1984; Josten, 1991).

Material examined.—Fourteen specimens from Unit 4.

Description.—Ultimate pinnae are linear and parallel-sided for most of their length, but can be slightly narrower at the base and taper to an obtusely rounded apex. Pinna axes are conspicuously robust. Terminal pinnules are large, 16–20 mm long and 9–14 mm wide (L:W ratio ~ 1.6; Table 5; Fig. 15), oblong-ovate to oblong-deltoid and asymmetric with a basal lobe on one or both sides, and have a very obtusely rounded apex; terminal pinnules are larger, more oblong, and more obtusely rounded in small pinnae (compare Fig. 11.2–11.4 with 11.11, 11.12). Lateral pinnules are 8–24 mm long and 4–10 mm wide (L:W ratio ~1.9; Table 5; Fig. 15). Pinnules are inserted slightly obliquely, closely spaced to slightly overlapping, ovate in the most distal positions (Fig. 11.4), but generally oblong and linguaeform with an obtusely rounded apex, and typically are bilaterally symmetrical, but somewhat subfalcate in the largest examples. Pinnule shape in distal parts of pinnae depends on the degree of development: ovate pinnules occur on short pinnae, and linguaeform pinnules occur on long pinnae. Pinnules are always sessile (resting on the rachis without an elongate petiolule), attached by a broad midvein (even in the smallest forms), have nearly equally rounded acroscopic and basiscopic bases (cordate), and are characterized by a narrow but thick compression margin (Fig. 11.11, 11.12). Midveins are slightly decurrent, very prominent and set within a deep furrow, extend about two-thirds of the pinnule length, and generally are straight, but can appear flexuous due to the wide angle of departure of lateral veins. Lateral veins are thin but depressed in the thick lamina, branch close to the midvein and one to three

more times before reaching the lateral margin at ~65–80°, and are sparse, with venation density typically 23–26 veins per cm (range: 20–32, mean: 25; Table 5). Near the midvein, lateral veins may extend straight between successive forks, conferring a somewhat flexuous appearance to the venation.

Remarks.—Specimens compare closely with the syntypes of *Neuropteris missouriensis* illustrated by Lesquereux (1879-80), although the fossil-species is otherwise rare and poorly documented. Distinguishing features include the robust pinnae axes and pinnule midveins, large obtusely rounded and oblong terminal pinnules, and sparse venation on lateral pinnules that invariably are sessile with a cordate base. Sellards (1908) emphasized the prominent compression margin on the pinnules, implying that margins were inrolled. The fact that lateral pinnules at the distal end of a pinna are attached only by the pinnule petiolule rather than being partly fused to the rachis, and that midveins are prominent and extend beyond the pinnule midpoint, suggests that *N. missouriensis* belongs in the fossil-genus *Laveineopteris* rather than *Neuropteris* (Cleal et al., 1990). White (1899a) illustrated a wide range of morphological variety in *N. missouriensis*, and demonstrated that the terminal pinnule in longer (more proximal) pinnae is smaller, less oblong, and less obtusely rounded than originally envisioned by Lesquereux (1879-80). However, the assertion by White (1899a) that terminal pinnules only have a single lobe is incorrect; some specimens have two lobes, although one is better developed.

White (1893, 1899a) stated that *Neuropteris missouriensis* most resembles *Neuropteris flexuosa*, and Darrah (1969) also implied that the species might belong to the '*Neuropteris ovata* complex'. However, *N. flexuosa* has larger terminal pinnules that are rhomboid to deltoid, lateral pinnules that are broadly attached (i.e., 'mixoneurid') in extreme distal positions and have a prominent basiscopic auricle, thin midveins that extend only to the midpoint of a pinnule, and a greater venation density (Table 5). Crookall (1959, pl. 53, figs. 1–3) reported *N. missouriensis* in the UK, but these examples may involve multiple species, including *Laveineopteris loshii* (Brongniart, 1831) Cleal, Shute, and Zodrow, 1990 and *Laveineopteris hollandica* (Stockmans, 1933) Cleal and Shute, 1995.

In many respects, particularly in the distinct shape of terminal pinnules, venation density, and cordate pinnule bases, *N. missouriensis* compares closely with *Laveineopteris dussartii* (cf., Laveine, 1967; Josten and Laveine, 1984; Josten, 1991), which only is known from the Bolsovian to Asturian of Western Europe. Nonetheless, *L. dussartii* differs in having less-robust pinnae axes and midveins. If synonymous, *N. missouriensis* has nomenclatural priority.

Neuropteris ovata Hoffmann, 1826a, b
Figure 9.2–9.4, 9.8

1826b	*Neuropteris ovata* Hoffmann, p. 266.
1826a	*Neuropteris ovata* Hoffmann, p. 158, pl. 1b, figs. 5–7 [lectotype: fig. 6].
(?)1879-80	*Neuropteris plicata* Sternberg; Lesquereux, p. 96, pl. 10, figs. 1–4.
(?)1879-80	*Neuropteris loschii* [sic] Brongniart; Lesquereux, p. 98, pl. 11.

1908	*Neuropteris ovata*; Sellards, p. 408, pl. 53, fig. 2, pl. 56, fig. 6(?).
(?)1925	*Neuropteris ovata*; Noé, pl. 21, fig. 4.
(?)1925	*Neuropteris capitata* Lesquereux; Noé, pl. 22, fig. 2.
1937c	*Neuropteris ovata* sensu ampl.; Jongmans, p. 417, pls. 37–39, 42.
1938	*Neuropteris* (*Mixoneura*) *ovata*; Bell, p. 60, pl. 52, fig. 4, pl. 53, fig. 3, pl. 54, figs. 1–3.
(?)1958	*Neuropteris plicata*; Langford, p. 207, text-fig. 361.
(?)1958	*Neuropteris capitata*; Langford, p. 207, text-fig. 362.
1958	*Neuropteris* (*Mixoneura*) *ovata*; Langford, p. 218, text-figs. 382, 383.
(?)1958	*Neuropteris* (*Mixoneura*) *jenneyi* White; Langford, p. 218, text-fig. 384.
1963	*Neuropteris obliqua*? (Brongniart) Zeiller; Wood, p. 59, pl. 9, fig. 10.
1963	*Odontopteris subcuneata* Bunbury; Wood, p. 61, pl. 10, fig. 5.
1968	*Neuropteris ovata* Hoffmann forma *flexuosa* Crookall; Basson, p. 98, pl. 23, figs. 1, 2(?).
1969	*Neuropteris ovata* Hoffmann forma *typica* Crookall; Darrah, p. 105, pl. 9., fig. 2, pl. 10, fig. 1, 2(?).
1969	*Imparipteris ovata* (Hoffmann) Gothan; Saltzwedel, pl. 24, figs. 1–3 [lectotype].
1977	*Neuropteris ovata* forma *typica*; Gastaldo, text-fig. 47.
(?)1978	*Neuropteris ovata*; Gillespie et al., p. 104, pl. 43, figs. 1, 2.
1979	*Mixoneura ovata* (Hoffmann) Zalessky; Janssen, p. 157, text-fig. 150.
(?)1979	*Neuropteris heterophylla* (Brongniart) Sternberg; Pfeiffer, pl. 6, fig. 63.
(?)1979	*Neuropteris ovata*; Pfeiffer, pl. 6, fig. 64.
(?)1979	*Neuropteris obliqua* (Brongniart) Zeiller; Pfeiffer, pl. 7, fig. 70.
1980	*Neuropteris* (*Mixoneura*) *ovata*; Zodrow and McCandlish, p. 44, pl. 28, fig. 3, pls. 29–32, pl. 33, fig. 1.
1988	*Neuropteris ovata*; Zodrow and Cleal, pls. 2, 3, pl. 4, fig. 4.
1982	*Neuropteris ovata* forma *typica*; Oleksyshyn, p. 111, text-figs. 21g, h, 22a–e.
1982	*Neuropteris ovata* forma *flexuosa*; Oleksyshyn, p. 114, text-fig. 23a, b.
1992	*Neuropteris ovata*; Mamay and Mapes, text-fig. 4a, c, e.
1997	*Neuropteris ovata*; Wagner and Lyons, pl. 8, fig. 5.
1997	*Neuropteris* cf. *ovata*; Wagner and Lyons, pl. 3, figs. 1, 2.
2002	*Neuropteris ovata*; Blake et al., pl. 21, fig. 7.
(?)2005	*Neuropteris ovata*; DiMichele et al., text-fig. 6b.
(?)2006	*Neuropteris flexuosa* Sternberg; Wittry, p. 49, figs. 1, 2.
2006	*Neuropteris ovata*; Wittry, p. 55, fig. 1.

2013b   *Neuropteris ovata*; DiMichele et al., p. 298, text-figs. 12, 12, 13(?).

Lectotype.—Geologisch-Paläontologische Sammlungen, Martin-Luther-Universität Halle-Wittenberg, Halle, from Dickenburg Coal, Osnabrück Formation (basal Asturian), Ibbenbüren Coalfield (Osnabrück Highlands), Germany.

Occurrence.—USA: upper Atokan to upper Virgilian, common in lower Desmoinesian to Missourian (Jongmans, 1937c; Wood, 1963; Read and Mamay, 1964; Darrah, 1969; Gillespie and Pfefferkorn, 1979; Oleksyshyn, 1982; Blake et al., 2002). Europe: rare in upper Bolsovian (Cleal, 1978), common from basal Asturian to Cantabrian (Cleal, 1978, 1997; Laveine, 1977, 1987, 1989; Josten, 1991; Cleal and Shute, 1995), some varieties extend up to Stephanian C (Wagner, 1963, 1984). Atlantic Canada: middle Asturian to lower Cantabrian (Bell, 1938; Zodrow and Cleal, 1985; Zodrow, 1986).

Material examined.—Twenty-six specimens from Units 2 to 4.

Description.—Ultimate pinnae are linear but rapidly taper to an acutely rounded apex. Terminal pinnules (Fig. 9.2, 9.3) are small, 13–23 mm long and 5–6 mm wide (L:W ratio ~3.4; Table 5; Fig. 15), elongate-rhomboid to lanceolate and asymmetric with a basal lobe on one or both sides, and have an acutely rounded or acuminate summit. Lateral pinnules are 5–14 mm long and 3–7 mm wide (L:W ratio ~1.8; Table 5; Fig. 15). Pinnules are inserted slightly obliquely (markedly so in distal positions, where pinnules are strongly decurrent), generally closely spaced, linguaeform to ovate with an obtusely rounded apex, and are characterized by a strongly incised, rounded acroscopic base and a pronounced, acutely rounded basiscopic auricle (Fig. 9.4, 9.8). Lateral pinnules are narrowly attached by a petiolule in proximal parts of pinnae, but in distal parts much of the base is affixed to the rachis ('mixoneurid' habit), particularly on the basiscopic side (Fig. 9.2–4), from whence subsidiary veins enter the pinnule. Midveins may comprise multiple thin strands, and are decurrent (more so apically) and depressed in a shallow crease; the central strand extends straight to near the pinnule midpoint before dissipating. Lateral veins are thin, arise at an acute angle, branch close to the midvein and generally two to three more times, broadly arch to reach the lateral margin at ~40–70°, and are dense, with the venation density typically 35–40 veins per cm (range: 29–44, mean: 37; Table 5).

Remarks.—Although *Neuropteris ovata* is a common Middle to Late Pennsylvanian medullosalean pteridosperm, its widespread distribution and polymorphic habit have resulted in a complex and unresolved taxonomic history (Crookall, 1959; Wagner, 1963; Laveine, 1967). Laveine (1989, pls. 47, 48) illustrated the array of morphological variation that can occur in the species concept from a single basin. Given the wide range of pinnule forms, previous workers have split the species into several taxa, based on differences in regional distribution (Bertrand, 1930), stratigraphic distribution (Wagner, 1963), or a combination of these factors together with differences in epidermal anatomy (Cleal and Zodrow, 1989). Although some of the resulting 'varieties' may represent distinct species (Cleal and Shute, 1995),

no attempt has been made to assign specimens in the assemblage to a variety because cuticles were not procured. The material at hand compares well with the lectotype of *N. ovata*, in addition to other specimens from the type area (Saltzwedel, 1969).

According to Darrah (1969, p. 105), in the USA the majority of specimens that Lesquereux (1879-80) assigned to *Neuropteris loschii* [sic] Brongniart belong to *Neuropteris ovata*. As discussed in the *Neuropteris flexuosa* section above, Jongmans' (1937c) study of *N. ovata* from American strata included three species (*N. ovata*, *N. flexuosa*, and *Neuropteris vermicularis*). Specimens in the assemblage belong to what Crookall (1959) and Darrah (1969) termed *N. ovata* forma *typica*. Based on illustrations in the literature and comparison between *N. ovata* and *N. flexuosa* in the study population (Table 5; Figs. 9, 15), the former has overall smaller lateral pinnules, a small elongate terminal pinnule with an acutely rounded tip, more-dense and non-flexuous venation, and broadly attached lateral pinnules that normally occur in distal and medial parts of an ultimate pinna. Small forms of *N. vermicularis* may be confused with *N. ovata* (e.g., Noé, 1925, pl. 20, fig. 3), but the former has larger and more symmetrical terminal pinnules with an obtusely rounded apex, a coarser venation, and more elongate lateral pinnules that may have only a slight basiscopic auricle. A single cyclopteroid pinnule with a fimbriate margin, referable to *Cyclopteris fimbriata* Lesquereux, 1854, in the assemblage presumably was part of the *N. ovata* frond, but other North American examples are not included in the synonymy list.

Neuropteris semireticulata Josten, 1962
Figure 11.6, 11.9

(?)1938   *Neuropteris heterophylla* (Brongniart) Sternberg; Bell, p. 56, pl. 50, fig. 2.
(?)1938   *Linopteris muensteri* (Eichwald) Potonié; Bell, p. 65, pl. 59, figs. 2, 3.
1962   *Neuropteris semireticulata* Josten, p. 39, pl. 3, figs. 2–5 [holotype: figs. 3, 3a].
(?)1962   *Neuropteris heterophylla*; Bell, p. 43, pl. 33, fig. 2, pl. 34, fig. 1.
2002   *Neuropteris semireticulata*; Blake et al., pl. 19, fig. 1, pl. 22, fig. 1.
2005   *Neuropteris semireticulata*; Bashforth, p. 62, pl. 16, pl. 17, figs. 1–11.

Holotype.—No. 927, Type Collection, Geologischen Landesamtes, Krefeld, from Dorsten Formation (Bolsovian), Ruhr Coalfield, near Bottrop, North Rhine-Westphalia, Germany.

Occurrence.—USA: upper Atokan to lower Desmoinesian (Blake et al., 2002). UK: middle Duckmantian to lower Asturian (Cleal, 1978, 2007; Cleal and Thomas, 1994). France: Bolsovian (Laveine, 1967, 1987). Germany: upper Duckmantian to upper Bolsovian (Josten, 1962, 1991). Atlantic Canada: upper Bolsovian to lower Asturian (Bell, 1938, 1962; Bashforth, 2005).

Material examined.—Two specimens from Unit 4.

Description.—Terminal pinnules are ~15 mm wide and of indeterminate length, and have a lobe on one side. Lateral

pinnules are 13–17 mm long and 5–8 mm wide (L:W ratio ~ 2.2). Pinnules are inserted obliquely, crowded to overlapping, subovate to linguaeform (more elongate proximally) with a broadly rounded top, and are characterized by a rounded acroscopic base that overlaps the pinna rachis. Lateral pinnules generally are cordate, but in distal positions the base becomes partly fused with the rachis and the midvein is accompanied above and below by subsidiary veins. Midveins are decurrent (more so apically), robust, flexuous, and extend beyond the pinnule midpoint before dissipating. Lateral veins are strong, arise at an open angle, branch close to the midvein and generally one to two more times on approach to the margin, which they reach at 70–80°. Lateral veins are markedly flexuous to pseudoreticulate (Fig. 11.9), closely approach or run alongside (but do not join) adjacent veins, and are relatively sparse, the venation density typically being 30–33 veins per cm (range: 28–36, mean: 32; Table 5). Midveins extend farther and lateral veins are denser in the longest pinnules.

Remarks.—*Neuropteris semireticulata* can be distinguished from other neuropterids by its flexuous to pseudoreticulate venation, and although easily recognized, the taxon has rarely been recorded in Euramerica. Whereas this may reflect genuine scarcity, it is more probable that the species has been incorrectly identified as *Neuropteris heterophylla* (Brongniart, 1822) Sternberg, 1825 or *Reticulopteris muensteri* (Eichwald, 1840) Gothan, 1941 at many localities. In West Virginia, for example, some specimens that Gillespie et al. (1978) referred to the latter species probably represent *N. semireticulata*, as Blake et al. (2002) also illustrated examples from the state. Similar misidentifications are probable in Atlantic Canada (see synonymy list), although *N. semireticulata* was documented in upper Bolsovian strata of Newfoundland (Bashforth, 2005). The American species *Dictyopteris rubella* Lesquereux, 1870 is a junior synonym of *R. muensteri* according to Janssen (1940).

Order Lyginopteridales Corsin, 1960
Family Lyginopteridaceae Potonié, 1900
Genus *Eusphenopteris* Gothan, 1913 ex Simson-Scharold, 1934
Eusphenopteris neuropteroides (Boulay, 1876) Novik, 1947
Figure 10.4, 10.5, 10.8

1854   *Sphenopteris squamosa* Lesquereux, p. 420.
(?)1868   *Sphenopteris lesquereuxii* Newberry; Lesquereux, p. 862, pl. 10, fig. 1.
1868   *Sphenopteris squamosa* Lesquereux, p. 862, pl. 10, fig. 3.
1876   *Pecopteris neuropteroides* Boulay, p. 32, pl. 2, figs. 6, 6bis [lectotype: fig. 6].
1879-80   *Pseudopecopteris anceps* Lesquereux, p. 207, pl. 38, figs. 1, 1a, 2(?)
1883   *Sphenopteris nevropteroides* (Boulay) Zeiller, p. 186.
1899b   *Pseudopecopteris squamosa* (Lesquereux) White, p. 474.
1938   *Sphenopteris neuropteroides*; Bell, p. 23, pl. 5, fig. 4(?), pl. 6, pl. 7, pl. 8, fig. 1.
(?)1943   *Diplothmema aldrichi* White var. *anthracitica* White, p. C98, pl. 33, figs. 6, 9, pl. 34, fig. 2.

1947   *Eusphenopteris neuropteroides* (Boulay) Novik, p. 277.
(?)1952   *Eusphenopteris neuropteroides*; Novik, p. 312, pl. 52, figs. 9, 10.
1975   *Eusphenopteris neuropteroides*; Van Amerom, p. 54, pl. 28, figs. 1, 2 [lectotype: fig. 1].
(?)1978   *Eusphenopteris neuropteroides*; Gillespie et al., p. 110, pl. 52, figs. 2, 3.
(?)1978   *Eusphenopteris* Gothan ex Simson-Scharold sp.; Gillespie et al., pl. 52, fig. 5.
1980   *Sphenopteris neuropteroides*; Zodrow and McCandlish, p. 54, pl. 56, figs. 2–4, pls. 57, 58.
1982   *Eusphenopteris neuropteroides*; Oleksyshyn, p. 58, text-fig. 13b(?), c(?), d, e, f(?).
(?)2002   *Eusphenopteris neuropteroides*; Blake et al., pl. 21, figs. 2, 4.
(?)2014   cf. *Eusphenopteris neuropteroides*; Moore et al., p. 44, pl. 7, fig. 16.

Lectotype.—Université Catholique de Lille, Lille, probably from the Faisceau de Six-Sillons or d'Ernestine (Bolsovian), Northern France Coalfield, France.

Occurrence.—USA: lower Atokan to lower Virgilian(?), common in Desmoinesian (Darrah, 1969; Oleksyshyn, 1982; Blake et al., 2002). UK: middle Langsettian to lower Cantabrian (Cleal and Thomas, 1994). Europe: extends into Stephanian C (Wagner, 1984). Atlantic Canada: Asturian (Bell, 1938).

Material examined.—Twenty-six specimens from Units 2 and 3.

Description.—Penultimate pinnae are linear, taper to an obtusely rounded apex topped by a small, lobate terminal pinnule, reach at least 50 mm long and 35 mm wide, and comprise alternate ultimate pinnae (becoming pinnatifid and then entire pinnules apically) that arise from a thick, straight, and longitudinally striated rachis with faint transverse ridges. Ultimate pinnae are perpendicular to slightly oblique, generally linear with a blunt apex, but can be subtriangular with a slightly more acutely rounded tip, typically 10–30 mm long and 5–15 mm wide, and have a pronounced, winged rachis that gives rise to 2 to 8 pairs of lateral pinnules. The shape and size of lateral pinnules are highly variable. In more proximal positions of a pinna (Fig. 10.4, 10.5), trilobate to bilobate pinnules (4–8 mm long, 4–7 mm wide) stand approximately perpendicular to the rachis, are attached by a wide footstalk, and pass apically into more or less entire pinnules (4–6 mm long, 3–5 mm wide) that are quadrate to ovate and affixed by most of their base. The most distal pinnules (2–6 mm long, 2–5 mm wide) are strongly decurrent, confluent, round, and fuse upwards with a small, lobate terminal pinnule (Fig. 10.4, 10.5, 10.8). Midveins are decurrent (less so in quadrate to lobate pinnules), thick, and divide into several branches shortly after entering the pinnule; in round, distal pinnules, one branch ascends nearly parallel to the pinna rachis before dichotomizing.

Remarks.—Despite having polymorphous foliage, *Eusphenopteris neuropteroides* is readily distinguished by having large quadrate pinnules that superficially resemble the habit and

venation of neuropteroid foliage. Van Amerom (1975) documented the full range of variation. In the USA, *E. neuropteroides* has been published under various names. Lesquereux (1854, 1868) introduced the earlier synonym *Sphenopteris squamosa*. Subsequently, Lesquereux (1879-80) erected *Pseudopecopteris anceps*, although he explicitly included *S. squamosa* as a synonym. However, the only syntype of *P. anceps* in the NMNH collections (Lesquereux, 1879-80, pl. 38, figs. 3, 4; USNM 13401) is not representative and may belong to *Eusphenopteris nummularia* (Gutbier, 1835) Novik, 1947 or *Eusphenopteris obtusiloba* (Brongniart, 1830-31) Novik, 1947. Zeiller (1883, 1886-88) recognized the identity between these two American taxa and the European form he referred to *Sphenopteris nevropteroides*, and White (1899b) synonymized all three taxa under *Pseudopecopteris squamosa*. However, Bell (1938) suggested that the epithet *neuropteroides* be retained because the original drawing and descriptions of *S. squamosa* were insufficient. Darrah (1969) supported this assertion and noted that the holotype of *S. squamosa* is missing. According to van Amerom (1975), *Diplothmema aldrichi* var. *anthracitica* of White (1943) could be accommodated in *E. neuropteroides*.

Although specimens illustrated by Gillespie et al. (1978) and Blake et al. (2002) exhibit the general characters of *Eusphenopteris neuropteroides*, they are included in the synonymy list with reservation because they have overall larger dimensions than is typical. These examples perhaps should be referred to the superficially similar fossil species "*Mariopteris*" *anthrapolis*.

Eusphenopteris sp. indet.
Figure 11.5

Material examined.—One specimen from Unit 4.

Description.—Penultimate pinnae reach 26 mm long, and comprise alternate to subopposite ultimate pinnae (becoming pinnatifid and then entire pinnules apically). The rachis is stiff and straight, bears faint longitudinal striations with no transverse ridges, and has a pronounced central groove flanked by elevated lateral margins. Ultimate pinnae reach 11 mm long and 7 mm wide, and have a winged rachis that gives rise to at least 3 pairs of vaulted, orbicular to obovate pinnules. In distal parts of the penultimate pinna, trilobate to bilobate(?) pinnules (at least 8 mm long and 5–8 mm wide) stand slightly obliquely, are attached by a wide and decurrent footstalk, and consist of one or two small orbicular basal lobes (larger on the basiscopic side) and a large apical lobe. Near the pinna apex, entire pinnules (~7 mm long and 5 mm wide) are ovate and affixed by most of their base. Midveins occupy a shallow groove, and lateral veins are difficult to discern, but appear to be relatively sparse.

Remarks.—Although the single penultimate pinna fragment clearly belongs to the fossil-genus *Eusphenopteris*, the specimen does not display enough morphological attributes to permit specific identification. The best comparison may be with *Eusphenopteris nummularia*, which is characterized by strongly vaulted foliage and essentially indiscernible venation (Van Amerom, 1975).

Incertae sedis
"*Mariopteris*" *anthrapolis* Langford, 1958
Figure 8.5, 8.9, 8.12, 8.13

1958   *Mariopteris anthrapolis* Langford, p. 268, text-figs. 488, 489(?), 490(?), 493.
(?)1969   *Mariopteris thompsonii* Darrah, p. 123, pl. 25, fig. 1.
(?)1978   *Eusphenopteris neuropteroides* (Boulay) Novik; Gillespie et al., p. 110, pl. 52, figs. 2, 3.
(?)1978   *Eusphenopteris* Gothan ex Simson-Scharold sp.; Gillespie et al., pl. 52, fig. 5.
(?)1982   *Mariopteris* cf. *inflata* White; Oleksyshyn, p. 63, text-fig. 13i.
(?)2002   *Eusphenopteris neuropteroides*; Blake et al., pl. 21, figs. 2, 4.
2006   *Mariopteris anthrapolis*; Wittry, p. 80, figs. 1, 2 [syntype: fig. 1].

Syntypes.—FMNH P31072 and P31113, Paleobotany Collections, The Field Museum, Chicago and Nos. 15722 and 15204, Illinois State Museum, Springfield, from Francis Creek Shale, Carbondale Formation (middle Desmoinesian), Illinois Basin, Wilmington Township, Will County, Illinois.

Occurrence.—Illinois: middle Desmoinesian (Langford, 1958; Wittry, 2006). If synonymy list accurate, in West Virginia: lower Atokan (Gillespie et al., 1978; Blake et al., 2002); and Pennsylvania: upper Atokan (Oleksyshyn, 1982).

Material examined.—Six specimens from Unit 2.

Description.—The foliage appears coriaceous. Ultimate pinnae are linear with a broadly rounded apex, 47 mm long and 20 mm wide (based on incomplete specimens), and are centered by an inflated and winged rachis (Fig. 8.9), within which sits a thin (~1 mm wide) and depressed vascular strand with faint longitudinal striations. At least four pairs of subopposite to alternate, strongly vaulted lateral pinnules are present on an ultimate pinna. In proximal parts (Fig. 8.5, 8.9, 8.12), markedly quadrate pinnules (9–14 mm long, 11–14 mm wide) are affixed to the rachis near their basiscopic margin, have a strongly incised acroscopic margin that runs parallel to the rachis, and exhibit a shallow incision on the outermost margin, manifest as two rounded lobes on the lowest pinnules. Toward the pinna apex, pinnules (10–14 mm long, 6–9 mm wide) are increasingly decurrent, more broadly attached, closely spaced, and spatulate to obovate, eventually merging with a large, lobate terminal pinnule (Fig. 8.13) that is ~15 mm long and 17 mm wide. Midveins are decurrent (particularly in distal positions), very short, and divide into a number of branches shortly after entering the pinnule; the uppermost branch may ascend nearly parallel to the pinna rachis before reaching the lateral margin. Lateral veins are sparse, gently arch toward the margin, and are depressed within the conspicuously vaulted lamina, resulting in a subtly crenulate lateral margin (Fig. 8.13).

Remarks.—Specimens are fragmentary, precluding confident assignment. The pinnule habit is distinctly 'eusphenopteroid,' although of unusually large size for the fossil-genus. Comparison initially was made with *Eusphenopteris scribanii* Van Amerom, 1975, which has the largest foliar elements known in the genus (Van Amerom, 1975). However, as exhibited in the

holotype and paratype illustrated by Kidston (1923, pl. 3, fig. 2, pl. 4, fig. 4, under *Sphenopteris obtusiloba* Brongniart, 1830-31), pinnules of *E. scribanii* have a denser venation that can be partly obscured by a finely striated surface; these features are inconsistent with the material at hand. Specimens documented by Moore et al. (2014, p. 44, pls. 8, 9, under *Eusphenopteris* sp.), which also are atypically large for the genus, share some similarities with the study examples, including an inflated winged rachis with a sunken vascular strand, a thick lamina, and subtly undulatory pinnule margins that correspond to lateral vein endings. However, the taxon described by Moore et al. (2014) has an overall more lax or loosely spaced appearance and fan-shaped pinnules that may be deeply incised into two or three lobes, rather than quadrate pinnules with only two lobes resulting from shallow incision.

The best comparison is with "*Mariopteris*" *anthrapolis*, particularly with two syntypes that have large, vaulted, quadrate to obovate pinnules, probably from proximal parts of a frond (Langford, 1958, text-figs. 488, 493). Wittry (2006, p. 80, fig. 1) reillustrated one syntype, in addition to an example (fig. 2) with a pinnule habit, subtly crenulate margin, and venation scheme identical to the study specimens. Two other syntypes of "*M.*" *anthrapolis* (Langford, 1958, text-figs. 489, 490), presumably from more distal parts of a frond, have a more 'mariopteroid' appearance, including subtriangular pinnules that show less resemblance to the present examples. Darrah (1969, p. 123) also noted the morphological differences among Langford's syntypes, and posited that they may include more than one species. Unfortunately, the full gamut of variability is not available in our assemblage for comparison, and it is possible that "*M.*" *anthrapolis* is highly polymorphic. Darrah (1969) erected *Mariopteris thompsonii* for a species he considered closely related to "*M.*" *anthrapolis*, although he did so hesitantly because his specimens came from the same stratigraphic unit and location as the syntypes of the latter. The slightly denser venation and trilobate pinnules of *M. thompsonii* resemble those of *Eusphenopteris scribanii*. The specimen Oleksyshyn (1982) identified as *Mariopteris* cf. *inflata* White, 1943 appears more similar to "*M.*" *anthrapolis* than what White (1943) probably envisioned.

The genus and systematic position of "*Mariopteris*" *anthrapolis* are ambiguous, hence the quotation marks and placement under *Incertae sedis*. The species could be assigned to *Eusphenopteris*, and Langford (1958) and Darrah (1969) noted that it could easily be mistaken for a large form of *Eusphenopteris neuropteroides*. A case in point may be specimens illustrated by Gillespie et al. (1978) and Blake et al. (2002), which are markedly larger than is typical of *E. neuropteroides*. Two syntypes (Langford, 1958, text-figs. 489, 490) may indeed belong to *Mariopteris* Zeiller, 1879b, or to the related genus *Karinopteris* Boersma, 1972 as speculated by Wittry (2006). Hence, more than one genus may be included in the type material, but the specimens on hand probably belong to *Eusphenopteris*.

<div align="center">

Order Cordaitanthales Meyen, 1984
Family Cordaitanthaceae Meyen, 1984
Genus *Cordaites* Unger, 1850
Cordaites spp. indet.
Figure 8.6, 8.10

</div>

Occurrence.—Euramerica: fossil-genus common throughout Carboniferous and Permian.

Material examined.—Seventy-five specimens in Units 1 and 2.

Description.—Leaves are thick, coriaceous, linear-lanceolate, and reach 150 mm long (although some probably an order of magnitude longer in life) and 8–60 mm wide (full width not always preserved). Lateral margins are entire, subparallel, and taper towards the base and apex, presumably resulting in a strap-shaped leaf. The basal attachment structure (Fig. 8.6) is thicker than the lamina, has a conspicuous wrinkled or cracked texture, and has a convex distal edge (where it adjoins the lamina) and a concave proximal edge (where it attached to the branch). Leaf surfaces comprise parallel, longitudinal ridges and furrows, representing primary veins and intervening lamina. Primary veins rarely bifurcate at a very low angle, and venation densities range from 11–30 veins per cm in central positions, becoming very dense near lateral margins. The trace of intermediate sclerotic strands, exhibited as faint longitudinal lines between primary veins, may be present. Some examples from Unit 1 have spirorbiform worm-tubes (microconchids) affixed to the surface (Fig. 8.10).

Remarks.—Attempts to classify *Cordaites* based on the size, shape, and venation pattern of leaves is recognized as wholly artificial (cf., Šimůnek, 2006). Different leaf types can be found on a single branch (Césari and Hünicken, 2013), and venation schemes are not diagnostic because the spacing of primary veins and the presence or absence (and number) of sclerotic strands between the veins can differ depending on placement on a branch, maturity of the plant, which leaf surface is exposed, and even position on a single leaf (Harms and Leisman, 1961; Crookall, 1970; Barthel, 1976; Bashforth, 2005). Furthermore, although *Cordaites* shows a relatively conservative morphology, cuticular studies highlight the diversity in the group (Zodrow et al., 2000; Šimůnek, 2006). Because no cuticles were procured from the study specimens, all leaves are assigned to *Cordaites* spp. indet.

During analysis, it was difficult to differentiate between *Cordaites* and axes with densely spaced longitudinal striations, which probably represent naked pteridosperm petioles. The fact that no apices and only rare bases of *Cordaites* were observed further compounded the problem. We emphasize that only specimens that could confidently be assigned to *Cordaites* were described and measured.

Acknowledgments

References

Abbott, M.L., 1958, The American species of *Asterophyllites, Annularia*, and *Sphenophyllum*: Bulletins of American Paleontology, v. 38, p. 289–390.

Algeo, T.J., and Heckel, P.H., 2008, The Late Pennsylvanian Midcontinent Sea of North America: a review: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 268, p. 205–221.

Allen, K.C., 1961, *Lepidostrobophyllum fimbriatum* (Kidston 1883) from the Drybrook Sandstone (Lower Carboniferous): Geological Magazine, v. 98, p. 225–229.

Archer, A.W., Feldman, H.R., Kvale, E.P., and Lanier, W.P., 1994, Comparison of drier- to wetter-interval estuarine roof facies in the Eastern and Western Interior coal basins, USA: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 106, p. 171–185.

Archer, A.W., Elrick, S., Nelson, W.J., and DiMichele, W.A., 2016, Cataclysmic burial of Pennsylvanian Period coal swamps in the Illinois Basin: Hypertidal sedimentation during Gondwanan glacial melt-water pulses, *in* Tessier, B., and Reynaud, J.-Y., eds., Contributions to Modern and Ancient Tidal Sedimentology: Proceedings of the Tidalites 2012 Conference: International Association of Sedimentologists Special Publication 47, p. 217–231.

Arnold, C.A., 1934, A preliminary study of the fossil flora of the Michigan Coal Basin: Contributions from the Museum of Paleontology, University of Michigan, v. 4, p. 177–204.

Arnold, C.A., 1949, Fossil flora of the Michigan Coal Basin: Contributions from the Museum of Paleontology, University of Michigan, v. 7, p. 131–269.

Barrick, J.E., Lambert, L.L., Heckel, P.H., Rosscoe, S.J., and Boardman, D.R., 2013, Midcontinent Pennsylvanian conodont zonation: Stratigraphy, v. 10, p. 55–72.

Barthel, M., 1976, Die Rotliegendflora Sachsens: Abhandlungen des Staatlichen Museums für Mineralogie und Geologie zu Dresden, v. 24, p. 1–190. pls. 1–97.

Barthel, M., 1997, Epidermal structures of sphenophylls: Review of Palaeobotany and Palynology, v. 95, p. 115–127.

Barthel, M., 2000, *Annularia stellata* oder *Annularia spinulosa*?: Veröffentlichungen des Naturkundemuseums Erfurt, v. 19, p. 37–42.

Barthel, M., 2004, Die Rotliegendflora des Thüringer Waldes. Teil 2: Calamiten und Lepidophyten: Veröffentlichungen Naturhistorisches Museum Schloß Bertholdsburg Schleusingen, v. 19, p. 19–48.

Bartling, F.G., 1830, Ordines Naturales Plantarum Eorumque Characteres et Affinitates Adjecta Generum Enumeratione: Göttingen, Sumptibus Dieterichianis, 498 p.

Bashforth, A.R., 2005, Late Carboniferous (Bolsovian) macroflora from the Barachois Group, Bay St. George Basin, southwestern Newfoundland, Canada: Palaeontographica Canadiana, v. 24, p. 1–123.

Bashforth, A.R., Falcon-Lang, H.J., and Gibling, M.R., 2010, Vegetation heterogeneity on a Late Pennsylvanian braided-river plain draining the Variscan Mountains, La Magdalena Coalfield, northwestern Spain: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 292, p. 367–390.

Bashforth, A.R., Drábková, J., Opluštil, S., Gibling, M.R., and Falcon-Lang, H.J., 2011, Landscape gradients and patchiness in riparian vegetation on a Middle Pennsylvanian braided-river plain prone to flood disturbance (Nýřany Member, Central and Western Bohemian Basin, Czech Republic): Review of Palaeobotany and Palynology, v. 163, p. 153–189.

Basson, P.W., 1968, The fossil flora of the Drywood Formation of southwestern Missouri: University of Missouri Studies, v. 44, p. 1–170.

Batenburg, L.H., 1977, The *Sphenophyllum* species in the Carboniferous flora of Holz (Westphalian D, Saar Basin, Germany): Review of Palaeobotany and Palynology, v. 24, p. 69–99.

Bell, W.A., 1938, Fossil flora of Sydney Coalfield, Nova Scotia: Geological Survey of Canada Memoir, v. 215, p. 1–334.

Bell, W.A., 1940, The Pictou Coalfield, Nova Scotia: Geological Survey of Canada Memoir, v. 225, p. 1–161.

Bell, W.A., 1944, Carboniferous rocks and fossil floras of northern Nova Scotia: Geological Survey of Canada Memoir, v. 238, p. 1–277.

Bell, W.A., 1962, Flora of Pennsylvanian Pictou Group of New Brunswick: Geological Survey of Canada Bulletin, v. 87, p. 1–71, pls. 1–56.

Bertier, P., Swennen, R., Lagrou, D., Laenen, B., and Kemps, R., 2008, Palaeo-climate controlled diagenesis of the Westphalian C & D fluvial sandstones in the Campine Basin (north-east Belgium): Sedimentology, v. 55, p. 1375–1417.

Bertrand, P., 1930, Bassin houiller de la Sarre et de la Lorraine. I. Flore fossile. Part 1. Neuroptéridées: Études des Gîtes Minéraux de la France, p. 1–58, pls. 1–30.

Bertrand, P., 1932, Bassin houiller de la Sarre et de la Lorraine. I. Flore fossile. Part 2. Alethoptéridées: Études des Gîtes Minéraux de la France, p. 61–107, pls. 31–60.

Blake, B.M. Jr., and Gillespie, W.H., 2011, The enigmatic Dunkard macroflora, *in* Harper, J.M., ed., Geology of the Pennsylvanian–Permian in the Dunkard Basin: Guidebook, 76th Annual Field Conference of Pennsylvania Geologists, Middletown, p. 103–143.

Blake, B.M. Jr., Cross, A.T., Eble, C.F., Gillespie, W.H., and Pfefferkorn, H.W., 2002, Selected plant megafossils from the Carboniferous of the Appalachian region, United States: geographic and stratigraphic distribution, *in* Hills, L.V., Henderson, C.M., and Bamber, E.W., eds., Carboniferous and Permian of the World: Canadian Society of Petroleum Geologists Memoir 19, p. 259–335.

Blakey, R., 2013, North America key time-slices paleotectonic and sedimentation maps: Carboniferous-Pennsylvanian: cpgeosystems.com/images/penn-facies.jpg (accessed August 2014).

Bode, H., 1958, Die floristichse Gliederung des Oberkarbons der Vereinigten Staaten von Nordamerika: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 110, p. 217–259.

Boersma, M., 1972, The Heterogeneity of the Form Genus *Mariopteris* Zeiller: a Comparative Morphological Study with Special Reference to the Frond Composition of West-European Species: Utrecht, Elinkwijk, 172 p., pls. 1–43.

Boneham, R.F., 1974, Chieftain No. 20 flora (Middle Pennsylvanian) of Vigo County, Indiana: Proceedings of the Indiana Academy of Science, v. 84, p. 89–113.

Boulay, N., 1876, Le Terraine Houiller du Nord de la France et ses végétaux fossiles [Ph.D. dissertation]: Caen, France, Académie de Caen, 74 p., pls. 1–4.

Brongniart, A., 1822, Sur la classification et la distribution des végétaux fossiles, et sur ceux des terrains de sédiment supérieur en particulier: Mémoires du Muséum d'Histoire Naturelle, v. 8, p. 203–240, 297–348, pls. 1–6.

Brongniart, A., 1828a, Histoire des Végétaux Fossiles, ou Recherches Botaniques et Géologiques sur les Végétaux Renfermés dans les Diverses Couches du Globe, vol. 1, part 2: Paris, G. Dufour, p. 81–136, pls. 9bis, 10, 12, 15, 19–27.

Brongniart, A., 1828b, Prodrome d'une Histoire des Végétaux Fossiles: Paris, F.G. Levrault, 223 p.

Brongniart, A., 1830, Histoire des Végétaux Fossiles, ou Recherches Botaniques et Géologiques sur les Végétaux Renfermés dans les Diverses Couches du Globe: Paris, G. Dufour, vol. 1, part 4, p. 169–208, pls. 29, 42, 43, 46–49, 51, 52, 54–56, 61, 66.

Brongniart, A., 1831, Histoire des Végétaux Fossiles, ou Recherches Botaniques et Géologiques sur les Végétaux Renfermés dans les Diverses Couches du Globe: Paris, G. Dufour, vol. 1, part 5, p. 209–248, pls. 50, 53, 57, 58, 61bis, 62, 64, 65, 67, 68, 70, 71, 73, 76.

Brongniart, A., 1833-34, Histoire des Végétaux Fossiles, ou Recherches Botaniques et Géologiques sur les Végétaux Renfermés dans les Diverses Couches du Globe: Paris, G. Dufour, vol. 1, parts 7–9, p. 265–336, pls. 82A, 83–114, 117, 118, 124, 127, 128, 130.

Buisine, M., 1961, Contribution à l'étude de la flore du terrain houiller. I. Flore fossile, Part 4. Les Aléthoptéridées du Nord de la France: Études géologiques pour l'Atlas de topographie souterraine, Service géologique des Houillères du Bassin du Nord et du Pas-de-Calais, p. 1–317, pls. 1–74.

Bunbury, C.J.F., 1847, On fossil plants from the coal formation of Cape Breton: Quarterly Journal of the Geological Society, v. 3, p. 423–438.

Butterworth, M.A., and Williams, R.W., 1958, The small spore floras of coals in the Limestone Coal Group and Upper Limestone Group of the Lower Carboniferous of Scotland: Transactions of the Royal Society of Edinburgh, v. 63, p. 353–392.

Calder, J.H., 1998, The Carboniferous evolution of Nova Scotia, *in* Blundell, D.J., and Scott, A.C., eds., Lyell: The Past is the Key to the Present: Geological Society of London Special Publications, v. 143, p. 261–302.

Cambier, R., and Renier, A., 1912, Observations sur *Cyclostigma macconochiei* Kidston sp. et *Omphalophloios anglicus* Sternberg sp.: Mémoires de la Société Géologique de Belgique, v. 3, no. 2, p. 56–88, pls. 6–11.

Canright, J.E., 1959, Fossil plants of Indiana: Indiana Geological Survey Report of Progress, v. 14, p. 1–45, pls. 1–5.

Cecil, C.B., 1990, Paleoclimate controls on stratigraphic repetition of chemical and siliciclastic rocks: Geology, v. 18, p. 533–536.

Cecil, C.B., Stanton, R.W., Neuzil, S.G., Dulong, F.T., Ruppert, L.F., and Pierce, B.S., 1985, Paleoclimate controls on late Paleozoic sedimentation and peat formation in the central Appalachian Basin (USA): International Journal of Coal Geology, v. 5, p. 195–230.

Cecil, C.B., Dulong, F.T., West, R.R., Stamm, R., Wardlaw, B.A., and Edgar,. T., N, 2003, Climate controls on the stratigraphy of a Middle Pennsylvanian cyclothems in North America, *in* Cecil, C.B., and Edgar, N.T., eds., Climate Controls on Stratigraphy: Society for Sedimentary Geology (SEPM) Special Publication, v. 77, p. 151–182.

Cecil, C.B., DiMichele, W.A., and Elrick, S.D., 2014, Middle and Late Pennsylvanian cyclothems, American Midcontinent: Ice-age environmental changes and terrestrial biotic dynamics: Comptes Rendus Geoscience, v. 346, p. 159–168.

Césari, S.N., and Hünicken, M., 2013, Heterophylly in *Cordaites*-like foliage from western Gondwana: Review of Palaeobotany and Palynology, v. 196, p. 9–18.

Cleal, C.J., 1978, Floral biostratigraphy of the upper Silesian Pennant Measures of South Wales: Geological Journal, v. 13, p. 165–194.

Cleal, C.J., 1991, Carboniferous and Permian biostratigraphy, in Cleal, C.J., ed., Plant Fossils in Geological Investigation: The Palaeozoic: Chichester, Ellis Horwood, p. 182–215.

Cleal, C.J., 1997, The palaeobotany of the upper Westphalian and Stephanian of southern Britain and its geological significance: Review of Palaeobotany and Palynology, v. 95, p. 227–253.

Cleal, C.J., 2002, Two new late Carboniferous Neuropteris species (Medullosales) from Saarland, Germany and their palaeobiogeographical significance: Botanical Journal of the Linnean Society, v. 139, p. 193–205.

Cleal, C.J., 2007, The Westphalian–Stephanian macrofloral record from the South Wales Coalfield, UK.: Geological Magazine, v. 144, p. 465–486.

Cleal, C.J., 2008a, Palaeofloristics of Middle Pennsylvanian lyginopteridaleans in Variscan Euramerica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 261, p. 1–14.

Cleal, C.J., 2008b, Palaeofloristics of Middle Pennsylvanian medullosaleans in Variscan Euramerica: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 268, p. 164–180.

Cleal, C.J., and Shute, C.H., 1995, A synopsis of neuropteroid foliage from the Carboniferous and Lower Permian of Europe: Bulletin of the British Museum (Natural History), Geology Series, v. 51, p. 1–52.

Cleal, C.J., and Shute, C.H., 2003, Systematics of the Late Carboniferous medullosalean pteridosperm Laveineopteris and its associated Cyclopteris leaves: Palaeontology, v. 46, p. 353–411.

Cleal, C.J., and Shute, C.H., 2012, The systematic and palaeoecological value of foliage anatomy in Late Palaeozoic medullosalean seed-plants: Journal of Systematic Palaeontology, v. 10, p. 765–800.

Cleal, C.J., and Thomas, B.A., 1994, Plant Fossils of the British Coal Measures: Palaeontological Association Field Guide to Fossils, v. 6, p. 1–222.

Cleal, C.J., and Thomas, B.A., 2010, Botanical nomenclature and plant fossils: Taxon, v. 59, p. 261–268.

Cleal, C.J., and Zodrow, E.L., 1989, Epidermal structure of some medullosan Neuropteris foliage from the middle and upper Carboniferous of Canada and Germany: Palaeontology, v. 32, p. 837–882.

Cleal, C.J., Shute, C.H., and Zodrow, E.L., 1990, A revised taxonomy for Palaeozoic neuropterid foliage: Taxon, v. 39, p. 486–492.

Cleal, C.J., Laveine, J.-P., and Shute, C.H., 1996, Architecture of the Upper Carboniferous pteridosperm frond Macroneuropteris macrophylla: Palaeontology, v. 39, p. 561–582.

Cleal, C.J., Laveine, J.-P., and Shute, C.H., 1998, Further observations on the Upper Carboniferous pteridosperm frond Macroneuropteris macrophylla: Palaeontology, v. 41, p. 383–386.

Cleal, C.J., Opluštil, S., Thomas, B.A., Tenchov, Y., Abbink, O.A., Bek, J., Dimitrova, T., Drábková, J., Hartkopf-Fröder, Ch., Van Hoof, T., Kędzior, A., Jarzembowski, E., Jasper, K., Libertín, M., McLean, D., Oliwkiewicz-Miklasinska, M., Pšenička, J., Ptak, B., Schneider, J.W., Schultka, S., Šimůnek, Z., Uhl, D., Waksmundzka, M.I., Van Waveren, I., and Zodrow, E.L., 2009, Late Moscovian terrestrial biotas and palaeoenvironments of Variscan Euramerica: Netherlands Journal of Geosciences, v. 88, p. 181–278.

Cleal, C.J., Uhl, D., Cascales-Miñana, B., Thomas, B.A., Bashforth, A.R., King, S.C., and Zodrow, E.L., 2012, Plant biodiversity changes in Carboniferous tropical wetlands: Earth-Science Reviews, v. 114, p. 124–155.

Comer, V.J., 1992, The first documentation of a lower Middle Pennsylvanian Upland flora from the eastern margin of the Eastern Interior Basin (Illinois Basin) [M.Sc. dissertation]: Charleston, Eastern Illinois University, 87 p.

Corsin, P., 1932, Guide paléontologique dans le terrain houiller du Nord de la France: Travaux et Mémoires de l'Université de Lille, v. 5, p. 1–44, pls. A–C, 1–40.

Corsin, P., 1960, Classification des Ptéridophytes et des Ptéridospermophytes du Carbonifère: Bulletin de la Société Géologique de France (Série 7), v. 2, p. 566–572.

Corsin, P., and Corsin, P., 1971, Zonation biostratigraphique due Houiller des bassins due Nord–Pas-de-Calais et de Lorraine: Comptes rendus hebdomadaires des séances de l'Académie des Sciences, Série D (Sciences naturelles), v. 273, p. 783–788.

Crookall, R., 1959, Fossil plants of the Carboniferous rocks of Great Britain (Second Section): Memoirs of the Geological Survey of Great Britain, Palaeontology, v. 4, pt. 2, p. 85–216, pls. 25–58.

Crookall, R., 1964, Fossil plants of the Carboniferous rocks of Great Britain (Second Section): Memoirs of the Geological Survey of Great Britain, Palaeontology, v. 4, pt. 3, p. 217–354, pls. 59–81.

Crookall, R., 1966, Fossil plants of the Carboniferous rocks of Great Britain (Second Section): Memoirs of the Geological Survey of Great Britain, Palaeontology, v. 4, pt. 4, p. 355–572, pls. 82–106.

Crookall, R., 1969, Fossil plants of the Carboniferous rocks of Great Britain (Second Section): Memoirs of the Geological Survey of Great Britain, Palaeontology, v. 4, pt. 5, p. 573–792, pls. 107–150.

Crookall, R., 1970, Fossil plants of the Carboniferous rocks of Great Britain (Second Section): Memoirs of the Geological Survey of Great Britain, Palaeontology, v. 4, pt. 6, p. 793–840, pls. 151–159.

Darrah, W.C., 1969, A Critical Review of the Upper Pennsylvanian Floras of Eastern United States with Notes on the Mazon Creek Flora of Illinois: Gettysburg, Privately published, 220 p., pls. 1–80.

Davydov, V.I., Crowley, J.L., Schmitz, M.D., and Poletaev, V.I., 2010, High-precision U–Pb zircon age calibration of the global Carboniferous time scale and Milankovitch band cyclicity in the Donets Basin, eastern Ukraine: Geochemistry, Geophysics, Geosystems, v. 11, Q0AA04 doi:10.1029/2009GC002736.

Demko, T.M., and Gastaldo, R.A., 1992, Paludal environments of the Mary Lee coal zone, Pottsville Formation, Alabama: stacked clastic swamps and peat mires: International Journal of Coal Geology, v. 20, p. 23–47.

DiMichele, W.A., 1979a, Arborescent lycopods of Pennsylvanian age coals: Lepidophloios: Palaeontographica Abteilung B (Palaeophytologie), v. 171, p. 57–77.

DiMichele, W.A., 1979b, Arborescent lycopods of Pennsylvanian age coals: Lepidodendron dicentricum C. Felix: Palaeontographica Abteilung B (Palaeophytologie), v. 171, p. 122–136.

DiMichele, W.A., 1983, Lepidodendron hickii and generic delimitation in Carboniferous lepidodendrid lycopods: Systematic Botany, v. 8, p. 317–333.

DiMichele, W.A., 1985, Diaphorodendron, gen. nov., a segregate from Lepidodendron (Pennsylvanian age): Systematic Botany, v. 10, p. 453–458.

DiMichele, W.A., 2014, Wetland-dryland vegetational dynamics in the Pennsylvanian Ice Age tropics: International Journal of Plant Sciences, v. 175, p. 123–164.

DiMichele, W.A., and Bateman, R.M., 1992, Diaphorodendraceae, fam. nov. (Lycopsida: Carboniferous): systematics and evolutionary relationships of Diaphorodendron and Synchysidendron, gen. nov.: American Journal of Botany, v. 79, p. 605–617.

DiMichele, W.A., and Bateman, R.M., 1993, Validation of Synchysidendron, gen. nov. (Fossiles): Taxon, v. 42, p. 647–648.

DiMichele, W.A., and Chaney, D.S., 2005, Pennsylvanian-Permian fossil floras from the Cutler Group, Cañon del Cobre and Arroyo del Agua areas, in northern New Mexico: New Mexico Museum of Natural History and Science Bulletin, v. 31, p. 26–33.

DiMichele, W.A., and Nelson, W.J., 1989, Small-scale spatial heterogeneity in Pennsylvanian-age vegetation from the roof shale of the Springfield Coal (Illinois Basin): Palaios, v. 4, p. 276–280.

DiMichele, W.A., and Phillips, T.L., 1996a, Clades, ecological amplitudes, and ecomorphs: phylogenetic effects and the persistence of primitive plant communities in the Pennsylvanian-age tropics: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 127, p. 83–105.

DiMichele, W.A., and Phillips, T.L., 1996b, Climate change, plant extinctions, and vegetational recovery during the Middle-Late Pennsylvanian transition: the case of tropical peat-forming environments in North America, in M. L. Hart, ed., Biotic Recovery from Mass Extinctions: Geological Society Special Publication, v. 102, p. 201–221.

DiMichele, W.A., Phillips, T.L., and Olmstead, R.G., 1987, Opportunistic evolution: abiotic environmental stress and the fossil record of plants: Review of Palaeobotany and Palynology, v. 50, p. 151–178.

DiMichele, W.A., Pfefferkorn, H.W., and Phillips, T.L., 1996, Persistence of Late Carboniferous tropical vegetation during glacially driven climatic and sea-level fluctuations: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 125, p. 105–128.

DiMichele, W.A., Phillips, T.L., and Nelson, W.J., 2002, Place vs. time and vegetational persistence: a comparison of four tropical mires from the Illinois Basin during the height of the Pennsylvanian Ice Age: International Journal of Coal Geology, v. 50, p. 43–72.

DiMichele, W.A., Tabor, N.J., and Chaney, D.S., 2005, Outcrop-scale environmental heterogeneity and vegetational complexity in the Permo-Carboniferous Markley Formation of North Central Texas: New Mexico Museum of Natural History and Science Bulletin, v. 30, p. 60–66.

DiMichele, W.A., Falcon-Lang, H.J., Nelson, W.J., Elrick, S.D., and Ames, P. R., 2007, Ecological gradients within a Pennsylvanian mire forest: Geology, v. 35, p. 415–418.

DiMichele, W.A., Elrick, S.D., and Bateman, R.M., 2013a, Growth habit of the late Paleozoic rhizomorphic tree-lycopsid family Diaphorodendraceae: Phylogenetic, evolutionary, and paleoecological significance: American Journal of Botany, v. 100, p. 1604–1625.

DiMichele, W.A., Wagner, R.H., Bashforth, A.R., and Álvarez-Vázquez, C., 2013b, An update on the flora of the Kinney Quarry of central New Mexico (Upper Pennsylvanian), its preservational and environmental significance: New Mexico Museum of Natural History and Science Bulletin, v. 59, p. 289–325.

Dix, E., 1934, The sequence of floras in the Upper Carboniferous, with special reference to South Wales: Transactions of the Royal Society of Edinburgh, v. 57, p. 789–838.

Douglass, R.C., 1987, Fusulinid biostratigraphy and correlations between the Appalachian and Eastern Interior basins: United States Geological Survey Professional Paper, v. 1451, p. 1–95.

Du Mortier, B.-C., 1829, Analyse des Familles des Plantes, avec l'Indication des Principaux Genres qui s'y Rattachent, Tournay, J. Casterman, 104 p.

Eichwald, E., 1840, Die Urwelt Russlands Durch Abbildungen Erlæutert, Erstes Heft: St. Petersburg, Journal de Saint-Petersbourg, 106 p.

Falcon-Lang, H.J., and DiMichele, W.A., 2010, What happened to the coal forests during Pennsylvanian glacial phases?: Palaios, v. 25, p. 611–617.

Falcon-Lang, H.J., Heckel, P.H., DiMichele, W.A., Blake, B.M. Jr., Easterday, C.R., Eble, C.F., Elrick, S., Gastaldo, R.A., Greb, S.F., Martino, R.L., Nelson, W.J., Pfefferkorn, H.W., Phillips, T.L., and Rosscoe, S.J., 2011, No major stratigraphic gap exists near the Middle-Upper Pennsylvanian (Desmoinesian-Missourian) boundary in North America: Palaios, v. 26, p. 125–139.

Felix, C.J., 1952, A study of the arborescent lycopods of southeastern Kansas: Annals of the Missouri Botanical Garden, v. 39, p. 263–288.

Fielding, C.R., Frank, T.D., and Isbell, J.L., 2008, The Late Paleozoic Ice Age: a review of current understanding and synthesis of global climate patterns, *in* Fielding, C.R., Frank, T.D., and Isbell, J.L., eds., Resolving the Late Paleozoic Ice Age In Time and Space: Geological Society of America Special Paper, v. 44, p. 343–354.

Gastaldo, R.A., 1977, A Middle Pennsylvanian nodule flora from Carterville, Illinois, *in* Romans, R.C., ed., Geobotany: New York, Plenum Press, p. 133–156.

Gastaldo, R.A., 1987, Confirmation of Carboniferous clastic swamp communities: Nature, v. 326, p. 869–871.

Gastaldo, R.A., and Boersma, M.A., 1983a, A reinvestigation of Early Pennsylvanian species of *Mariopteris* from the Appalachian Region. I. *Karinopteris*, *Mariopteris* and the "Pottsvillea Complex": Review of Palaeobotany and Palynology, v. 38, p. 185–226.

Gastaldo, R.A., and Boersma, M.A., 1983b, A reinvestigation of Early Pennsylvanian species of *Mariopteris* from the Appalachian Region. II. *Eusphenopteris* and *Sphenopteris*: Review of Palaeobotany and Palynology, v. 38, p. 227–247.

Gastaldo, R.A., Stevanoviç-Walls, I.M., Ware, W.N., and Greb, S.F., 2004, Community heterogeneity of Early Pennsylvanian peat mires: Geology, v. 32, p. 693–696.

Gillespie, W.H., and Pfefferkorn, H.W., 1979, Distribution of commonly occurring plant megafossils in the proposed Pennsylvanian System stratotype, *in* Englund, K. J., Arndt, H.H., and Henry, T.W., eds., Proposed Pennsylvanian System Stratotype: Virginia and West Virginia: American Geological Institute Selected Guidebook Series, v. 1, p. 87–96.

Gillespie, W.H., Clendening, J.A., and Pfefferkorn, H.W., 1978, Plant fossils of West Virginia and adjacent areas: West Virginia Geological and Economic Survey Educational Series, ED-3A, p. 1–172.

Göppert, H.R., 1836, Die fossilen Farrnkräuter (Systema filicum fossilium): Verhandlungen der kaiserlichen Leopoldinischen-Carolinischen Akademie der Naturforscher, v. 17 (supplement), p. 1–486, pls. 1–44.

Göppert, H.R., 1848, *in* Bronn, H.G., Index Palaeontologicus oder Übersicht der bis jetzt bekannten fossilen Organismen, Nomenclator palaeontologicus in alphabetischer Ordnung, vol. 2, parts N–Z: Stuttgart, E. Schweizerbart'sche Verlagsbuchhandlung und Druckerei, p. 777–1381.

Gothan, W., 1913, Die oberschlesische Steinkohlenflora. I. Farne und farnähnliche Gewächse (Cycadofilices bezw. Pteridospermen): Abhandlungen der königlichen Preussischen Geologischen Landesanstalt (Neue Folge), v. 75, p. 1–278, pls. 1–53.

Gothan, W., 1941, Paläobotanische Mitteilungen. 5–7. Die Unterteilung der karbonischen Neuropteriden: Paläontologische Zeitschrift, v. 22, p. 421–438.

Gothan, W., and Remy, W., 1957, Steinkohlenpflanzen, Leitfaden zum Bestimmen der wichtigsten pflanzlichen Fossilien des Paläozoikums im rheinisch-westfälischen Steinkohlengebiet: Essen, Verlag Glückauf, 248 p.

Greb, S.F., Andrews, W.M., Eble, C.F., DiMichele, W.A., Cecil, C.B., and Hower, J.C., 2003, Desmoinesian coal beds of the Eastern Interior and surrounding basins: the largest tropical peat mires in earth history, *in* Chan, M.A., and Archer, A.W., eds., Extreme Depositional Environments: Megaend Members in Geologic Time: Geological Society of America Special Paper, v. 370, p. 127–150.

Gutbier, A., von, 1835, Abdrücke und Versteinerungen des Zwickauer Schwarzkohlengebirges und seiner Umgebungen: Zwickau, G. Richter'sche Buchhandlung, 80 p., pls. 1–11.

Gutbier, A., von, 1837, Pflanzenabdrucke des Rothliegenden und der Kohlenformation der gegend von Zwickau: Isis, encyclopädische Zeitschrift vorzüglich für Naturgeschichte, vergleichender Anatomie und Physiologie, v. 5–7, p. 435–436.

Gutbier, A., von, 1849, Die Versteinerungen des Rothliegenden in Sachsen, *in* Geinitz, H.B., and Gutbier, A., eds., Die Versteinerungen des Zechsteingebirges und Rothliegenden Oder des Permischen Systemes in Sachsen: Dresden, Arnold, vol. 2, p. 1–39.

Harms, V.L., and Leisman, G.A., 1961, The anatomy and morphology of certain *Cordaites* leaves: Journal of Paleontology, v. 35, p. 1041–1064.

Hatcher, R.D., 2002, Alleghanian (Appalachian) orogeny, a product of zipper tectonics: rotational transpressive continent-continent collision and closing of ancient oceans along irregular margins, *in* Martinez Catalán, J.R., Hatcher, Jr., R.D., Arenas, R., and Díaz García, F., eds., Variscan-Appalachian Dynamics: The Building of the Late Paleozoic Basement: Geological Society of America Special Paper, v. 364, p. 199–208.

Hatcher, R.D., 2010, The Appalachian orogen: a brief summary, *in* Tollo, R.P., ed., From Rodinia to Pangea, the Lithotectonic Record of the Appalachian Region: Geological Society of America Memoir, v. 206, p. 1–19.

Haughton, S., 1860, On *Cyclostigma*, a new genus of fossil plants from the Old Red Sandstone of Kiltorcan, co. Kilkenny; and on the general law of phyllotaxis in the natural orders Lycopodiaceæ, Equisetaceæ, Filices, & c.: Annals and Magazine of Natural History, Third Series, v. 5, p. 433–445.

Heckel, P.H., 1977, Origin of phosphatic black shale facies in Pennsylvanian cyclothems of Mid-Continent North America: American Association of Petroleum Geologists Bulletin, v. 61, p. 1045–1068.

Heckel, P.H., 1980, Paleogeography of eustatic model for deposition of Midcontinent Upper Pennsylvanian cyclothems, *in* Fouch, T.D., and Magathan, E.R., eds., Paleozoic Paleogeography of West-Central United States: Society of Economic Paleontologists and Mineralogists, Rocky Mountain Section, Paleogeography Symposium, v. 1, p. 197–215.

Heckel, P.H., 1986, Sea-level curve for Pennsylvanian eustatic marine transgressive-regressive depositional cycles along midcontinent outcrop belt, North America: Geology, v. 14, p. 330–334.

Heckel, P.H., 2013, Pennsylvanian stratigraphy of Northern Midcontinent Shelf and biostratigraphic correlation of cyclothems: Stratigraphy, v. 10, p. 3–39.

Hirmer, M., 1927, Handbuch der Paläobotanik. Band I, Thallophyta—Bryophyta—Pteridophyta: Berlin, R. Oldenbourg, 708 p.

Hoffmann, F., 1826a, Über die Pflanzenreste des Kohlengebirges von Ibbenbühren und vom Piesberge bei Osnabrück, *in* Keferstein, C., ed., Teutschland, Geognostisch-geologisch Dargestellt, mit Charten und Durchschnittszeichnungen, Welche Einen Geognostischen Atlas Bilden, v. 4, pt. 2, p. 151–168, figs. 1–10.

Hoffmann, F., 1826b, Untersuchungen über die Pflanzen-Reste des Kohlengebirges von Ibbenbühren und vom Piesberge bei Osnabrück, *in* Karsten, C.J.B., ed., Archiv für Bergbau und Hüttenwesen, v. 13, pt. 2, p. 266–282.

Houseknecht, D.W., 1983, Tectonic-sedimentary evolution of the Arkoma basin and guidebook to deltaic facies, Hartshorne Sandstone: Society of Economic Paleontologists and Mineralogists, Midcontinent Section, v. 1, p. 1–119.

Hutchison, H.C., 1976, Geology of the Catlin-Mansfield area, Parke and Putnam counties, Indiana: Indiana Geological Survey Bulletin, v. 54, p. 1–57.

Jackson, T.F., 1916, The description and stratigraphic relationships of fossil plants from the Lower Pennsylvanian rocks of Indiana: Proceedings of the Indiana Academy of Science, v. 26, p. 405–439.

Janssen, R.E., 1940, Some fossil plant types of Illinois: a restudy of the Lesquereux types in the Worthen Collection of the Illinois State Museum, augmented by descriptions of new species from Mazon Creek: Illinois State Museum Scientific Papers, v. 1, p. 1–124.

Janssen, R.E., 1979, Leaves and stems from fossil forests: Illinois State Museum Popular Science Series, v. 1, p. 1–190.

Jongmans, W.J., 1937a, Contribution to a comparison between the Carboniferous floras of the United States and of Western Europe: Compte Rendu du Deuxième Congrès pour l'Avancement des Études de Stratigraphie Carbonifère (Heerlen, 1935), v. 1, p. 363–387.

Jongmans, W.J., 1937b, Comparison of the floral succession in the Carboniferous of West Virginia with Europe: Compte Rendu du Deuxième Congrès pour l'Avancement des Études de Stratigraphie Carbonifère (Heerlen, 1935), v. 1, p. 393–415, pls. 11–36.

Jongmans, W.J., 1937c, Some remarks on *Neuropteris ovata* in the American Carboniferous: Compte Rendu du Deuxième Congrès pour l'Avancement des Études de Stratigraphie Carbonifère (Heerlen, 1935), v. 1, p. 417–422, pls. 37–42.

Jongmans, W.J., and Gothan, W., 1934, Florenfolgen und vergleichende Stratigrafie des Karbons der östlichen Staaten Nord-Amerika's. Vergleich mit West-Europa: Geologisch Bureau voor het Nederlandsche Mijngebied te Heerlen, Jaarverslag over 1933, p. 17–44.

Josten, K.-H., 1962, *Neuropteris semireticulata*, eine neue Art als Bindeglied zwischen den Gattungen *Neuropteris* und *Reticulopteris*: Palaontologische Zeitschrift, v. 36, p. 33–45.

Josten, K.-H., 1991, Die Steinkohlen-Floren Nordwestdeutschlands: Fortschritte in der Geologie von Rheinland und Westfalen, v. 36, p. 1–434, pls. 1–220.

Josten, K.-H., and Laveine, J.-P., 1984, Paläobotanisch-stratigraphische Untersuchungen im Westfal C-D von Nordfrankreich und Nordwestdeutschland: Fortschritte in der Geologie von Rheinland und Westfalen, v. 32, p. 89–117.

Kerp, J.H.F., 1984, Aspects of Permian palaeobotany and palynology. V. On the nature of *Asterophyllites dumasii* Zeiller, its correlation with *Calamites gigas* and the problem concerning its sterile foliage: Review of Palaeobotany and Palynology, v. 41, p. 301–317.

Kidston, R., 1888, On the fossil flora of the Radstock Series of the Somerset and Bristol Coal Field (Upper Coal Measures). Part I.: Transactions of the Royal Society of Edinburgh, v. 33, p. 335–417, pls. 18–28.

Kidston, R., 1923, Fossil plants of the Carboniferous rocks of Great Britain (First Section): Memoirs of the Geological Survey of Great Britain, Palaeontology, v. 2, pt. 1, p. 1–110, pls. A–E, 1–22.

Knoll, A.H., 1985, Exceptional preservation of photosynthetic organisms in silicified carbonates and silicified peats: Philosophical Transactions of the Royal Society of London, v. 311B, p. 111–122.

Kosanke, R.M., 1950, Pennsylvanian spores of Illinois and their use in correlation: Illinois State Geological Survey Bulletin, v. 74, p. 1–128.

Kvaček, J., and Straková, M., 1997, Catalogue of Fossil Plants Described in the Works of Kaspar M. Sternberg: Prague, National Museum, 201 p.

Kvale, E.P., Mastalerz, M., Furer, L.C., Engelhardt, D.W., Rexroad, C.B., and Eble, C.F., 2004, Atokan and early Desmoinesian coal-bearing parasequences in Indiana, U.S.A., in Pashin, J.C., and Gastaldo, R.A., eds., Sequence Stratigraphy, Paleoclimate, and Tectonics of Coal-bearing Strata: American Association of Petroleum Geology Studies in Geology, v. 51, p. 71–88.

Langenheim, R.L., and Nelson, W.J., 1992, The cyclothemic concept in the Illinois Basin: a review, in Dott, R.H., ed., Eustasy: The Historical Ups and Downs of a Major Geological Concept: Geological Society of America Memoir, v. 180, p. 55–72.

Langford, G., 1958, The Wilmington Coal Flora from a Pennsylvanian Deposit in Will County, Illinois: Downers Grove, Illinois, ESCONI Associates, 360 p.

Langford, G., 1963, The Wilmington Coal Fauna and Additions to the Wilmington Coal Flora from a Pennsylvanian Deposit in Will County, Illinois: Downers Grove, Illinois, ESCONI Associates, 280 p.

Laveine, J.-P., 1967, Contribution à l'étude de la flore du terrain houiller. I. Flore fossile, Part 5. Les Neuroptéridées du Nord de la France: Études géologiques pour l'Atlas de topographie souterraine, Service géologique des Houillères du Bassin du Nord et du Pas-de-Calais, 344 p., pls. 1–84.

Laveine, J.-P., 1977, Report on the Westphalian D, in Holub, V.M., and Wagner, R.H., eds., Symposium on Carboniferous Stratigraphy: Prague, Ústřední ústav geologický, p. 71–87.

Laveine, J.-P., 1987, La flore du bassin houiller du Nord de la France. Biostratigraphie et méthodologie: Annales de la Société géologique du Nord, v. 106, p. 87–93.

Laveine, J.-P., 1989, Guide Paléobotanique dans le Terrain Houiller Sarro-Lorrain: Documents des Houillères du Bassin de Lorraine, 154 p., pls. 1–64.

Laveine, J.-P., 2005, The Cyclopteris of Laveineopteris (Late Carboniferous pteridosperm). Fancies and facts: methodological and taxonomical implications: Revue de Paléobiologie, v. 24, p. 403–487.

Laveine, J.-P., and Belhis, A., 2007, Frond architecture of the seed-fern Macroneuropteris scheuchzeri, based on Pennsylvanian specimens from the Northern France coal field: Palaeontographica Abteilung B (Palaeophytologie), v. 277, p. 1–41.

Laveine, J.-P., and Oudoire, T., 2015, Partial alopecia for the Permo-Pennsylvanian seed-fern Macroneuropteris scheuchzeri: Review of Palaeobotany and Palynology, v. 216, p. 132–142.

Laveine, J.-P., Zhang, S., and Lemoigne, Y., 2000, Palaeophytogeography and palaeogeography on the basis of examples from the Carboniferous: Revue Paléobiologie Genève, v. 19, p. 409–425.

Leighton, M.W., Kolata, D.R., Oltz, D.F., and Eidel, J.J., eds., 1991, Interior Cratonic Basins: American Association of Petroleum Geologists Memoir, v. 51, 819 p.

Lesnikowska, A.D., and Willard, D.A., 1997, Two new species of Scolecopteris (Marattiales), sources of Torispora securis Balme and Thymospora thiessenii (Kosanke) Wilson et Venkatachala: Review of Palaeobotany and Palynology, v. 95, p. 211–225.

Lesquereux, L., 1854, New species of fossil plants, from the Anthracite and Bituminous coal-fields of Pennsylvania; collected and described by Leo Lesquereux. With introductory observations by Henry Darwin Rogers: Boston Journal of Natural History, v. 6, n. 4., p. 409–431.

Lesquereux, L., 1861, Report of the fossil flora, and the stratigraphical distribution of the coal in the Kentucky coal fields, in Owen, D.D., ed., Fourth Report of the Geological Survey in Kentucky, made during the years 1858 and 1859, Frankfurt, Kentucky, A.G. Hodges, public printer, p. 331–437, pls. 6, 7.

Lesquereux, L., 1866, Enumeration of the fossil plants found in the Coal Measures of Illinois, with descriptions of new species: Geological Survey of Illinois, vol. 2 (Palæontology), Section 3 (Fossil Plants), p. 425–470, pls. 33–50.

Lesquereux, L., 1868, Fossil plants of the coal strata of Pennsylvania, in Rogers, H.D., ed., The Geology of Pennsylvania. A Government Survey, with a General View of the Geology of the United States, Essays on the Coal-Formation and its Fossils, and a Description of the Coal-Fields of North America and Great Britain, Philadelphia, J.B. Lippincott & Co., v. 2, pt. 2, p. 835–884, pls. 1–21.

Lesquereux, L., 1870, Report on fossil plants of Illinois: Geological Survey of Illinois, v. 4 (Geology and Palæontology), Pt. 2 (Palæontology of Illinois), Section 2, p. 375–508, pls. 5–31.

Lesquereux, L., 1879-1884, Description of the coal flora of the Carboniferous formations in Pennsylvania and throughout the United States: Second Geological Survey of Pennsylvania, Report of Progress P, v. 1, p. 1–354 (1880), v. 2, p. 355–694 (1880), v. 3, p. 695–922 (1884), pls. 1–85 (1879), pls. 88–111 (1884).

Lindley, J., and Hutton, W., 1831, The Fossil Flora of Great Britain, or Figures and Descriptions of the Vegetable Remains Found in a Fossil State in this Country: London, James Ridgway and Sons, v. 1, p. 1–48.

Lindley, J., and Hutton, W., 1832, The Fossil Flora of Great Britain, or Figures and Descriptions of the Vegetable Remains Found in a Fossil State in this Country: London, James Ridgway and Sons, v. 1, p. 49–166.

Lindley, J., and Hutton, W., 1833, The Fossil Flora of Great Britain, or Figures and Descriptions of the Vegetable Remains Found in a Fossil State in this Country: London, James Ridgway and Sons, v. 1, p. 167–218.

Mamay, S.H., and Mapes, G., 1992, Early Virgilian plant megafossils from the Kinney Brick Company Quarry, Manzanita Mountains, New Mexico: New Mexico Bureau of Mines and Mineral Resources Bulletin, v. 138, p. 61–85.

Mastalerz, M., Stankiewicz, A.B., Salmon, G., Kvale, E.P., and Millard, C.L., 1997, Organic geochemical study of sequences overlying coal seams; example from the Mansfield Formation (Lower Pennsylvanian), Indiana: International Journal of Coal Geology, v. 33, p. 275–299.

Mastalerz, M., Padgett, P.L., and Eble, C.F., 2000, Block coals from Indiana: inferences on changing depositional environment: International Journal of Coal Geology, v. 43, p. 211–226.

Mastalerz, M., Ames, P.R., and Padgett, P.L., 2003, Coals of the Brazil Formation (Pennsylvanian) in Indiana: observations of correlation inconsistencies and their implications: International Journal of Coal Geology, v. 54, p. 209–222.

Meyen, S.V., 1978, An attempt at a radical improvement of suprageneric taxonomy of fossil plants: Phyta, v. 1, p. 76–86.

Meyen, S.V., 1984, Basic features of gymnosperm systematics and phylogeny as evidenced by the fossil record: The Botanical Review, v. 50, p. 1–111.

Moore, L.C., Wittry, J., and DiMichele, W.A., 2014, The Okmulgee, Oklahoma fossil flora, a Mazon Creek equivalent: Spatial conservatism in the composition of Middle Pennsylvanian wetland vegetation over 1100 km: Review of Palaeobotany and Palynology, v. 200, p. 24–52.

Moore, R.C., Wanless, H.R., Weller, J.M., Steele Williams, J., Read, C.B., Bell, W.A., Ashley, G.H., Cheney, M.G., Cline, L.M., Condra, G.E., Dott, R.H., Dunbar, C.O., Elias, M.K., Glenn, F.C., Greene, T.A., Hendricks, J.M., Jewett, J.M., Johnson, J.H., King, P.B., Knight, J.B., Levorsen, A.I., Miser, H.D., Newell, N.D., Plummer, F.B., Thompson, M.L., Tomlinson, C.W., and Westheimer, J., 1944, Correlation of Pennsylvanian formations of North America: Geological Society of America Bulletin, v. 55, p. 657–706.

Nelson, W.J., Trask, C.B., Jacobson, R.J., Damberger, H.H., Williamson, A.D., and Williams, D.A., 1991, Absaroka Sequence, Pennsylvanian and Permian Systems, in Leighton, M.W., Kolata, D.R., Oltz, D.F., and Eidel, J.J., eds., Interior Cratonic Basins: American Association of Petroleum Geologists Memoir, v. 51, p. 143–194.

Nelson, W.J., Greb, S.F., and Weibel, C.P., 2013, Pennsylvanian Subsystem in the Illinois Basin: Stratigraphy, v. 10, p. 41–54.

Neves, R., 1958, Upper Carboniferous plant spore assemblages from the Gastrioceras subcrenatum horizon, North Staffordshire: Geological Magazine, v. 95, p. 1–19.

Newberry, J.S., 1891, The genus Sphenophyllum: Journal of the Cincinnati Society of Natural History, v. 13, p. 212–217.

Noé, A.C., 1925, Pennsylvanian flora of northern Illinois: Illinois State Geological Survey Bulletin, v. 52, p. 1–113.

Novik, E.O., 1947, Classification of Carboniferous pteridosperms: Doklady Akademii Nauk, SSSR, v. 58, p. 277–279.

Novik, E.O., 1952, Carboniferous flora of the European part of the U.S.S.R: Paleontologija SSSR (Novaya Seriya), v. 1, p. 1–468, pls. 1–71.

Oleksyshyn, J., 1982, Fossil plants from the anthracite coal fields of eastern Pennsylvania: Pennsylvania Geological Survey, General Geology Report, v. 72, p. 1–157.

Opluštil, S., Pšenička, J., Libertín, M., Bashforth, A.R., Šimůnek, Z., Drábková, J., and Dašková, J., 2009a, A Middle Pennsylvanian (Bolsovian) peat-forming forest preserved in situ in volcanic ash of the Whetstone Horizon in the Radnice Basin, Czech Republic: Review of Palaeobotany and Palynology, v. 155, p. 234–274.

Opluštil, S., Pšenička, J., Libertín, M., Bek, J., Dašková, J., Šimůnek, Z., and Drábková, J., 2009b, Composition and structure of an in situ Middle Pennsylvanian peat-forming plant assemblage buried in volcanic ash, Radnice Basin (Czech Republic): Palaios, v. 24, p. 726–746.

Peppers, R.A., 1984, Comparison of miospore assemblages in the Pennsylvanian System of the Illinois Basin with those in the Upper Carboniferous of western Europe: Compte Rendu Neuvième Congrès Internationale de

Stratigraphie et Géologie du Carbonifère (Washington and Champaign-Urbana, 1979), v. 2, p. 483–502.

Peppers, R.A., 1993, Palynological correlation of the Lewisport coal bed (early Desmoinesian) and equivalent coal in the Illinois Basin [unpublished manuscript]: Champaign, Illinois State Geological Survey, 65 p.

Peppers, R.A., 1996, Palynological correlation of major Pennsylvanian (Middle and Upper Carboniferous) chronostratigraphic boundaries in the Illinois and other coal basins: Geological Society of America Memoirs, v. 188, p. 1–112.

Peppers, R.A., and Pfefferkorn, H.W., 1970, A comparison of the floras of the Colchester (No. 2) Coal and Francis Creek Shale, *in* Smith, W.H., Nance, R.B., Hopkins, M.E., Johnson, R.G., and Shabica, C.W., eds., Depositional Environments in Parts of the Carbondale Formation: Geological Society of America Coal Division Field Trip, Illinois State Geological Survey Guidebook Series, v. 8, p. 61–74.

Pfefferkorn, H.W., 1979, High diversity and stratigraphic age of the Mazon Creek Flora, *in* Nitecki, M.H., ed., Mazon Creek Fossils: New York, Academic Press, p. 129–142.

Pfefferkorn, H.W., and Gillespie, W.H., 1980a, A bibliography of compression-impression floras of Pennsylvanian age in North America 1821 to 1977, *in* International Working Group on Carboniferous and Permian Compression Floras, eds.: Philadelphia, Schlotheimiana, p. 1–44.

Pfefferkorn, H.W., and Gillespie, W.H., 1980b, Biostratigraphy and biogeography of plant compression fossils in the Pennsylvanian of North America, *in* Dilcher, D.L., and Taylor, T.N., eds., Biostratigraphy of Fossil Plants: Successional and Paleoecological Analyses, Stroudsburg, Dowden, Hutchinson & Ross, p. 93–118.

Pfefferkorn, H.W., and Thomson, M.C., 1982, Changes in dominance patterns in upper Carboniferous plant-fossil assemblages: Geology, v. 10, p. 641–644.

Pfefferkorn, H.W., Mustafa, H., and Hass, H., 1975, Quantitative Charakterisierung oberkarboner Abdruckfloren: Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 150, p. 253–269.

Pheifer, R.N., 1979, The paleobotany and paleoecology of the unnamed shale overlying the Danville Coal Member (VII) in Sullivan County, Indiana [Ph.D. dissertation]: Bloomington, Indiana University, 285 p.

Potonié, H., 1900, Cycadofilices und sonstige Mittelgruppen zwischen Filicales und höheren Gruppen, *in* Engler, A., and Prantl, K., eds., Die natürlichen Pflanzenfamilien nebst ihren Gattungen und wichtigeren Arten insbesondere der Nutzpflanzen, Teil I, Part 4: Leipzig, W. Engelmann, p. 780–798.

Pryor, J.S., and Gastaldo, R.A., 2000, Paleoecological analysis of two Early Pennsylvanian mineral-substrate wetlands: Palaios, v. 15, p. 3–13.

Read, C.B., and Mamay, S.H., 1964, Upper Paleozoic floral zones and floral provinces of the United States: United States Geological Survey Professional Paper 454K, 35 p., pls. 1–19.

Remy, W., and Remy, R., 1977, Die Floren des Erdaltertums: Einführung in Morphologie, Anatomie, Geobotanik und Biostratigraphie der Pflanzen des Paläophytikums: Essen, Verlag Glückauf, 468 p.

Rex, G., 1983, The compression state of preservation of Carboniferous lepidodendrid leaves: Review of Palaeobotany and Palynology, v. 39, p. 65–85.

Rexroad, C.B., Brown, L.M., Devera, J.A., and Suman, R.J., 1998, Conodont biostratigraphy and paleoecology of the Perth Limestone Member, Staunton Formation (Pennsylvanian) of the Illinois basin, U.S.A.: Palaeontologia Polonica, v. 58, p. 247–259.

Roscher, M., and Schneider, J.W., 2006, Permo-Carboniferous climate: Early Pennsylvanian to Late Permian climate development of central Europe in a regional and global context, *in* Lucas, S.G., Cassinis, G., and Schneider, J.W., eds., Non-Marine Permian Biostratigraphy and Biochronology: Geological Society of London, Special Publications, v. 265, p. 95–136.

Rygel, M.C., Fielding, C.R., Frank, T.D., and Birgenheier, L.P., 2008, The magnitude of Late Paleozoic glacioeustatic fluctuations: a synthesis: Journal of Sedimentary Research, v. 78, p. 500–511.

Saltzwedel, K., 1969, Revision der *Imparipteris ovata* (Hoffmann) Gothan, 1. Teil: Typus und Typoid-Material vom locus typicus: Argumenta Palaeobotanica, v. 3, p. 131–162, pls. 24–27.

Schabilion, J.T., and Reihman, M.A., 1985, Anatomy of petrified *Neuropteris scheuchzeri* pinnules from the Middle Pennsylvanian of Iowa: a paleoecological interpretation: Compte Rendu Neuvième Congrès Internationale de Stratigraphie et Géologie du Carbonifère (Washington and Champaign-Urbana, 1979), v. 5, p. 3–12.

Scheihing, M.H., and Pfefferkorn, H.W., 1980, Morphologic variation in *Alethopteris* (Pterisperms, Carboniferous) from St. Clair, Pennsylvania, USA: Palaeontographica Abteilung B (Palaeophytologie), v. 172, p. 1–9.

Schenk, A., 1883, Pflanzen aus der Steinkohlenformation, *in* Richthofen, F. von, ed., China. Ergebnisse eigner Reisen und darauf gegründeter Studien, 4: Berlin, D. Reimer, p. 211–244.

Scott, A.C., 1978, Sedimentological and ecological control of Westphalian B plant assemblages from West Yorkshire: Proceedings of the Yorkshire Geological Society, v. 41, p. 461–508.

Sellards, E.H., 1908, Fossil plants of the Upper Paleozoic of Kansas: The University Geological Survey of Kansas, v. 9 (Special Report on Oil and Gas), p. 386–480, pls. 44–69.

Seward, A.C., 1898, Fossil Plants. A Text-book for Students of Botany and Geology. Vol. I: Cambridge, Cambridge University Press, 452 p.

Shaver, R.H., 1984, Atokan Series concepts with special reference to the Illinois Basin and Iowa, *in* Sutherland, P.K., and Manger, W.L., eds., The Atokan Series (Pennsylvanian) and its Boundaries–A Symposium: Oklahoma Geological Survey Bulletin, v. 136, p. 101–113.

Shaver, R.H., and Smith, S.G., 1974, Some Pennsylvanian kirkbyacean ostracods of Indiana and Midcontinent series terminology: Indiana Geological Survey Report of Progress, v. 31, p. 1–59.

Shute, C.H., and Cleal, C.J., 1987, Palaeobotany in museums: Geological Curator, v. 4, p. 553–559.

Simson-Scharold, E., 1934, Zur Kenntnis der Carbonflora des Saargebietes: Palaeontographica Abteilung B (Palaeophytologie), v. 79, p. 1–66, pls. 1–7.

Šimůnek, Z., 2006, New classification of the genus *Cordaites* from the Carboniferous and Permian of the Bohemian Massif, based on cuticle micromorphology: Sborník Národního muzea v Praze, Řada B, Přírodní vědy, v. 62, p. 97–210.

Šimůnek, Z., and Cleal, C.J., 2011, Imparipinnate neuropteroid foliage (Medullosales) from the middle Westphalian of the West and Central Bohemia Coal Basin, Czech Republic: Review of Palaeobotany and Palynology, v. 166, p. 163–201.

Smith, A.H.V., and Butterworth, M.A., 1967, Miospores in the coal seams of the Carboniferous of Great Britain: Palaeontological Association, Special Papers in Palaeontology, v. 1, 324 p.

Staplin, F.L., and Jansonius, J., 1964, Elucidation of some Paleozoic densospores: Palaeontographica Abteilung B (Palaeophytologie), v. 114, p. 95–117.

Sternberg, K.M., 1820, Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt: Leipzig, F. Fleischer, v. 1, pt. 1, 24 p., pls. 1–13.

Sternberg, K.M., 1821, Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt: Leipzig, F. Fleischer, v. 1, pt. 2, 33 p., pls. 14–26.

Sternberg, K.M., 1823, Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt: Regensburg, Ernst Brenck's Wittwe, vol. 1, pt. 3, p. 1–39, pls. 27–39.

Sternberg, K.M., 1825, Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt: Regensburg, Ernst Brenck's Wittwe, vol. 1, pt. 4, p. 1–48, pls. 40–59, A–E.

Sternberg, K.M., 1833, Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt: Prague, Johann Spurny, v. 2, pts. 5, 6, p. 1–80, pls. 1–26, A–E.

Stockmans, F., 1933, Les Neuroptéridées des bassins houillers belges (première partie): Memoires du Musée Royal d'Histoire Naturelle de Belgique, v. 57, p. 1–61, pls. 1–16.

Storch, D., 1980, *Sphenophyllum*-Arten aus drei intramontanen Karbonbecken—pflanzengeographische Besdonderheiten im mitteleuropäischen Karbon, *in* Daber, R., ed., Evolution/Naturgeschichte Pflanzen: Schriftenreihe für Geologische Wissenschaften, v. 16, p. 171–273.

Stull, G.W., DiMichele, W.A., Falcon-Lang, H.J., Nelson, W.J., and Elrick, S., 2012, Palaeoecology of *Macroneuropteris scheuchzeri*, and its implications for resolving the paradox of 'xeromorphic' plants in Pennsylvanian wetlands: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 331–332, p. 162–176.

Stull, G.W., Labandeira, C.C., DiMichele, W.A., and Chaney, D.S., 2013, The "seeds" on *Padgettia readi* are insect galls: reassignment of the plant to *Odontopteris*, the gall to *Ovofoligallites* n. gen., and the evolutionary implications thereof: Journal of Paleontology, v. 87, p. 217–231.

Sutherland, P.K., and Manger, W.L., 1984, The Atokan Series: an interval in search of a name, *in* Sutherland, P.K., and Manger, W.L., eds., The Atokan Series (Pennsylvanian) and its Boundaries–A Symposium: Oklahoma Geological Survey Bulletin, v. 136, p. 1–8.

Tabor, N.J., Romanchock, C.M., Looy, C.V., Hotton, C.L., DiMichele, W.A., and Chaney, D.S., 2013, Conservatism of Late Pennsylvanian vegetational patterns during short-term cyclic and long-term directional environmental change, western equatorial Pangea, *in* Gąsiewicz, A., and Słowokiewicz, M., eds., Palaeozoic Climate Cycles: Their Evolutionary and Sedimentological Impact: Geological Society of London, Special Publications, v. 376, p. 201–234.

Taylor, T.N., 1978, The ultrastructure and reproductive significance of *Monoletes* (Pteridospermales) pollen: Canadian Journal of Earth Sciences, v. 56, p. 3105–3118.

Teichmüller, M., and Teichmüller, R., 1982, The geologic basis of coal formation, *in* Stach, E., Mackowsky, M.-Th., Teichmüller, M., Taylor, G.H., Chandra, D., and Teichmüller, R., eds., Stach's Textbook of Coal Petrology, 3rd edition: Berlin–Stuttgart, Borntraeger, p. 5–86.

The Tri-State Committee on Correlation of the Pennsylvanian System in the Illinois Basin 2001, Toward a more uniform stratigraphic nomenclature for rock units (formations and groups) of the Pennsylvanian System in the Illinois Basin: Illinois Basin Consortium Study, v. 5, 26 p.

Tidwell, W.D., 1967, Flora of the Manning Canyon Shale. Part I: a lowermost Pennsylvanian flora from the Manning Canyon Shale, Utah, and its stratigraphic significance: Brigham Young University Geology Studies, v. 14, p. 3–66.

Tidwell, W.D., Jennings, J.R., and Bues, S.S., 1992, A Carboniferous flora from the Surprise Canyon Formation in the Grand Canyon, Arizona: Journal of Paleontology, v. 66, p. 1013–1021.

Tidwell, W.D., Ash, S.R., Kues, B.S., Kietzke, K.K., and Lucas, S.G., 1999, Early Permian plant megafossils from Carrizo Arroyo, central New Mexico: New Mexico Geological Society Guidebook, v. 50, p. 297–304.

Unger, F., 1840, Abhandlung über die Struktur der Calamiten und ihre Rangordnung im Gewächsreiche: Flora, v. 2, p. 654–662.

Unger, F., 1842, *in* Endlicher, S.L., Genera Plantarum Secundum Ordines Naturales Disposita, Supplementum Secundum: Vienna, F. Beck, 114 p.

Unger, F., 1850, Genera et Species Plantarum Fossilium: Vienna, Wilhelmum Braumüller, 627 p.

Van Amerom, H.W.J., 1975, Die eusphenopteridischen Pteridophyllen aus der Sammlung des geologischen Bureaus in Heerlen, unter besonderer Berücksichtigung ihrer Stratigraphie bezüglich des Südlimburger Kohlenreviers: Mededelingen Rijks Geologische Dienst, Serie C, v. 3–1(7), p. 1–208.

Van Hoof, T.B., Falcon-Lang, H.J., Hartkopf-Fröder, C., and Kerp, H., 2013, Conifer-dominated palynofloras in the Middle Pennsylvanian strata of the De Lutte-6 borehole, The Netherlands: implications for evolution, palaeoecology and biostratigraphy: Review of Palaeobotany and Palynology, v. 188, p. 18–37.

Van Leckwijck, W.P., 1964, Rapport sur les résultats des travaux de la Sous-commission de Stratigraphie du Carbonifère: Compte Rendu Cinquième Congrès Internationale de Stratigraphie et Géologie du Carbonifère (Paris, 1963), v. 1, p. 35–41.

Wagner, R.H., 1963, Stephanian B flora from the Ciñera-Matallana Coalfield (León) and neighbouring outliers. I: introduction, *Neuropteris*: Notas y Comunicaciones del Instituto Geológico y Minero de España, v. 72, p. 5–70.

Wagner, R.H., 1968, Upper Westphalian and Stephanian species of *Alethopteris* from Europe, Asia Minor and North America: Mededelingen Rijks Geologische Dienst, Serie C, v. 3–1(6), p. 1–319.

Wagner, R.H., 1984, Megafloral zones of the Carboniferous: Compte Rendu Neuvième Congrès Internationale de Stratigraphie et Géologie du Carbonifère (Washington and Champaign-Urbana, 1979), v. 2, p. 109–134.

Wagner, R.H., and Álvarez-Vázquez, C., 2008, A revision of the lower Pennsylvanian *Alethopteris lonchitica* (*auctorum*) and its identity with *Alethopteris urophylla*: Revista Española de Paleontología, v. 23, p. 157–192.

Wagner, R.H., and Lyons, P.C., 1997, A critical analysis of the higher Pennsylvanian megafloras of the Appalachian region: Review of Palaeobotany and Palynology, v. 95, p. 255–283.

Wahlman, G.P., 2013, Pennsylvanian to Lower Permian (Desmoinesian-Wolfcampian) fusulinid biostratigraphy of Midcontinent North America: Stratigraphy, v. 10, p. 73–104.

Walton, J., 1936, On the factors which influence the external form of fossil plants; with descriptions of the foliage of some species of the Palaeozoic equisetalean genus *Annularia* Sternberg: Philosophical Transactions of the Royal Society of London, Series B–Biological Sciences, v. 226, p. 219–237.

Wanless, H.R., and Shepard, F.P., 1935, Permo-Carboniferous coal series related to Southern Hemisphere glaciation: Science, v. 81, p. 521–522.

Wanless, H.R., and Shepard, F.P., 1936, Sea level and climatic changes related to late Paleozoic cycles: Geological Society of America Bulletin, v. 47, p. 1177–1206.

Watney, W.L., Wong, J.-C., and French, J.A., 1989, Computer simulation of Upper Pennsylvanian (Missourian) carbonate-dominated cycles in western Kansas, *in* Franseen, E.K., Watney, W.L., Kendall, C.G.S., and Ross, W., eds., Sedimentary Modeling: Computer Simulations and Methods for Improved Parameter Definition: Kansas Geological Survey Bulletin, v. 233, p. 415–430.

Weiss, C.E., 1881, Beobachtungen an Calamiten und Calamarien: Neues Jahrbuch für Mineralogie, Abhandlungen, v. 2, p. 272–274.

Weiss, C.E., and Sterzel, J.T., 1893, Die Sigillarien der preußichen Steinkohlen und Rothleigenden Gebiete. Teil 2: Abhandlungen der Königlich Preussischen geologischen Landesanstalt, Neue Folge, v. 2, p. 1–255.

White, D., 1893, Flora of the outlying Carboniferous basins of southwestern Missouri: United States Geological Survey Bulletin, v. 98, p. 1–139.

White, D., 1899a, Fossil Flora of the Lower Coal Measures of Missouri: United States Geological Survey Monographs, v. 37, p. 1–467, pls. 1–73.

White, D., 1899b, Report on fossil plants from the McAlester Coal Field, Indian Territory, collected by Messrs. Taff and Richardson in 1897: Nineteenth Annual Report of the United States Geological Survey to the Secretary of the Interior (1897–1898), Part 3 (Economic Geology), p. 457–538, pls. 67, 68.

White, D., 1909, The Upper Paleozoic floras, their succession and range: Journal of Geology, v. 17, p. 320–341.

White, D., 1943, Lower Pennsylvanian species of *Mariopteris*, *Eremopteris*, *Diplothmema*, and *Aneimites* from the Appalachian region: United States Geological Survey Professional Paper, v. 197C, p. C85–C140, pls. 8–39.

Willard, D.A., Phillips, T.L., Lesnikowska, A.D., and DiMichele, W.A., 2007, Paleoecology of the Late Pennsylvanian-age Calhoun coal bed and implications for long-term dynamics of wetland ecosystems: International Journal of Coal Geology, v. 69, p. 21–54.

Wilson, L.R., and Venkatachala, B.S., 1963, *Thymospora*, a new name for *Verrucososporites*: Oklahoma Geological Survey, Oklahoma Geology Notes, v. 23, p. 75–79.

Wing, S.L., and DiMichele, W.A., 1995, Conflict between local and global changes in plant diversity through geological time: Palaios, v. 10, p. 551–564.

Wittry, J., 2006, The Mazon Creek Fossil Flora: Downers Grove, ESCONI Associates, 154 p.

Witzke, B.J., 1990, Palaeoclimatic constraints for Palaeozoic palaeolatitudes of Laurentia and Euramerica, *in* McKerrow, W.S., and Scotese, C.R., eds., Palaeozoic Palaeogeography and Biogeography: Geological Society of London Memoir, v. 12, p. 57–73.

Wnuk, C., 1985, The ontogeny and paleoecology of *Lepidodendron rimosum* and *Lepidodendron bretonense* trees from the Middle Pennsylvanian of the Bernice Basin (Sullivan County, Pennsylvania): Palaeontographica Abteilung B (Palaeophytologie), v. 195, p. 153–181.

Wood, H.C., 1860, Contributions to the Carboniferous flora of the United States: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 12, p. 236–240, pls. 4–6.

Wood, H.C., 1869, A contribution to the knowledge of the flora of the Coal Period in the United States: Transactions of the American Philosophical Society (New Series), v. 13, p. 341–349, pls. 8, 9.

Wood, J.M., 1963, The Stanley Cemetery Flora (Early Pennsylvanian) of Greene County, Indiana: Indiana Geological Survey Bulletin, v. 29, p. 1–73, pls. 1–12.

Zeiller, R., 1878-79a, Explication de la Carte Géologique de la France, Tome Quatrième, Seconde Partie, Végétaux Fossiles du Terrain Houiller (1879), pls. CLIX–CLXXVI (1878): Service de la Carte Géologique de la France, Paris, p. 1–185.

Zeiller, R., 1879b, Presentation de l'Atlas du Tome IV de l'Explication de la Carte Géologique de la France, et note sur le genre *Mariopteris*: Bulletin de la Société Géologique de France (Série 3), v. 7, p. 92–99.

Zeiller, R., 1883, Fructifications de fougères du terrain houiller: Annales des Sciences Naturelles, (Sixième Série, Botanique), v. 16, p. 177–209, pls. 9–12.

Zeiller, R., 1886-88, Bassin Houiller de Valenciennes. Description de la Flore Fossile. Études des Gîtes Minéraux de la France: Paris, Ministère des Travaux Publics, p. 1–729 (1888), pls. 1–94 (1886).

Zenker, F.C., 1833, Beschreibung von *Galium sphenophylloides*: Neues Jahrbuch für Mineralogie Geognosie, Geologie und Petrefaktenkunde, v. 4, p. 398–400.

Zodrow, E.L., 1986, Succession of paleobotanical events: evidence for mid-Westphalian D floral changes, Morien Group (Late Pennsylvanian, Nova Scotia): Review of Palaeobotany and Palynology, v. 47, p. 293–326.

Zodrow, E.L., 1989, Revision of Silesian sphenophyll biostratigraphy of Canada: Review of Palaeobotany and Palynology, v. 58, p. 301–331.

Zodrow, E.L., 2003, Foliar forms of *Macroneuropteris scheuchzeri* (Pennsylvanian, Sydney Coalfield, Nova Scotia, Canada): Atlantic Geology, v. 39, p. 23–37.

Zodrow, E.L., and Cleal, C.J., 1985, Phyto- and chronostratigraphical correlations between the late Pennsylvanian Morien Group (Sydney, Nova Scotia) and the Silesian Pennant Measures (south Wales): Canadian Journal of Earth Sciences, v. 22, p. 1465–1473.

Zodrow, E.L., and Cleal, C.J., 1988, The structure of the Carboniferous pteridosperm frond *Neuropteris ovata* Hoffmann: Palaeontographica Abteilung B (Palaeophytologie), v. 208, p. 105–124.

Zodrow, E.L., and Cleal, C.J., 1998, Revision of the Pteridosperm foliage *Alethopteris* and *Lonchopteridium* (Upper Carboniferous), Sydney Coalfield, Nova Scotia, Canada: Palaeontographica Abteilung B (Palaeophytologie), v. 247, p. 65–122.

Zodrow, E.L., and Mastalerz, M., 2009, A proposed origin for fossilized Pennsylvanian plant cuticles by pyrite oxidation (Sydney Coalfield, Nova Scotia, Canada): Bulletin of Geosciences, v. 84, p. 227–240.

Zodrow, E.L., and McCandlish, K., 1980, Upper Carboniferous Fossil Flora of Nova Scotia in the Collections of the Nova Scotia Museum; with Special Reference to the Sydney Coalfield: Halifax, Nova Scotia Museum, 275 p.

Zodrow, E.L., Šimůnek, Z., and Bashforth, A.R., 2000, New cuticular morphotypes of "*Cordaites principalis* (Germar) Geinitz" from the Canadian Carboniferous Maritimes Basin: Canadian Journal of Botany, v. 78, p. 135–148.

Zodrow, E.L., D'Angelo, J.A., Werner-Zwanziger, U., and Chen, B., 2014, Hair-trichomes-files, and spectrochemistry of *Macroneuropteris scheuchzeri* (Basal Cantabrian, Sydney Coalfield, Canada): Palaeontographica Abteilung B (Palaeophytologie), v. 290, p. 141–153.