



## Research paper

# The Okmulgee, Oklahoma fossil flora, a Mazon Creek equivalent: Spatial conservatism in the composition of Middle Pennsylvanian wetland vegetation over 1100 km

Lillien C. Moore<sup>a</sup>, Jack Wittry<sup>b</sup>, William A. DiMichele<sup>a,\*</sup><sup>a</sup> Department of Paleobiology, NMNH Smithsonian Institution, Washington, DC 20560, USA<sup>b</sup> Science and Education, The Field Museum, Chicago, IL, 60605, USA

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## ABSTRACT

Temporal compositional conservatism of late Middle Pennsylvanian wetland vegetation and persistence of its dominance–diversity structure through time spans of millions of years have been documented from many places in North America and Europe. This conservatism occurs within the context of glacial–interglacial fluctuations that force spatial migration of that vegetation or its restriction to refugia during periodic sea-level changes on the craton. Although known from long temporal sequences, there have been few studies of spatial variability in these wetland floras over more than relatively small distances, generally much less than a km. Here we report a late Middle Pennsylvanian (Desmoinesian) flora from above the Henryetta Coal, near Okmulgee, Oklahoma, in the American Midcontinent. This flora is exactly correlative with the Mazon Creek flora, above the Colchester Coal of northern Illinois; the Colchester Coal and its equivalents may have been the largest, contiguous peat accumulating swamp of the Pennsylvanian. Okmulgee and Mazon Creek are separated by 1100 km, but the depositional context of the two floras is the same and they can be considered isotaphonomic. Though a much smaller sample, and thus of lower overall biodiversity, the known composition of and dominance–diversity structure of the Okmulgee flora is convergent with Mazon Creek. The overwhelmingly dominant elements of both the Okmulgee and Mazon Creek floras are pectopterid tree-fern foliage mostly attributable to *Lobatopteris vestita* (Lesquereux) Wagner and the pteridosperm *Macroneuropteris scheuchzeri* (Hoffman) Cleal, Shute and Zodrow. Both of these floras likely represent wetlands that were being drowned during the early phases of sea-level rise associated with ice melting. Each sampled a broad area, and a variety of subhabitats that fringed the Pennsylvanian coastline.

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## 1. Introduction

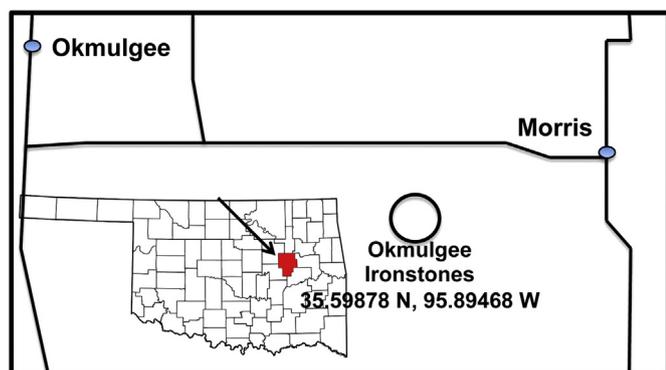
The late Middle Pennsylvanian was a time of major vegetational change across the Euramerican tropics. This change saw a rise in tree ferns in most wetland habitats (Pfefferkorn and Thomson, 1982; Phillips and Peppers, 1984; Zodrow, 1986; Cleal et al., 2009; Bashforth et al., 2010), coincident with major environmental changes in the equatorial region reflected in terrestrial sedimentary patterns (e.g., Bertier et al., 2008), the morphology of peat-forming swamps from predominantly domed to planar (Greb et al., 2002), and in the chemistry (increase in sulfates and carbonates) of terrestrial sedimentary rocks (Cecil et al., 1985). Early studies of this fern expansion, based on macrofossil adpressions, suggested that it began in mineral substrate wetlands (Pfefferkorn and Thomson, 1982), prior to a similar but slightly later expansion documented by the coal-ball record (mainly North

American – e.g., Phillips et al., 1985). More recent palynological data, however, suggest dominance or co-dominance of tree ferns in peat swamps fringing the Variscan mountain belt in Europe as early as the middle Middle Pennsylvanian (earliest Asturian) (Dimitrova et al., 2005; Cleal et al., 2009; Falcon-Lang et al., 2012; Pendleton et al., 2012; Stolle, 2012). This increase in tree ferns during the late Middle Pennsylvanian, principally the Late Moscovian (Desmoinesian, Asturian), was punctuated by a much larger vegetational turnover at the Middle–Late Pennsylvanian boundary (Desmoinesian–Missourian, approximately Moscovian–Kasimovian, within the Cantabrian), following which tree ferns became the dominant plants in Late Pennsylvanian (Kasimovian, Stephanian) peat swamps, and dominant-to-subdominant in many other kinds of wetland habitats (Phillips et al., 1974; Pfefferkorn and Thomson, 1982; Wagner and Álvarez-Vázquez, 2010; Bashforth et al., 2011).

Although such temporal patterns are now reasonably well established, there have been few studies of the spatial variation in the affected vegetation, and most of these have been on scales of meters to less than a kilometer (e.g., Gastaldo et al., 2004; DiMichele et al., 2007; Opluštil et al., 2009; Wang et al., 2012). These smaller scale studies

\* Corresponding author.

E-mail addresses: [dinoexpert@gmail.com](mailto:dinoexpert@gmail.com) (L.C. Moore), [wittry@yahoo.com](mailto:wittry@yahoo.com) (J. Wittry), [dimichel@si.edu](mailto:dimichel@si.edu) (W.A. DiMichele).



**Fig. 1.** Location of Okmulgee Ironstone collecting site. Inset: Okmulgee County (shaded, at arrow). Location of sample site south at circle, between Morris and Okmulgee. State map courtesy of Wikipedia.

have revealed a great deal of compositional variation from site to site, leaving open the question of the degree to which such heterogeneity “scales up” to larger, broad landscape scales. Widespread homogeneity would suggest that smaller scale variability may reflect the effects of local dispersal limitation and may be averaged-out, disappearing into the background of the widespread and low diversity, wetland species pool. The major constraints on comparisons over broad spatial scales are confident correlation at a sufficiently fine scale to be able to bracket time to within an “ecological” time frame of 10 s to 100 s of years, and to limit the comparison to assemblages preserved in similar depositional settings, so-called “isotaphonomic” comparisons (Behrensmeyer and Kidwell, 1985).

The flora described here, from the roof of the Henryetta Coal in eastern Oklahoma, is temporally, sedimentologically and taphonomically comparable to the much larger and better known Mazon Creek flora from north-central Illinois (Peppers and Pfefferkorn, 1970; Pfefferkorn, 1979). The floras come from shales that rest directly on coals that, by a variety of means, have been correlated as time equivalent (Meyers, 1967; Smith, 1970). Both floras are preserved in near-shore fresh to brackish water mudstones, with the plants preserved in siderite concretions. Each flora also represents a variety of coastal habitats extant during the early phases of coastal flooding during Late Glacial or Early Interglacial phases of the Verdigris glacial–interglacial cycle (Cecil et al., 2003).

In addition, the Okmulgee flora is one of comparatively few adpression floras described in the past 50 years from the critical late Middle Pennsylvanian interval. In contrast to many such floras described from Europe (e.g., Wagner, 1962, 1971; Thomas and Cleal,

2001; Cleal, 2004, 2005, 2007; Cleal et al., 2004; Šimůnek, 2008; Libertín et al., 2009; Opluštil et al., 2009; Bashforth et al., 2010; Wagner and Álvarez-Vázquez, 2010), there are relatively few from the United States (Langford, 1958; Basson, 1968; Boneham, 1974; Gastaldo, 1977; Pheifer, 1979; Oleksyshyn, 1982; Wittry, 2006). The current study thus is a baseline that helps establish the composition and structure of coastal wetlands prior to the major changes in vegetation that took place at the Middle–Late Pennsylvanian boundary.

## 2. Geological background

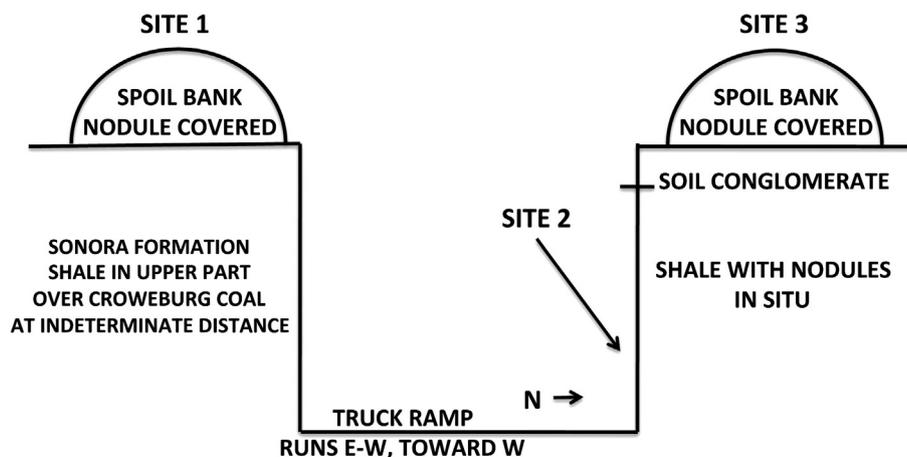
### 2.1. Location and stratigraphy

The fossils described in this report were collected in an abandoned mine east of Okmulgee, Oklahoma (Fig. 1) by Joseph Wood, then of the University of Missouri. The mine is located on the Okmulgee North 71/2' Quadrangle, E 1/2 SE 1/4 Section 14 T13N R14E, which translates to 35.59878° N, 95.89468° W. According to Wood (1961 – field notes), natural exposures of the nodule-bearing shales crop out in the hills of the local area.

The Henryetta coal bed was being mined at this location. It is stratigraphically equivalent to the better known Croweberg coal of northeastern Oklahoma (Meyers, 1967). The Croweberg coal, based on physical stratigraphy (Wanless, 1955) and palynological composition (Peppers, 1970; Wilson, 1979), is equivalent to the Colchester (No. 2) Coal Member of the Illinois Basin. Together these coal beds, and their Appalachian equivalent, the Lower Kittanning coal, may have formed one of the areally most extensive, contemporaneous peat forming environments of the Middle Pennsylvanian (Greb et al., 2003). The collecting site lies within the western Arkoma Basin and is within 70 km of the northern margin of the Ouachita Mountains. The Ouachita Orogeny, which culminated in Late Atokan time (Late Bolsovian, Middle Moscovian), uplifted the Ouchita Mountains, which were a major source of sediment to the Arkoma Basin (Houseknecht, 1983).

Wood's field notes indicate that the collecting area was mined circa 1945–1948. An exposure of the coalface remained, revealing a seam about 75 cm (2 1/2 ft) thick. The coal bed may have been thicker in the mined-out areas and Wood estimated maximum thickness to have been 1.2–2 m or more (4–>6 ft). He suggests, for reasons not elaborated in his field notes, that the area of thick coal was of limited areal extent.

The ironstone nodules described herein were collected from spoils in this mine prior to 1959 and from June 4, 1961 to July 5, 1961, based on Wood's field notes and correspondence. Collections were made at five sites. Sites one, two and three (Fig. 2) all were in the same general location. Site four was 200 yards from a truck ramp into the abandoned



**Fig. 2.** Location of sampling sites 1–3 in abandoned strip mine. Redrawn from field notes of Dr. Joseph Wood, Monday, June 5, 1961. Original notes in National Museum of Natural History collections

**Table 1**

Okmulgee ironstone flora. Taxa organized by Linnean Class, occurrences by quadrat (hand sample), and frequency of occurrence (percentage of hand-samples on which the plant category was identified). *Incertae sedis* is unreported in the table but included in calculations: Indeterminate axes (250 occurrences, 15.6%), roots (39 occurrences, 2.4%), interesting unidentified things (15 occurrences, <1%).

Taxon	Count	Frequency
<b>LYCOPSIDA</b>		
<i>Lepidodendron aculeatum</i>	2	<1
<i>Synchysidendron andrewsii</i>	145	9.1
<i>Diaphorodendron rimosum</i>	82	5.1
<i>Lepidodendron wortheni</i>	1	<1
Indeterminate lepidodendrids	33	2.1
Lycopsid leaves & reproductive organs	117	7.3
<b>SPHENOPSISIDA</b>		
<i>Annularia spinulosa</i>	58	3.6
<i>Annularia radiata</i>	6	<1
<i>Annularia sphenophylloides</i>	173	10.8
<i>Asterophyllites equisetiformis</i>	8	<1
Calamitalean stems	122	7.6
<i>Sphenophyllum</i>	2	<1
<b>FILICOPSIDA</b>		
<i>Lobopteris vestita</i>	442	27.6
<i>Pecopteris subcrenulata</i>	8	<1
<i>Pecopteris unita</i>	3	<1
Indeterminate pecopterids	128	8.0
<i>Oligocarpia gutberi</i>	4	<1
<b>SPERMATOPSIDA—PTERIDOSPERMS</b>		
<i>Macroneuropteris scheuchzeri</i>	433	27.1
<i>Odontopteris subcuneata</i>	2	<1
<i>Odontopteris aequalis</i>	1	<1
<i>Eusphenopteris neuropteroides</i>	1	<1
<i>Laveineopteris rarineris</i>	91	5.7
<i>Alethopteris serlii</i>	1	<1
<i>Alethopteris lonchitica</i>	1	<1
<i>Karinopteris plumosa</i>	95	5.9
<i>Eusphenopteris</i> sp.	9	<1
<i>Codontotheca caduca</i>	57	3.6
<b>SPERMATOPSIDA—CORDAITALES</b>		
Cordaitalean remains	15	<1
Specimens with >1 taxon	300	
Total specimens examined	1600	

mine, which was located near site two. Site five, is approximately 3/4 of a mile north of the other sites, but still on the east side of the local hills.

The gray roof-shale facies of the Colchester coal in the northern portion of the Illinois Basin is designated the Francis Creek Shale Member. This shale contains the ironstone nodules from which the Mazon Creek flora and fauna have been collected (see Wittry, 2006, 2012), and is equivalent to shales overlying the Croweburg–Henryetta coals in Oklahoma (Smith, 1970). These rocks are of Late Desmoinesian Age

(Peppers, 1996), equivalent to the Late Moscovian. Based on the number of major and minor cyclothem (glacial–interglacial cycles), with an average of approximately 140,000 years each, grouped into larger cycles of approximately 400,000 years (Heckel, 2008; Falcon-Lang et al., 2011a; Eros et al., 2011), the Colchester coal and its equivalents are as much as 1.5–2 million years older than the wetland plant turnover that takes place at the Desmoinesian–Missourian (Middle–Late Pennsylvanian) boundary (Phillips et al., 1974; Falcon-Lang et al., 2011a).

## 2.2. Collection history

The Okmulgee ironstone nodule collection was made in an unbiased manner by Wood and his assistants. Wood's notes explain that the specimens were not prepared in the field. As a consequence, there was no pre-selection targeting certain taxa or qualities of preservation. Furthermore, no mention is made of later collection culling, which is consistent with the composition of the NMNH collection, which includes all manner of plant remains, including unidentifiable organic debris. As such, this is a good example of a museum collection that effectively captures original compositional character of the fossil assemblage (King et al., 2011). The 1600 specimens that make up the collection presumably were kept because of their fossiliferous content, while non-fossiliferous nodules were being disposed of.

Of the five sites from which fossils were collected, specimens from sites one, three, and five form the basis of this paper. Sites one and three were both spoil banks and covered with nodules. Site five had both compressions preserved in shales and surface nodules. Only compression fossils, which were not considered in this analysis because of small sample sizes, were collected at sites two and four.

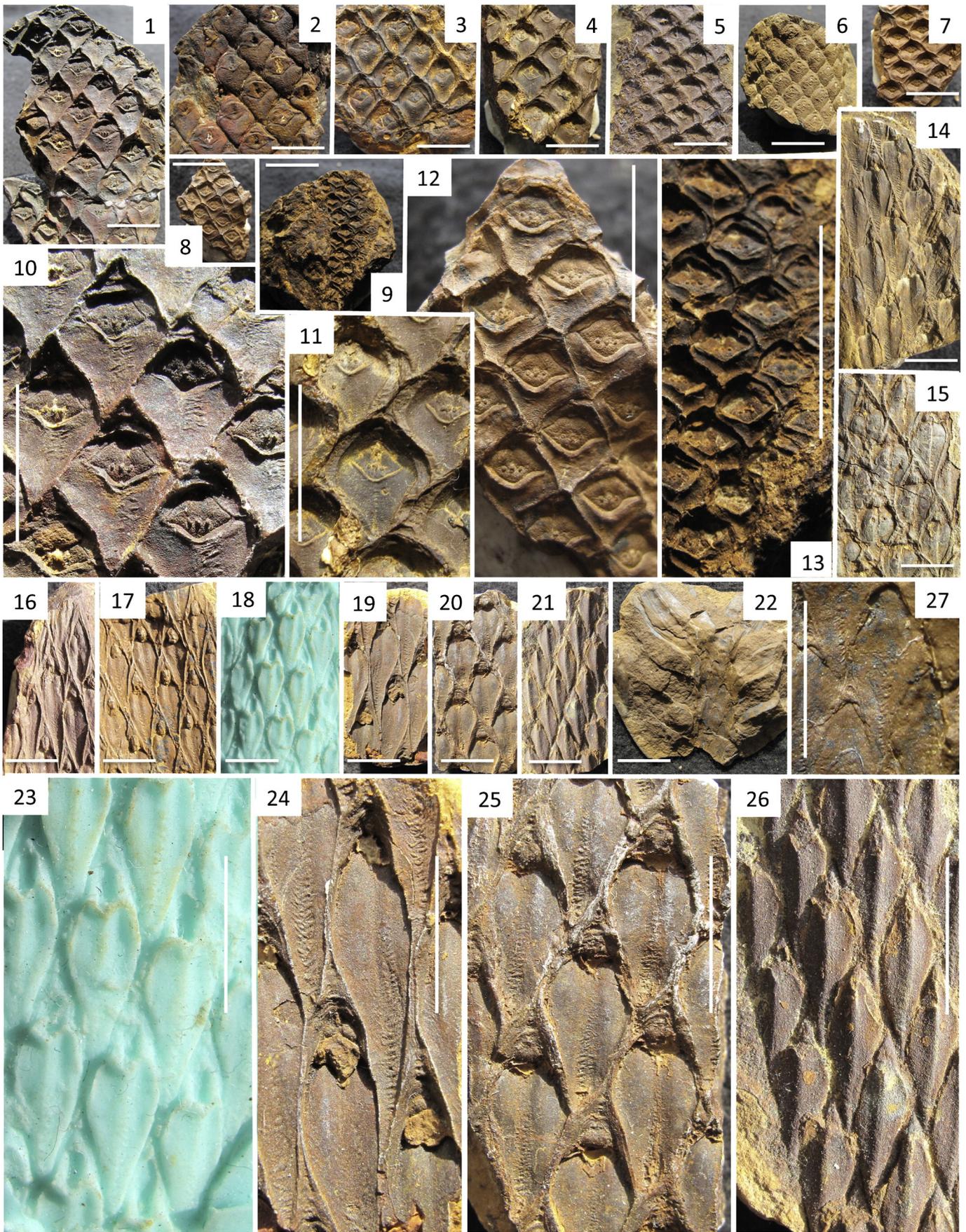
## 3. Flora

### 3.1. Quantitative composition

The Okmulgee flora contains 22 whole-plant species, based on stem remains as proxy for whole plants in arborescent lycopsids, and vegetative foliage as proxy in ferns, sphenopsids, pteridosperms and cordaitaleans (Table 1). The flora was quantified by treating each nodule as a “quadrat”, a technique developed by Pfefferkorn et al. (1975), in which any number of single specimens on a given quadrat is recorded as one occurrence. This means, of course, that more than one taxon may be recorded and that the final count data represent frequencies.

**Plate I.** Diaphorodendraceae: *Synchysidendron andrewsii* and *Diaphorodendron rimosum*. Sequences of specimens showing progression from larger to smaller diameter axes, proximal to distal stages of determinate growth.

- 1–13. *Synchysidendron*. Diminution of stem diameter is accompanied by progressive diminution of leaf-cushion size and shape change from more to less elongate.
- 1 & 10. Specimen USNM546911, surface mold, scale bars = 1 cm.
2. Specimen USNM546912, surface cast, scale bar = 1 cm.
3. Specimen USNM546917, surface mold, scale bar = 1 cm.
- 4 & 11. Specimen USNM546918, surface mold, scale bars = 1 cm.
5. Specimen USNM546919, surface mold, scale bar = 1 cm.
6. Specimen USNM546916, surface cast, scale bar = 1 cm.
7. Specimen USNM546916, surface mold, scale bar = 1 cm.
- 8 & 12. Specimen USNM546915, surface mold, scale bars = 1 cm.
- 9 & 13. Specimen USNM546914, surface mold, scale bars = 1 cm. Note enlargement of this specimen is greater than that of others.
- 14–27. *Diaphorodendron*. Leaf cushion proportions are retained as stem diameter diminishes. Specimen illustrated in 9 has leaves still adherent to the stem. Leaf scars are obscured in most specimens suggesting the presence of attached leaves preserved to outside of mold surfaces or separated from cast surfaces along fracture plane.
14. Specimen USNM546923, surface mold, scale bar = 1 cm.
15. Specimen USNM546925, surface mold, scale bar = 1 cm.
16. Specimen USNM546926, surface mold, scale bar = 1 cm.
17. Specimen USNM546921, surface mold, scale bar = 1 cm.
- 18 & 23. Specimen USNM546921, silicone cast of specimen illustrated in Plate I, 17, scale bars = 1 cm.
- 19 & 24. Specimen USNM546927, surface mold, scale bars = 1 cm.
- 20 & 25. Specimen USNM546920, surface mold, scale bars = 1 cm.
- 21 & 26. Specimen USNM546924, surface cast, scale bars = 1 cm.
- 22 & 27. Specimen USNM546922, surface mold. Specimen with attached leaves visible in Plate I, 22. Very small leaf cushions enlarged in Plate I, 27. Scale bars = 1 cm.



Hypothetically, each taxon could be represented on 100% of the quadrats. Of 1600 nodules examined, 300 contained more than one taxon.

The most abundant group is the pectopterid ferns. Among the pectopterids, *Lobopteris vestita* sensu Wagner was the most abundant, consisting of 442 occurrences, a frequency of 27.6%. The other most common taxon was *Macroneuropteris scheuchzeri*, which at 433 occurrences, 27.1%, was nearly as common as *L. vestita* sensu Wagner. Calamitaleans (257 occurrences, ~16% frequency) and lycopsids (380 occurrences, ~24% frequency) were only slightly less abundant. These abundances are reported as approximations because of error that will result from adding frequency occurrences; there is a small amount of co-occurrence of various reported categories, such as foliage and stems that will inflate apparent abundance. The most common calamitalean foliage was *Annularia sphenophylloides* (173 occurrences, 10.8% frequency), with *Annularia spinulosa* a distant second (58 occurrences, 3.6% frequency). The most common lycopsid stem remains were *Synchysidendron andrewsii* (145 occurrences, 9.1% frequency) and *Diaphorodendron rimosum* (82 occurrences, 5.1% frequency). Of minor importance were *Karinopteris plumosa* (95 occurrences, 5.9% frequency) and *Laveinopteris rarineris* (91 occurrences, 5.7% frequency). All other taxa are present only in minor amounts. A common, but taxonomically uninformative category was “indeterminate axes”, likely a mixture of stems and foliar axes, which accounted for 250 occurrences (15.6% frequency). In this category there may be “hidden” occurrences of cordaitalean foliage, which, in fragmentary preservation, may be difficult to separate from axes of pteridosperms and ferns, wherein longitudinally disposed sclerenchyma bands may appear similar to leaf veins in poor preservation, especially if the axes are highly flattened and essentially two dimensional.

### 3.2. Systematics

Division Tracheophyta

Class Lycopsidea

Order Isoetales

Family Diaphorodendraceae

Genus ***Synchysidendron*** DiMichele and Bateman (1992)

*Synchysidendron andrewsii* (Lesquereux) Moore, Wittry and DiMichele comb. nov., nov. emend.

**Basionym;** Lesquereux, 1880. Description of the coal flora of the Carboniferous Formation in Pennsylvanian and throughout the United States, Volume I. Second Geological Survey of Pennsylvania: Report of Progress, P, Text, 1880, p. 389; Atlas, 1979, pl. LXIV, fig. 6.

**Emended diagnosis.**—Arborescent lycopsid stem. Leaf cushions longer than wide, shape changing from elongate to nearly equidimensional as stem diameter decreases. Leaf cushions protuberant, clearly distinct from adjacent leaf cushions, with upper and lower angles rounded, straight to slightly curved oppositely. Upper and lower keels present, weakly developed, with plications on lower keel in many specimens. Lateral lines present, extending from lateral angles of leaf scar to leaf-cushion margin in low arc, weakly developed. Leaf scar wider than

high, in upper 1/2 of leaf cushion, occupying progressively more of leaf-cushion area as leaf-cushion size diminishes. Vascular trace scar flanked at same horizontal level by two parichnos scars. No infrafoliar parichnos present below leaf scar.

**Description.**—*Synchysidendron andrewsii* is a lycopsid stem with leaf cushions that are generally longer than wide (Plate I, 1–4, 10–11) but become nearly equidimensional on smaller axes as cushion size becomes smaller overall (Plate I, 5–9, 12–13). A series of specimens with progressively smaller leaf cushions illustrates this change in shape (Plate I, 1–13). Details of these leaf cushions show that they are somewhat protuberant from the stem surface (note particularly Plate I, 2, the positive counterpart of Plate I, 1). They have weakly developed upper and lower keels with folds on the lower keels in many, but not all specimens (Plate I, 10–12). The leaf scar is generally wider than high and bears the typical leaf scar in which a vascular strand is flanked by foliar parichnos strands in the lower part of the scar. Leaf scars also are smaller on smaller cushions, but take up a proportionally larger part of the cushion surface as stem diameter shrinks; consequently the scar becomes more prominent on the smaller cushions (Plate I, 12–13). The leaf cushions are clearly distinct from one another and may be separated by thin interareas. Their tails may be slightly curved, in opposite directions. The upper and lower tips of the cushions, while triangular, are bluntly rounded.

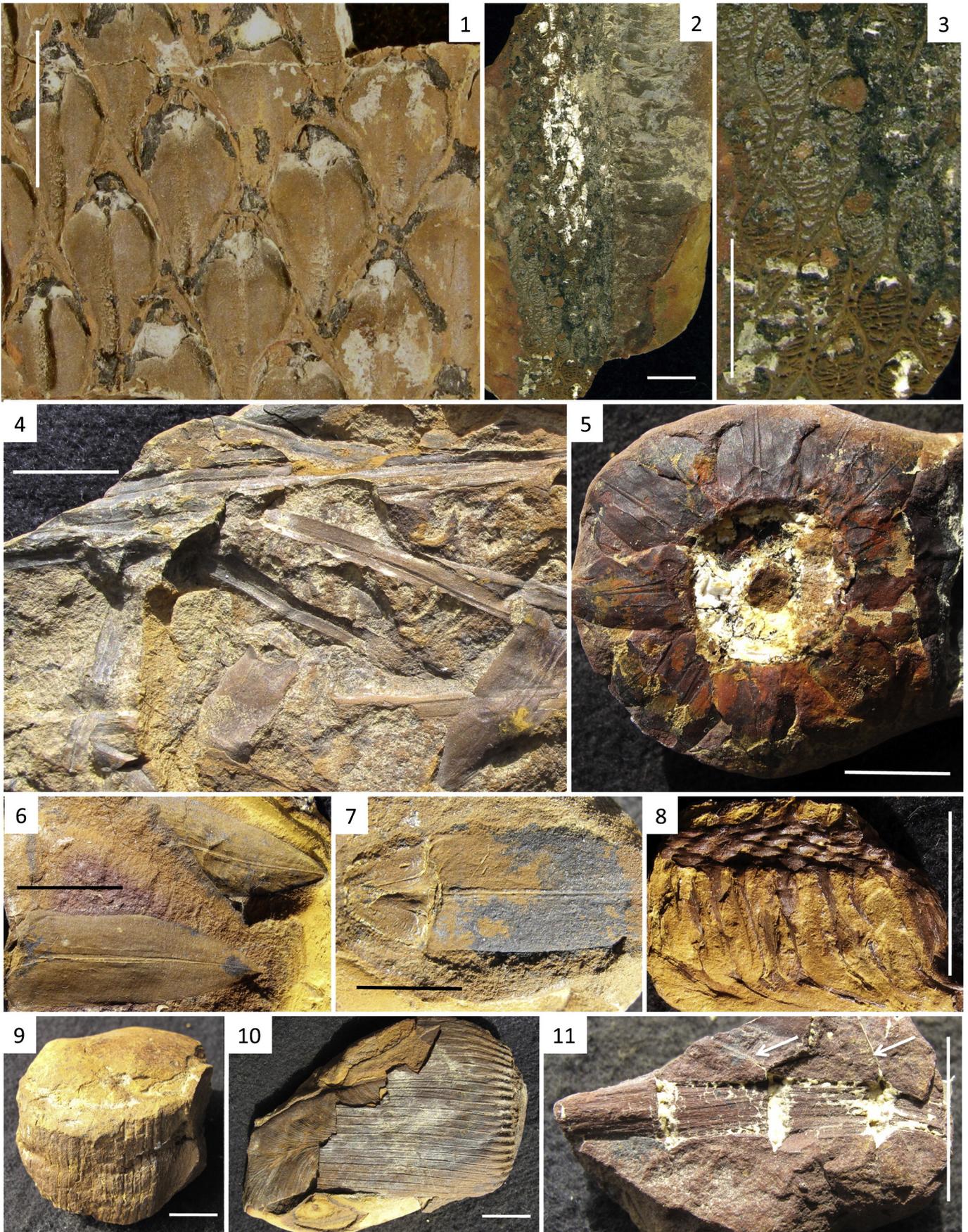
**Type specimen.**—United States National Museum Specimens 15430 and 15431 (part and counterpart), Francis Creek Shale, Carbondale Formation, Middle Pennsylvanian (Desmoinesian), Illinois.

**Occurrence.**—Middle Pennsylvanian

**Remarks.**—*Synchysidendron andrewsii* was originally described by Lesquereux (1880) from an ironstone nodule collected from the Francis Creek Shale Member of the Carbondale Formation, source of the Mazon Creek flora. The original specimen is small, likely from the more terminal portions of a lateral branch system, and leaf cushions consequently have the somewhat square, protuberant nature found in all smaller specimens of this species. It is rediagnosed here in light of a larger sample size that shows a greater range of morphological variation. The species has been considered to belong to *Lepidodendron* on the basis of higher-than-wide leaf cushions that also bear a clear leaf scar in the upper half, and have upper and lower keels. The traditional generic concept is based upon this small number of characteristics of which all are plesiomorphic (Bateman et al., 1992; DiMichele and Bateman, 1992), characteristic of a wide array of lepidodendrids. Phylogenetically informative attributes of leaf-cushions are revealed by their correlation with the much larger suite of anatomical characteristics known from these plants (see papers by DiMichele, 1979, 1980, 1983, 1985; DiMichele and Bateman, 1992; Bateman et al., 1992, and further references cited in these papers), including correlations with reproductive organs. The change in leaf-cushion shape, as a function of stem diameter, characteristic of this species, accompanies developmental determinate growth, a process that Eggert (1961) described as apogogenesis, the final phase of growth prior to termination. Recent evidence (DiMichele et al., 2013)

**Plate II.** *Lepidodendron aculeatum*, *Lepidodendron worthenii*, lycopsid leaves and reproductive structures, sphenopsid stems.

1. *Lepidodendron aculeatum*, Field Museum of Natural History Specimen PP55127, Morris, Okmulgee County, Oklahoma. Scale bar = 1 cm.
- 2 & 3. *Lepidodendron worthenii*, Field Museum of Natural History Specimen PP55129, Ben Hur Mine, Henryetta, Oklahoma. Note leaves attached on both sides, but particularly visible on the right-hand side of the specimen. Enlargement of leaf cushions showing characteristic serpentine shape, long upper and lower tails, and wrinkles across the entire leaf-cushion surface. Scale bars = 1 cm.
4. Typically narrow, elongate, single-veined lycopsid leaves. Note also the *Lepidostrobohyllum* in the lower right corner, Specimen USNM546931, scale bar = 1 cm.
5. Lycopsid cone, transverse fracture providing a view of the bottom of a helix of *Lepidostrobohyllum* attached to the central cone axis, Specimen USNM546928, scale bar = 1 cm.
6. *Lepidostrobohyllum*, distal laminae from lycopsid cones, probably megasporangiate, Specimen USNM546929, scale bar = 1 cm.
7. *Lepidostrobohyllum*, distal lamina from lycopsid cone, probably megasporangiate, Specimen USNM558405, scale bar = 1 cm.
8. Lycopsid cone, probably microsporangiate, in longitudinal section, showing low-angle sporophyll laminae and high-angle distal laminae, Specimen USNM546930, scale bar = 1 cm.
9. Calamitalean stem cast, likely originally preserved in upright position, cast in siltstone, Specimen USNM546942, scale bar = 1 cm.
10. Calamitalean stem adpression, showing internode with node at top of specimen. Note *Macroneuropteris scheuchzeri* pinnule immediately below calamitalean stem, Specimen USNM546944, scale bar = 1 cm.
11. Sphenopsid stem of sphenophyllalean type. Arrows indicate leaves preserved in section, Specimen USNM546945, scale bar = 1 cm.



indicates that *Synchysidendron* main trunks produced deciduous lateral branch systems, in which the cones were borne. Thus, most stem specimens of this plant are likely derived from these deciduous branch systems. Members of the Diaphorodendraceae can be distinguished most easily from true *Lepidodendron* (sensu DiMichele, 1983) by the absence of infrafoliar parichnos below the leaf scar flanking the top of the lower keel.

Álvarez-Vázquez and Wagner (in press) suggest that *Leidodendron andrewsii* is a junior synonym of *Lepidodendron decurtatum* Dawson, 1868, which they assign to the Diaphorodendraceae.

Lesquereux (1880, p. 389) bestowed the specific epithet *andrewsii* without etymological attribution. However, immediately following the description of this new species, Lesquereux (1880, p. 389) describes *Lepidodendron quadralaterale* Andrews, with which he places *Lepidodendron lesquereuxii* Andrews (1875) in synonymy. It may be presumed, therefore, that *Lepidodendron andrewsii* was named for E.B. Andrews, the author of *L. lesquereuxii*, as a reciprocal honor.

*Synchysidendron andrewsii* was the most frequently encountered of the lycopsid stems in the Okmulgee flora. The plant is by no means common, however.

Division Tracheophyta

Class Lycopsidea

Order Isoetales

Family Diaphorodendraceae

Genus **Diaphorodendron** DiMichele (1985) emend DiMichele and Bateman (1992)

*Diaphorodendron rimosum* (von Sternberg, 1820–1838) Moore, Wittry and DiMichele comb. nov., nov. emend.

**Basionym:** von Sternberg (1820). Versuch einer geognostischbotanischen Darstellung der Flora der Vorwelt: Pt. 1, Leipzig and Prague, p. 23, Taf. X, fig. 1.

**Emended diagnosis.**—Arborescent lycopsid stem. Leaf cushions significantly longer-than-wide, on stems of all diameters, do not protrude greatly from stem surface thus appearing flattened against stem, well differentiated and sometimes separated by well developed interareas. Upper and lower leaf-cushion apices acuminate pointed, tails may curve slightly. Lateral lines present, generally well developed, curving steeply from lateral angles of leaf scar to widest part of leaf cushion. Leaf scar above vertical mid-point of leaf cushion, often very near apex, somewhat longer-than-wide. Leaf trace flanked by foliar parichnos within leaf scar. Leaf trace and parichnos may be obscured by attached leaves. Lower keel prominent, generally bearing wrinkles in lower 1/2 to 1/3, where keel may expand slightly in width. Upper keel generally short but may be wrinkled. Infrafoliar parichnos lacking below leaf scar.

**Description.**—*Diaphorodendron rimosum* is a species of arborescent lycopsid stem. The leaf cushions, which clothe the outer surface of the stem, often appear narrowly spindle shaped (Plate I, 14–26). Leaf cushions have acuminate pointed tails that may curve slightly and are not confluent with one another. The cushions do not protrude greatly from the stem surface (Plate I, 23, 26). The leaf scar lies above the vertical mid-point of the cushion, and can be very near the apex. The leaf scar is somewhat longer than wide, biconvex to equilaterally triangular when well developed, and has the typical leaf trace flanked by foliar parichnos. However, most of the specimens of this study, all of which were relatively small and probably from the outer portions of crown or deciduous lateral branches, have obscure leaf scars, likely indicating the presence of attached leaves; this was clearly visible on one specimen (Plate I, 22), which had the smallest leaf cushions (Plate I, 27) of any

specimen identified as *D. rimosum*. Due to the position of the leaf scar high on the cushion, the lower keel is a prominent feature. It generally bears wrinkles in its lower 1/2 to 1/3, where the keel may expand slightly in width (Plate I, 24–25). *D. rimosum* always lacks infrafoliar parichnos flanking the upper part of the lower keel, immediately below the leaf scar.

**Type specimen.**—National Museum, Prague Specimen number E 1836. Kladno–Radnice Basin, Czech Republic, Bolsovian age, Middle Pennsylvanian. Sternberg's holotype has been photographically reillustrated by Kvaček and Straková (1997) as Plate 44, Figure 4.

**Occurrence.**—Lower and Middle Pennsylvanian.

**Remarks.**—*Diaphorodendron rimosum* was described by von Sternberg (1820–1838) from the Middle Pennsylvanian of the Czech Republic. Opluštil (2005) discusses the depositional setting of this basin. *D. rimosum*, like *Synchysidendron andrewsii*, has been considered a species of *Lepidodendron* on the basis of its higher-than-wide leaf bases, the presence of a clear leaf scar in the upper half of the leaf base, and clearly demarcated upper and lower keels and lateral lines. Wnuk (1985) was the first to suggest affinities with *Diaphorodendron*, although he did not formally emend the taxon. Similarly, Álvarez-Vázquez and Wagner (in press) suggest that this species may not belong in *Lepidodendron* sensu stricto. As a member of the Diaphorodendraceae, *D. rimosum* always lacks infrafoliar parichnos flanking the upper part of the lower keel, immediately below the leaf scar, which, as in *S. andrewsii* readily permits differentiation from true *Lepidodendron* of the Lepidodendraceae (see Bateman et al., 1992). *D. rimosum* produced deciduous lateral branch systems, in which the cones were borne, and thus the vast majority of fossiliferous material is most likely derived from these lateral branches, rather from main trunks or the crown branches.

The name *Diaphorodendron* is derived from the Greek words diaphoros (different) and dendron (tree) (DiMichele, 1985). The specific epithet *rimosum* refers to elongate “cracked” nature of the interareas found between leaf bases of the type specimen, characteristic of larger stems of the species (“cortice inter squamas distantes rimoso” — von Sternberg, 1820–1838).

*Lepidodendron rimosum* was a common, but by no means abundant, element in the Okmulgee collection.

Division Tracheophyta

Class Lycopsidea

Order Isoetales

Family Lepidodendraceae

Genus **Lepidodendron** von Sternberg (1820)

*Lepidodendron aculeatum* von Sternberg (1820)

**Description.**—This species is represented by a single specimen in the NMNH collections that has the typical features of relatively large leaf cushions with distinct lower and upper keels, distinct lower keel “bars” or folds, slightly to highly curved tails, and well marked lateral lines that define the upper field. Above the cushion midpoint, there is a relatively small and nearly equidimensional leaf scar that bears the prints of the vascular trace and flanking foliar parichnos. Flanking the keel, slightly below the leaf scar, is a pair of infrafoliar parichnos.

**Remarks.**—One specimen of this iconic lepidodendrid lycopsid was found in the NMNH collections. An additional specimen was located at the Field Museum of Natural History (Plate II, 1). *Lepidodendron* has a distinctive anatomy (DiMichele, 1983) that distinguishes it from other Euramerican lepidodendrids with higher-than-wide leaf cushions.

**Plate III.** Calamitalean foliage.

- 1 & 2. *Annularia spinulosa* of a form similar to *A. radiata*, part (1) and counterpart (2), Specimen USNM546934, scale bars = 1 cm.
3. *Annularia spinulosa*, Specimen USNM546938, scale bar = 1 cm.
4. *Annularia spinulosa*, Specimen USNM546939, scale bar = 1 cm.
5. *Annularia spinulosa*, Specimen USNM546935, scale bar = 1 cm.
- 6 & 7. *Annularia sphenophylloides*, Specimen USNM546937, scale bars = 1 cm.
- 8 & 9. *Asterophyllites equisetiformis*, Specimen USNM546936, scale bars = 1 cm.



Such anatomy is similar to that of, and phylogenetically links it with, *Lepidophloios* (DiMichele, 1979) and *Hizemodendron Bateman and DiMichele* (1991) in the Lepidodendraceae (sensu Bateman et al., 1992; DiMichele and Bateman, 1996).

Division Tracheophyta

Class Lycopsidea

Order Isoetales

Family Flemingitaceae

Genus *Bergeria* Presl in von Sternberg (1838)

Species *Bergeria worthenii* (Lesquereux) Álvarez-Vázquez and Wagner (in press)

**Description.**—Leaf cushions are typical of this species and are the key characters for identification. These are higher than wide, serpentine in shape, with the tails strongly curved and confluent with leaf cushions above and below (Plate II, 2–3). The leaf scar lies above the center of the cushion and is not flanked by strongly marked lateral lines. The cushion is neither divided clearly into an upper and lower field nor does it bear clearly defined keels. The cushion surface is intensely wrinkled, both above and below the leaf scar. Infracoliar parichnos have not been identified. Leaves remain attached, though they are visible only along the margins, having been sheared off along the fracture plane on which the specimen is exposed (Plate II, 2).

**Remarks.**—*Lepidodendron worthenii* was not present in the Okmulgee collections that were analyzed in this study. The illustrated specimen (Plate II, 2–3) is from the collections of the Field Museum of Natural History and was obtained from the Ben Hur mine, near Henryetta, Oklahoma, by Dr. E.N. Kjellesvig-Waering (see Baird et al., 1985b, p. 93). The specimen is from the shale above the Henryetta coal bed.

Described as a species of *Lepidodendron* by Lesquereux (1866), this species has been so classified until very recently. Álvarez-Vázquez and Wagner (in press) suggest affinity with the genus *Bergeria*, Presl in von Sternberg, 1820–1838, which they place in the family Flemingitaceae. We concur that species may be a distinct entity at the generic level, based on the peculiar and singular aspects of its leaf cushions. The affinities of *Bergeria worthenii* would be clarified, perhaps, if anatomically preserved specimens were known. Ainsworth (1936) described the anatomy of a supposed *Lepidodendron worthenii* cone axis. However, axes of this size with wrinkled leaf cushions could equally belong to *Hizemodendron serratum* (Felix) Bateman and DiMichele (1991). This species has been identified from coal balls in coals from the Langsettian (Westphalian A) and Duckmantian (Westphalian B) of Britain and Europe, and from the Atokan through the Middle Desmoinesian of the United States and Nova Scotia (Bolsovian and Asturian), encompassing most of the Early and Middle Pennsylvanian. Additionally, small specimens of *Paralycopodites brevifolius* (Williamson) DiMichele (1980) also may have wrinkled leaf cushions and anatomy very similar to that of *H. serratum*, and *P. brevifolius* permanently retained its leaves. *P. brevifolius* likewise is known from the entire Westphalian, whereas no petrifications unquestionably identifiable as *B. worthenii* have yet been reported from this stratigraphic interval. Whereas these observations do not rule out *B. worthenii* as the identity of Ainsworth's specimen, they broaden the possible affinities.

These observations also raise the possibility that *Bergeria worthenii* might be closely related to *Paralycopodites* Morey and Morey (1977).

This latter genus, by virtue of its bisporangiate cones, would also reside in the family Flemingitaceae of Thomas and Brack-Hanes (1984). DiMichele and Bateman (1996) placed it in the parataxon Ulodendrineae, and suggested a close relationship between *Paralycopodites* and *Ulodendron* sensu Thomas (1967). Álvarez-Vázquez and Wagner (in press) refer *Ulodendron* sensu Thomas (1967) to *Bergeria*. This whole complex, according to the phylogenetic analysis of Bateman et al. (1992) and DiMichele and Bateman (1996) encompasses the basal group of lycopsids in the rhizomorphic clade.

Division Tracheophyta

Class Lycopsidea

Order Isoetales

Leaves and reproductive organs

**Leaves.**—Among the specimens in the collection are rare, fragmentary leaves of arborescent lycopsids (Plate II, 4). The leaves of these plants are narrow, with a single median vein, sessile in their attachment, and thus with a broad base, and tapered apices. They have been reported to reach lengths of over 75 cm (Kosanke, 1979). Lycopsid leaves have been assigned to several genera, including *Lepidophylloides Snigirevskaya* (1958), *Lepidophyllum* Lindley and Hutton (1831–1833) and *Cyperites* (Lindley and Hutton, 1831–1833), with the latter being the valid name for compression specimens.

**Reproductive organs.**—Reproductive organs include four strobilus fragments between 15 and 25 mm in diameter (Plate II, 8). These appear to be microsporangiate strobili, or the microsporangiate portions of bisporangiate strobili in the size range of smaller forms of *Flemingites* Carruthers (1865) (see Brack-Hanes and Thomas, 1983), the kind associated with *Paralycopodites*. Two additional strobili are fragmentary cross-sections >30 mm in diameter, with a central column approximately 13 mm in diameter (Plate II, 5). The basal laminae of the sporophylls are short, and are not well enough exposed in the study specimens to determine their length. The distal laminae are triangular in shape, approximately 2× longer than wide, with a broad base and a broadly acute apex. Larger, isolated specimens of distal laminae appear to have a sporangium at the base and are overall of larger size than those still in attachment to the central columnar axis (Plate II, 6–7). These structures in dispersed form are assignable to *Lepidostrobophyllum Hirmir* (1927).

Division Tracheophyta

Class Sphenopsida

Order Equisetales

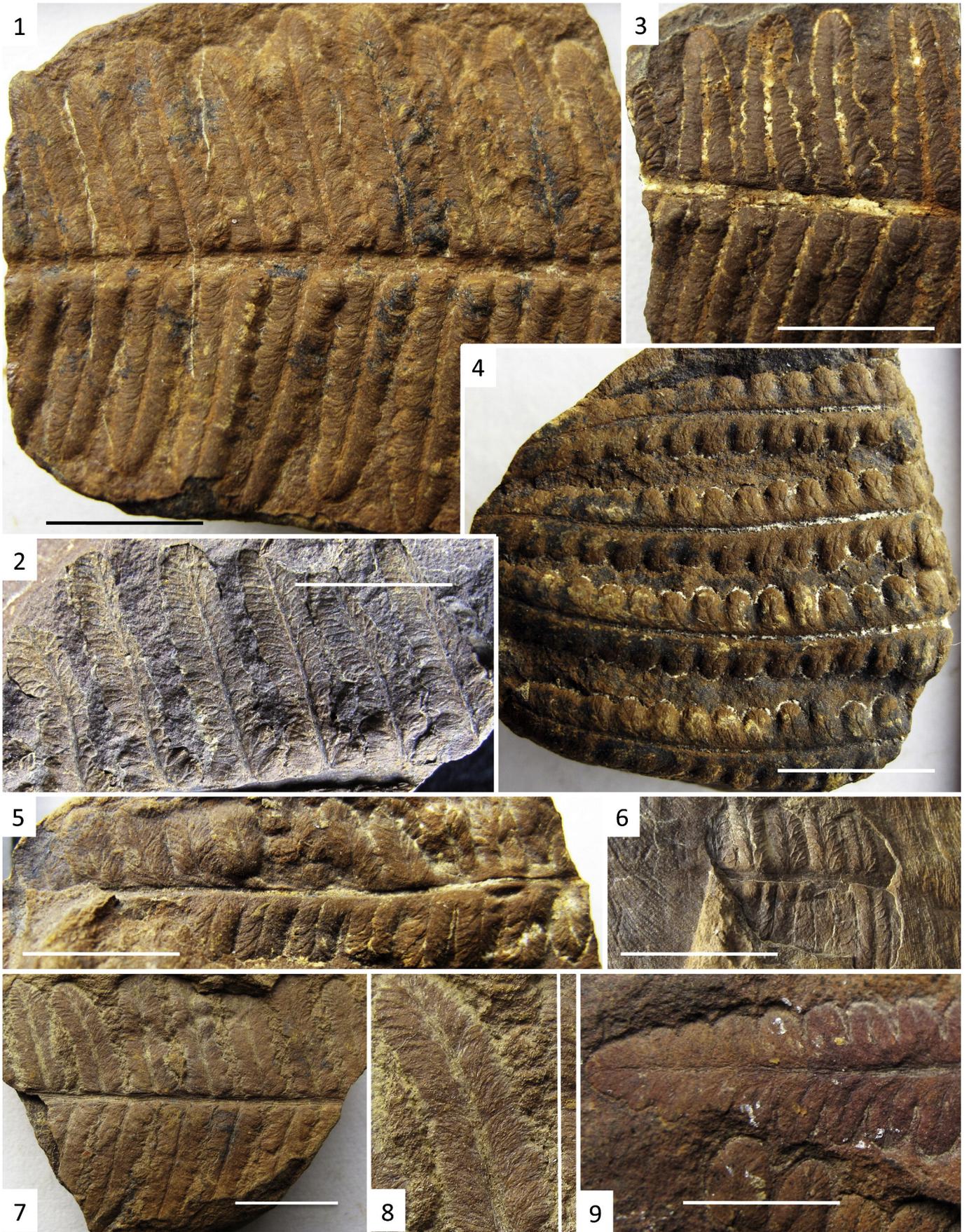
Calamitalean stems

**Description.**—Calamitalean stem remains in the Okmulgee flora were identifiable by their characteristic strong vertical ribs and node–internode organization. Most were highly fragmentary. A few specimens were found to be preserved “in the round”, as casts of calamitalean stems (Plate II, 9). All others are preserved as flattened compressions (Plate II, 10). Several specimens represent nodal plates preserved from disarticulated calamitalean stems.

**Remarks.**—The stem remains of calamitaleans are a common component of Pennsylvanian-age floras from the equatorial region. These are

**Plate IV.** Marratialean ferns—*Lobatopteris vestita* sensu Wagner. Typical morphological expression of lobate pectopterid foliage showing different degrees of pinnule development and complexity of venation.

- 1–3. Pinnae with margins showing increasing apical to proximal lobation (left to right). Venation is complex, candelabra form. 1. Specimen USNM546949, 2. Specimen USNM546942, 3. Specimen USNM546953. Scale bars = 1 cm.
- 4–6. Pinnae with sufficiently deep marginal lobation that pinnules are individuated. Secondary venation is much simplified, consisting of at most two bifurcations, the second on upper limb of the first. 4. Specimen USNM546951, 5. Specimen USNM546953, 6 Specimen USNM546950. Scale bars = 1 cm.
7. Pinnae showing progressive apical to proximal lobation (left to right), Specimen USNM546946, scale bar = 1 cm.
8. Weakly lobed pinna from distal portion of specimen illustrated in Plate IV, 8, higher magnification showing venation only weakly visible beneath surface ramentum, Specimen USNM546946, scale bar = 1 cm.
9. Lateral pinna apex, Specimen USNM546948, scale bar = 1 cm.



very similar in gross form to the modern plant *Equisetum* L., with some subtle differences, but close enough to warrant placement of the calamitaleans in the order Equisetales (e.g., Cichan, 1986). Typically referred to as “pith casts”, such fossils are more likely stem casts reflecting the original size and external appearance of the plants in life; this is particularly indicated by flattened specimens, such as that illustrated in Plate II, 10, which does not have a central core of sediment (DiMichele et al., 2009; DiMichele and Falcon-Lang, 2012).

Division Tracheophyta  
Class Sphenopsida  
Order Sphenophyllales  
Genus **Sphenophyllum** Brongniart (1822)

*Description.*—Axes weakly ribbed with distinct, somewhat swollen nodes. Foliage attached in whorls.

*Remarks.*—No unquestionable specimens of *Sphenophyllum* foliage were identified in the Okmulgee collections. However, two small stems with the gross morphology typical of *Sphenophyllum* were found. There appears to be foliage attached at the nodes on one of the specimens (Plate II, 11), but it is entirely embedded within the rock matrix at an angle that precludes sufficient preparation to permit identification.

Division Tracheophyta  
Class Sphenopsida  
Order Equisetales  
Calamitalean foliage

Calamitalean foliage could be attributed with certainty to three major taxa, and possibly to one other.

Genus and species **Annularia spinulosa** von Sternberg (1821)

*Description.*—Foliage is organized in elliptical-shaped whorls of leaves consisting of 20 or more elongate, single veined leaves with a linear shape, tapered at both ends, the widest point about half-way from base to tip (Plate III, 3–5). The tips taper to a point, but do not appear to be notably mucronate. In some instances, the whorls are quite large, approaching 8 cm in diameter at the widest point, in which case a confident attribution to *Annularia spinulosa* could be made (e.g., Plate III, 5). In other instances, particularly where multiple foliage whorls were attached to stems (Plate III, 1–3), attribution was more problematic because the number of leaves per whorl was less than what is typical for *A. spinulosa* and, in a few instances, the whorls were more round than elliptical in overall shape (Plate III, 3). However, for the most part, even these less-populated whorls were elliptical in shape. Their small size and reduced number of leaves may be attributable to terminal positions on lateral branch systems, as is clear from the diminution of leaf size along some axes that bear multiple whorls (Plate III, 1–3).

*Remarks.*—Foliage of this form, with large-diameter, elliptical whorls of leaves, has for many years been attributed by most authors to *Annularia stellata* (Schlotheim) Wood (1860), a name that has come to encompass a considerable range of morphological variation. This variation ranges from the linear, fusiform leaves attributed here to *Annularia spinulosa* to large-diameter whorls in which the leaves are spatulate in shape. Barthel (2004) reexamined this problem and concluded that

*A. spinulosa* was the correct name for the fusiform-type of foliage and had priority over *A. stellata*, which should be considered an invalid name. Barthel's (2004) determination is followed here.

Some specimens that we assign to *Annularia spinulosa* bear similarities to *Annularia radiata* (Brongniart) von Sternberg (1820–1838) (Plate III, 1–2), particularly the narrowness of the leaves and the symmetrical nature of the whorls. However, given natural morphological variation, taphonomic effects, and the degree of overlap among specimens in the collection, we believe that all specimens are likely *A. spinulosa*.

Genus and species **Annularia sphenophylloides** (Zenker) von Gutbier (1837)

*Description.*—Specimens consist of nearly round whorls of 12–20 leaves, with whorls reaching about 1 cm in diameter (Plate III, 6–7). In many specimens the leaves on one side of the whorl are somewhat shorter than those on the other three sides, rendering the whorls bilaterally symmetrical. The leaves are obovate in shape and have a single midvein. The leaf lamina is generally vaulted, so that the midvein appears sunken when viewed from the adaxial surface.

Genus and species **Asterophyllites equisetiformis** (Schlotheim) Brongniart (1828, 1828–1837)

*Description.*—All specimens have narrowly lanceolate, single veined leaves with acutely tapered, pointed tips that form upswept whorls (Plate III, 8–9). The small size of most of these specimens, and the tight adpression of their leaves to the stem, suggest that they were terminal portions of branches.

*Remarks.*—Only a few specimens in the Okmulgee collection are attributable to *Asterophyllites equisetiformis*, showing the typical form of the species (e.g., Wittry, 2006, p. 93).

Division Tracheophyta  
Class Filicopsida  
Order Marattiales

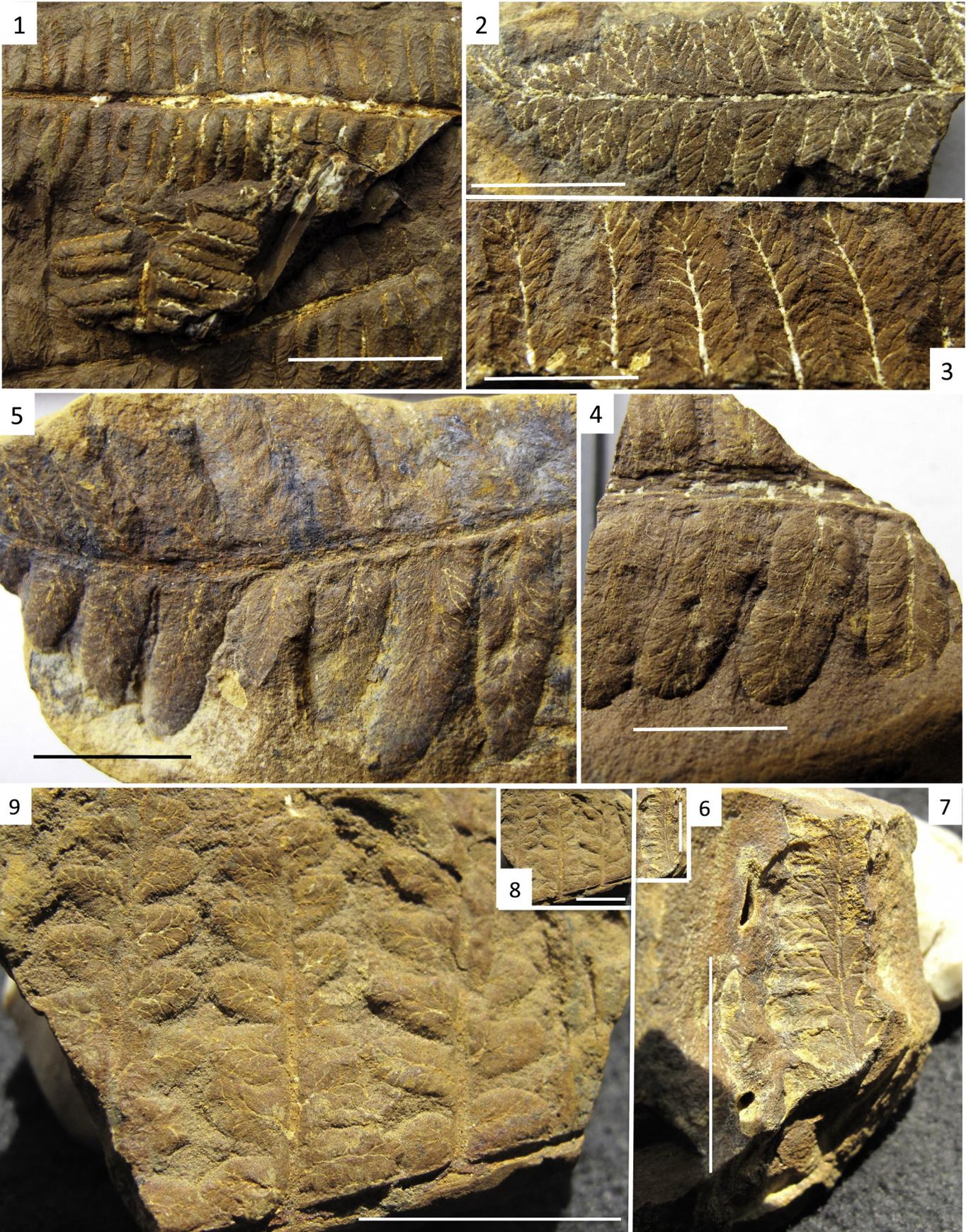
The remains of marattialean ferns in the Okmulgee collections consist of foliage attributable to the genus *Pecopteris* Brongniart (1828, 1828–1837), or to the segregate genus *Lobatopteris* Wagner (1958), and of axes suspected to be rachis fragments. A large number of *Pecopteris* species have been described, often differing in miniscule ways. Paradoxically, certainty of identification is often more difficult for large suites of specimens, if fragmentary, than for single occurrences or small sample populations. This is due to the large amount of morphological variability within most species, even within individual fronds, the extent and pattern of which are poorly understood for most species, leading to a lack of clear morphological boundaries and morphological overlap between species.

Genus and species **Lobatopteris vestita** (Lesquereux) Wagner, 1958

*Description.*—All specimens are characterized by a dense cover of what appear to be fine hairs on the adaxial surface of the pinnules (Plate IV, 1–9) that often obscures the venation. Pinnules are highly variable in form. Most are well individuated, slightly decurrent, and

**Plate V.** Marattialean and filicalean ferns.

- |        |   |
|--------|---|
| 1–5.   | <i>Pecopteris subcrenulata</i> .  |
| 1.     | Pinnae bearing multiple, small pinnules, Specimen USNM546954, scale bar = 1 cm.                                 |
| 2.     | Pinnae apex, Specimen USNM546957, scale bar = 1 cm.   |
| 3.     | Large pinnules, clearly marked vein bifurcations in middle of lamina, Specimen USNM546955, scale bar = 1 cm.    |
| 4.     | Large pinnules, somewhat rounded, vein bifurcations in middle of lamina, Specimen USNM546956, scale bar = 1 cm. |
| 5.     | Lateral pinna apex, large, elongate pinnules, Specimen USNM546947, scale bar = 1 cm.                            |
| 6 & 7. | <i>Pecopteris unita</i> , Specimen USNM546932, scale bars = 1 cm.   |
| 7 & 8. | <i>Oligocarpia gutbieri</i> , Specimen USNM546933, scale bars = 1 cm.   |





**Plate VI.** Pteridosperms—*Macroneuropteris scheuchzeri*.

1. Mat of caducous pinnules, Specimen USNM546959, scale bar = 1 cm.
2. Isolated pinnule with rounded tip and base, Specimen USNM546958, scale bar = 1 cm.
3. Isolated pinnule with tapering, acuminate tip, Specimen USNM546961, scale bar = 1 cm.
4. Terminal and lateral pinnules in connection, Specimen USNM546962, scale bar = 1 cm.
5. Pinnule surface showing characteristic apically directed, hairs, Specimen USNM546960, scale bar = 1 cm.

variably confluent with adjacent pinnules (Plate IV, 4–6, 9). Pinnules may be as small as 1.5 mm in length and 1 mm in width or as large as 12 mm in length and 6 mm in width. In between these extremes, pinnules of various sizes may have entire or variably deeply lobed margins (Plate IV, 1–3, 7–8). Ultimate pinnae will typically have ten lobes per side. Such slight marginal undulation is relatively common (e.g., Plate IV, 3) but more deeply lobed forms, with the margin 50% or more incised, are rare. Pinnules have bluntly rounded tips. The terminal pinnules of ultimate pinnae are small, and lateral pinnules may be fused close to the apex of an ultimate pinna (Plate IV, 1, 9). Venation is complex. The midvein is decurrent in entire pinnules and extends through 90% or more of the pinnule, except in the smallest pinnules, where the midvein may be variably to poorly developed (depending on where these pinnules were in relationship to lobed, transitional regions). Most specimens also have fine lateral veins that fork 3 times: typically the upper limb of the initial dichotomy is again forked (Plate IV, 1–3). In more deeply lobed or undulate pinnules, those that might be considered transitional between different stages of lobing, the venation takes on a candelabra form, typical of *Lobopteris* as described by Wagner (1958). In these cases a third vein dichotomy occurs in the lower limb of the second (upper) dichotomy derived from the initial fork. Rarely subsequent dichotomies occur and are directed progressively inward, alternating position between the lower and upper limbs of the preceding dichotomy, forming a fascicle (Plate IV, 2). Pinnule insertion on the rachis is nearly at right angles to slightly acropetally inclined. The basal most, basipetal pinnule of ultimate pinnae can be slightly enlarged in size, although this may be a very subtle feature.

**Remarks.**—*Lobopteris vestita* was first described by Lesquereux (1880) as *Pecopteris vestita* Lesquereux and has been treated as a species of *Lobopteris* due to the complex lobation and associated changes in venation (Wagner, 1958). Lesquereux's description and the illustrations he provides are not strictly congruent. Using both, there are distinct similarities between *L. vestita* and the Okmulgee specimens. These include the tomentose adaxial surface of the pinnules and the complex and variable venation that depends on the size and degree of lobation of the pinnules. Lesquereux (1880) illustrated several different pinnule sizes and venation types. For the most part, the pinnules are about 1 cm in length, but may be much smaller on lobate specimens. The midvein of the pinnules is decurrent and strong at the base and extends to near the pinnule tip, however it is effectively absent in the smallest pinnules, in which the venation resembles a vein fascicle in the lobed pinnules. In the larger pinnules, it is most common to find lateral veins branched once, with a second dichotomy occurring in the upper limb of the initial fork. Pinnules and pinnae are inserted at a slight angle to the supporting rachis. Pinnules are slightly confluent at the base, decurrent, and have bluntly pointed tips.

We initially classified nearly all the pecopterid foliage specimens in the Okmulgee collections as either *Lobopteris vestita* sensu Wagner or *Lobopteris miltoni* (Artis) Wagner (1958; see also Shute and Cleal, 1989), which Pšenička et al. (2009) place in synonymy under *Pecopteris miltoni* (the type species of *Lobopteris* is *L. vestita*). These species can share similar morphology, with *L. miltoni* occurring mainly in the Early through early Middle Pennsylvanian (Langsettian through Bolsovian; Morrowan–Atokan) and *L. vestita*, as the name has come to be applied, occurring mainly in the late Middle Pennsylvanian (Asturian and Early Cantabrian; Desmoinesian), according to Blake et al. (2002) for American occurrences, and Pšenička et al. (2009) for its European distribution. Wittry (2006) does not include *L. vestita* among species found at Mazon Creek, but he does identify a highly lobate pecopterid as *Lobopteris lamuriana* (Heer) Wagner (1958), noting that this is very abundant in the Mazon Creek flora and is a taxonomic name that has been subject to considerable confusion. As of this writing, Blake et al. (2002) restrict *P. lamuriana* to the Stephanian, and identify *P. vestita* as the common lobate form of the late Middle Pennsylvanian (Asturian and Cantabrian).

In light of the junior synonym status of *Lobopteris vestita* as established by Pšenička et al. (2009), *Pecopteris acadica* Bell (1962) appears to be the most likely correct name for specimens of the kind described here as *L. vestita* (Wittry, in preparation). If the name *L. vestita* is a synonym of *Pecopteris miltoni*, and if the specimens described here, according to authoritative sources are not *P. miltoni* sensu stricto, then we are left with a pecopterid for which there is presently no validly established name. Consequently, we have chosen to continue to use the name *L. vestita* in light of a suitable alternative, recognizing that this material will likely fall under the name *P. acadica* once this synonymy is formally established.

We have chosen to illustrate a fairly large number of specimens (Plate IV) in order to document the high levels of variability in the Okmulgee material. As currently understood, these species may be said to belong to the same “species complex”, differentiable as end points but with a high degree of morphological overlap (Scheihing and Pfefferkorn, 1980). The similarities and key differences between the Okmulgee specimens and the vegetative foliage of *Lobopteris miltoni* are clear, when comparison is based on the detailed characterization of *L. miltoni* by Dalinval (1960). Similarities include covering of the pinnule adaxial surfaces by fine hairs that may mask the venation, a great diversity of pinnule size and form reflective of shape changes related to marginal lobing that is further associated with changes in the patterns and complexity of venation. In both species, the pinnules end in a bluntly rounded apex and there may be a slight enlargement of the basalmost, basipetal pinnule of a pinna (see Dalinval, 1960, Plate 37, fig. 2a). Possible differences include slightly more inclination of pinnules and pinnae on the rachis in *L. miltoni* than in *L. vestita* sensu Wagner, but this, again, is subtle and appears to vary greatly based on Dalinval's illustrations, and perhaps some differences in the venation, such as more common forking of the lower vein following the initial dichotomy in *L. miltoni*. The midvein in *L. miltoni*, if present, is strong at the base, and tends to be more decurrent.

*Lobopteris vestita* sensu Wagner and *Lobopteris miltoni* have been confused with other species such as *Pecopteris pseudovestita* White (1899) and *Pecopteris buttsii* White in Adams et al. (1926); see discussion in Gastaldo (1984) and Pšenička et al. (2009). The Okmulgee specimens also compare favorably with several forms illustrated by Wittry (2006) from the Mazon Creek flora, in equivalent-age rocks of the Francis Creek Shale of Illinois. These include *Pecopteris subcrenulata* (Lesquereux) Wittry (2006), in which *Pecopteris serpillifolia* Lesquereux (1880) is subsumed, *Pecopteris mazoniana* (Lesquereux) Langford (1963), and *Pecopteris clintonii* (Lesquereux) White (1899). All of these species illustrate different pinnule sizes and shapes, accompanied by changes in the complexity and composition of venation, possibly associated with lobing. Pinnules of *P. daubreei* Zeiller (1888), as identified by Wittry (2006), are similar to some of the unlobed forms we have identified as part of the *L. vestita* complex, and have a dense adaxial covering of hairs that obscure venation, as in *L. vestita*. The commonness of surface hairs appears to be primarily taphonomic; specimens show great variation in the degree to which the adaxial surface is obscured by hairs, and a search for this characteristic sometimes reveals a pinnule or two on a specimen in which veins are well exposed.

Genus and species ***Pecopteris subcrenulata*** (Lesquereux) Wittry (2006)

**Description.**—Pinnules of this type are generally relatively large, but with considerable size variation, and have slightly angular insertions that are acropetally directed. The margins are mostly straight to slightly undulatory, and taper gently to a bluntly rounded tip. The midvein extends to the tip of the pinnule and is somewhat decurrent and inflated at the base. The lateral veins are distant and generally fork once between their base and 1/2 of the distance to the margin of the pinnule. They meet the margin at various angles. The vein bundles near the base of the pinnule are generally more developed.

The veins are relatively straight and the angle of vein bifurcation varies. The upper limb of the vein fork most often arcs initially at a steep angle subparallel to the midvein, then strongly bends toward the margin and continues in parallel with the lower limb of the fork. In addition, there are rare trifurcations, the second dichotomy occurring in the upper limb resulting from the initial division. Pinnules do not appear to have adaxial surface hairs.

**Remarks.**—Although there are a variety of other types of tree-fern foliage in the Okmulgee collections, all are either represented by small scraps, or are of questionable affinity with *Lobopteris vestita* sensu Wagner. An example of this kind of foliage is illustrated in Plate V, 1–5. These specimens are quite similar to *Pecopteris mazoniana*, as characterized by Wittry (2006, see particularly Plates 6–11). There are only a few such specimens in the collection. Some of the material Lesquereux (1880, Plate XXXII) attributed to this species, however, has clearly lobate margins, reinforcing its possible affinities with *L. vestita* sensu Wagner, given the morphological variability of the entire specimen suite from the Okmulgee sites.

In isolation from consideration of the larger specimen suite, these few Okmulgee specimens assigned to *Pecopteris subcrenulata* also bear strong resemblance to *P. raconensis* Němejc (1940). *Pecopteris raconensis* was originally described by Němejc (1940) from Bohemia, based on fertile material illustrated by Kidston (1925) from Great Britain. Numerous similarities include angular pinnule attachment, a midvein that is slightly decurrent, lateral venation that is relatively widely spaced, with veins that branch largely once (sometimes the basal most acroscopic vein is forked a second time in larger pinnules), the fork occurring about 1/3 of the distance to the margin, and relatively broad pinnules with rounded apices. Wagner (1965) illustrated and gave a detailed characterization of this species from NW Spain, which is very similar to the descriptions of *Pecopteris mazoniana* by Lesquereux (1880) and Wittry (2006). Wagner also illustrates it from the Guardo coalfield in Spain (Wagner, 1983) and Bashforth et al. (2010) describe the species from Bohemia. It appears to be most common in the later Middle Pennsylvanian. We hesitate to assign these specimens to this latter species because of their small number and fragmentary nature, particularly when considered in light of the undulatory margins of the material originally illustrated by Lesquereux (1880) and the high variability within the Okmulgee tree-fern foliage, most of which seem to fall within the circumscription of *Lobopteris vestita*.

#### Genus and species *Pecopteris unita* Brongniart, 1828, 1828–1837

**Description.**—Three specimens in the Okmulgee collection were identified tentatively as *Pecopteris unita*. Pinnules are small, 3.5–5 mm long and 2.5–3.5 mm wide, mostly free, but fused through their lower 1/3, and decurrent. The midvein is decurrent and extends 2/3 of the distance from the base to the tip of the pinnule. Lateral veins are simple and upswept, particularly at the base, however, it cannot be determined if they extend all the way to the pinnule apex or terminate along the lateral margin. Pinnules become progressively more fused toward the pinna tip, which terminates in a bluntly rounded end (Plate V, 6–7).

**Remarks.**—Some authors (Castro, 2005; Van Waveren et al., 2007; Wagner and Álvarez-Vázquez, 2010) assign species of this form to the

genus *Diplazites* Goepfert, 1841, a name originally used for fertile material associated with *P. unita*-type foliage.

Division Tracheophyta

Class Filicopsida

Order ? Filicales

Genus and species *Oligocarpia gutbieri* Goepfert (1841) emend. Brousmiche (1983)

**Description.**—Specimens assigned to this species are characterized by rounded to slightly elongate pinnules with blunt apices and smooth to slightly scalloped margins. The venation is well marked, thready, sparse, and slightly flexuose. The midvein is decurrent, strong at the base and extends about 2/3 the length of the pinnule. Lateral veins are mostly once forked, occasionally unforked, and arc only slightly. Only one ultimate pinnae terminal pinnule was observed and it was very small, part of a progression of pinnule size reduction approaching the terminus; this reduction in pinnule size occurs in the larger specimen also, but the terminal was not preserved (Plate V, 8–9).

**Remarks.**—*Oligocarpia gutbieri* is a true fern, characterized by delicate foliage that demonstrates some variation throughout the frond, particularly in the degree of individuation of pinnules, which may be fused to various degrees. This is well illustrated by Brousmiche (1983, see plates 57–59), who designated a neotype for the species. Rare in the Okmulgee collections, only four specimens were identified, all fragmentary, and no fertile material was found.

There is discussion in the literature about the validity of applying this name to American specimens (see White, 1899; Wittry, 2006), preference being given to *Oligocarpia alabamensis* Lesquereux (1880) or *Oligocarpia missouriensis* White (1899). Both of these uniquely American species were segregated from *O. gutbieri* by the respective authors, each of whom also tentatively recognized *O. gutbieri* in the floras they were describing. The morphological differentiation of *O. gutbieri*, *O. alabamensis* and *O. missouriensis* appears to be quite subtle, and given the range of variation in form illustrated by Brousmiche (1983), perhaps the American specimens all fall within the expectations of variation within a single species. Thus, we feel it is most advisable to place the Okmulgee specimens in the best known species of this group. *Oligocarpia gutbieri* is typically found in rocks ranging from the Duckmantian (Atokan) through the earliest Stephanian (Missourian).

Division Tracheophyta

Class Spermatoopsida

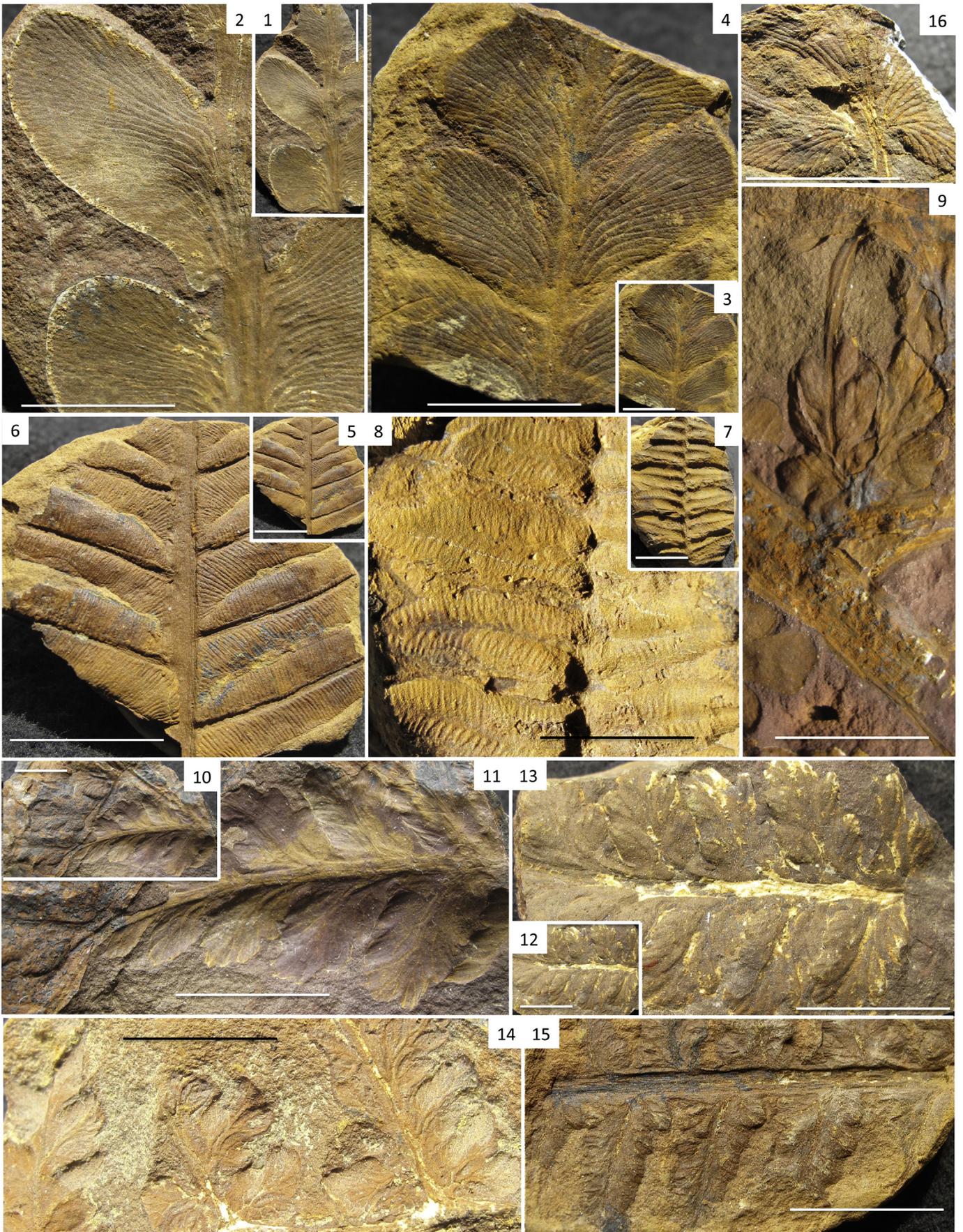
Order Medullosales

Genus and species *Macroneuropteris scheuchzeri* (Hoffman) Cleal et al. (1990)

**Description.**—Pinnules of *Macroneuropteris scheuchzeri* in the Okmulgee collection generally are large, 8–9 cm long, 1–2 cm wide (in the upper third) and 4–5 cm wide at base. Pinnules are straight to slightly falcate, with the margins arcing toward the acroscopic side. The apex of the pinnule is acute and can be sharply or bluntly angular. The base is generally cordate. Sometimes a single opposite pair of smaller, rounded pinnules are found at the base of the main pinnule lamina. The midvein is well marked and extends nearly to the apex. Lateral

#### Plate VII. Pteridosperms—mixed taxa.

- 1 & 2. "*Odontopteris subcuneata*" form of *Macroneuropteris scheuchzeri*, Specimen USNM546967 scale bars = 1 cm.
- 3 & 4. *Odontopteris aequalis*, Specimen USNM546968, scale bars = 1 cm.
- 5 & 6. *Alethopteris serlii*, Specimen USNM546969, scale bar = 1 cm.
- 7 & 8. *Alethopteris lonchitica*, Specimen USNM546971, scale bar = 1 cm. 9–15. *Karinopteris plumosa*. All scale bars = 1 cm.
9. Pinna tip with spine-like prolongation, Specimen USNM546973.
- 10 & 11. Pinnae illustrating various degrees of lobation and venation, Specimen USNM546974.
- 12 & 13. Pinnae illustrating various degrees of lobation and venation, Specimen USNM546977.
14. Pinnae illustrating various degrees of lobation and venation, Specimen USNM546979.
15. Pinnae illustrating various degrees of lobation and venation, Specimen USNM546978.
16. Cf. *Eusphenopteris neuropteroides*, USNM546972, scale bar—1 cm.



veins are fine and dense. They arc from the midvein and meet the margin at a shallow angle. Small trichomes (hairs) are found on the surface of the pinnule; they point apically, are sparse, and tend to be concentrated near the midvein, though they may occur across the pinnule surface. In some *M. scheuchzeri* specimens, the pinnule lamina may be subdivided into pinnules that bear a close resemblance to *Odontopteris*, which has caused taxonomic confusion; such specimens were described as *Odontopteris subcuneata* Bunbury (1847).

**Remarks.**—*Macroneuropteris scheuchzeri* is represented in the collections almost entirely by isolated pinnules (Plate VI, 1–3) with only a few pinna fragments (e.g., Plate VI, 4). In some of the larger specimens, the pinnules form dense accumulations without preferential orientation, suggesting little transport or settling in still water (Plate IV, 1). Gross morphology and the presence of hairs on many specimens (Plate IV, 4–5) allow certain attribution of specimens to this species.

American specimens of *Macroneuropteris scheuchzeri* reach larger sizes than those typically found in Europe (e.g., Laveine, 1967; see discussions in Darrah, 1969; Pfefferkorn, 1979; Cleal et al., 2007). Large specimens from Mazon Creek were described as *Neuropteris decipiens* Lesquereux (1880) and later included in *Neuropteris scheuchzeri* Hoffman and described as *N. scheuchzeri* forma *decipiens* Gastaldo (1977), Lesquereux (1880) split a range of apparently continuous morphological variation into several species and did not designate a type specimen for *N. decipiens* nor did he provide an illustration to accompany the original description. Darrah (1969) attributed the large size of these plants remains to “gigantism”, and suggested that larger pinnules indicated larger parent plants. Large size also may be due to preservational factors, specifically the rapid fossilization that accompanies preservation of organic matter in ironstones (Laveine, 1990) preventing significant shrinkage; Cleal and Shute (2007) discuss this specifically with regard to Mazon Creek fossils, noting that this is probably not the explanation, given the extremely large size of many of the specimens from that flora. In addition, a study of leaf shrinkage (Blonder et al., 2012) indicates that preservation of leaves in mud prevents most shrinkage, as does rehydration of dried leaves. Thus, shrinkage should be an issue only if specimens were exposed to severe dehydration before being buried rapidly, without sufficient opportunity to rehydrate. Discussions of the taxonomic and morphological patterns surrounding American *M. scheuchzeri* material can be found in Darrah (1969), Pfefferkorn (1979), Wittry (2006) and Cleal et al. (2007).

The large size of some American specimens also is accompanied by reduced vein densities (Darrah, 1969). This observation may take on new significance in light of work by Zwieniecki et al. (2004) on the mechanisms underlying so-called sun and shade leaves. These authors find that variance in leaf size and vein density, traditionally attributed to sun vs. shade exposure at maturity, actually reflect differences in the local hydraulic environment driving leaf expansion during early development. Leaves close to the base of the canopy are larger than those near the top, with accompanying changes in the packing of veins. At the time of Spring leaf expansion in the temperate species they studied, all leaves were equally exposed to sun such that their “sun” and “shade” mature characteristics were set at a time when all leaves had sun exposure, so that there was no sun-shade environmental dichotomy during early development, when leaf morphological characteristics were being set. For *M. scheuchzeri* this may mean that larger pinnules, with lower vein densities, may have come from positions within fronds that were closer to the frond base than smaller pinnules with higher vein densities. Darrah (1969) noted that vein-density varied with size in the specimens he examined, which would be expected under the Zwieniecki et al. (2004) developmental scenario. This explanation, of course, does not account for the failure to find such large specimens in the European record, and may indicate that specimens were overall larger in the environments colonized by these plants in the American wetlands (Cleal et al., 2007).

Variation in foliar morphology in fossil plants can lead to the recognition of different species and genera that are, in fact, parts of the same

plant. Such is the case with *Odontopteris subcuneata*. Originally described by Bunbury (1847), this species was subsequently recognized (Bell, 1938) as a developmental form of *Macroneuropteris scheuchzeri* (see Zoderow, 2003; Wittry, 2006). “*Odontopteris subcuneata*” is represented in the Okmulgee collections by two specimens (Plate VII, 1–2). It has the odontopterid venation typical of the genus *Odontopteris*, in which multiple veins enter the base of the pinnule, without forming a distinct midvein. Atypical of *Odontopteris*, and thus helping to indicate distinctiveness from that genus, are the auriculate, basicopic bases of the pinnules.

#### Genus and species *Odontopteris aequalis* Lesquereux (1866)

**Description.**—The pinnules of this single specimen are broadly attached to the pinna rachis, decurrent and slightly incised acroscopically. Their basicopic margins are quite straight, with some curvature of the acroscopic margin. Pinnule apices are broad and rounded. There is no distinct midvein; however, the veins of the pinnule appear to arise entirely or mostly from one point, near the base of the basicopic end of the pinnule, from which subsequent vein divergences occur and turn steeply into the pinnule lamina. Veins are of medium thickness and moderately spaced. They contact the pinnule margin beginning about 1/3 of the distance from the base of the pinnule. The veins are straight on the acroscopic half of the pinnule lamina and arc slightly in the basicopic half, but mainly in their lower 1/3, after which they run straight to the margin.

**Remarks.**—The type specimen of *Odontopteris aequalis* is poorly illustrated making comparisons difficult. Consequently, assignment of the Okmulgee specimen (Plate VII, 3–4) to this species must be tentative. Based on its patterns of occurrence and morphological variation, as established in other studies (see discussion in Wittry, 2006), *O. aequalis* appears to be a specifically distinct entity based.

Cleal (1997, 2007) considered *Odontopteris aequalis* to be possibly conspecific with *Odontopteris cantabrica* Wagner differing simply in size, though the fragmentary nature of the type of *O. aequalis* and its lack of cuticle may be barriers to establishing synonymy (Cleal et al., 2007). If *O. aequalis* and *O. cantabrica* were the same, Cleal (1997) suggests this would be further evidence for assigning the Francis Creek Shale to the *O. cantabrica* biozone of Wagner (1984), thus making this deposit Cantabrian in age, using terrestrial European stage boundaries. Cleal (personal communication 2012) notes that the vein density is too high in the Okmulgee specimen for it to be equivalent to *O. cantabrica*.

#### Genus and species *Alethopteris serlii* (Brongniart) Göppert (1836).

**Description.**—*Alethopteris von Sternberg* (1825) of the form we designate *Alethopteris serlii* is represented in the Okmulgee ironstone collections by only a single, fragmentary specimen (Plate VII, 5–6). The ambiguous suite of characters in this specimen render identification to specific level difficult. Pinnules generally are elongate, with slightly convex sides, reaching the greatest width near the middle. Pinnule apices are not preserved. Pinnules are inserted on the rachis at an angle. The base of each pinnule is basicopically decurrent and pinnules are narrowly confluent. The acroscopic side of the pinnule is usually somewhat to strongly contracted. The pinnule lamina appears to have been vaulted, though not strongly so. Pinnules have a strong midvein that extends as far as could be followed through the pinnule in this specimen. Lateral veins arc slightly, mainly on the basicopic side, and then follow a nearly straight course through the pinnule lamina to the margin. Lateral veins on the acroscopic side are largely unforked; those on the basicopic side are a mixture of forked and unforked, and the bifurcations occur primarily within the inner half of the pinnule lamina before proceeding to the margin. Rachial veins are confined to the basicopic side and are largely unforked, though the rachial vein closest to the midvein may fork once. Venation is rather dense at nearly 42–45 veins/cm of margin.



**Plate VIII.** Pteridosperms—*Eusphenopteris* sp.

1 & 2. Tangled mat of foliage with thin rachises and relatively long inter-pinna distances, Specimen USNM546980, scale bars = 1 cm.

**Remarks.**—The specimen illustrated here can be compared with several species that have varying degrees of overlap in their characteristics. According to Wagner (1968), the vein density of *Alethopteris serlii* is considerably lower than that of the Okmulgee specimen (about 30–35 veins/cm), the midvein is generally less robust, and the lamina is more broadly confluent between pinnules, with rachial veins on both the acroscopic and basiscopic sides. Lateral venation of *A. serlii* also is somewhat more highly branched and the patterns on the acroscopic and basiscopic sides are not notably different. However, a morphometric study of a large sample of this type of alethopterid foliage led Scheihing and Pfefferkorn (1980) to conclude that *A. serlii* encompassed within its range of variation a number of other species, delimited on smaller sample sizes, including *Alethopteris missouriensis* White (1899) and *Alethopteris densinervosa* Wagner (1968), to which we compare the Okmulgee specimen below. Other comparable species include *Alethopteris robusta* Lesquereux (1884), and *Alethopteris corsinii* Buisine (1961).

*Alethopteris missouriensis* has a number of similarities with the Okmulgee specimen including pinnules that are relatively elongate with slight development of the pinnule margin convexity, high lateral vein density of over 40 veins/cm, relatively straight lateral veins, and a well marked midvein. However, *A. missouriensis* typically is more broadly decurrent and demonstrates both acroscopic and basiscopic rachial veins.

*Alethopteris densinervosa* compares favorably in terms of pinnule shape and size, and lateral vein density, and the relatively low number of dichotomies seen in the lateral veins. The pinnules also may be constricted at the base and somewhat inflated in the middle, and vein densities are between 40 and 45 veins/cm (Wagner, 1968). The species is known only from the Bolsovian (Westphalian C) of northern France and the Asturian (Westphalian D) of the Appalachian Basin (Scheihing and Pfefferkorn, 1980).

*Alethopteris robusta*, particularly the varietal form *A. robusta* var. *longipinnata* Wagner (1968), bears many strong similarities to the Okmulgee specimen, included are possible pinnule insertion obliquely on the rachis, obscuring some portion of the rachis or pinnule attachment, the non-decurrent midvein, the large proportion of unforked veins, particularly on the acroscopic side of the pinnule, the small number of forked rachial veins, and vein densities in the 40 s/cm. The degree of pinnule confluence is somewhat greater than in the Okmulgee fragment but this appears to be a highly variable trait, based on the specimens illustrated by Wagner (1968).

*Alethopteris corsinii* compares favorably in terms of the shape and size of pinnules, the relatively narrow confluence of the lamina between adjacent pinnules, and the rather straight disposition of the veins relative to the midvein and margin. Vein density is generally too low, though there appears to be intra-frond variation in this trait. Several larger, subapical pinnules illustrated by Buisine, 1961 (see Plate XXI, fig. 1 and a) bear a striking resemblance to the Okmulgee fragment, but are considerably more widely spaced. The more distal pinnules are distinguishably different from these near apical ones, and represent the predominant morphology throughout the frond, with venation that is more distant, much more thready, and with a significantly less robust midvein. This species reaches its apogee in the mid-Bolsovian, extending into the Early Asturian.

Genus and species *Alethopteris lonchitica* von Schlotheim (1820) ex von Sternberg (1825)

**Description.**—The single Okmulgee specimen attributed to *Alethopteris lonchitica* has pinnules that are weakly connate, but not markedly decurrent, standing close to right angles with the rachis. The

pinnule apex is triangularly pointed, a characteristic that apparently varies among populations of the species, some of which have bluntly rounded pinnule apices. The veins are well marked, particularly in ventral view. The midvein is strong and proceeds to nearly the apex of the pinnule. Lateral veins are widely spaced, leave the midvein at nearly right angles, and arc little or not at all in their path across the lamina to the pinnule margin, branching once, sometime twice.

**Remarks.**—This species is best known from the upper Middle Pennsylvanian. The morphology of single Okmulgee specimen, though fragmentary, conforms very closely to the species characteristics (Plate VII, 7–8) and is congruent in its stratigraphic position.

The morphology of this species, and its taxonomic implications, have been discussed in detail recently by Wagner and Álvarez-Vázquez (2010). They conclude that *Alethopteris lonchitica* has been used incorrectly for many years for Lower Pennsylvanian specimens attributable to *Alethopteris urophylla* (Brongniart) Göppert, 1836. Based on the holotype, which was rediscovered and typified (Kvaček and Straková, 1997) and then reillustrated (Zodrow and Cleal, 1998), they conclude that *A. lonchitica* is properly used for specimens of a form that generally is referred to *Alethopteris ambigua* Lesquereux emend. White (1899). We initially identified the Okmulgee specimen as *A. ambigua* sensu Wagner (1968), a description accompanied by copious illustrations and a lengthy discussion of the complexity of sorting out the proper application of this name. Witrty (2006) comments at some length on *A. ambigua* as described originally by Lesquereux (1880), noting that both Mazon Creek specimens and those described by Wagner (1968) differ from the specimens described and illustrated by either Lesquereux (1880) or White (1899). In these latter specimens the pinnules are generally bluntly rounded at the tip rather than triangularly pointed, may have a more oblique insertion, greater basal confluence, and lateral veins that are more distant and less commonly branched. Although he did not describe the Mazon Creek material as a new species, Witrty (2006) suggested that a new species, closely related to *A. ambigua*, might be warranted.

The Okmulgee specimen (Plate VII, 7–8) more closely resembles specimens described and illustrated as *Alethopteris ambigua* by Witrty (2006) and Wagner (1968) than by Lesquereux (1880) and White (1899) in having the following characteristics: right-angle insertion, straight sided pinnules with a relatively acute apex and narrow basal confluence, strongly marked venation, strong midvein and once-to-twice forked lateral veins borne at nearly right angles to the midvein. Given that the Lesquereux (1880) description is the original for *A. ambigua*, we have chosen to follow Wagner and Álvarez-Vázquez (2010) and use *Alethopteris lonchitica*, recognizing that there may remain significant taxonomic issues to be resolved with regard to this morphotype and these names (Cleal, personal communication, 2012).

Division Tracheophyta

Class Spermatopsida

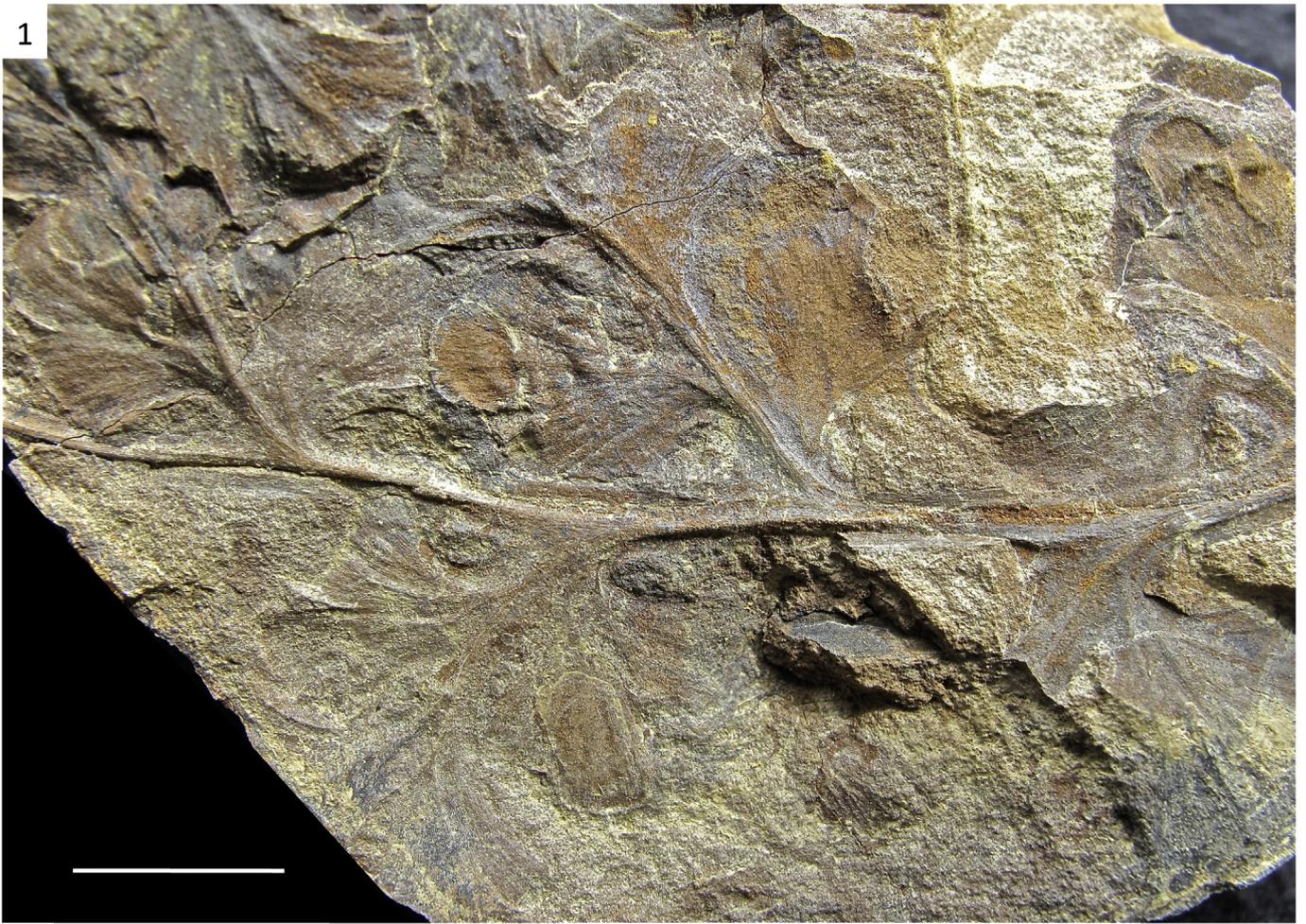
Order Lyginopteridales

Genus and species *Karinopteris plumosa* (Kidston) Boersma (1972)

**Description.**—A relatively large number of specimens in Okmulgee collections have features that link them to the lyginopterids and more specifically to the mariopterids, such as spine-like prolongations at the end of pinnae, instead of terminal pinnules (Plate VII, 9), horizontal sclerotic plates in the stems and rachises (Plate VII, 9) and lobed pinnules at the base of pinnae on the basiscopic side (Plate VII, 15). Pinnules of these specimens might be described as lobate, where the triangular pinnules are fused over more than 1/3 of their lateral margins, thus reducing their apparent individuality (Plate VII, 10–11). They, in effect, form large pinnules with toothed lateral margins. In some instances, the

**Plate IX.** Pteridosperms—*Eusphenopteris* sp.

1. Stem or pinna rachis bearing multiple pinnae. Long inter-pinnae distances, possible sclerotic nests in the rachis/stem, Specimen USNM546981, scale bar = 1 cm.
2. Pinnule venation and lobing, Specimen USNM546982, scale bar = 1 cm.
3. Pinnule venation and lobing, Specimen USNM546976, scale bar = 1 cm.



confluent pinnules rarely form a group elongate enough to present as an additional pinna order (Plate VI, 12–15). Venation, where visible, includes a clear and decurrent midvein that extends to near the tip of the pinnule and from which arise steep, arching lateral veins that are widely spaced and fork at a variable distance from the midvein, each lateral vein again potentially forking in the larger pinnules, particularly in the basal portions of the lamina. Veins are deeply embedded in the pinnule lamina.

*Remarks.*—We have identified the material described above as *Karinopteris plumosa* based on Christopher Cleal's suggestion (personal communication, 2011) that we examine the description and illustrations in Kidston (1925). The only record of this plant is the type specimen of Kidston (1925), which is from the well-known Radstock beds of England, of a similar, Late Westphalian or Early Cantabrian Age to the Okmulgee material. This identification is congruent with the totality of the morphologies shown by these specimens, particularly the rather acute nature of the pinnule apices, the patterns of vein branching, and the deeply embedded venation.

A closely comparable mariopterid to the Okmulgee specimens is *Mariopteris muricata* (Schlotheim) Zeiller, 1879. It too has somewhat elongate pinnules that can fuse to form toothed pinnae (e.g., Kidston, 1925, plate CXLV; Boersma, 1972, see particularly Plate 25), though its venation is more delicate and the toothed pinnae are more regular than those of *Karinopteris plumosa*. It is commonly found in older strata (e.g., Eble et al., 2009, for the American distribution).

*Mariopteris nervosa* (Brongniart) Zeiller (1879), which has a stratigraphic range encompassing that of *Karinopteris plumosa*, has more triangular pinnules, and although these may fuse to form toothed pinnae they are more coarsely toothed and less common than found in the Okmulgee specimens.

Other species of *Mariopteris* illustrated from Mazon Creek by Wittry (2006) are sufficiently distinct to be excluded as possible identities.

*Karinopteris plumosa* is part of the mariopterid lineage of lyginopterids, which may warrant segregation as a distinct family of pteridosperms. However, the lack of broad understanding of mariopterid anatomy and reproductive biology led Cleal (2008) to suggest their inclusion within the Lyginopteridaceae. Most of the mariopterids were vines or scrambling thicket formers (see Krings et al., 2003).

Division Tracheophyta

Class Spermopsida

Genus and species cf. *Eusphenopteris neuropteroides* (Boulay) Novik

(1947)

*Description.*—A tiny fragment of what may be *Eusphenopteris neuropteroides* is illustrated in Plate VII, 16, the only specimen of this species recognized in the collection. It is a pinna fragment bearing three incomplete pinnules, each of which have multiple veins entering their bases. These veins are coarse, widely spaced, arching toward the margin immediately from their point of entry into the pinnule, and undergo as many as five divisions within the preserved segments of lamina. The pinnules appear to be rounded at the base, typical of this species. Overall pinnule shape is not revealed by the specimen.

*Remarks.*—Although this fragmentary specimen is too small to assign with confidence, it is morphologically distinct from other forms in the flora and is most suggestive of *E. neuropteroides*.

Genus and species cf. *Eusphenopteris* Simson-Scharold (1934) *E. sp.*

*Description.*—Ultimate pinnae bearing rounded to lobed pinnules, the largest of which are about 1.5 cm in length, from base to apex. Pinnules vary from entire and rounded, to two lobed or three lobed and broadly fan-shaped. There may be some muted undulations at the pinnule margin corresponding to vein endings. Pinnule venation is open dichotomous. Veins are widely spaced, originate from a single point at the pinnule base, straight, non-flexuose, and fork between 2 and 4

times before reaching the pinnule margin. The veins are difficult to see on some pinnules, either because the pinnule lamina was thick and the veins embedded, or because of adaxial surface hairs. An ultimate pinna may bear several pinnules, each pinnule has a highly constricted attachment, but with a narrow strip of lamina running along the sides of the pinnule petiole, which is 1 or 2 mm long. A similar thin strip of lamina, <1 mm wide, flanks the pinna rachis throughout its length. The ultimate pinna rachis is decurrent at its point of attachment to the penultimate pinna rachis. The lamina of the basicopic pinnule is continuous with the penultimate pinna rachis, though rachial veins do not appear to be present. The penultimate rachises are flexuose, and the distance between successive ultimate pinnae is about 1 cm on the larger specimens. Horizontally disposed sclerotic plates were not observed on any of the axes to which pinnules are attached.

*Remarks.*—These specimens are perhaps the most perplexing in the Okmulgee collection. They occur as somewhat tangled masses of foliage with a *Eusphenopteris* aspect, but of a larger size than described, contemporary, late Middle Pennsylvanian species (van Amerom, 1975); some of the variability in this species can be seen in the illustrated specimens (Plate VIII, 1–2; Plate IX, 1–3). The gross form of these few specimens suggests a vine-like habit, appearing tangled, with flexuose penultimate rachises (Plate VIII, 1) and relatively wide spacing between adjacent ultimate pinnae (Plate IX, 1).

The shapes of the pinnules, the nature of their lobing (Plate VIII, 2; Plate IX, 2–3), and the surface aspects of the pinnule laminae are not unlike those of such species as *Eusphenopteris obtusiloba* (Brongniart) Novik, 1947 or *Eusphenopteris striata* (Gothan) Novik, 1947. We hesitate to describe this as a new species at this time, due to the fragmentary nature of the material at hand.

The specimens in the Okmulgee collection are intimately intermixed with specimens of *Karinopteris plumosa*. However, there is no evidence of attachment between them to suggest that these are different growth forms of the same plant. Both are quite fragmentary in preservation and their co-occurrence, both probably vines, may be a consequence of intermixing in the habitat of growth, perhaps climbing on the same host plant, or growing together in a thicket.

Division Tracheophyta

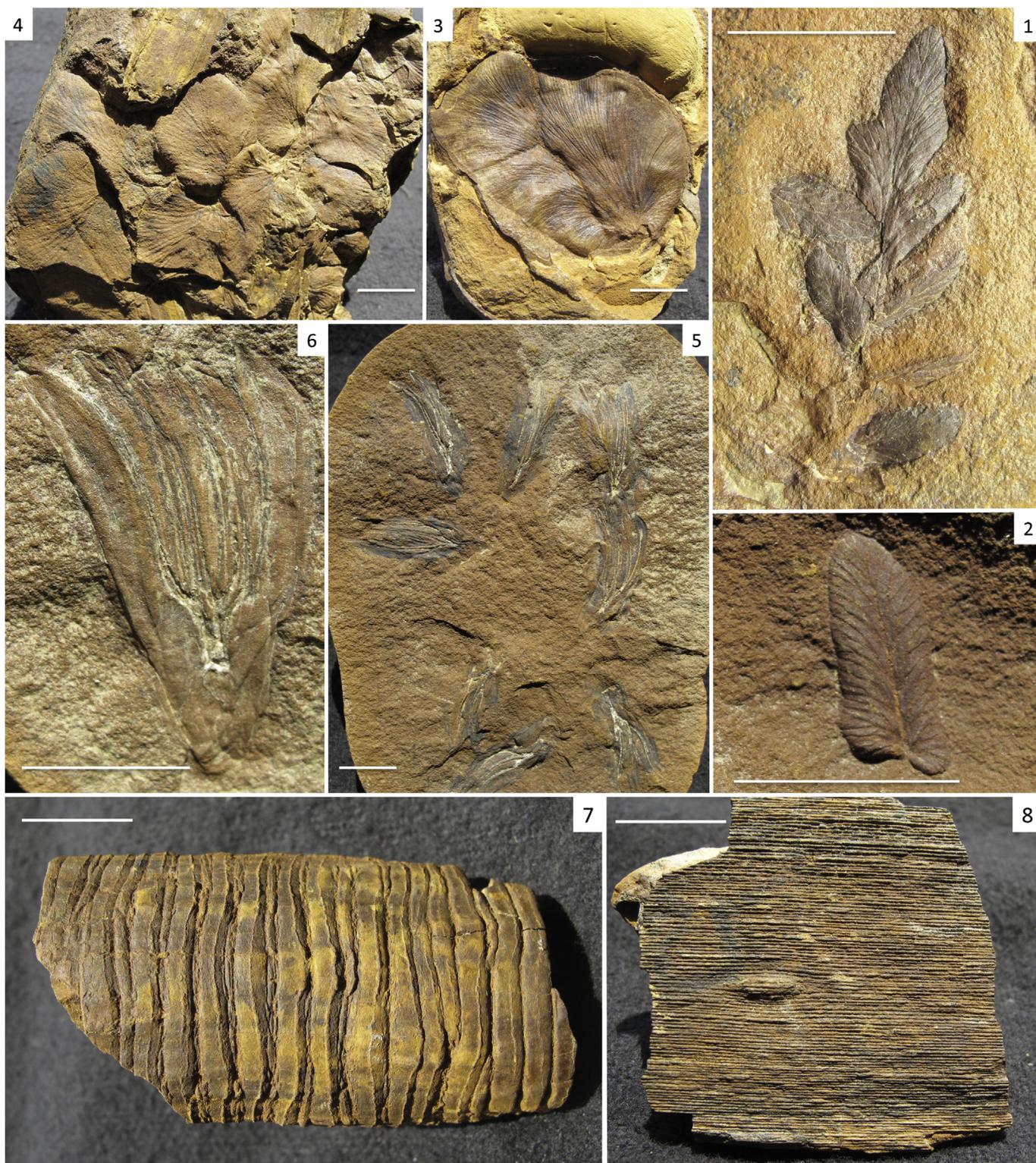
Class Spermopsida

Order Medullosales

Genus and species *Laveineopteris rarinervis* (Bunbury) Cleal et al. (1990)

*Description.*—Pinnules of this species in the collection are generally small, up to 1.8 cm in length, and elongate (2 or more times longer than wide) with a rounded to bluntly pointed, asymmetrical tip, straight but slightly undulatory lateral margins and slightly inflated base. They are narrowly attached to the rachis generally at an angle. Veins are well marked and probably protruded slightly from the abaxial side of the pinnule in life. The midvein is well defined, slightly flexuose and extends up to 2/3 of the length of the pinnule, breaking into secondary veins at its tip. Lateral veins are widely spaced and typically forked one to three times, the first fork nearly at the midvein and later forks more commonly occurring in the upper limb of the initial vein dichotomy. In most specimens pinnules are strongly adherent to the rachis and pinna fragments are more commonly encountered than isolated pinnules. Terminal pinnules are somewhat elongate and about the same size and shape as lateral pinnules. Approaching the terminal pinnule the lateral pinnules become more broadly attached and fused at the base of the terminal.

*Remarks.*—*Laveineopteris rarinervis* is a species of medullosan pteridosperm foliage with characteristic and easily recognized morphology (Plate X, 1–2). The foliage of this plant, though highly fragmentary, is not rare in the Okmulgee collection. The most commonly encountered specimens were fragments of pinnae, some with terminal pinnules.



**Plate X.** Pteridperms—*Laveineopteris*; Cordaitales.

1. *Laveineopteris rarinervis*, pinna tip with terminal pinnule, Specimen USNM546975, scale bar = 1 cm.
2. *Laveineopteris rarinervis*, pinnule with sparse, well marked venation, Specimen USNM546970, scale bar = 1 cm.
3. Cyclopterid pinnule, probably of *Laveineopteris rarinervis*, Specimen USNM546966, scale bar = 1 cm.
4. Large orbiculoid to slightly lobed pinnules, possibly cyclopterids of *Laveineopteris rarinervis*, Specimen USNM546965, scale bar = 1 cm.
5. *Codonothea caduca* cluster, Specimen USNM546963, scale bar = 1 cm.
6. *Codonothea caduca*, Specimen USNM546964, scale bar = 1 cm.
7. *Artisia*, cordaitalean pith cast, Specimen USNM546983, scale bar = 1 cm.
8. Striate axis or *Cordaites* leaf impression, Specimen USNM546984, scale bar = 1 cm.

The Okmulgee specimens conform in all respects to descriptions of this species in the literature (e.g., [Wittry, 2006](#)).

A few specimens were encountered that appear to be cyclopterid pinnules of *Laveineopteris* (Plate X, 3–4). The morphology of these structures and matters surrounding their placement within the frond of the plant are discussed in point and counterpoint by [Clea and Shute \(2003\)](#) and [Laveine \(2005\)](#), and are further discussed in [Clea and Shute \(2012\)](#).

#### Genus and species *Codonothea caduca* [Sellards \(1903\)](#)

*Description.*—Specimens assigned to *Codonothea* in the Okmulgee collection consist of a cup or bell-shaped structure, composed of fused lobes, up to six of which are visible on some specimens. These lobes are fused laterally at their bases and surround a central hollow area. The lobes are free for the upper 2/3 or more of their length. Most of the Okmulgee material is <20 mm to about 30 mm in length, and about 10 mm or less in maximum width.

*Remarks.*—*Codonothea* [Sellards](#) emend [Drinnan and Crane \(1994\)](#) is a rare but conspicuously identifiable element of the Okmulgee flora. [Sellards \(1903\)](#) first described this genus from Mazon Creek and recognized it as a pollen-producing organ, assigning his materials to the species *Codonothea caduca*. Through preparation, [Sellards \(1903\)](#) determined that the organ consists of a cup or bell-shaped body, composed of six lobes that were fused laterally at their bases and free for the upper 40–50% of their length, thus surrounding a central hollow area; [Drinnan and Crane \(1994\)](#) emended this description to note that the average size of specimens, measured longitudinally from base to tip, is 3–5 cm, with a width of about 1.3 cm, measured near the end of free lobes. They found lobes to be free for 69–83% of their length. [Sellards](#) also inferred that the base of the organ had been covered with somewhat softer, more “fleshy” material. *Monoletes*-type prepollen were found in these organs, overlying the interior portions of the lobes, from base to tip, but without evidence of the sporangia in which they were originally borne; the prepollen were monolete and fusiform in shape. [Millay et al. \(1978\)](#) found the prepollen to average 329 μm × 233 μm. [Drinnan and Crane \(1994\)](#) found there to be a single, elongate, segmented sporangium running the length of each lobe, displaced toward the interior. The Okmulgee material agrees in all respects with the emended diagnosis of [Drinnan and Crane \(1994\)](#) with the exception of size, the Okmulgee specimens being somewhat smaller in both length and width.

[Sellards \(1903\)](#) speculated that these organs might have been produced by the plant that bore *Macroneuropteris scheuchzeri* foliage (cited as *Neuropteris decipiens* in [Sellards' paper](#)), noting a 10:1 ratio of the foliage to the spore-producing organs in the Yale University collections. He later ([Sellards, 1907](#)) restated this opinion somewhat less tentatively. [Darrah \(1969\)](#) agreed with this interpretation. Certainly, the attribution of this organ to the medullosans is widely accepted based on its morphology and that of the pollen grains it contains ([Wieland, 1924](#); [Millay et al., 1978](#); [Millay and Taylor, 1979](#); [Stidd, 1981](#); [Mapes, 1982](#)). It also is noteworthy that these pollen organs often are massed, suggesting (perhaps seasonal) synchronicity of production on the parent plant, and possible attachment in groups (Plate X, 5–6).

Division Tracheophyta

Class Spermatopsida

Order Cordaitales

Genus *Artisia* [Presl in von Sternberg \(1838\)](#)

*Description.*—*Artisia* is the cast of the pith area of woody cordaitalean stems. It is recognized by its circular to oval shape in cross section and horizontal to subhorizontal lines, representing parenchymatous plates originally crossing the pith area.

*Remarks.*—Specimens of the pith-cast *Artisia* (Plate X, 7) strongly suggest the presence of cordaitaleans in a flora. Cordaitaleans were woody plants, some of considerable sizes (e.g., [Falcon-Lang and Bashforth,](#)

[2005](#)), and often produced thick secondary xylem. Such woody axes have been attributed to a number of fossil genera (e.g., [Costanza, 1985](#); [Trivett, 1992](#); [Wang et al., 2003](#)), but all have a broad pith traversed by parenchymatous plates or septae. This pith area evidently could be filled with sediment that would filter in around these parenchymatous septae and create a cast of the pith region, in which the anatomical aspects were preserved. Several specimens of *Artisia* were identified in the Okmulgee collection, providing a reasonably strong case for the presence of cordaitaleans in the flora.

Wide septate piths recently have been recognized in stems possibly of coniferalean affinity ([Falcon-Lang et al., 2011b](#)). No conifer foliage was found in the Okmulgee flora nor, given its taphonomic and sequence stratigraphic settings, would such plants be expected. Consequently, we consider such an affinity unlikely.

#### Genus *Cordaites* [Unger \(1850\)](#)

*Description.*—All specimens attributed to *Cordaites* are fragmentary, relatively flat and wide, resembling axes. They have fine striations, sometimes thickened by encrustation with iron, that do not anastomose and occasionally can be found to fork in one direction only, thus consistent with an interpretation as veins, as opposed to sclerenchyma strands. No positively identifiable bases or tips of leaves were found.

*Remarks.*—In the Okmulgee flora, we have identified very few specimens that might qualify as *Cordaites*. Cordaitalean foliage is among the most difficult Pennsylvanian wetland plant elements to recognize in fragmentary, parautochthonous to allochthonous preservation. The leaves assigned to *Cordaites* [Unger, 1850](#) are strap-like and have numerous parallel veins (see discussion of anatomy in [Good and Taylor, 1970](#), and of cuticular features in [Šimůnek, 2000, 2007](#)). Fragments of such leaves can be difficult to differentiate from flattened medullosan or tree fern rachis or petiolar remains, which also may have abundant longitudinally elongate bundles in their tissues, consisting of sclerenchyma, resin ducts, etc. Although in detail the longitudinal striations in these latter organs do not have the consistent thickness, spacing, or dichotomous branching patterns of leaf veins, these different organs nonetheless are exceedingly difficult to differentiate under many forms of preservation (Plate X, 8). Leaf apices or clasping bases are positive indicators of cordaitalean foliage and permit more confident assignment of less diagnostic fragments to *Cordaites*. Consequently, such leaves may be among the most under-recognized of any of the common taxa present from Pennsylvanian wetlands.

#### 3.3. Comparison of the Okmulgee and Mazon Creek floras

The Okmulgee flora is compared directly to the large Mazon Creek collection held by the Field Museum of Natural History in Table 2. The first half of this table compares the 27 taxonomic categories (varying from species to major lineages, and including various kinds of organs) identified at Okmulgee with the 27 most abundant taxa at Mazon Creek, and considering, though not listing, any Mazon Creek taxonomic categories not among the top 27. The second comparison is based upon the 20 species-level taxa identified at Okmulgee with the 23 most abundant species identified at Mazon Creek (excluding species based on reproductive organs unassignable to a vegetatively-based species). Comparisons between these two floras are complicated by the variably resolved taxonomy of Pennsylvanian compression–impression plants, which is plagued by many duplicate names, dubious names based on fragmentary material, and inconsistencies in taxonomic practice. In addition, there is a large fraction of the specimens that cannot be identified to anything other than a major group (e.g., pectopterid ferns, or lycopsid reproductive organs). In some instances this introduces a conflict in comparing dominance patterns; for example, in a comparison of all taxonomic categories, it is clear that pectopterid ferns are twice as abundant as any other category in the Field Museum Mazon Creek collection, whereas in a species level ranking, the most abundant tree fern,

**Table 1**

Comparison of quantitative composition of the Okmulgee and Mazon Creek floras. Part 1 illustrates the top 27 categories in each flora and the number of specimens on which that category was identified. Symbols preceding the category name: 1—shared between top 10 categories, 2—shared between categories 11 to 27, 3—an Okmulgee category present at Mazon Creek but ranked >27th, X—present at Mazon Creek, but not present in the smaller Okmulgee collection. Part 2 lists the 20 species identified at Okmulgee and the top 23 species identified at Mazon Creek, each in rank abundance based on specimen occurrences. The numbers or symbols preceding the species name indicate: the rank of the species in that flora followed the rank of the species in the other flora. X—present at Okmulgee but ranked >25 at Mazon Creek. Z—present at Mazon Creek but not present in the Okmulgee flora. 12 of the 20 Okmulgee species are among top 25 at Mazon Creek.

Okmulgee		Mazon Creek	
Count	Taxon	Taxon	Count
442	1-Lobopteris vestita	1-Pecopteris sp.	2376
435	1-Macroneuropteris scheuchzeri	1-Lycopside leaves and reproductive organs	1273
173	1-Annularia sphenophylloides	1-Macroneuropteris scheuchzeri	1079
145	3-Synchysidendron andrewsii	1-Lobopteris (P. acadica) vestita	574
128	1-Pecopteris sp.	2-Pecopteris unita	495
122	1-Calamitalean stems	1-Annularia sphenophylloides	486
117	1-Lycopside leaves and reproductive organs	1-Laveinopteris rarinervis	485
95	3-Karinopteris plumosa	1-Calamitalean stems	441
91	1-Laveinopteris rarinervis	2-Sphenophyllum emarginatum	396
82	3-Diaphorodendron rimosum	X-Annularia sp.	380
58	2-Annularia spinulosa	X-Neuropteris vermicularis	379
57	3-Condotheca caduca	2-Annularia radiata	364
33	2-Indeterminate lepidodendrids	X-Lepidophloios protuberans	347
15	3-Cordaitaleans	2-Odontopteris aequalis	277
9	3-Eusphenopteris sp.	X-Alethopteris sullivantii	274
8	2-Asterophyllites equisetiformis	2-Alethopteris serlii	262
8	3-Pecopteris subcrenulata	2-Asterophyllites equisetiformis	251
6	2-Annularia radiata	X-Cyclopteris trichomanoides	251
4	3-Oligocarpia gutbieri	X-Neuropteris sp.	210
3	2-Pecopteris unita	X-Rhacophyllum sp.	210
2	3-Lepidodendron aculeatum	2-Annularia (stellata) spinulosa	217
2	2-Sphenophyllum sp.	2-Lepidodendron sp.	185
1	3-Lepidodendron wortheni	X-Stephanospermum konopeonus	180
1	2-Odontopteris aequalis	X-Macroneuropteris macrophylla	158
1	3-Eusphenopteris neuropteroides	X-Pecopteris fontainei	148
1	2-Alethopteris serlii	X-Lepidodendron diplotegioides	137
1	3-Alethopteris lonchitica	X-Neuropteris ovata	136

Okmulgee		Mazon Creek	
Count	Taxon	Taxon	Count
442	1/2-Lobopteris vestita	1/2-Macroneuropteris scheuchzeri	1079
435	2/1-Macroneuropteris scheuchzeri	2/1-Lobopteris (P. acadica) vestita	574
173	3/4-Annularia sphenophylloides	3/14-Pecopteris unita	495
145	4/21-Synchysidendron andrewsii	4/3-Annularia sphenophylloides	486
95	5/X-Karinopteris plumosa	5/6-Laveinopteris rarinervis	485
91	6/5-Laveinopteris rarinervis	6/Z-Sphenophyllum emarginatum	396
82	7/X-Diaphorodendron rimosum	7/Z-Neuropteris vermicularis	379
58	8/14-Annularia spinulosa	8/12-Annularia radiata	364
57	9/X-Condotheca caduca	9/Z-Lepidophloios protuberans	347
8	10/13-Asterophyllites equisetiformis	10/16-Odontopteris aequalis	277
8	10/X-Pecopteris subcrenulata	11/Z-Alethopteris sullivantii	274
6	12/8-Annularia radiata	12/16-Alethopteris serlii	262
4	13/X-Oligocarpia gutbieri	13/10-Asterophyllites equisetiformis	251
3	14/4-Pecopteris unita	14/Z-Pecopteris/Crossotheca fontainei/sagittata	224
2	15/X-Lepidodendron aculeatum	15/8-Annularia (stellata) spinulosa	217
1	16/X-Lepidodendron wortheni	16/Z-Macroneuropteris macrophylla	158
1	16/10-Odontopteris aequalis	17/Z-Lepidodendron diplotegioides	137
1	16/X-Eusphenopteris neuropteroides	18/Z-Neuropteris ovata	136
1	16/11-Alethopteris serlii	19/Z-Neuropteris inflata	111
1	16/22-Alethopteris lonchitica	20/Z-Rhacophyllum comutum	108
		21/4-Synchysidendron (Lepidodendron) andrewsii	107

**Table 2 (continued)**

Okmulgee		Mazon Creek	
Count	Taxon	Taxon	Count
		22/16-Alethopteris (ambigua) lonchitica	100
		23/Z-Pecopteris mazoniana	86

*Pecopteris vestita*, is second overall, about half as common as *Macroneuropteris scheuchzeri*.

The comparison presented in Table 2 demonstrates unequivocally that the Okmulgee flora is a compositional subset of that known from Mazon Creek. Both are dominated by a combination of pecopterid tree-fern foliage and pteridosperm foliage. The single most abundant species of tree fern is *Lobopteris vestita*; the overwhelmingly most abundant pteridosperm is *Macroneuropteris scheuchzeri*. On a clade basis, tree ferns and pteridosperms are most abundant, followed by lycopsids and calamitaleans. The diversity at Okmulgee is, of course, lower than that encountered at Mazon Creek because the Okmulgee locality has not attracted the attention of collectors, with the resultant examination of massive numbers of specimens. Mazon Creek may be the most heavily collected Pennsylvanian-age fossil flora in the United States, by contrast. Nonetheless, the Okmulgee collection is quite large compared to many Pennsylvanian collections and yet reveals a remarkably monotonous vegetation that when linked to Mazon Creek can be extended over a vast area.

Coastal regions of the modern tropics also may be quite homogeneous and taxonomic similarity over large areas has been noted: consider the low diversity of coastal fringe mangrove communities (Fromard et al., 1998; Ukpong, 2000), or the assemblages dominated by *Montrichardia arborescens* described by Pfefferkorn et al. (2001) from both the Amazon and Orinoco deltas. This lends support to hypotheses such as that of Falcon-Lang (2009) that *Macroneuropteris scheuchzeri* or some populations thereof, may have been mangroves or had wide tolerances of disturbance and salinity. Certainly, the data reported here suggest that it may have combined with tree ferns in such communities.

Pfefferkorn (1979) estimates the described diversity of the Mazon Creek flora to stand at 96 species belonging to 41 genera. This would need revision given changes in taxonomy of such groups as *Neuropteris* sensu lato, in the years since the publication of his paper (e.g., Cleal et al., 1990). We count about 70 species, in round numbers, in Wittry (2006), which of course depends on what one counts as a “species” — in this case, not considering reproductive structures of any sort, focusing only on foliage of calamitaleans, pteridosperms, cordaitaleans and ferns, and stems of lycopsids. The census of the Field Museum Mazon Creek flora includes nearly 200 species of pteridosperm, cordaitalean, fern and sphenopsid foliage and lycopsid stem taxa, over 70 of which are represented by a single specimen, and many more by two specimens. In addition, there are many more named reproductive organs that cannot be assigned with confidence to any existing vegetatively-based species. Considering how many of these groups are in need of taxonomic revision, the standing estimates of diversity in Pfefferkorn (1979) and Wittry (2006) appear to remain reasonable, order of magnitude approximations.

Darrah (1969) collected an unbiased sample of nodules and estimates that 4 species comprise 60% of the Mazon Creek flora: *Neuropteris decipiens* (which we would classify as *Macroneuropteris scheuchzeri*), *Pecopteris lamuriana* (which we would classify as *Lobopteris vestita* sensu Wagner), *Neuropteris ovata* (in this name he included specimens of *Neuropteris flexuosa* and the much more common *Neuropteris vermicularis* as forms of *N. ovata*), and *Neuropteris rarinervis* (now *Laveinopteris rarinervis*). Five additional species bring this number up to 80%: *Alethopteris serlii*, *Alethopteris sullivantii*, *Annularia stellata* (which we identify as *Annularia spinulosa*), *Pecopteris unita*, and *Pecopteris arborescens* (Darrah included several distinct forms under

this latter name, including *Pecopteris subcrenulata* and *Pecopteris oreopteridia*, which greatly outnumber *P. arborescens* sensu stricto; see Wittry, 2006). Darrah further notes that *Lepidodendron*, *Calamites* and *Cordaites* seldom occur in small samples, although they certainly are present in the flora. Peppers and Pfefferkorn (1970) compared several different Mazon Creek dominance estimates at the major-group level and determined that pteridosperms, as a group, generally are the most abundantly represented, followed by ferns. In rank order, the sphenopsids, lycopsids and cordaitaleans are less abundant, in keeping with the findings of Darrah (1969) and Wittry (2006). Pfefferkorn (personal communication, 2012) notes, however, that there is a great deal of site-to-site variation in the Mazon Creek collections when such collections can be constrained to small geographic areas.

Pfefferkorn and Thomson (1982) quantified numerous Pennsylvanian floras and found that those older than the middle of the Westphalian D (as used prior to the establishment of the Cantabrian, thus approximately equal to the Westphalian–Cantabrian boundary as presently used in Western European terrestrial sections) are never dominated by ferns, whereas younger floras commonly may be. The Okmulgee and Mazon Creek floras occur during the early parts of this time interval marked by a sharp rise in tree fern abundance.

#### 4. Discussion

The Okmulgee collection adds a distinctive geographic component to the much better known and studied Mazon Creek flora of the Illinois Basin. Occurring at the same stratigraphic position, the Okmulgee flora is compositionally similar to Mazon Creek (Peppers and Pfefferkorn, 1970; Janssen, 1979; Pfefferkorn, 1979; Wittry, 2006). Separated by over 1100 km, but in the same depositional context and in the same form of preservation, the Okmulgee and Mazon Creek collections are isotaphonomic (sensu Behrensmeyer and Kidwell, 1985; Behrensmeyer and Hook 1992), which strengthens comparisons between them. The great distance separating these assemblages illustrates the spatial extent over which Middle Pennsylvanian floras could be effectively compositionally homogeneous. There have been few opportunities in the fossil record to examine narrowly time equivalent deposits, preserved in the same way and representing the same biome over such large distances, other than studies of reliably correlated coal beds, in which floristic studies can be carried out with spore and pollen data (e.g., Peppers, 1996). The flatness of much of the Pennsylvanian cratonic area in present day North America, then west-central and western Pangaea, is an important factor underlying the dynamics and areal distribution of sedimentary processes in such environments. The low gradient would have permitted relatively rapid flooding of the land surface during times of ice melting and early sea-level rise, which is the likely phase of a glacial–interglacial cycle during which these floras were preserved. The depositional environment of the enclosing deposits appears to have been a shallow, extremely broad, lake-like embayment, or series of embayments with variable salinity reflective of distance from the coastline (Baird et al., 1985a). In the Francis Creek Shale, source of the Mazon Creek assemblage, plants are preserved in the lowest salinity facies, where they are associated with a variety of terrestrial animal remains (Richardson and Johnson, 1971; Wittry, 2012). Such deposits have been interpreted as deltaic in origin (Wright, 1965; Shabica, 1970), and are represented by several mudstone lobes, collectively the Francis Creek Shale, that immediately overlie the Colchester (No. 2) coal bed in a five county area of northern Illinois. Baird et al. (1985b) note the presence of animals typical of transitional brackish-to-marine environments in the basal portion of the Francis Creek Shale.

Fossiliferous shales above the Croweburg–Henryetta Coal in Oklahoma were deposited in a setting similar to that of the Francis Creek Shale. Wright (1965), Smith (1970) and Baird et al. (1985a) illustrate clastic wedges above the coal in Oklahoma similar to those in Illinois, though such sediments would have been derived from a different clastic source area than those of the Francis Creek Shale (Houseknecht, 1983). Similar

animal fossils to those of Mazon Creek also are found above the Croweburg–Henryetta in what are interpreted as brackish-to-fresh water deposits, positioned, as in the Francis Creek Shale of Illinois, seaward of the plant-bearing shales. The Francis Creek Shale and its equivalents must have been deposited very rapidly and prior to widespread flooding of the craton as evidenced by extensive, overlying marine rocks. For example, Shabica (1970) illustrates a tall, upright tree trunk, rooted in muds, just above the top of the Colchester coal and buried in Francis Creek Shale. Given the expected short duration that such a tree would last if covered with marine or brackish water, probably a decade to a century, its burial to such a height would need to have been rapid. Furthermore, the Mecca Quarry black shale, which forms the roof shale of most of the Colchester coal and its equivalents, was deposited after the gray shale wedges, and onlaps them. It is succeeded, as in a typical late Middle Pennsylvanian cyclothem, by marine limestone.

The alternation of terrestrial and marine rocks is repeated throughout the later Middle Pennsylvanian in both the Illinois Basin and Midcontinent. Localized gray-shale wedges immediately above the Springfield (No. 5), Herrin (No. 6), and Danville (No. 7) coals of the Illinois Basin are overlapped successively by marine black shales and limestones, all formed during successive phases of marine transgression during a glacial-to-interglacial transition. Sedimentological reevaluation of these gray-shale wedges (Elrick et al., 2008; Nelson et al., 2008; Elrick and Nelson, 2010) indicates a non-marine origin in tidally influenced, shallow-water coastlines, perhaps beginning as mudflats flanking rivers that had been converted to estuaries. Accommodation space for the non-marine to brackish muds was created by a combination of sea-level rise and peat compaction. Such deposits also tie closely to changes in clastic transport patterns due to climate change, linked further to glacial melting and sea-level rise (Cecil et al., 2003). The clastics were essentially avulsed onto the peat surface as rising sea-level backed up downstream sediment transport and forced sediment upriver.

Although such a model cannot be asserted with certainty for the Francis Creek Shale, the patterns of distribution for that deposit, its sedimentary features, and its relationship to other, later-deposited sediments, are consistent with the patterns observed for other late Middle Pennsylvanian coal beds and the rocks that overlie them. In light of these similarities and their implications for the origin of the fossiliferous gray-shale wedges, it is unlikely that the Francis Creek Shale or its equivalents in Missouri and Oklahoma were deposited in high-constructive deltaic settings. More likely, they originated as a mixture of mudflats fringing drowning channels or off-shore mudstones being driven landward by a combination of rising sea-levels and siliciclastic transport associated with late lowstand to early transgressive phase climate changes during the onset of an interglacial. This is important because it has some very specific implications for the paleoecology of the Mazon Creek and the Okmulgee plant assemblages.

Deltaic deposits of a high constructive nature are most expected to have formed at sea-level highstand or during falling stages of sea-level, when polar ice was at a minimum or starting to build again. At these times, during highstands, the most recent climate models (Cecil et al., 2003; Poulsen et al., 2007; Eros et al., 2011; Horton et al., 2012) predict the driest climates of a glacial–interglacial cycle. The Mazon Creek and Okmulgee floras are, however, fairly typical wetland, Pennsylvanian floras. In contrast, if the enclosing deposits formed during early transgression, the plants they contain would represent the last elements of the coastal wetland flora fringing the encroaching sea, a time of transition from the wettest humid climates of a glacial–interglacial cycle (the peat forming period) to the increasing seasonality of a wet sub-humid climate during early transgression. Thus, they may be composed mostly of “coal swamp” elements mixed with smaller numbers of plants drawn from terra firma wetland assemblages. Consider the tall, in situ lycopsid trees at the interface of the Colchester coal and Francis Creek Shale, one of which is illustrated by Shabica (1970, Figure 4). Burial of such trees had to happen during very early phases of peat-swamp surface flooding or the trees would have rotted away.

The source area from which both the Mazon Creek and Okmulgee floras were drawn was a wet, probably very low lying, coastal plain that included a mixture of habitats from within that kind of physiographic setting (Pfefferkorn, 1979). These would have included clastic swamps, stream side vegetation, flood plain and interfluvial areas, but all filtered through any vegetation that specifically colonized and was characteristic of shoreline habitats. Thus, the original vegetation from which both fossil floras originated probably did not grow in exclusively “swampy” (nearly permanently flooded) habitats, in which homogeneity might be expected, given the narrow physical breadth and peculiar conditions of such environments. The vegetation dominating the margins of coastal estuaries was most probably dominated of tree ferns (primarily *Lobatopteris vestita*) and the pteridosperm *Macroneuropteris scheuchzeri*, given the abundance of these plants in both assemblages.

Baird et al. (1985a) make a strong case for the conservatism of the brackish-to-marine nearshore fauna, which has been tagged with the name “Essex Fauna” (Richardson and Johnson, 1971). Following Schram (1979), they argue that the Essex-type fauna was characteristic of physically unstable, high-stress, marginal marine environments. This kind of compositional persistence, or recurrence also has been documented in terrestrial wetland vegetation from Carboniferous lowland environments (e.g., DiMichele et al., 2002), and for normal marine benthic faunas from Mississippian environments (e.g., Bonelli and Patzkowski, 2011). These kinds of patterns in both terrestrial and marine environments have been attributed to relatively narrow ranges of physical environmental tolerance by most organisms, resulting in strong patterns of habitat tracking through space and time (e.g., Brett et al., 2007; DiMichele et al., 2008), and, as observed by Ivany et al. (2009), may account for observed larger spatio-temporal scale, evolutionary–ecological patterns.

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