

ATLAS OF SELECTED KINNEY QUARRY PLANT FOSSILS, LATE PENNSYLVANIAN, CENTRAL NEW MEXICO

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Abstract—During the Late Pennsylvanian, seasonality and rainfall increased in western Pangea, which led to the expansion of “mixed” floras composed of a combination of wetland and drought-tolerant plants. One notable example is the flora of the Kinney Brick Quarry, a Missourian Lagerstätte southeast of Albuquerque, New Mexico, USA, deposited in an embayment by a prograding delta in a seasonal, subhumid climate. A controlled excavation of the quarry and bed-by-bed quantitative analyses of the floral composition revealed a transition from dominance by wetland plants to drought-tolerant plants. In this study, we provide a visual reference of important plant taxa from each of the six productive beds in the controlled excavation. Pteridosperms, conifers, and filicalean ferns are present in all six beds; lycopsids, marattialeans ferns, and cordaitaleans range through Beds 2-5; sphenopsids, dicranophylls, and noeggerathialeans span Beds 2-6; and *Taeniopteris* species are present only in Bed 4. The stratigraphic ranges of plants at Kinney suggest that, although there were changes in species dominance patterns, the overall species pool stayed consistent throughout deposition of the strata. We also hypothesize the habitat preferences of fossil plant taxa from Kinney based on morphological adaptations, modeled physiological requirements, and depositional environment interpretations of other localities where the same plant species occur. These interpretations suggest a landscape with varied microhabitats accommodating plants with an array of moisture tolerance levels, with wetland plants colonizing the shoreline, along rivers, and other moist substrates, and meso- and xeromorphic plants occupying areas experiencing seasonal drought.

INTRODUCTION

The Kinney Brick Quarry, southeast of Albuquerque, New Mexico, preserves fossil plants, invertebrates, and vertebrates from the Missourian (Late Pennsylvanian) of western Pangea. The flora of the Kinney Quarry is a “mixed” flora, consisting of xeromorphic and mesomorphic plants associated with seasonally-dry climates intermixed with hygromorphic species typical of wetland environments. Early studies of the flora focused on systematic descriptions of unusual new species, including *Dicranophyllum readii* (Mamay, 1981), *Charliea manzanitana* (Mamay, 1990), and *Sphenopteridium manzanitanum* (Mamay, 1992). Detailed studies on the entire macroflora were conducted by Mamay and Mapes (1992) and DiMichele et al. (2013). Willard (1992) described the palynoflora from two collections from different parts of the quarry, finding cordaitalean, conifer, and pteridosperm pollen, and fern spores. *Cordaites kinneyensis* Šimůnek was recently described from cuticle (Šimůnek, 2018). Two charophyte oogonia were illustrated by Kietzke and Kaesler (1992). Possible piscine eggs (Mamay, 1994; but reinterpreted as gastropod eggs by Lucas et al., 2021a, this volume) and arthropod and pathogen damage associated with the flora (Donovan and Lucas, 2021, this volume) have also been described.

Although detailed floristic studies have previously been published (Mamay and Mapes, 1992; DiMichele et al., 2013c), these studies did not tie the plant fossils from Kinney to specific localities or beds in the quarry. Therefore, whether the fossil plant assemblages changed through time as a result of local environmental fluctuations was unknown. In 2014, a joint team from the New Mexico Museum of Natural History and Science in Albuquerque, New Mexico, and Technical University Bergakademie Freiberg, Germany, carried out a controlled excavation of the Kinney Quarry, identifying six distinct beds with fossil plants. The succession of lithological and biotic patterns revealed by the controlled excavation served as a basis to sort the collections of the National Museum of Natural

History, which were made by the U.S. Geological Survey in the late 1960s. DiMichele et al. (2021, this volume) characterized the taphonomy of the plant fossils in the quarry by analyzing changes in composition and diversity through the strata and evolving depositional environments. Their study revealed that the flora is an allochthonous mixture of wetland and drought-tolerant plants. When moving upsection, the mean fragment size of the fossil plants increases, related to decreasing distance from the paleo-shoreline (DiMichele et al., 2021, this volume). Wetland taxa are dominant in the lower beds, and xeromorphic species increase in relative abundance in the upper beds, possibly related to minor changes in climate over the course of deposition, and/or to changes in the number of terrestrial source areas contributing to the local floral assemblage (DiMichele et al., 2021, this volume).

The primary purpose of this article is to provide a visual reference to common fossil plants that occur in beds of the Kinney Quarry, which accompanies the companion manuscript focusing on fossil plant taphonomy and bed-by-bed changes in the flora (DiMichele et al., 2021, this volume). Here, we illustrate many of the important plant taxa by bed level and provide notes on taxonomic identifications, stratigraphic ranges of the plant taxa, and hypothesized habitat preferences of many of the plant taxa.

GEOLOGY

The Kinney Brick Company Quarry, part of the Atrasado Formation, is located in section 18, T9N, R6E of the Sedillo 7 ½' Quadrangle, ~12 km south of Tijeras, Bernalillo County, New Mexico, in the Manzanita Mountains (Fig. 1). Strata at the locality were deposited during the Missourian (Late Pennsylvanian; approximately 305 Ma) based on conodont and fusulinid biostratigraphy (Lucas et al., 2011). The Missourian corresponds approximately to the Kasimovian in the International Commission on Stratigraphy time scale (Schneider et al., 2020).

The deposit was likely formed in a sheltered coastal

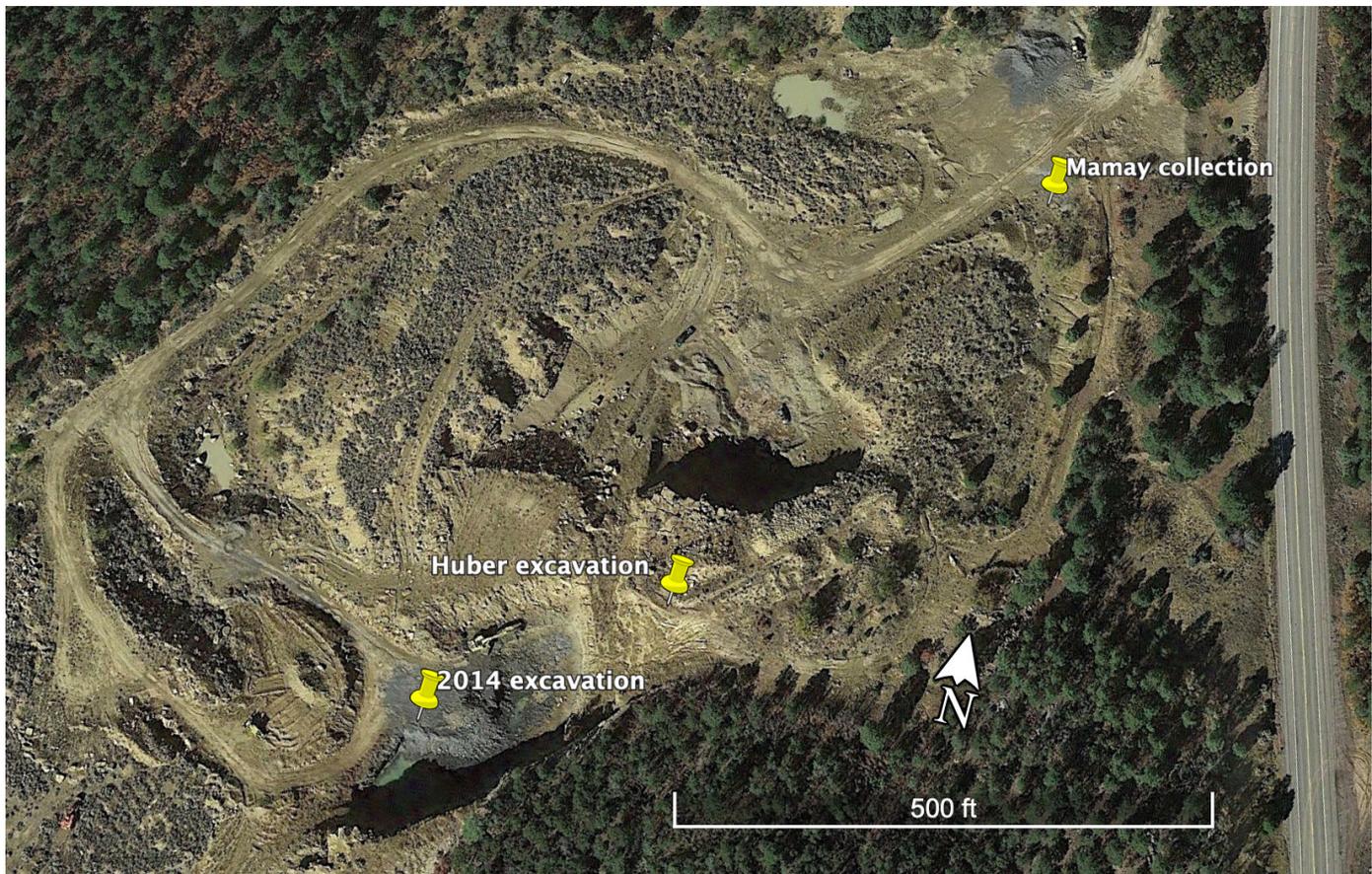


FIGURE 1. Map of the Kinney Quarry with locations of the Mamay collection at NMNH, the Huber collection at NMMNHS, and the 2014 controlled excavation. Image courtesy of Google Earth.

embayment fed by one or more streams and rivers, which became closer to the paleoshoreline as a river delta prograded and siliciclastic sediments were deposited (Archer and Clark II, 1992; Feldman et al., 1992; Kues and Lucas, 1992; Lorenz et al., 1992; Schneider et al., 2021, this volume). The climate is interpreted as being seasonal and monsoonal (Huber, 1992; Schneider et al., 2021, this volume). The fossil plants are preserved in six beds spanning 2.5 m of section (Fig. 2). Bed 2 through Bed 5 exhibit millimeter-scale laminations, which are interpreted as the result of seasonal river floods. Based on counts and estimations of the number of laminae, the total time to deposit the plant-bearing section (Beds 1 to 6) was probably somewhat longer than 2000 years (Kues, 1992; Schneider et al., 2021, this volume). Brief facies descriptions and interpretations of the depositional environments of Beds 1-6 are discussed in the following section.

COLLECTIONS

The collections we analyzed are housed at the New Mexico Museum of Natural History and Science (NMMNHS) and the National Museum of Natural History (NMNH or USNM). They come from three discrete spots in the area excavated for clay to make bricks by the Kinney Brick Company (Fig. 1). The USNM collections were made primarily during the late 1960s, by the late Sergius Mamay and crew. Philip Huber, then an undergraduate student at the University of New Mexico, made the largest portion of the NMMNHS plant-fossil collection during the early 1990s (Fig. 1). Since that time, there have been additional collecting trips to the quarry by NMMNHS staff and volunteers, including a large field trip on May 21, 2013, held in conjunction with a professional meeting at the NMMNHS. Some of the specimens photographed at that time appear in this paper.

In 2014, coauthors Schneider and Lucas, together with a team of collaborators from their respective institutions, carried out a controlled excavation at the Kinney Quarry (Fig. 3). During the excavation, researchers systematically stripped back layers of rock and collected plant and animal fossils, as well as analyzed the sedimentology of the deposit. Plant-fossil specimens that were possible to collect were accessioned into the collections of NMMNHS. The portion of the excavation that included the main layers in which plant fossils were found was divided into six beds, numbered Bed 1 through Bed 6 (Fig. 2, 3). All contained plant remains, although the principal foci were Beds 2-5, which encompassed a thickness of 2.5 m. Beds 1 and 2 are marine limestones deposited in a restricted, low energy lagoon on a shallow marine carbonate shelf. Beds 3-5 are finely laminated brackish-marine mudstones, which allowed many specimens to be split along large, continuous surfaces into relatively thin, plate-like sheets. Bed 6 is an indistinctly laminated mudstone intercalated with unbedded claystone layers of brackish marine origin with elevated fluvial influence.

The USNM collections were made under the supervision of U.S. Geological Survey (USGS) paleobotanist Sergius H. Mamay, and, as USGS collections, were housed in the NMNH until formally transferred to NMNH jurisdiction in the early 1980s. Mamay and his assistant, Arthur D. Watt, collected in the Kinney Quarry in 1967 and 1969. Their collections were made near the then entry to the quarry (Fig. 1), thus in a different area from those made by Huber and the area of the controlled excavation. Although the USNM collections were not originally made with regard to bed and were mixed in the collections, it was possible to re-sort them to original bed based on lithological characters, described below (DiMichele et al., 2021, this volume).

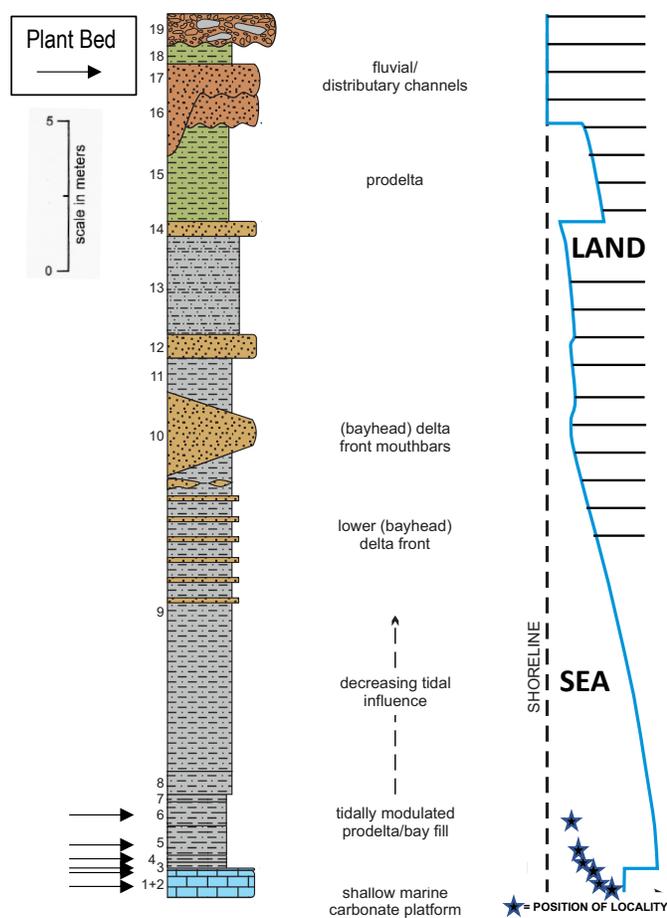


FIGURE 2. Stratigraphic column of the 2014 controlled excavation at Kinney Quarry.

All plant remains in the Kinney deposit are allochthonous, although studies of fragment size (DiMichele et al., 2021, this volume) based on bed-by-bed analyses suggest a decrease in long-distance transport from the lowermost (Bed 2) to the uppermost (Bed 5) excavated (or inferred equivalent) beds. Bed 6 again demonstrates fragmentary preservation, likely due to the higher energy of the deposit. Specimens were generally rare in the matrix. This was revealed during the controlled excavation. However, it also proved to be the case in a quantitative analyses, wherein approximately 50% of the hand samples were barren on one face, and where it was most common to encounter only a single taxon per informative surface (DiMichele et al., 2021, this volume).

Bed 1 is a gray, bioclastic, irregularly-laminated limestone with various marine invertebrate remains dominated by brachiopods (Kues and Lucas, 1992). Plant fossils are rare in the matrix, but, when present, they are often reasonably well preserved. The bed was deposited in a shallow marine environment (Schneider et al., 2021, this volume).

Bed 2 is an olive black micritic limestone. The bed splits irregularly in the basal portion and is laminated at the top. Plant fossils are uncommon in Bed 2 and tend to be fragmentary. Like Bed 1, the depositional environment of Bed 2 is interpreted as shallow marine (Schneider et al., 2021, this volume).

Bed 3 (the “Fish bed”) is a gray to buff, distinctly laminated bituminous limestone to calcareous siltstone, which weathers mostly ocher-colored. Hand samples often have distinctive iron (Liesegang) banding, giving some specimens a yellowish appearance. Liesegang banding is rare in Beds 4 and 5, which was revealed during the controlled excavation. This feature allowed us to attribute specimens from the NMNH-USGS

collections from the 1960s and the NMMNHS collections from the 1990s to Bed 3. The bed tends to split into thin sheets. Although most plant-fossil specimens in Bed 3 are small and fragmentary, occasional larger specimens also are present. Bed 3 was deposited when the embayment deepened, which may be a result of tectonics (Schneider et al., 2021, this volume).

Bed 4 in the excavation is a gray, calcareous, finely laminated siltstone with fossils of the brackish to freshwater bivalve *Dunbarella* Newell. These fossils are increasingly abundant up section through the thickness of the bed. Plant remains can be relatively large, again, mainly in the upper portions of the bed. Bed 4 is interpreted as muds deposited in the prodelta (Kues and Lucas, 1992; Schneider et al., 2021, this volume).

Bed 5, a gray, laminated siltstone that splits into large, plate-like sheets, is similar in many ways to Bed 4 of the excavation. *Dunbarella* fossils are most dense in this bed. The plant fossil remains in this bed are very variable in size, but, on average, larger than in any of the other beds, and with many very large remains present. Similar to Bed 4, the siltstones of Bed 5 are interpreted as prodeltaic muds (Schneider et al., 2021, this volume).

Bed 6 is a poorly-bedded gray siltstone intercalated with layers of unbedded claystone. The bed is of brackish water origin, deposited most probably in the closest proximity to land, or actually on the delta top. Fractures are irregular and rounded. Plant fossils tend to be fragmentary and sparse.

The pre-excavation collections housed in both the NMNH and NMMNHS contain an additional facies, which appears to have been roughly equivalent to a portion of Bed 4 of the excavation. This facies is generally more buff and less gray in color. Furthermore, although laminated, it does not split into large sheets, or expose large surfaces. Rather, it breaks irregularly, across laminae, so it generally exposes small size fragments. Due to its presence in the NMMNHS collections, and its labeling there, this facies has been treated as equivalent to Bed 4. The facies is also very abundant in the NMNH collections.

DOMINANCE-DIVERSITY PATTERNS

Based on count data for each bed, dominance-diversity summaries were generated separately for the NMNH and NMMNHS collections (DiMichele et al., 2021, this volume). Count data were collected in DiMichele et al. (2021, this volume) using the quadrat method of Pfefferkorn et al. (1975) modified by Bashforth and Nelson (2015). In this method, plant fossils are counted as present or absent on the front and back of a hand sample, and each side is considered a separate quadrat. The rankings are presented here in Table 1 for the most common elements of the respective collections. Photographic plates are presented by bed to illustrate many of the dominant taxa from each bed. However, not all of the most common forms are depicted, because we have not been able to access the NMNH collection during the writing of this manuscript due to the COVID-19 lockdown. Consequently, we have not been able to photograph the best or most representative specimens from each bed. The illustrations are those of specimens that either were photographed in the field at the time of excavation, as part of Kinney quantitative studies (DiMichele et al., 2021, this volume), for earlier publications on the Kinney flora, or of arthropod and pathogen damage (Donovan and Lucas, 2021, this volume).

KINNEY FOSSIL FLORA BY BED

The taxonomic data reported below are based on the “reduced matrices” from DiMichele et al. (2021, this volume, tables 3 and 4). In these compilations, the “taxa” referred to were first considered to be “plant objects” that could be recognized repeatedly, and that would be relevant to a taphonomic study (All Data matrices: DiMichele et al., 2021, this volume, tables



FIGURE 3. Photograph of the 2014 controlled excavation of the Kinney Brick Quarry.

1 and 2). Some of these plant objects were not taxonomically specific, or were objects that might overlap taxonomically, but to an uncertain degree (such as foliage and stems or reproductive organs). The reduced matrices lessen the redundancy of taxonomic organ categories, and remove non-taxonomically identifiable plant objects from consideration for statistical analyses. Counts of taxa below, therefore, may be resolved to the level of genus, or even more encompassing groups. All are taxonomically identifiable.

The Bed 1 collection at NMMNHS, from the lowermost bed of the controlled excavation, includes nine informative quadrats and five taxa. No Bed 1 specimens were recognized in the NMNH collections. Taxa from Bed 1 include the medullosan pteridosperms *Neuropteris ovata* Hoffmann (Fig. 4A), *Mixoneura/Odontopteris* sp., and *Mixoneura (Odontopteris) cantabrica/schlotheimii* (Fig. 4B); the conifer *Walchia piniformis* (Schlotheim) Sternberg (Fig. 4C); and *Sphenopteris* Brongniart sp., a filicalean fern (Fig. 4D). A striate axis, probably from a pteridosperm, is also figured (Fig. 4E). Although the sample size of Bed 1 is small, so that our ability to interpret the flora is limited, the flora represents a mix of wetland (*N. ovata*, *Mixoneura/Odontopteris* sp., *M. (O.) cantabrica/schlotheimii*) and drought-tolerant (*W. piniformis*) plants.

The Bed 2 collection at NMMNHS includes 30 quadrats with 12 taxa. The dominant species in the NMMNHS collection are *Neuropteris ovata*, the coniferophyte *Dicranophyllum readii* Mamay, the calamitalean foliage *Phyllothea* Brongniart sp.

(Fig. 5C), *Walchia piniformis*, and marattialean fern foliage. Also illustrated is *Annularia sphenophylloides* (Fig. 5D). In the NMNH Bed 2 collection, there are 51 informative quadrats and 15 taxa with a composition similar to that of the NMMNHS collection (Table 1). We were unable to illustrate NMNH specimens because of the museum lockdown due to COVID-19. Although the order of the most frequent taxa varies between the NMMNHS and NMNH collections, the overall taxa are similar, especially considering the small sample size. The most frequent taxa from the NMNH collection include *Phyllothea* sp., *W. piniformis*, *N. ovata*, and *Cordaites* Unger sp. *Dicranophyllum readii* is tied for the fifth most frequent taxon with four other species (Table 1). Both Bed 2 collections suggest a “mixed” flora composed of hygromorphic taxa (*N. ovata*, *Phyllothea* sp., marattialean foliage) blended with xeromorphic plants (*D. readii*, *W. piniformis*).

The Bed 3 collection at NMMNHS has 31 taxa from 306 quadrats. Dominant species include *Neuropteris ovata* (Figs. 6A, C, 8), *Phyllothea* sp. (Fig. 6E), *Annularia spinulosa* Sternberg (calamitalean foliage; Fig. 7D), marattialean fern foliage, *Cordaites* sp. (Fig. 7A), *Asterophyllites equisetiformis* (Schlotheim ex Sternberg) Brongniart (calamitalean foliage; Fig. 7E), the noeggerathialean *Charliea manzanitana* Mamay, *Walchia* Sternberg sp., and *Annularia* Sternberg sp. We also illustrate a calamitalean stem (Fig. 7G) and *Dicranophyllum Grand'Eury* sp., probably *D. readii* (Fig. 7H). At NMNH, 32 taxa were found on 503 quadrats from Bed 3. The most frequently

TABLE 1. Taxon rankings for Beds 1-6.

NM Bed 1	NM Bed 2	US Bed 2	NM Bed 3	US Bed 3	NM Bed 4
<i>Neuropteris ovata</i>	<i>Neuropteris ovata</i>	<i>Phyllothea</i> sp.	<i>Neuropteris ovata</i>	<i>Neuropteris ovata</i>	<i>Neuropteris ovata</i>
<i>Mixoneura (Odontopteris)</i> sp.	<i>Dicranophyllum readii</i>	<i>Walchia piniformis</i>	<i>Phyllothea</i> sp.	<i>Charliea manzanitana</i>	<i>Sphenopteridium manzanitanum (Sphenopteris germanica)</i>
<i>Mixoneura (Odontopteris) cantabrica</i>	<i>Phyllothea</i> sp.	<i>Neuropteris ovata</i>	<i>Annularia spinulosa</i>	<i>Phyllothea</i> sp.	<i>Charliea manzanitana</i>
<i>Walchia piniformis</i>	<i>Walchia piniformis</i>	<i>Cordaites</i> sp.	Marattialean foliage	<i>Dicranophyllum readii</i>	<i>Walchia</i> sp.
<i>Sphenopteris</i> sp.	Marattialean foliage	<i>Annularia spinulosa</i>	<i>Cordaites</i> sp.	Marattialean foliage	<i>Dicranophyllum readii</i>
	Others	<i>Dicranophyllum readii</i>	<i>Asterophyllites equisetiformis</i>	<i>Sphenopteris</i> sp.	<i>Neuropteris</i> sp.
		<i>Mixoneura subcrenulata</i>	<i>Charliea manzanitana</i>	<i>Neuropteris</i> sp.	<i>Danaeites</i> sp.
		<i>Sphenopteridium manzanitanum (Sphenopteris germanica)</i>	<i>Walchia</i> sp.	<i>Cordaites</i> sp.	Marattialean foliage
		<i>Calamostachys tuberculata</i>	<i>Annularia</i> sp.	<i>Remia pinnatifida</i>	<i>Walchia piniformis</i>

US Bed 4	NM Bed 5	US Bed 5	NM Bed 6
<i>Sphenopteridium manzanitanum (Sphenopteris germanica)</i>	<i>Sphenopteridium manzanitanum (Sphenopteris germanica)</i>	<i>Dicranophyllum readii</i>	<i>Walchia piniformis</i>
<i>Walchia piniformis</i>	<i>Walchia piniformis</i>	<i>Sphenopteridium manzanitanum (Sphenopteris germanica)</i>	<i>Walchia</i> sp.
Marattialean foliage	<i>Neuropteris ovata</i>	<i>Neuropteris ovata</i>	<i>Sphenopteridium manzanitanum (Sphenopteris germanica)</i>
<i>Cordaites</i> sp.	<i>Cordaites</i> sp.	<i>Cordaites</i> sp.	<i>Macroneuropteris. scheuchzeri</i>
<i>Dicranophyllum readii</i>	<i>Charliea manzanitana</i>	<i>Neuropteris</i> sp.	<i>Neuropteris ovata</i>
<i>Mixoneura subcrenulata</i>	<i>Dicranophyllum readii</i>	<i>Charliea manzanitana</i>	<i>Mixoneura subcrenulata</i>
<i>Charliea manzanitana</i>	<i>Walchia</i> sp.	<i>Neurodopteris auriculata</i>	<i>Sphenopteris</i> sp.
<i>Sphenopteris</i> sp.	<i>Neurodopteris auriculata</i>	Marattialean foliage	<i>Dicranophyllum readii</i>
<i>Annularia carinata</i>	<i>Mixoneura (Odontopteris)</i> sp.	<i>Otoviccia hypnoides</i>	Others

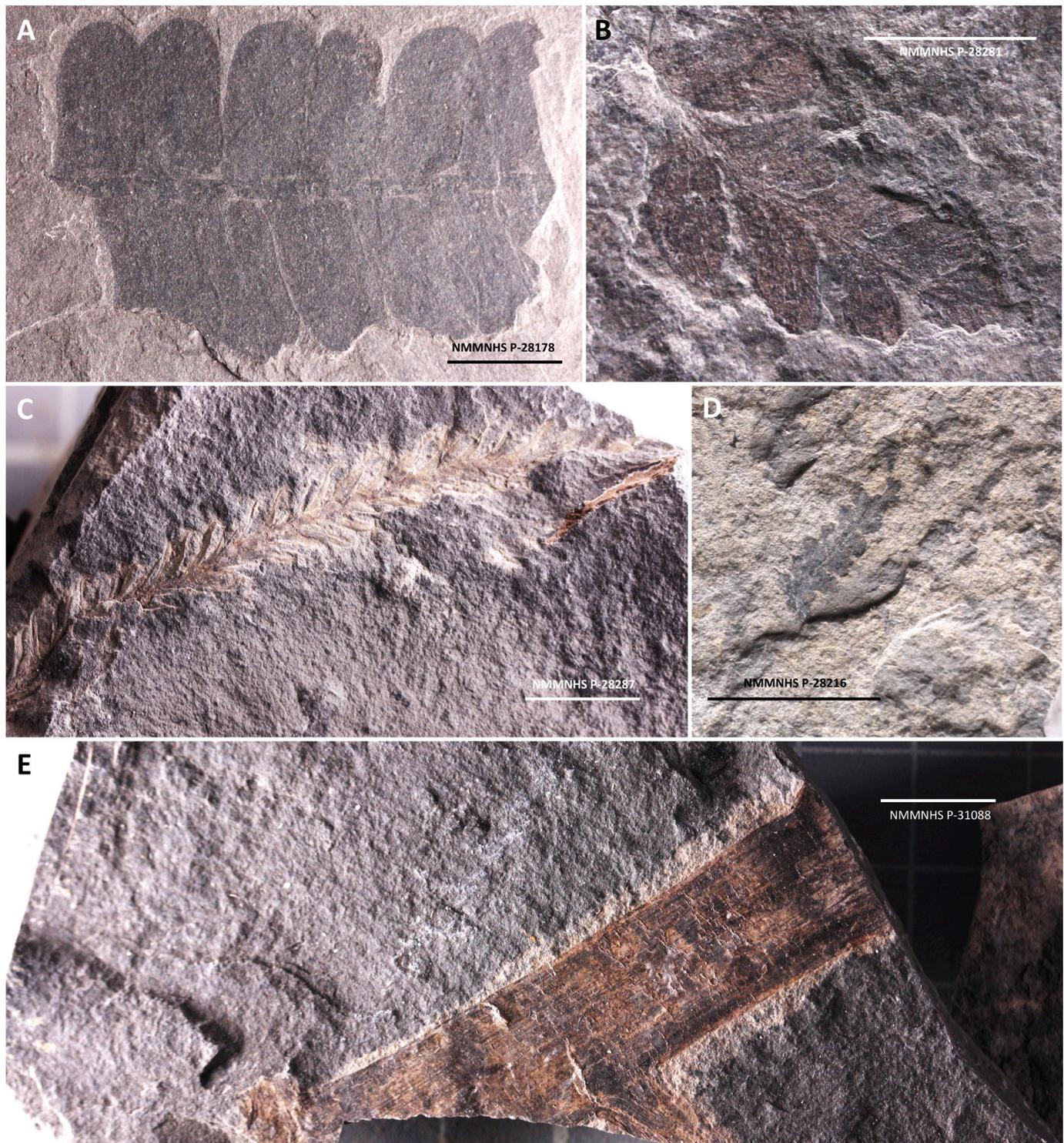


FIGURE 4. Bed 1. Plant fossils from Bed 1 in the NMMNHS collections. **A.** *Neuropteris ovata*. NMMNHS specimen P-28178. **B.** *Mixoneura (Odontopteris) cantabrica/schlotheimii*. More likely the former, based on size. NMMNHS specimen P-28281. **C.** *Walchia piniformis*. NMMNHS specimen P-28287. **D.** *Sphenopteris* sp. (filicalean fern). NMMNHS specimen P-28216. **E.** Striate axis, likely of pteridosperm origin. NMMNHS specimen P-31088. Scale bars = 1 cm.

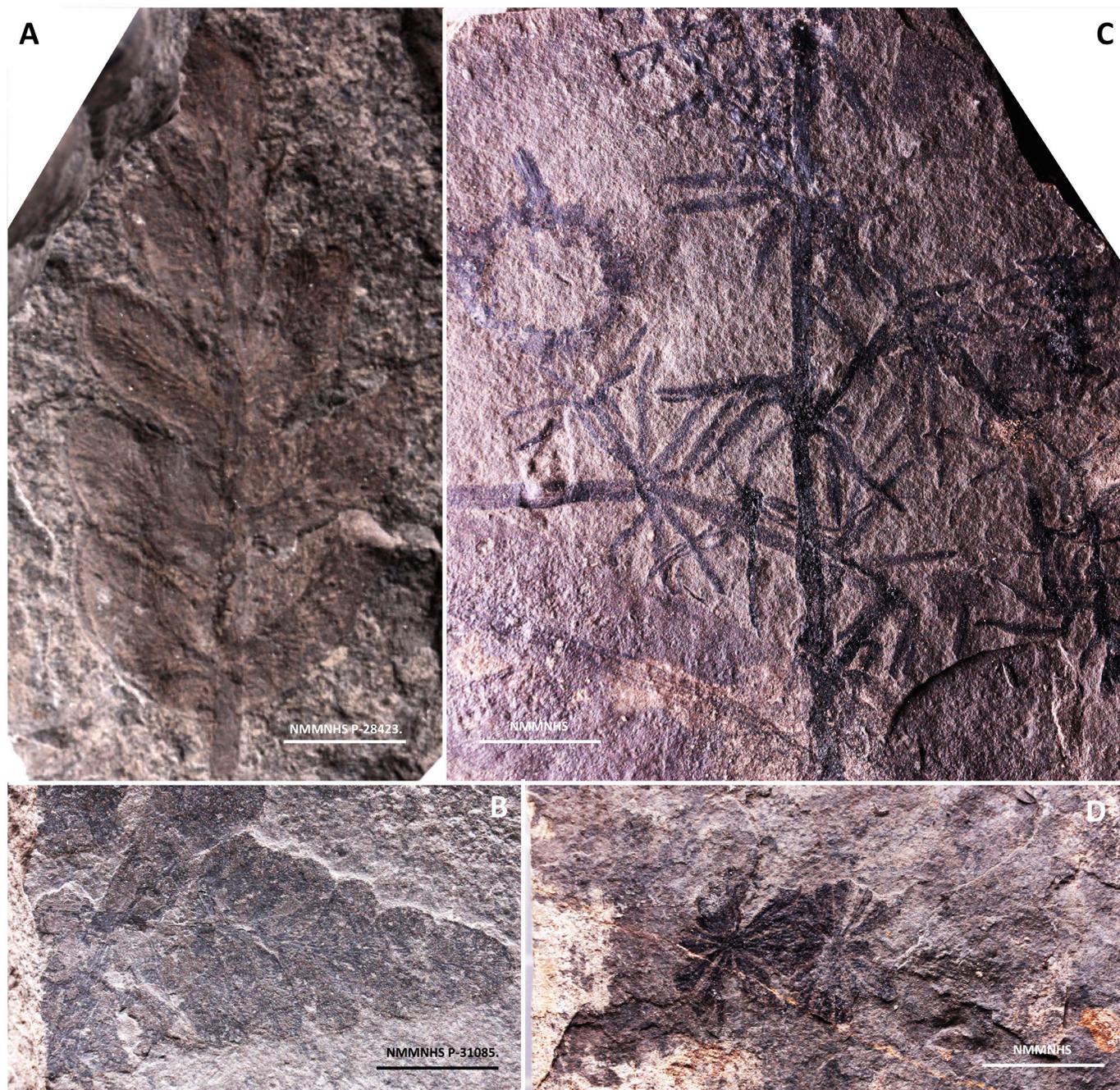


FIGURE 5. Bed 2 Fossil-plant remains from Bed 2, NMMNHS collections. **A.** *Neuropteris ovata*. NMMNHS specimen P-28423. **B.** *Neuropteris ovata*. NMMNHS specimen P-31085. **C.** *Phyllothea* sp. Note calamitalean stem node flattened in transverse view, to left of leafy shoot. NMMNHS specimen, uncatalogued. **D.** *Annularia sphenophylloides*. NMMNHS specimen, uncatalogued. Scale bars = 1 cm.

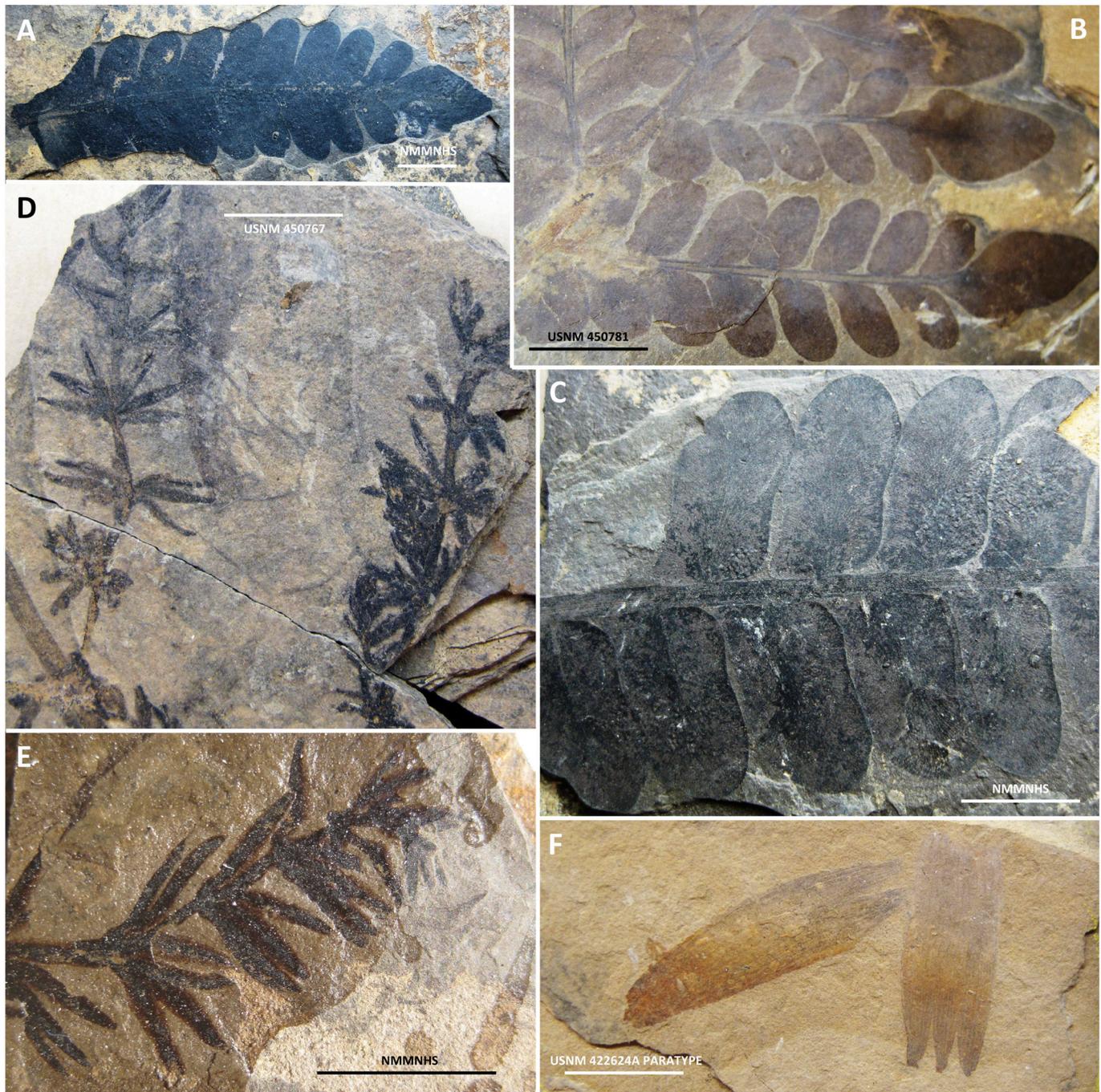
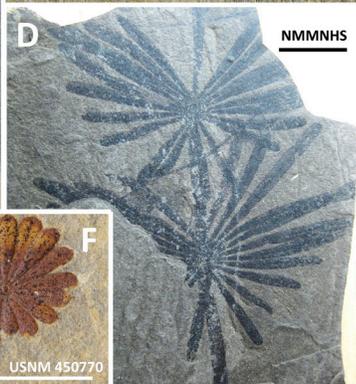
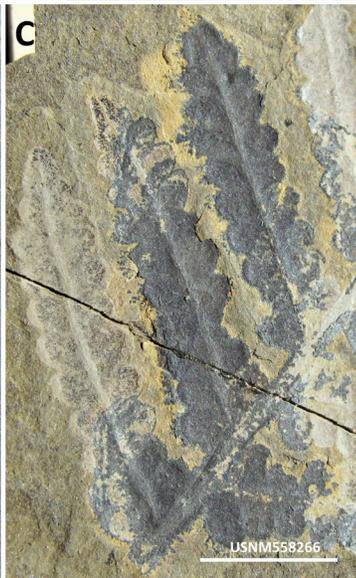
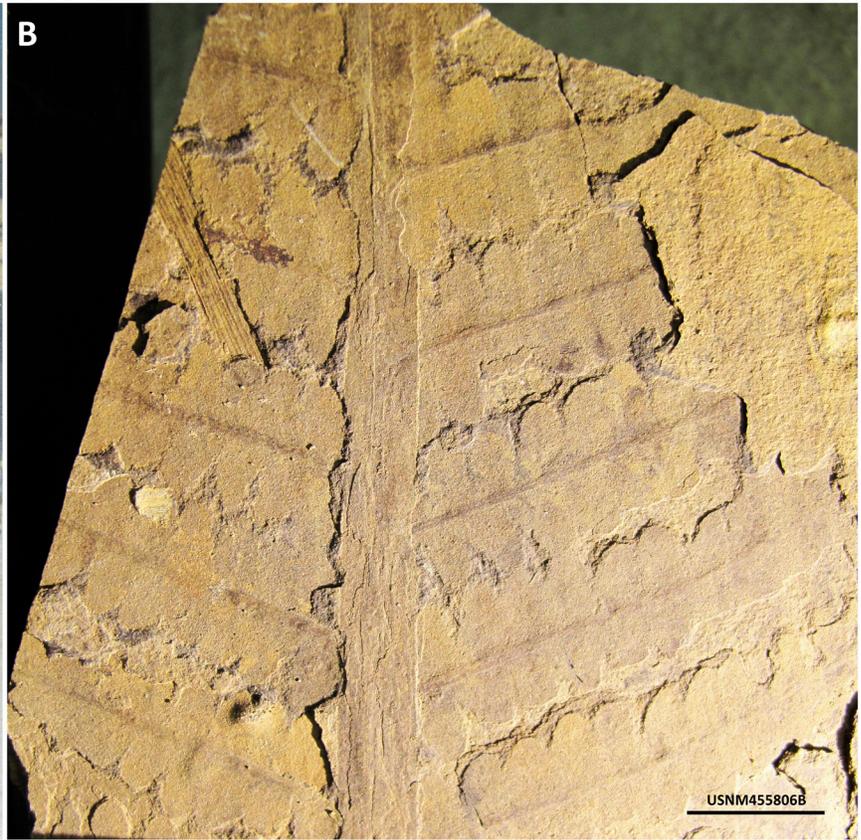


FIGURE 6. Bed 3 (1). Plant fossils from Bed 3. NMMNHS and USNM collections are combined. **A.** *Neuropteris ovata*. NMMNHS specimen. **B.** *Neuropteris ovata*. USNM 450781. **C.** *Neuropteris ovata*. NMMNHS specimen. **D.** *Phyllotheca* sp. USNM 450767. **E.** *Phyllotheca* sp. NMMNHS specimen. **F.** *Charliea manzanitana*. USNM 422624A Paratype. Scale bars = 1 cm.

FIGURE 7. (facing page) Bed 3 (2). Plant fossils from Bed 3. NMMNHS and USNM collections are combined. **A.** *Cordaites* leaf with attached microconchids. NMMNHS specimen. **B.** Marattialean fern foliage. USNM 455806B. **C.** Marattialean fern foliage. USNM 5583266. **D.** *Annularia spinulosa*. NMMNHS specimen. **E.** *Asterophyllites equisetiformis*. NMMNHS specimen. **F.** cf. *Annularia sphenophylloides*. Identity is questionable because of the asymmetry of the leaf whorl. An alternative identification is *A. carinata/mucronata*, however, the whorls in that species are ovate in shape, not round. Leaf tips are distinctly mucronate. USNM 450770. **G.** Calamitalean stem. NMMNHS specimen. **H.** *Dicranophyllum* sp., probably *D. readii*. Note Liesegang banding, characteristic of many specimens from this bed. NMMNHS specimen. Scale bars = 1 cm.



occurring taxa include *N. ovata* (Fig. 6B), *C. manzanitana* (Fig. 6F), *Phyllothea* sp., *D. readii*, marattialean fern foliage (Fig. 7B-C), *Sphenopteris* sp., *Neuropteris* sp., *Cordaites* sp., and the marattialean fern foliage *Remia pinnatifida* (Gutbier) Knight emend. Kerp et al. We also illustrate cf. *Annularia sphenophylloides* (Zenker) Gutbier or possibly *Annularia carinata* Gutbier/*A. mucronata* Schenk (Fig. 7F). *Charliea manzanitana* is much more common in the NMNH than in the NMMNHS collection, which may be a collecting bias from the original collectors searching for new species (Mamay, 1990). Plants requiring high moisture levels (*N. ovata*, *Phyllothea* sp., *A. spinulosa*) dominate Bed 3, but taxa that were presumably meso- or xeromorphic (*C. manzanitana*, *Walchia* sp., *D. readii*) are also present.

The Bed 4 collection at NMMNHS has 27 taxa on 115 quadrats. Dominant taxa include *Neuropteris ovata* (Fig. 9A, C), *Sphenopteridium manzanitanum* Mamay (*Sphenopteris germanica* Weiss) (Figs. 9E), *Charliea manzanitana*, *Walchia* sp. (Fig. 10C), *Dicranophyllum readii* (Fig. 9D), *Neuropteris* sp., the marattialean fern foliage *Danaeites* Goeppert sp., unidentified marattialean fern foliage, and *Walchia piniformis* (Fig. 10A-B). Also illustrated are a neuropterid of uncertain affinity, possibly *Neurodopteris auriculata* (Brongniart) Potonié (Fig. 9B), the arborescent lycopsid *Sigillaria brardii* Brongniart (Fig. 9E), and *Phyllothea* sp. (Fig. 10D). At NMNH, 54 taxa were identified on 848 quadrats, including *S. manzanitanum* (*S. germanica*) (Figs. 11A, 13), *W. piniformis* (Fig. 4B), marattialean fern foliage (Fig. 13), *Cordaites* sp., *D. readii*, *Mixoneura subcrenulata* (Rost) Zeiller (Fig. 12C, F), *C. manzanitana* (Figs. 4F, 12A), *Sphenopteris* sp., and *Annularia carinata*. We also illustrate *Danaeites* cf. *emersonii* Lesquereux (Fig. 11C), *N. ovata* (Fig. 12B), *Annularia spinulosa* (Fig. 12D), cf. *Lobatannularia* Kawasaki sp. (a sphenopsid), the noeggerathialean *Plagiozamites planchardii* (Renault) Zeiller (Fig. 12G), and cf. *Neurodopteris auriculata* (Fig. 12H). An unexpected difference in dominance-diversity patterns between the two collections is that *N. ovata* is the most frequent taxon in the NMMNHS collection, but not common in the NMNH collection. With the exception of *N. ovata* and *Danaeites* sp. and other marattialean foliage, the dominant plant taxa from Bed 4 are drought-tolerant plants. Notably, *S. manzanitanum* (*S. germanica*), a probable lyginopterid pteridosperm and drought-tolerant species, makes its first appearance as a dominant component of the flora.

The Bed 5 collection from NMMNHS (24 taxa on 199 quadrats) is dominated by *Sphenopteridium manzanitanum* (*Sphenopteris germanica*) (Figs. 14A, 15A-B), *Walchia piniformis* (Fig. 14B), *Neuropteris ovata* (Fig. 14G), *Cordaites* sp., *Charliea manzanitana* (Fig. 14F), *Dicranophyllum readii*, *Walchia* sp., *Neurodopteris auriculata*, and *Mixoneura/Odontopteris* sp. We also illustrate *Culmitzschia speciosa* (Florin) Clement-Westerhof (conifer; Fig. 14C), *Mixoneura subcrenulata* (Fig. 14D), cf. *Dicranophyllum* sp. (Fig. 14E), and *Arnophyton kuesii* (Ash and Tidwell) (Fig. 15C), which is likely a juvenile *S. manzanitanum* (*S. germanica*). Another probable juvenile of *S. manzanitanum* (*S. germanica*) is shown in Figure 15D. At NMNH, 31 taxa on 308 quadrats are present, and common taxa include *D. readii* (Fig. 16A), *S. manzanitanum* (*S. germanica*), *N. ovata* (Fig. 16C-D), *Cordaites* sp., *Neuropteris* sp., *C. manzanitana*, *N. auriculata*, marattialean foliage, and the conifer *Otoviccia hypnoides* (Brongniart) Kerp, Poort, Swinkels and Verwer. We also show photographs of *D. readii* (Fig. 16B, paratype) and *M. subcrenulata*. *Dicranophyllum readii* was more frequent in the NMNH collection, which most likely is another example of biased collecting of a new species (Mamay, 1981). Overall, the dominant taxa are similar in both collections, made up of mostly drought-tolerant plants with a smaller number of wetland plants.

Bed 6 had 16 taxa on 53 informative quadrats at NMMNHS. The dominant taxa include *Walchia piniformis*, *Walchia* sp. (Fig. 17A-C), *Sphenopteridium manzanitanum* (*Sphenopteris germanica*), *Macroneuropteris scheuchzeri* (Hoffmann) Cleal, Shute and Zodrow, *Neuropteris ovata* (Fig. 17F), *Mixoneura subcrenulata* (Fig. 17D), *Sphenopteris* sp., and *Dicranophyllum readii*. We also illustrate *Annularia* cf. *carinata* (Fig. 17E). *Incertae sedis*, a possible coniferophyte similar to *Podozamites* Braun (Fig. 17G), was present in a small collection of Bed 6 specimens at NMNH (DiMichele et al., 2020). Most of the taxa from Bed 6 are meso- to xeromorphic, drought-tolerant plants, except for *M. scheuchzeri* and *N. ovata*, common hygromorphic taxa.

The stratigraphic ranges of fossil plant taxa across beds at Kinney (combined NMMNHS and NMNH collections) are presented in Figure 18. Out of 75 taxa, 43 occur in multiple beds. Most of the recurring taxa are present in consecutive beds: only eight taxa have gaps between appearances. Thirty-one taxa occur only in a single bed. Most of the major plant groups at Kinney span at least four beds. Filicalean ferns (*Sphenopteris* sp.), pteridosperms (the medullosan seed ferns *Neuropteris ovata* and *Mixoneura* (*Odontopteris cantabrica/schlotheimii*), and conifers (*Walchia piniformis*) span all six beds. Lycopsids, marattialean ferns, and cordaitaleans span Beds 2-5, and sphenopsids, dicranophylls, and noeggerathialeans range from Beds 2 through 6. *Taeniopteris* Brongniart species are only present in Bed 4. Bed 4 had the highest number of unique taxa (19), but also was the most heavily sampled. The absence of many taxa and broader groups from Beds 1 and 6 is probably a result of the small sample sizes from both beds. Overall, the species pool is similar throughout the Kinney deposit, and common taxa persist through most of the beds. The dominance of taxa varies by beds, however, and shifts from wetland dominated to seasonally-dry adapted taxa moving upward in the section. The pattern may have been a result of decreasing transport distance and an increase in proximity to the source of the vegetation along the shoreline, as well as minor changes in climate (DiMichele et al., 2021, this volume).

NOTES ON IDENTIFICATIONS

DiMichele et al. (2013) presented the most recent comprehensive taxonomic revision of the Kinney flora, and most of the identifications here follow their taxonomy. Notes on some of the identifications are presented below.

Sphenopsids

The identity of *Phyllothea* sp. (Figs. 5C, 6D-E, 10D) is open to discussion. The only description of this genus in North America is that of Mamay and Read (1956), who described *Phyllothea paulinensis* Mamay and Read from the Lower Pennsylvanian Spotted Ridge flora of Oregon. The specimen in Figure 6D was originally illustrated by Mamay and Mapes (1992) as *Annularia* cf. *radiata* Brongniart. DiMichele et al. (2013) identified material of this type as *Annularia spicata* (Gutbier) Schimper, but, as discussed in that text, there was disagreement among the authors as to the plant's identity. The specimens we assigned to *Phyllothea* sp. differ from *A. spicata* in a number of ways. Whorls are larger, the bases of the leaves are wide, and they narrow to acuminate apices. The leaves are likely fused at the base, which is indicated by the widening of the leaf blade downward, without a basal contraction. The specimens differ from the Spotted Ridge, Oregon material (Mamay and Read, 1956) in that the leaves are wider. Also, the Spotted Ridge specimens have whorls composed of up to 20 leaves, whereas the Kinney specimens have <10 (typically around 6). Thus, we do not assign the Kinney *Phyllothea* sp. specimens to *Phyllothea paulinensis*.

The specimen identified as cf. *Lobatannularia* sp. (Fig.

12E, Bed 4) has distinctive upswept leaves characteristic of the genus. However, the specimen may, in fact, simply be a preservational form of *Annularia spinulosa* (see Figs. 7D, 12D for comparison). Nonetheless, the similarity of whorl shape to that of *Lobatannularia* is worthy of note.

Kerp (1984) notes that *Annularia carinata* often is confused with *Annularia sphenophylloides* and *Annularia stellata* when there are populations that vary in whorl size. In *A. carinata*, which may be conspecific with *Annularia mucronata*, leaf whorls exhibit anisophylly, with leaves of different lengths on arcs of the whorl, and are therefore oval in shape. Leaf shape is spatulate, similar to that of the other two species. The whorls of *A. carinata* are composed of 8-18 leaves (Kerp, 1984). In comparison, *A. stellata* has a higher number of leaves per whorl, up to 30, and individual leaves are longer (Kerp, 1984). A possible specimen of *A. carinata* is shown in Figure 17E from Bed 6, which exhibits oval-shaped leaf whorls and mucronate tips. From Bed 3, we identified a specimen of *A. sphenophylloides* (Fig. 7F). *Annularia carinata/mucronata* is an alternative identification for this specimen, because the leaf whorl is asymmetrical and composed of leaves of varying lengths. A rounded whorl, characteristic of *A. sphenophylloides*, is shown in Figure 5D from Bed 2.

As a side note, the taxonomy of these *Annularia* foliage species is confusing, and confused. Barthel (2004) noted that *Annularia stellata* is a later homonym of *A. spinulosa*. However, the very concept itself has drifted, so that the type concept of *A. spinulosa/stellata* has changed from leaf whorls with relatively straight-sided narrow leaves, to encompassing, and being treated typically as distinctly spatulate leaves, often quite large. This, particularly, has become the *A. stellata* concept, even though the type material of that species is the same as for *A. spinulosa*, and not of the broad, spatulate form.

Pteridosperms

Several kinds of neuropterids with relatively large pinnules, similar to *Neuropteris ovata* or *Neurodontopteris auriculata*, are present in the Kinney collections, and are described and illustrated in DiMichele et al. (2013). Illustrated here are problematic forms similar to *Neurodontopteris auriculata* (Figs. 9B, 12H), a form with large, somewhat variable pinnule morphology. These identifications are considered tentative.

In recent papers focused on Pennsylvanian floras from western Pangea, the application of the generic names to mixoneurid taxa has been inconsistent, suggesting the need for stabilization of the nomenclature. For example, mixoneurid foliage has recently been referred to by either generic name alone (e.g., *Mixoneura*: DiMichele et al., 2013; *Odontopteris*: DiMichele et al., 2017), or as either *Odontopteris* (*Mixoneura*) (e.g., DiMichele et al., 2017) or *Mixoneura* (*Odontopteris*) (e.g., Lucas et al., 2021b). Laveine and Legrand (2019) suggest that *Mixoneura* fronds have a different basic architecture than those of *Odontopteris*, sensu stricto (“bifurcate outer-inner semi-pinnate” vs. “bifurcate outer semi-pinnate” fronds). The distinction in frond architecture allows other features of these plants to be magnified, and thus to be used more effectively than in the past to differentiate *Mixoneura* from *Odontopteris*. In light of the findings of Laveine and Legrand (2019), we suggest the use of *Mixoneura* for the identifiable mixoneurid species in the Kinney flora, including *M. subcrenulata* and *M. lingulata* (both emended in Laveine and Legrand, 2019), and *M. gimmii* (Wagner and Mayoral, 2007). We refer to the final mixoneuroid/odontopteroid species at Kinney as *Mixoneura* (*Odontopteris cantabrica/schlotheimii* because their determination is uncertain without a clear understanding of the frond architecture (see comments in Laveine and Legrand, 2019). The close relationship between *M. (O.) schlotheimii* and *M. (O.) cantabrica* seems increasingly clear (Zodrow et al., 2020), and we here treat them

together as either the same species or members of a lineage.

Only a small fragment of foliage found at Kinney has been attributed to *Mixoneura gimmii* (DiMichele et al., 2013c). This species was attributed to *Mixoneura* by Wagner and Mayoral (2007) and had earlier been synonymized with *Neurocallipteris neuropteroides* by Barthel (Barthel, 2006). Laveine and Legrand (2019) discuss the problem and note that no clear determination can be made. Given that the identification of the Kinney material was made by Robert Wagner (in DiMichele et al., 2013), and in light of his familiarity with the taxon, we have chosen to place it in *Mixoneura gimmii*, recognizing its distinct form.

The distinction between *Mixoneura* (*Odontopteris cantabrica*) and *Mixoneura* (*O.*) *schlotheimii* (Fig. 4B) is one mainly of their stratigraphic position (Wagner et al., 1969). Both are characterized by sparse pinnule venation. Barthel and Amelang (2011) describe *O. schlotheimii* in some detail. Cleal et al. (2007) describe cuticle from *O. cantabrica* and note that cuticle is not known from *O. schlotheimii*, but that cuticle characters will be necessary to differentiate the two species. Recently, however, Zodrow et al. (2020) have reexamined specimens of *O. schlotheimii* from the type section of the Manebach Formation in Germany, and found trichomes identical to those of specimens identified as *O. cantabrica* from the Late Pennsylvanian of the Sydney Coalfield in Canada. Although these latter authors demur from drawing taxonomic conclusions in their paper, the implications seem to indicate strongly that these two species either are the same, or are close enough relatives to form an evolutionary continuum. Because the stratigraphic separation between *O. cantabrica* and *O. schlotheimii* is not sufficient grounds for differentiating species, and because of taxonomic issues with *Mixoneura* and *Odontopteris*, we refer to the Kinney specimens as *Mixoneura* (*Odontopteris cantabrica/schlotheimii*).

The identity of the plant described as *Sphenopteridium manzanitanum* (Figs. 9E, 11A, 13, 14A, 15A-B) by Mamay (1992) has been a subject of some uncertainty. The genus *Sphenopteridium* is nominally Mississippian, so its presence in the Late Pennsylvanian is unexpected. *Sphenopteridium manzanitanum* is presumably a pteridosperm, based on the presence of transverse lines on the axes interpreted as sclerotic plates (Mamay, 1992). In addition, Mamay (1992) described an isolated, poorly-preserved lyginopterid fertile axis, *Telangiopsis Eggert and Taylor* sp., and suggested that the foliage and fertile axis may have been part of the same plant, *Diplopteridium* Walton. A similar association, but again lacking attachment, was found in an early Permian assemblage from Texas (DiMichele et al., 2019). *Arnophyton kuesii*, from Pennsylvanian-Permian boundary beds of the Bursum Formation in New Mexico, is a probable juvenile form of *Sphenopteridium manzanitanum* (Fig. 15C-D; Ash and Tidwell, 1986, 1987). *Sphenopteris manzanitanum* is identical in vegetative morphology to *Sphenopteris germanica*, a widespread plant, as identified from fragmentary material, in Late Pennsylvanian and early Permian strata in the western U.S. (see, for example, Pfefferkorn and Resnik, 1980; DiMichele et al., 2013, 2019). Identical features include bifurcate frond structure, pinnule shape, and fan-shaped venation. A lyginopterid pollen organ was recently described from the late Permian of Jordan, and occurs in the same deposit as a fragmentary *S. germanica* specimen (Zavialova et al., 2020). Similar pollen organs have previously been found in deposits with *S. germanica*, further suggesting a pteridosperm affiliation (Remy, 1978). Pending further evidence, we refer to this plant as *Sphenopteridium manzanitanum* (*Sphenopteris germanica*), given the current concerns about its affinities and identity.

Incertae sedis

The incertae sedis USNM specimen from Bed 6 (Fig. 17G) is discussed in DiMichele et al. (2013). Mamay and Mapes (1992)



FIGURE 8. Bed 3 (3). Plant fossil from Bed 3, NMMNHS collections. *Neuropteris ovata*, with matrix marked by distinct Liesegang banding, characteristic of many specimens from this bed. NMMNHS specimen P-81450. Scale bar = 1 cm.

suggested the specimen was most similar to the coniferophyte *Podozamites*. The leaves appear to be arranged helically, rather than in a two-ranked disposition. Overall, the leaves are very similar to what Mamay called *Russellites* from the Emily Irish flora in Texas, of Artinskian age (Mamay, 1968), which was later synonymized with *Yuania* H.C. Sze by Wang and Chaney (2010). Similarities include the leaf shape, the scooped apex, and the relatively wide, parallel veins. However, the leaves of *Russellites* differ in that they are arranged in a single plane, unlike the *Podozamites*-like specimen (Mamay and Mapes, 1992). In either case, this would be a very early occurrence of a plant of this type, as *Podozamites* is typically found in the Mesozoic (Anderson, 1978; Shi et al., 2018), and *Yuania* was a component of Permian floras (Wang and Chaney, 2010).

HABITAT PREFERENCES OF KINNEY PLANT TAXA

The Kinney Brick Quarry deposit was probably formed under subhumid climatic conditions (DiMichele et al., 2021, this volume; Schneider et al., 2021, this volume) and preserves a “mixed” flora, meaning that plants typical of wetland environments are fossilized alongside drought-tolerant plants presumed to have grown in well-drained soils. The presence of hygromorphic, mesomorphic, and xeromorphic plants in the same beds suggests that the plants were growing in multiple microhabitats located in close proximity to each other. Elements of the seasonally-dry and wetland floras are present in all six beds. Wetland plants, including lycopsids, sphenopsids, ferns, and medullosan pteridosperms, required nearly continuously high moisture levels and probably grew along the coastline

and rivers. The seasonally-dry flora, including coniferophytes, callipterid peltasperms, noeggerathialeans, and taeniopterids, grew in well-drained soils, which may have covered more of the landscape than the wetter areas. Below, we summarize evidence for the moisture level tolerances of plant taxa from Kinney based on morphological characteristics, modeled physiological requirements, and occurrences in particular sedimentary facies.

A note about terms. We use the term “wetland species” here to mean those plants requiring high soil moisture at nearly all times throughout the year. The term “drought-intolerant species” could be substituted, and might be more accurate because many of these plants probably did not live, obligately, or even at all, under flooded conditions. Yet they form a repeatedly associated suite of species and genera through time and space in the Euramerican tropics. Similarly, the term “dryland” is sometimes used to stand in contrast to “wetland”, and is effectively the same as “drought-tolerant” when referring to particular taxonomic groups. Extant drought-tolerant plants range greatly in the length of time they can tolerate moisture deficits and can be ecologically segregated quite finely along moisture gradients. This almost certainly was true in the late Paleozoic, and we expect that many of the more mesomorphic taxa, particularly pteridosperms, perhaps callipterids, and others, and the more xeromorphic taxa, varied widely in the extent of their drought tolerance. They, too, comprise repeated associations. Our combined experience suggests, however, that there are several, overlapping, drought-tolerant species pools. Thus, assemblages dominated by these plants will be more variable through space and time than those composed of drought-intolerant plants.

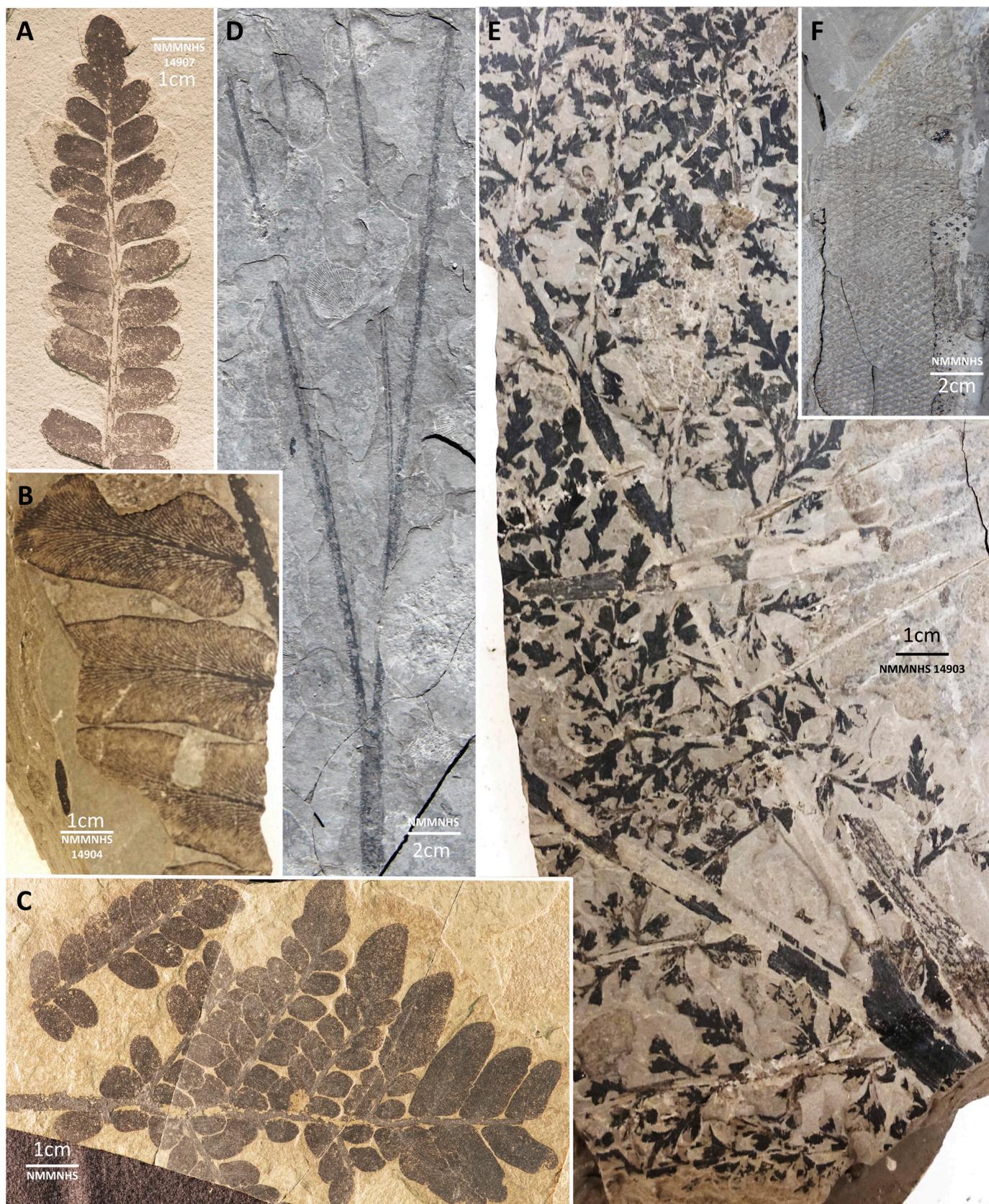


FIGURE 9. Bed 4 NMMNHS (1). Plant fossils from Bed 4 in the NMMNHS collections. **A.** *Neuropteris ovata*. NMMNHS P-14907. **B.** Neuropterid of uncertain affinity, possibly *Neurodontopteris auriculata*. NMMNHS P-14904. **C.** *Neuropteris ovata*. NMMNHS specimen. **D.** *Dicranophyllum readii*. NMMNHS specimen. **E.** *Sphenopteridium manzanitanum* (*Sphenopteris germanica*). NMMNHS P-14903. **F.** *Sigillaria brardii*. Note narrow “growth band” interval. NMMNHS specimen. Scale bar sizes noted on image.

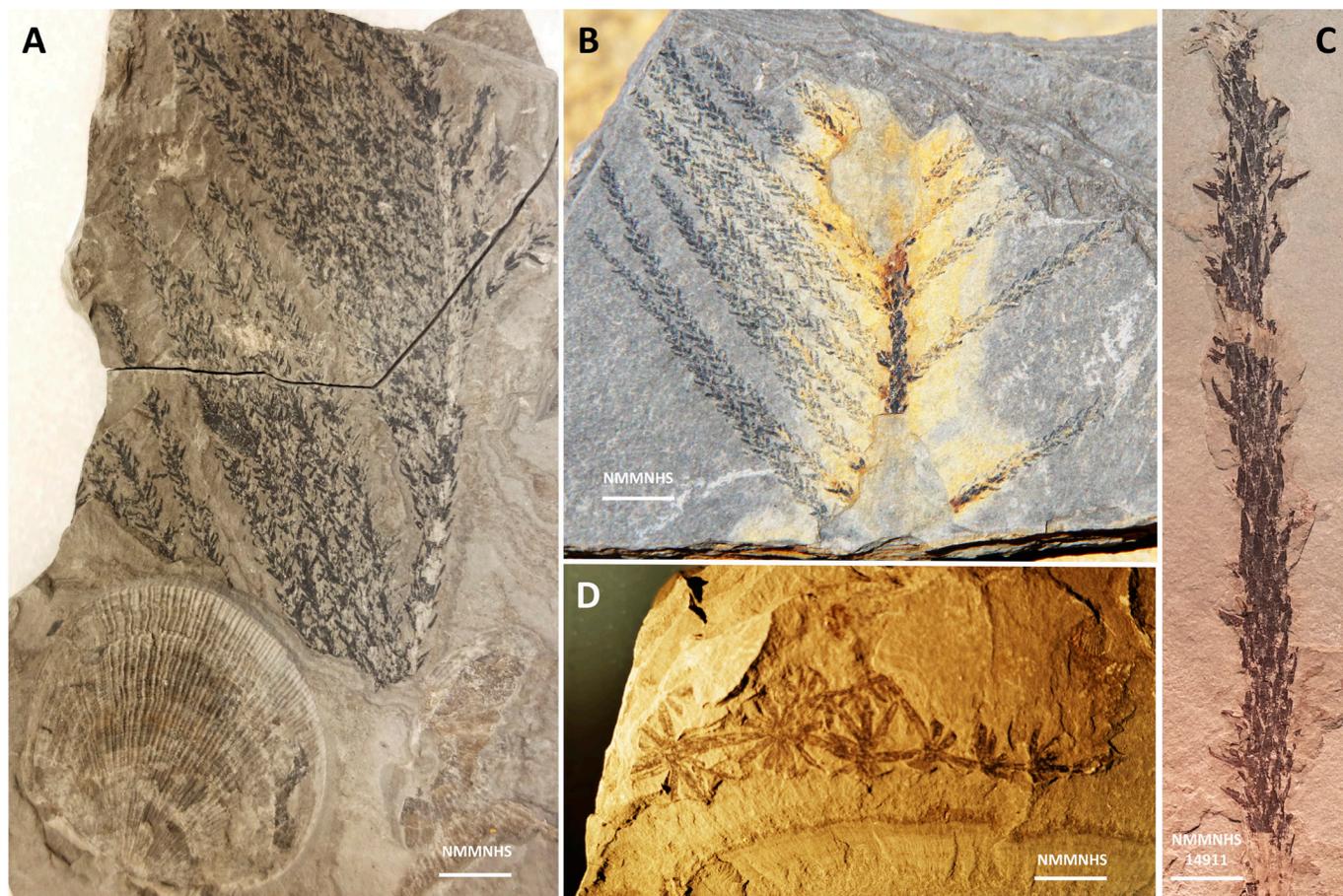


FIGURE 10. Bed 4 NMMNHS (2). Plant fossils from Bed 4 in the NMMNHS collections. **A.** *Walchia piniformis*. Note large *Dunbarella* specimen in lower left. NMMNHS specimen. **B.** *Walchia piniformis*. NMMNHS specimen. **C.** *Walchia* sp. NMMNHS P-14911. **D.** *Phyllothecca* sp. NMMNHS specimen. Scale bars = 1 cm.

Wetland Flora

Lycopsids

Arborescent lycopsids were a dominant plant group in swamp forests during the Pennsylvanian. Most species grew in water-logged soils and were probably submerged in standing water for periods of time (DiMichele and Phillips, 1985; Phillips and DiMichele, 1992). Evidence for their close association with wet substrates includes a heterosporous life history (Bateman and DiMichele, 1994; Petersen and Burd, 2017), probable water-dispersed female reproductive organs (Phillips, 1979), and extensive but shallow root systems (Phillips and DiMichele, 1992). *Sigillaria* Brongniart, a common arborescent lycopsid often found in wetland deposits, was also capable of surviving in areas that experienced seasonal dryness (Phillips and DiMichele, 1992; Pfefferkorn and Wang, 2009). Sigillariaceae, the family that *Sigillaria* belongs to, survived the extinction and ecosystem restructuring that occurred at the Desmoinesian-Missourian boundary, unlike many of the other arborescent lycopsid families (Phillips and Peppers, 1984; Phillips et al., 1985; Kosanke and Cecil, 1996; Falcon-Lang et al., 2011a; Elrick et al., 2017). *Sigillaria* roots may have penetrated deep into the substrate, helping them access groundwater during dry periods, and providing stability (Phillips and DiMichele, 1992; Pfefferkorn and Wang, 2009). Sigillarians grew along the margins of wetlands, streams, and levees (Gastaldo, 1987; Phillips and DiMichele, 1992; DiMichele et al., 2009). Based on sigillarian habitat preferences, it is unsurprising that *Sigillaria brardii* is present at Kinney. Because of the fragmented nature of the specimens and the small size of the leaf cushions, we

are unable to determine the adult size of the plant, although sigillarians are interpreted as arborescent based on preserved trunks. Either way, *S. brardii* and other *Sigillaria* species were able to successfully colonize wet areas in otherwise dryland environments, as evidenced by their presence in western Pangean “mixed” floras (DiMichele et al., 2006).

Sphenopsids

Sphenopsids, including calamitaleans and sphenophylls, were common wetland plants during the Pennsylvanian, and both groups are present at Kinney. The calamitaleans, relatives of extant Equisetales, lived in a variety of wet environments across the Pennsylvanian landscape, including peat swamps (Andrews, 1951; Willard and Phillips, 1993; Galtier, 1997), clastic wetlands (Abbott, 1958; Mencl et al., 2013; Opluštil et al., 2016), lake margins (Scott, 1979), and riversides (Falcon-Lang, 2004; Falcon-Lang et al., 2012; Bashforth et al., 2014). Calamitaleans had rhizomatic root systems capable of clonal growth, which enabled them to thrive in disturbance-prone environments (Pfefferkorn et al., 2001; DiMichele et al., 2009) and survive burial by sediment (Gastaldo, 1992). Although common in wetland floras, calamitaleans are found in many “mixed” floras, too, where they survived in wetter parts of the environment. *Arthropitys bistrinata* Frenzel, large calamitalean trees from the early Permian fossil forest in Chemnitz, Germany, show high amounts of secondary growth and a high percentage of parenchyma (up to 50%) in the secondary xylem, potentially helping the trees survive periods of seasonal dryness (Rößler et al., 2012, 2014). The species at Chemnitz also exhibit growth rings (Rößler et al., 2012) and may have abscised leafy branches

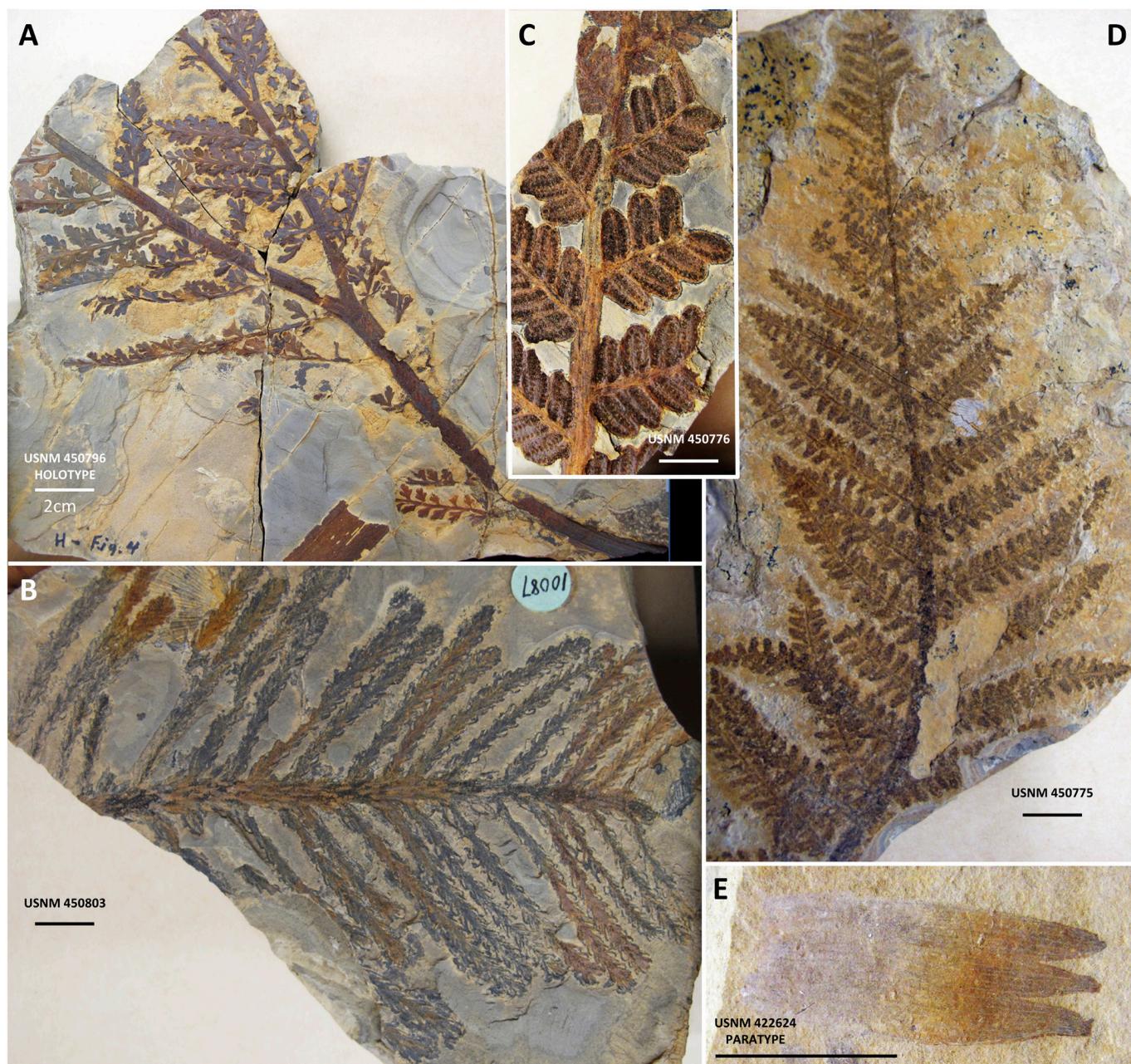


FIGURE 11. Bed 4 USNM (1). Plant fossils from Bed 4 in the NMNH collections. **A.** *Sphenopteridium manzanitanum* (*Sphenopteris germanica*). USNM 450796 Holotype. **B.** *Walchia piniformis*. USNM 450803. **C.** *Danaeites* cf. *emersonii*. USNM 450776. **D.** Marattialean fern foliage. USNM 450775. **E.** *Charliea manzanitana*. USNM 422624 Paratype. Scale bars = 1 cm except A, as marked.

seasonally (Röbner and Noll, 2010). Calamitaleans at Kinney are represented by a variety of foliage taxa, including *Asterophyllites equisetiformis*, *Annularia spinulosa*, *Annularia carinata*, *Annularia galioides* (Lindley and Hutton) Kidston, *Annularia spicata*, and *Phyllothea* sp., and a cone, *Calamostachys tuberculata* (Sternberg) Jongmans. At Kinney, the calamitaleans may have grown in wetter parts of the landscape along the paleo-shoreline, riverbanks, and point bars where there was consistently high moisture availability.

Sphenophylls were common understory plants in the Late Pennsylvanian to early Permian with shrubby, climbing, or scrambling growth habits (Batenburg, 1977; Galtier and Daviero, 1999; Bashforth and Zodrow, 2007). Sphenophyll species grew in clastic and peat-forming wetlands (Hoskins and Cross, 1943;

Good, 1978; Pryor and Gastaldo, 2000; Opluštil et al., 2016), possibly along channels or on floodplains (Scott, 1979). Some sphenophyll species exhibited adaptations to clastic vs. peat-forming environments. This is demonstrated by the growth of adventitious roots in species occupying peat substrates (Batenburg, 1982), whereas some species growing in clastic swamps lacked adventitious roots (Batenburg, 1977, 1981, 1982). In addition, the climbing or scrambling habit is associated with species growing in clastic swamps, and a prostrate, rooted main axis is associated with species in peat-forming environments (Batenburg, 1982). At Kinney, *Sphenophyllum miravallis* Vetter is the only identifiable sphenophyll species we found. Hooks have previously been described on the most dissected leaves of the species, suggesting a climbing lifestyle (Batenburg, 1981,

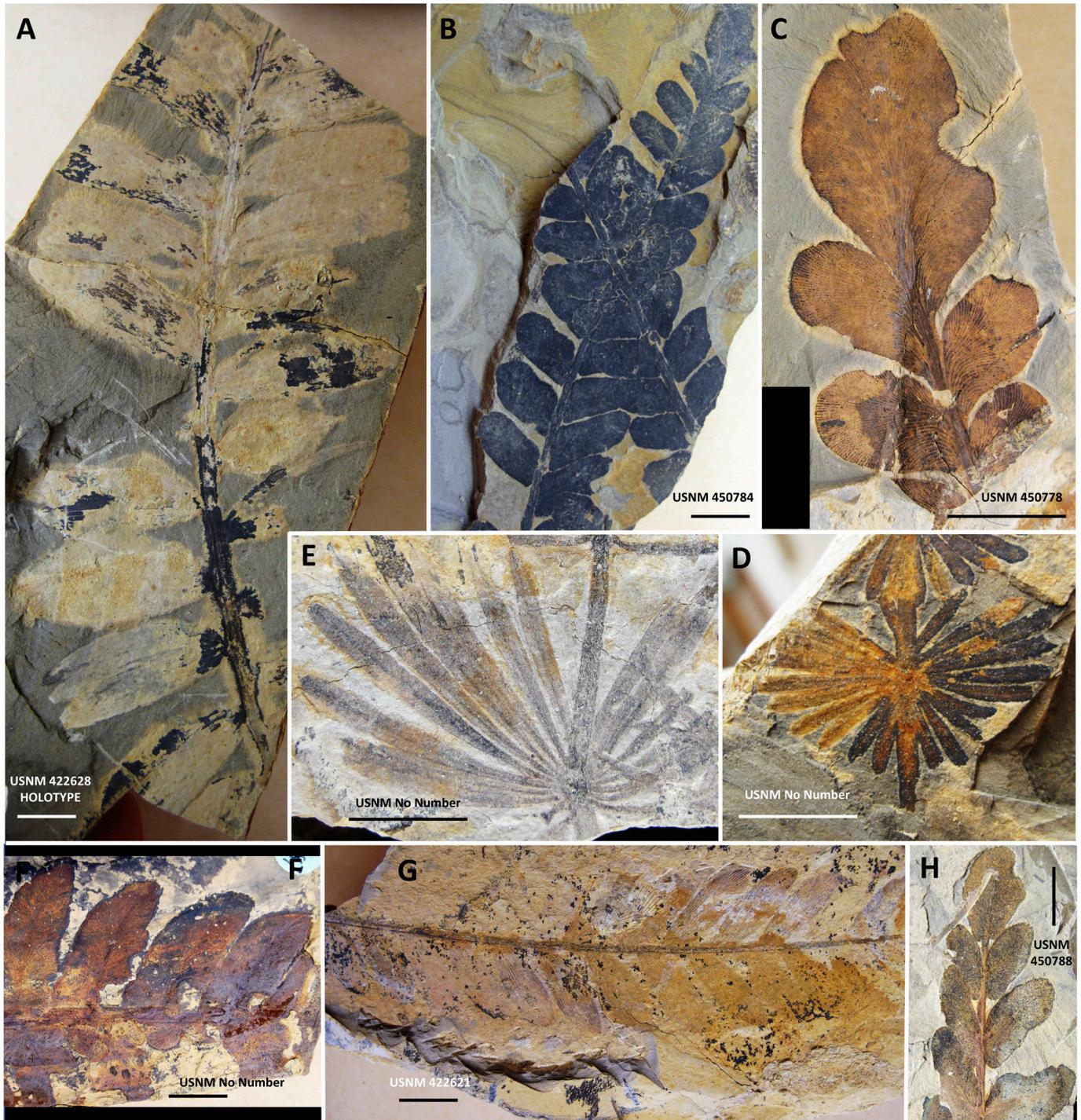


FIGURE 12. Bed 4 USNM (2). Fossils from Bed 4 in the NMNH collections. **A.** *Charliea manzanitana*. USNM 422628 Holotype. **B.** *Neuropteris ovata*. USNM 450784. **C.** *Mixoneura subcreulata*. USNM 450778. **D.** *Annularia spinulosa*. USNM specimen 770966. **E.** Cf. *Lobatannularia* sp. USNM specimen 770967. **F.** *Mixoneura subcrenulata*. USNM specimen 770968. **G.** *Plagiozamites planchardii*. USNM 422621. **H.** Cf. *Neurodopteris auriculata*. Scale bars = 1 cm.

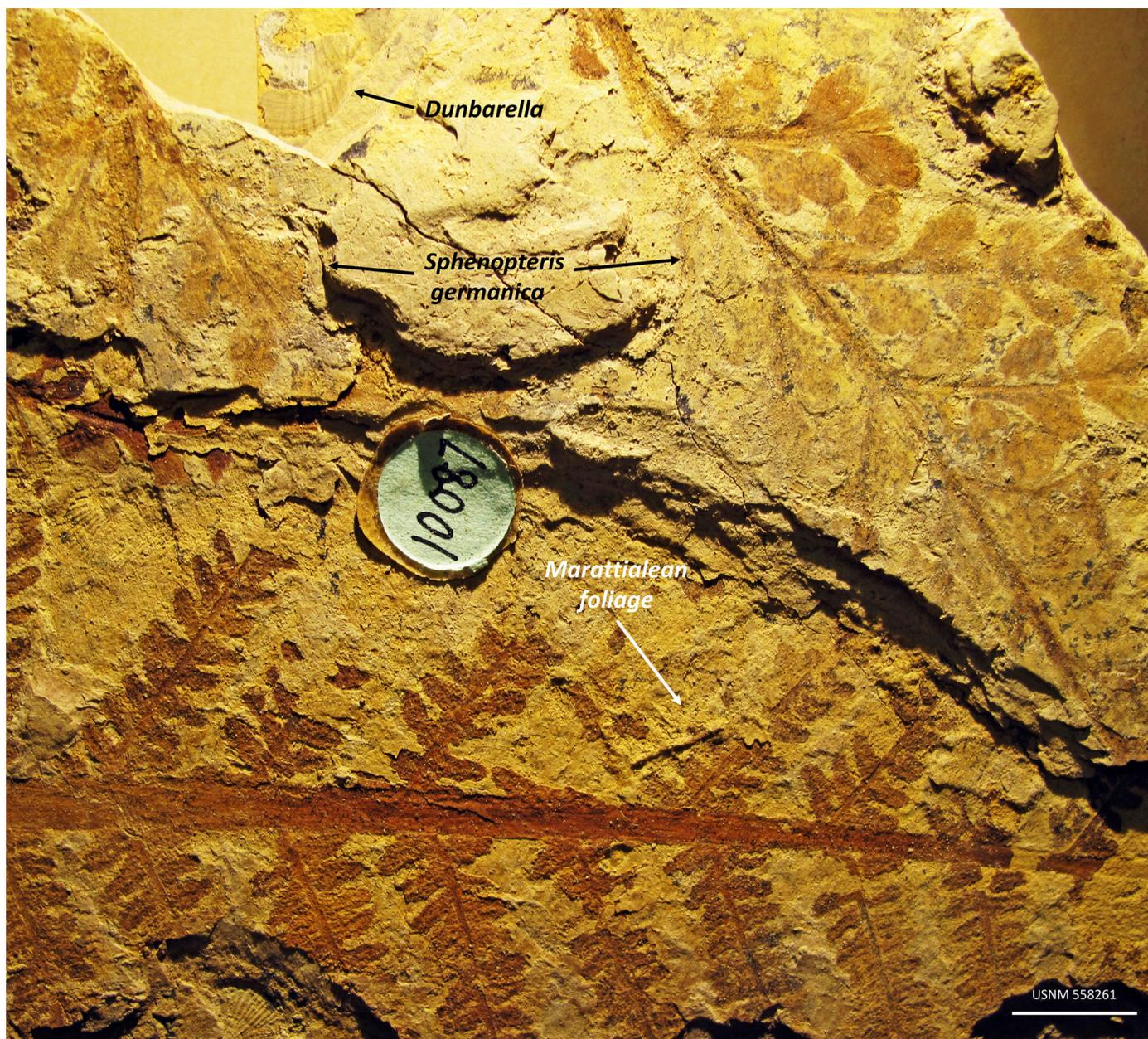


FIGURE 13. Bed 4 USNM (3). Plant fossils from Bed 4 in the NMNH collections demonstrating the close occurrence of *Sphenopteridium manzanitanum* (*Sphenopteris germanica*) and marattialean tree fern foliage. Note the somewhat clayey fracture of the rock and the presence of *Dunbarella*, typical of the USNM Bed 4 facies. USNM 558261. Scale bar = 1 cm.

1982; Hettterscheid and Batenburg, 1984).

Ferns

Together with lycopsids, sphenopsids, and medullosan pteridosperms, ferns were important members of plant communities growing in wet substrates in the Pennsylvanian. Marattialean tree ferns were dominant components of tropical peat-forming swamps, particularly from the Middle Pennsylvanian into the Permian (Phillips and Peppers, 1984; Phillips et al., 1985), and exhibit a variety of characteristics suggesting growth in moist substrates (DiMichele and Phillips, 2002). Marattialean ferns then as now are homosporous, and their spores need moist conditions to grow. The cortical areas of the adventitious roots of late Paleozoic tree ferns had many air spaces (Ehret and Phillips, 1977; Baker and DiMichele, 1997), a feature typically associated with plants that grow in water-saturated conditions (Kozłowski, 1984). The large fronds

supported high numbers of sporangia, which produced massive numbers of spores. This allowed marattialeans to colonize wet areas across Pennsylvanian landscapes, including in locally wetter areas of otherwise seasonally dry habitats (DiMichele et al., 2006; DiMichele, 2014). At Kinney, marattialean foliage includes indeterminate (to genus or species) foliage, *Danaeites* sp., and *Remia pinnatifida*, which have previously been found in other “mixed” floras (Šimůnek and Martinek, 2009; DiMichele et al., 2018). In their discussion of “extrabasinal” elements, Wagner and Álvarez-Vásquez (2010) noted that *R. pinnatifida* follows a pattern exhibited by many well-established seasonal-drought-tolerant plants in Pennsylvanian floras from Spain. The species appears in the Stephanian B of Spain (Knight, 1985), despite being considered a characteristic aspect of the German Lower Rotliegendes flora (Barthel, 2005).

Small filicalean ferns exhibited many growth habits during the Pennsylvanian, but were often groundcover plants (DiMichele



FIGURE 14. Bed 5 NMMNHS (1). Plant fossils from Bed 5 in the NMMNHS collections. **A.** *Sphenopteridium manzanitanum* (*Sphenopteris germanica*). Field specimen in private hands. **B.** *Walchia piniformis*. NMMNHS P-55540. **C.** *Culmitschia speciosa*. NMMNHS P-55534. **D.** *Mixoneura subcrenulata*. NMMNHS P-55549. **E.** cf. *Dicranophyllum* sp. NMMNHS specimen. **F.** *Charliea manzanitana*. NMMNHS P-55542. **G.** *Neuropteris ovata*. NMMNHS P-55548. Scale bars = 1 cm.

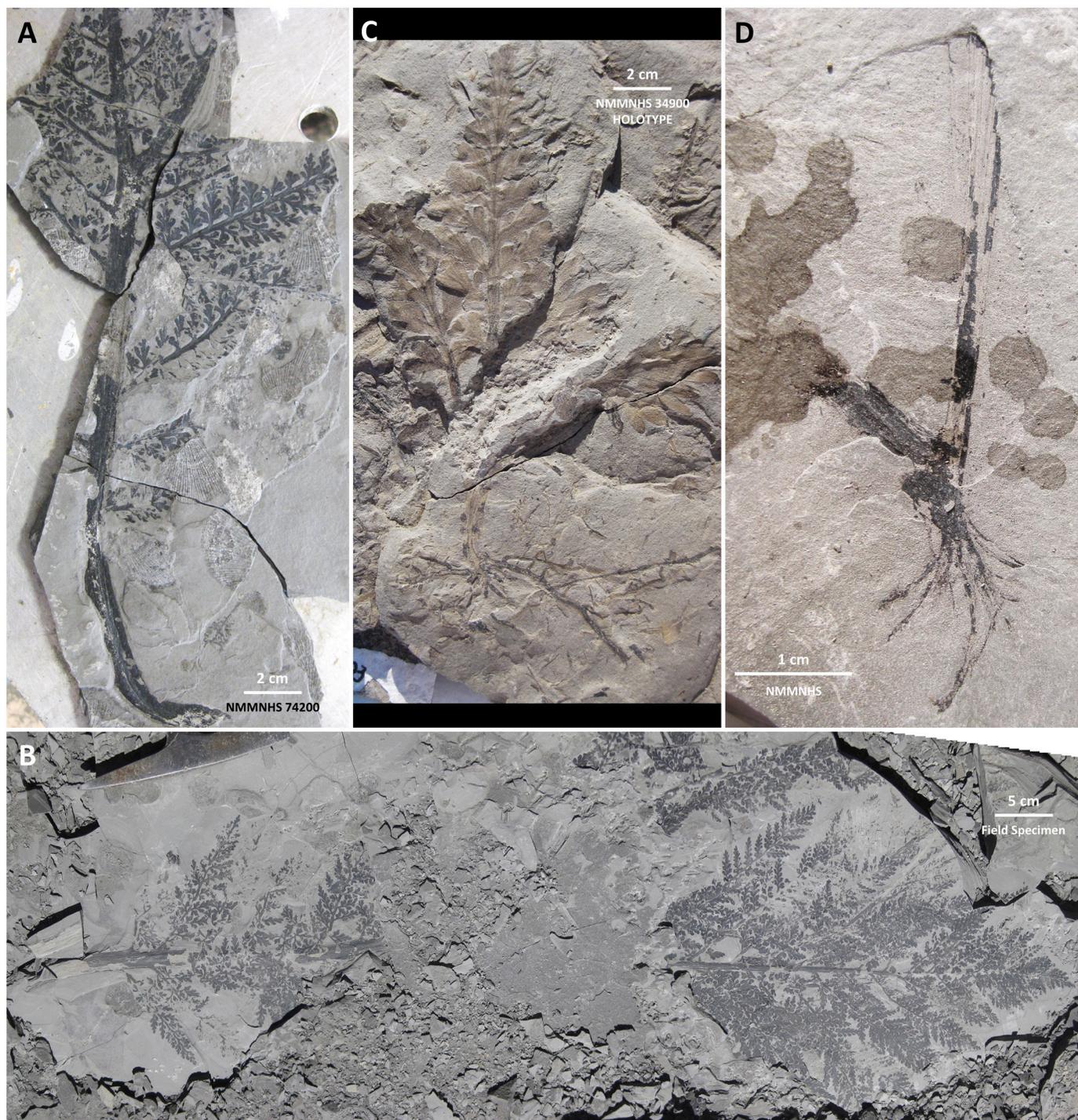


FIGURE 15. Bed 5 NMMNHS (2). Plant fossils from Bed 5 in the NMMNHS collections. **A.** *Sphenopteridium manzanitanum* (*Sphenopteris germanica*). NMMNHS 74200. **B.** *Sphenopteridium manzanitanum* (*Sphenopteris germanica*). Probably half of a larger, forked leaf. Field specimen, not collected. **C.** *Arnophyton kuesii*, likely juvenile of *Sphenopteridium manzanitanum* (*Sphenopteris germanica*). NMMNHS P-34900 Holotype. **D.** Juvenile plant, possibly *Sphenopteridium manzanitanum* (*Sphenopteris germanica*). Scale bars as marked on image.

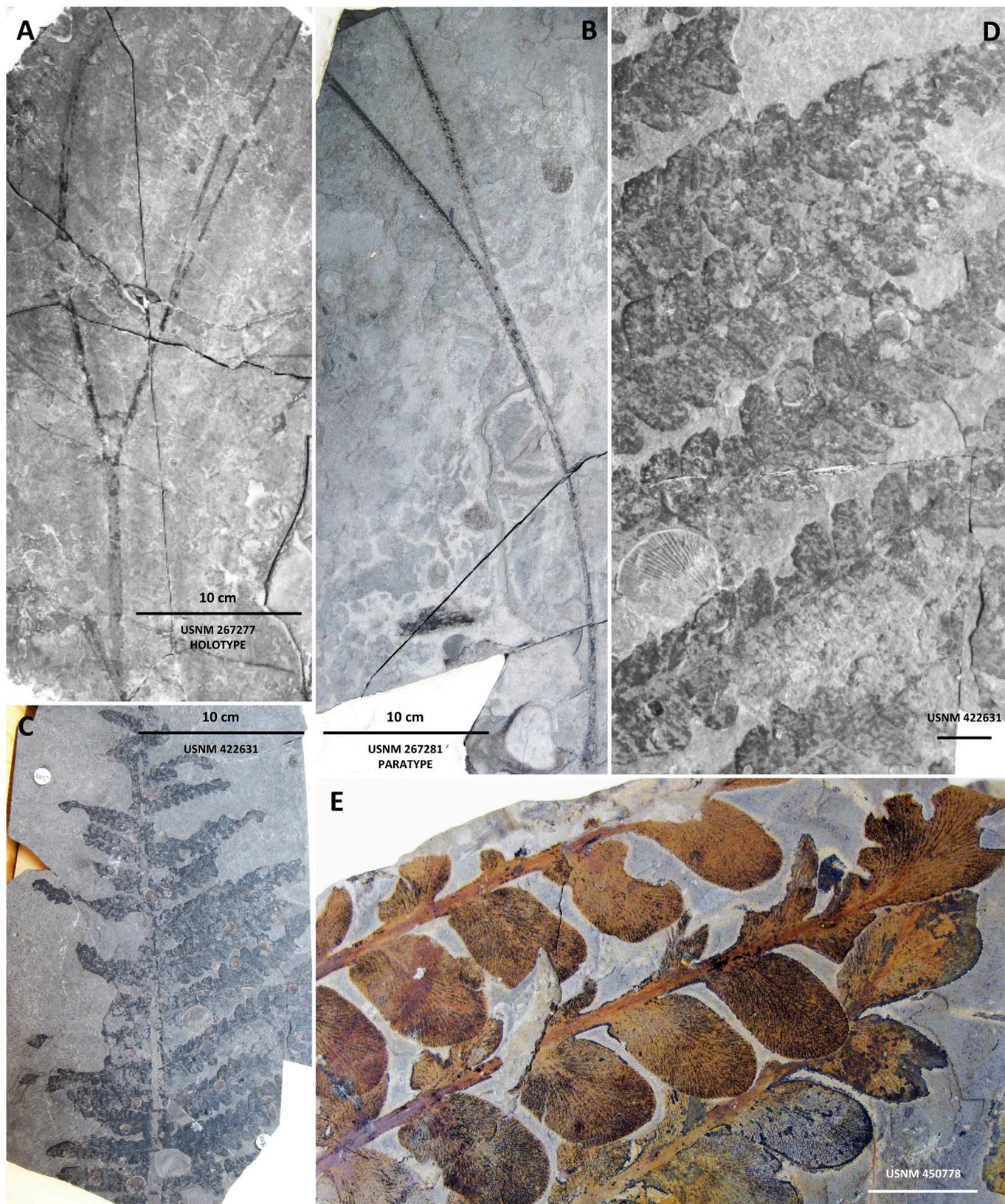


FIGURE 16. Bed 5 USNM. Plant fossils from Bed 5 in the NMNH collections. **A.** *Dicranophyllum readii*. USNM 267277. Holotype. **B.** *Dicranophyllum readii*. USNM 267281. Paratype. **C.** *Neuropteris ovata*. USNM 422631. **D.** *Neuropteris ovata*. Detail of specimen illustrated in (C). USNM 422631. **E.** *Mixoneura subcrenulata*. USNM 450778. Scale bars = 1 cm, except as marked in (A), (B), and (C).

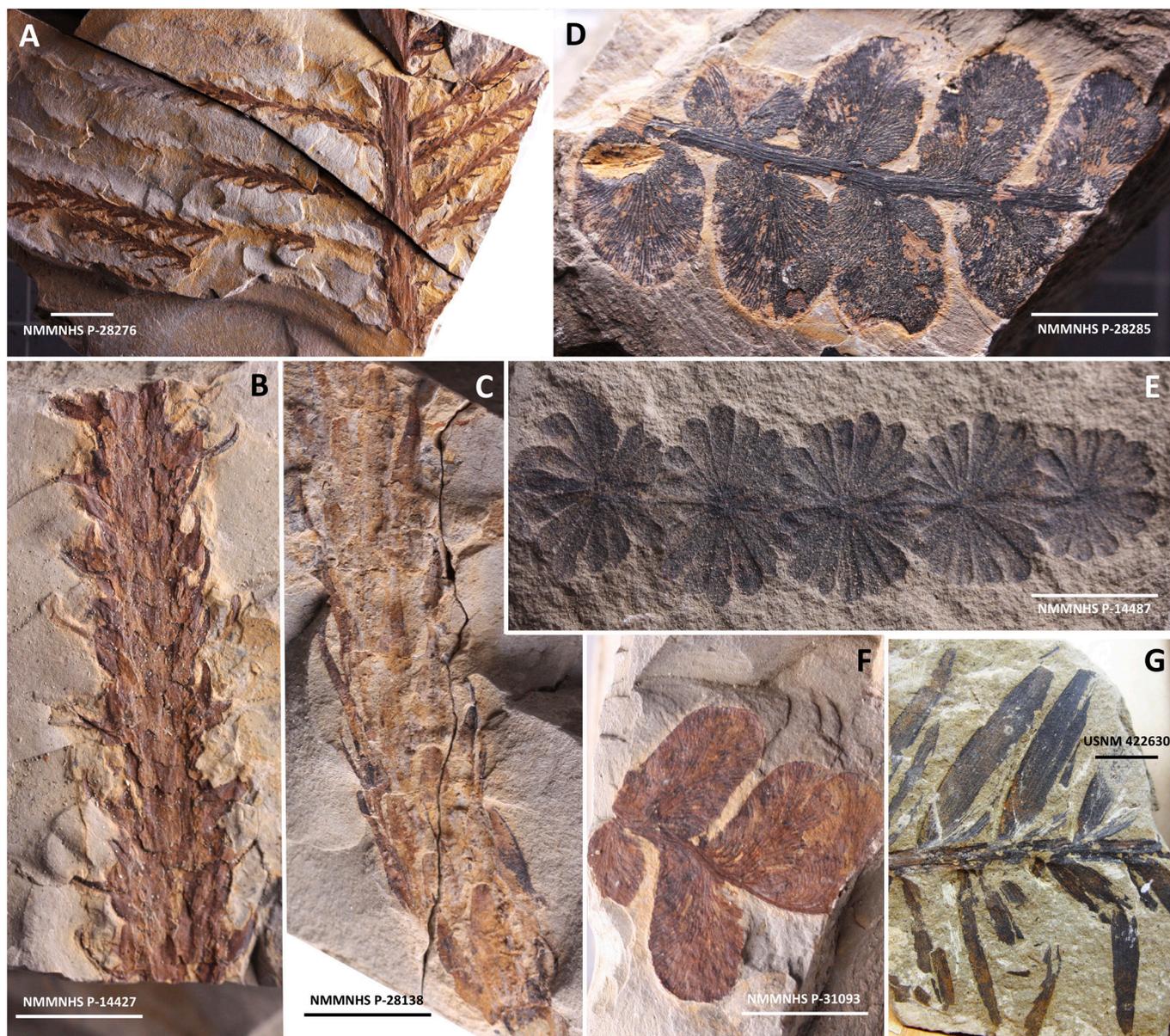


FIGURE 17. Bed 6. Plant fossils from Bed 6 in the NMMNHS and NMNH collections. **A.** *Walchia* sp. NMMNHS specimen P-28276. **B.** Walchian conifer axis. Leaves are exposed both in longitudinal section and in face view, the latter revealing a relatively broad, scoop shape. NMMNHS specimen P-14427. **C.** Walchian conifer axis with closely adpressed and overlapping, broad-based leaves, tapering to an elongate apex. NMMNHS specimen P-28138. **D.** *Mixoneura subcrenulata*. NMMNHS specimen P-28285. **E.** *Annularia* cf. *carinata*. Leaf whorls are oval in shape. Leaves have mucronate tips. NMMNHS specimen P-14487. **F.** *Neuropteris ovata*. NMMNHS specimen P-31093. **G.** Incertae sedis, possible coniferophyte with helical leaf arrangement, parallel veins, similar in some respects to *Podozamites*. USNM specimen 422630. Scale bars = 1 cm.

and Phillips, 2002). The filicalean taxa present at Kinney, including *Sphenopteris mathetii* Zeiller and *S. hadrophylla* Knight (Wagner and Alvarez-Vázquez, 2010; Knight and Wagner, 2012), the gleicheniaceous ferns *Oligocarpia gubieri* Goepfert and *O. leptophylla* (Bunbury) Grauvogel-Stamm and Doubinger (Wagner and Alvarez-Vázquez, 2010; Bashforth et al., 2011; Glasspool et al., 2013; Moore et al., 2014a), and the zygopterids *Nemejcopteris feminaeformis* (Schlotheim) Barthel (Zodrow, 1986; DiMichele et al., 2010; Wang and Pfefferkorn, 2013; Pšenička et al., 2014) and *Corynepteris angustissima* (Sternberg) Nemejc (Galtier, 2004; Tenchov, 2010; Wagner and Alvarez-Vázquez, 2010), have been previously documented in numerous wetland assemblages.

Pteridosperms

Medullosan pteridosperms were another key component of wetland environments in the Pennsylvanian. Medullosan growth habits were ecologically diverse and included trees (Stewart and Delevoryas, 1956; Laveine, 1986), lianas, and vines (Dunn et al., 2003; Rothwell, 2020). Physiological modeling of *Medullosa* Cotta, anatomically preserved medullosan stems, suggests that they required high water availability (Wilson et al., 2008, 2015; Wilson and Knoll, 2010; Wilson, 2013). Features of their vascular systems, including large conducting cells, tracheids with thin walls and a large pit membrane area, unique vascular cambium growth patterns, and high numbers of leaf traces in the petioles allowed them to rapidly transport water and support the

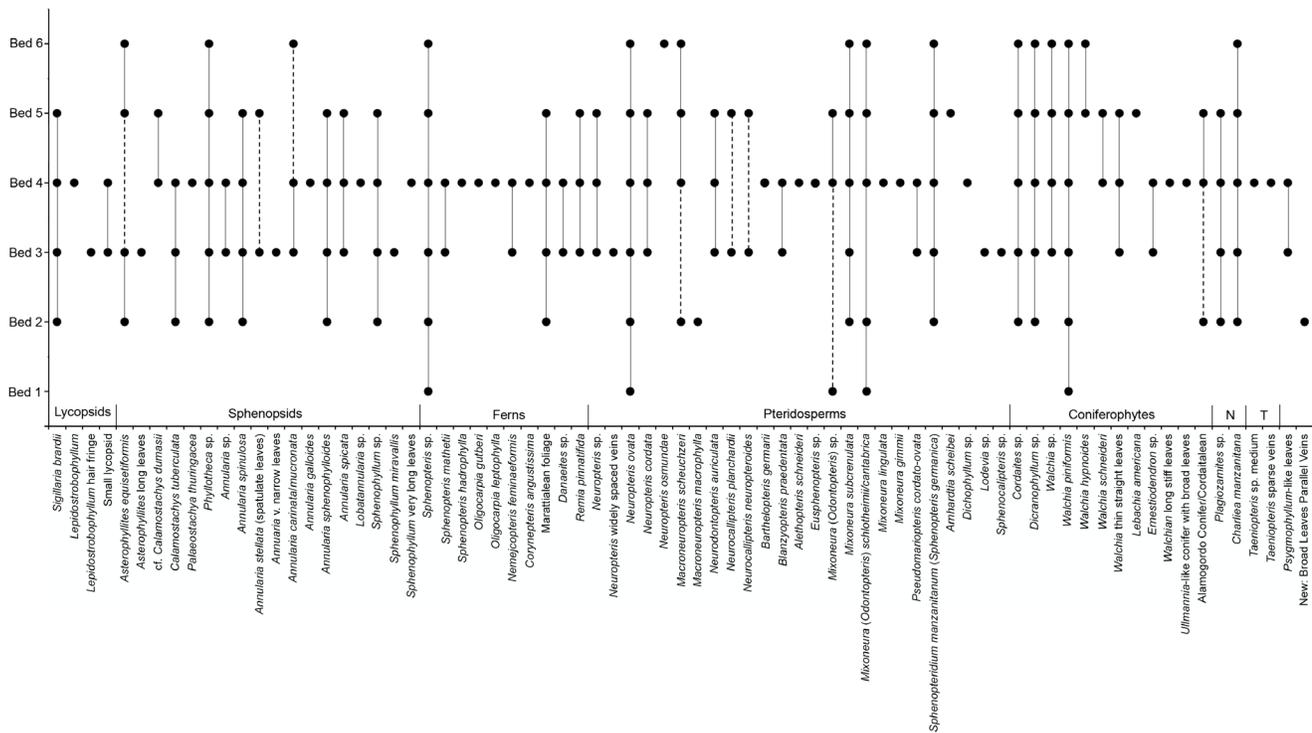


FIGURE 18. Stratigraphic ranges of fossil plant taxa from the Kinney Quarry. Points mark the presence of a specific taxon from a bed. Solid lines connect taxa found in subsequent beds, and dashed lines connect through gaps where a taxon was not found. N = Noeggerthiales; T = *Taeniopteris*

evapotranspiration requirements of the large leaf areas. These tracheidal features allowed the plants to move large amounts of water, but also opened them up to greater risk of cavitation under frost or drought conditions (Wilson et al., 2008, 2015; Wilson and Knoll, 2010; Wilson, 2013). Although medullosans were apparently physiologically confined to wetlands, some species, as discussed below in the “Seasonally-dry Flora” section, tend to be associated with “mixed” floras and probably grew in moist substrates in environments that experienced seasonally dry periods.

Neuropteris ovata was a widespread pteridosperm foliage taxon, which was present in Pennsylvanian wetlands, both peat swamps (Beeler, 1983) and on wet or flooded clastic substrates (Wnuk and Pfefferkorn, 1984). Cuticle characters, including thin cuticles, plentiful stomata, and low density of trichomes, suggest *N. ovata* was not well adapted to dry conditions and grew in moist substrates (Cleal and Zodrow, 1989). Based on chemical analyses of fronds, tannins were likely produced by the plants, which may be related to a preference for open, high light environments with moist, nitrogen-poor soils (Zodrow et al., 2016; D’Angelo and Zodrow, 2016). The pinnules may have been long-lasting, another possible adaptation to nutrient poor, wet soils (D’Angelo and Zodrow, 2018). *Neuropteris ovata* has previously been found in “mixed” floras from seasonally-dry habitats, where the plants probably grew in areas where there was consistent moisture. The other *Neuropteris* foliage taxa at Kinney, *N. cordata* Brongniart and *N. osmundae* (Artis) Kidston, probably occupied environments similar to those occupied by *N. ovata* (DiMichele et al., 1991; Charbonnier et al., 2008; Šimůnek and Martínek, 2009).

Macroneuropteris scheuchzeri was an important component of tropical wetland habitats in the Middle-Late Pennsylvanian

of Euramerica. Pinnules of the species feature many characters associated with xeromorphic plants, including thick cuticles, sunken stomata, and sparse adaxial stomata (Cleal and Zodrow, 1989; Zodrow, 2003). In addition, the pinnules of *M. scheuchzeri* may be caducous (individually deciduous prior to whole-leaf abscission) (Knaus and Lucas, 2004), and when a pinnule abscises, it leaves behind a rachial spine (Stull et al., 2012). The pinnules are characterized by the presence of dense “hairs,” originally thought to be a xeromorphic feature. However, the “hairs” may actually be internal, immediately sub-epidermal, resin canals, and not an adaptation to dry environments (Laveine and Oudoire, 2015). Interestingly, *Macroneuropteris scheuchzeri* also exhibits adaptations associated with water-saturated habitats. The pinnules have possible hydathodes, which are pores that allow the plant to secrete excess water, even when stomata are closed (Schabillion and Reihman, 1985). Also, as discussed above, the vascular systems of medullosan pteridosperms were not well-adapted to drier environments (Wilson et al., 2008, 2015; Wilson and Knoll, 2010; Wilson, 2013). Despite the variety of xeromorphic features, *M. scheuchzeri* is strongly associated with wetland deposits formed before and after coal-producing peat swamps (Stull et al., 2012). With increased temperatures and drying in the Late Pennsylvanian, *M. scheuchzeri* went extinct in Europe, but persisted in wet areas of western Euramerica until the beginning of the Permian (Stull et al., 2012). Judging by its habitat preference, the xeromorphic characters may have been an adaptation to growing in nutrient poor conditions (Haworth and McElwain, 2008; Stull et al., 2012).

Macroneuropteris macrophylla (Brongniart) probably lived in wet parts of the landscape based on cuticle characters. The pinnules of *M. macrophylla* from the Sydney Coalfields, Canada, have dense epidermal papillae that obscure the stomata (Cleal

and Zodrow, 1989; Zodrow et al., 2010). Epidermal papillae occur on hydrophilic leaves of some extant plants and can help prevent water from entering the stomata (Barthlott et al., 2017). The papillae may have prevented *M. macrophylla* pinnules from becoming waterlogged in high rainfall environments (Zodrow et al., 2010).

Seasonally-dry Flora

Coniferophytes

Dicranophyllum is a genus of gymnosperms and a probable coniferophyte, although its affinity is still debated (Meyen and Smoller, 1986; Rothwell et al., 2005; Van Der Pas et al., 2017). *D. readii*, a common component of the Kinney flora, particularly in upper beds 4 and 5 of the section, has long, slender leaves that usually bifurcate twice (Mamay, 1981). *Dicranophyllum* leaves are characterized by a central vein and two rows of stomatal furrows on the abaxial side. The stomatiferous furrows of *Dicranophyllum* are reminiscent of stomata positioned in grooves along the leaves of many Proteaceae species, suggested to be an adaptation to arid or semi-arid habitats (Jordan et al., 2008). Although *Dicranophyllum* ranges from the Late Mississippian to early Permian, the genus is uncommon in typical Pennsylvanian wetland floras, which suggests that the various species inhabited drought-prone environments less likely to be preserved than the wetlands (Wagner, 2005). Van Der Pas et al. (2017) noted that *D. gallicum* Grand'Eury specimens from central and western Europe were preserved in tuffs, interpreted as mesic-xeric environments on volcanic slopes, and in shales, where plant remains were interpreted as drawn from wetland environments. These observations suggest that *D. gallicum* colonized multiple habitat types opportunistically. *Dicranophyllum* is often associated with other presumed drought-tolerant plants in deposits likely formed during seasonally-dry climatic conditions (Wagner, 2005; Correia et al., 2016), and is common in deposits in western Pangaea (DiMichele et al., 2001, 2013c; Lucas et al., 2021b).

Walchian conifers, represented at Kinney by *Walchia piniformis*, *Walchia* sp., *Lebachia americana* Florin, and *Otovicia hypnoides*, are common components of Pennsylvanian-Permian seasonally-dry floras. Walchian conifers possess features to reduce transpiration, including thick cuticle, sunken stomata, and a sclerenchymatous hypodermis, which allowed them to thrive in water-stressed habitats. The surface-area-to-volume ratio of the leaves is low, because of their needle-like structure. Walchian conifers were wind pollinated (Rothwell, 1982; Mapes and Rothwell, 1984; Rothwell and Mapes, 1988). Also, active abscission of the branches may have been an adaptation to fire; dropping the lower branches can protect the tree crown from the upward spread of ground fires (Looy, 2013).

Walchian conifers were important components of moisture-stressed habitats in the Late Pennsylvanian-Permian (DiMichele et al., 2001, 2015; Falcon-Lang et al., 2009; Martino, 2017; Lucas et al., 2021b). The earliest walchian conifer fossils occur in rocks of Middle Pennsylvanian age (Falcon-Lang et al., 2009; Plotnick et al., 2009), coinciding with increased seasonality of rainfall (Cecil, 1990). In the Illinois Basin, walchian conifers grew along channels in seasonally-dry tropical lowlands during early glacial phases (Falcon-Lang et al., 2009). Occurrences of *Walchia* are rare in the Upper Pennsylvanian Conemaugh Group, Appalachian Basin (Darrach, 1936, 1975; McComas, 1988; Lyons and Darrach, 1989; Martino, 2017), and all occur after the extinction of most arborescent lycopsids in the region near the Desmoinesian-Missourian boundary, and after the onset of calcic vertisols and aridisols (Martino, 2017). In New Mexico (western Pangaea), walchian conifers have been found in early Permian red beds deposited in seasonally-dry conditions (Mack et al., 2010; DiMichele et al., 2015b). By the Asselian-Sakmarian (early Permian), *Walchia* ranged across subtropical

and tropical Euramerica in seasonally-dry environments (Ziegler et al., 2002).

Cordaitaleans were an ecologically diverse group of coniferophytes that lived in both wetland (Phillips et al., 1985; Raymond et al., 2010) and seasonally-dry environments (Falcon-Lang, 2003; Falcon-Lang et al., 2011c; Bashforth et al., 2014; Šimůnek, 2018). Growth forms include small (Cridland, 1964) and large trees (Falcon-Lang and Scott, 2000; Šimůnek et al., 2009; Wan et al., 2020; Trümper et al., 2020). (Falcon-Lang and Scott, 2000; Šimůnek et al., 2009; Wan et al., 2020), and scrambling species (Rothwell and Warner, 1984). Cordaitalean foliage is often fragmentary, and species are difficult to differentiate based on the gross morphology of leaves. However, detailed cuticle analysis suggests previously unrecognized diversity and morphological differences between species inhabiting wet vs. well-drained soils (Šimůnek, 2000, 2007, 2018; Šimůnek and Florjan, 2013). In clastic soils in dryland environments, cordaitalean species had broad and deep root systems (Falcon-Lang, 2003, 2004; Bashforth et al., 2014). Conifer and cordaitalean remains found in the same sediments with abundant charcoal suggest that these plants lived in environments prone to wildfires (Scott et al., 2010).

In the Kinney flora, cordaitaleans are represented by *Cordaites* sp. in Beds 2-6 and *Cordaitanthus* Feistmantel (reproductive axis) on three quadrats from Bed 4. The *Cordaites* sp. macrofossils tend to be fragmentary and preserve few macroscopic details useful for separating the specimens into species. However, *Cordaites kinneyensis* was described based on cuticle from Kinney (Šimůnek, 2018). Mamay and Mapes (1992) noted that *Cordaites* was a rare component of the Kinney flora. However, when separated into beds, *Cordaites* sp. is one of the most common plants in the NMNH Bed 2, NMNH and NMMNHS Beds 3 and 5, and NMNH Bed 4 collections (Table 1; DiMichele et al., 2021, this volume). Cordaitalean pollen is dominant in sediment from the NMNH collections made by Mamay and Watt and abundant in the Huber collection at NMMNHS (Willard, 1992). Presumably, as with many other seasonally moisture-limited environments in the Late Pennsylvanian-Permian (Trümper et al., 2020), cordaitaleans and walchian conifers occupied moisture-stressed parts of the landscape.

Pteridosperms

The modeled physiological requirements of medullosans suggest the necessity of high moisture availability (Wilson et al., 2008, 2015; Wilson and Knoll, 2010; Wilson, 2013), and medullosan species were common in peat-forming and clastic swamps. Some species, however, consistently occur in floras growing in seasonally-dry environments, and therefore may have preferred better-drained substrates, or at least wetter areas in those landscapes. For example, *Neurocallipteris planchardii* (Goeppert) Cleal, Shute and Zodrow and *N. neuropteroides* (Zeiller) Cleal, Shute and Zodrow both are present at Kinney, and one or both of the species have been found in association with meso- and xeromorphic plants in the Late Pennsylvanian of New Mexico (DiMichele et al., 2010), the Late Pennsylvanian and early Permian of the Czech Republic (Šimůnek, 2004; Šimůnek and Martínek, 2009), the early Permian of Texas (Glasspool et al., 2013), Austria (Paalman, 2017), and Germany (Feng et al., 2012). In the Middle Pennsylvanian Nýřany Member, Central and Western Bohemian Basin, Czech Republic, *N. planchardii* was interpreted as living in stable settings near abandoned channels, such as raised banks with better-drained soils compared to plants growing right on the margins of the water (Bashforth et al., 2011). *Neurocallipteris? planchardii*, considered a characteristic taxon of the Stephanian B of France, was found in older Stephanian rocks in Spain together with numerous drought-tolerant plant taxa (Bouroz and Wagner,

1972; Wagner and Álvarez-Vázquez, 2010).

Four species of the medullosan foliage genus *Mixoneura* appear at Kinney, including *M. subcrenulata*, *M. lingulata*, *M. gimmii*, and *M. (Odontopteris) cantabrica/schlotheimii*. Given the controversy regarding *Mixoneura* and *Odontopteris* discussed in the “Notes on Identifications” section above, we follow the designations in the cited publications when referring to species in this paragraph. *Odontopteris cantabrica* is widespread in Euramerica and is used as an index fossil for the base of the Cantabrian Substage in terrestrial deposits (Zodrow and Cleal, 1985). Cleal et al. (2007) suggested that *O. cantabrica* may have been a scrambling plant based on the presence of dense forked hairs on the pinnules, which may have helped the pinnules cling together. The species may have grown in open parts of forests, where there was less shade and increased transpiration, evidenced by the lower density of hydathodes compared to some other medullosans (Cleal et al., 2007). The cuticle of *O. cantabrica* does not necessarily suggest xeromorphy, and the species is found in roof shale deposits (Zodrow and Cleal, 1985; Zodrow and D’Angelo, 2019), suggesting a tolerance for high moisture substrates. *Odontopteris cantabrica* has been compared, morphologically, to *O. schlotheimii* of the later Pennsylvanian and early Permian. A recent study of *O. schlotheimii* from the type section of the Manebach Formation in Germany (Zodrow et al., 2020) found trichomes similar to those of *O. cantabrica*, although the authors did not suggest formally that these taxa are conspecific. *Mixoneura subcrenulata* and *M. lingulata* appear to be more consistently associated with seasonally-dry environments, however. For example, *O. lingulata* was documented in a conifer-dominated flora collected in a lacustrine deposit from the Rotliegend in Oberhausen, Germany (Kerp et al., 1989). The species has also been collected in Late Pennsylvanian seasonally dry deposits in western Pangea (DiMichele et al., 2017; Lucas et al., 2021b). *Mixoneura subcrenulata* was interpreted as an extrabasinal taxon, which can also mean having a preference for seasonally-dry habitats (Wagner and Álvarez-Vázquez, 2010).

Another medullosan pteridosperm from Kinney often found in seasonally-dry floras is *Neurodopteris auriculata* (DiMichele and Chaney, 2005; Šimůnek and Martinek, 2009; Boyarina, 2010; Šimůnek et al., 2012). Pinnules have been found in Late Pennsylvanian and early Permian deposits from New Mexico (DiMichele and Chaney, 2005; DiMichele et al., 2017b) and Texas (DiMichele et al., 2005b, 2018; Glasspool et al., 2013).

The medullosan *Barthelopteris germarii* (Giebel) Zodrow and Cleal was found on one Bed 4 specimen from the NMMNHS Kinney collection. Pinnules of the species exhibit multiple characters associated with drier, stressed conditions (Krings and Kerp, 1998). The leaf veins of *B. germarii* anastomose, which may have enhanced water transport ability by increasing the area of contact between veins and mesophyll (Zodrow and Cleal, 1993). Krings and Kerp (1998) noted the presence of peltate glandular trichomes on *B. germarii* specimens from the Stephanian of Blanzky-Montceau, France. The trichomes may have excreted lipophilic substances (Krings and Kerp, 1998), which could have helped reduce transpiration (Dell, 1977). The stomatal subsidiary cells were adorned with papillae, which also may have functioned to reduce transpiration (Krings and Kerp, 1998). Of stratigraphic interest, *B. germarii* is considered characteristic of the Stephanian B flora from France, but has been found along with many xero- or mesomorphic plants from older Stephanian rocks in Spain (Bouroz and Wagner, 1972; Wagner and Álvarez-Vázquez, 2010).

Callipterid peltasperms, including *Arnhardtia scheibei* (Gothan) Haubold and Kerp, *Lodevia* Haubold and Kerp sp., *Dichophyllum* Elias sp., and *Sphenocallipteris* Haubold and Kerp sp., are another pteridosperm group found at Kinney.

Callipterids occupied seasonally moisture-stressed parts of the landscape. In the Late Pennsylvanian and early Permian, peltasperms first appear in strata deposited under seasonally-dry conditions, including channel fills, flood basins, and shallow marine settings (Remy, 1975; Boyarina, 1994, 2010; Kerp et al., 2001; DiMichele et al., 2013b; Falcon-Lang et al., 2015). Based on their absence from nearly all Pennsylvanian wetland floras, callipterid peltasperms may have evolved in seasonally dry habitats in areas less likely to be fossilized, and diversified as the aridity increased in the Permian (DiMichele et al., 2005a; Booi et al., 2009; Bomfleur et al., 2011; Wan et al., 2016). Callipterid peltasperm leaves in general are coriaceous, and some possible adaptations to mesic or xeric conditions have been noted for certain species. Andrews (1941) suggested the “well-developed cuticle” of *Dichophyllum* may have been a xeromorphic adaptation. *Autunia conferta* (Sternberg) Kerp from the lower Permian of Germany has a thick adaxial cuticle and thinner abaxial cuticle. Guard cells on the abaxial side have papillae that overlie the stomatal opening (Kerp and Barthel, 1993). *Peltaspermum martinsii* (Germar) Poort and Kerp from the upper Permian of Europe has a thick upper cuticle, sunken stomata, and papillae covering the stomatal pores (Poort and Kerp, 1990). Hinting at the complexity of dryland environments in the Pennsylvanian and Permian, callipterids often are found in different assemblages from conifers (Kerp, 2000) despite both being considered indicators of seasonally-dry conditions. Although exceptions exist (Galtier and Broutin, 2008; DiMichele et al., 2015a), the combination of conifers and callipterids suggests heterogeneity in the seasonally-dry environment of Kinney.

Sphenopteris manzanitanum (*Sphenopteris germanica*) and its probable juvenile form, *Arnophyton kuesii*, were likely lyginopterid pteridosperms (Mamay, 1992; Zavalova et al., 2020). *Sphenopteris manzanitanum* (*Sphenopteris germanica*) has recently been documented in a number of Late Pennsylvanian and early Permian assemblages from New Mexico and Texas (Tabor et al., 2013; DiMichele et al., 2017, 2018, 2019; Lucas et al., 2021b), suggesting the species was widespread in seasonally-dry environments in western Pangea. For example, *S. manzanitanum* (*S. germanica*) is the dominant species in the lowermost bed at the lower Permian Kola Switch locality in Clay County, Texas, which was interpreted as forming under a seasonally-dry climate, and lacks fossils of wetland plants (DiMichele et al., 2019). In Europe, Permian occurrences of *S. manzanitanum* (*S. germanica*) tend to be associated with typical drought-tolerant taxa (Barthel, 2006; Šimůnek and Martinek, 2009; Opluštil et al., 2013).

Taeniopteris

Taeniopteris, a form genus encompassing cycadophyte and fern foliage (van Konijnenburg-van Cittert et al., 2017), was a widespread, sub-dominant component of floras deposited in seasonally-dry climates during the Late Pennsylvanian and Permian. The earliest appearance of the genus is in Middle Pennsylvanian deposits of the Illinois Basin (Indiana) (Bashforth et al., 2016; DiMichele et al., 2016) associated with other meso- or xeromorphic taxa (for example, *Cordaites* and *Lesleya* Lesquereux). This association with drought-tolerant floras continued into the Late Pennsylvanian and Permian (Kerp and Fichter, 1985; Opluštil et al., 2017). In addition to the depositional environments in which *Taeniopteris* is found, its thick lamina is a possible xeromorphic adaptation (Barthel, 1960). At Kinney, taeniopterids are represented by two unidentified morphotypes, one with medium size leaves and the other with sparse venation. The plants may have been grown in the understory in parts of the landscape that experienced seasonally dry conditions (Cridland and Morris, 1963; Bashforth et al., 2016).

Noeggerathiales

Noeggerathiales is an enigmatic group of heterosporous plants from the Carboniferous and Permian characterized by pinnate leaves on unbranched stems and adaxial sporangia attached to sporophylls arranged in cone structures (Wang et al., 2009; Pfefferkorn and Wang, 2016). Noeggerathiales from tropical regions that grew on nutrient-rich soils (Pfefferkorn and Wang, 2016) or were common components of peat-forming swamps, adapted to wet conditions, have been found both in the Central European part of Euramerica (Šimůnek and Bek, 2003) and in Cathaysia (Wang et al., 2009, 2012, 2014, 2020; Pfefferkorn and Wang, 2016; Zhou et al., 2017). In western Euramerica, however, noeggerathialeans species are typically not abundant and are associated with facies deposited in seasonally-dry environments (Read, 1946; Leary and Pfefferkorn, 1977; Mamay, 1968; Wang and Chaney, 2010; Koll and DiMichele, 2020). *Charliea manzanitana* is assigned to Noeggerathiales, in part based on the plagiotropic arrangement of the leaves (Mamay, 1990; Tidwell and Ash, 2003), and is common at Kinney (the type locality). Like most other western Euramerican noeggerathialeans, *C. manzanitana* grew in seasonally-dry environments, exhibited by its presence in deposits of an age similar to Kinney in New Mexico (DiMichele et al., 2017a; Lucas et al., 2021b). Near Socorro, New Mexico, *C. manzanitana* and other seasonally dry-adapted plants were found in a channel fill 1-2 m below an in-place stand of coniferopsid tree fossils, interpreted to have grown on a coastal sabkha during the Missourian (Kasimovian) (Falcon-Lang et al., 2011b). The coniferophyte trees exhibit growth rings, evidence of seasonality (Falcon-Lang et al., 2011b). The Tinajas locality from the Missourian of Socorro County, New Mexico, is a lacustrine deposit, which preserves a “mixed” flora, containing typical wetland elements and plants adapted to seasonally water-stressed environments, like *C. manzanitana* (Lerner et al., 2009).

Plants assigned to *Plagiozamites* Zeiller have been considered cycadophytes (Bassler, 1916) or noeggerathialeans (Zeiller, 1894). Recent analysis of cuticle of *Plagiozamites oblongifolius* Halle from the upper Permian of Southwest China suggests that species is a cycad (Feng et al., 2017). In western Euramerica, the genus is associated with facies deposited in soils that experience seasonal moisture stress (DiMichele et al., 2013a; DiMichele, 2014; Bashforth et al., 2016). The Bassler (1916) specimen, assigned to *P. planchardii* (Renault) Zeiller, is from the Central Appalachian Basin but lacks sufficient geologic context to permit an assessment of the environmental conditions of its preservation.

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Artist's conception of *Acanthodes kinneyi*. Artwork by Ken McKeighen.