FOSSIL VEGETATIONAL TRANSECT FROM BELOW THE COLCHESTER COAL TO THE ROOF OF THE CARDIFF (SURVANT) COAL (DESMOINESIAN, UPPER MIDDLE PENNSYLVANIAN), ILLINOIS BASIN

JOHN H. CALDER[1], W. JOHN NELSON[2], ARDEN R. BASHFORTH[3], JACK WITTRY[4], SCOTT D. ELRICK[2] and WILLIAM A. DIMICHELE[5]

[1]Halifax, Nova Scotia, B3J 2L4, Canada, [2]Illinois State Geological Survey, 615 E. Peabody Drive, Champaign, IL 61820 USA, [3]Natural History Museum of Denmark, University of Copenhagen, 1718 Copenhagen K, Denmark, [4]Field Museum of Natural History, Chicago, IL, 60605 USA, [5]Department of Paleobiology, NMNH Smithsonian Institution, Washington, DC 20560, USA email: dimichel@si.edu

Abstract—Four collections of Middle Pennsylvanian plant fossils create an opportunity to examine a transect from below the Colchester Coal through the roof shale of the Cardiff (Survant) Coal of the Illinois Basin. The collections come from the Colchester Coal seat earth, the Colchester Coal roof shale (two collections), and the roof shale of the Cardiff Coal. The Colchester Coal is one of the most widespread coals in the American Pennsylvanian, extending from the Appalachian Basin (Lower Kittanning Coal) to the Midcontinent Region (Whitebreast and Croweburg coals). The Colchester Coal has been made famous by the fossilized plants and soft-bodied animals preserved in a facies of its roof shale, the Francis Creek Shale, host of the Mazon Creek biota. The collections reported here are much smaller than the Mazon Creek flora, and so represent local assemblages. The collection from the Cardiff Coal, which is no longer mined, is the first report of a flora associated with that coal bed. The three roof shale floras, collected in 1906, are small and likely were collected from the surface area at the mine tipple. They appear to represent the flora preserved close to the coal-bed surface and thus capture the final flora of the peat swamp. Accordingly, they represent the early phases of transition from a humid to a subhumid climate at the time of glacial melting and sea-level rise. Similarly, the Colchester Coal seat-earth collection likely represents a local landscape preserved during the time of climate change from a wet sub-humid to a humid climate, just preceding the onset of peat formation.

INTRODUCTION

The middle of the Desmoinesian Stage, upper Middle Pennsylvanian, in coal basins of the eastern and midwestern United States encompasses the most widespread and economically significant coal beds of the Pennsylvanian in the United States (Greb et al., 2003). These coal beds comprise parts of the first appearance of well developed cyclic sedimentation patterns recording the alternation of marine and terrestrial strata (Wanless and Weller, 1932; Langenheim and Nelson, 1992; Cecil et al., 2014). This pattern begins with the so-called Verdigris Cycle, which includes the Colchester Coal bed (Cecil et al., 2003), the main object of this study.

Cyclic sedimentation, as was recognized early (Wanless and Shepard, 1936), reflects glacial fluctuations primarily in the southern hemisphere, which also induced and were thus synchronized with changes in sea level and climate (Cecil et al., 1985; Cecil, 1990; Montañez et al., 2016). These oscillations were driven most likely by Earth orbital factors (Horton et al., 2012). The resultant glaciations were not, however, equally intense, even if they followed a more-or-less regular temporal rhythm (Heckel et al., 2007). Like modern glacial-interglacial cycles, magnitude of sea-level changes varied, resulting in temporally variable thicknesses and extents of the resulting strata (Heckel, 2008).

In this study, we examine several local plant-fossil assemblages that come from different terrestrial phases of the extensive glaciation that produced the Verdigris cyclothem and the Colchester Coal, and the subsequent much less extensive glaciation that includes the Survant Coal. Local occurrences of the Survant, situated at the most landward fringes of its development have been described by several different names over time, reflecting their limited and unconnected areal extents. Among these names was the Cardiff Coal, which is of secondary interest here. The Colchester Coal is superseded by the Francis Creek Shale, which hosts the famous Mazon Creek biota, with which these local assemblages can be contrasted.

GEOLOGICAL AND HISTORICAL BACKGROUND

The Colchester Coal originated as part of one of the most extensive peat deposits in geologic history. Although too thin to mine in many places, the Colchester occurs throughout the Illinois Basin, which covers much of Illinois, southwestern Indiana, and western Kentucky. West of Illinois the Colchester correlates into the Midcontinent Basin as the Whitebreast Coal of Iowa and the Croweburg Coal of Missouri, eastern Kansas, and northeastern Oklahoma. Eastward, the Colchester is correlative with the Lower Kittanning coal bed in the northern Appalachian Basin of eastern Ohio, western Pennsylvania, and parts of West Virginia. These correlations are based on biostratigraphy of spores in coal (Peppers, 1996) and conodonts in associated marine rocks (Heckel, 2013), in addition to lithologic similarities. Cecil et al. (2003) compared the paleoclimate of the Colchester Coal to its correlatives (including rocks that lack coal) from the northern Appalachian Basin as far west as California.

In the southern part of the Illinois Basin the Colchester Coal is too thin to mine, ranging from a few cm to about 50 cm and averaging around 20 to 30 cm. Directly overlying the coal is the Mecca Quarry Shale, which is black, highly fissile, phosphatic marine shale typically 50 to 75 cm thick (Fig. 1). Although thin, these units are readily recognized on most types of borehole logs. Thicker Colchester Coal is confined to the northern half of Illinois where thickness is commonly 75 to 125 cm and the coal was mined extensively from the middle 19th into the middle 20th century. The growth of heavy industry in the Chicago area spurred mining of the Colchester Coal, but gradually the thicker coal deposits of southern Illinois came to prominence and the northern mines went out of production.

Lying between the Colchester Coal and the Mecca Quarry Shale in much of northern Illinois is a gray, non-marine to marginal marine shale unit called the Francis Creek Shale. Thickness of the Francis Creek increases from zero on the south and west to more than 25 m at the northeastern corner of the basin near Kankakee (Smith, 1970; Fig. 2). The Francis Creek Shale is famous for its “Mazon Creek” flora and fauna, including soft-

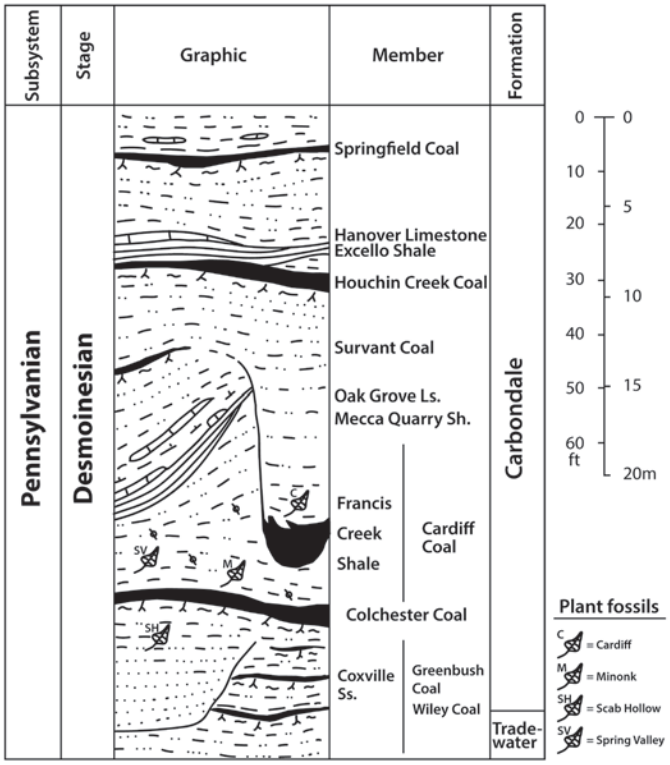

FIGURE 1. Generalized stratigraphic section discussed in report with approximate stratigraphic position of plant-fossil localities.

bodied invertebrates, preserved in siderite concretions (Wittry, 2012, 2020). In addition, the Francis Creek Shale contains a diverse flora preserved as compressions within the shale, and locally the casts of flat-lying logs and stumps in growth position rooted at the top of the Colchester. Mainly because of difficulty in collecting, these fossils have received less attention than those of the Mazon Creek concretions. The low seam height in underground mines made walking upright impossible; the last deep mine closed more than 70 years ago. Surface mining continued into the 2000s but collecting generally was confined to random gathering of siderite nodules from spoil banks.

A highly localized deposit of thick coal younger than the Colchester is known as the Cardiff Coal (Fig. 1). This coal was mined underground more than a century ago at the village of Cardiff in northeastern Illinois (Fig. 3) and later was extracted, together with the Colchester, from a nearby surface mine. As detailed below, the Cardiff Coal apparently represents peat that accumulated in an abandoned stream channel. Plant fossils (compressions) were collected from shale overlying the coal in a mine at Cardiff but information on their precise geologic setting is not available.

This article describes and illustrates plant fossils from three localities associated with the Colchester Coal and one with the Cardiff Coal (Fig. 3). Two of the Colchester collections came from the lower part of the Francis Creek Shale in underground mines (Minonk and Spring Valley) and the third came from shale a short distance below the Colchester exposed along a county road (Scab Hollow). The Cardiff collection came from shale overlying the Cardiff Coal in an underground mine.

Scab Hollow Locality: Colchester Coal Seat Earth

This name refers to a flora collected by coauthors DiMichele and Nelson in July 1983 near Scab Hollow (USNM locality 38404), a ravine in Schuyler County, western Illinois (Fig. 3). We have not learned the origin of this peculiar name. Judging by a field photograph and Google Earth imagery, the legal location is: roadcut on west side of Scab Hollow Road approximately 300 feet from north line and 1,200 feet from east line of Section 24, T2N, R1W, on the Ray 7.5-minute topographic quadrangle.

We sought this locality based on mention of plant fossils in a measured section here from Wanless (1957, p. 189). Field notes that H.R. Wanless made in 1930 (ISGS, open files) provide further information. Wanless identified "well preserved fern leaves, including *Annularia sphenophylloides, Neuropteris rarinervis, Neuropteris sp., Odontopteris, Pecopteris sp., Cordaites, Calamites,* etc. Collection made by Messrs. Milligan, Livingston, and Wanless". We have not learned the disposition of the collection nor the identity of Livingston and Milligan. Possibly, they were students of Dr. Wanless.

The section that Wanless described is shown graphically (Fig. 4). Plant fossils occur in the upper 1 to 2 feet (30 to 60 cm) of gray, micaceous shale that becomes increasingly sandy downward and lies approximately 45 to 65 cm beneath the base of the Colchester Coal, which is approximately 1.5 feet (45 cm) thick at this site. Wanless interpreted the plant-bearing shale as the upper part of a channel phase of the unit then called the Isabel sandstone, now considered to be the Coxville Sandstone Member of the Carbondale Formation.

The plant-bearing siliciclastic bed beneath the Colchester Coal is a "seat earth" only in the broadest terms: it is a rock unit immediately below a coal bed. Rooting by the lycopsid root system, *Stigmaria*, is concentrated in the upper parts of the bed, almost certainly derived from the initial development of the Colchester peat swamp. A typical paleosol "underclay", of the type that underlies the Colchester Coal in most of the Illinois Basin, was not noted either by Wanless or in the fieldnotes of the authors (Nelson and DiMichele).

Minonk Mine: Colchester Coal Roof Shale

David White, of the U.S. Geological Survey, acquired a collection (USGS collection 4146) from the Minonk Coal Company's mine on August 27, 1906. Minonk is about 50 km north of Bloomington in north-central Illinois (Fig. 3) and at the time was a junction point for branches of the Illinois Central and Santa Fe Railroads. A shaft 100 m (329 feet) deep was completed in 1869 and production from the Danville Coal began, but this operation proved unprofitable, so the company deepened the shaft to 168 m (550 feet), where higher quality coal from the Colchester Coal Member was available (Moore, 1913). More than 1.9 million tons of coal were produced until 1902, when the first mine was closed. Mine No. 2 commenced operation in 1905 from shafts about 1 km north of the original portal and remained in production through 1951, at the time of closure being one of the last underground mines in Illinois extracting the Colchester Coal. Total output of Mine No. 2 was approximately 1.28 million tons, having had average annual production less than half that of Mine No. 1. According to available maps, workings of the two mines connected underground.

Like most mines in the Colchester Coal, both Minonk mines used the longwall system of coal extraction that evolved to maximize recovery from thin coal seams. Generally, the mine layout was circular or semi-circular having haulage roads radiating from the shafts to the working faces around the perimeter. After setting wooden props and building walls of waste rock to protect roads and work areas, the miners removed coal and as the face advanced, allowed overburden to subside into the worked-out area. In this manner, more than 90% of the coal in place could be extracted. Most of the work was carried out by hand: undercutting the coal with a pick, drilling shot holes, blasting with explosives, and loading by shovel into cars pulled by mules or other animals. By contrast, the longwall system of mining in use today is fully mechanized and uses massive hydraulic jacks to support the roof at the working face.

No field notes from David White's visit to Minonk have

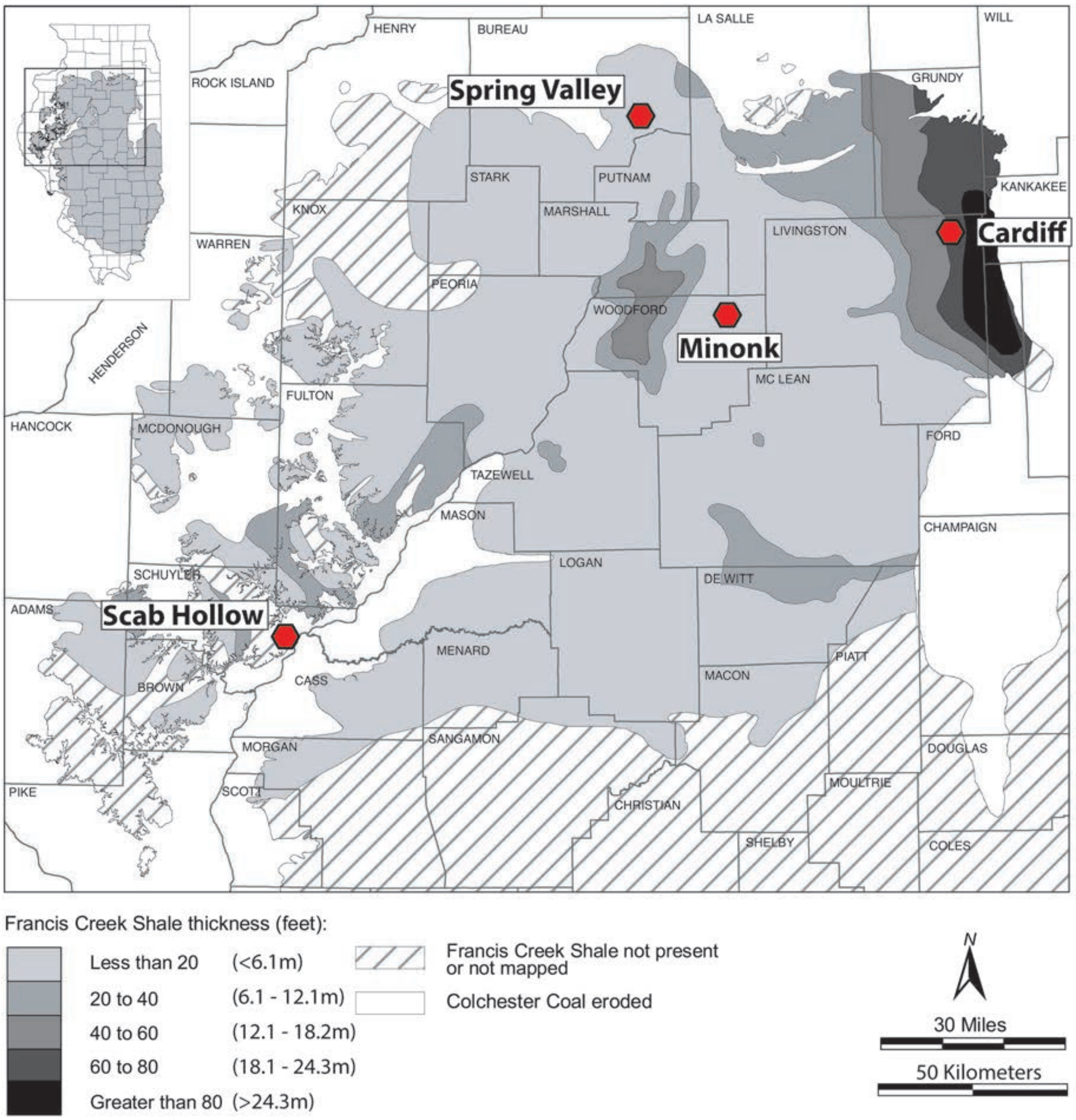

FIGURE 2. Thickness of Francis Creek Shale, from Korose (2003), with plant-fossil localities from this report.

come to light. We do not know whether he collected fossils underground or from waste piles on the surface. Geologists from the Illinois State Geological Survey (ISGS) visited the Minonk No. 2 Mine on several occasions. In field notes from circa 1912, K.D. White reported, "The shale above the coal has many plant impressions, mostly fern fronds. Also in the roof, up to a height of 10 feet [3 m] there are many flattened trunks with the diamond patterned imprints on the surface. These were observed in places to be 12 inches [30 cm] wide, 1½ inches [4 cm] thick, and as long as 10 feet [3 m]. One vertical stem 6 inches [15 cm] in diameter was observed in place, the others being horizontal or nearly so."

Spring Valley No. 2 Mine: Colchester Coal Roof Shale

A plant-fossil collection (USGS 4149) was made by David White and H. Foster Bain, the latter from the ISGS, on August 17, 1906, at an unnamed mine operated by the Spring Valley Coal Company, noted in the USGS collection records as operating near LaSalle, Illinois. The Spring Valley Coal Company operated five longwall underground mines in the Colchester Coal at Spring Valley, which lies about midway between Joliet and the Quad Cities in northern Illinois (Fig. 3). The No. 1 Mine opened in 1884, No. 2 following a year later and operating until 1908 having produced more than 5.2 million tons of coal. The city of Spring Valley was born with and grew up around the mines.

No field notes on the Spring Valley No. 2 Mine by David White, H.F. Bain, or other geologists have been found. J.A. Udden, however, then working for the ISGS, went underground at spring Valley No. 1. His fieldnotes state that the coal averaged 1.1 m (3.5 feet) thick and contained partings of pyrite and "bone". The roof was hard gray shale as thick as 6 m (20 feet) having thin "draw slate" at the base, whereas the floor consisted of fire clay, grading down to sandstone.

In the Spring Valley No. 5 Mine, bordering No. 2 on the northeast, Gilbert Cady (ISGS) reported that the coal varied from 73 to 122 cm (2.4 to 4.0 feet) thick, and the "soapstone" roof thinned toward the northeast, where black shale (Mecca

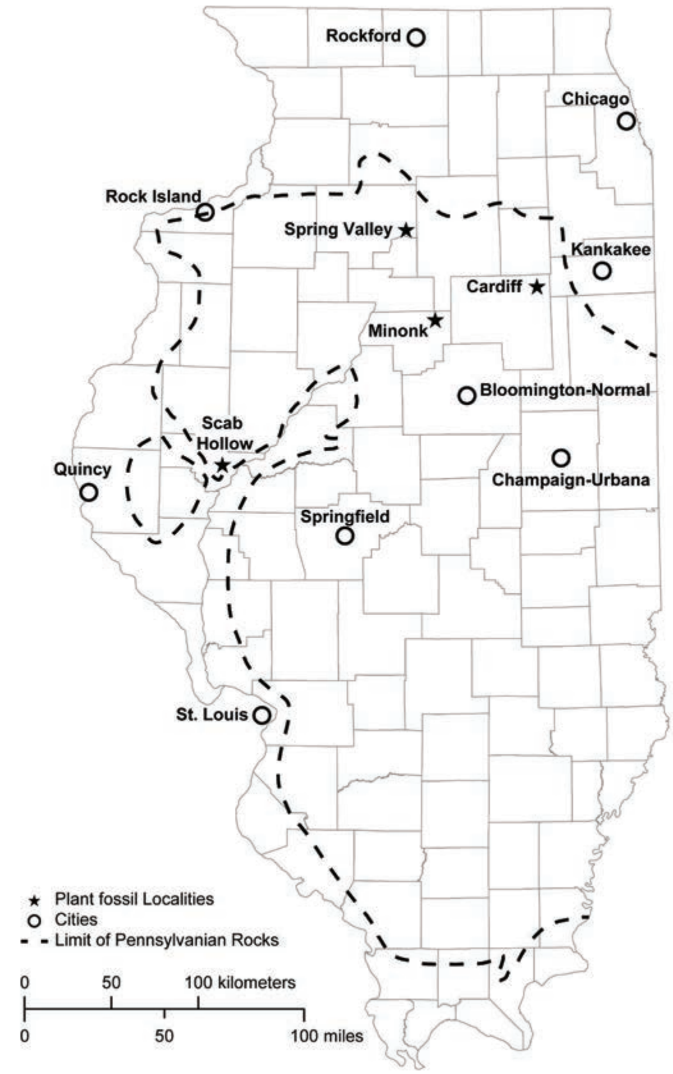

FIGURE 3. Map of Illinois showing plant-fossil localities discussed in this report.

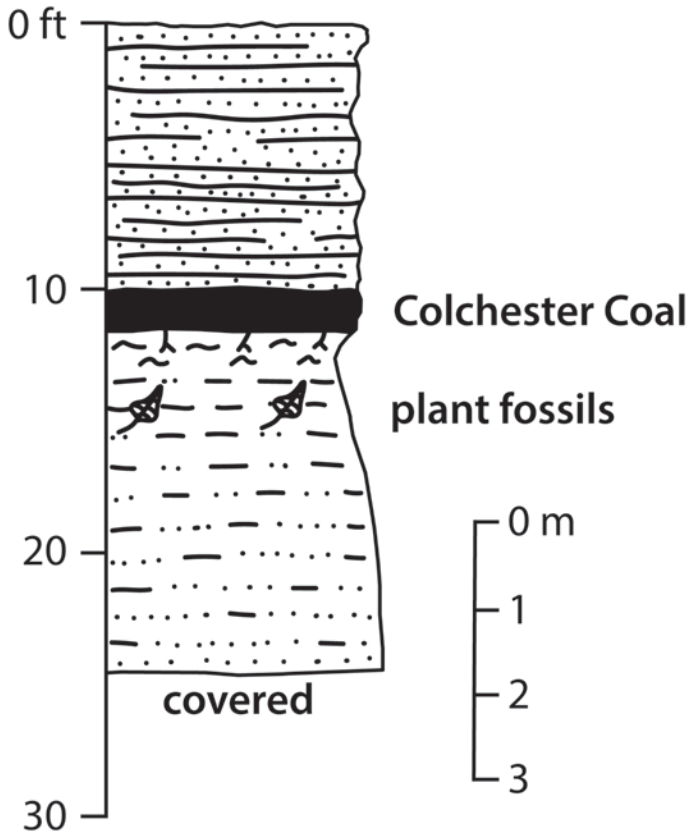

FIGURE 4. Graphic section of Scab Hollow plant-fossil locality as described in field notes of H.R. Wanless, 1930 (ISGS field notes archive).

Quarry) came close to the top of the coal. In notes dated 1912, K.D. White (ISGS) stated the gray shale varied up to 9 m (0 to 30 feet) thick, with about 3 m (10 feet) of black shale containing limestone and ironstone concretions (again, Mecca Quarry Shale). Neither Cady nor White mentioned plant fossils, which almost certainly occurred in the gray Francis Creek Shale and not the black Mecca Quarry Shale.

Cardiff Mine: Cardiff/Survant Coal Roof Shale

David White and H. Foster Bain collected plant fossils (USGS collection 4150) on August 17, 1906, from the Cardiff Coal Company's mine at Cardiff, Illinois. This is the same day on which they collected at the Spring Valley Mine noted above. Now a ghost town, Cardiff was situated in Livingston County, northeastern Illinois about 30 km west of Kankakee.

Coal was discovered at Cardiff (probably by drilling), a shaft was sunk, and production began in September 1899. The town that blossomed around the mine was named for the city in Wales, long known for its collieries. Within four years the mine employed 400 workers and Cardiff's population grew to 2,000. Then in March of 1903 a series of explosions (probably of methane gas and/or coal dust) ripped through the underground workings, killing nine workers and injuring 16 more. The Cardiff Coal Company then sealed the shafts and opened a new mine, Cardiff Coal Company No. 2, less than 1 km northwest of the first. Production grew until in September 1912 when the Wabash Railroad canceled its contract with Cardiff claiming that coal quality had declined and was no longer suitable as fuel for steam locomotives. Thus, Mine No. 2 closed, people moved away, and most of the buildings in town were dismantled and moved (Ridings, 2008). Given the timing, White and Bain obtained their collection from Cardiff's Mine No. 2.

As with the other sites from this time, no field notes of White and Bain are on file for the Cardiff Mine. Considering that their Cardiff and Spring Valley collections carry the same dates, most likely they gathered fossils from waste piles on the surface and did not go underground.

The two mines extracted both the Colchester Coal and the younger, lenticular seam that came to be called the Cardiff Coal. Cady (1915, p. 35) provided a map and three cross sections (Fig. 5) and described the Cardiff Coal as follows: "…a thick, lenticular bed of coal which seems to have been deposited in a small channel-like basin running in a quarter circle for about two miles [3.2 km], with a breadth of 1000 to 1200 feet [300 to 420 m]. At the bottom of this trough this coal (the 'big vein') lies a few feet, as a rule not over 10 [3 m], above coal No. 2 [Colchester]; at a few points the beds are in contact. The bottom of the coal rises to a height of 15 [4.5 m] to over 30 feet [9 m] above coal No. 2 at the sides of the trough. Twelve feet [3.6 m] of coal has been encountered, but the average thickness in the trough is about 9 feet [2.7 m]."

Coal having the same characteristics was encountered in 1958 in Peabody Coal Company's Northern Mine, Pit 15, a surface mine about 11 km north-northeast of Cardiff (ISGS field notes; Smith, 1970). Whether the Cardiff and Clarke City deposits are continuous has not been determined. At both localities the Cardiff coal body is crescent-shaped and concave

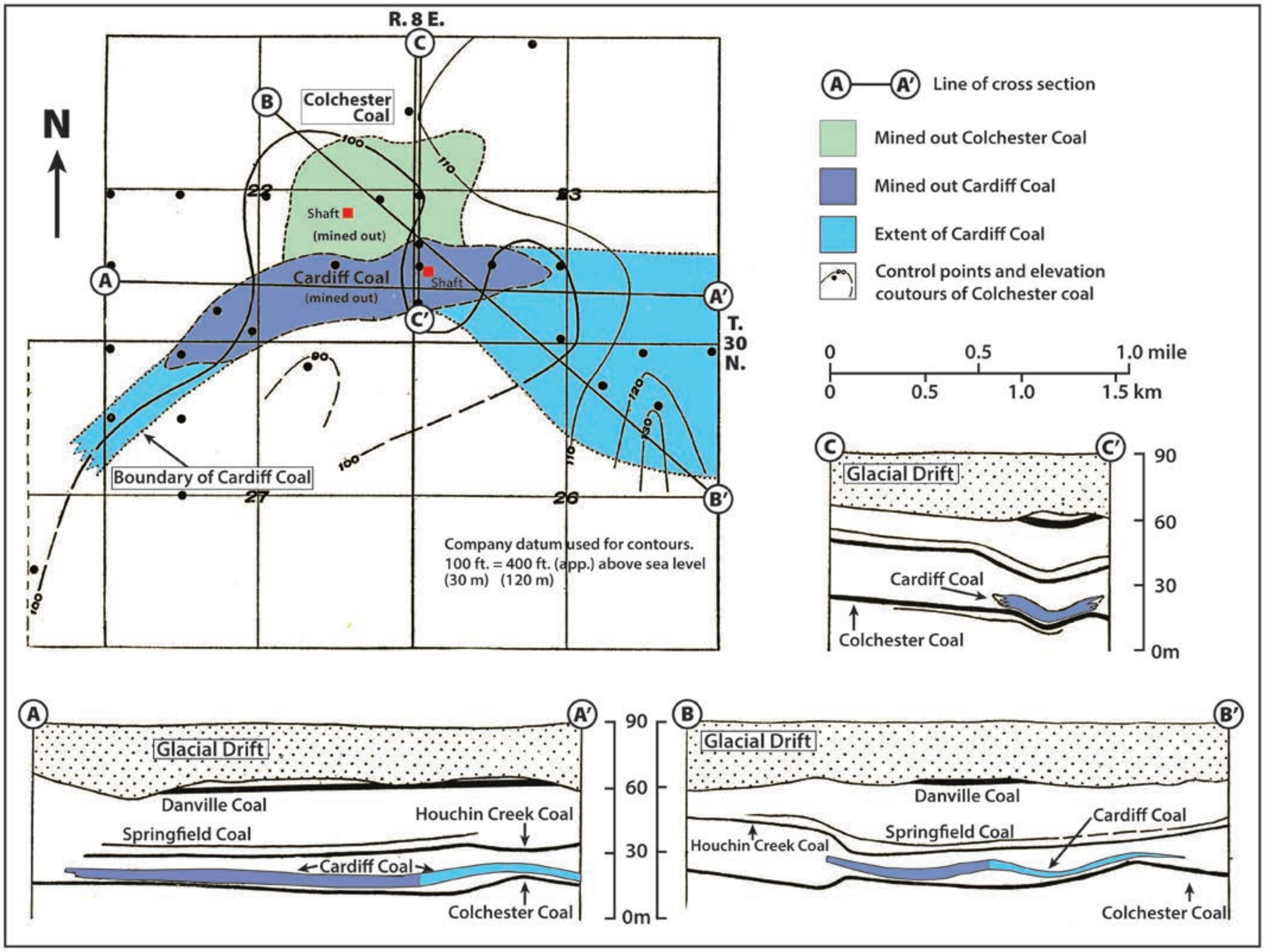

FIGURE 5. Maps and cross sections modified from Cady (1915, Plate V) showing configuration of Cardiff Coal in the mines at Cardiff, Illinois.

upward in cross section. Interbeds of shale and claystone are numerous. In places the coal terminates abruptly at its margins, elsewhere it interfingers and grades laterally to shale.

A columnar section (Fig. 6) for the Cardiff area was assembled using drilling records from the Cardiff Coal Company. As interpreted by Nelson et al. (2022a), the Cardiff coal is the Wheeler or lower Survant Coal Member and represents peat that accumulated in one or more channel-form depressions. That conclusion agrees with Peppers (1970, p. 49), who examined fossil spores from Cardiff and concluded, “The Cardiff Coal is interpreted as an earlier abandoned channel phase of deposition of the Lowell [Survant] Coal. It may actually be a little older than the Lowell Coal of other parts of the Illinois Basin because the spore assemblage has some aspects of the No. 2 [Colchester] Coal assemblage.” Also interpreted as Survant equivalents are the Kerton Creek and Roodhouse coal beds of western Illinois (Nelson et al., 2022b, 2022c). The Survant Coal occurs extensively in the deeper part of the Illinois Basin but was not deposited outside of local depressions on the northern and western shelves of the basin where regional subsidence was slower.

QUANTITATIVE ANALYSIS OF THE FLORAS

Methods

The floras analyzed in this study were quantified using the “hand-sample = quadrat” method of Pfefferkorn et al. (1975). At the time these quantifications were carried out, each hand sample, both sides together, were treated as a single quadrat. Identical areas of Part-Counterpart faces were counted only once. On each quadrat, the occurrence of a taxon was noted once, regardless of how many individual specimens of that taxon were present. This method adjusts for the great size differences among plant remains in a typical Pennsylvanian-age wetland flora. For example, recalling that the objective is an estimate of biomass, how many marattialean-fern pinnules can be taken to be equivalent to a fragment of a *Lepidodendron* trunk? Because, hypothetically, every taxon or recognized object could be present on every quadrat, the resulting data reflect commonness not relative abundance (i.e., the method produces frequency data). In practice, however, the method preserves rank-order abundance and generally reflects absolute abundance. As shown by Wing and DiMichele (1995), this method tends to underestimate, within the context of an assemblage, the relative commonness of the more common forms and overestimate the relative commonness of the rarer forms.

Frequencies of taxonomic or recognized-object occurrence were normalized by being expressed as a percentage occurrence relative to the total number of quadrats examined. The additive percentages of all recognized categories, however, will not add up to 100% because of the above-mentioned characteristics of

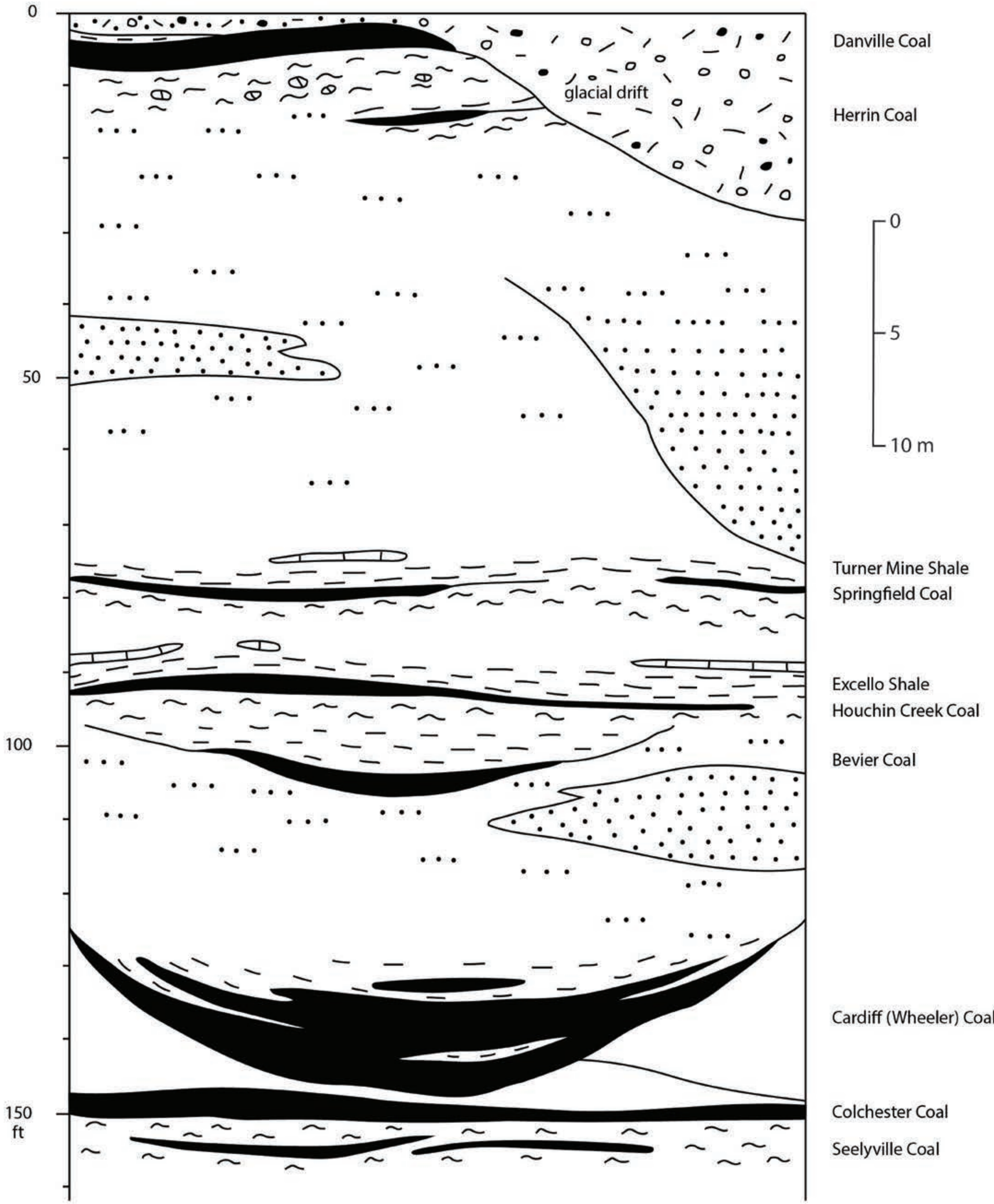

FIGURE 6. Generalized section in Cardiff area, northeastern Livingston County, Illinois, based on a composite of drilling records, interpreted by Nelson et al. (2022a).

the sampling process. Nonetheless, they preserve the basic rank order of the objects recognized and can be shown in dominance-diversity graphs.

The counts were performed by two different individuals. Calder examined the Colchester seat-earth collection (USNM 38404), one of the Colchester roof-shale collections (USGS 4146), and the Cardiff roof-shale collection (USGS 4150). DiMichele examined one of the Colchester roof-shale collections (USGS 4149). Furthermore, Bashforth reassessed the taxonomic composition of the three roof-shale collections and Wittry reassessed the Cardiff roof-shale flora.

Results of Quantitative Analyses

The results of the quantitative analyses are presented in Table 1. For each taxon or object category, this table shows both the raw frequencies (the count data itself) and the corresponding percentage of the sample that frequency entails. The table also shows the reranking of the taxa from most to least frequent, not including axes, seeds, or roots; due to uncertainties caused by preservation, some of the categories in fact may be duplicates, lowering overall diversity. Dominance-diversity curves based on the rankings and frequencis in Table 1 for each of the four samples are presented in Figure 7.

Possibly the most interesting result of these analyses is the similarity of the Colchester Coal seat-earth flora (USNM 38404) to the Cardiff Coal roof-shale flora. Both are dominated to a relatively high degree by species of *Neuropteris*, *N. ovata* in the seat-earth assemblage and *N. vermicularis* in the Cardiff flora. Both assemblages also contain small proportions of marattialean fern foliage and only single occurrences of aerial arboreous lycopsid remains. *Laveineopteris rarinervis* occurs in all four collections. The rarity of some of the remains more common in the Colchester Coal roof shale may reflect the small size of the Cardiff sample.

The two Colchester Coal roof-shale assemblages also are very similar. Both are more diverse than either of the other two assemblages, despite each being considerably smaller than the Colchester Coal seat-earth collection. Dominance in both collections also is lower with a longer tail of less frequent taxa. In both cases, the arboreous lycopsid *Synchysidendron andrewsii* is either the most frequently encountered taxon or just slightly below that position. Both collections also contain small numbers of lycopsid remains attributable to *Diaphorodendron* cf. *rimosum*. Together these species constitute the Diaphorodendraceae (sensu DiMichele and Bateman, 1996), thus, as a group, the most frequently encountered in the assemblages. Illinois State Geological Survey fieldnotes, taken at the time of active mining at the Spring Valley mine (USGS 4149), make note of the abundance of large lycopsid trunks in the roof shale. Other elements in these floras include various calamitalean remains, *Sphenophyllum*, tree-fern foliage, and other pteridosperms, such as *Macroneuropteris scheuchzeri* and *Laveineopteris rarinervis*.

FLORISTICS

Selected elements of the floras are shown in Figures 8 - 20. They are described below beginning with the stratigraphically lowest of the assemblages, the Colchester Coal seat earth flora from the Scab Hollow location, proceeding to the two Colchester Coal roof shale collections, and ending with the Cardiff Coal roof shale collection.

Colchester Coal Seat Earth, Scab Hollow (USNM 38404)

The flora at Scab Hollow (Fig. 8 a) was described initially by Wanless (1957). It was preserved in a fine sandstone, that grades upward into a hard silty clay, reflecting pedogenesis in its upper portion. The upper part of the deposit was heavily penetrated by stigmarian rooting systems (Fig. 8 b-d) that

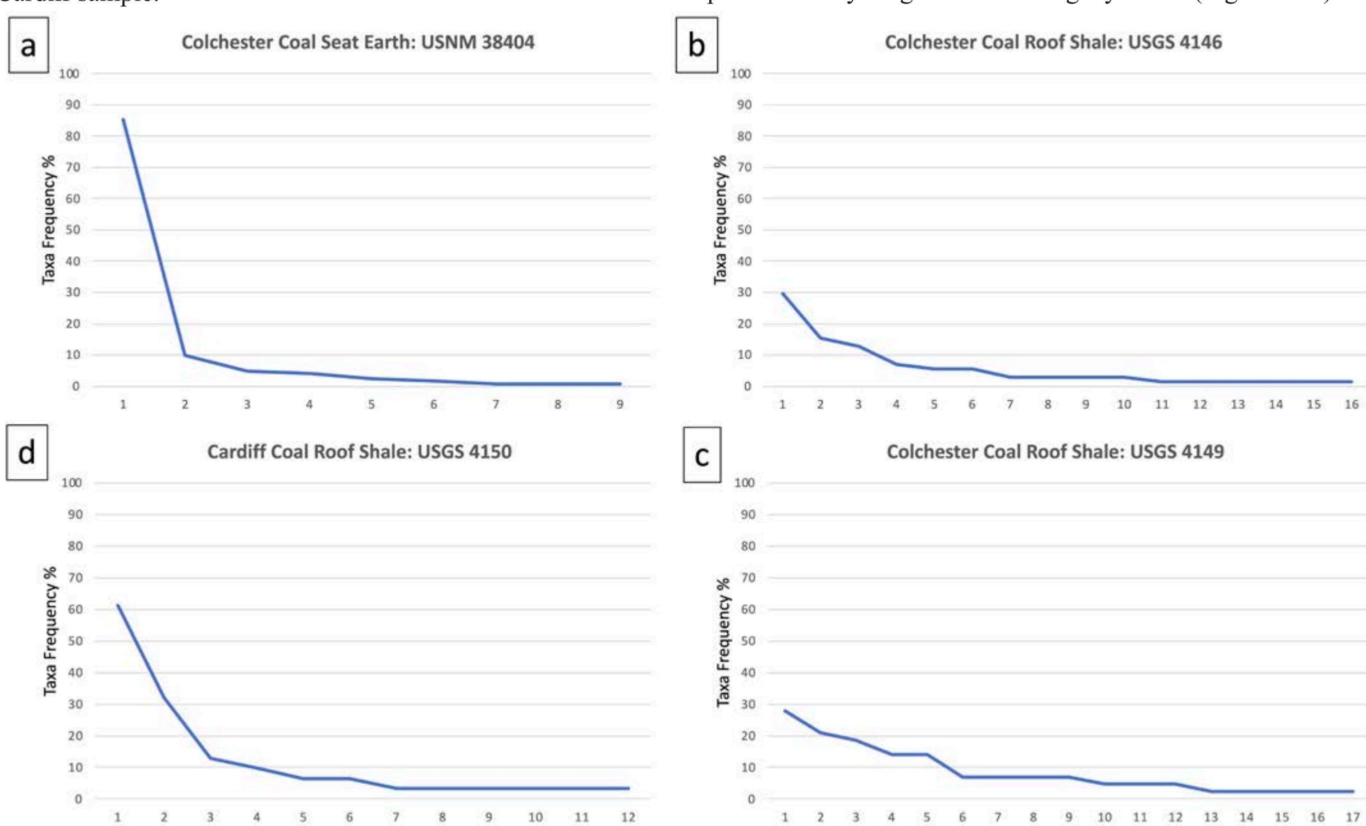

FIGURE 7. Dominance-Diversity curves for the collections discussed herein. Data on Frequency is derived from Table 1. **a**, USNM 38404, Colchester Coal seat earth, Scab Hollow locality. **b**, USGS 4146. Colchester coal roof shale, Minonk Mine. **c**, USGS 4149, Colchester Coal roof shale, Spring Valley No. 2 Mine. **d,** USGS 4150. Cardiff Coal roof shale, Cardiff Mine.

TABLE 1. Quantitative analyses of Colchester and Cardiff coal macrofloras.

Cardiff Coal roof shale (Cardiff Mine)	**USGS 4150**	
Quadrats	31	
TAXA	*Frequency*	*Percentage*
Neuropteris vermicularis	19	61.29
Neuropteris ovata	10	32.26
Cyclopteris spp.	4	12.90
Laveineopteris rarinervis	3	9.68
Neuropteris sp.	2	6.45
"*Pecopteris*" cf. *cyathea*	2	6.45
Diaphorodendron sp.	1	3.23
Macroneuropteris macrophylla	1	3.23
Crenulopteris sp.	1	3.23
Senftenbergia plumosa	1	3.23
Seeds	1	3.23
cf. Small fern	1	3.23
Medullosan axes	numerous	

Colchester Coal roof shale (Spring Valley)	**USGS 4149**	
Quadrats	43	
TAXA	*Frequency*	*Percentage*
Calamitalean tissue sheets	12	27.91
Synchysidendron andrewsii	9	20.93
striate axes	8	18.60
Crenulopteris cf. *acadica*	6	13.95
Marattialean foliage sp.	6	13.95
Diaphorodendron cf. *rimosum*	3	6.98
Annularia sp.	3	6.98
Sphenophyllum emarginatum	3	6.98
Alethopteris serlii	3	6.98
Crenulopteris cf. *subcrenulata*	2	4.65
cf. *Neuropteris anomala*	2	4.65
Pteridosperm foliage	2	4.65
Lepidodendrid indeterminate	1	2.33
Sphenophyllum cf. *oblongifolium*	1	2.33
Calamites sp.	1	2.33
Macroneuropteris cf. *scheuchzeri*	1	2.33
Lavineopteris rarinervis	1	2.33
comminuted plant debris	1	2.33
bivalves	3	6.98
snails	1	2.33
charcoal	2	4.65

TABLE 1 (continued). Quantitative analyses of Colchester and Cardiff coal macrofloras.

Colchester Coal roof shale (Minonk Mine)	**USGS 4146**	
Quadrats	71	
TAXA	*Frequency*	*Percentage*
Synchysidendron andrewsii	21	29.58
Oligocarpia/Mariopteris	11	15.49
Lepidodendrid indeterminate	9	12.68
Diaphorodendron cf. *rimosum*	5	7.04
Macroneuropteris scheuchzeri	4	5.63
Laveineopteris rarinervis	4	5.63
Senftenbergia plumosa	2	2.82
Sphenophyllum sp.	2	2.82
Marattialean foliage	2	2.82
Lepidodendron cf. *aculeatum*	2	2.82
cf. *Lepidodendron mannabachense*	1	1.41
Bergeria sp.	1	1.41
Annularia radiata	1	1.41
Sphenophyllum emarginatum	1	1.41
Crenulopteris cf. subcrenulata	1	1.41
Sphenopteris sp.	1	1.41
Seeds	1	1.41
Medullosan axes	numerous	
Lepidophylloides sp.	numerous	
Dunbarella (pectinacean bivalve)	2	2.82

Colchester Coal seat earth (Scab Hollow)	**USNM 38404**	
Quadrats	121	
TAXA	*Frequency*	*Percentage*
Neuropteris ovata	103	85.12
"Pecopteris" cf. *cyathea*	12	9.92
Crenulopteris acadica	6	4.95
Cyclopteris fimbriata	5	4.13
Calamites spp.	4	2.48
Lepidophylloides sp.	1	0.83
Stigmaria ficoides	1	0.83
Laveineopteris rarinervis	1	0.83
Medullosan axes	numerous	
Stigmarian rootlets	numerous	

FIGURE 8. USNM 38404. Colchester Coal seat earth (Scab Hollow). **a,** Roadside ditch collection location. USNM locality 38404, July 6, 1983. **b,** Stigmarian rhizomorph with attached rootlets USNM 787712. **c,** Closeup, 2X magnification increase, of stigmarian axis with attached rootlets. Rootlet attachment points are vague but can be identified on the axis. **d,** Stigmarian rootlets penetrating downward in seat-earth matrix. USNM 787711. **e,** Stigmarian rootlets penetrating downward in seat-earth matrix. USNM 787710. Scale bar in (c) = 1 cm. Scale bars in (b, d, e) = 2 cm (1/2 X at published plate size - 18.4 cm width).

diminished downward in the deposit.

The taxonomic composition changed through the 1 m thickness of the deposit that was excavated. In the lower parts, plant remains were sparse and comprised primarily axes, including striate axes typical of calamitalean stems (Fig. 9 a-c), pteridosperms, and marattialean ferns. The *Calamites* stems were preserved mainly as sandstone-filled stem casts, a preservation type commonly referred to as "pith casts" but that, in nearly all instances, are casts of stems (see DiMichele and Falcon-Lang, 2012; Falcon-Lang, 2015; the cited papers discuss the pith-cast explanation in detail). Rare remains of tree-fern foliage also were found. In his examination of the site in 1930, H.R. Wanless noted the presence of *Annularia sphenophylloides* among the plant remains; we did not encounter any calamitalean foliage in the collection.

The upper parts of the deposit were the richest in marattialean tree-fern foliage, attributable to *Crenulopteris acadica* (Wittry et al., 2015), a lobate form of tree-fern foliage (Fig.9 d-e). In these plants, pinnule shape varies systematically through the large fronds, and are associated with characteristic forms of pinnule venation and lobing (Wagner, 1959). This foliage type has long been characterized as *Lobatopteris vestita*, a form of foliage that includes a number of species within the genus *Lobatopteris* (Wagner, 1959). The introduction of the genus *Crenulopteris* by Wittry et al. (2015) challenged lobatopterid taxonomy, and a response can be found in Wagner and Álvarez-Vázquez (2016). *Crenulopteris acadica* is found most commonly in the later part of the Middle Pennsylvanian, consistent with its occurrence here.

There may be other tree-fern species present, but poor preservation hampers identification. The specimen illustrated in Figure 9 f is one of the better preserved examples of these questionable specimens. Although venation is unclear, it could be cyatheoid, that is with lateral veins dichotomized no more than once; whether all or some are dichotomized is one of the characteristic traits on which species of this group are separated. In addition, the apparent lack of marginal pinnule lobation also weighs against a lobate-marattialean affinity.

Neuropteris ovata nearly entirely dominates the middle part of the deposit and also occurs frequently in the upper portions. The plant remains (Fig. 10) are relatively well preserved and occur in considerable abundance where present. In addition, the foliage is commonly intermixed with fine roots typical of pteridosperms and calamitaleans (Fig. 10 c). The *N. ovata* specimens are typical of this species. Pinnules are basipetally auriculate and acropetally somewhat incised, having a relatively weak midvein that extends through about 2/3 of the pinnule length, flanked by thin, dense, arching lateral veins, straight to slightly curved lateral margins, and a blunt and broadly rounded apex. In more distal parts of pinnae, secondary veins can be found entering directly from the rachis on both sides of the midvein. There is considerable variation in pinnule size, but the basic characteristics are consistent. In addition, where pinna apices are preserved (Fig. 10 a - c), apical pinnules are bluntly rounded and not notably inflated or constricted, and the lateral pinnules are increasingly fused to one another and to the apical pinnule. Associated with these pinnules is a cyclopterid, *Cyclopteris fimbriata* (Fig. 10 d), that is part of the *N. ovata* frond.

It is possible that other neuropterids are present as rare elements in the assemblage. The specimen illustrated in Figure 10 f, shown at the same magnification of that in Figure 10 e, is much larger than pinnules of most of the *N. ovata* specimens, lacks an auricle and has a tapering apical region. The identity of this particular specimen is uncertain. Wanless, in his aforementioned 1930 field notes, also recorded the presence of "*Neuropteris*"

FIGURE 9. USNM 38404. Colchester Coal seat earth (Scab Hollow). Pteridophytes. **a - b,** Opposite sides of calamitalean stem cast from sandstone portion of seat earth. This specimen is not a "pith cast" (see discussion of this form of preservation in DiMichele and Falcon-Lang, 2012; Falcon-Lang, 2015). USNM 787708. **c,** Calamitalean stem cast. USNM 787707. **d,** *Crenulopteris acadica* (*Lobatopteris vestita*) lobate marattialean fern foliage. USNM 543927. **e,** *Crenulopteris acadica* (*Lobatopteris vestita*) lobate marattialean fern foliage. USNM 543926. **f,** Marattialean foliage, possibly "*Pecopteris*" *cyathea* or a member of the cyathea group. Lateral venation is not clear but may be once bifurcate, and there is no evidence of marginal lobing. USNM 787704. Scale bars = 1 cm.

(now *Laveineopteris*) *rarinervis* and *Odontopteris* sp. We found no indication of *Odontopteris* and note that in certain parts of the frond, particularly near the apex of pinnae, *N. ovata* pinnules can be broadly attached, lack a midvein, and be partially fused to one another and the apical pinnules, thus appearing much like a form of *Odontopteris*. As noted below, *Laveineopteris rarinervis* was identified in the Colchester Coal roof-shale collections analyzed here, so its presence in this collection is not unexpected.

As a final note, Wanless recorded the presence of *Cordaites*. Cordaitalean gymnosperms are a common, if not dominant, element in coal balls, thus of the coal-swamp floras themselves, from coals older and younger than the Colchester (Phillips et al., 1985). Coal balls are rare in the Colchester Coal, and in those we have examined the peat is too poorly preserved to identify the plant composition. In addition, it can be quite difficult to distinguish flattened striate axes of pteridosperms and ferns, wherein the striae are strands of supportive sclerenchyma cells, from cordaitalean leaves, wherein the striae are mostly bundles of vascular tissue (leaf veins). There were, in our collection, striate axis-or-leaf remains that could not be classified unequivocally as cordaitalean leaves. Consequently, Wanless' identification would not be atypical for a wetland flora of this time period, but it also cannot be affirmed.

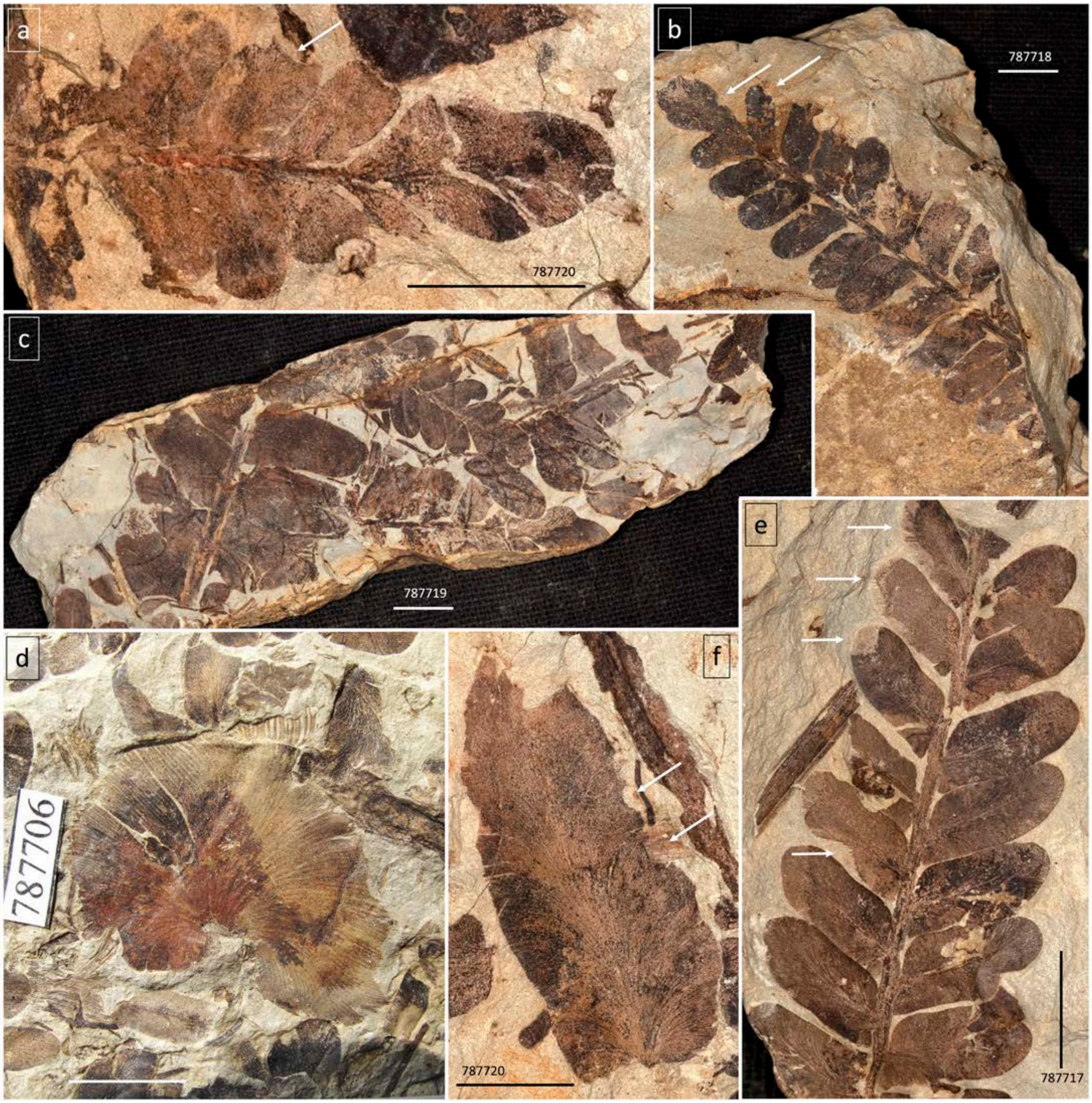

FIGURE 10. USNM 38404. Colchester Coal seat earth (Scab Hollow). Pteridosperms. **a,** *Neuropteris ovata* pinna tip. USNM 787720. **b,** *Neuropteris ovata* pinna. USNM 787718. **c,** *Neuropteris ovata* litter of various sizes (from different parts of the frond), mixed with fine roots of pteridosperm or calamitalean origin. USNM 787719. **d,** *Cyclopteris fimbriata*, cyclopterid pinnule of *N. ovata*. USNM 787706. **e,** *Neuropteris ovata* pinna. USNM 787717. **f,** Neuropterid pinnule, possibly a large *N. ovata* pinnule. USNM 787720. In all images: arrows point to areas of suspected arthropod damage. Scale bars = 1 cm.

Colchester Coal Roof Shale, Minonk Mine (USGS 4146)

The collection from the Minonk Mine (USGS 4146) is the larger of the two USGS Colchester Coal roof shale collections, consisting of 71 non-empty quadrats. The flora is dominated by lycopsids, consistent with the observations of ISGS geologist K.D. White, who noted when visiting the Minonk Mine that "... in the roof, up to a height of 10 feet [3 m] there are many flattened trunks with the diamond patterned imprints on the surface." Second in abundance is a fern-like plant that may be either *Oligocarpia* or *Mariopteris*. Other elements are rare, but include the spectrum of typical wetland plants, including pteridosperms, calamitaleans, marattialean tree ferns, and groundcover plants, *Sphenophyllum* and small ferns.

Most of the collected lycopsid remains can be attributed to *Synchysidendron andrewsii* (Fig, 11 a-e) and *Diaphorodendron* cf. *rimosum* (Fig. 11 f-g). Both genera are characterized by deciduous-lateral branch architecture (DiMichele et al., 2013). Leaf cushions of *Synchysidendron* protrude more from the stem surface than those of *Diaphorodendron*. *Synchysidendron* leaf

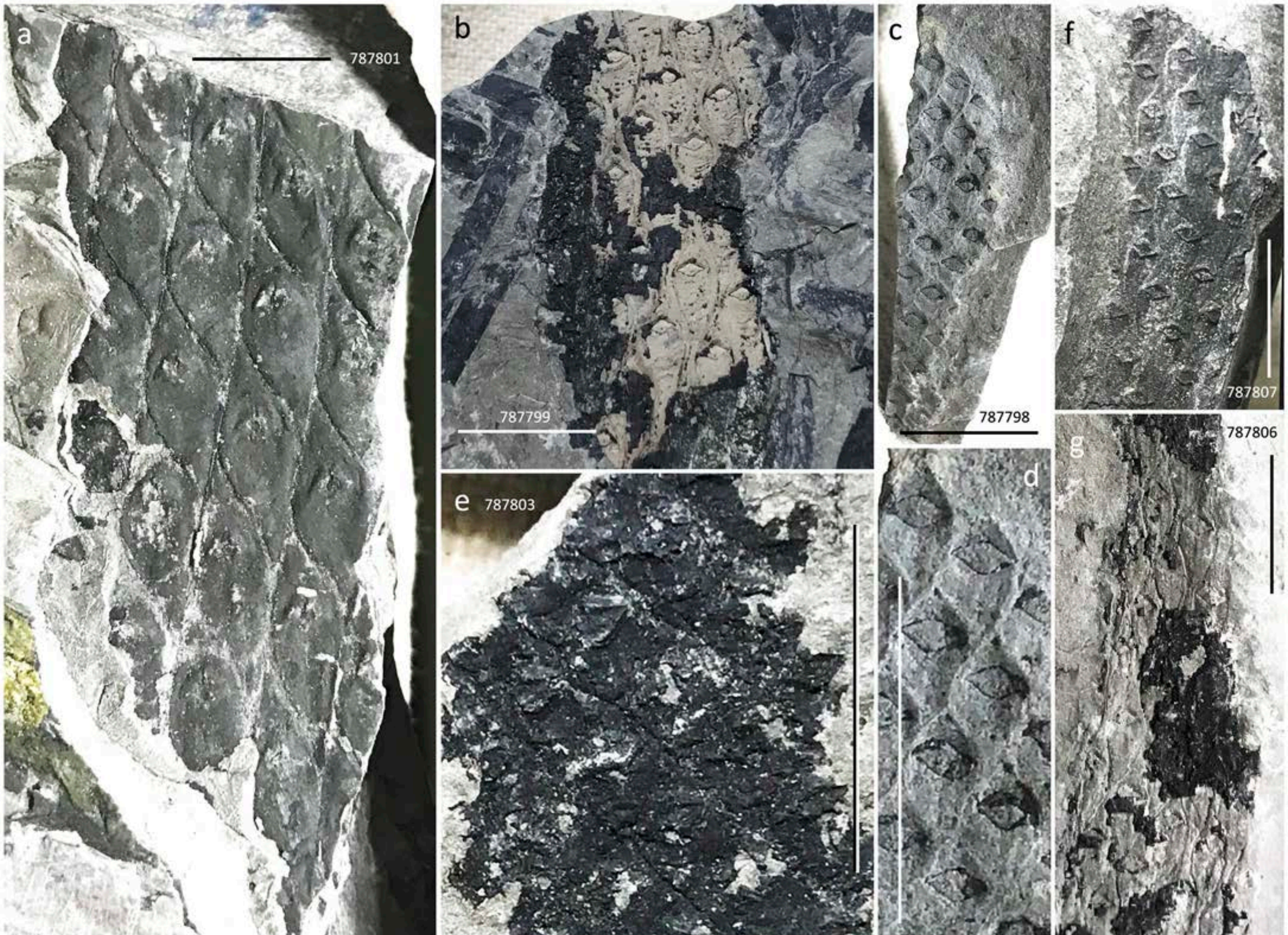

FIGURE 11. USGS 4146. Colchester Coal roof shale (Minonk Mine). Lycopsids. Diaphorodendraceae. **a,** *Synchysidendron andrewsii*. USNM 787801. **b,** *Synchysidendron andrewsii* USNM 787799. **c,** *Synchysidendron andrewsii* USNM 787798. **d,** Enlargement of image (c). **e,** *Synchysidendron andrewsii* USNM 787803. **f.** *Diaphorodendron* cf. *rimosum* USNM 787807. **g,** *Diaphorodendron* cf. *rimosum* USNM 787806. Scale bars = 1 cm.

cushions also change shape from larger diameter branches, where they are much longer than wide, to the smaller branches, where they approach equidimensional in height and width. *Diaphorodendron* leaf cushions, in contrast, remain narrow and elongate on branches of all diameters. Other kinds of lycopsids also are present. One form, Figure 12, is a form of *Lepidodendron* sensu stricto (DiMichele, 1983), possibly *L. aculeatum*, with curved tails, lower keel folds, a relatively small leaf scar, and sub-leaf-scar infrafoliar parichnos. These specimens are somewhat more rounded than typical of the species and lack so-called lateral lines, running in downward arcs from the edges of the leaf scar, so the *L. aculeatum* identification must remain speculative. One specimen has leaf cushions with nearly equal height and width (Fig. 12 c-d). The upper angle of the leaf cushions on this specimen is sharply angular, whereas the lower angle is rounded. There are wrinkles in the lower portion, below the leaf scar, possibly due to compression given that these leaf cushions appear to be rather thick and protuberant. There may be infrafoliar parichnos beneath the distinctive, protuberant leaf scar. Rare specimens (Fig. 12e) with attached leaves and obscure leaf cushions, typical of specimens with still attached and somewhat adpressed leaves, may be attributable to *Bergeria*, or simply be a branch of one of the other forms (Thomas and Cleal, 2022). Figure 13 shows the same specimen illustrated in Figure 12 c-d, but inverted (Fig. 13 a-b; Fig. 13 c-d re-illustrates the specimen in the other orientation for direct comparison) suggesting an affinity with *Lepidophloios*, possibly *L. acerosus*; this identification seems unlikely given the position of what may be infrafoliar parichnos strands (Fig. 13 d, arrows) and the location of extensive plications above the leaf scar in the *Lepidophloios* orientation (Fig. 13 a-b), but must be considered.

Small numbers of marattialean fern remains were encountered in the collection. The name *Pecopteris*, long used for marattialean sterile foliage, is an invalid name as applied to that group; the type species of *Pecopteris* belongs to a different group of ferns (see Cleal, 2015). The USGS 4146 specimens are difficult to identify with confidence; they are similar to "*Pecopteris*" *cyathea* or "*Pecopteris*" *oreopteridia* (Fig. 14 a-b) in being approximately twice as long as wide, with midveins that are inserted orthogonally on the rachis, and lateral veins that fork once once or are unforked. Due to the state of preservation and the small size of the remains, certain identification is not possible. The specimen illustrated in Figure 14c, preserved in a siderite concretion, is similar to *Crenulopteris* cf. *subcrenulata*. Its pinnules are deeply lobed and might be described as a pinna bearing small, rounded pinnules with typically lobatopterid, candelabra-type venation (Fig. 14d).

Sphenopsid remains, also rare, are represented by both calamitaleans and sphenophyllaleans. Rare foliage is tentatively assigned to *Annularia radiata* (Fig. 15a), given its relatively

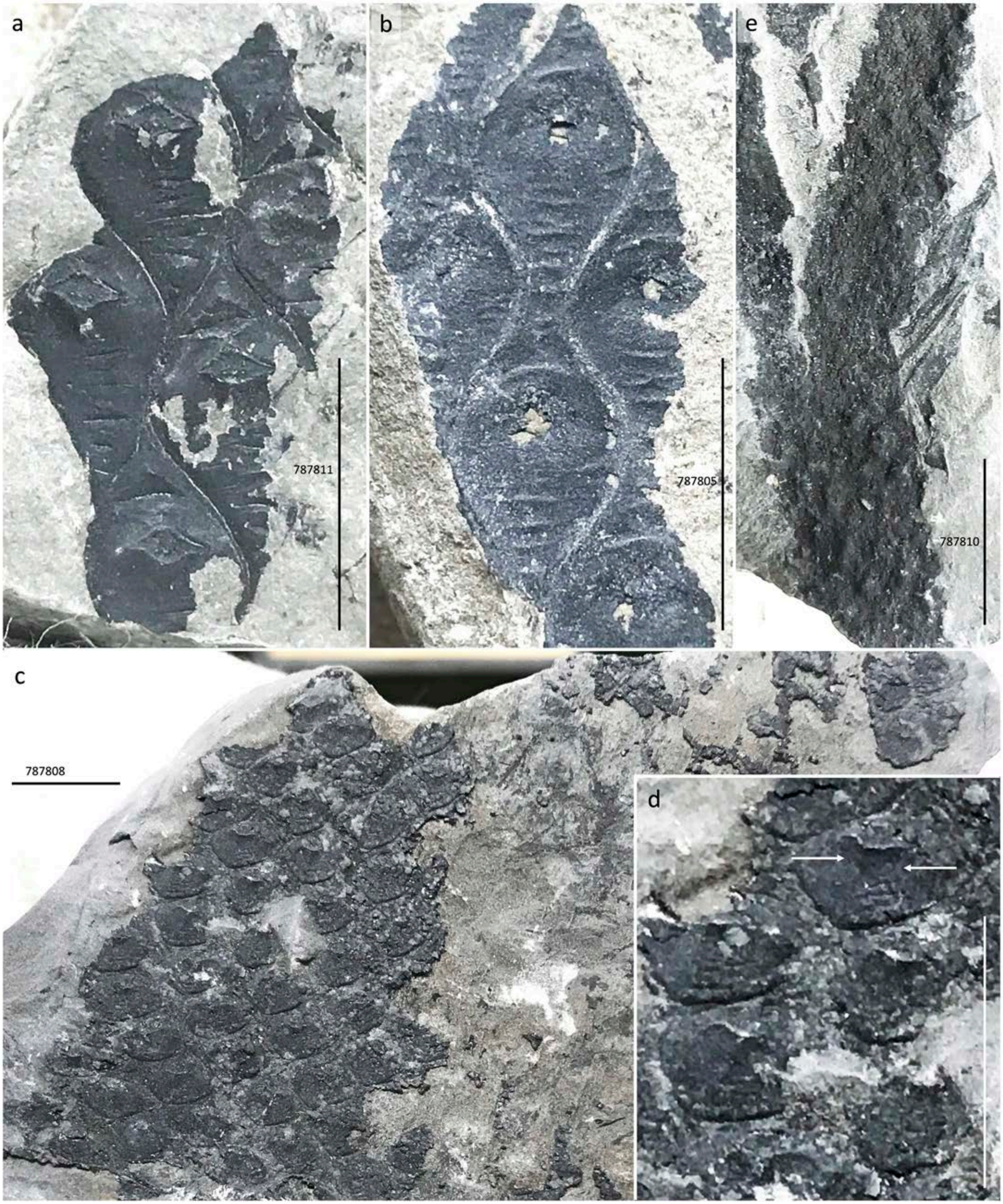

FIGURE 12. USGS 4146. Colchester Coal roof shale (Minonk Mine). Lycopsids. **a,** *Lepidodendron* cf. *aculeatum*. USNM 787811. **b,** *Lepidodendron* cf. *aculeatum*. USNM 787805. **c,** cf. *Lepidodendron mannabachense*, USNM 787808. **d,** Higher magnification of parts of specimen in image (c). White arrows point to what possibly are infrafoliar parichnos. See also Figure 13, which also examines the possibility that this specimen is a species of *Lepidophloios*. **e,** *Bergeria* sp. (*Paralycopodites*-type) with attached leaves. USNM 787810. Scale bars = 1 cm.

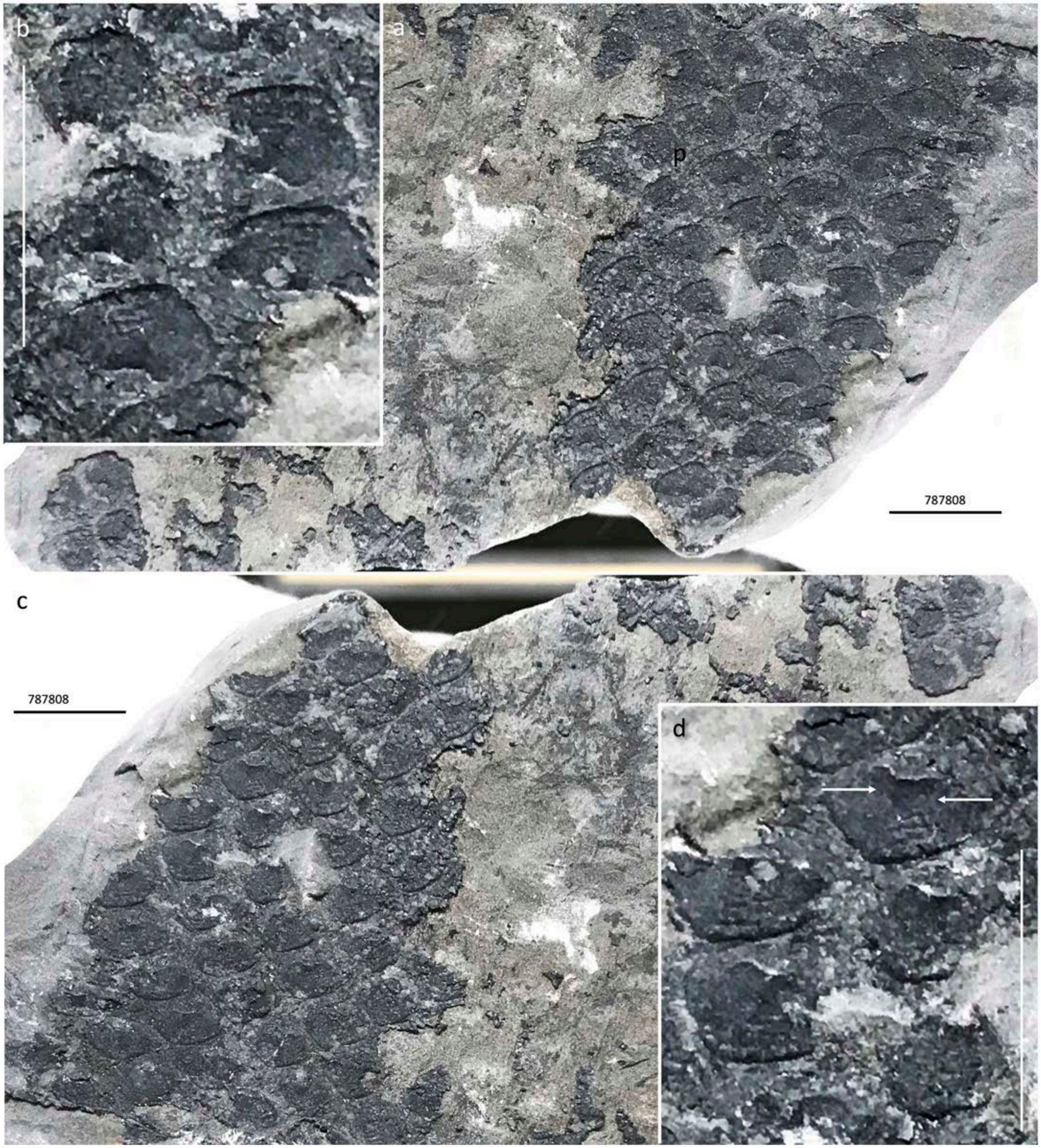

FIGURE 13. USGS 4146. Colchester Coal roof shale (Minonk Mine). This plate represents two views of the specimen illustrated in Figure 12, demonstrating the possibility that this specimen is a species of *Lepidophloios* rather than *Lepidodendron*. In the rotated views of images (a) and (b) the specimen bears some resemblance to *Lepidophloios acerosus*. Scale bars = 1 cm.

narrow, straight-sided leaves and acuminate leaf apices. Sphenophylls, which constitute some of the rare groundcover components of the flora, are assignable to *Sphenophyllum emarginatum* (Fig. 15 b-c).

Additional small groundcover plants were rare but include unidentified sphenopterid-fern remains that appear to bear pinnule-margin sporangia (Fig. 15d). Also tentatively identified is a single specimen of the small fern cf. *Senftenbergia plumosa* (Fig. 16d/upper bracket). This latter foliage fragment has short, falcate pinnules of triangular shape with an acuminate apex. A midvein is well marked and proceeds from the pinnule base to the apex. Lateral veins are sparse, dichotomize at least one time, and are borne at approximately 45°.

Another possible fern is part of a complex of plants that

FIGURE 14. USGS 4146. Colchester Coal roof shale (Minonk Mine). Marattialean ferns. **a,** Cyatheoid marattialean foliage, possibly "*Pecopteris*" *cyathea* or "*Pecopteris*" *oreopteridia*. USNM 787792. **b,** Cyatheoid marattialean foliage, possibly "*Pecopteris*" *cyathea* or "*Pecopteris*" *oreopteridia*. USNM 787791. **c,** *Crenulopteris* cf. *subcrenulata* USNM 787789. **d,** Enlargement of right-side basal portion of image (c) showing lobate pinna margins and lobatopterid venation. Scale bars = 1 cm.

proved difficult to identify to species, and may represent more than one group, artificially combined in Table 1 as *Oligocarpia*/*Mariopteris*. This group includes what we think might be the true fern *Oligocarpia leptophylla* (Fig. 15 e-f), which has elongate, largely straight-sided pinnules with bluntly triangular apices. A midvein is weakly developed and lateral veins are ascendent and dichotomizing. The basiscopic basal pinnule, sometimes two, of each pinna are rounded with a slightly undulatory margin. Another form of foliage that we have lumped into this group is shown in Figure 15 g-h. In such specimens, the pinnules are more rounded than elongate, but with an undulatory margin and a bluntly convergent apex, and fused together in the apical parts of the ultimate pinnae in the terminal portion of the penultimate pinna. The pinnules are generally more uniform in shape than in Figure 15 e-f, although the basalmost pinnules of a pinna are likewise enlarged compared to the more distal pinnules. As seen especially in Figure 15h the penultimate rachis is relatively thin and flexuous, leading us to conclude that this is likely a fern rather than a pteridosperm, possibly *Oligocarpia gutbieri*. Additional specimens of this complex are illustrated in Figure 16 c-d/lower bracket. These specimens are intermediate in form between the others illustrated in having robust, straight, penultimate pinna rachises. The pinnules are uniformly short and rounded with undulate margins but with bluntly pointed apices. The basal basiscopic pinnule is more triangular and enlarged with a slightly constricted base. A midvein is present through about 2/3 of the pinnule length and lateral veins are thick and coarse. Progressively along the ultimate pinna the pinnules become fused to those adjacent. Overall, were these pinnules larger, the specimens would bear comparison with *Mariopteris* cf. *nervosa*, a seed plant.

Two seed plants in the flora are attributable to the Medullosales, *Macroneuropteris scheuchzeri* (Fig. 16 a-b) and *Laveineopteris rarinervis* (Figs. 15e, 16e). The former is recognizable by its large size, thin but well marked midvein, and fine, arching lateral venation. Most distinctively, however, are the "hairs" that mark its surface, which Laveine and Oudoire (2015) showed to be subepidermal resin ducts. *Laveinopteris rarinervis*, a common late Middle Pennsylvanian species, is characterized by generally small pinnules that are strongly adherent to the rachis, with straight sides, a rounded apex, strong midvein, and sparse but robust lateral venation (Cleal and Shute, 2003). A single seed was found in the collection (Fig. 16e); it is round and may be platyspermic, but otherwise lacks identifiable features.

Among animal remains in the collection were pectenoid bivalves. One of these is illustrated in Figure 16f.

FIGURE 15 (facing page). USGS 4146. Colchester Coal roof shale (Minonk Mine). **a,** *Annularia radiata* USNM 787784. **b,** *Sphenophyllum emarginatum* USNM 787786. **c,** *Sphenophyllum emarginatum*, longitudinally preserved axis USNM 787785. **d,** Unidentified fertile sphenopterid fern with marginally borne sporangia on pinnules. USNM 787788. **e,** *Oligocarpia leptophylla* USNM 787787 counterpart. **f,** *Oligocarpia leptophylla* USNM 787787 part; note *Laveineopteris rarinervis* pinnules, upper left of image. **g,** *Oligocarpia* cf. *mixta*, *Mariopteris* cf. *nervosa*, or possibly *Senftenbergia plumosa*; compare with Figure 16 c, d, perhaps reflective of intraspecific, even intra-frond, variation. USNM 787790. **h,** Enlargement of lower portion of image (g), showing sinuousness of the rachis, sparseness of the venation, and lobate pinnule margins. Scale bars = 1 cm.

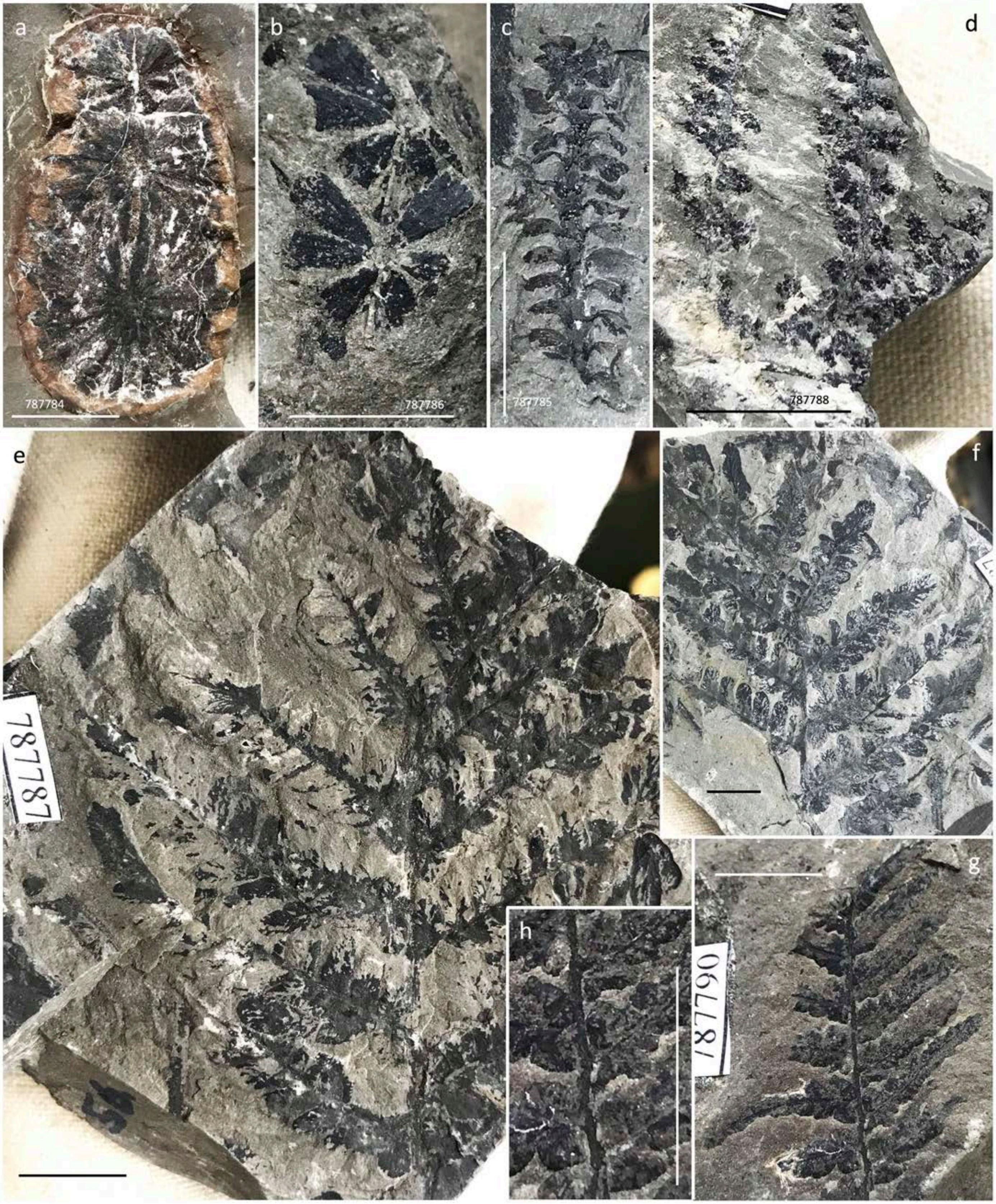
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FIGURE 16. USGS 4146. Colchester Coal roof shale (Minonk Mine). Seed plants. **a,** *Macroneuropteris scheuchzeri*. Arrows point to areas with subcutaneous resin canals ("hairs"). USNM 787782. **b,** *Macroneuropteris scheuchzeri*. Arrows point to areas with subcutaneous resin canals ("hairs"). USNM 787783. **c,** *Mariopteris* cf. *nervosa* USNM 78794. **d,** cf. *Senftenbergia plumosa* (upper bracket) and *Mariopteris* cf. *nervosa* (lower bracket) USNM 78793. **e,** Seed (arrow) and cf. *Laveineopteris rarinervis* USNM 787795. **f,** *Dunbarella* (pectinacean bivalve) USNM 787796. Scale bars = 1 cm.

Colchester Coal Roof Shale, Spring Valley Mine (USGS 4149)

The collection from the Spring Valley Mine, USGS 4149, is about half the size of the other Colchester Coal roof-shale collection from the Minonk Mine (USGS 4146). Both roof shale collections are more diverse than the seat-earth collection from Scab Hollow, which contains three times as many specimens. Species dominance differs between the Spring Valley and Minonk localities. At Spring Valley, the most commonly encountered and recognizable specimens in the assemblage were isolated sheets of parenchyma cells, contextually associated with calamitalean stem remains. Of the more definitive remains, the lycopsid *Synchysidendron andrewsii* is the most commonly encountered species from Spring Valley, as at Minonk. However, overall, marattialean tree ferns, which are very rare in the other roof-shale collection, are the most commonly encountered larger taxonomic group of plants. Lesser components of the flora include calamitalean remains, pteridosperms, and the lycopsid *Diaphorodendron* cf. *rimosum*.

Examples of pteridophytes are illustrated in Figure 17 and Figure 18 a-d. *Synchysidendron* cf. *andrewsii* is illustrated in Figure 17 a-b. Its characteristics are described above, in the Minonk flora. The two specimens illustrated demonstrate the basic features of the species: elongate leaf cushions that are somewhat protuberant and that change in height-width ratio on progressively smaller stems.

Sphenopsid remains include rare *Calamites* stems (Fig. 17c) and *Annularia* sp. (Fig. 17d). The latter is characterized by an asymmetrical leaf whorl with long, narrow leaves, but the absence of leaf tips and insufficient preservation prevent a positive species identification (see Wittry, 2020). The groundcover or climbing sphenopsid, *Sphenophyllum emarginatum* is represented by a few leaf whorls (Fig. 17 e-f). The specimen illustrated in Figure 17f is similar to *S. oblongifolium* in the narrowness of its leaves and the leaf arrangement (opposite laterally projecting pairs and downward facing "bib"). The marginal teeth, however, are rounded rather than acuminate, so there is a possibility this is a taphonomic effect and that the specimen is *S. emarginatum*.

Marattialean tree-fern foliage is illustrated in Figures 17 g-h and 18 a-d. Figure 17g may be "*Pecopteris*" cf. *cyathea*; it appears to have elongate, straight-sided pinnules with a well developed midvein that extends to near the tip of the pinnule, and sparse, dichotomized lateral veins (Fig. 17h). The marattialean foliage illustrated in Figure 18 a-d is a lobate form that is most likely *Crenulopteris*. The most common species of *Crenulopteris* in the upper Middle Pennsylvanian is *C. acadica* (*Lobatopteris vestita* – see comment by Wagner and Álvarez-Vázquez, 2016) (Wittry et al., 2015). A specimen attributable to this species is illustrated in Figure 18 a-b. The pinnules are elongate with lobate margins; they might be described as pinnae with small, rounded pinnules, particularly on some larger specimens where the lobation is deeper. The midvein of the pinnule is strong and proceeds to near the pinnule tip. Lateral veins are candelabra-like, typical of the lobatopterid marattialeans. Additional fragmentary remains of lobatopterids were found (Fig. 18 c-d). We have tentatively assigned these to *Crenulopteris* cf. *subcrenulata* given their lobate form, (both species are lobate), but the lateral veins that are more widely spaced and, where visible (as in Fig. 18d), the ultimate rachis is more robust. Nonetheless, given the small size of the flora, these fragments may be *C. acadica*. See Wittry (2020) for a discussion of various forms of marattialean foliage found in the Mazon Creek flora.

Pteridosperms in both of the Colchester roof-shale floras, surprisingly, do not include *Neuropteris ovata*, which is abundant in the Colchester Coal seat-earth flora from Scab Hollow. In addition to single specimens of *Macroneuropteris scheuchzeri* and *Laveineopteris rarinervis*, several specimens of *Alethopteris serlii* were identified (Fig. 18f) on the basis of the elongate, obovate shape of the pinnules with bluntly pointed tips, somewhat constricted bases, and dense lateral veins strongly orthogonal to the midvein, the latter extending almost to the pinnule apex. A number of unusual pteridosperm foliage specimens or fragments were found that are not clearly identifiable (e.g., Fig 18e, cf. *Macroneuropteris scheuchzeri*; cf. *Neuropteris anomala*). These mostly were large with fine, dense, curved veins, but lacking critical characteristics for further identification.

Cardiff Coal Roof Shale (USGS 4150)

Only a small collection of specimens was made from the roof shales of the Cardiff Coal, which, at the time, was being mined underground. Unfortunately, we have no information on geologic context of the Cardiff fossils. It is likely that the collection was made from spoils at the mine tipple. Clearly, this collection is not representative of the full flora that was present during the final phases of the channel in which the Cardiff Coal was accumulating. This vegetation may have come from the channel margins or have been the final phases of a drowning swamp flora. Diversity of the flora is low (Fig. 7d). What is of interest, however, is the dominance of the neuropterid pteridosperm, *Neuropteris vermicularis*. The remainder of the common plants in the flora also are pteridosperms, with a small number of tree ferns and the lycopsid *Diaphorodendron*.

Neuropteris vermicularis is likely a more widespread species than is generally reported. As noted by Bashforth et al. (2016, p. 620), *N. vermicularis* is difficult to differentiate from *Neuropteris flexuosa*, particularly when a large spectrum of specimens is not available. In particular, large pinnules of *N. vermicularis* with a dense venation are virtually indistinguishable from equally large forms of *N. flexuosa*. In smaller specimens and near the pinna terminus, however, *N. vermicularis* pinnules remain elongate whereas in *N. flexuosa* the pinnules become more squat and rounded. *N. vermicularis* typically has no lateral veins entering the pinnule lamina directly from the rachis, and the pinnules lack an auricle on the basiscopic side except in those nearest the terminal pinnule. The basic characteristics of *N. vermicularis* can be seen in Figure 19 a-d.

Other medullosan remains in the collection include *Neuropteris ovata* (Figs. 19 e-f, 20d [box 2]), which also is relatively abundant. These have typical characteristics of this species. The pinnules are parallel-sided with rounded apices that are "truncated" on the basiscopic side, and they are auriculate. The midvein is weakly developed and extends about 1/2 - 2/3 of the length of the pinnule. Lateral venation is fine, arching, and asymmetrical on the acroscopic and basiscopic sides. The identity of the isolated, elongate, narrow pinnule in Figure 19g is uncertain. We suggest comparison with *Macroneuropteris macrophylla*, which has been identified in the American literature as *Neuropteris clarksonii* (see Wittry, 2020, p. 195). *Laveineopteris rarinervis* (Fig. 19h) is typical of the species, with relatively small, non-deciduous pinnules. Enlargement of pinnules from image (h) in Figure 19i shows the coarseness of the lateral venation typical of this species. Cyclopterid pinnules, typical of portions of pteridosperm fronds, are rare in the collection. Most are similar to *C. fimbriata*, typical of *N. ovata*, in having fine venation, although a fimbriate margin is not clearly visible (e.g., Fig. 20a). In contrast, the large cyclopterid in Figure 20b is coarse veined and the veins are particularly low density at the base of the pinnule, possibly indicating affinity with *L. rarinervis*. A tiny, ribbed seed/ovule with a compression border is seen in Figure 20d [box 3].

Small numbers of pteridophytes occur in the flora. The small fern *Senftenbergia plumosa* (Fig. 20c) is represented by a single specimen, which is enlarged in Figure 20d [box 1]. It is similar to the *S. plumosa* specimen illustrated in Figure 16d. Both have characteristic short, falcate pinnules that terminate in a pointed

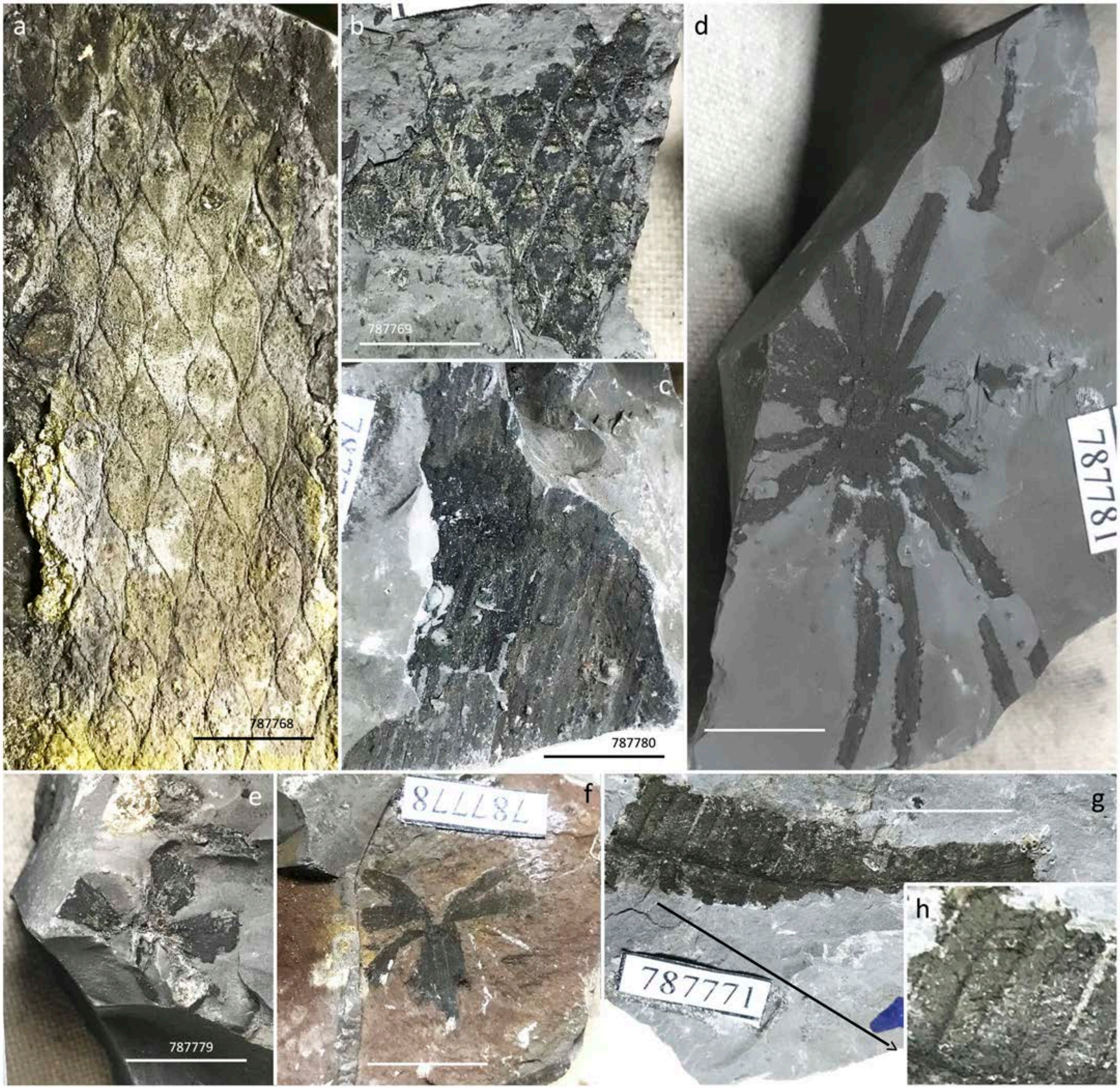

FIGURE 17. USGS 4149. Colchester Coal roof shale (Spring Valley Mine). Pteridophytes. **a,** *Synchysidendron andrewsii* USNM 787768. **b,** *Synchysidendron andrewsii* USNM 787769. **c,** *Calamites* stem. USNM 787780. **d,** *Annularia* sp. USNM 787781. **e,** *Sphenophyllum emarginatum* USNM 787779. **f,** *Sphenophyllum oblongifolium* or *S. emarginatum*. Leaf narrowness and arrangement suggests the former; rounded rather than acuminate teeth, the latter. USNM 787778. **g,** "*Pecopteris*" cf. *cyathea*, marattialean foliage. USNM 787771. **h,** Enlargement of basal-most pinnules illustrated in image (g) to show venation. Scale bars = 1 cm; scale bar for image (g) is angular with arrowhead at lower end.

apex. The midvein is strong and traverses the pinnule with sparse, lateral veins that dichotomize at least one time. Other pteridophytes include a possible lobatopterid marattialean fern, perhaps *Crenulopteris acadica* or *C. subcrenulata*, with lobate pinnule margins and candelabra-like lateral venation (Fig. 20e). Questionable calamitalean remains are only a coarsely ribbed axis, but without clear nodes (Fig. 20f). A small pinna (Fig. 20g) is perhaps a fragment of a filicalean fern, a marattialean or even *Laveineopteris rarinervis*; the flexuous rachis suggests a small, filicalean fern.

DISCUSSION

The late Middle Pennsylvanian (Desmoinesian) was a time period during which significant changes took place in tropical terrestrial landscapes. These temporal changes were reflected in compositional changes in Pennsylvanian tropical floras, best studied for floras from wetland settings. These floras are preserved in coals, either as coal-balls (Phillips et al., 1985) or palynofloras (Peppers, 1996; Eble et al., 2001; Bek and Opluštil, 2021), and in siliciclastic rocks both as palynofloras (e.g., Juncal et al., 2019) and as an extensive adpression flora record, mainly

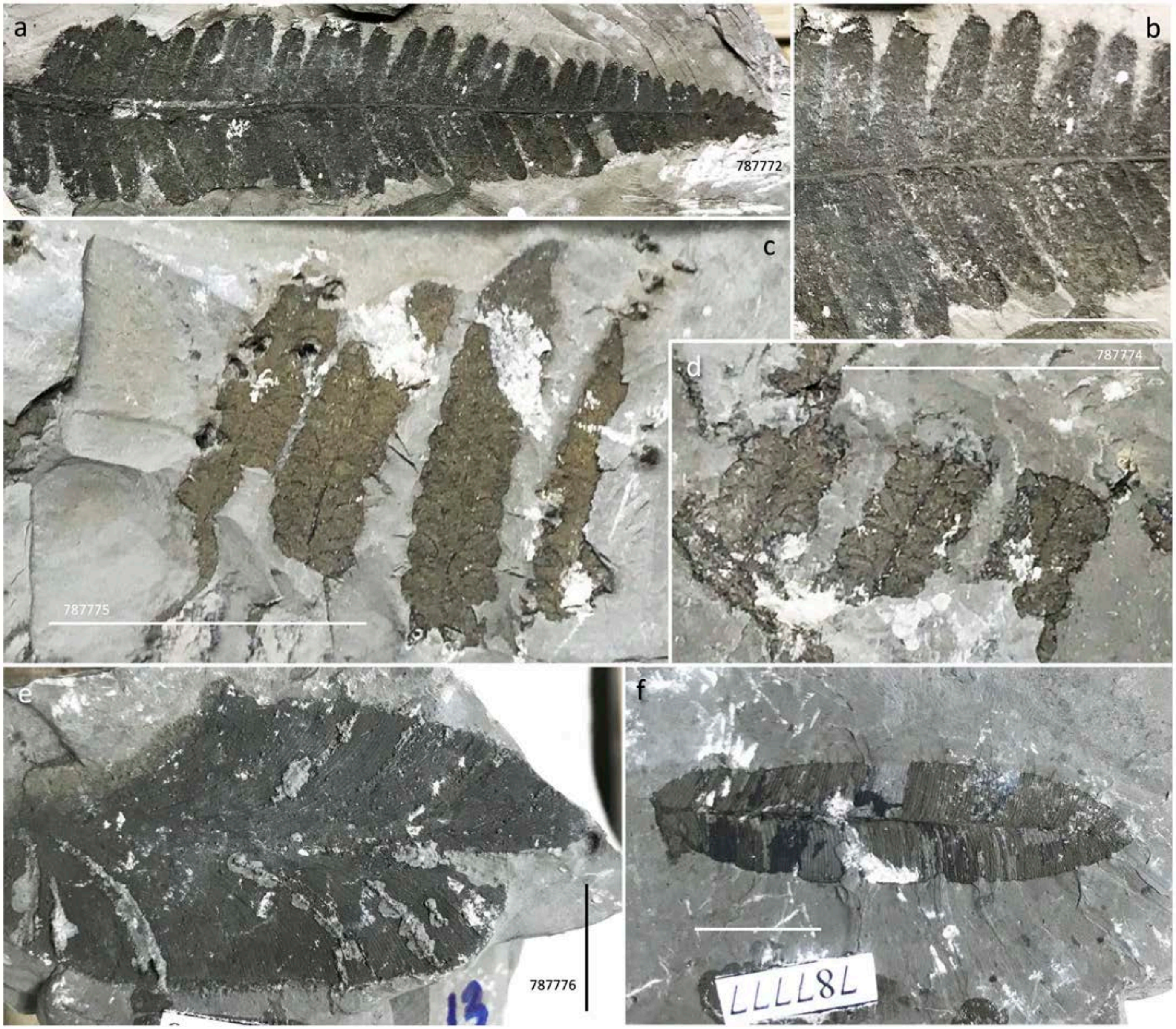

FIGURE 18. USGS 4149. Colchester Coal roof shale (Spring Valley Mine). Marattialean ferns and pteridosperms. **a,** *Crenulopteris acadica*. USNM 787772. **b,** Enlargement of portion of specimen in image (a) showing pinnule marginal lobation and lobatopterid venation. **c,** *Crenulopteris* cf. *subcrenulata* or *C. acadica*. USNM 787775. **d,** *Crenulopteris* cf. *subcrenulata* or *C. acadica* USNM 787774. **e,** Neuropterid of uncertain affinity, cf. *Neuropteris anomala* or *N. inflata*. USNM 787776. **f,** *Alethopteris serlii*. USNM 787777. Scale bars = 1 cm.

in association with coal bearing strata. There are numerous examples documented from Europe Europe (e.g., Kidston, 1923–1925; Crookall, 1955–1976; Wagner, 1983; Cleal, 1997, 2018; Wagner and Álvarez-Vázquez, 2010; Bashforth et al., 2011; King et al., 2011; Opluštil et al., 2022), but also a relatively small number in the U.S. (e.g., Boneham, 1974; Gastaldo, 1977; Pheifer, 1979; Blake, 2002; Wittry 2006) and Canada (e.g., Bell, 1938; Calder et al., 1996). The prevalence of these plants in association with tropical wetlands has led to the establishment of both palynological and macrofloral biostratigraphic schemes (e.g., Peppers, 1970, 1996; Wagner, 1984; Cleal, 1991; Wagner and Álvarez-Vázquez, 2010; Opluštil et al., 2022).

Coal balls and palynofloras from coal beds of Desmoinesian age indicate that early Desmoinesian floras were rich in lycopsids and cordaitaleans of various kinds, as well as a variety of pteridosperms, but relatively small numbers of marattialean tree ferns (e.g., Costanza, 1985; Phillips et al., 1985; Raymond et al., 2010). By about the middle of the Desmoinesian, there was a decrease in the abundance and diversity of cordaitaleans, and a change in their taxonomic composition, but they remained quantitatively important; this change took place during what Phillips and Peppers (1984) labelled their “Second Cordaitalean Interval”. The drop in cordaitaleans and change in the dominant form thereof (based on ovule/seed type) also witnessed the beginnings of the rise in abundance and diversity of marattialean ferns. A similar change was noted in the adpression floras across Euramerica (Pfefferkorn and Thomson, 1982). A second change was noted in the late Desmoinesian, at which time cordaitalean abundance dropped consistently below 1% of swamp-floral biomass, and marattialean abundance continued to increase. During this general time period, some of the most extensive peat-forming swamps of all time developed across the coastal

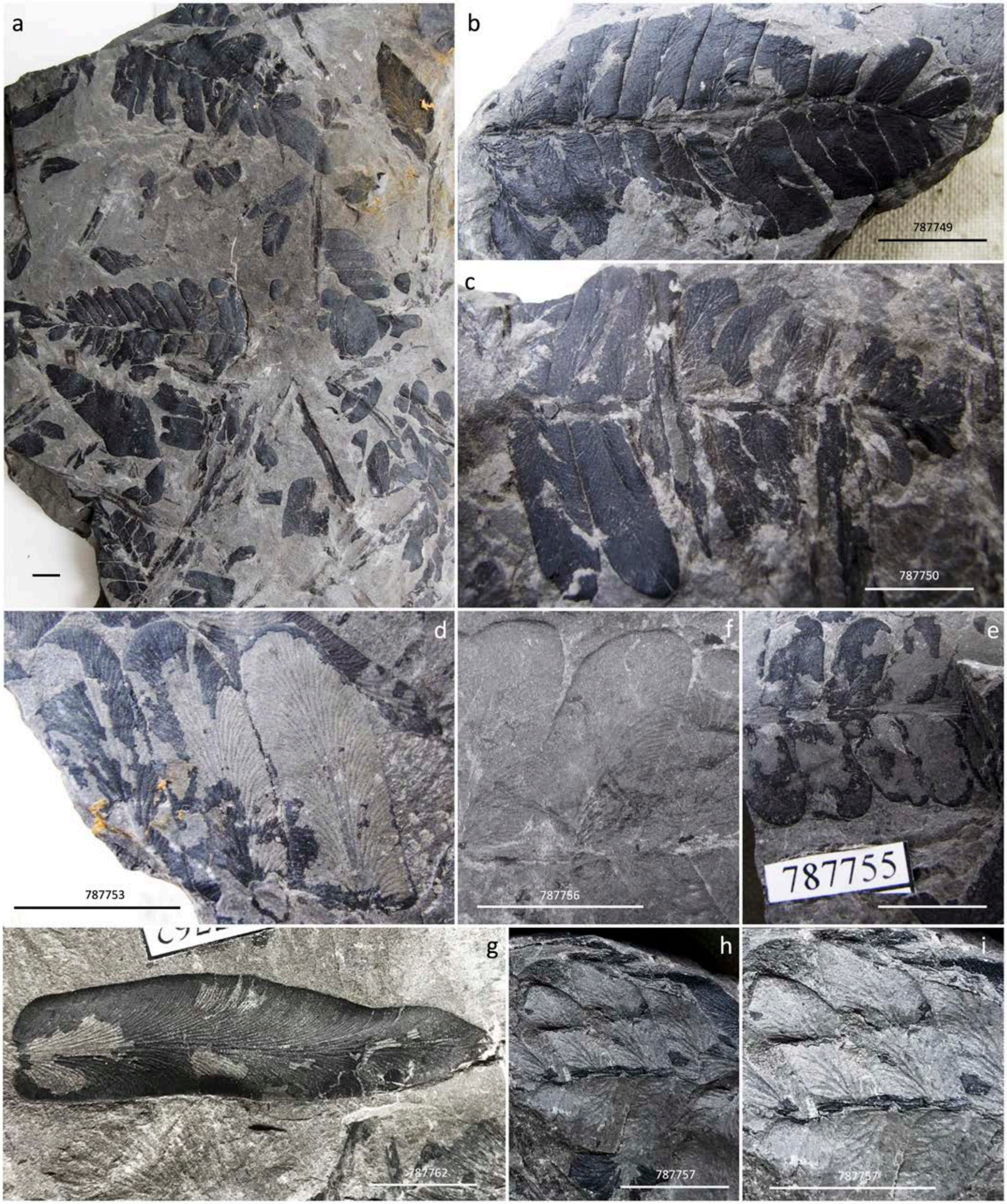

FIGURE 19. USGS 4150. Cardiff Coal roof shale (Cardiff Mine). Pteridosperms. **a,** *Neuropteris vermicularis* pinna fragments and dispersed pinnules. Specimen is 1/2 natural size on printed page with full plate at 18.4 cm wide. **b,** *Neuropteris vermicularis*. USNM 787749. **c,** *Neuropteris vermicularis*. USNM 787750. **d,** *Neuropteris vermicularis* impression showing pinnule venation. USNM 787753. **e,** *Neuropteris ovata* impression showing venation. USNM 787756. **f,** *Neuropteris ovata*. USNM 787755. **g,** *Macroneuropteris macrophylla*. USNM 787762 part. **h,** *Laveineopteris rarinervis*. USNM 787757. **i,** Enlargement of pinnules from image (h) showing coarseness of the lateral venation. Scale bars = 1 cm.

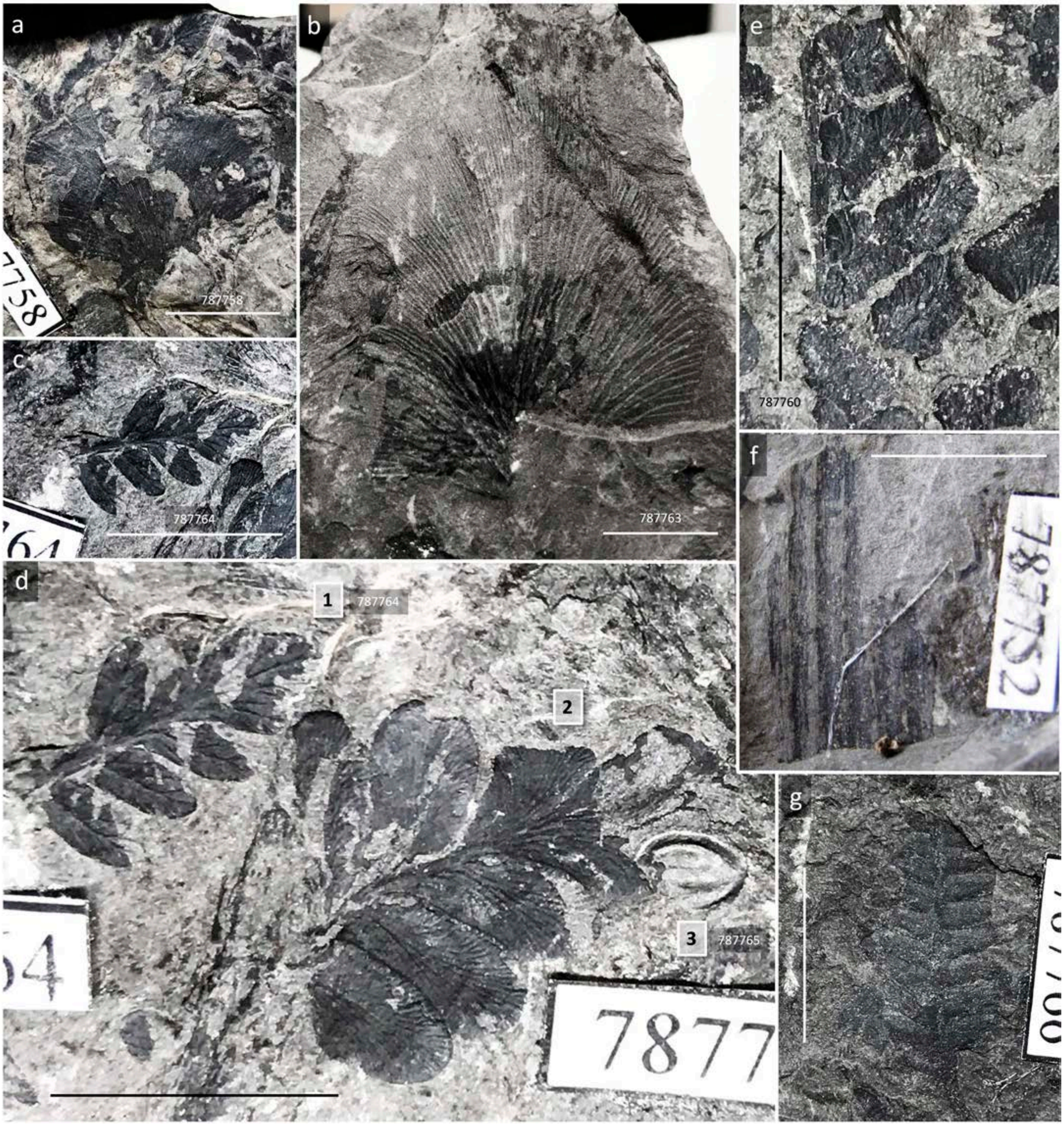

FIGURE 20. USGS 4150. Cardiff Coal roof shale (Cardiff Mine). Pteridosperms and pteridophytes. **a,** *Cyclopteris* sp. USNM 787758. **b,** *Cyclopteris* sp. Low density venation, particularly in the lower portion, suggests affinity with *Laveinopteris rarinervis*. USNM 787763. **c,** *Senftenbergia plumosa*. USNM 787764. **d,** *Senftenbergia plumosa* (higher magnification image of specimen in image [c]) box 1, *Neuropteris ovata* box 2, Seed box 3. USNM 787764. **e,** Lobatopterid marattialean fern, possibly *Crenulopteris acadica* or *C. subcrenulata*. Note lobate pinnule margins and candelabra-like lateral venation. USNM 787760. **f,** *Calamites* stem. USNM 787752. **g,** Pteridophyte foliage, possibly a small fern, a marattialean fern, or even *Laveineopteris rarinervis*. The flexuous rachis suggests a small, filicalean fern. USNM 787766. Scale bars = 1 cm.

lowlands, west of the Appalachians (Cecil et al., 2003; Greb et al., 2003). The Colchester and Cardiff coals fall within the latter part of the period of cordaitalean abundance, the Middle Desmoinesian interval during which their importance was in decline and during which marattialeans were beginning to increase in diversity and abundance. The uppermost coal bed in the Illinois Basin that includes this "Second Cordaitalean Interval" is the Houchin Creek (the Illinois No. 4) Coal, the next significant coal above the Survant/Cardiff Coal bed (Fig. 1). Thus, although we have no coal-ball floras from the immediate interval under investigation here, we do have reference to one of the best known adpression floras of the Pennsylvanian, that from Mazon Creek, with which to compare.

Colchester and Cardiff Floras in Environmental Context

The major, underlying driver of floristic changes during the Desmoinesian was a long-term, 10^6-year time scale, trend toward greater aridity. Superimposed on the longer term trend were short-term glacial-interglacial cycles on 10^5-year time scales. These shorter term cycles are marked stratigraphically by an alternation of climatically sensitive terrestrial strata, reflecting climate changes accompanying glacial-interglacial cycles (Cecil, 1990). Coals, formed from peat beds, reflect perhumid and humid climates (10 months or more when rainfall exceeded evapotranspiration, sensu Cecil, 2003). Paleosols and various kinds of fluvial-deltaic sediments reflect periods of greater seasonality, ranging from sub-humid to semi-arid. These shorter term cyclic patterns are reflected differently in strata formed on the great coastal plains west of the Variscan-Appalachian mountain ranges (e.g., Heckel, 2008) in the present day United States, or in physiographically similar regions on the eastern side of the ranges in, for example, the Donets Basin (e.g., Eros et al., 2012), than they are in the various intermountain regions (e.g., Opluštil et al., 2015, 2019) or north and south of those regions (e.g., Van Hoof et al., 2013) in modern Europe. In addition to changes in climate co-occurring with the different phases of glacial-interglacial cycles, there also were little-investigated changes in temperature (Fredericksen, 1972; Tabor et al., 2013; Matthaeus et al., 2021), which would have been pantropical, even if affected by local topography.

Glacial cycles also would have been accompanied by changes in sea level (Heckel, 2008; Rygel et al., 2008). These latter fluctuations, however, although worldwide, were manifested mainly in those areas directly fronting the ocean, such as in the Appalachian Basin and westward, or in the Donets Basin in eastern Euramerica. Such regular fluctuations gave rise, particularly in the Midcontinent and Eastern Interior basinal regions of the United States, to so-called cyclothems, alternating packages of marine and terrestrial strata. A cyclothem typically contains within the terrestrial phase a coal bed, sometimes only fluvial-deltaic strata and paleosols, recording glacial maxima. The marine phase includes shales and limestones of various origins, recording phases from glacial melting through re-expansion. The present study has focused on one such cycle, which likely represents the transition from glacial maximum through the early stages of deglaciation - the Colchester Coal cycle and associated floras, a widespread glacial event of significant magnitude based on the extent of correlative stratigraphic units. This cycle has been traced across the United States from the Appalachian Basin in the east to areas of Utah in the west (Cecil et al., 2003; Greb et al., 2003). The next cycle, that represented by the Cardiff Coal, was of lesser magnitude, based on the extent and thickness of correlative units (see Fig. 2).

Patterns in the data

Interpreting the patterns in the data represented by the four collections is closely tied to the environments of deposition in which the plant remains were preserved. These environments differ to a considerable degree but, in all instances, the plant remains appear to have been subject to little transport and most likely are parachthonous (sensu Bateman, 1991). The sub-Colchester seat-earth deposit and the Cardiff Coal roof shale may have many aspects of deposition and taphonomy in common and differ from the conditions under which the Colchester Coal roof-shale deposits formed. None of these accumulations are similar to those under which the Mazon Creek biota was preserved.

The oldest assemblage at Scab Hollow is the sub-Colchester Coal channel fill, which accumulated during the transition from a more seasonal subhumid climate to a less seasonal humid climate during glacial maximum, ultimately transitioning to a coal swamp flora (the source of the stigmarian root systems in the top of the deposit, immediately below the coal bed). The two Colchester roof floras are preserved in what were likely mudflats, formed during the early phases of sea-level-driven inundation of the peat swamp, perhaps by increasingly brackish water, preserving a peat-swamp-type vegetation. The Colchester Coal, from which we do not have a macroflora, lies between these deposits and represents the wettest part of a glacial-interglacial cycle, possibly formed at glacial maximum and in the early phases of ice melting. Lastly, the Cardiff Coal roof flora may be too small to account fully for the local flora; unfortunately, the ISGS geologists who visited the Cardiff mines while they were active did not leave any records of plant fossils they observed. It is possible, however, that, given the channel form of the coal bed, the same channel may have been occupied during the sea-level inundation that terminated formation of the Survant (Cardiff) peat swamp. Such inundation may have tracked inland in these depressions, thereby capturing a flora that included both peat-swamp elements and plants that lived alongside the channel on wet mineral soils of floodplains lateral to the peat body.

The most unusual of the four collections is that from the Colchester Coal seat earth, from the Scab Hollow Road ditch (USNM 38404). This collection was deposited in what Wanless (1957, and 1930 fieldnotes) characterized as a small, sandstone-filled channel. Rooted by stigmarian axes in its upper portions, but lacking remains of arboreous lycopsids, one is led to conclude that the stigmarian remains penetrated the deposit well after the aerial plant remains had been deposited, originating from obligate wetland lycopsid trees that populated the developing peat swamp. Furthermore, the flora preserved in the channel changes vertically through the deposit, initially dominated by calamitalean remains, with scraps of marattialean foliage (and possibly calamitalean foliage, reported by Wanless but not found by us). The preservation of calamitalean stems as casts, some angular in the bedding, suggests that they may have been growing in streamside settings or on bars within the active channel. The midpart of the deposit is heavily dominated by the medullosan *Neuropteris ovata*, of classic form. The lack of directional orientation and the mixed, but relatively large sizes of leaf fragments found abundantly in the deposit indicate standing water. This inference is supported further by the common presence of fine roots that do not penetrate across the bedding surfaces of the deposit but lie on the same planes as the foliage - they likely represent bank collapse material washed into the deposit. Marattialean tree-fern foliage becomes most abundant in the upper portions, documenting plants occupying a surface with an ever higher water table (consider their aerenchymatous root systems - Ehret and Phillips, 1977 - giving them access to flooded substrates). What is surprising is the lack of lycopsids in the uppermost parts of the seat earth.

Almost as unusual is the small flora collected in 1906 from the Cardiff Coal (USGS 4150). According to the USGS collections records, White and Bain visited both the Cardiff and Spring Valley mines on the same day. These mines are 80 km (50 miles) apart, suggesting that they either did not enter the mines and simply collected from gob or spoils exposed in the course of mining, or that they did not explore the mines thoroughly. We have not been able to locate fieldnotes of either individual that might shed additional light on the nature of fieldwork or on any plant remains that may have been observed but not collected. The Cardiff Coal collection is of interest not only because of its stratigraphic position but because of its potential depositional environment. Clearly deposited in a shallow channel (Fig. 5a), and well inland of the more continuously developed Survant peat swamp, the Cardiff Coal represents the finger-like edge of planar peat formation. The channel was filled as downstream flow was dammed by the developing more extensive peat swamp, permitting organic matter to accumulate and clog the channel; marginal interfingering with shale reflects the vagaries of swamp expansion and contraction through time. During the time of peat formation, this swampy area was almost certainly surrounded by a flora adapted to growth on wet, siliciclastic soils - a rainforest in more classic conception than would be peat-swamp vegetation. We are inclined to believe that as ice-melting ensued and coastal transgression began, the channel containing the precursor Cardiff peat accumulation was flooded, capturing some of the later stage swamp plants mixed with remains from the vegetation occupying the wetland floodplains flanking the channel. This may explain why the flora bears similarity to the Colchester seat-earth assemblage, in being pteridosperm-dominated, but also containing rare remains of lycopsid trees.

The Colchester Coal roof shale assemblages at Minonk (USGS 4146) and Spring Valley (USGS 4149) are both typical of coal beds from the upper Desmoinesian, dominated by lycopsids, particularly members of the Diaphorodendraceae, pteridosperm foliage, and marattialean tree-fern remains, with minor amounts of calamitalean remains and groundcover pteridosperms, ferns, and sphenopsids. This makes these assemblages overall more diverse than the other two. From a taphonomic perspective, they also may have a greater degree of intra-environmental transport and mixing, thus capturing remains from a larger spatial domain. Although no coextensive river channel has been identified that is contemporaneous with and lateral to the Colchester Coal bed, it is likely that the strata containing these two floras were inland of the now well known and extensively studied lagoonal facies of the Francis Creek Shale, the facies in which the Mazon Creek biota is preserved. Fortunately, ISGS geologist K.D. White made some helpful observations on the plant fossils he observed in the Minonk Mine (USGS 4146), noting fern fronds (probably mostly pteridosperms) and lycopsid trunks with diamond shaped bark, up to 30 cm in diameter, occurring upward of 3 meters into the roof; there must have been some roof falls for him to make this observation in 1912. In our plant collections we note the presence of the pectinacean bivalve *Dunbarella* and small snails, both characteristic of brackish to near-marine water conditions. In combination, these various observations indicate a similarity of the Colchester Coal roof deposits to those found flanking channels in underlying Desmoinesian coals, such as the Murphysboro (Treworgy and Jacobson, 1985), and overlying Desmoinesian coals such as the Springfield, Herrin, and Danville, in all of which contemporaneous river channels have been documented or strongly suspected (Eggert, 1982; Nelson, 1983; Burk et al., 1987; Elrick et al., 2017; Nelson et al., 2020). These channels were converted to estuaries in the latter phases of peat formation (Archer et al., 2016). In combination with changing climate, the channels are suspected of changing from largely black-water rivers, draining the lowland, peat-covered landscapes and mineral-soil wetlands farther inland, to estuaries carrying an increased sediment load, resulting in the development of mudflats flanking and progressively burying peat beds as sea-level rise progressed (e.g. Archer and Kvale, 1993), often rapidly as part of meltwater pulses (Archer et al., 2016). We suspect that the roof-shale deposits documented herein formed in the same way.

Comparison of the Colchester and Cardiff floras with the Mazon Creek flora

The Mazon Creek flora is an obvious point of comparison for the floras discussed here, given that the two Colchester Coal roof-shale floras are, like the Mazon Creek flora, enclosed in the Francis Creek Shale. The Mazon Creek flora is one of the most extensively collected, well researched, and publicly accessible fossil floras of the Pennsylvanian Subperiod (e.g., Janssen, 1979; Wittry, 2006, 2020). A comparative analysis of the Mazon Creek flora and a stratigraphically equivalent, similarly preserved flora from Okmulgee, Oklahoma was presented in Moore et al. (2013, table 2). Quantitative lists of the most common Mazon Creek taxa (compiled by Wittry) were compared with the entire Okmulgee taxonomic list (compiled by Moore and DiMichele, with identifications validated by Wittry for consistency).

Based on large numbers of specimens, generally with each nodule containing only a single specimen, seven of the 10 most commonly encountered taxa were shared by the two nodule collections from Mazon Creek and Okmulgee. These include the tree ferns *Crenulopteris acadica* (*Lobatopteris vestita*) and indeterminate marattialean fern foliage, the pteridosperms *Macroneuropteris scheuchzeri* and *Laveineopteris rarinervis*, calamitalean stems and the foliage form *Annularia sphenophylloides*, and, lastly, various remains of arboreous lycopsids, mainly the combination of leaves and reproductive structures. There were an additional eight shared taxa ranked between 11 and 27, including the marattialean *Diplazites unitus*, the pteridosperms *Alethopteris serlii* and *Odontoperis aequalis*, the calamitalean foliage forms *Annularia radiata*, *Annularia spinulosa*, and *Asterophyllites equisetiformis*, the shrubby sphenopsid *Sphenophyllum emarginatum*, and the arboreous lycopsid *Lepidodendron* sp. (distinguished from members of the Diaphorodendraceae, which also were recognized in the assemblages). 11 of the 27 most quantitatively abundant taxa from the smaller Okmulgee assemblage were not among the most common Mazon Creek taxa, but were reported from Mazon Creek, according to Wittry's census. Conversely, 12 of the top 27 categories in Wittry's Mazon Creek compilation did not occur in the Okmulgee assemblage.

The two Colchester roof-shale floras (Minonk and Spring Valley) studied here consist of 71 and 43 hand-specimens respectively, making them much smaller than the Mazon Creek flora by several orders of magnitude. These two floras share the major elements of lobate marattialeans (such as *Crenulopteris acadica*, specimens of which were identified in one of the collections), the pteridosperms *Macroneuropteris scheuchzeri* and *Lavineopteris rarinervis*, different species of the calamitalean foliage *Annularia*, the shrubby sphenopsid *Sphenophyllum emarginatum*, and the lycopsid *Diaphorodendron* cf. *rimosum*. Species of *Neuropteris*, *Alethopteris, Senftenbergia*, *Mariopteris*, *Lepidodendron*, and *Lepidophloios* were identified in one or the other of the collections. Given the small size of these collections, they might be considered replicates rather than being suitable examples of spatial variation in the composition of the flora, and together provide a picture of the flora of the Colchester Coal in its final phases as the landscape was turned from a peat swamp to a mudflat. In toto, these floras are compositionally comparable to that known from Mazon Creek or Okmulgee. What is noteworthy is the absence of *Neuropteris* species (either *N. ovata* or *N. vermicularis*) from either of these Colchester Coal roof-shale collections. Both of these species occur in the Mazon Creek collection, although only *N. vermicularis* is among the most abundant taxa in Wittry's analysis in Moore et al. (2013). In conclusion, the roof shale floras of the Colchester Coal, collected inland from the brackish-to-marine facies of the Francis Creek Shale from which nodular floras have been so widely collected, are consistent with the more broadly known Mazon Creek floral assemblage.

Turning to the Colchester Coal seat-earth assemblage from Scab Hollos, one finds a quantitative, but not qualitative, difference from the Mazon Creek assemblage, indicating its assembly from a common species pool but reflecting differences in microhabitat conditions. The presence of lobate marattialean foliage, most likely attributable to *Crenulopteris acadica*, is a consistent feature, particularly its increasing abundance in the upper portion of the seat-earth flora, wherein it can be inferred that seasonality of rainfall was decreasing progressively into the beginnings of peat formation. The dominance of *Neuropteris ovata*, however, differs from the Mazon Creek pattern wherein this species is the 25th most common taxon in Wittry's compilation. The other elements of the seat-earth flora, calamitaleans and *Annularia sphenophylloides* (the latter in Wanless' fieldnotes) also are consistent with the broader species pool. Perhaps of interest also is the larger size of the collection than the roof-shale assemblages, but, nonetheless, its much lower diversity.

The small collection (31 specimens) from the Cardiff Coal certainly is inadequate to provide a full sense of the local flora. However, experience suggests that were the collection "random" (that is, not a trophy hunt), it likely captures the most common elements of the assemblage. The dominant elements of the assemblage are very similar to what is found at Mazon Creek. The assemblage is overwhelmingly dominated by *Neuropteris*, with *N. vermicularis* and *N. ovata* numbers 1 and 2 in the count, with *Cyclopteris* cf. *fimbriata* as number 3. A few specimens of *Laveineopteris rarinervis*, a single specimen of *Diaphorodendron*, and a marattialean foliage specimen identified as *Pecopteris* cf. *cyathea* are, again, all consistent with the Mazon Creek flora. The marattialean specimen could easily be a part of one of the more complex lobate marattialean fronds of the *Crenulopteris*/*Lobatopteris* form, given the many venation patterns found in different parts of those fronds. In addition, although *Diaphorodendron* is not among the dominants in the Wittry quantitative assessment, it is present in the Mazon Creek flora (Wittry, 2020) and ranks among the top 10 taxa reported from the Okmulgee collection. As noted above, the similarity, quantitatively, of the Cardiff macroflora to the Colchester Coal seat-earth flora, suggests similarities to their microhabitats, with the dominant pteridosperm foliage possibly drawn from siliciclastic soils flanking the peat soils that had formed in the choked, and/or abandoned channel, mixing the immediately surrounding vegetation with the remnants of the dying peat-swamp flora.

As a final note, it should be emphasized that the Mazon Creek biota is not the only such large-scale plant and animal assemblage preserved in siderite concretions. There are two other published examples from the American Eastern Interior Basin. One is the Carterville flora (Gastaldo, 1977) from the roof shales of the Herrin (No. 6) Coal of southern Illinois. The Herrin Coal is several cycles above the Colchester Coal, but is part of the late Middle Pennsylvanian interval during which thick, widespread peats blanketed the coastal regions of west-central Pangea (Greb et al., 2003). As with the relationship between the two Colchester Coal roof floras described here, and the Mazon Creek flora, the allochthonous Carterville flora was preserved in shales flanking the lower reaches of the Walshville Channel, in a brackish to marine setting, whereas upstream of this area roof floras are preserved in tidalite mudflats flanking the channel (Archer and Kvale, 1993; Nelson et al., 2020). In a somewhat different depositional setting, the Stanley Cemetery flora of Indiana (Wood, 1963), preserved in siderite nodules, is found above the Lower Block Coal of the Indiana Brazil Formation. Other, unpublished, siderite floras have been collected from several other localities in the shales above one or more of the Block coals of Indiana by the authors. The Block Coal interval is Atokan in age, and thus older than the Carbondale Formation that includes the Colchester Coal. The interval is situated below a major environmental and floristic change that occurred at the Atokan-Desmoinesian boundary (Bsshforth and Nelson, 2015), one that also saw a change in peat-forming environments from more domed to more planar in form (Mastalerz et al., 2018), likely reflecting a major step change in rainfall seasonality during the wettest parts of glacial-interglacial cycles (Montañez, 2016). Most of the Brazil Formation flora is preserved in tidalite sediments that are thought to have formed on a drowning coastline (Kvale and Archer, 1990). Most Brazil Formation plant fossils are preserved as adpressions; the relationship of the siderite-preserved assemblages to the more typical and widespread compression-impression assemblages is unstudied, but these kinds of preservation appear to be spatially separated.

CONCLUSIONS

The four floras described in this study, three associated with the Colchester Coal and one with the Cardiff Coal, are all typically late Middle Pennsylvanian in character. The absence of conspicuous cordaitalean remains is a key factor separating them from what is known, primarily from palynological studies (e.g., Phillips et al, 1985; Peppers, 1996), of the peat-swamp floras they precede or supercede stratigraphically, which had a small, but significant cordaitalean component. This difference is of interest because of the great range of ecological tolerance exhibited by the cordaitaleans, as a group; elements of this broad taxonomic group might be expected to have inhabited a broad range of wetland habitats.

Of particular interest are the two Colchester Coal roof-shale floras, which are paleogeographically inland of that part of the Francis Creek Shale that is rich in siderite nodules and preserves the well known Mazon Creek flora. These floras likely formed in the early phases of marine transgression of the peat, which involved a transition from a freshwater peat-forming landscape to one of mudflats and an increasingly inundated landscape. Nonetheless, plant-fossil assemblages reflect, even in their small sample sizes, basic compositional similarity to the Mazon Creek assemblage, despite being much less diverse. By all indications, the Mazon Creek assemblage was allochthonous, drawn from a broad swath of landscape, thus from many small patches of vegetation like those preserved in these two assemblages.

The Cardiff Coal roof flora is of additional interest because there has been no mining of this coal in over 65 years as of this date, and there is unlikely to be any additional collecting possible from those strata. That said, there may be collections from the Cardiff roof shales present in the drawers of one or more museum, university, or private collections that may one day appear. More information would be most welcome given the unusual conditions under which the parent peat formed.

ACKNOWLEDGEMENTS

We acknowledge the great David White for his commitment to documenting the plant fossils from across the United States at a time, late 1800s through the 1930s, when relatively little was known or published from many areas, particularly using active coal mines as the source of specimens. He left a large, and largely unexplored, collection at the National Museum of Natural History. We thank reviewers Christopher Cleal and Michael Donovan for their careful reading, comments, and suggestions helpful in the revision of an earlier version of this paper.

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